

PHOTOSYNTHETIC RESPONSE AND NUTRIENT UPTAKE DYNAMICS OF
PHYTOPLANKTON IN THE ROSS SEA, ANTARCTICA

A Thesis

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In Partial Fulfillment

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Master of Science

By

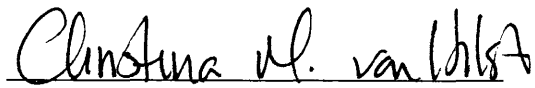
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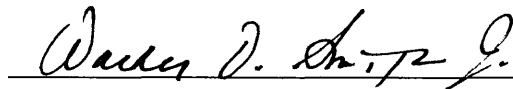
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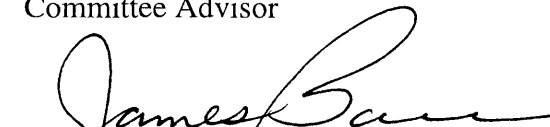
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Master of Science



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I dedicate this work to my family, those in heaven and on earth, without their love and support none of it would have been possible...

Thanks for the inquisitive mind.

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ABSTRACT

Phytoplankton bloom dynamics in the Ross Sea, Antarctica were investigated during austral spring (1994) and austral summer (1995-96) to determine the possible causes of the segregation of phytoplankton species characteristically found in this region.

Phaeocystis antarctica, a colonial haptophyte, tends to dominate in the south central polynya while diatoms are more dominant at the western ice edge. Both photosynthesis/irradiance relationships and nutrient uptake dynamics were investigated. Significant differences in the photosynthetic parameters derived from the P/E relationships of these species were not detected in either the field or culture experiments. Differences were detected for both nitrate and ammonium uptake. *P. antarctica* had significantly lower uptake of both nitrogen species when compared to diatom-dominated assemblages. C:N uptake ratios for these species were also significantly different and deviated from calculated particulate ratios. This study found that while nutrient uptake dynamics were different for these species they alone were not responsible for the segregation of taxa within the phytoplankton bloom in the Ross Sea polynya. This study suggests that a complex set of environmental factors control the growth and dominance of phytoplankton in this region.

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INTRODUCTION

The Ross Sea exhibits seasonal extremes in physical and environmental variables, most notably irradiance. Advance and retreat of the annual sea ice, opening of the polynya (a region of reduced ice cover surrounded by greater concentrations of ice), water column stratification, and surface irradiance levels are all physical features that in turn create relatively predictable biological processes in this area (Arrigo *et al.*, 1998). The phytoplankton bloom in the Ross Sea is one of the largest in the Southern Ocean, with chlorophyll concentrations increasing by over two orders of magnitude during the growing season (Smith *et al.*, in press). Recently much attention has been focused on the Southern Ocean as a possible location for sequestration of anthropogenic CO₂ from the atmosphere (Sarmiento and Orr, 1991; Sarmiento and LeQuéré 1996; Caldiera and Duffy, 2000). Although the biological processes, including primary productivity, in this area are relatively predictable as a result of the physical forcing, a full understanding of the initiation of growth and the phytoplankton dynamics within the bloom has not yet been achieved. The goal of this project was to determine if *Phaeocystis antarctica* exhibits characteristics that allow it to establish itself early and dominate in the seasonal bloom, either by enhanced photosynthetic capabilities or by enhanced specific uptake rates of carbon and/or nitrogen. The answers to these questions will increase our understanding of the bloom dynamics in this region and how the phytoplankton ecology of the Ross Sea

influences the region's biogeochemistry, including cycling of nutrients and flux of biogenic material to depth.

BACKGROUND

The Ross Sea – Physical Characteristics

The movement and concentrations of the sea ice in the Ross Sea change in a relatively predictable annual cycle. The entire Ross Sea is ice-covered during winter, except for coastal polynyas that remain open due to katabatic winds (Zwally *et al.*, 1983; van Woert, 1999). Coastal polynyas are ice-free areas hundreds of kilometers long that form primarily near ice shelves due to off-shore winds. Ice concentrations and extent in the Ross Sea start decreasing rapidly in spring (November) due to increased irradiance (and hence, increased heat flux). The Southern Ross Sea is open but not necessarily ice-free in late December and throughout January (Zwally *et al.*, 1983, Comiso *et al.*, 1993); generally ice begins forming again in early March. As the polynya expands, the water column stratifies as a result of the added fresh water via ice ablation, although the strength of stratification varies spatially and depends on the amount of melt-water input. Weaker stratification has been seen in waters that have reduced ice due to horizontal advection induced by winds and decreased *in situ* melting (Smith and Asper, in press). Stratification traps nutrient-rich water near the surface, and reduction of ice concentration results in irradiance levels that support maximal phytoplankton growth. Irradiance continues to increase throughout the spring finally reaching a maximum during summer. This combination of factors leads to the spring phytoplankton bloom, as algal production is closely linked to sea ice dynamics and available irradiance. The onset of the bloom

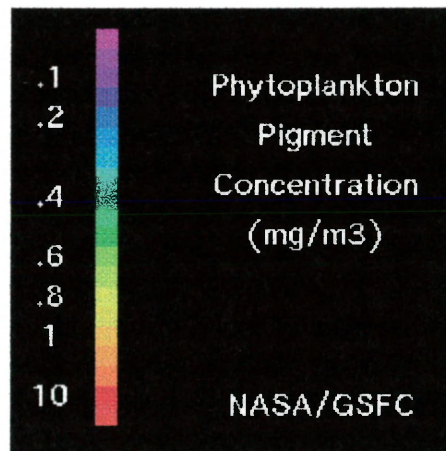
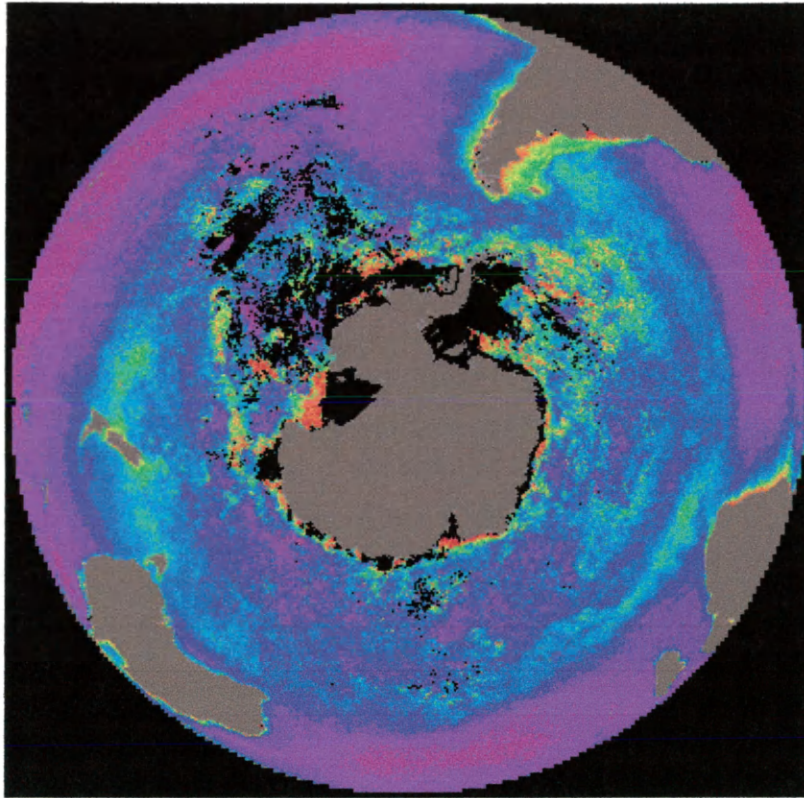
results from vertical stabilization and the increase in photosynthetically available radiation (PAR) (Sverdrup, 1953; Smith and Nelson, 1985; Nelson and Smith, 1991).

The Ross Sea is also a site of deep-water formation and may play an important role in global elemental cycles. Antarctic Bottom Water is formed from a mixture of Circumpolar Deep Water and Ice Shelf Water in the Northern Ross Sea during the summer over the continental slope in the eastern Ross Sea (Jacobs *et al.*, 1970). Because of the deep-water formation, the potential for flux of biogenic material to depth is significant. These relationships are complicated, however, due to the temporal uncoupling of the spring phytoplankton bloom and the formation of deep water in the Austral winter. Large deposits of biogenic silica also occur in this region (DeMaster *et al.*, 1992), thus suggesting a significant role in the global silica budget.

The Ross Sea – Phytoplankton Bloom Dynamics

Within the Southern Ocean the Ross Sea is the site of the most extensive seasonal phytoplankton bloom (Figure 1) (Comiso *et al.*, 1993). This bloom is unique for two reasons. First, the initiation of the bloom begins quite early in the growing season when compared to other regions at the same latitude (Smith and Gordon, 1997). Second, the distribution of phytoplankton taxa appears to be spatially distinct (DiTullio and Smith, 1996; Smith *et al.*, 1996; Arrigo *et al.*, 1999; Smith and Asper, in press). *Phaeocystis antarctica* has been found primarily in the south central polynya, and diatoms dominate in the western region near Victoria Land. The causes for these distinct distributions are unknown. Past studies have not demonstrated differences in the two chemical and physical environments, although mixed layers may be slightly shallower in the west due

Figure 1. Coastal Zone Color Scanner composite image (1978-86) showing high primary productivity throughout the Southern Ocean and in the Ross Sea.



to greater *in situ* ice melt and stratification (Arrigo *et al.*, 1999), whereas the relatively shallow (ca. 30 m.) mixed layers in the central region appear to persist for longer time periods (Smith *et al.*, in press). This spatial difference occurs both in the phytoplankton assemblage composition as well as the distribution of vertical flux of organic matter. Near the coast of Victoria Land, where diatoms tend to dominate, sinking material generally has a high silica content, while export in the central Ross Sea is comprised of loose, organic aggregates that are relatively low in silica content (Nelson *et al.*, 1996). *P. antarctica*'s dominance has been attributed to superior photosynthetic abilities in the form of higher uptake and assimilation rates at low irradiance levels (Arrigo *et al.*, 1999), and it has also been hypothesized that this species may have different nutrient uptake capabilities as well (Arrigo *et al.*, 1999). However, neither of these abilities has been demonstrated conclusively. Smith and Asper (in press) concluded that the distribution of these taxa reflects the complex relationships that control production in this system rather than a single factor.

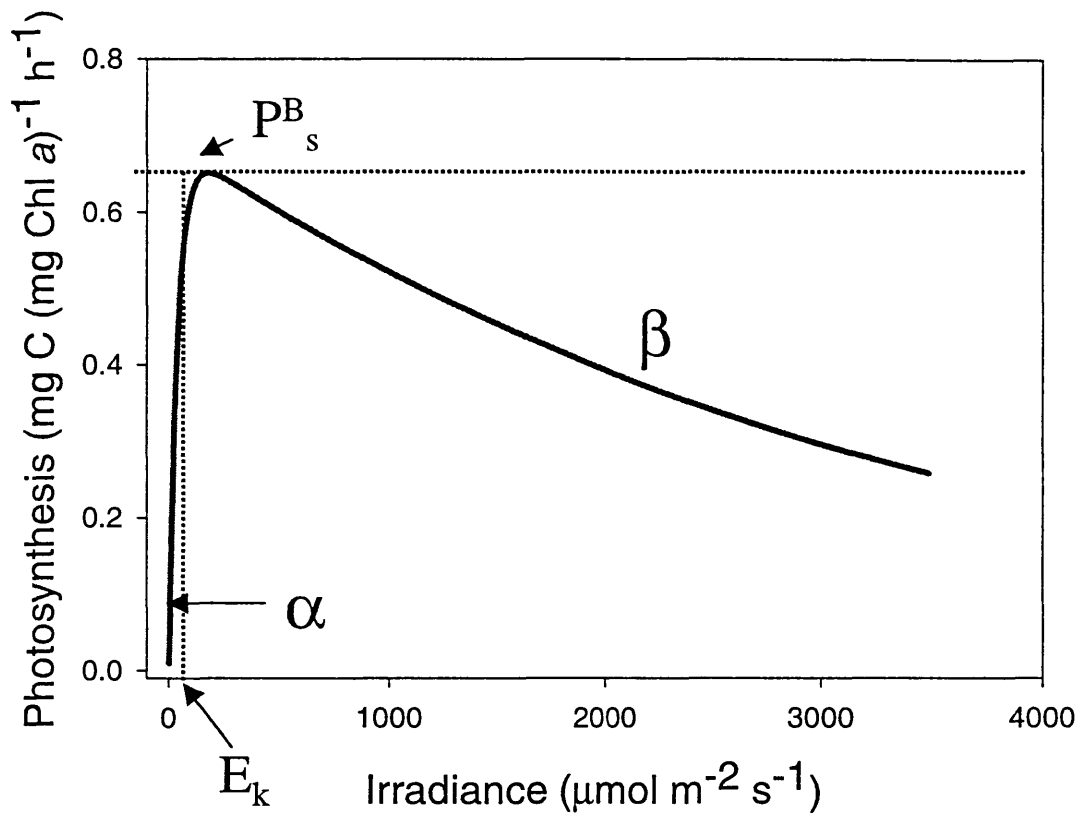
The Photosynthesis/Irradiance Relationship

The relationship between photosynthesis and irradiance has been modeled in several forms (Jassby and Platt, 1976; Platt *et al.*, 1980; Platt *et al.*, 1983). Platt *et al.* (1980) defined a model that incorporated irradiance levels that range from limiting to saturating conditions based on natural irradiance, and hence allowed for a full investigation of the irradiance regimes experienced *in situ*. These bio-optical models are empirical, and questions have been raised as to how accurately they model the photosynthetic/irradiance relationship. This empirical method of describing the

Table 1. The photosynthetic parameters as described by Platt *et al.*, 1980

Parameter	Description and Units
P^B	Photosynthetic rate $\text{mg C (mg Chl } a)^{-1} \text{ h}^{-1}$
P_s^B	Theoretical max photosynthetic rate in the absence of photoinhibition $\text{mg C (mg Chl } a)^{-1} \text{ h}^{-1}$
α	Initial slope of curve or rate of photosynthesis per unit irradiance $\text{mg C (mg Chl } a)^{-1} \text{ h}^{-1} (\mu\text{mol m}^{-2} \text{ s}^{-1})$
β	Measure of photoinhibition $\text{mg C (mg Chl } a)^{-1} \text{ h}^{-1} (\mu\text{mol m}^{-2} \text{ s}^{-1})$
P_m^B	Actual max photosynthetic rate calculated by $P_m^B = P_s^B(\alpha/(\alpha+\beta)) * (\beta/(\alpha+\beta))^{\alpha/\beta}$ $\text{mg C (mg Chl } a)^{-1} \text{ h}^{-1}$
E_k	Index of photoadaptation calculated by $E_k = P_m^B/\alpha$ $\mu\text{mol m}^{-2} \text{ s}^{-1}$

Figure 2. Photosynthesis/irradiance curve with parameters labeled.



photosynthesis/irradiance relationship has been compared to other methods, including oxygen evolution, and has been found to be comparable (Falkowski and Raven, 1997). The photosynthetic parameters (Table 1, Figure 2) that are defined by this relationship provide information about the initial rate of photosynthesis per unit chlorophyll (α), roughly equivalent to the optimum yield, the theoretical maximum rate of production (P_m^B), and a measure of photoinhibition (β). These parameters provide insights into the physiological state of the phytoplankton species in question. In particular, α and P_m^B can be influenced by nutrient status, irradiance regime, and adaptation status. It is known that these parameters are overestimates because neither dark reactions or respiratory losses are considered. This relationship has been used to model production of phytoplankton worldwide and has become an important part of several global production models (Sathyendranath *et al.*, 1999).

Many studies in polar regions have investigated how the photosynthetic parameters change depending on environmental conditions and with season (Table 2). Brightman and Smith (1989) investigated the P/E relationships of Antarctic phytoplankton during austral winter and found that the phytoplankton assemblage had adapted to the relatively low irradiance regime by reaching saturation at low light intensities. Lizotte and Sullivan (1991) and Palmisano *et al.* (1987) both examined sea ice microalgae and found that these diatom-dominated communities are very sensitive to environmental factors. Ice thickness can affect irradiance, temperature, and salinity, all of which can influence growth. Another study in McMurdo Sound looked at how these parameters were affected as a *Phaeocystis*-dominated assemblage was advected under the sea ice. Palmisano *et al.* (1986) found that when the phytoplankton were advected

Table 2. Photosynthesis/Irradiance parameters from other studies in Polar Regions. Numbers given are either averages given in study with standard deviations in parentheses, or ranges of values reported.

Study	Location	Species composition	%I	Z (m)	α^*	P_s^B **	P_m^B **	E_k ***
Platt et al., 1982	Baffin Bay	Mixed assemblage dominated by diatoms	50		0.049 (0.007) 0.035 (0.009)		1.32 (0.19) 1.29 (0.51)	25 (3.3) 24 (7.3)
Palmisano et al., 1986	McMurdo Sound	<i>Phaeocystis</i>	1	3	0.025 - 0.124	4.57 - 9.55	3.52 - 8.08	47 - 144
Sakshaug and Holm-Hansen, 1986	Antarctic Polar Front	Mixed assemblage		5 - 100	0.0094 - 0.049		.75 - 4.4	
Palmisano et al., 1987	McMurdo Sound	Mixed assemblage of sea-ice microalgae		0-25 cm	0.004 - 0.038	0.063 - 0.157	0.055 - 0.150	2.8 - 13.5
Brightman and Smith, 1989	Bransfield Strait	Mixed assemblage		0 50	0.21 (0.01) 0.031 (0.02)	1.53 (0.9) 1.24 (0.7)	1.19 (0.6) 1.10 (0.6)	60 (37) 40 (11)
Lizotte and Sullivan, 1991	Wedell - Scotia Sea	Mixed assemblage of sea-ice microalgae		0-150 cm	0.0036 - 0.058		0.091 - 4.57	14 - 144
Cota et al., 1994	Greenland Sea	<i>Phaeocystis</i> dominated	100 0.1		0.092 (0.035) 0.097 (0.036)		13.0 (5.7) 13.3 (5.3)	140 (32) 131 (33)
This Study	Ross Sea	<i>Phaeocystis</i> and diatoms	50 1		0.08 0.11		2.44 2.86	36 26

* Units for α : $\text{mg C (mg chl } a)^{-1} \text{ h}^{-1}$ ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)⁻¹

** Units for P_s^B , P_m^B : $\text{mg C (mg chl } a)^{-1} \text{ h}^{-1}$

*** Units for E_k : $(\mu\text{mol m}^{-2} \text{ s}^{-1})^{-1}$

underneath the ice (where the irradiance was reduced by 2 orders of magnitude), the rate parameter α increased significantly while P_m^B changed very little. This result demonstrates that *Phaeocystis* was able to utilize the lower irradiance more efficiently and still maintain maximal photosynthetic rates (Palmisano *et al.*, 1986). Harrison and Platt (1986) looked at the variation in P/E relationships over broad geographical and temporal scales. They found that, in polar regions especially, the parameters and therefore production were largely under physical control, namely temperature and irradiance.

Carbon and Nitrogen Assimilation

The Southern Ocean is an area of seasonally high biological productivity. Estimates of short-term productivity in the Ross Sea during Austral spring/summer range from 3.53 – 6 g C m⁻² d⁻¹ (Smith and Gordon, 1997). Smith and Gordon (1997) also investigated new production (based on nitrate disappearance) and found a mean value of 1.52 g C m⁻² d⁻¹, indicating that new production is large in this region during austral spring (see Table 3 for more estimates).

There are considerable temporal changes in production throughout spring and summer, and spatial variations in production are also significant. Estimates of productivity away from the continental shelf have been as low as 0.33 g C m⁻² d⁻¹ (El-Sayed, 1983). Some of the variation is primarily a result of sampling patterns because of the short growing season and difficulty in studying these remote areas, but much of this variability can be attributed to the increasing irradiance and retreat of sea ice in this region.

Table 3. Summary table of Primary Production values for the Ross Sea

Study	Location	Primary Production *		Season	Notes
		Mean	Range		
Holm-Hansen et al., 1977	Ross Sea Sector	0.17	0.04 - 0.30	Late Summer	
El Sayed et al., 1983	Ross Sea	0.04	- 0.95	Summer	Ross Ice Shelf
Arrigo and McClain, 1994	Ross Sea	3.90		Spring	modeled from CZCS and SMMR satellite imagery
Smith et al., 1996	Ross Sea		0.15 - 2.85	Spring/Summer	
Smith and Gordon, 1997	Ross Sea	5.53	- 6.00	Spring	
Arrigo et al., 1998	Ross Sea	1.33 1.35		Spring/Summer Spring/Summer	<i>P. antarctica</i> assemblage Diatom assemblage
Smith et al., in press	Ross Sea	1.94 0.01		Spring Autumn	
This Study	Ross Sea	1.95 1.10		Spring Summer	

*Units for Primary production $g C m^{-2} d^{-1}$

Smith *et al.* (1996) investigated the spatial and temporal variability in primary productivity on the Ross Sea continental shelf. This study found a clear difference in the northern (72°30'S) and southern (76°30'S) transects occupied, with the southern transect having primary production values nearly two times those measured in the northern transect. Other parameters supported these findings including biomass measurements and concentrations of POC and PON. Smith *et al.* (in press) found a clear seasonal trend in primary productivity and biomass, although the maximum biomass lagged the maximum production by approximately 25 days. They attributed this lag to slow biomass accumulation over time until loss processes balanced or exceeded growth later in the season. In this study primary productivity increased rapidly during the austral spring reaching its maximum in December and declined throughout January and February (Smith *et al.*, in press).

Smith *et al.* (1991) found rates of new production to be around $1.2 \text{ g C m}^{-2} \text{ d}^{-1}$ in the Greenland Sea. This value is roughly similar to values found in the “hyperproductive” Bransfield Strait. It is unknown if these hyperproductive blooms result from the shorter, more intense growing season experienced in polar regions, and the possible effects of these hyperproductive blooms on the flux of particulate material to depth are not well documented. It would be expected that highly productive events would support the export of a greater amount of organic material (Buesseler, 1998). The Ross Sea Polynya is one of these “hyperproductive” areas, with high rates of production, over short time scales (weeks to months), contributing significantly to the total production measured for the continental shelves of the Antarctic (Smith and Gordon, 1997).

Cycling of inorganic nutrients is an important part of understanding bloom dynamics because nutrient uptake may affect transport of carbon to depth. Carlson *et al.* (1998) investigated DOC distribution and concentration change in the Ross Sea. This study found that little DOC accumulation occurred throughout the austral spring/summer, indicating that the Ross Sea phytoplankton assemblage, dominated by *P. antarctica*, retained most organic carbon in particulate form. Only approximately 4% of the seasonal primary production accumulated in the DOC pool. The response of the bacterial community indicated a significant uncoupling of bacterial and phytoplankton processes. Bacterial production was initially detected at background levels and lagged that of phytoplankton production as the bloom progressed (Carlson *et al.* 1998).

Environmental factors are known to affect nutrient uptake. For example, irradiance has a direct effect on NO_3^- and NH_4^+ uptake. Although uptake continues in the dark there is evidence of increased uptake with increasing irradiance (Dortch, 1990). Uptake of these nutrients, both in the dark and at low irradiance (1% I_0), has been found at several locations, including the Ross Sea (Smith and Harrison, 1991). Some studies have found a light dependence for nitrate uptake (Muggli and Smith, 1993). The evidence is conflicting, and the exact relationship between irradiance and uptake of nitrogen is not fully understood.

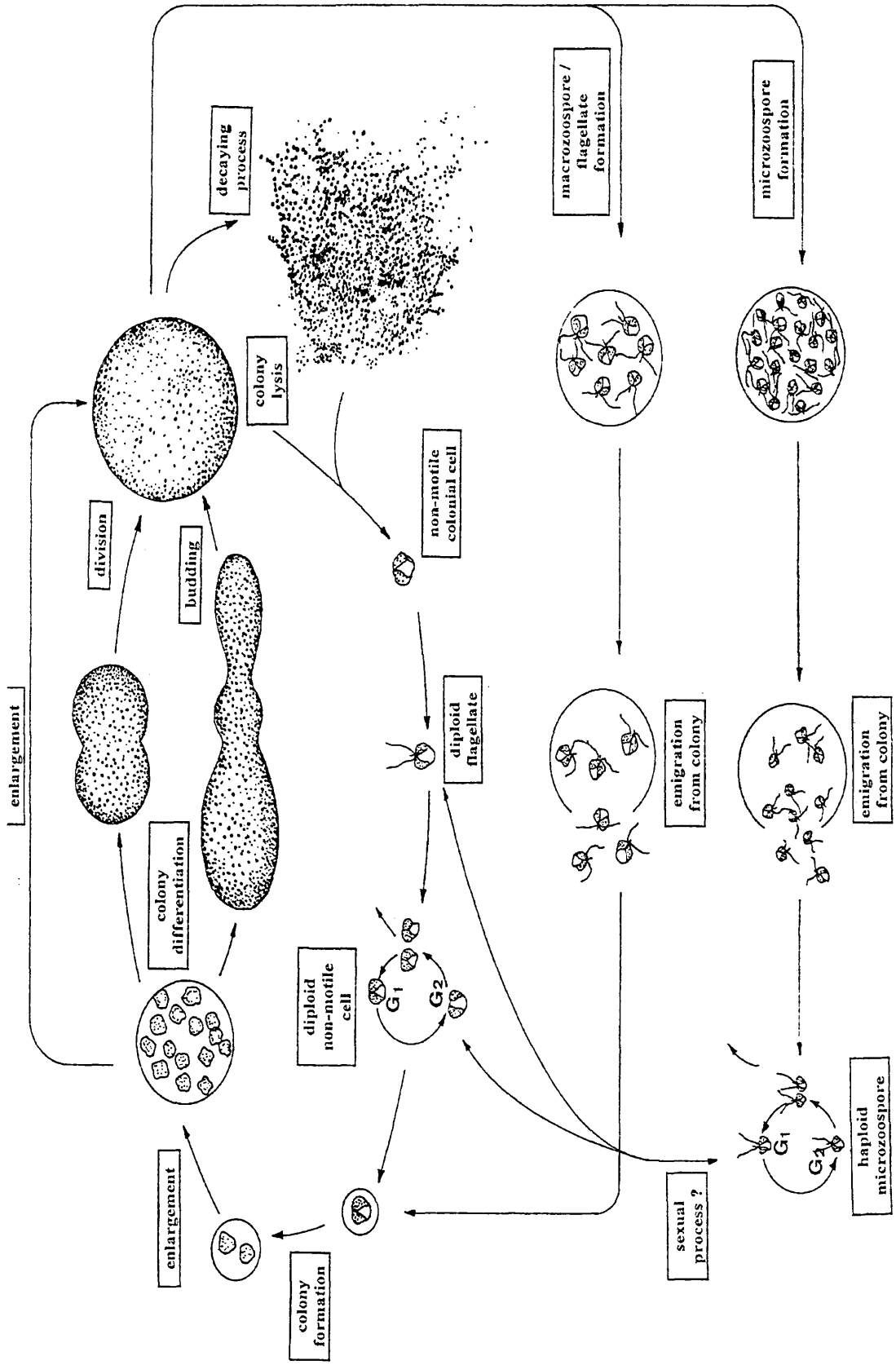
It has been well established that preferential uptake of NH_4^+ decreases the rate of NO_3^- uptake as nitrogen is recycled by bacteria and other heterotrophs in the system (Harrison, 1983). This relationship is reflected by the *f*-ratio (ratio of new:total production; Eppley and Peterson, 1979). Smith and Harrison (1991) found *f*-ratios to decrease as NH_4^+ concentrations increased in both polar and temperate regions. Most of

the spring growth in the Ross Sea appears to be supported by NO_3^- (Smith and Gordon, 1997), but nitrate is rarely reduced to limiting concentrations at any time. Ammonium only begins to become a significant term in production towards the end of the bloom, resulting in lowered *f*-ratios (Smith and Nelson, 1990). Arrigo *et al.* (1999) suggested from disappearance ratios, calculated from the slope of $([\text{NO}_3^-]+[\text{NH}_4^+])$ over $[\text{PO}_4]$, that diatom species utilized NH_4^+ more efficiently than *P. antarctica*. Disappearance ratios may not be ideal way to assess preferential uptake of N forms, since all NH_4^+ must have originally been reduced from NO_3^- (ammonium concentrations in late winter – early spring are zero; Sweeney *et al.*, in press). Arrigo *et al.* (1999) further suggested that *P. antarctica* fulfilled its nitrogen needs entirely with the NO_3^- available.

Phaeocystis antarctica

P. antarctica is the Southern Ocean member of the genus *Phaeocystis* in the Prymnesiophyceae, in the Chrysophyta or golden brown algae. This genus has a cosmopolitan distribution, and a full understanding of the various species within this genus has not yet been achieved due to its complex life cycle (Baumann *et al.*, 1994). *P. antarctica* is found in both colonial and single-celled motile forms (Fig. 3). In most cases the colonial form dominates in coastal Southern Ocean blooms. The colonies tend to be hollow and spherical or cylindrical in shape, with the cells held in a mucus matrix (Hamm *et al.*, 1999). *P. antarctica* has received much attention for several reasons, including its unique colonial structure and the large amount of mucus the colonies apparently produce under certain conditions (Mathot *et al.*, in press). It is unknown what role *P. antarctica* plays in the complex food web of the Southern Ocean, and only limited

Figure 3. Life cycle of *Phaeocystis sp.*, taken from Rousseau *et al.*, 1994



work has been done to determine grazing rates (Liss *et al.*, 1994; Haberman, 1998; Caron *et al.*, in press). Studies investigating the flux of material from the euphotic zone have found little evidence of *P. antarctica* in fecal pellets. It appears that in most cases the colonies coagulate to form large aggregates and sink, although the loss processes acting on this species in particular are not well understood (Smith *et al.*, in press).

P. antarctica is a producer of dimethylsulfide (DMS).

Dimethylsulfidepropionate (DMSP) is formed within the cell and DMS and acrylic acid are released in an equal molar ratio from the phytoplankton cells. Many studies have established a positive correlation of DMS concentration with the presence of *P. antarctica* (Gibson *et al.*, 1990; Crocker *et al.*, 1995; Liss *et al.*, 1994; DiTullio and Smith, 1996). When released from the ocean, DMS is oxidized and forms cloud condensation nuclei. Additionally, DMS is a major contributor to the acidity of atmospheric aerosols, and is an environmentally important molecule (Liss *et al.*, 1994; Crocker *et al.*, 1995). The Southern Ocean has recorded some of the largest concentrations of DMS worldwide, indicating that this region may have an important role in the global sulfur cycle (Andreae *et al.*, 1986; Liss *et al.*, 1994). It is not fully understood whether this production of DMS benefits *P. antarctica*. DMSP is thought to be an osmoregulator and possible cryoprotectant. In addition, several studies have found that acrylic acid, a byproduct of DMS production, may act as a broad spectrum antibiotic, thereby reducing the bacterial production occurring in the mucus of the *Phaeocystis* colonies (Liss *et al.*, 1994), but at acrylic acid concentrations found in the Ross Sea, no antibacterial effect has been found (DiTullio *et al.*, unpublished).

The role the colonial mucus matrix plays in *P. antarctica* is also not well understood. Higher-than-Redfield ratios of nutrient uptake by *P. antarctica* suggest that this matrix may act as a storage facility for nutrients (Lancelot and Mathot, 1985). It has also been hypothesized that the main function of the mucus matrix is to reduce grazing pressure (Lancelot *et al.*, 1998). The proportion of carbon partitioned to the matrix can be large (30 – 50%), but Mathot *et al.* (in press) found relatively minor fractions occurred in the colonial matrix. It is unknown if the relatively minor amounts of mucilage found in the Ross Sea are found throughout the Antarctic.

GENERAL APPROACH AND SIGNIFICANCE

Using both field and experimental laboratory approaches the photosynthetic/irradiance relationships of both *Phaeocystis antarctica*-dominated assemblages and diatom-dominated assemblages were investigated. Experimental manipulations were performed to derive the photosynthetic parameters. Nutrient uptake dynamics of these different assemblages *in situ* were determined from primary production (CO₂) and nitrogen (NO₃⁻ and NH₄⁺) uptake incubations. Collectively, these data were used to assess the causal mechanisms for the temporal and spatial distribution of *P. antarctica* and diatoms in the Ross Sea Polynya.

This area of the Southern Ocean is important because it is the location of the most spatially extensive phytoplankton bloom in the entire Antarctic. This unique separation of taxa provides an opportunity to investigate how community structure affects processes within the system. Dominance by either diatoms or *P. antarctica* may have effects on higher trophic levels, cycling of nutrients, and flux of dissolved and particulate organic

matter to depth. Therefore, it is important to understand how these two species differ in their nutrient uptake and assimilation capabilities and explore the causes and effects of the spatial segregation of these species in the Ross Sea

HYPOTHESES

- *Phaeocystis antarctica* and diatoms will exhibit different photosynthetic characteristics that allow *P. antarctica* to grow more rapidly than diatoms at the low irradiance conditions found early in the growing season of the Ross Sea.
- The photosynthetic characteristics of these *P. antarctica* and diatom species will change in both time and space as the irradiance environment in the Ross Sea Polynya changes, thereby allowing the growth of diatoms to increase to levels similar to those of *P. antarctica*.
- *P. antarctica* will exhibit higher carbon and nitrogen uptake rates, relative to diatoms, early in the growing season, which allows *P. antarctica* to grow and accumulate more rapidly early in the growing season.

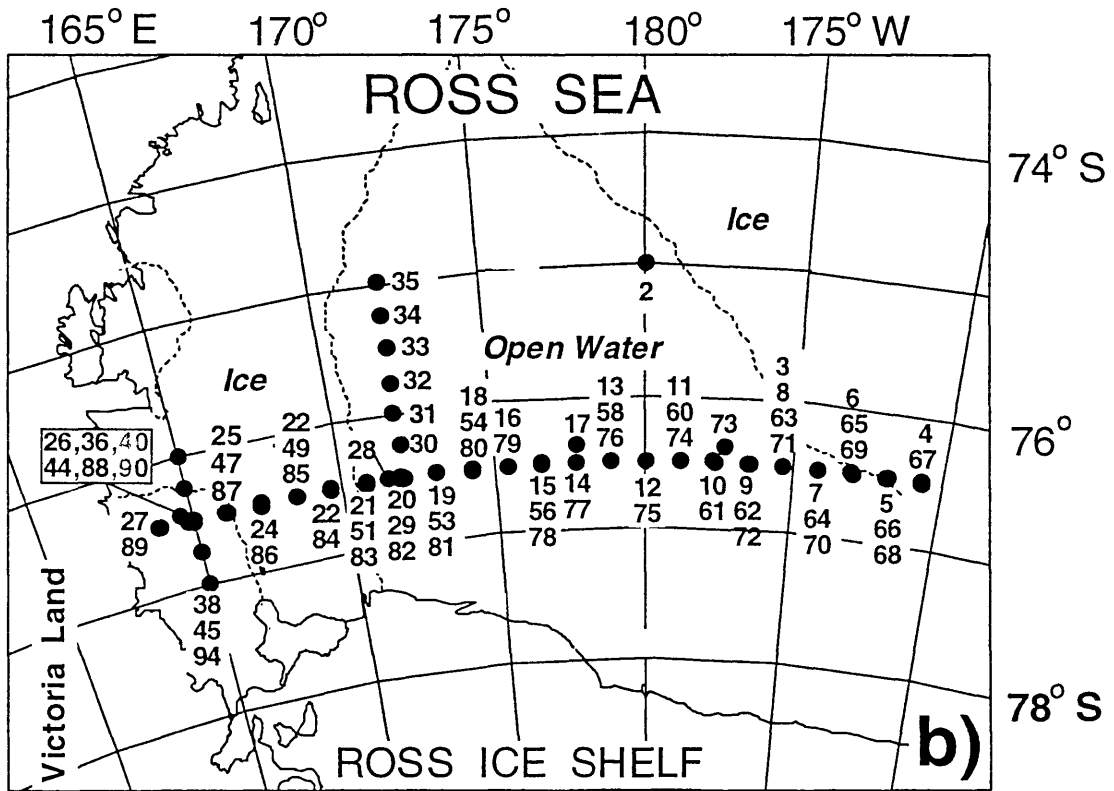
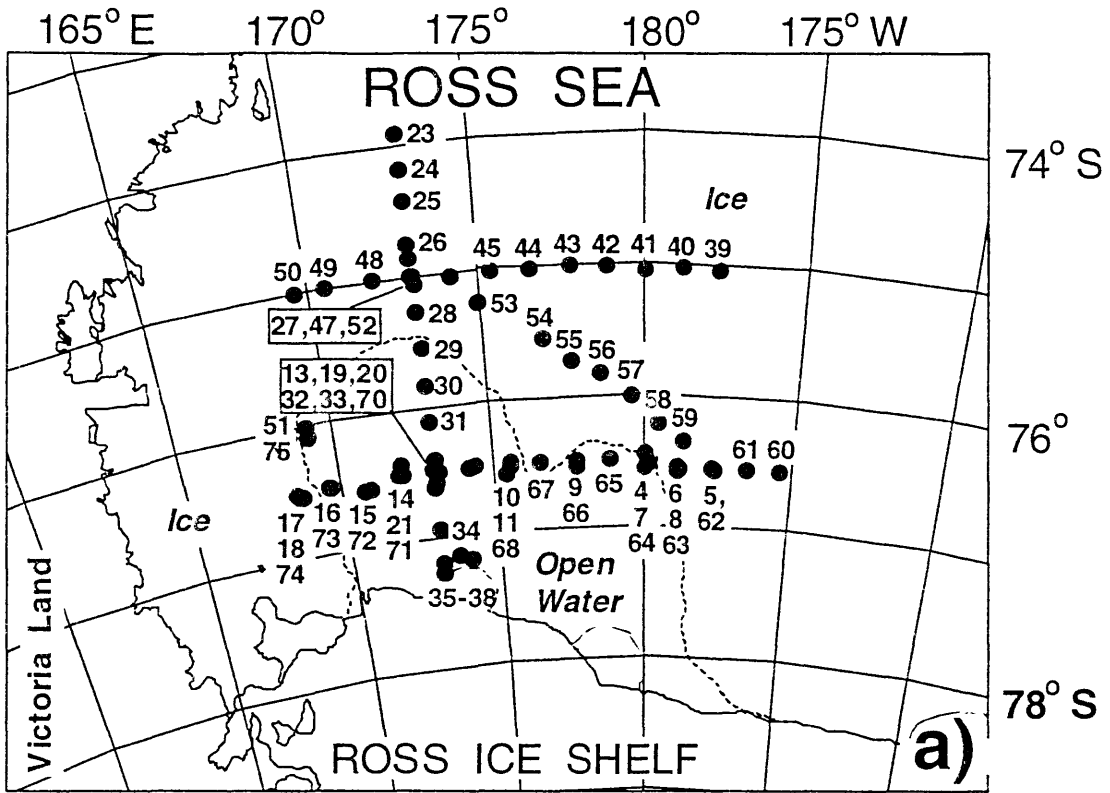
METHODS

Field Sampling

Field samples were collected in the Ross Sea Polynya during two cruises on the RVIB *Nathaniel B. Palmer* (November – December 1994 and December 1995 – January 1996) that sampled the austral spring and summer, respectively. Stations were occupied primarily along 76°30'S and the surrounding areas (Figure 4). Walker O. Smith, Jim Rich, Naomi Parker, Scott Polk, Lisa Smith, and Ann Marie White collected and processed shipboard samples. Continuous light measurements were made using a Biospherical Instruments 4 pi sensor. Isolumes (100, 50, 30, 15, 5, 1, and 0.1% surface irradiance) were determined from secchi depths or under water quantum sensor measurements at each station, and sampling depths were determined from these values. Samples were collected using a Seabird 911+ sampling rosette with 12-liter Niskin bottles fitted with Teflon-coated closing springs. The sampling rosette was equipped with sensors to measure temperature, salinity, and depth, in addition to a Chelsea Instruments fluorometer, underwater PAR sensor, and a Sea-Tech transmissometer.

Chlorophyll *a* concentrations at each isolume were determined in the field by filtering known volumes of seawater through 25 mm filters and then following a two-step extraction process. First, 10 mL of 90% acetone were added and the samples were allowed to extract on ice in the dark for 15 minutes. Samples were then sonicated on ice for another 15 minutes to aid in the breakage of membranes and extraction of the

Figure 4. Location of stations in the Ross Sea polynya, Antarctica a) December 1994 b) December 1995- January 1996.



chlorophyll from the cells. Concentrations were then determined fluorometrically before and after acidification using a Turner Designs fluorometer (Model 10 series). The fluorometer was calibrated using known concentrations of commercially purified chlorophyll *a* (Sigma).

Photosynthesis/Irradiance Experiments

Photosynthesis/irradiance relationships were measured in the field using a method adapted from Lewis and Smith (1983). Seventy-five mL of sample were inoculated with ca. 750 $\mu\text{Ci NaH}^{14}\text{CO}_3$. Then 32, two-mL sub-samples in 7 mL scintillation vials were incubated for two hours within an artificial light gradient. Incubations were terminated by acidifying with 1 mL 10% HCl. Samples were then dried, rehydrated with 1 mL deionized water, and 5 mL of scintillation cocktail (Ecolume) were added. Time zero controls were treated the same way except that they were acidified immediately. Total added $\text{NaH}^{14}\text{CO}_3$ was measured by collecting 0.1 mL of sample, adding 0.1 mL of β -phenylethylamine (which acts as a CO_2 trap), and immediately adding scintillation cocktail. Samples were counted on a liquid scintillation counter.

The incubators (photosynthetrons) consisted of a sample block with 32 wells that each held 7 mL scintillation vials and a main block containing the main light source. This block allowed the samples to be exposed to a range of irradiances from limiting to saturating conditions ($0\text{-}2000 \mu\text{mol m}^{-2} \text{s}^{-1}$) by covering the bottom of each well with different combinations of neutral density screens. The source light was provided by two halogen lamps that projected onto a surface that then reflected onto the bottom of the sample wells. The irradiance within the wells was measured using a Biospherical

Instruments quantum meter before the start of all incubations. The sample block was attached to a water bath that allowed the samples to incubate at ambient water temperature (approximately from -1.8 to 0° C). In addition to the water bath, heat from the lights was vented by a fan in the side of the photosynthetron.

Uptake Measurements

Primary productivity was measured in the field as both carbon and nitrogen assimilation with on-deck incubations. The incubator mimicked the *in situ* light environment and ambient surface water temperatures. These incubators were constructed of clear plexiglass and had troughs covered with neutral density screen to simulate 100, 50, 30, 15, 5, 1 and 0.1 % of the surface irradiance, with surface waters continually circulating through to maintain ambient temperatures. Irradiance was monitored continuously using a quantum meter throughout the cruise. Changes in spectral quality with depth were adjusted by using blue filters on the relevant incubator troughs.

Carbon Uptake

To measure carbon assimilation, small volume samples (280 mL in polycarbonate bottles) were spiked with ca. 20 μ Ci of $\text{NaH}^{14}\text{CO}_3$. The samples were then incubated for ca. 24 hours. Incubations were stopped by filtration, and the filters acidified to remove any remaining inorganic ^{14}C . Filters were then placed in scintillation vials and scintillation cocktail was added. Time zero controls (filtered and acidified immediately) were used to correct for abiotic adsorption. Samples for total added $\text{NaH}^{14}\text{CO}_3$ were collected following the same methods used in the P/E experiments. All samples were

counted on a liquid scintillation counter and DPMs were converted to production using the following equation

$$\text{Photosynthesis (mg C m}^{-3} \text{ h}^{-1}) = \frac{(24,000) * (\text{DPM}_s) * V_{\text{inc}}}{V_F * t * \text{DPM}_{\text{TOT}}} \quad (1)$$

Where $\text{DPM}_{\text{TOT}} = V_{\text{inc}} * 10 * \text{DPM}_T$, DPM_s =disintegrations per minute of sample, V_{inc} =volume incubated, V_F =volume filtered, t =incubation time, and 24,000 for the approximate concentration in mg m^{-3} of inorganic C in seawater (Sweeney *et al.*, in press).

Nitrogen Uptake

To measure nitrogen assimilation similar field incubations were performed using stable isotope methods. Additions of ^{15}N were made using 99% carrier-free $\text{Na}^{15}\text{NO}_3$ and $^{15}\text{NH}_4\text{Cl}$. A 10% enrichment, based on ambient NO_3^- and NH_4^+ concentrations, was made for the nitrate additions. Ambient concentrations of ammonium rarely exceeded $0.5 \mu\text{M}$. Because the limit of detection for ammonium is ca. $0.05 \mu\text{M}$ using standard procedures, and because a minimum amount of isotopic incorporation is needed for analytical detection on the emission spectrometer, $0.025 \mu\text{mol}$ were added to these treatments, unless NH_4^+ concentrations exceeded $0.05 \mu\text{M}$, when a 10% addition was used. Incubations were performed in 500 mL polycarbonate bottles in on-deck incubators for 24 h, in parallel with the ^{14}C -incubations. Incubations were stopped by filtering known volumes onto precombusted (450°C for 2 h) GF/F filters, rinsed with cold filtered seawater, placed in combusted glass vials capped with combusted foil, dried at 60°C , and stored for analysis in the laboratory. Care was taken not to disrupt cells or colonies by filtering under low vacuum. Samples were analyzed for ^{15}N -content by micro-Dumas

combustion in evacuated ampoules followed by emission spectrometry (Jasco). Plankton incorporation rates were calculated using initial particulate N values. Specific uptake was modeled using the following equation where uptake is assumed to be constant through time:

$$V_N = (1/T) \ln ((^{15}\text{N}_{\text{enr}} - F)/(^{15}\text{N}_{\text{enr}} - ^{15}\text{N}_s)) \quad (2)$$

where V_N is the specific nitrate uptake rate in h^{-1} , $^{15}\text{N}_s$ is the atom per cent of ^{15}N in the sample, $^{15}\text{N}_{\text{enr}}$ is the atom per cent in the initially labeled stock, F is the natural abundance of ^{15}N (0.366), and T is the incubation time in hours (Dugdale and Wilkerson, 1986). No correction was made for either isotope dilution of DO^{15}N release due to the slow turnover times in the Ross Sea.

Laboratory Experiments

Additional experiments to investigate the photosynthetic parameters of Antarctic phytoplankton were performed in the laboratory at the Virginia Institute of Marine Science using cultured phytoplankton species. Cultures of *Phaeocystis antarctica* (CCMP1871) and the diatom *Pseudonitzschia sp.* (CCMP1445) were acquired from the Provasoli – Guillard National Center for Culture of Marine Phytoplankton in Booth Bay Harbor, ME (CCMP). Both of these cultures originated from phytoplankton isolated near McMurdo Sound in the Ross Sea. The cultures were initially grown at 0°C and at approximately $200 \mu\text{mol m}^{-2} \text{s}^{-1}$, in filter sterilized *f/2* media for the diatom and filter sterilized *f/2 - Si* for *P. antarctica* (Guillard, 1983). Once the cultures were visibly established, 280 mL Qorpak bottles filled with culture media were inoculated with 10 mL of actively growing culture of each species. These bottles were covered with neutral

density screen to simulate three different irradiance regimes (332, 149, and 41 $\mu\text{mol m}^{-2} \text{s}^{-1}$). The bottles were placed in the incubator randomly and allowed to grow/acclimate for 13 days. After acclimation, samples were collected for chlorophyll *a*, HPLC determination of pigments, POC, PON and photosynthesis/irradiance experiments.

The photosynthesis/irradiance method that was used closely followed that described above with one minor modification: one mL samples were incubated for one hour. The incubation volume and time were decreased due to the high biomass in the cultures. Lewis and Smith (1983) reported that shorter incubation times for higher biomass samples give a more accurate representation of photosynthetic processes occurring on time scales equal to or less than adaptation times. Chlorophyll *a* concentrations were again determined fluorometrically, but these extractions were done in 90% acetone in the dark at 4° C for 24 h.

The full suite of phytoplankton pigments were analyzed using High Performance Liquid Chromatography (HPLC). Known volumes were filtered onto GF/F filters and quick-frozen in liquid N₂ until analysis. These samples were analyzed by first extracting the pigments by grinding in 90% acetone, then separating the filter from the extracted photosynthetic pigments by high speed centrifugation. This extracted sample was then diluted (2:1) with deionized water before being injected onto the sample column for analysis. Identification and quantification of the plankton pigments were performed using a Waters HPLC system consisting of a 600 controller/dual pump, a 717 Autosampler, a 996 Photodiode Array Detector and a 747 Scanning Fluorescence Detector (Waters, Milford, MA, USA). Solvents were degassed using an in-line degasser. Samples were injected onto, and pigments separated using, a Waters

Spherisorb 5 mm ODS2 analytical column. A Waters guard column preceded the analytical column, containing the same above packing material. System functions, data collection and data analysis was accomplished using Waters Millennium³² software.

POC and PON samples were filtered onto combusted (450° C for 2 hours) GF/F filters, dried at 60° C, and analyzed on a Fisons CHNSO elemental analyzer. Blanks were run by analyzing unused, combusted filters.

Data Analysis

All photosynthesis/irradiance data were normalized to chlorophyll *a* biomass and then fitted to the empirical equation described by Platt *et al.* (1980):

$$P^B = P_s^B \left(1 - e^{-\alpha E / P_s^B}\right) e^{-\beta E / P_s^B} \quad (3)$$

using Sigma Plot 4.0 to perform the nonlinear regression. The parameters from this equation and other parameters calculated from these initial values and their units are found in Table 2. Sigma Plot uses the Marquardt-Levenberg algorithm to derive parameters for the curves. This process is iterative and starts from given estimates of the parameters and iterates until the difference between the residual sum of squares no longer decreases significantly.

In cases when the numerical routine within Sigma Plot failed to converge (making reliable estimates of parameter values impossible), these parameter values (11 of 88 experiments) were discarded from the analysis. In addition, parameter values that were more than two standard deviations from the mean (of all values) were eliminated (Sokal and Rohlf, 1981). The parameter values were first analyzed using a linear regression over time to determine if a temporal trend could be detected. For both the field and

laboratory experiments, photosynthetic parameter values were pooled by irradiance and taxonomic dominance, as determined by HPLC pigment concentrations (see Smith and Asper, in press). These parameters were next examined using the general linear model for analysis of variance (ANOVA) to evaluate effects due to taxonomic dominance and irradiance and possible interaction effects. For the culture experiments a two way ANOVA was applied to determine if there was any interaction between irradiance and species.

The uptake data were analyzed using analysis of variance (ANOVA). Much of these data did not meet the assumptions of parametric statistics (i.e. normally distributed, homogeneity of variance). Whenever possible the data were transformed to yield homogeneous variance, using either a logarithmic or square root transformation. In all cases, except for the integrated NO_3^- uptake data, transformation of the data was corrected for variance (Cochran's test for heteroscedasticity) but not non-normality. However, analysis of variance is a statistically robust test for data that are not normally distributed (Underwood, 1997). In addition to ANOVA, *a posteriori* comparisons (Tukey test and Student-Newman-Keuls test) were performed to further define significant effects. Underwood (1997) stated that analysis of variance is still a robust analysis when data sets exhibit departure from the assumptions, particularly when sample sizes are large.

RESULTS

Field Conditions

Average daily irradiance, calculated using the model of Legendre *et al.* (1993), for the austral spring (1994) cruise was $578 \pm 172 \mu\text{mol m}^{-2} \text{s}^{-1}$ (data not shown).

Although this model makes the assumption of cloud-free weather conditions that are rarely met in the Ross Sea, the modeled values were similar to the values from the ship-board collected PAR data (Parker, 1997). (Model results were used to fill large gaps in PAR data.) The average depth of the euphotic zone ($0.1\% I_0$) was 53 ± 31 m (data not shown). Chlorophyll *a* values increased throughout the cruise, starting at less than $1 \mu\text{g L}^{-1}$ and increasing to over $7 \mu\text{g L}^{-1}$, with the mean chlorophyll *a* concentration being $3.17 \pm 2.41 \mu\text{g L}^{-1}$. Chlorophyll concentrations were relatively constant through out the water column. Average integrated production for the early spring was $1.95 \pm 1.71 \text{ g C m}^{-2} \text{ d}^{-1}$.

Average calculated daily irradiance for the austral summer cruise (1995-96) was $572 \pm 281 \mu\text{mol m}^{-2} \text{s}^{-1}$, and the average depth of the euphotic zone was 42 ± 17 m (data not shown). Chlorophyll *a* values remained relatively constant for most of the cruise but declined towards its end. The average chlorophyll *a* concentration was $3.68 \pm 2.76 \mu\text{g L}^{-1}$ (Range: $>1-12 \mu\text{g L}^{-1}$). The average chlorophyll *a* concentrations for the 1 and 0.1% irradiance levels were 4.37 and 4.05, respectively, which were higher than the averages at higher isolumes. Average integrated production for the summer was $1.10 \pm 0.83 \text{ g C m}^{-2} \text{ d}^{-1}$.

Mixed layer depths for the composite of both cruises decreased from early spring into the austral summer. Mixed layer depths for the spring cruise ranged from 16 – 150 m, while the summer mixed layer depths ranged from 0 – 73 m. Degree of stratification was found to vary seasonally. The south-central region was generally less strongly stratified when compared to the western region. Stations closer to the coast initially had deeper mixed layers that were reduced by the addition of low density melt-water (Data not shown).

Taxonomic dominance at each station was determined by calculating pigment ratios from HPLC data. Those stations where the integrated euphotic zone fucoxanthin:19'-hexanoyloxyfucoxanthin ratios (FUCO:HEX) were > 1.0 were considered to be diatom dominated, those with a FUCO:HEX ratio < 0.2 were considered to be dominated by *Phaeocystis antarctica*. All stations not classified as diatom or *Phaeocystis*-dominated were considered to be a mixed assemblage, (see Smith and Asper (in press) for a full discussion of taxonomic dominance as determined by pigment ratios).

Photosynthesis/Irradiance Experiments

Field Data

Parameter values (α , β , P_m^B , E_k) were calculated for all 88 photosynthesis/irradiance measurements following the method of Platt *et al.*, (1980) (Table 4). Of these, 11 were discarded because of failure to converge on a parameter value. In many cases β was equal to 0 or not detectable, and β was excluded from all analyses. (P/E curves in Appendix I).

Table 4. Calculated parameters for field experiments

STATION	%I ₀	α	P ^b _m	E _k	STATION	%I ₀	α	P ^b _m	E _k
1994									
13	50	0.204	8.006	39	23	1	0.130	2.802	22
19	50	0.055	2.169	40	25	50	0.047	1.855	40
22	50	0.038	1.674	44	25	1	0.116	2.861	25
25	50	0.006	0.231	38	26	1	0.043	1.374	32
36	50	0.200	4.159	21	28	50	0.060	1.914	32
38	50	0.067	2.137	32	35	1	0.052	0.709	14
64	50	0.067	2.373	35	47	50	0.073	2.858	39
68	50	0.065	3.033	47	54	50	0.064	1.365	21
77	50	0.031	0.756	24	61	1	0.080	1.956	24
1995-96									
5	50	0.043	1.495	35	68	50	0.052	1.786	35
7	50	0.074	2.956	40	68	1	0.099	2.337	24
7	1	0.122	3.059	25	70	50	0.046	0.950	21
9	50	0.067	1.287	19	70	1	0.077	2.150	28
9	1	0.037	0.828	22	71	50	0.059	2.250	38
10	50	0.070	1.747	25	71	1	0.311	7.426	24
12	50	0.111	3.124	28	73	50	0.038	1.556	41
12	1	0.173	6.895	40	73	1	0.075	1.592	21
14	50	0.090	2.837	31	75	50	0.193	3.791	20
14	1	0.086	3.170	37	75	1	0.112	3.485	31
16	50	0.186	2.922	16	78	50	0.145	2.672	18
16	1	0.320	4.080	13	78	1	0.083	1.785	21
17	50	0.175	2.257	13	80	50	0.067	2.164	32
17	1	0.090	1.884	21	81	50	0.055	2.847	52
18	50	0.071	2.018	28	83	50	0.022	2.023	94
18	1	0.063	2.606	42	83	1	0.101	1.078	11
20	1	0.065	1.423	22	84	1	0.061	1.926	31
21	50	0.047	3.991	85	85	1	0.184	4.699	26
21	1	0.116	3.827	33	86	50	0.133	2.913	22
22	50	0.063	3.192	51	86	1	0.097	2.778	29
22	1	0.137	7.448	55	87	50	0.073	3.228	44
23	50	0.027	1.241	45	87	1	0.077	1.285	17
					88	1	0.119	1.866	16

The mean α value for both cruises was $0.094 \pm 0.062 \text{ mg C (mg Chl } a)^{-1} \text{ h}^{-1} (\mu\text{mol m}^{-2} \text{ s}^{-1})^{-1}$, ranging from $0.006 - 0.311 \text{ mg C (mg Chl } a)^{-1} \text{ h}^{-1} (\mu\text{mol m}^{-2} \text{ s}^{-1})^{-1}$. The mean P_m^B value was $2.621 \pm 1.571 \text{ mg C (mg Chl } a)^{-1} \text{ h}^{-1}$, and ranged from $0.231 - 8.006 \text{ mg C (mg Chl } a)^{-1} \text{ h}^{-1}$. The mean E_k value was $32 \pm 15 \mu\text{mol m}^{-2} \text{ s}^{-1}$, and values ranged from $11 - 94 \mu\text{mol m}^{-2} \text{ s}^{-1}$.

Statistical Analyses

No temporal variations were detected for any of the photosynthetic parameters (α , P_m^B , or E_k) (Figure 5). When regressed over time, the slopes of α , P_m^B , and E_k were not significantly different from zero ($P=0.79, 0.46, 0.39$, respectively). The mean α , P_m^B , and E_k values for both cruises are presented in Table 5. When analyzed as a function of irradiance level (50 or 1% I_0), there were no interaction effects between taxa and irradiance for all three parameters, suggesting that these factors have independent effects on photosynthetic response. Each photosynthetic parameter was investigated individually. These data were not normally distributed but did have homogeneous variance (as determined by Levene's test for heterogeneous variance). The two-way analysis of variance detected a significant effect due to the irradiance levels for both α and E_k (Table 6). Values for α (the photosynthetic efficiency) at the 1% irradiance level are greater than those for the 50% irradiance level, while values for E_k , the adaptation parameter, are less at the 1% isolume. When analyzed relative to taxonomic dominance, neither the analyses of variance nor a Tukey's Studentized Range multiple means comparison detected a significant difference among the parameters for the taxonomic groupings.

Figure 5. Plot of P/E parameters over time, indicating no detectable change in the parameters with time. Data shown are means and standard errors.

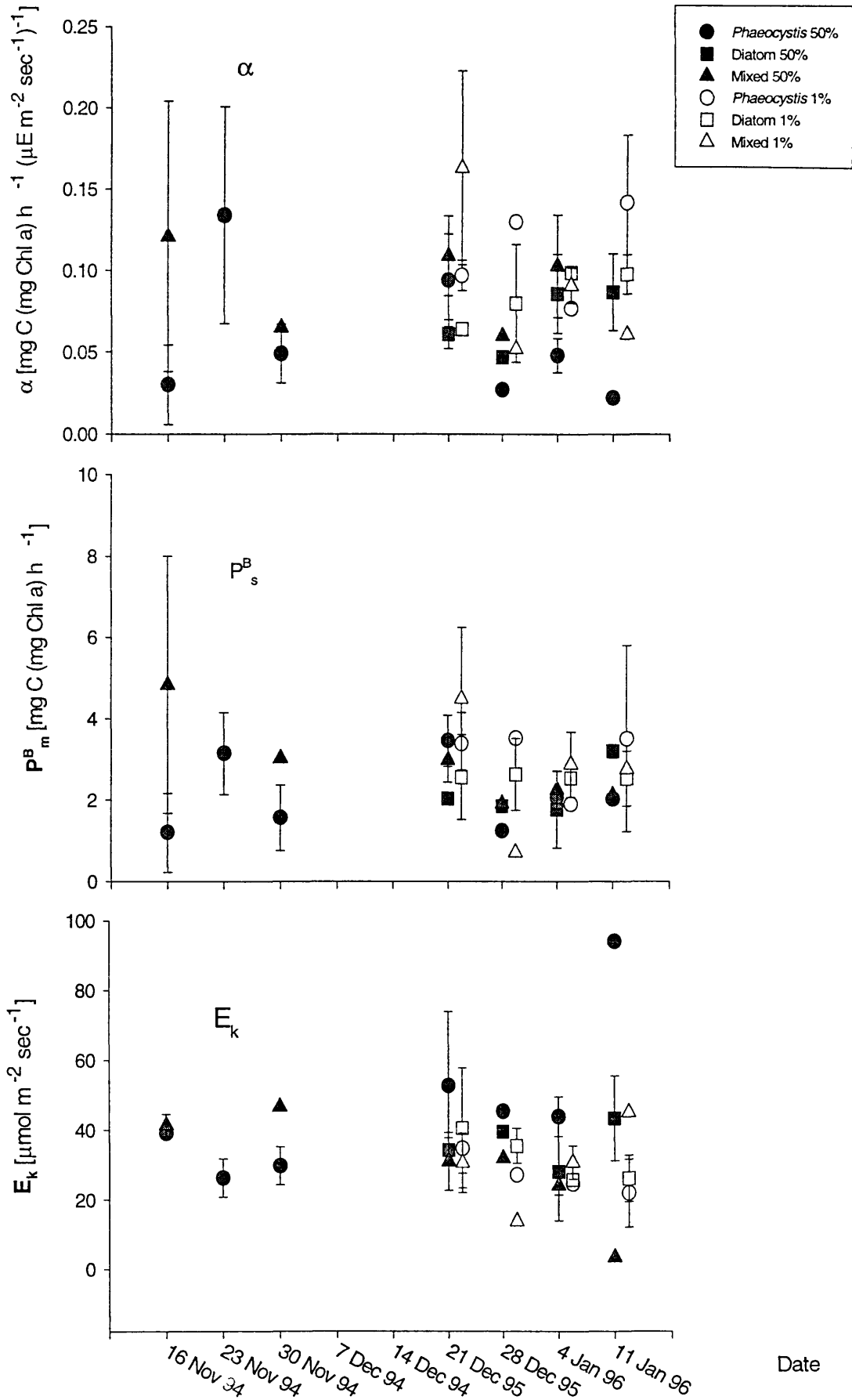


Table 5. Mean response of P/E experiments grouped by different factors

	1994	1995-96	50%	1%	<i>P. antarctica</i>	Diatom	Mixed Assemblage
α	0.08	0.10	0.08	0.11	0.09	0.08	0.11
P_m^B	2.73	2.72	2.44	2.86	2.79	2.19	2.76
E_k	36	34	36	26	36	31	27

Table 6. F and P values for two-way analysis of variance for Photosynthesis/irradiance experiments in both the laboratory and field.

	α		P_m^B		E_k	
	F	P	F	P	F	P
Laboratory Experiments						
Irradiance	5.91	0.02	6.17	0.01	12.61	0.00
Taxa	0.74	0.41	7.70	0.02	0.08	0.78
Irradiance*Taxa	0.38	0.69	3.39	0.07*	0.04	0.96
Field Experiments						
Irradiance	4.84	0.03	1.31	0.26	7.49	0.01
Taxa	1.30	0.28	0.89	0.42	2.20	0.12
Irradiance*Taxa	1.21	0.30	1.63	0.20	0.85	0.43

* indicates questionable result

Laboratory Experiments

The Platt *et al.* (1980) model was also fit to the data from the laboratory experiments to estimate the photosynthetic parameters. A total of 18 experiments were completed, and parameter values were estimated for α , β , P_m^B , and E_k (Table 7). Again, β was excluded from the analyses because it was either very close to zero or inadequately estimated by the model. Only the parameter α met both of the assumptions for analysis of variance, normal distribution and homogenous variance. The other two parameters, P_m^B and E_k , were not normally distributed, but both parameter values had homogenous variance and therefore the data were not transformed before analysis.

The mean responses (α , P_m^B , and E_k) grouped by the three irradiance levels and two taxa are presented in Table 8. The two-way analysis of variance detected a significant effect due to irradiance for both α and E_k (Table 6), similar to the findings in the field. The Tukey's multiple means comparison test further defined this effect, at the lower irradiance levels α was higher while the values for E_k were lower, as in the field experiments (Table 9).

The results for P_m^B were more complicated. No interaction was detected, but the P value was close to being significant ($P=0.07$), making interpretation of these results difficult. This test had low power due to poor replication within the experiment. Significant effects were detected for both irradiance and taxa. The mean P_m^B value was 1.14 for *Phaeocystis antarctica* and 0.68 for *Pseudonitzschia sp.* A two-sample t-test indicated that the P_m^B response for *P. antarctica* was greater than *Pseudonitzschia* ($P=0.04$) and a multiple means comparison of the values at the different irradiance levels indicated that the response at $322 \mu\text{mol m}^{-2} \text{s}^{-1}$ was significantly different from the lower

Table 7. Calculated parameters for laboratory experiments

Irradiance ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Taxa	α	P_m^B	E_k
332	<i>P. antarctica</i>	0.013	2.709	204
332	<i>P. antarctica</i>	0.005	1.636	334
332	<i>P. antarctica</i>	0.006	1.232	205
332	<i>Pseudonitzschia</i>	0.007	0.798	117
332	<i>Pseudonitzschia</i>	0.001	0.583	416
332	<i>Pseudonitzschia</i>	0.006	0.966	167
149	<i>P. antarctica</i>	0.010	0.820	81
149	<i>P. antarctica</i>	0.015	1.647	114
149	<i>P. antarctica</i>	0.006	0.583	94
149	<i>Pseudonitzschia</i>	0.013	0.927	74
149	<i>Pseudonitzschia</i>	0.005	0.415	83
149	<i>Pseudonitzschia</i>	0.009	0.660	72
41	<i>P. antarctica</i>	0.008	0.614	73
41	<i>P. antarctica</i>	0.013	1.252	94
41	<i>P. antarctica</i>	0.019	0.875	46
41	<i>Pseudonitzschia</i>	0.018	0.650	37
41	<i>Pseudonitzschia</i>	0.018	0.624	35
41	<i>Pseudonitzschia</i>	0.019	0.460	24

Table 8. Mean response for laboratory P/E experiments.

	α	P_m^B	E_k
$\mu\text{mol m}^{-2} \text{s}^{-1}$			
322	0.0064	1.32	241
149	0.0112	0.73	74
41	0.0178	0.67	41
Taxa			
<i>Phaeocystis</i>	0.0130	1.14	123
<i>Pseudonitschiza</i>	0.0106	0.68	114

Table 9. Post Hoc Results for Photosynthesis/irradiance experiments for both field and laboratory experiments. The Tukey Studentized Range (HSD) test was performed.

Laboratory Experiments		α	P_m^B	E_k
Irradiance Level	322	A	A	A
($\mu\text{mol m}^{-2} \text{s}^{-1}$)	149	A B	B	B
	41	B	B	B

Field Experiments				
Taxa	<i>Phaeocystis</i>	A	A	A
	Diatom	A	A	A
	Mixed Assemblage	A	A	A

two levels (Table 9). The P_m^B value at $322 \mu\text{mol m}^{-2} \text{s}^{-1}$ was nearly two times greater than the values at 149 and $41 \mu\text{mol m}^{-2} \text{s}^{-1}$.

Differences in chlorophyll *a*, chlorophylls *c1* and *c2*, 19'-hexanoyloxyfucoxanthin (*P. antarctica* only), and fucoxanthin (*Pseudonitzschia sp.* only) concentrations due to irradiance and taxa within the cultures were investigated. The analysis indicated that both irradiance level and taxa had an effect on chlorophyll *a* and chlorophyll *c1* and *c2* concentrations. When averaged by irradiance, all of the chlorophylls had increased concentrations as irradiance decreased (Table 10). *P. antarctica* had an average chlorophyll *a* concentration of $25 \mu\text{g L}^{-1}$ while the *Pseudonitzschia* culture had an average concentration of $187 \mu\text{g L}^{-1}$. This difference is partially a function of cell number and size within the different cultures. A Kruskal-Wallis Test found significant differences among the mean concentrations of 19'-hexanoyloxyfucoxanthin at the three irradiance levels ($p=0.03$). The 19'-hexanoyloxyfucoxanthin concentrations in the *P. antarctica* cultures increased with decreasing irradiance. However, there was no significant difference in fucoxanthin concentrations at the different irradiance levels. The POC:Chl ratio calculated from HPLC values of chlorophyll *a* were 53 and 387 for *Pseudonitzschia* and *P. antarctica*, respectively. The C:N ratios (*Pseudonitzschia* 5.01 ± 0.24 and *P. antarctica* 5.64 ± 0.09) for these two cultured species were also significantly different (t-test, $P=0.001$).

Carbon and Nutrient Uptake Dynamics

Primary productivity ($\text{g C m}^{-2} \text{d}^{-1}$), primary productivity normalized to chlorophyll ($\text{g C (g Chl } a)^{-1} \text{m}^{-2} \text{d}^{-1}$), uptake of NO_3^- normalized to particulate nitrogen

Table 10. HPLC Pigment Concentrations in $\mu\text{g L}^{-1}$ from cultures

	<i>P. antarctica</i>			<i>Pseudonitzschia</i>		
	322 $\mu\text{mol m}^{-2} \text{s}^{-1}$	149 $\mu\text{mol m}^{-2} \text{s}^{-1}$	41 $\mu\text{mol m}^{-2} \text{s}^{-1}$	322 $\mu\text{mol m}^{-2} \text{s}^{-1}$	149 $\mu\text{mol m}^{-2} \text{s}^{-1}$	41 $\mu\text{mol m}^{-2} \text{s}^{-1}$
Chlorophyll <i>a</i>	7.63	21.57	44.52	110.50	186.89	264.09
Chlorophylls <i>c1, c2</i>	0.69	2.69	6.62	6.33	13.71	25.09
19' Hexanoyloxyfucoxanthin	0.24	1.81	5.46			
Fucoxanthin				0.12	0.18	0.26

($\text{mmol NO}_3^- (\text{mmol PN})^{-1} \text{m}^{-2} \text{d}^{-1}$) or d^{-1} , uptake of NH_4^+ normalized to particulate nitrogen ($\text{mmol NH}_4^+ (\text{mmol PN})^{-1} \text{m}^{-2} \text{d}^{-1}$) or d^{-1} and total N uptake, also normalized to particulate nitrogen, ($\text{mmol N} (\text{mmol PN})^{-2} \text{m}^{-2} \text{d}^{-1}$) or d^{-1} were calculated for vertically integrated daily uptake (through the euphotic zone) and instantaneous water column uptake at each isolume. A total of 45 stations were sampled during the 1994 early spring cruise and 51 stations were sampled during the 1995-96 summer cruise (Appendix II).

Vertically Integrated Daily Values

Regressions of nutrient uptake over time were first performed to determine if there was a temporal change in the data. Each cruise was examined individually to more accurately determine the relationship with time. All of the regressions were significant, except for total N uptake in both cruises and primary productivity normalized to chlorophyll in the 1995-96 cruise (Table 11). Although the regressions were significant, the R^2 values were extremely low, explaining little of the variance within the data and making interpretation of the results difficult. Because the relationship of nutrient uptake over time could not be resolved via regression analysis, temporal variation was incorporated into the analysis of variance as the factor season [early spring (1994) and summer (1995-96)]. The factors taxa and season were used in all analyses of nutrient uptake.

Primary Productivity/Carbon Uptake

Primary production at the sampled stations ranged from $0.13 - 7.50 \text{ g C m}^{-2} \text{ d}^{-1}$ for both cruises combined. The overall mean primary production was $1.50 \text{ g C m}^{-2} \text{ d}^{-1}$ (Table 12). A significant effect was detected due to taxonomic dominance, although a multiple means comparison did not further define this effect (Tables 13, 14). The P .

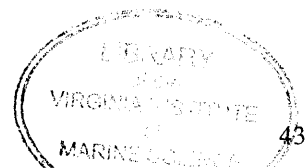


Table 11. Regression results for nutrient uptake measurements and biomass measurements. Rho values were normalized using PN values.

	1994		1995-96	
	P	R2	P	R2
Primary Productivity				
g C m⁻² d⁻¹	*	0.07	*	0.04
Chl a				
μg L⁻¹	*	0.28	*	0.51
Primary Productivity/Chl a				
g C (g Chl a)⁻¹ m⁻² d⁻¹	*	0.02	N.S.	
ρ NO₃				
d⁻¹	*	0.05	*	0.09
ρ NH₄				
d⁻¹	*	0.04	N.S.	
Total N Uptake				
d⁻¹	N.S.		N.S.	

Table 12. Mean uptake parameters from all field measurements

	1994	1995-96	Assemblage Composition		
			<i>P. antarctica</i>	Diatom	Mixed
Primary Productivity g C m ⁻² d ⁻¹	1.95	1.10	1.93	1.34	1.23
Primary Productivity/Chl <i>a</i> g C (g Chl <i>a</i>) ⁻¹ m ⁻² d ⁻¹	0.85	0.35	0.64	0.68	0.52
ρ NO₃ d ⁻¹	5.81	6.89	4.48	8.09	6.99
ρ NH₄ d ⁻¹	1.47	2.84	1.15	2.65	2.71
Total N d ⁻¹	7.44	9.74	5.91	10.73	9.78
<i>f</i>-ratio	0.77	0.62	0.75	0.70	0.63

Table 13. P values from two way analysis of variance on integrated station values for nutrient uptake. All data (except Rho NO₃) were transformed to have homogeneous variance.

	Taxa*Season	Taxa	Season	ANOVA FIT
Primary Productivity g C m ⁻² d ⁻¹	0.481	0.039	0.063	0.048
Chl a μg L ⁻¹	0.011	**	**	0.002
Primary Productivity/Chl a g C (g Chl a) ⁻¹ m ⁻² d ⁻¹	0.012	**	**	0.000
ρ NO₃* d ⁻¹	0.155	0.027	0.864	0.055
ρ NH₄ d ⁻¹	0.001	**	**	0.000
Total N Uptake d ⁻¹	0.039	**	**	0.003

** indicates uninterpretable due to significant interaction between factors Taxa and Season

* Data do not meet the assumptions of ANOVA

Table 14. Post Hoc Results for Nutrient uptake experiments field experiements. Both the SNK and Tukey Studentized Range (HSD) tests were performed.

	<i>Phaeocystis</i>	Diatom	Mixed
Primary Productivity g C m ⁻² d ⁻¹	A	A	A
Chl a μg L ⁻¹	A	A	A
Primary Productivity/Chl a g C (g Chl a) ⁻¹ m ⁻² d ⁻¹	A	A	A
ρ NO₃ d ⁻¹	A	B	A B
ρ NH₄ d ⁻¹	A	B	B
Total N Uptake d ⁻¹	A	B	B

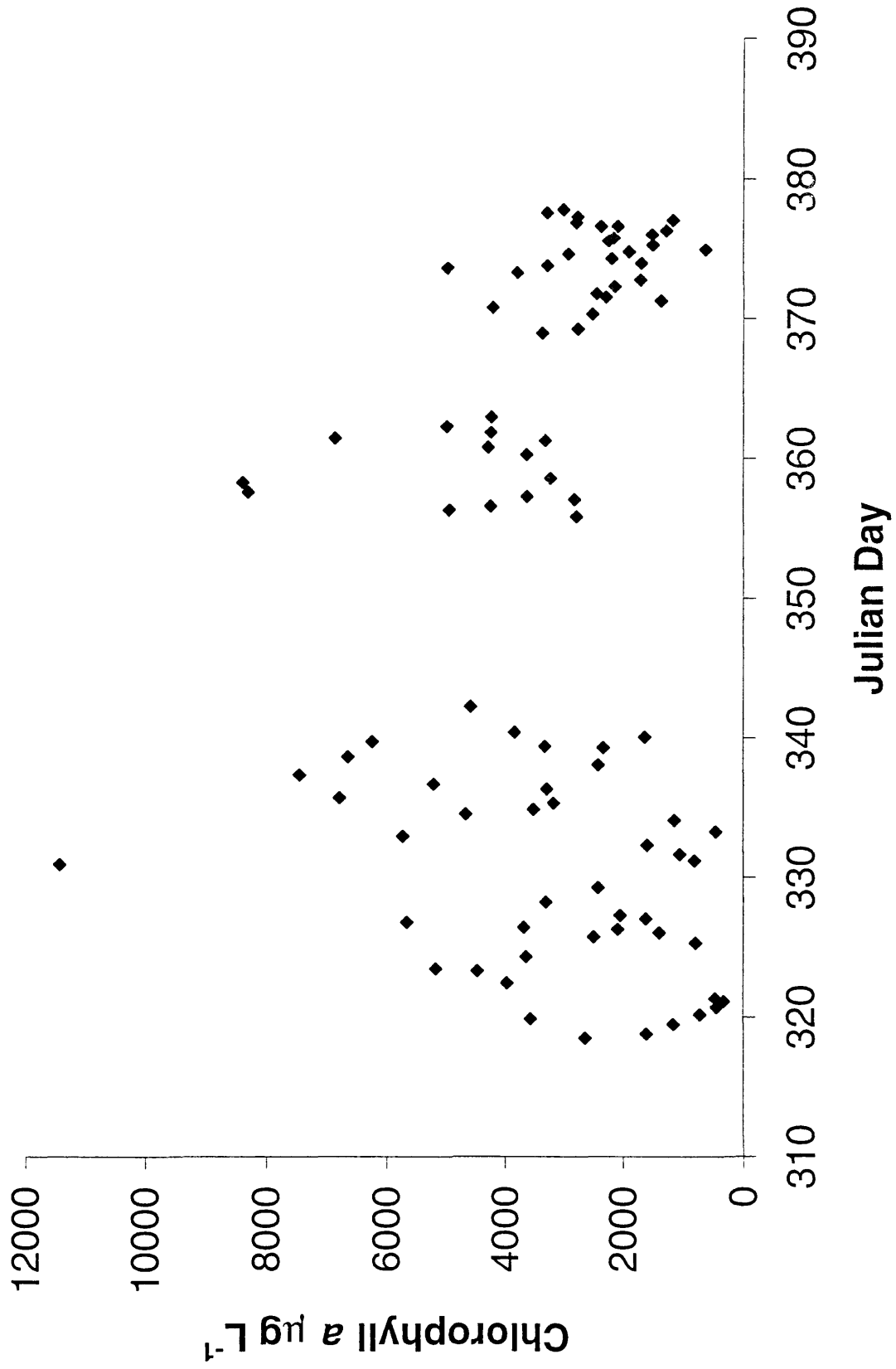
antarctica dominated stations had a higher mean primary productivity ($1.93 \text{ g C m}^{-2} \text{ d}^{-1}$) when compared to the diatom and mixed assemblages (1.34 and $1.23 \text{ g C m}^{-2} \text{ d}^{-1}$, respectively). This difference is likely due to differences in biomass among the groups.

When averaged for both cruises the mean primary productivity normalized to chlorophyll *a* concentration was $0.61 \text{ g C (g Chl } a)^{-1} \text{ m}^{-2} \text{ d}^{-1}$, and values ranged from $0.07 - 2.90 \text{ g C (g Chl } a)^{-1} \text{ m}^{-2} \text{ d}^{-1}$. Significant interactions between taxa and season were detected for primary productivity normalized to chlorophyll *a* concentration, making the interpretation of the individual factors within the ANOVA impossible. A multiple means comparison of the primary productivity normalized to chlorophyll *a* values did not detect a significant difference between the three taxonomic groupings. A two-sample t-test determined that the responses were not equal for the spring and summer season ($P=0.001$). The mean chlorophyll-normalized primary production was $0.85 \pm 1.30 \text{ g C (g Chl } a)^{-1} \text{ m}^{-2} \text{ d}^{-1}$ for the spring cruise and $3.50 \pm 2.20 \text{ g C (g Chl } a)^{-1} \text{ m}^{-2} \text{ d}^{-1}$ for the summer cruise.

Chlorophyll a

Vertically integrated chlorophyll *a* values remained relatively constant throughout (Figure 6); mean concentrations were $3.10 \text{ g Chl } a \text{ m}^{-2}$ and $3.20 \text{ g Chl } a \text{ m}^{-2}$ for spring and summer, respectively. Values for both cruises ranged from $0.33 - 11.00 \text{ g Chl } a \text{ m}^{-2}$. The analysis found a significant interaction between taxa and season when investigating the integrated chlorophyll values (Table 13). Further investigation using a multiple means comparison did not detect a difference for the three taxonomic groupings (Table 14). In addition, no significant difference was detected for chlorophyll *a* between the two seasons when a two-sample t-test was performed.

Figure 6. Integrated Chlorophyll *a* biomass over Julian day for all stations sampled.



Nitrogen Uptake

Mean integrated NO_3^- uptake for both cruises was $6.57 \text{ mmol NO}_3^- (\text{mmol PN})^{-1} \text{ m}^{-2} \text{ d}^{-1}$. Means for each cruise were 5.64 ± 4.57 and $7.21 \pm 4.43 \text{ mmol NO}_3^- (\text{mmol PN})^{-1} \text{ m}^{-2} \text{ d}^{-1}$ for spring and summer, respectively (Figure 7). Although the data for normalized uptake of NO_3^- did not meet the assumptions of ANOVA the results of the two-way ANOVA are still valuable (Underwood, 1997). No interaction was detected between taxa and season. A significant effect was detected due to taxa, suggesting that these species may utilize nitrogen at different rates. A multiple means comparison indicated a significant difference in mean uptake rates for *P. antarctica* and diatom-dominated stations, while neither of these was different from the mixed assemblage (Table 14). No significant effect was detected due to season.

Integrated NH_4^+ uptake increased over time for both cruises (Figure 8). Mean uptake in the spring and summer was $1.43 \pm 1.64 \text{ mmol NH}_4^+ (\text{mmol PN})^{-1} \text{ m}^{-2} \text{ d}^{-1}$ and $2.86 \pm 1.57 \text{ mmol NH}_4^+ (\text{mmol PN})^{-1} \text{ m}^{-2} \text{ d}^{-1}$, respectively. Total N uptake did not change dramatically during the two cruises. Mean total N uptake for both cruises was $8.64 \pm 5.14 \text{ mmol N } (\text{mmol PN})^{-1} \text{ m}^{-2} \text{ d}^{-1}$. Interaction was detected in the two-way ANOVAs for both uptake of NH_4^+ and total N uptake. Multiple means comparison showed that in both cases mean uptake for *P. antarctica* was significantly lower than both the diatom and mixed assemblage stations. A two sample t-test detected a significant difference in specific uptake of NH_4^+ for the two seasons. Uptake of NH_4^+ was greater during the summer season.

A C:N ratio was calculated using molar carbon uptake to molar nitrogen uptake as a short term look at the coupling between carbon and nitrogen metabolism (e.g. daily

Figure 7. Integrated NO_3^- uptake over Julian Day for all stations sampled.

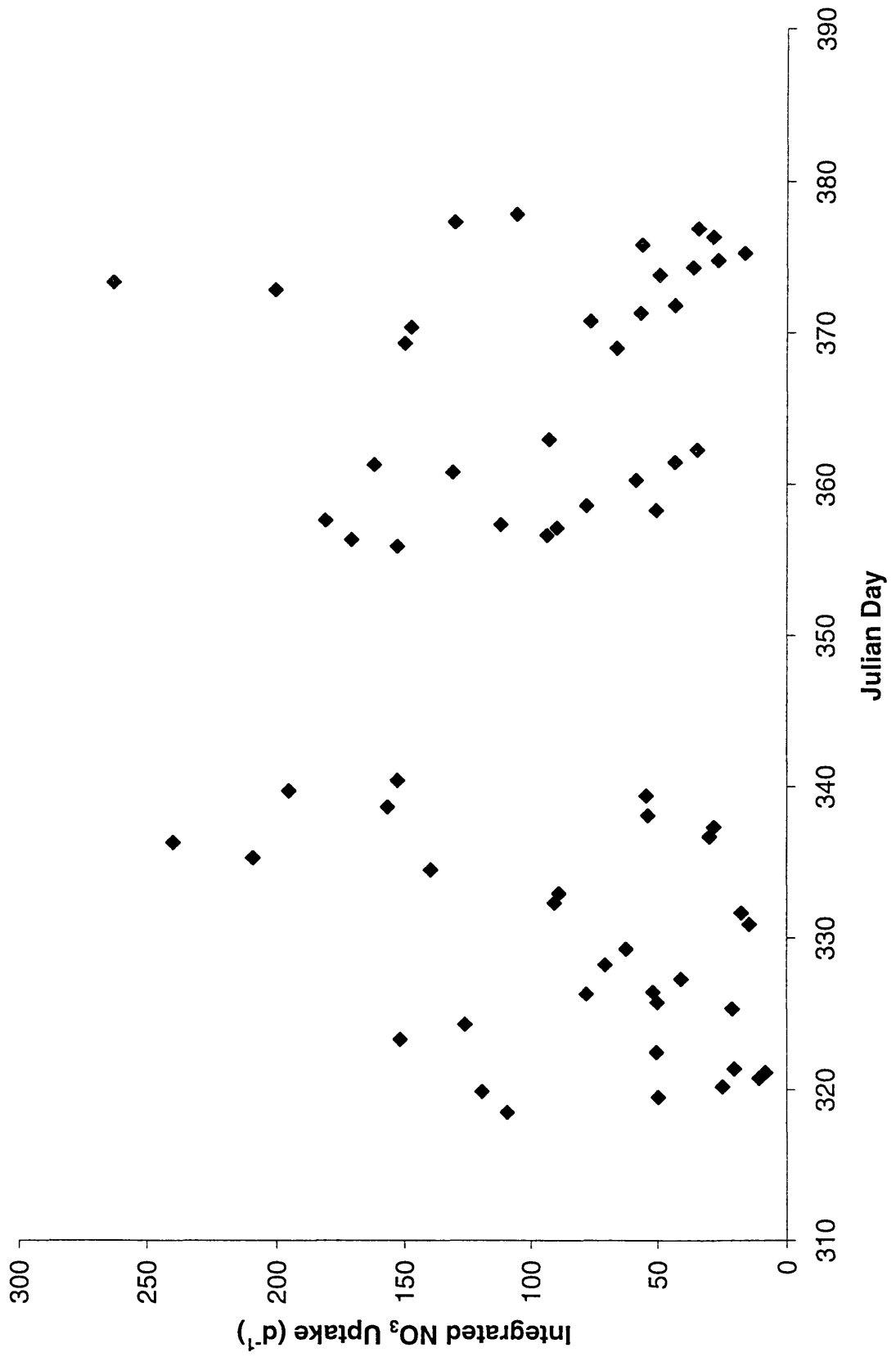
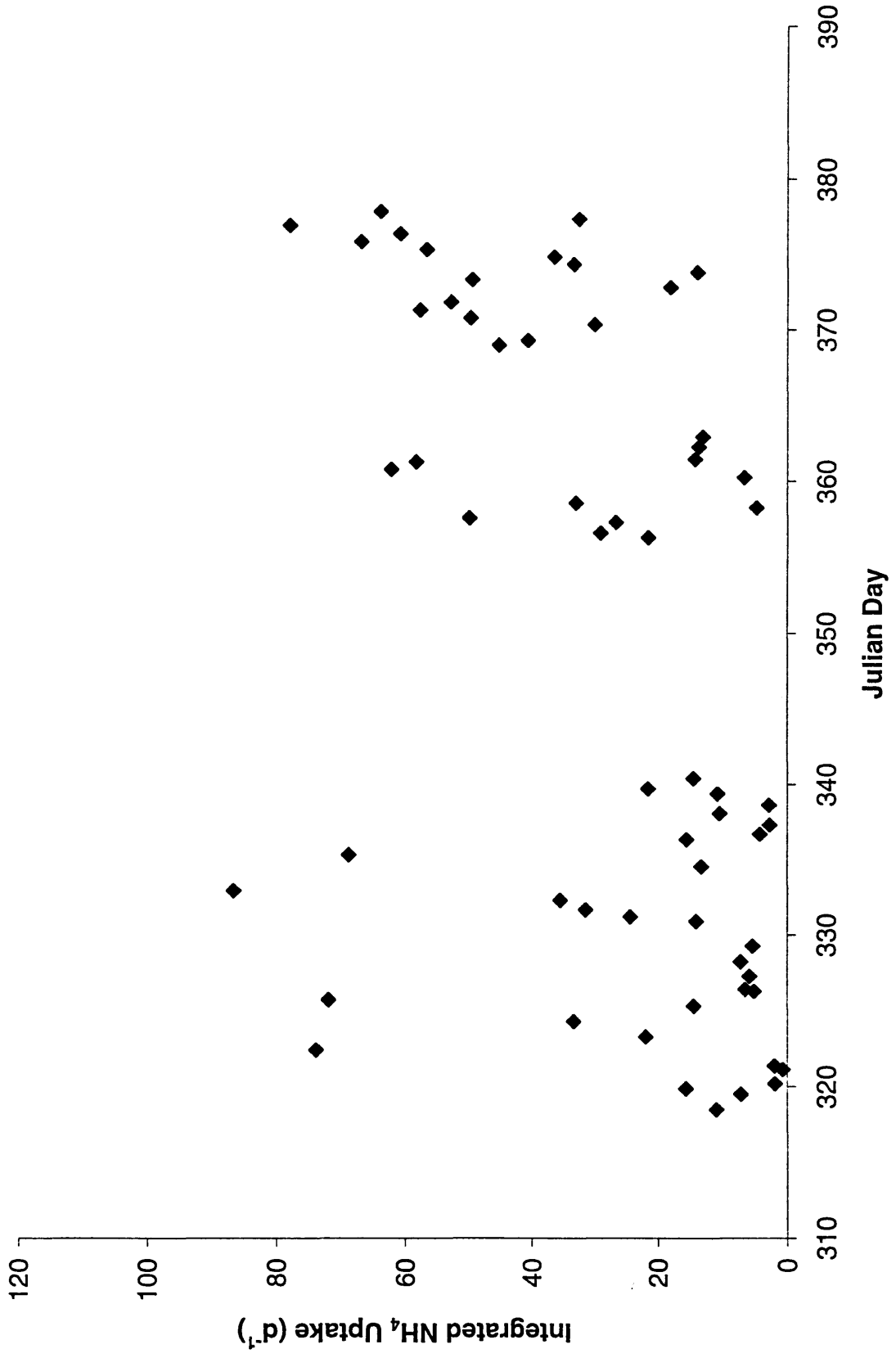


Figure 8. Integrated NH_4^+ uptake over Julian day for all stations sampled.



rates) and these data were analyzed as a function taxonomic dominance. A graphical representation of the ratio indicates possible differences among the different taxonomic groups (Figure 9). Due to the scatter in the data traditional regression analysis was not used to determine differences in the slopes. A Kruskal-Wallis test was used to evaluate the differences in the ratios for the taxonomic groupings. This test is often referred to as an analysis of variance by ranks and is robust when data do not meet the assumptions of parametric statistics (Zar, 1996). The analysis found that the mean C:N ratios calculated from the uptake values were indeed significantly different between taxa ($P=0.01$) (Table 14). The ratio calculated for *P. antarctica* was the highest at 38. In contrast, the ratios calculated from the particulate ratios were not significantly different for the taxonomic groupings (Figure 10). A regression of these data gave a POC:PON ratio of 5.61 for diatom-dominated stations and 5.69 for *P. antarctica* dominated stations ($R^2 = 0.97, 0.93$).

The f -ratio can be measure of the extent of nitrogen recycling and ammonium use within a system. The average f -ratio for both cruises combined was 0.69. The analysis found no indication that the f -ratios differed between the taxonomic groupings. The average integrated f -ratio for *P. antarctica*, diatom-dominated, and mixed assemblage stations was 0.75, 0.71 and 0.63, respectively and there was a significant effect due to season ($P=0.001$). The mean f -ratio for the spring was 0.77 and for summer was 0.63 indicating a slight increase in nitrogen recycling over time. A plot of integrated f -ratio versus integrated primary production (Figure 11) indicates that as production increases the f -ratio also tended to increase. The highest f value occurred when primary production was less than $1.00 \text{ g C m}^{-2} \text{ d}^{-1}$, and hence the f values do not decrease as primary

Figure 9. Plot of molar C:N uptake ratio for all sampled stations.

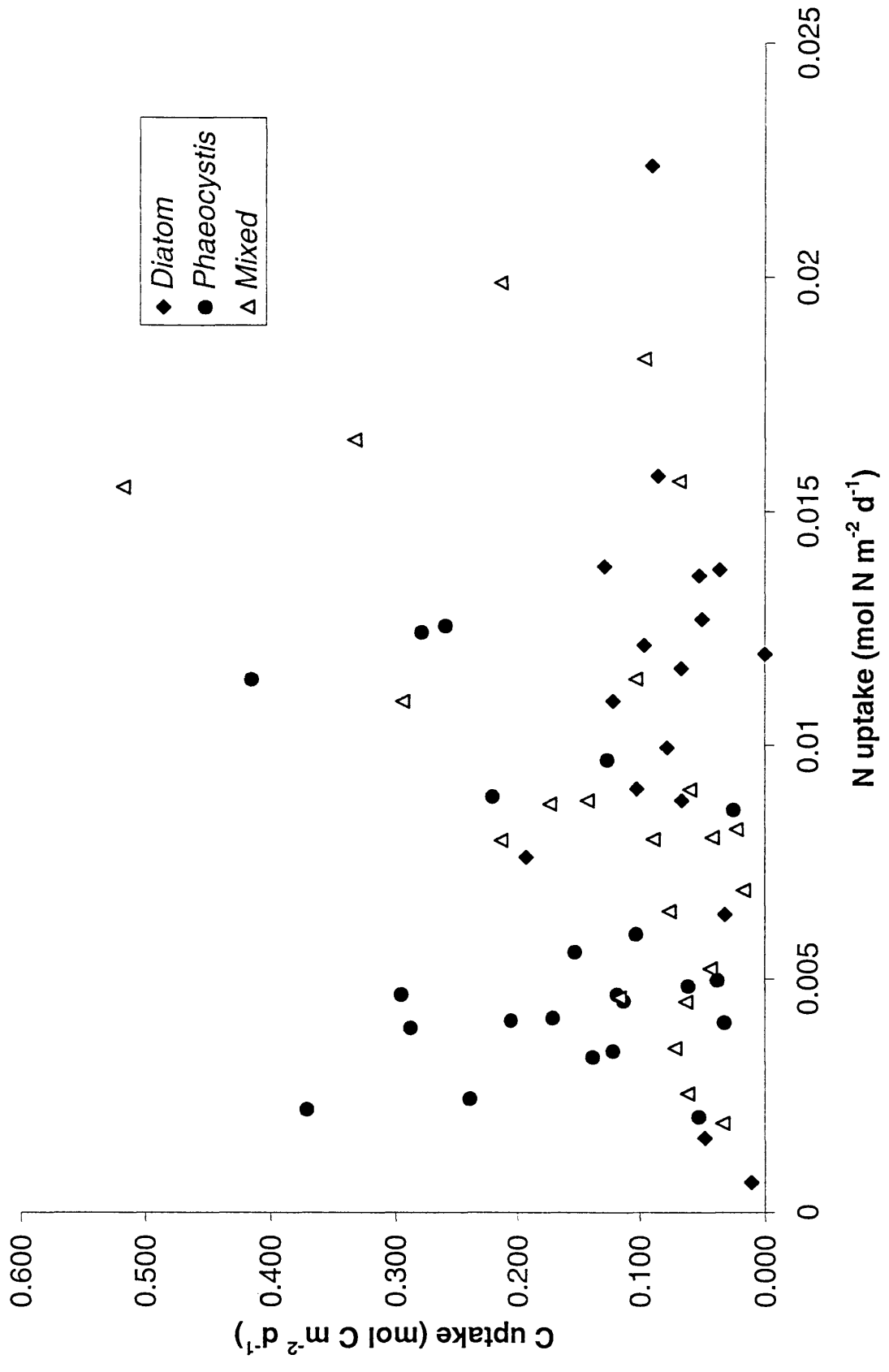


Figure 10. Plot of C:N particulate ratio for all sampled stations.

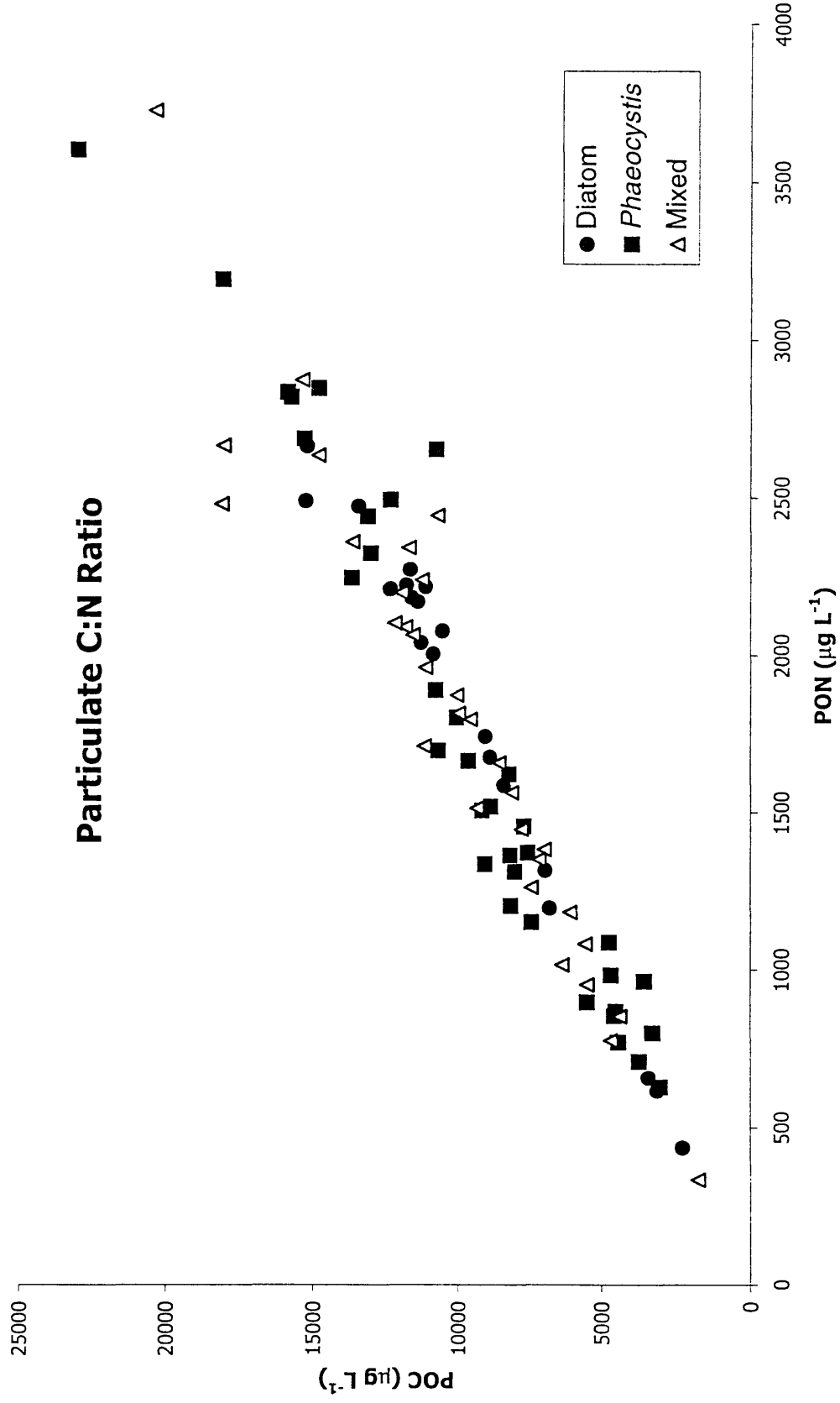
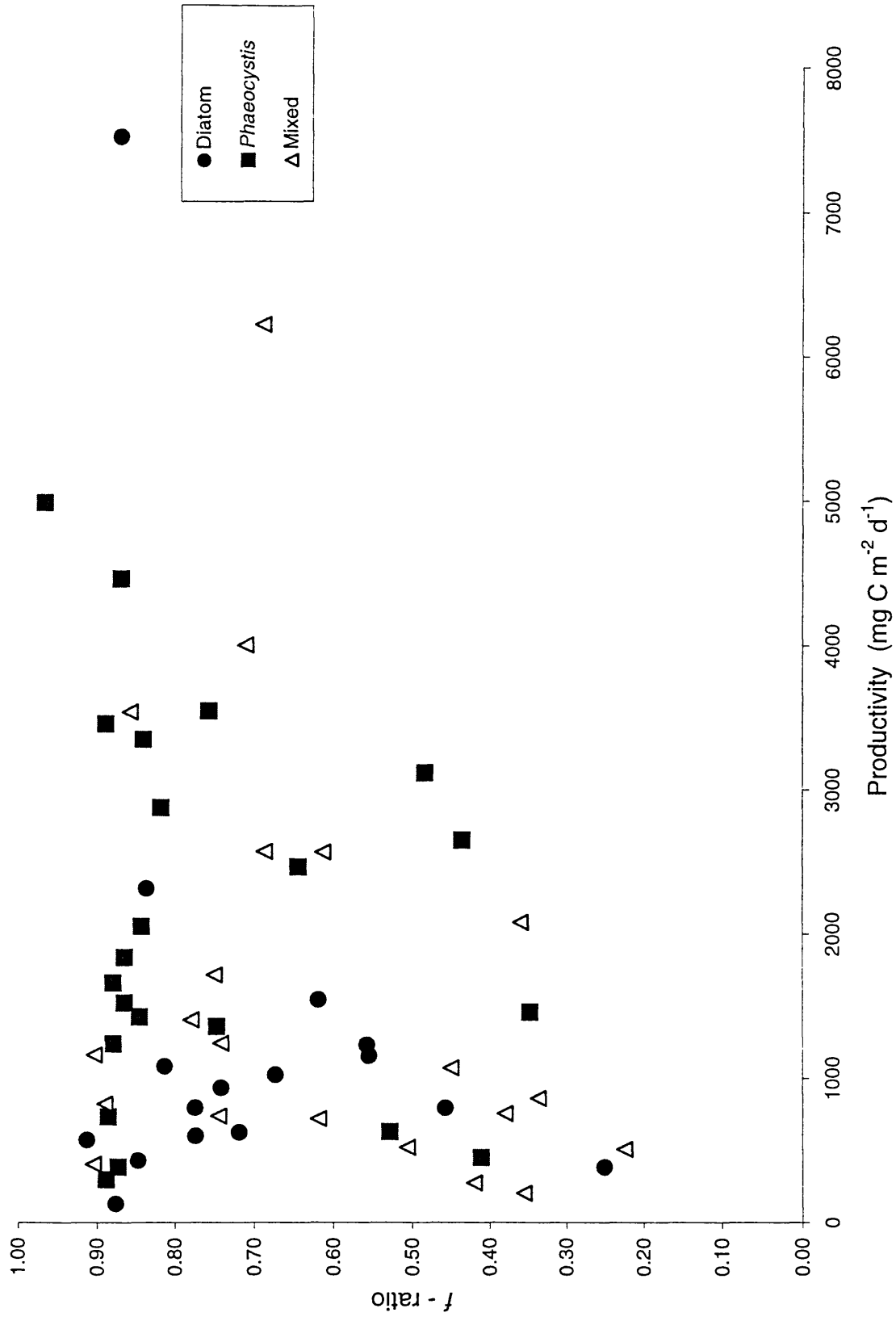


Figure 11. Plot of f -ratio vs. Primary productivity for all stations sampled.



production increases. No clear relationship between f -ratio and production is visible in this data.

Water Column Uptake Values

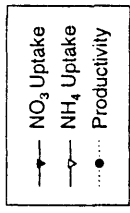
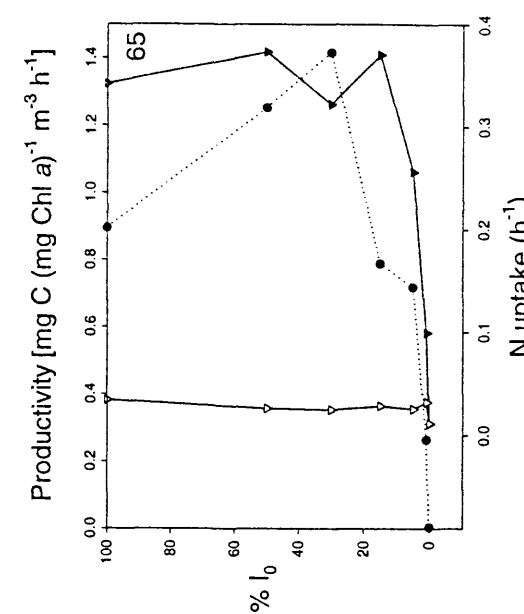
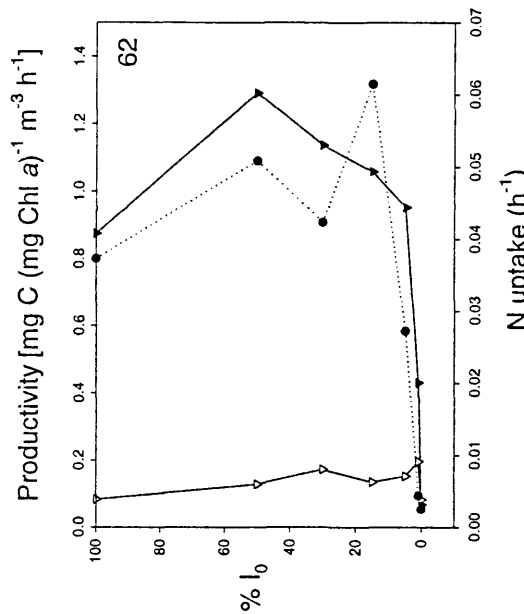
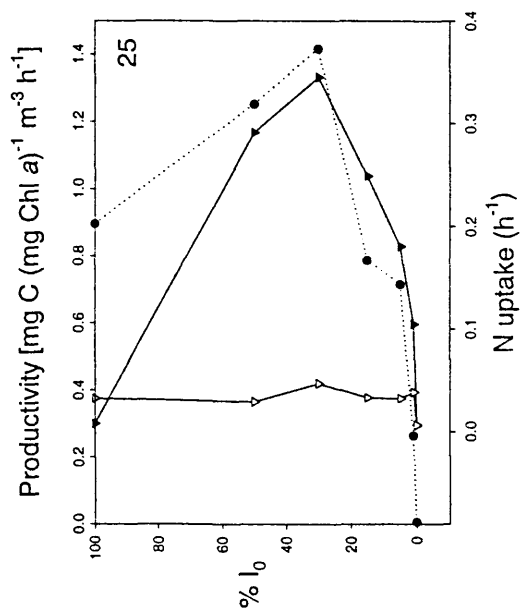
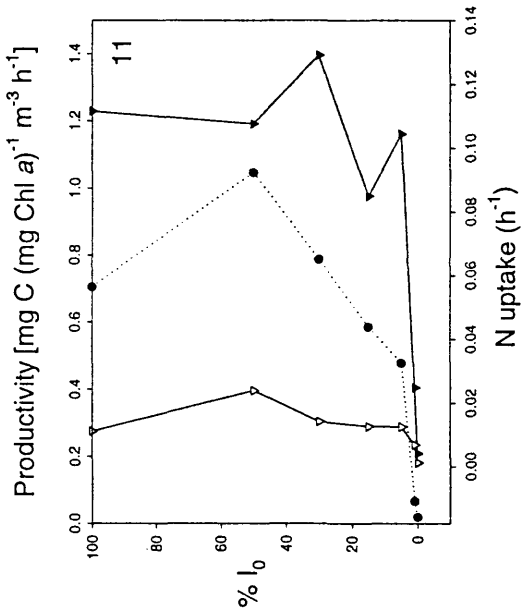
Three uptake parameters were investigated to determine differences in uptake at the sampled irradiance depths (100, 50, 30, 15, 5, 1, 0.1% surface): primary productivity normalized to chlorophyll, normalized NO_3^- uptake (ρ), and normalized NH_4^+ uptake (ρ) (Table 15). Plots of these data for representative stations from both cruises show the relationship of uptake with decreased irradiance (Figure 12). The figure shows that NH_4^+ uptake was not affected by decreased irradiance levels while both NO_3^- uptake and primary productivity were. There was even evidence of photoinhibition at the surface for the productivity data. When plotted the primary production (CO_2 uptake) first increases with decreasing irradiance but then declines as irradiance levels decrease. These values also did not meet the assumptions of parametric statistics, but the analyses were still performed because of their predictive values and the ability to discern trends. Analysis of Covariance was performed with irradiance treated as a covariant and taxonomic dominance as the main factor. For the ANCOVA data were transformed to remove heterogeneous variances.

No effect due to taxa was detected in the ANCOVA for primary productivity normalized to chlorophyll. This result was confirmed by a multiple means comparison that showed no difference in mean response among the three taxonomic groupings. Although no effect due to taxa was detected for NO_3^- uptake, the multiple means comparison did determine that diatoms and *Phaeocystis* did have significantly different mean responses. Mean uptake of NO_3^- was significantly lower at *Phaeocystis* dominated

Table 15. Mean uptake rates at isolumes for Primary productivity normalized to chlorophyll *a*, Rho NO₃ and Rho NH₄.

$\%I_0$	Primary Production / Chl <i>a</i> mg C (mg Chl <i>a</i>) ⁻¹ m ⁻² h ⁻¹	ρ NO ₃ h ⁻¹	ρ NH ₄ h ⁻¹
100	0.86	0.010	0.003
50	0.91	0.013	0.003
30	0.91	0.013	0.003
15	0.84	0.011	0.003
5	0.57	0.011	0.003
1	0.26	0.004	0.003
0.1	0.05	0.001	0.002

Figure 12. Plots showing representative nutrient uptake at the sampled irradiance depths for stations 11 and 62 from 1994 and stations 25 and 65 from 1995-96.



stations (0.006 h^{-1}) than for diatom dominated stations (0.013) and the mixed assemblage (0.018) stations. Neither diatoms or *Phaeocystis* were different from the mixed assemblage. The ANCOVA for NH_4^+ uptake also found a significant effect due to taxa. This was confirmed by the multiple means comparison that found diatoms and *Phaeocystis* to be significantly different. The mean diatom response was not significantly different from the mixed assemblage response.

To examine changes in uptake as irradiance decreased and to relate these data to the photosynthesis/irradiance results, the uptake rates were modeled following the nonlinear regression of Platt *et al.* (1980) after setting $\beta = 0$. The data were grouped by taxonomic dominance, and then uptake values for each taxonomic group were fit to the model. For both primary productivity normalized to chlorophyll and NO_3^- uptake, the model fit the grouped data significantly except for NO_3^- uptake for the mixed assemblage grouping (Table 16). In all cases uptake increased with the initial increase in irradiance but then plateaued as irradiance decreased (Figure 13). Specific uptake of NH_4^+ showed no significant relationship with depth and no regression model fit these data. A two sample t-test did detect a difference in mean uptake for a comparison of *P. antarctica* and diatoms ($P=0.001$). The mean NH_4^+ uptake for *P. antarctica* was 0.002 h^{-1} and for diatoms 0.004 h^{-1} .

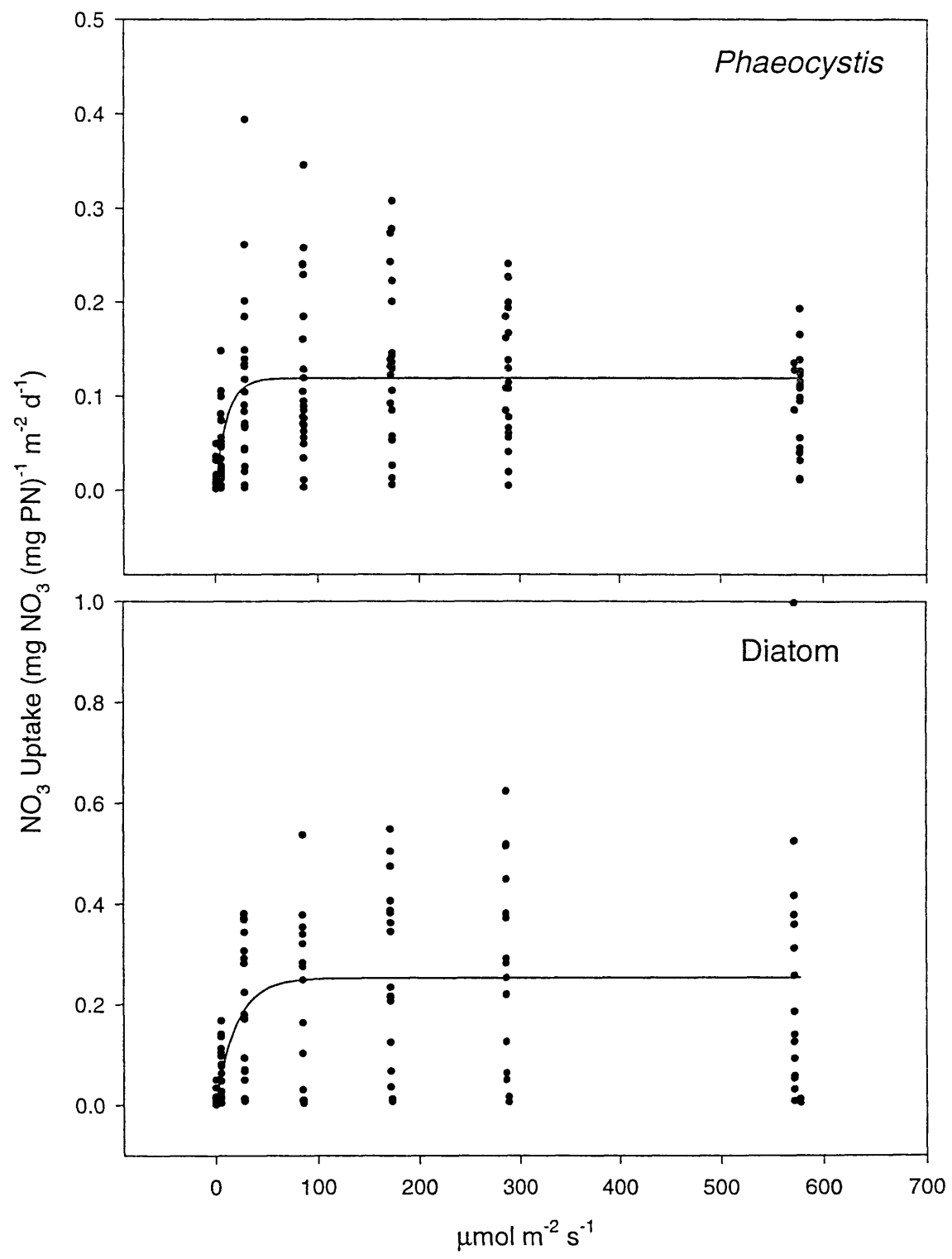
Temporal Analysis

Due to the structure of the data set, a qualitative approach was taken to determine the onset of *Phaeocystis* growth in the Ross Sea Polynya. All of the stations from one occupation of the $76^\circ 30'$ transect were considered together, and then numbers of stations

Table 16. Nonlinear regression fits of normalized productivity (Chl *a*) and nitrate (PN) uptake following the model of Platt *et al.*, 1980.

		α	P_m^B	P
Primary Productivity/Chl <i>a</i>				
mg C (mg Chl <i>a</i>) ⁻¹ m ⁻² d ⁻¹	<i>Phaeocystis</i>	0.0386	0.9394	<0.0001
	Diatom	0.0331	0.7660	<0.0001
	Mixed assemblage	0.0297	0.8277	<0.0001
ρ NO ₃				
mg NO ₃ (mg PN) ⁻¹ m ⁻² d ⁻¹	<i>Phaeocystis</i>	0.0106	0.1188	<0.0001
	Diatom	0.0123	0.2535	<0.0001
	Mixed assemblage	N.S.	N.S.	N.S.

Figure 13. Nonlinear fit (following Platt *et al.*, 1980) of NO₃ uptake vs. irradiance for *Phaeocystis*- and diatom-dominated stations.



dominated by the different taxonomic grouping were plotted in a histogram (Figure 14). This shows that both diatoms and *Phaeocystis* occur in the early occupations of the transect, but that the number of stations that are dominated by *Phaeocystis* is greater than those dominated by diatoms. Over the spring - summer a transition occurred and the number of diatom stations encountered increases.

Spatial Analysis

A similar analysis was done to determine if there was a clear signal of taxonomic dominance based on spatial analysis. All stations to the east of 172° E were considered to be the eastern stations near Victoria Land. All stations to the west of 172° E were considered to be western stations within the south central polynya. This longitude was chosen because a natural ice bridge often occurs at this location on the Ross Ice Shelf (Figure 15). This ice bridge separates two large ice-free regions, the Ross Sea polynya and a smaller polynya along the western most ice edge of Victoria Land. This ice bridge is a reoccurring feature within the Ross Sea, and is usually half the width of Ross Island. When stations were grouped in this manner it was evident that *Phaeocystis* was the dominant taxa in the south central polynya during these two cruises (Figure 16).

Figure 14. Histogram showing number of stations dominated by *Phaeocystis antarctica*, diatoms and mixed assemblages over time.

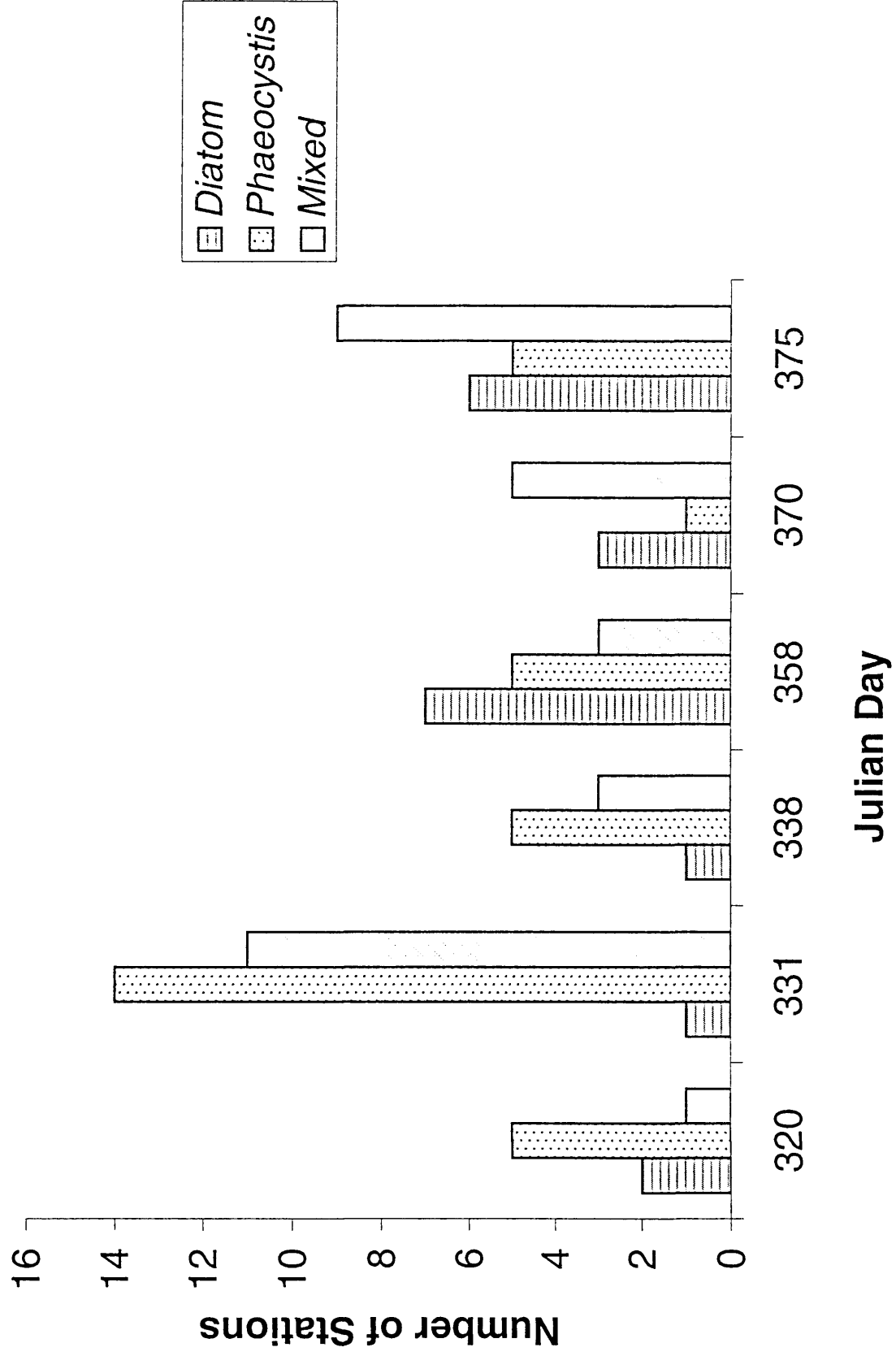


Figure 15. Images showing %Ice Cover and location of ice bridge near 172°E.

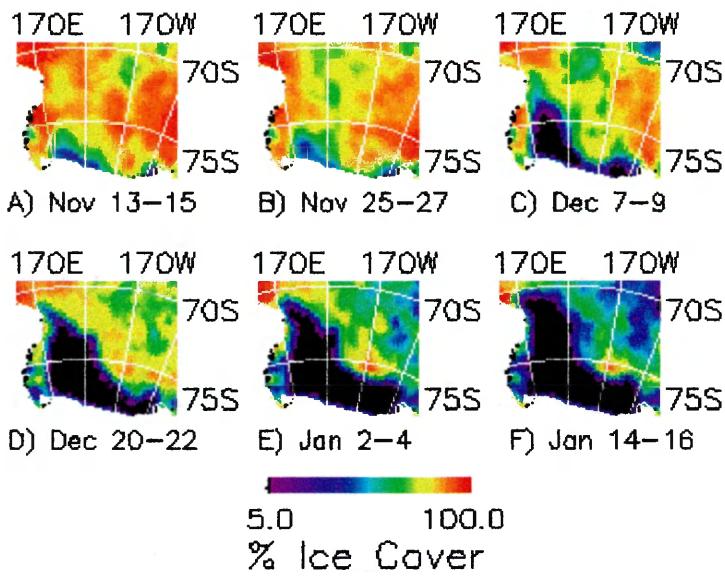
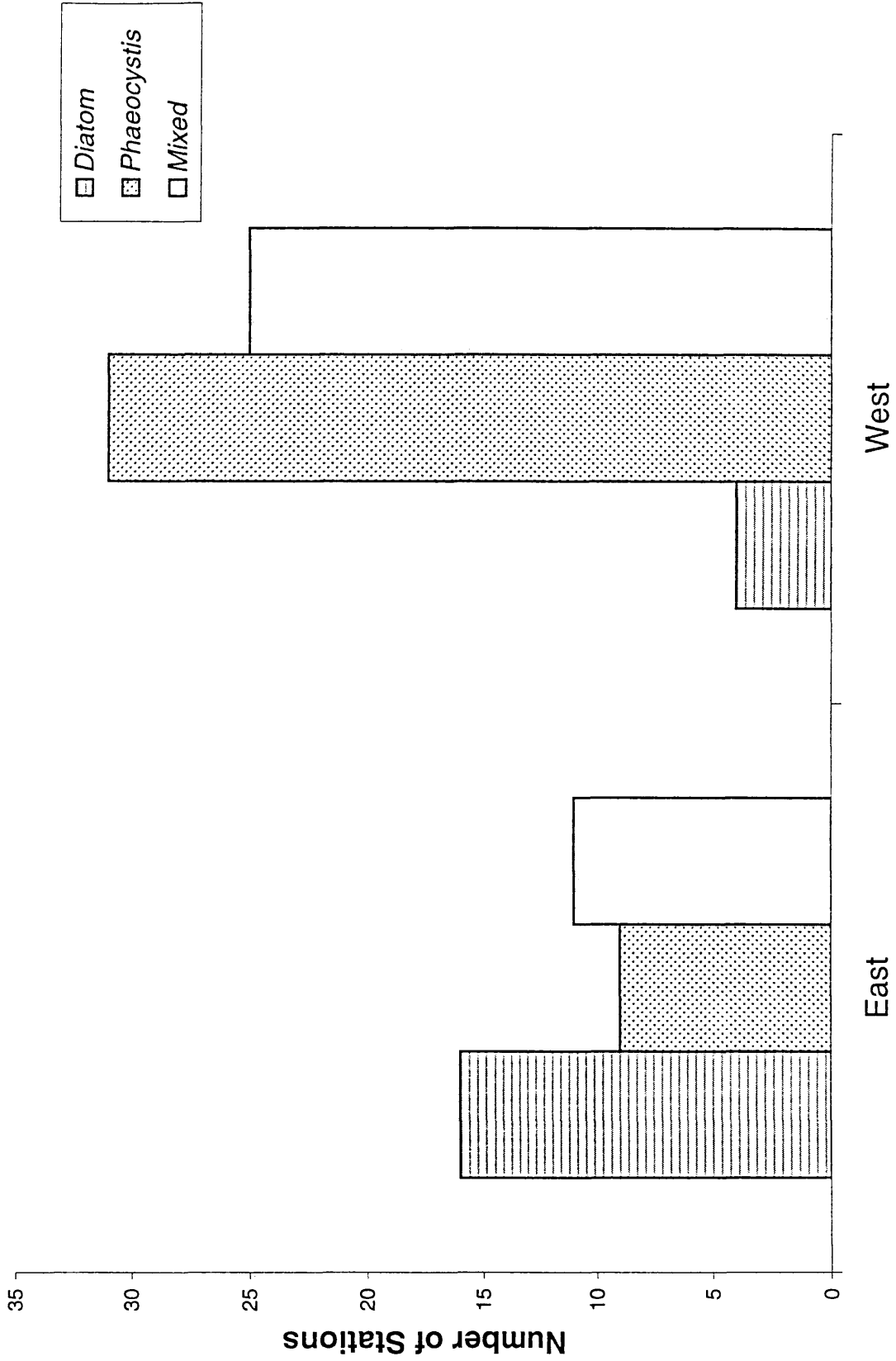


Figure 16. Histogram showing number of stations dominated by *Phaeocystis antarctica*, diatoms and mixed assemblages to the east and west of the ice bridge at 172°E.



DISCUSSION

Photosynthesis/irradiance Relationships

The results from both the field and laboratory experiments demonstrate that irradiance is the major factor controlling the photosynthetic parameters. Harrison and Platt (1986) stated that temperature and irradiance are the most important factors when explaining variation in P/I parameters for high latitude phytoplankton assemblages. Temperature variations in the Ross Sea are small and therefore likely to have a small influence. Although the temperature does vary (-1.8 to 2.0°C), it does not vary annually to the same extent as photosynthetically available radiation and photoperiod. In the Antarctic at 60° S the average photoperiod is 6 hours in midwinter, increasing to 19 hours in summer (Smith and Sakshaug, 1990). The low zenith angle at the poles results in decreased irradiance and high reflectance (Kirk, 1996). In addition, the light environment in polar oceans is highly variable, with cloud and fog formation quite common; snow and ice also attenuate the light significantly. Even with these extremes, the integrated daily irradiance at the poles in spring can be higher than values in temperate regions (Holm-Hansen et al., 1977; Smith and Sakshaug, 1990). Ice melt and increased daily insolation in the spring are the likely triggers of the austral spring bloom in the Ross Sea Polynya (Arrigo *et al.*, 1998; Smith *et al.*, in press). The early onset of the spring bloom is unusual at this high latitude and is most likely due to early opening of the polynya due to winds and increasing irradiance (increased heat flux).

Both the field and laboratory results indicate that both *Phaeocystis antarctica* and Antarctic diatoms are well adapted to low irradiance levels. At almost all stations the photosynthetic efficiency (α) was higher at lower irradiances, indicating that these taxonomic groups are able to maintain maximal photosynthetic output at the low irradiance regime early in the austral spring. Although the exact adaptation employed by these phytoplankton is not clear, it can be seen from the chlorophyll *a* data that the adaptation is not a simple increase in chlorophyll content in the cells. Palmisano *et al.* (1986) found similar results when investigating the changes in photosynthetic parameters when an assemblage of *P. antarctica* was advected under the sea ice in McMurdo Sound. Their study suggested that increased cellular accessory pigments or possible enhancement of electron flow between photosystems were the possible causes for enhanced photosynthetic efficiency at lower irradiance levels. The HPLC data from both of the cultures demonstrated that the concentrations of accessory pigments increased with decreasing irradiance. Brightman and Smith (1989) also found that Antarctic phytoplankton were well adapted to low irradiance conditions. They measured photosynthetic efficiencies ranging from $0.01 - 0.06 \text{ mg C (mg Chl } a)^{-1} (\mu\text{mol m}^{-2} \text{ s}^{-1})^{-1} \text{ h}^{-1}$ during the winter in the Bransfield Strait region when the mean daily irradiance was $0.795 \text{ mol m}^{-2} \text{ s}^{-1}$. The α values ($0.006 - 0.320$) for this study overlap those of the Bransfield Strait study, even though these cruises experienced different irradiance conditions, adding support to the statement that Antarctic phytoplankton are well adapted to low irradiance regimes.

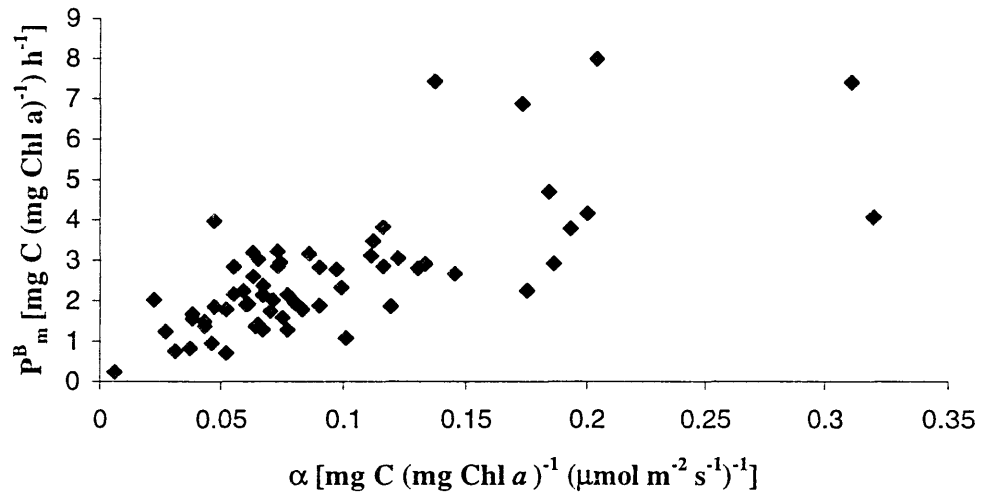
The E_k values of this study also support the conclusion that these species are well adapted to low irradiance regimes. E_k , the adaptation parameter, is an estimate of the

optimal irradiance for maximal photosynthesis. The field results show that the lower irradiance assemblages have low E_k (26 at 1% I_0 , 36 at 50% I_0) values when compared to the upper assemblage, indicating that a lower irradiance still allows for maximal assimilation. This is further supported by a lack of a significant difference between the P_m^B values at the difference irradiance levels in the field. The laboratory E_k values also followed this trend. For the cultures grown at the lower irradiance levels, the E_k values were lower than the culture grown at the highest irradiance. It is clear that these taxa are well adapted to the highly variable irradiance regime in their high latitude, polar environment and are able to maximize their photosynthetic potential at very low irradiances. The relatively low E_k values indicate a slow rate of adaptation due to the irradiance regime and low mixing environment these phytoplankton species experience. A plot of the E_k values demonstrates the different adaptation rates for different irradiance regimes (Figure 17). The values from the laboratory experiments verify that different irradiance regimes result in different rates of adaptation.

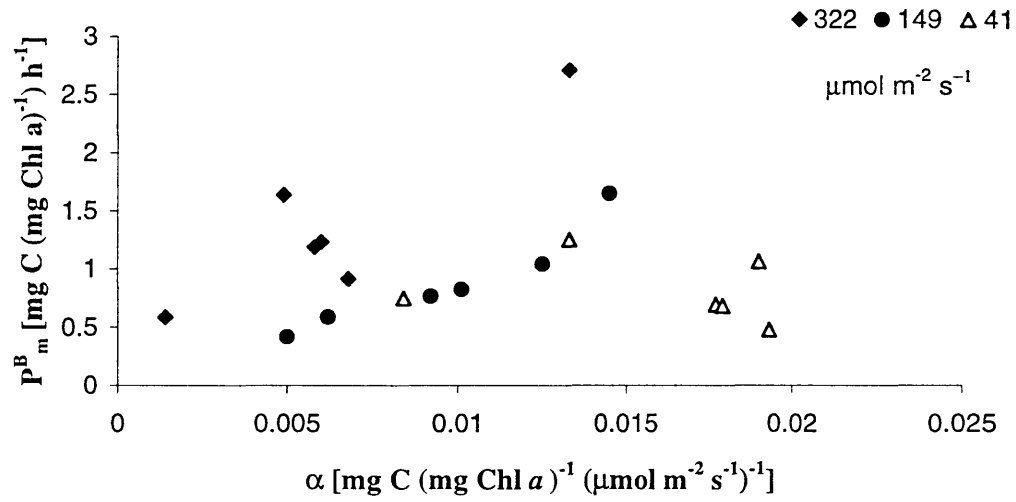
Chlorophyll *a* concentrations remained relatively constant throughout both the spring and summer and began to decline towards the end of the summer cruise. Although the difference is not statistically significant, the mean chlorophyll *a* concentrations at the lower two isolumens (1 and 0.1% I_0) were greater than the mean concentrations at the upper isolumens. This suggests several things. The increased concentration may be a result of settling of phytoplankton and export out of the euphotic zone. It is also possible that these species are aggregating in a lower, possibly preferred, irradiance regime. This phenomenon has been seen throughout the world's oceans when the chlorophyll maximum is found in deeper waters (e.g. Cullen et al., 1981; Bienfang et al., 1983)

Figure 17. Plot of E_k values for both field and laboratory experiments.

a)



b)



The field data showed no significant difference for all of the photosynthetic parameters among the three taxonomic groups. Both *P. antarctica*- and diatom-dominated stations showed similar photosynthetic responses. The results differ from those of Arrigo *et al.* (1999), who hypothesized that *P. antarctica* dominated in more deeply mixed waters with lower irradiance levels due to its ability to maintain maximal photosynthetic rates at lower irradiance levels. In this study both *P. antarctica* and diatoms were found in deeper waters at the base of the euphotic zone ($1\% I_0$), maintaining maximal photosynthetic rates, and hence there was no evidence of a difference in photosynthetic capabilities as a function of taxonomic dominance.

P. antarctica was found to dominate in the south central polynya where mixed layers tended to be deeper and less strongly stratified. Because there is no evidence indicating that photosynthetic capabilities are the cause of this dominance, one can speculate that the deeper mixed layers may support more growth due to higher concentrations of nutrients, including trace metals, supplied via mixing from deeper waters. Unfortunately, at this time, the data on trace metal fluxes are not available to test this hypothesis directly.

The results of the laboratory experiments indicate that there may have been a difference in response due to taxonomic dominance. As stated earlier these results are difficult to interpret because of a probable interaction effect between the taxa and irradiance treatments. In the culture experiments the differences in P_m^B may also be a result of a “colony effect”. The *P. antarctica* cultures formed very large colonies similar to those found in the field (Mathot *et al.*, in press) and the higher P_m^B values may result from different chlorophyll concentrations in the cultures. The *P. antarctica* cultures did

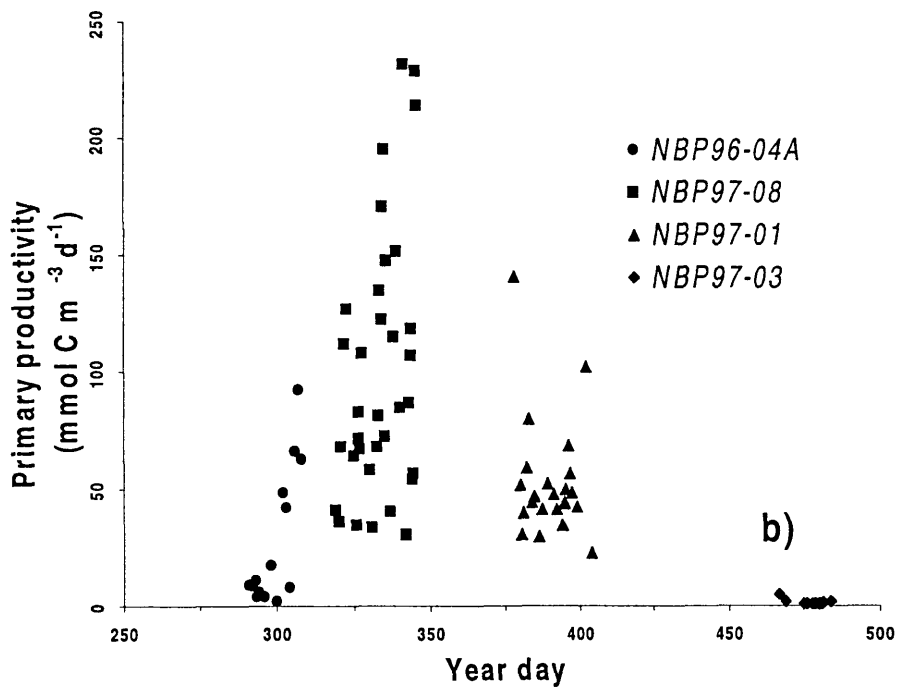
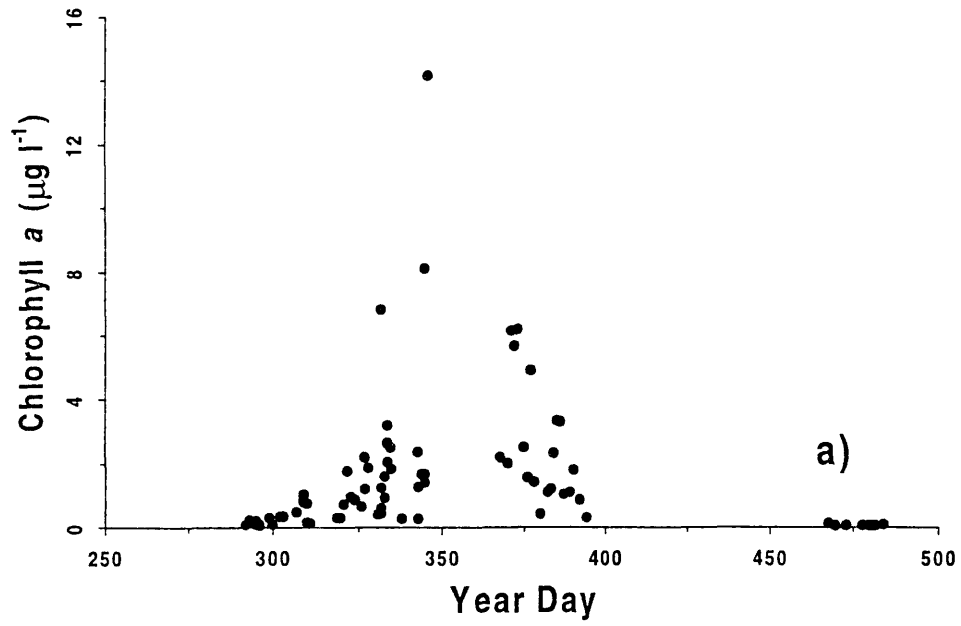
have lower concentrations of chlorophyll when compared to the *Pseudonitzschia* cultures at each irradiance level.

Another potential explanation lies in the differences in community structure between the cultures and field experiments. While the stations sampled in the polynya may have been dominated by a single species, in no cases were the stations completely unialgal. In addition, several groups of diatoms are present in the Ross Sea Polynya, including *Pseudonitzschia subcurvata*, *Thalassiosira sp.*, and *Fragilariopsis sp.* The response of the diatom community as a whole is unlikely to be exactly that of a single species culture.

Primary Production and Nutrient Uptake

Several studies and recent satellite images of the Ross Sea have established that this region has the most spatially extensive phytoplankton bloom in the Southern Ocean (Sullivan *et al.*, 1993; Arrigo and McClain, 1994; Arrigo *et al.*, 1999; Smith *et al.*, in press). The average daily primary production values of this study ($1.95 \text{ g C m}^{-2} \text{ d}^{-1}$ 1994, $1.1 \text{ g C m}^{-2} \text{ d}^{-1}$ 1995/96) were roughly equal to other measurements of primary productivity in this region (Holm-Hansen *et al.*, 1977; El-Sayed *et al.*, 1983; Smith *et al.*, 1996; Smith and Gordon, 1997). The unimodal pattern of primary productivity described in Smith *et al.* (in press) was also seen in this study, with integrated primary production peaking in early December prior to the biomass maximum that occurred approximately 18 days later (Figure 18). No clear signal of taxonomic dominance could be discerned from either the primary productivity or chlorophyll *a*-normalized primary productivity values (for both integrated station data and also isolume values). These data suggest that

Figure 18. Plot of Chlorophyll *a* biomass and primary productivity showing unimodal pattern of biomass maximum in the Ross Sea. Taken from Smith *et al.*, in press.



the spatial segregation of phytoplankton species and apparent dominance of *P. antarctica* in the south central polynya may be the result of many processes acting at once, rather than a single response to a single environmental variable.

The ^{15}N -incubation measurements detected differences in nitrogen utilization between the taxonomic groups, in that, *P. antarctica* had lower average uptake rates for both NO_3 and NH_4 relative to diatoms. Overall the uptake rates of these phytoplankton were low relative to other oceanic systems, most likely due to temperature limitations on uptake kinetics (Harrison, 1983). The modest uptake rates are unusual considering the high ambient nutrient concentrations (Cochlan and Bronk, submitted). Macronutrient concentrations are rarely limiting in the Southern Ocean (Nelson and Smith, 1986; Holm-Hansen *et al.*, 1989), but micronutrients (including trace metals) often can limit growth (Martin *et al.*, 1990; Sedwick and DiTullio, 1997; Olson *et al.*, in press). It is known that iron is required for many processes within a phytoplankton cell, including pigment synthesis as well as both nitrate and nitrite reduction. Sedwick and DiTullio (1997) found limiting concentrations of iron in the central polynya in the late spring. It is possible that all phytoplankton taxa are limited by iron as the bloom progresses. It is unclear why *P. antarctica* dominated stations have lower uptake rates of both nitrate and ammonium (when compared to diatoms), but this does not appear to be a disadvantage. Iron addition experiments have demonstrated that smaller cells are better suited to limiting concentrations of nutrients, partially because their larger surface to volume ratio aids in uptake (Chisholm, 1992). For example *in situ* iron enrichment experiments found that picoplankton dominated before iron enrichment, but after iron addition a shift to larger diatoms occurred (Coale *et al.*, 1996). It can be hypothesized that in the Ross Sea

the colonial matrix of *P. antarctica* no longer allows it to have advantages conferred to the small cell, making iron limitation a factor in its ability to assimilate nitrogen at optimal rates.

Another indicator pointing to possible nutrient limitation is the C:N uptake ratio calculated with molar uptake values. This ratio calculated from molar C uptake to molar N ($\text{NO}_3^- + \text{NH}_4^+$) uptake is an daily measure of the C:N ratio and provides insight into the coupling of carbon and nitrogen metabolism, compared to a C:N ratio calculated from particulate carbon and nitrogen values that describes the end-product of net assimilation. The C:N uptake ratios were higher than particulate ratios, and although there was scatter within these data, the differences among the taxa were significant. The difference in this ratio between *P. antarctica* dominated stations and diatom dominated stations may be a result of several processes. The production of the mucus matrix by *P. antarctica* is one of the most likely explanations for the increased values. It is also possible that *P. antarctica* is utilizing dissolved organic nitrogen (DON) as a source of nitrogen in addition to nitrate and ammonium. Although uptake of DON by phytoplankton has not been measured in the Ross Sea, other studies have shown that DON is a preferred source of nitrogen for many phytoplankton species (Bronk and Gilbert, 1993). The low concentrations of DON measured in the Ross Sea may indicate intense recycling of this pool or that very little DON is available for uptake or what is present is refractory (Carlson *et al.*, in press). A more likely explanation is that the elevated C:N ratio is a result of unbalanced growth due to micronutrient limitation.

Lipizer *et al.*, (2000) also found C:N uptake ratios that were higher than particulate ratios for phytoplankton assemblages in the Ross Sea polynya. Particulate

ratios remained relatively constant and close to Redfield Ratio (6.6), while C:N uptake ratios were as high as 25. The differences in the ratios were primarily attributed to seasonal maturity of the bloom and a possible uncoupling of photosynthetic processes and nutrient assimilation. Early in the bloom carbon assimilation is most likely exceeding nutrient assimilation due to the energy requirements of the phytoplankton. Their study did not look at trace metal concentrations but macronutrients were not limiting throughout the study period.

The C:N ratios calculated from particulate concentrations indicate no difference between the different phytoplankton taxa. The particulate C:N ratio provides information about the end process of nutrient uptake and biomass production. It becomes clear when the C:N ratio calculated from the uptake rates and the particulate C:N ratio are compared for *P. antarctica* that other processes are occurring between uptake and assimilation. One explanation for the decrease in the different C:N ratios is that *P. antarctica* is not storing the excess carbon it is taking up in the particulate pool but exuding it as dissolved organic carbon. Other studies have found that *Phaeocystis* produces and excretes DOC (Lancelot and Mathot, 1985). Carlson *et al.* (1998) found that DOC concentrations increased in the Ross Sea over the course of the bloom and that this pool of substrate was relatively labile.

Nitrate and Ammonium Uptake Interactions

It has been well established that the uptake dynamics of nitrate and ammonium are complex and that interactions between these nitrogen species occur (Dortch, 1990). Concentrations of ammonium greater than 1 μM have been shown to inhibit nitrate

uptake in many systems, and it has been reported that in most cases phytoplankton species utilize ammonium more readily than nitrate because of its reduced state (McCarthy, 1977). Dortch (1990) stated that 'inhibition' or 'preference' is neither universal nor as severe as has generally been believed, and that these processes may be affected very differently by environmental conditions. The fact that nitrate is rarely reduced to limiting concentrations in the Southern Ocean complicates the nitrogen uptake dynamics in this region. The current data set does not indicate that ammonium is present in inhibiting concentrations; in fact, the data indicate that nitrate is the most utilized form of nitrogen in the Ross Sea. This is most likely due to saturating concentrations of nitrate throughout the growing season and very low ammonium concentrations in spring.

The effect of irradiance on nitrate and ammonium uptake has been extensively studied but remains incompletely understood (MacIsaac and Dugdale, 1972; Muggli and Smith, 1993; Hu and Smith, 1998). It has been demonstrated that while uptake of nitrate increases with increased irradiance, uptake continues in the absence of light. Muggli and Smith (1993) found a light dependence for nitrate uptake in *Phaeocystis pouchetii* in the Greenland Sea. Other studies have found that nitrate uptake is only weakly dependent on irradiance (Nelson and Smith, 1986). In this study the vertical profiles of NO_3 uptake indicate decreased uptake with depth (i.e., decreased irradiance) while NH_4^+ uptake did not vary with depth. When the nitrate data were modeled following Platt *et al.* (1980), the uptake response followed that of photosynthesis, suggesting that nitrate uptake was controlled by irradiance levels and possibly dependent on available irradiance (Figure 13). It is possible that other cellular processes might indirectly affect inorganic nitrogen uptake, such as iron limitation affecting enzyme production.

Nelson and Smith (1986) investigated nitrogen uptake rates at the western ice edge of the Ross Sea in late austral summer (January – February) within an intense diatom bloom. Their study found no indication of light dependence for nitrate uptake but a clear decrease in uptake with depth for ammonium. The species composition of the bloom was mostly diatoms and the time of the study was later in the season than this one. It is possible that the ammonium uptake in this study is reduced due to low concentrations of ammonium in the water column. It is also possible that as the bloom progresses, a transition in nitrogen utilization occurs as nitrate concentrations in the Ross Sea decrease. It is clear that the nitrogen uptake dynamics in the Ross Sea vary temporally as the bloom progresses. Hu and Smith (1998) hypothesized that uptake dynamics differed due to the taxonomic composition of the bloom and the stage of the bloom. The coupling of phytoplankton and heterotrophs may also explain uptake variability (Hu and Smith, 1998; Carlson *et al.*, 1998; Cochlan and Bronk, submitted). Cochlan and Bronk (submitted) suggested that mutualism between phytoplankton and bacteria can result in the creation of nutrient microzones due to intense remineralization, resulting in variable uptake capabilities throughout the bloom.

Cochlan and Bronk (submitted) investigated the nitrogen nutrition of the phytoplankton bloom in the Ross Sea Polynya. They found concentrations of NH_4^+ that appeared to limit uptake of NO_3^- , but also measured the highest uptake of NO_3^- in relatively elevated concentrations of NH_4^+ ($0.16 \mu\text{M N L}^{-1}$). They also determined that in the early bloom phytoplankton utilized mostly NO_3^- , then NH_4^+ , and lastly urea. This apparent preference in utilization shifted at the end of January with NH_4^+ being utilized

more than NO_3^- . The data from this study indicate that no shift had occurred, possibly due to a shorter sampling season.

The generally high f -ratios calculated in this study suggest that only limited N recycling is occurring in this system and suggest that most of the production is NO_3^- based. While this may be the case in the Ross Sea and possibly throughout much of the Southern Ocean, this number does not then correlate to export production directly. The classic view as presented by Eppley and Peterson (1979) calculates export based on import to the system via slow diffusive flux and/or upwelling on short time scales. Eppley and Peterson (1979) specifically excluded polar oceans in their calculations because the short growing season and high ambient nutrient concentrations did not fit their model. As stated previously, nitrate concentrations are rarely reduced to limiting concentrations in the Ross Sea (Nelson and Smith, 1986). This, coupled with low concentrations of ammonium, leads to a high f -ratio as seen in this study.

CONCLUSIONS

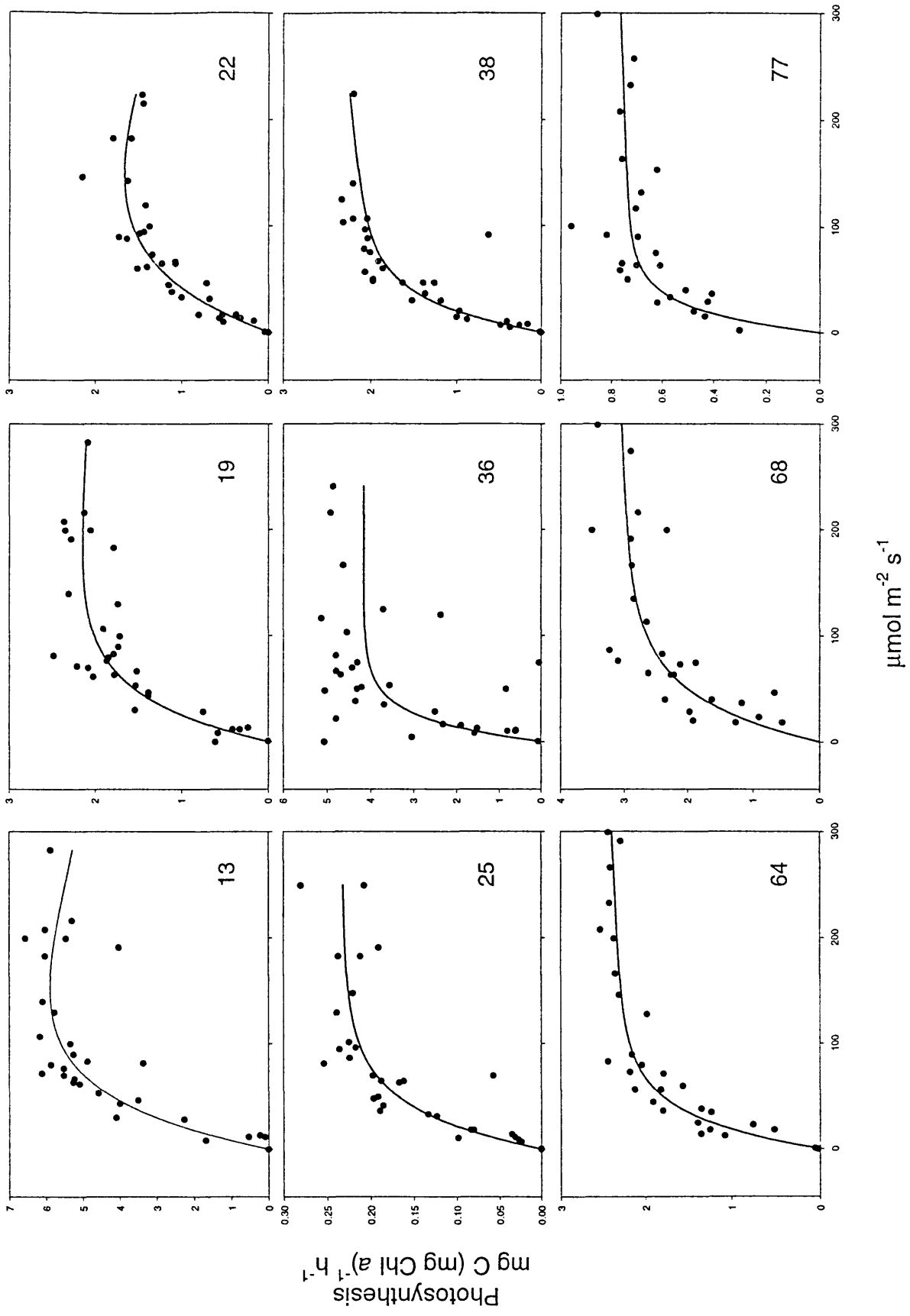
There was no evidence to support the hypothesis that *P. antarctica* and diatoms have different photosynthetic capabilities that allows *P. antarctica* to grow more rapidly in the Ross Sea Polynya. The data showed that the detectable differences occurred between irradiance levels but not taxonomic groupings. It is clear from this data set that all of the Antarctic phytoplankton species encountered were well adapted to the low irradiance conditions encountered throughout the Ross Sea Polynya. In addition, the photosynthetic parameters (at either irradiance level or between taxa) did not change over time. Because no differences could be detected over time or between species, it can be concluded that both of these species exhibit a maximal response throughout the growing season.

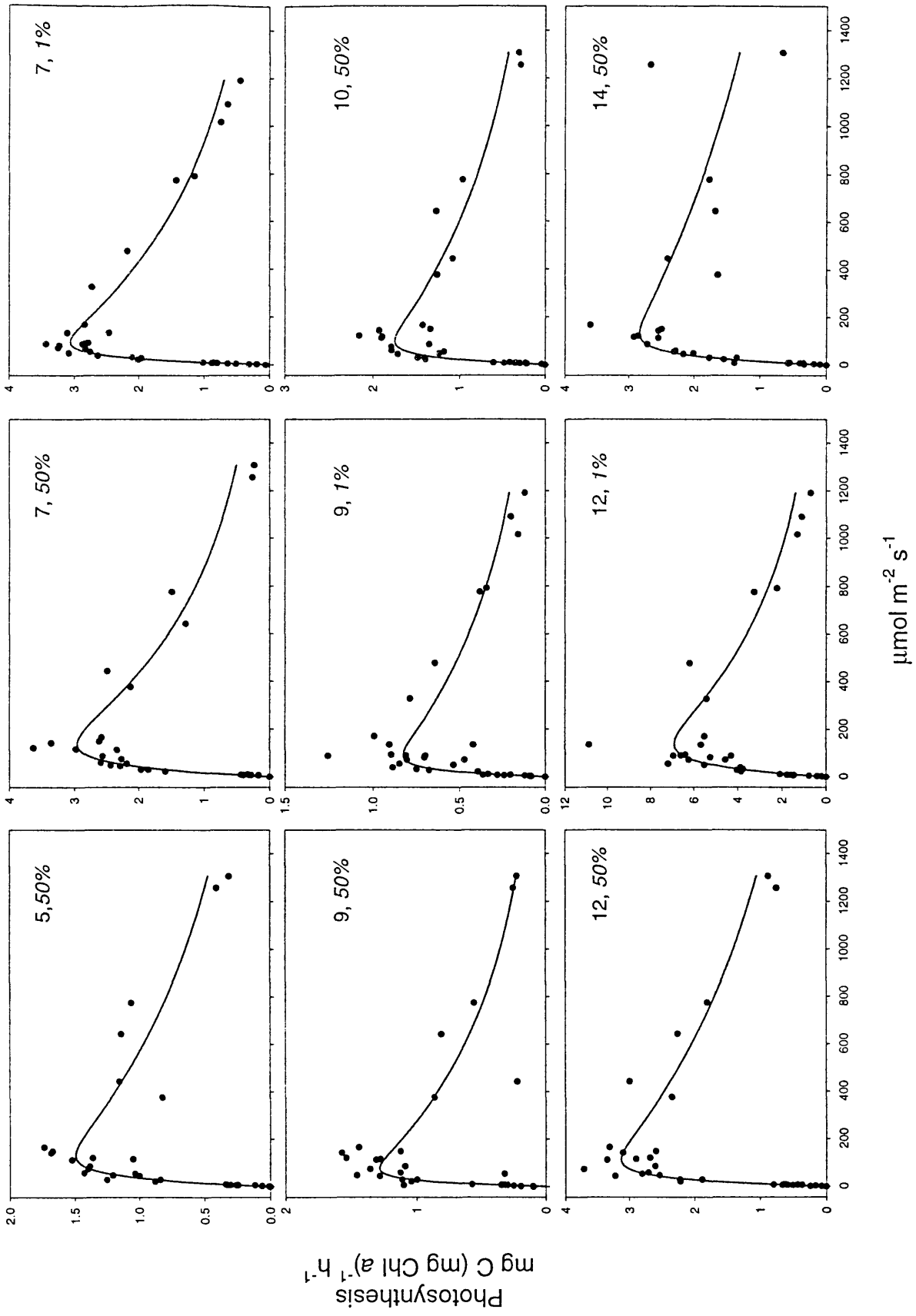
There was evidence to support differential utilization of nutrients by *P. antarctica* and diatoms. *P. antarctica* did have higher carbon uptake rates as detected by the C:N uptake ratio and also had a higher mean primary productivity. In contrast to expectation, *P. antarctica* did not have higher uptake rates for either nitrate or ammonium. The particulate ratios indicate that these phytoplankton assimilate both C and N in Redfield ratio. The differences between *P. antarctica* and diatoms in their nutrient uptake dynamics are not clearly explained by these data.

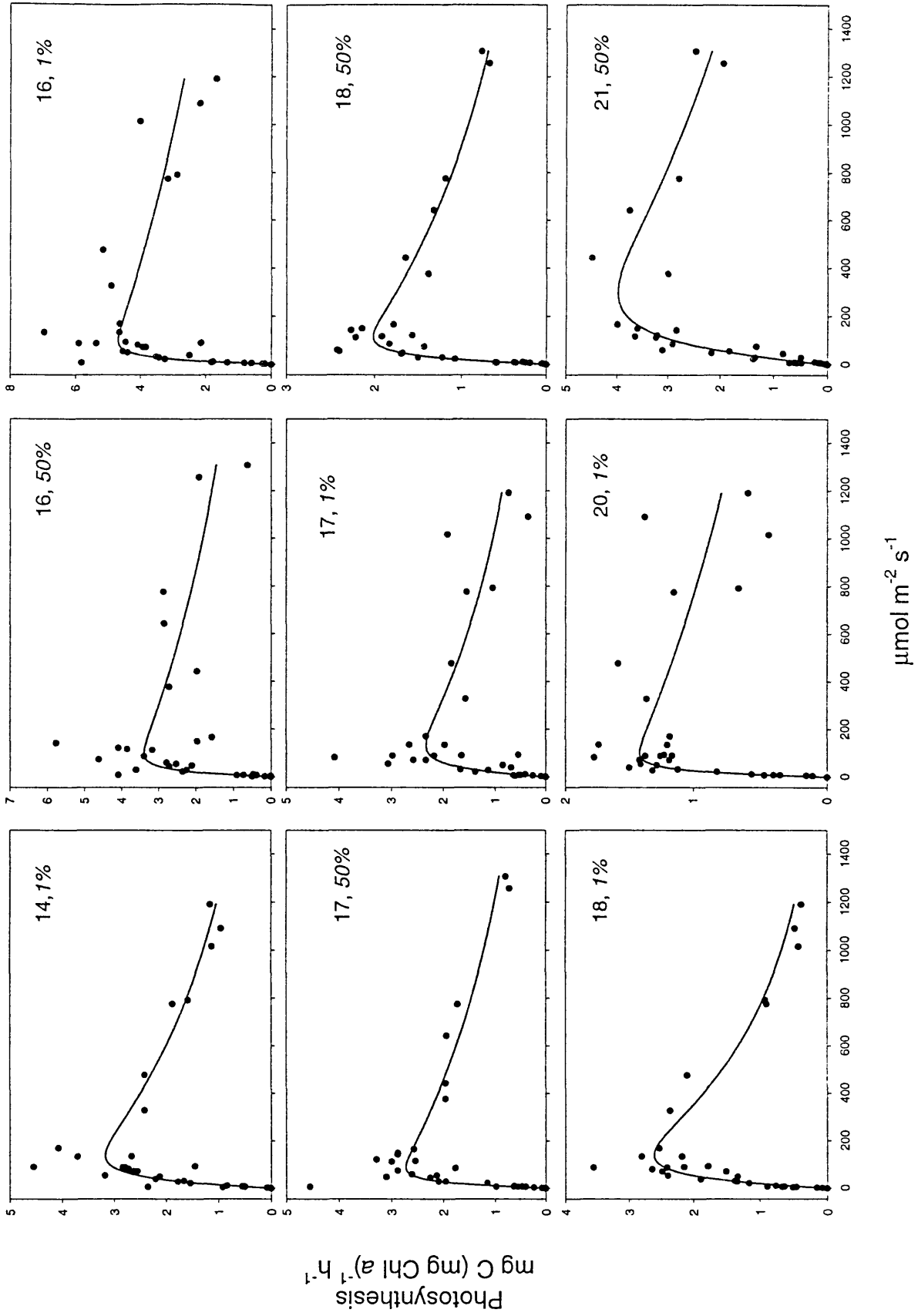
While *P. antarctica* is found at more stations early in the growing season, it is not clear that this is because it has superior photosynthetic or nutrient uptake capabilities. *P.*

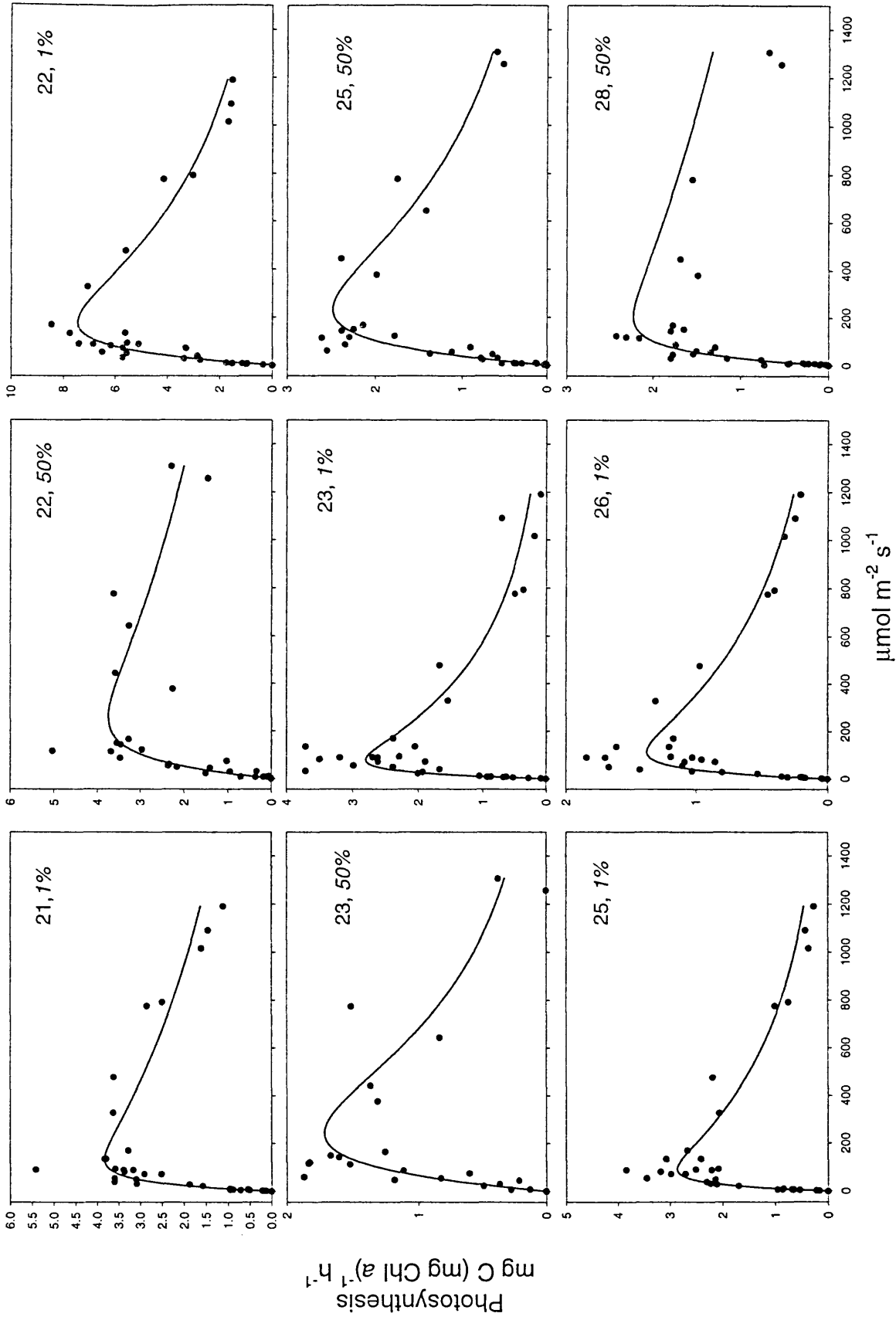
antarctica's dominance in the south central polynya is also not explained. It is likely that many environmental factors are at work controlling the phytoplankton bloom dynamics in the Ross Sea Polynya. Possible explanations for the differences in these taxa include different micronutrient (iron) limitations, differences in mixing regime due to strength of stratification and depth of mixing, and quite possibly a lack of grazing by herbivores. This study does not define the causes of spatial and temporal segregation in the Ross Sea phytoplankton bloom but it does indicate that in polar environments, where there is high variability, it is unlikely that a single process controls the dynamics of the phytoplankton bloom.

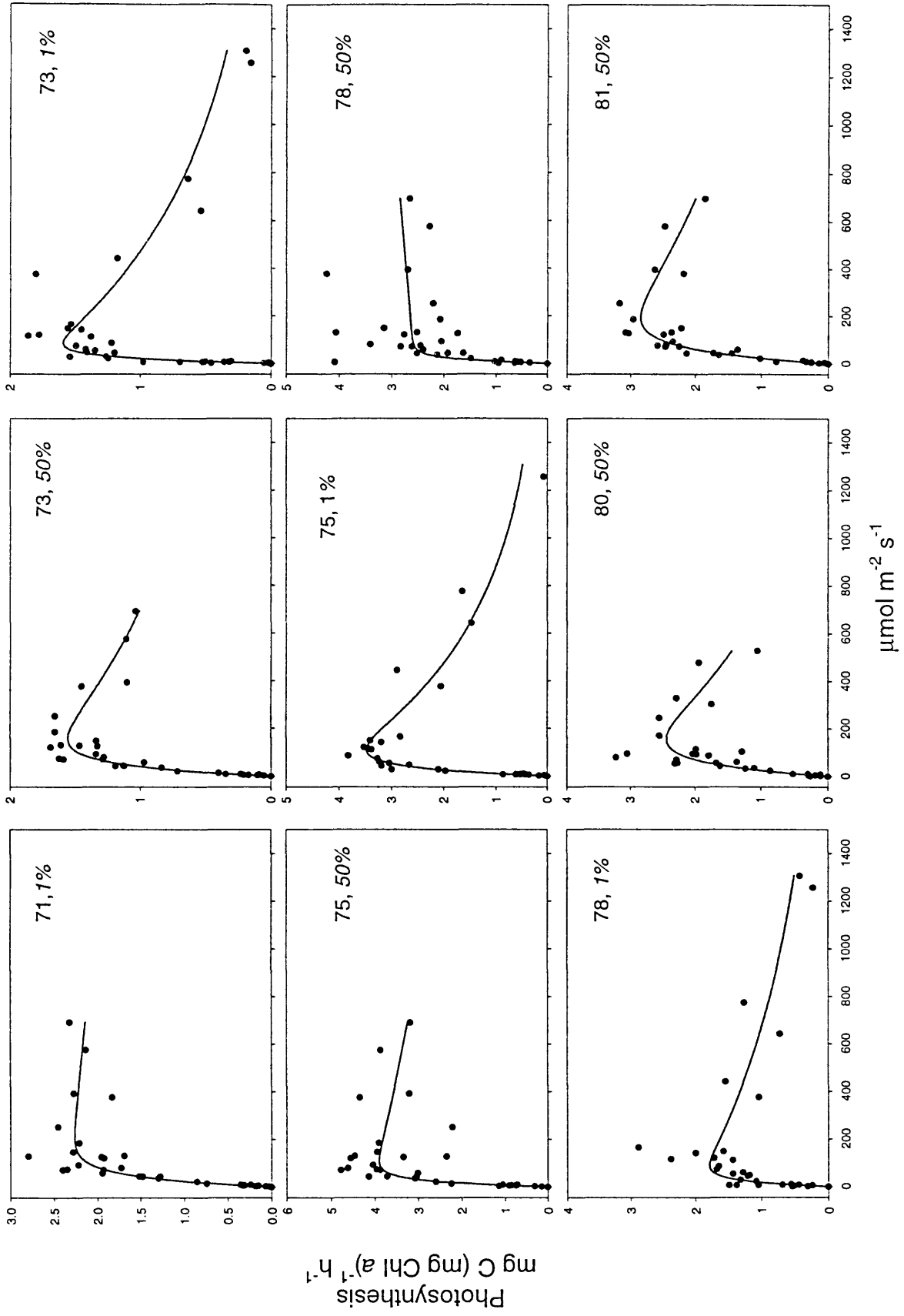
Appendix I. P/E curves for all experiments performed.

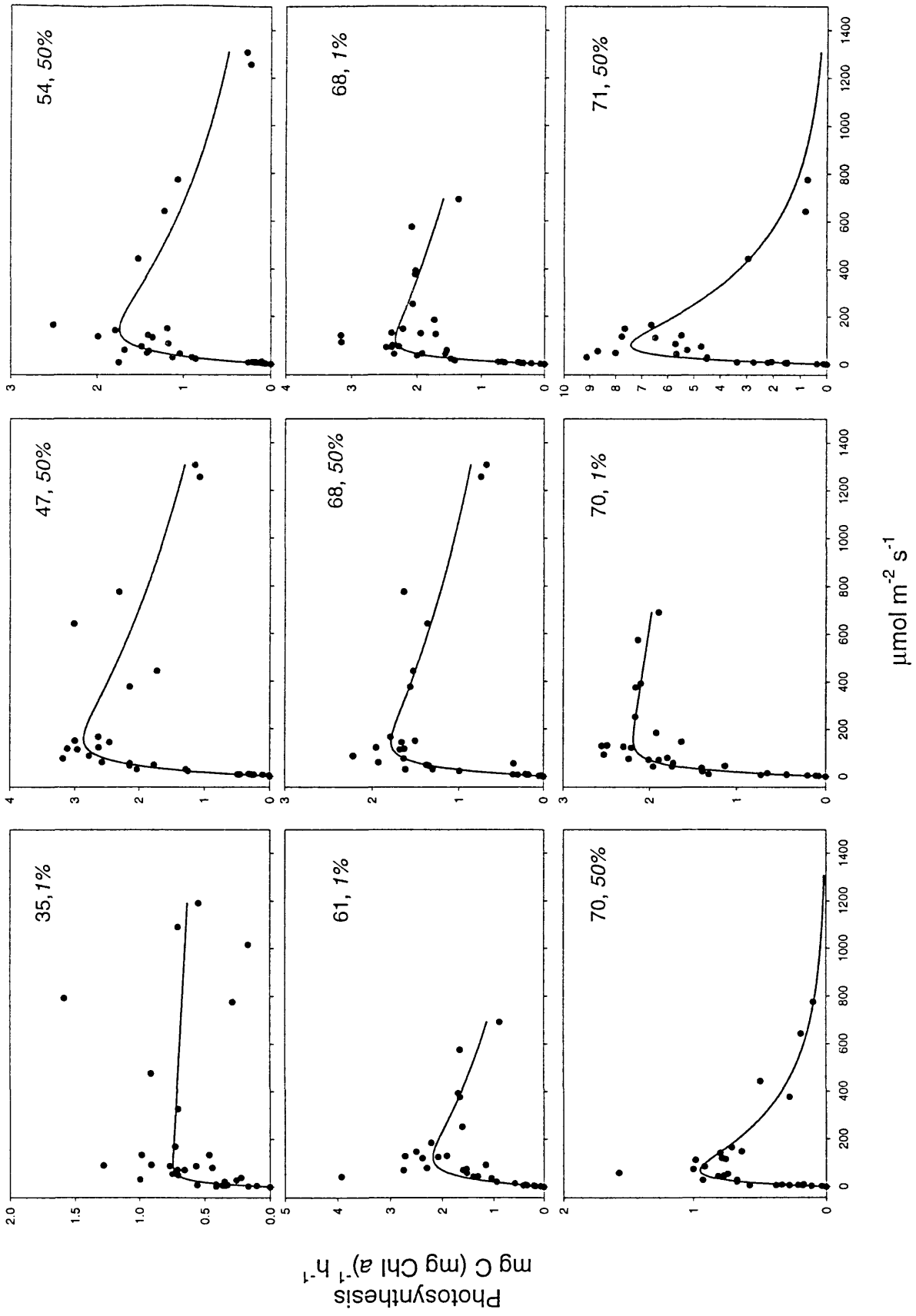


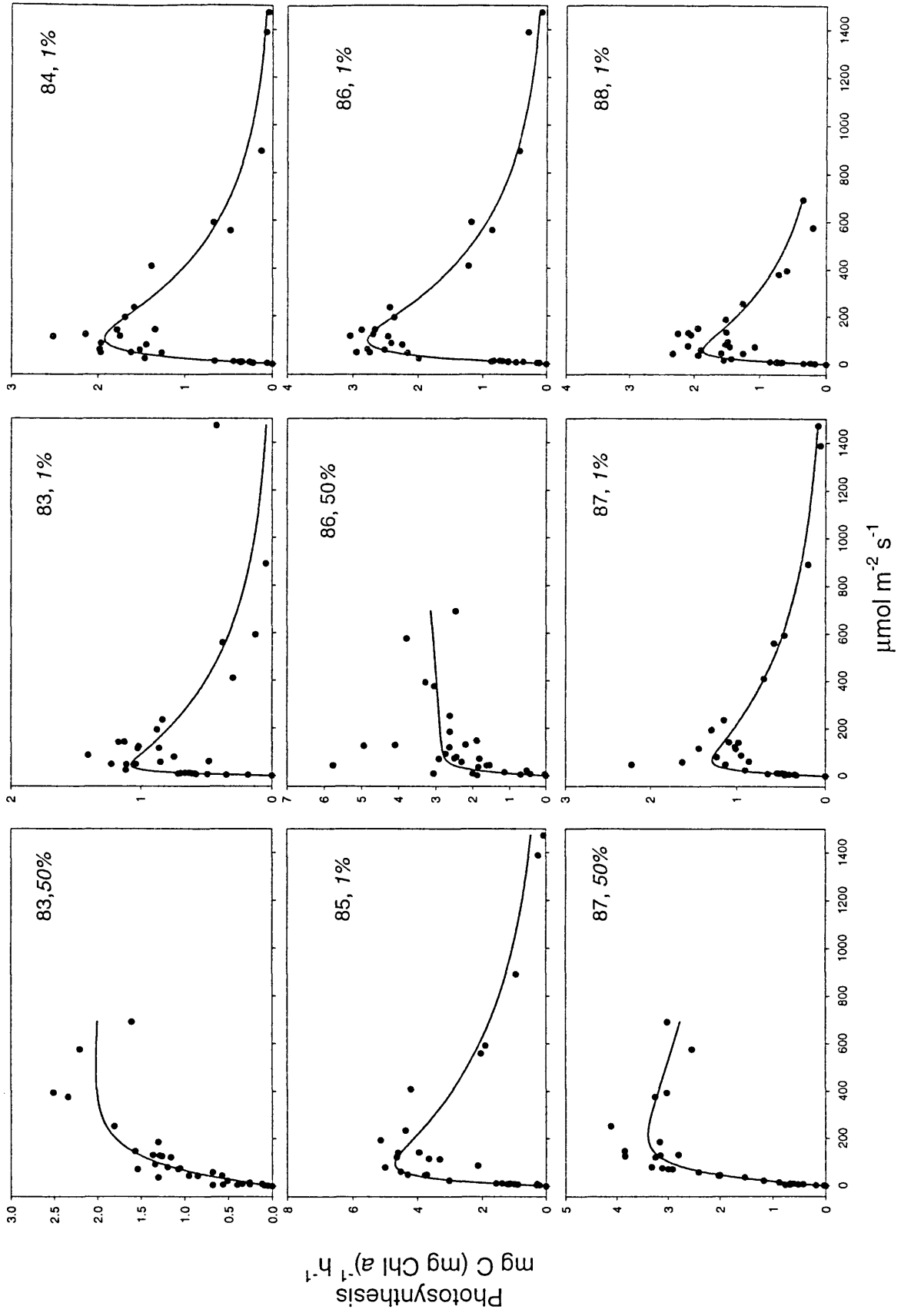












Appendix II. Table of parameters measured at each station.

Appendix II. Table of parameters measured at each station.

Station #	Julian Day	Dominant taxa	¹⁴ C Primary Production	¹⁵ N Uptake	Photosynthesis/Irradiance
1994					
7	318	<i>P. antarctica</i>	✓	✓	
9	319	<i>P. antarctica</i>	✓	✓	
11	319	<i>P. antarctica</i>	✓	✓	
13	320	Mixed Assemblage	✓	✓	✓
15	320	<i>P. antarctica</i>	✓	✓	
17	321	Diatom	✓	✓	
18	321	Diatom	✓	✓	
19	322	<i>P. antarctica</i>	✓	✓	✓
20	323	<i>P. antarctica</i>	✓	✓	
21	323	<i>P. antarctica</i>	✓	✓	
22	324	Mixed Assemblage	✓	✓	✓
23	324	Mixed Assemblage		✓	
25	325	Mixed Assemblage	✓	✓	✓
27	325	Mixed Assemblage	✓	✓	
29	326	Mixed Assemblage	✓	✓	
30	326	<i>P. antarctica</i>	✓	✓	
31	326	<i>P. antarctica</i>	✓	✓	
33	326	<i>P. antarctica</i>	✓		
35	327	<i>P. antarctica</i>	✓		
36	327	<i>P. antarctica</i>	✓	✓	✓
37	328	<i>P. antarctica</i>	✓	✓	✓
38	329	<i>P. antarctica</i>	✓	✓	✓
39	330	<i>P. antarctica</i>	✓	✓	
41	330	<i>P. antarctica</i>	✓	✓	
43	331	Mixed Assemblage	✓	✓	
45	331	Mixed Assemblage	✓	✓	
47	332	Mixed Assemblage	✓	✓	
49	332	<i>P. antarctica</i>	✓	✓	
51	333	Diatom	✓	✓	

Station #	Julian Day	Dominant taxa	¹⁴ C Primary Production	¹⁵ N Uptake	Photosynthesis/Irradiance
52	334	Mixed Assemblage	✓		
53	334	Mixed Assemblage	✓	✓	
54	334	Mixed Assemblage	✓		
56	335	Mixed Assemblage	✓	✓	
58	335	<i>P. antarctica</i>	✓		
60	336	Mixed Assemblage	✓	✓	
62	336	<i>P. antarctica</i>	✓	✓	
64	337	<i>P. antarctica</i>	✓	✓	✓
66	338	<i>P. antarctica</i>	✓	✓	
68	338	Mixed Assemblage	✓	✓	
70	339	<i>P. antarctica</i>	✓	✓	
72	339	Mixed Assemblage	✓	✓	
74	340	Diatom	✓		
75	340	Diatom	✓	✓	
77	342	<i>P. antarctica</i>	✓	✓	✓
1995-96					
4	355	Diatom	✓	✓	✓
5	356	Diatom	✓	✓	✓
7	356	Mixed Assemblage	✓	✓	✓
9	357	Mixed Assemblage	✓	✓	✓
10	357	Diatom	✓	✓	✓
12	357	Mixed Assemblage	✓	✓	✓
14	358	<i>P. antarctica</i>	✓	✓	✓
16	358	Mixed Assemblage	✓	✓	✓
17	360	<i>P. antarctica</i>	✓	✓	✓
18	360	Diatom	✓	✓	✓
20	361	Diatom	✓	✓	✓
21	361	<i>P. antarctica</i>	✓	✓	✓
22	361	<i>P. antarctica</i>	✓		✓
23	362	<i>P. antarctica</i>	✓	✓	✓
25	362	Diatom	✓	✓	✓
26	362	Diatom	✓	✓	✓

Station #	Julian Day	Dominant taxa	14C Primary Production	15N Uptake	Photosynthesis/Irradiance
28	364	Mixed Assemblage		✓	✓
35	365	Mixed Assemblage		✓	✓
36	365	Mixed Assemblage		✓	
40	2	Mixed Assemblage		✓	
43	3	Mixed Assemblage	✓	✓	
44	4	Diatom	✓	✓	
47	5	Diatom	✓	✓	✓
49	5	Diatom	✓	✓	✓
54	6	Mixed Assemblage	✓	✓	✓
56	7	Mixed Assemblage	✓		
58	7	Mixed Assemblage	✓		
61	7	<i>P. antarctica</i>	✓	✓	✓
65	7	Mixed Assemblage	✓		
68	8	Diatom	✓	✓	✓
70	8	Mixed Assemblage	✓		
71	8	<i>P. antarctica</i>	✓	✓	✓
72	8	Mixed Assemblage	✓		
73	9	<i>P. antarctica</i>	✓	✓	✓
74	9	Mixed Assemblage	✓		
75	9	Mixed Assemblage	✓	✓	✓
76	9	Mixed Assemblage	✓		
77	10	Mixed Assemblage	✓	✓	
78	10	Mixed Assemblage	✓		✓
79	10	Diatom	✓	✓	✓
80	10	Mixed Assemblage	✓		
81	11	Diatom	✓	✓	✓
83	11	<i>P. antarctica</i>	✓		✓
84	11	Mixed Assemblage	✓	✓	✓
85	12	<i>P. antarctica</i>	✓		✓
86	12	Diatom	✓	✓	✓
87	12	Diatom	✓		✓
88	12	Diatom	✓	✓	✓
92	13	Mixed Assemblage	✓	✓	✓

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