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Photosynthesis/irradiance relationships in the Ross Sea, Antarctica, and their control by phytoplankton assemblage composition and environmental factors

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ABSTRACT: The photosynthetic parameters of natural phytoplankton assemblages from the Ross Sea, Antarctica, as well as unialgal cultures of the diatom *Pseudonitzschia* sp. and the colonial haptophyte *Phaeocystis antarctica* were investigated to determine if differential responses to irradiance could explain the distribution of phytoplankton in the Ross Sea. Field assemblages had photosynthetic responses that suggested acclimation to low irradiance levels, and the initial rate of photosynthesis per unit chlorophyll (α) and the theoretical maximum rate of production (P^B_{max}) averaged 0.083 mg C (mg chl *a*)$^{-1}$ h^{-1} (µmol m^{-2} s^{-1})$^{-1}$ and 2.40 mg C (mg chl *a*)$^{-1}$ h^{-1}, respectively. An increase in both α and P^B_{max} were noted as the season progressed. However, no differences existed between the photosynthetic responses of phytoplankton assemblages dominated by diatoms and those dominated by *P. antarctica*. A significant influence of irradiance (reflected in changes in α and the photoadaption index E_k) was observed in the field observations, and this effect was corroborated by laboratory experiments. The carotenoid accessory pigment 19′-hexanoyloxyfucoxanthin in *P. antarctica* also varied with irradiance, but fucoxanthin did not. These results suggest that the spatially distinct distribution of *P. antarctica* and diatoms that is often observed in the Ross Sea probably does not result simply from different photosynthetic responses, but from a complex series of controls, potentially including trace metal effects, vertical mixing, and other factors.

KEY WORDS: Photosynthesis · Diatoms · *Phaeocystis* · Accessory pigments

INTRODUCTION

The Ross Sea exhibits seasonal extremes in physical and environmental variables, most notably irradiance. Irradiance is influenced by solar angle, the advance and retreat of the annual sea ice, opening of the Ross Sea polynya (a region of reduced ice cover surrounded by greater concentrations of ice), and water-column stratification. These physical processes in turn initiate relatively predictable biological processes in this area, especially the growth and accumulation of phytoplankton (Arrigo et al. 1998). The seasonal phytoplankton bloom in the Ross Sea is one of the most spatially extensive in the Southern Ocean (Comiso et al. 1993), with chlorophyll concentrations increasing by over 2 orders of magnitude during the growing season (Smith et al. 2000).

This bloom is unique for 2 reasons. First, initiation of growth begins early in the growing season, especially compared to other regions at the same latitude. Phytoplankton growth is initiated in the south central polynya in the vicinity of the Ross Ice shelf in November (Smith & Gordon 1997), and expands both towards the coast of Victoria Land and to the north as ice disappears from the region (generally in late December and early January; Nelson et al. 1996, Fabiano et al. 2000, Lipizer et al. 2000). Second, the distribution of phytoplankton taxa appears to be spatially distinct (DiTullio & Smith 1996, Arrigo et al. 1999, Smith & Asper 2001). *Phaeocystis antarctica*, a colonial hapto-

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phyte, is found primarily in the south central polynya in spring, and diatoms generally become dominant during summer in the western coastal region. While some locations are clearly dominated by a single form both in terms of numbers and biomass, many locations also represent mixtures of the 2 major groups (and others: Smith & Asper 2001). *P. antarctica* remains as an important constituent of the phytoplankton throughout the growing season in the south central Ross Sea, although by mid-summer its biomass has decreased and its physiological state is approaching senescence (Smith & Asper 2001). On the other hand, diatoms continue to grow at low rates over much of the entire region (Smith et al. 1996, 1999).

The causes for these spatially distinct distributions remain controversial. Past studies have not demonstrated differences in the 2 chemical and physical environments, although mixed layers may be slightly shallower in the west due to greater *in situ* ice melt and stratification (Arrigo et al. 1999). In contrast, Smith & Asper (2001) compared mixed layer depths of stations dominated by diatoms and *Phaeocystis antarctica* and found no difference between the 2 taxa in either spring or summer. Mixed layers of ca 30 m are formed in the south central region (along with ice-free conditions) and persist longer (from November through early March: Smith et al. 2000) than the even shallower mixed layers (ca 20 m) that are formed from late December through mid-February near the coast. Variations in the depth of the mixed layer, its persistence over time, and its strength make it difficult to attribute control of the phytoplankton assemblage composition to any single factor.

The spatial difference in the distribution of phytoplankton assemblage composition is also reflected in the distribution of the vertical flux of organic matter. Near the coast of Victoria Land, where diatoms generally dominate, sinking material generally has a high silica content (often enriched with fecal pellets), whereas export in the central Ross Sea is comprised of loose, organic aggregates that are relatively low in silica (Nelson et al. 1996, Dunbar et al. 1998). *Phaeocystis antarctica*'s dominance in the south central Ross Sea has been attributed to superior photosynthetic abilities in the form of higher carbon uptake at low irradiance levels (Arrigo et al. 1999), and based on ambient nutrient ratios it has also been hypothesized that this species may have different nutrient uptake capabilities as well (Arrigo et al. 1999; but see Sweeney et al. 2000). Smith & Asper (2001) concluded that the distribution of diatoms and *P. antarctica* reflects the complex relationships that control production and losses in the Ross Sea rather than a single factor.

The relationship between photosynthesis and irradiance has been modeled in several forms (Jassby & Platt 1976, Platt et al. 1980, 1982). Platt et al. (1980) defined a model that incorporated irradiance levels ranging from limiting to inhibiting conditions of irradiance, and hence allowed a full investigation of the irradiance regimes experienced *in situ*. The photosynthetic parameters defined by this relationship provide information about the initial rate of photosynthesis per unit chlorophyll (α), roughly equivalent to the quantum yield, the theoretical maximum rate of production ($P^B_{\max}$), and a measure of photoinhibition (β). These parameters also provide insights into the physiological state of the phytoplankton population or assemblage tested. In particular, α and $P^B_{\max}$ can be influenced by nutrient status, irradiance regime, and adaptation status. 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).

Several studies have investigated the role of nutrient limitation on photosynthetic parameters in an attempt to clearly understand the effects of both macronutrient and in particular trace metal limitation on photosynthetic abilities. Trace metal limitation, particularly of iron, is thought to be responsible for maintaining the high-nutrient, low-chlorophyll (HNLC) condition found in many of the world's oceans, as iron is essential for both photosynthesis and nutrient uptake. Specifically, it is an essential element in pigment synthesis, a component of both enzymes necessary for nitrogen uptake, and an obligate requirement for a functional electron transport system (Falkowski et al. 1998). Kolber et al. (1994), Lindley et al. (1995) and Lindley & Barber (1998) suggested that the primary production and quantum yield of photosynthesis are limited by iron, and based on reduced quantum yields concluded that trace metal limitation was a common occurrence in the equatorial Pacific. Lindley & Barber (1998) found that the addition of iron increased photosynthetic capacity of the phytoplankton in HNLC waters and ultimately resulted in an increase in biomass. If iron limitation occurs in the austral summer on the Ross Sea continental shelf, as suggested by Olson et al. (2000) and Sedwick et al. (2000), we would expect to find a temporal trend in $P^B_{\max}$.

Although biological processes, including primary productivity, in the Ross Sea are seemingly 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 study was 2-fold: to determine if *Phaeocystis antarctica* exhibits enhanced photosynthetic capabilities that allow it to become established earlier than diatoms and therefore to dominate the seasonal bloom, and to discover if any temporal progression of photosynthetic responses within the seasons

occurs. Measurements were conducted in both the field and laboratory to assess the relative photosynthetic capabilities of *P. antarctica* and diatoms and the environmental factors that control photosynthesis.

MATERIALS AND METHODS

Field sampling. Field samples were collected in the Ross Sea polynya during 2 cruises on the RVIB 'Nathaniel B. Palmer' (November/December 1994 and December 1995/January 1996) which sampled the austral spring and summer, respectively. Stations were occupied primarily along 76° 30′ S and the surrounding area (Fig. 1). Continuous irradiance measurements were made using a BioSpherical Instruments 4π sensor mounted on the ship's mast. Electrical problems resulted in substantial quantities of unusable data, and the PAR was also calculated using the model of Legendre et al. (1993). The depths to which 50 and 1% of surface irradiance (E_0) penetrated were determined from Secchi depths or from underwater irradiance measurements at each station, and water was collected from these depths. Samples were collected using a 911+ CTD system (Sea-Bird Electronics, Bellevue, WA) coupled with a sampling rosette fitted with 24 Niskin bottles (12 l) with Teflon-coated closing springs. The CTD was equipped with sensors to measure temperature and salinity continuously with depth, and also included a fluorometer (Chelsea Instruments, West Molesey, UK), underwater PAR sensor (BioSpherical Instruments, San Diego, CA), and a transmissometer (Sea-Tech, Los Angeles, CA).

Chlorophyll determinations: Chlorophyll *a* (chl *a*) concentrations at each isolume were determined by filtering known volumes of seawater through Whatman 25 mm GF/F filters and then extracting with a 2-step process. First, 10 ml 90% acetone were added and the samples were allowed to extract on ice in the dark for 15 min. Samples were then sonicated on ice for another 15 min to aid in the breakage of membranes and extraction of the chlorophyll. Concentrations were then determined fluorometrically before and after acidification using a Model 10 series fluorometer (Turner Designs, Sunnyvale, CA). The fluorometer was calibrated using known concentrations of commercially purified chl *a* (Sigma).

Photosynthesis/irradiance experiments: Photosynthesis/irradiance relationships were measured using a method adapted from Lewis & Smith (1983). Samples (75 ml) were inoculated with ca 750 µCi $NaH^{14}CO_3$. Then 32 × 2 ml sub-samples in 7 ml scintillation vials were incubated for 2 h within an artificial light gradient. Incubations were terminated by acidifying with 1 ml 10% HCl. Samples were then dried and rehydrated with 1 ml deionized water, to which 5 ml of scintillation cocktail (Ecolume) were added. Time-zero controls were treated identically, except that they were acidified immediately. Total added $NaH^{14}CO_3$ was measured by collecting 0.5 ml sample, adding 0.1 ml β-phenylethylamine (which acts as a CO_2 trap), and immediately adding scintillation cocktail. Samples were quantified using a liquid scintillation counter.

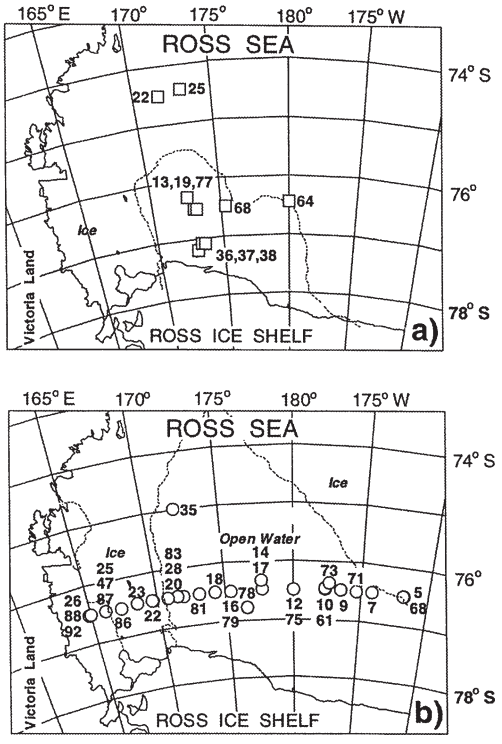

Fig. 1. Stations (numbered symbols) at which photosynthesis/irradiance experiments were conducted in (a) austral spring 1994 and (b) summer 1995/1996

The incubators (photosynthetrons) consisted of a sample block with 32 wells, each of which held a 7 ml scintillation vial. A main block contained the light source. This block allowed the samples to be exposed to a range of irradiances from limiting to saturating conditions (0 to 2000 µmol photons m^{-2} s^{-1}) by covering the bottom of each well with different combinations of neutral-density screens. The source light was provided by 2 halogen lamps projecting onto a surface that then reflected onto the bottom of the sample wells. The irradiance within the wells was measured with 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 (from –1.8 to 0°C).

Laboratory experiments. Additional experiments to investigate the photosynthetic parameters of Antarctic phytoplankton clones were performed in the laboratory using cultured phytoplankton species. Cultures of

Phaeocystis antarctica (CCMP1871) and the diatom *Pseudonitzschia* sp. (CCMP1445) were obtained from the Provasoli — Guillard National Center for Culture of Marine Phytoplankton (CCMP) in Booth Bay Harbor, Maine. Both cultures originated from phytoplankton isolated near McMurdo Sound in the Ross Sea. The cultures were initially grown at 0°C and ca 200 µmol photons m^{-2} s^{-1} (cool-white fluorescent lights) in filter-sterilized f/2 media (for the diatom) and filter-sterilized f/2 – Si for *P. antarctica* (Guillard 1983). Once the cultures had been established, 280 ml Qorpak bottles filled with culture media were inoculated with 10 ml actively growing culture of each species. These bottles were covered with neutral-density screen to simulate 3 different irradiance regimes (332, 149 and 41 µmol m^{-2} s^{-1}). The bottles were placed in the growth chamber randomly and allowed to grow and acclimate for 13 d. After this period, samples were collected for chl *a*, HPLC determination of pigments, POC, PON and photosynthesis/irradiance (P/E) experiments. Laboratory measurements of P/E parameters were similar to those employed in the field except that 1 ml samples were incubated for 1 h. Chl *a* concentrations were again determined fluorometrically, but extractions were done in the dark at 4°C for 24 h.

The full suite of phytoplankton pigments was analyzed using high-performance liquid chromatography (HPLC). Known volumes were filtered onto GF/F filters and quick-frozen in liquid N_2 until analysis. Samples were analyzed by first extracting the pigments by grinding with a mortar and pestle in 90% acetone and then separating the filter from the extracted photosynthetic pigments by high-speed centrifugation. The 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). Solvents were degassed using an in-line degasser. Pigments were separated using a Waters Spherisorb 5 mm ODS2 (C18) analytical column. A Waters guard column preceded the analytical column, containing the same packing material as described above. System functions, data collection and data analysis was accomplished using Waters Millenium© software.

Taxonomic dominance at each station was determined with the calculated pigment ratios. Those stations at which the integrated euphotic zone fucoxanthin:19′-hexanoyloxyfucoxanthin ratios (FUCO:HEX) were >1.0 were considered to be diatom-dominated, those with an integrated euphotic zone FUCO:HEX ratio of <0.2 were considered to be dominated by *Phaeocystis antarctica*. Those stations that did not fit these criteria were considered to be a mixed assemblage (Smith & Asper 2001).

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

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

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

using Sigma Plot 2000 to perform the nonlinear least-squares regression. P^B_s is the theoretical maximum for photosynthesis in the absence of photoinhibition [mg C (mg chl *a*)$^{-1}$ h^{-1}], α is the initial rate of photosynthesis [mg C (mg chl *a*)$^{-1}$ h^{-1} (µmol m^{-2} s^{-1})$^{-1}$], and β is a measure of photoinhibition (mg C (mg chl *a*)$^{-1}$ h^{-1} (µmol m^{-2} s^{-1})$^{-1}$). Using the parameters from this equation, several other parameters were calculated from:

$$P^B_{max} = P^B_{max}[\alpha/(\alpha+\beta)][\beta/(\alpha+\beta)]^{\alpha/\beta} \quad (2)$$

where P^B_{max} is the actual maximal photosynthetic rate [mg C (mg chl *a*)$^{-1}$ h^{-1}] and incorporates photoinhibition or β. An index of photoadaptation (µmol m^{-2} s^{-1}) was estimated from:

$$E_k = P^B_{max}/\alpha \quad (3)$$

E_k is also an estimate of the optimal irradiance for photosynthesis. In cases when the numerical routine failed to converge (making reliable estimates of parameter values impossible), these parameter values (11 of 88 experiments) were discarded from the statistical analysis. In addition, parameter values that were more than 2 SD from the mean of all values were eliminated (Sokal & Rohlf 1981). Surprisingly, in many cases β was very low or not detectable, and it was excluded from all statistical analyses. Mean values for β are, however, presented.

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. 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 2-way ANOVA was applied to determine if there was any interaction between irradiance and species.

Mixed-layer depths were calculated as the depth which exhibited a change of 0.05 σ_T unit from a stable surface value (Smith et al. 2000). The average irradiance available in the mixed layer was calculated by:

$$E_{mix} = \frac{1}{z_{mix}} \int_0^{z_{mix}} E_0 e^{kz} dz \quad (4)$$

where E_{mix} is the mean irradiance available to the phytoplankton in the mixed layer (z_{mix}), k is the observed attenuation coefficient, and E_0 is the daily irradiance corrected for air-sea reflectance (Figueiras et al. 1998).

RESULTS

Field observations

Average daily irradiance, calculated using the model of Legendre et al. (1993), for the austral spring (1994) cruise was 49.9 ± 14.9 mol photons m^{-2} s^{-1} (Table 1). 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 few ship-board PAR data collected (Parker 1997). The average depth of the euphotic zone (0.1 % E_0) was 52 m. Chl *a* values increased throughout the cruise, initially being much less than 1 µg l^{-1} and increasing to >11 µg l^{-1}, with the mean surface chl *a* concentration being 3.47 µg l^{-1} (Table 1). Chlorophyll concentrations were relatively invariant throughout the mixed layer. Average calculated daily irradiance for the austral summer cruise (1995/96) was 49.5 ± 24.3 mol photons m^{-2} s^{-1}, and the average depth of the euphotic zone was 42 m. Chl *a* values remained elevated for most of the cruise, but declined towards the end. The average surface chl *a* concentration was 3.20 µg l^{-1} (max. 10.8 µg l^{-1}).

Mixed-layer depths declined from early spring into the summer (Fig. 2a). Mixed-layer depths for the spring cruise ranged from 16 to 150 m, while the summer mixed-layer depths ranged from 0 to 73 m. The strength of stratification varied seasonally, and the south-central region was generally less strongly stratified than the western region (Smith & Asper 2001). However, stations closer to the coast initially had deeper mixed layers that were reduced by the addition of low-density melt-water. The contribution of *Phaeocystis antarctica* to phytoplankton biomass relative to diatoms (Fig. 2b) suggests that while the former dominates during spring under conditions of deeper mixing, the relationship between mixed-layer depth and assemblage composition varies with time.

Table 1. Average ± SD and range (in parentheses) of various environmental variables during austral spring and summer in the Ross Sea (all cruise data). Euphotic zone depth defined as the depth of the 0.1 % isolume

Variable	Spring	Summer
Mixed-layer depth (m)	61 ± 42 (16–150)	23 ± 15 (0–73)
Daily irradiance (mol photons m^{-2} d^{-1})[a]	49.90 ± 14.88 (26.85–77.57)	49.45 ± 24.27 (17.16–88.48)
Euphotic zone depth (m)	52 ± 30 (17–136)	42 ± 19 (17–137)
PAR in mixed layer (mol photons m^{-2} d^{-1})	9.73 ± 6.91 (1.77–26.0)	25.8 ± 20.0 (3.71–65.9)
Surface chlorophyll (µg l^{-1})	3.47 ± 2.49 (0.16–11.5)	3.20 ± 2.37 (0.31–10.8)

[a]From Parker (1997)

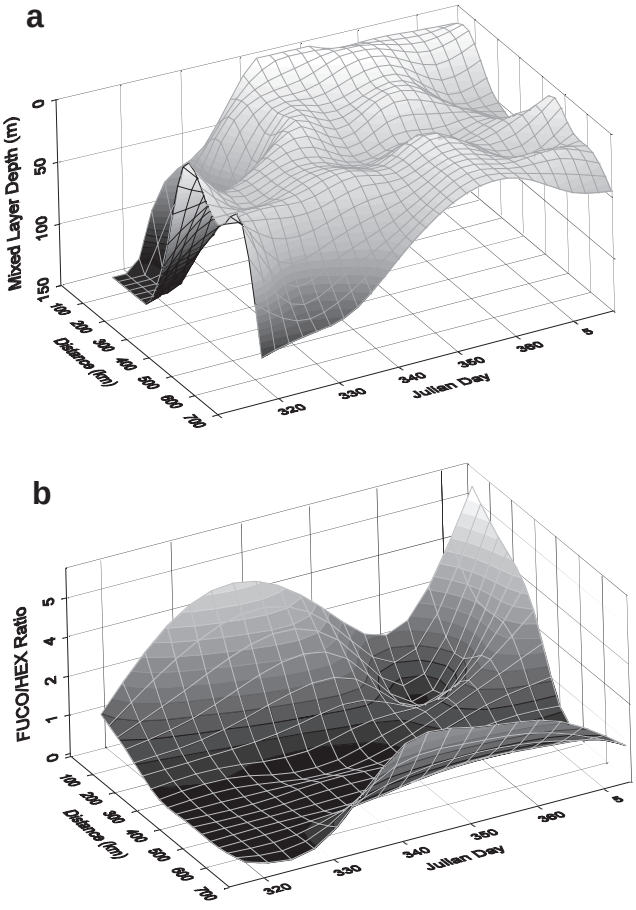

Fig. 2. Variation in (a) mixed-layer depth (m), and (b) phytoplankton assemblage composition (expressed as the ratio of 19′-hexanoyloxyfucoxanthin: fucoxanthin concentrations, since 19-HEX occurs in *Phaeocystis antarctica* whereas FUCO occurs in diatoms) over space and time for the spring-summer period

Photosynthesis/irradiance experiments

Field observations

As expected, photosynthesis exhibited a saturation response as a function of irradiance (Fig. 3). The mean α value for both cruises was 0.083 mg C (mg chl *a*)$^{-1}$ h^{-1}

(µmol m^{-2} s^{-1})$^{-1}$, ranging from 0.006 to 0.193 mg C (mg chl *a*)$^{-1}$ h^{-1} (µmol m^{-2} s^{-1})$^{-1}$ (Table 2). The mean P^B_{max} value was 2.40 mg C (mg chl *a*)$^{-1}$ h^{-1} [range 0.231 to 7.45 mg C (mg chl *a*)$^{-1}$ h^{-1})], and the average E_k value was 32 µmol photons m^{-2} s^{-1}. β, the photoinhibition parameter, averaged 0.005 mg C (mg chl *a*)$^{-1}$ h^{-1} (µmol m^{-2} s^{-1})$^{-1}$ (Table 2). The median values of α, P^B_{max} and E_k were 0.071 mg C (mg chl *a*)$^{-1}$ h^{-1} (µmol m^{-2} s^{-1})$^{-1}$, 2.17 mg C (mg chl *a*)$^{-1}$ h^{-1}, and 31 µmol photons m^{-2} s^{-1}, respectively (Fig. 4).

The photosynthetic parameters α, P^B_{max}, and E_k increased as the growing season progressed (Fig. 5). When regressed over time, the slopes of α, P^B_{max}, and E_k were significantly different from zero ($p < 0.05$ for all 3 variables), indicating a temporal acclimation to the changing irradiance regime. When analyzed as a function of irradiance level (50 or 1% E_0), there were no interaction effects between taxa and irradiance for all 3 parameters, suggesting that these factors have independent effects on photosynthetic response. As such, each photosynthetic parameter was investigated individually. These data were not normally distributed, but did display homogeneous variance (as determined by Levene & Cochran's test for heterogeneous variance: Underwood 1997). A 2-way ANOVA detected a significant effect of the irradiance levels on both α and E_k. Values for α (the photosynthetic efficiency) at the 1% irradiance level were greater than those for the 50% irradiance level, while values for E_k, the adaptation parameter, were smaller at the 1% isolume. When analyzed relative to taxonomic dominance, neither the analyses of variance or a Tukey's Studentized range multiple means comparison detected a significant difference among the parameters as a function of taxonomic grouping. As such, we conclude that phytoplankton assemblage composition played a minor role in regulating photosynthetic performance. We further concluded that the assemblages were well adapted to maximizing photosynthesis at the low light levels encountered.

Laboratory

The Platt et al. (1980) model was also used to estimate the photosynthetic parameters from the laboratory experiments. Only α met both of the assumptions (i.e. normal distribution and homogenous variance) that allowed an analysis of variance. The other 2 parameters (P^B_{max} and E_k) were not normally distributed,

Table 2. Average ± SD (in parentheses) and range of photosynthetic parameters during austral spring and summer in the Ross Sea. α: initial rate of photosynthesis per unit chlorophyll; β: photoinhibition; and E_k: photoadaptation index. Data presented as a function of season, irradiance (% surface value) and taxonomic dominance. Units for α and β = mg C (mg chl *a*)$^{-1}$ h^{-1} (µmol m^{-2} s^{-1})$^{-1}$, for P^B_{max} = mg C (mg chl *a*)$^{-1}$ h^{-1}, and for E_k = µmol photons m^{-2} s^{-1}

Season	α	β	P^B_{max}	E_k
All samples	0.083 ± 0.043 (0.006–0.193)	0.005 ± 0.006 (0.001–0.017)	2.40 ± 1.27 (0.23–7.45)	32 ± 15 (11–94)
Spring	0.047 ± 0.023 (0.006–0.067)	No data No data	1.77 ± 0.97 (0.023–3.03)	37 ± 7.5 (24–47)
Summer	0.087 ± 0.043 (0.022–0.19)	0.005 ± 0.004 (0.001–0.017)	2.48 ± 1.29 (0.709–7.45)	31 ± 16 (11–94)
All 50%	0.073 ± 0.045 (0.006–0.193)	0.003 ± 0.0014 (0.0013–0.0063)	2.22 ± 0.86 (0.233–3.99)	36 ± 17 (13–94)
All 1%	0.096 ± 0.036 (0.037–0.184)	0.0058 ± 0.0043 (0.0008–0.017)	2.63 ± 1.67 (0.71–7.45)	27 ± 9.6 (11–55)
All diatom-dominated	0.076 ± 0.027 (0.043–0.13)	0.0034 ± 0.0024 (0.0008–0.0090)	2.19 ± 0.64 (1.29–3.22)	31 ± 10 (16–52)
All *Phaeocystis antarctica*-dominated	0.079 ± 0.047 (0.006–0.184)	0.0057 ± 0.0047 (0.002–0.017)	2.52 ± 1.53 (0.231–7.45)	37 ± 20 (11–94)
All mixed assemblage	0.092 ± 0.049 (0.037–0.19)	0.005 ± 0.004 (0.001–0.015)	2.43 ± 1.39 (0.71–6.90)	28 ± 9.5 (14–47)
Diatom-dominated (50%)	0.068 ± 0.027 (0.043–0.133)	0.0021 ± 0.0005 (0.0013–0.0028)	2.31 ± 0.65 (1.50–3.23)	35 ± 9.5 (22–52)
Phaeocystis antarctica-dominated (50%)	0.057 ± 0.042 (0.006–0.175)	0.0032 ± 0.0013 (0.0017–0.0043)	2.08 ± 0.99 (0.23–3.99)	44 ± 23 (13–94)
Mixed assemblage (50%)	0.0093 ± 0.0053 (0.038–0.193)	0.0041 ± 0.0018 (0.0021–0.0063)	2.32 ± 0.89 (0.95–3.79)	28 ± 11 (16–47)
Diatom-dominated (1%)	0.085 ± 0.027 (0.043–0.119)	0.0044 ± 0.0028 (0.0008–0.0090)	2.07 ± 0.66 (1.28–2.86)	26 ± 8.5 (16–42)
Phaeocystis antarctica-dominated (1%)	0.111 ± 0.035 (0.075–0.184)	0.0068 ± 0.0053 (0.0024–0.017)	3.16 ± 1.98 (1.08–7.45)	28 ± 13 (11–55)
Mixed assemblage (1%)	0.090 ± 0.044 (0.037–0.173)	0.0063 ± 0.0049 (0.0012–0.015)	2.61 ± 1.98 (0.71–6.90)	27 ± 7.9 (14–40)

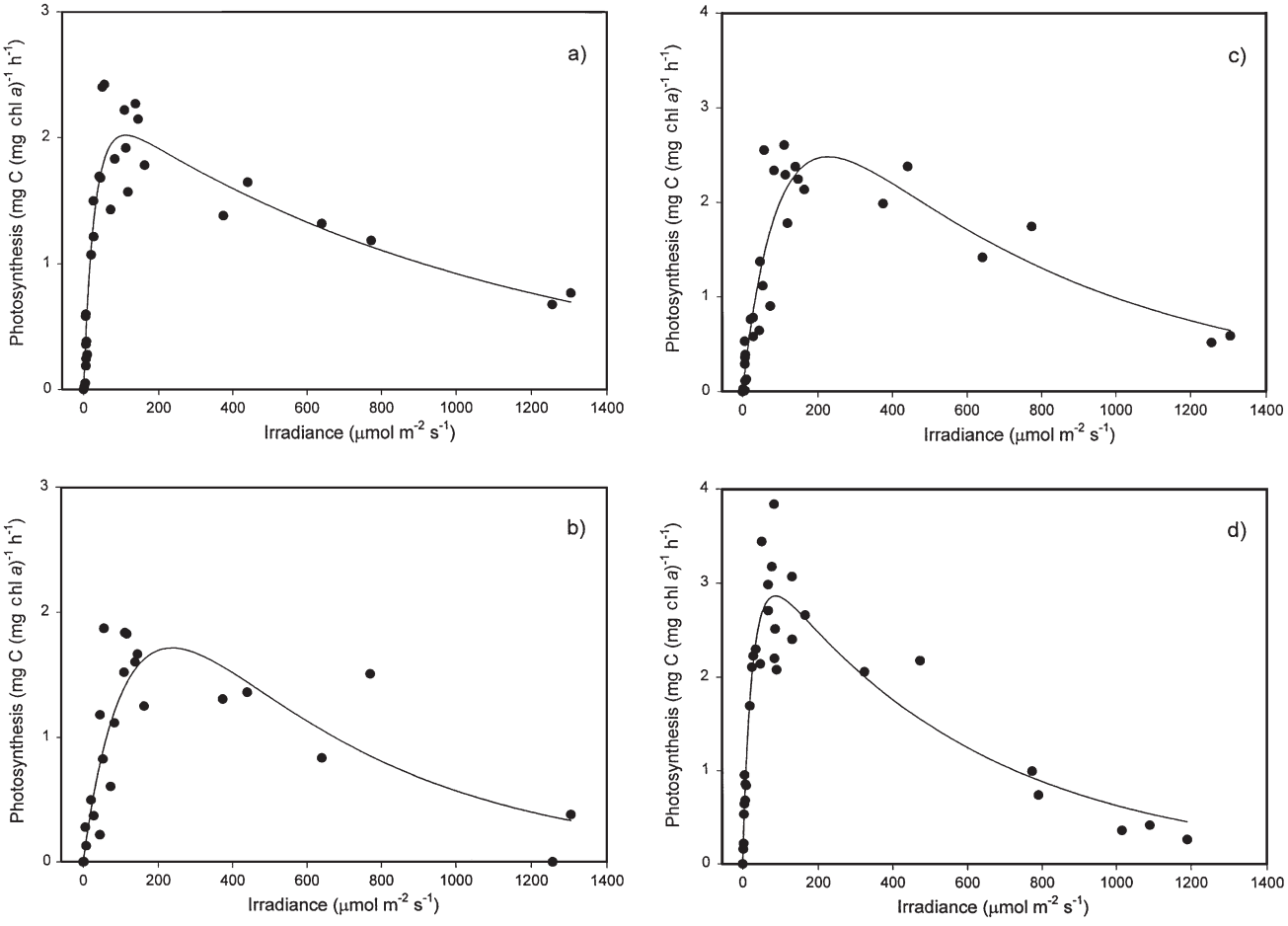

Fig. 3. Representative photosynthesis/irradiance experiments at selected stations. (a) Stn 18, dominated by diatoms, sampled from the 50% isolume; (b) Stn 23, dominated by *Phaeocystis antarctica*, sampled from the 50% isolume; (c) Stn 25, from a mixed assemblage, sampled from the 50% isolume; (d) Stn 25, from a mixed assemblage, sampled from the 1% isolume

but both parameter values displayed homogenous variance; therefore, the data were not transformed before analysis.

The mean responses of α, $P^B_{\max}$, and E_k grouped by the 3 irradiance levels and 2 taxa are presented in Table 3. The 2-way ANOVA detected a significant effect of irradiance for both α and E_k, similar to the findings in the field. The Tukey's multiple means comparison test further defined this effect, and suggested that at the lower irradiance levels α was higher and values for E_k were lower, again similar to the results of the field observations.

The results for $P^B_{\max}$ 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. The mean $P^B_{\max}$ values (1.14 for *Phaeocystis antarctica* and 0.68 for *Pseudonitzschia* sp.) were significantly different ($p < 0.05$), and a

Table 3. *Phaeocystis antarctica* and *Pseudonitzschia* sp. average and standard deviation of photosynthetic parameters α, $P^B_{\max}$, and E_k determined from laboratory experiments on unialgal cultures. Parameters and units as in Table 2

Species	Irradiance	α	$P^B_{\max}$	E_k
Phaeocystis antarctica	332	0.0080 ± 0.0045	1.86 ± 0.76	248 ± 75
Phaeocystis antarctica	149	0.010 ± 0.0045	1.02 ± 0.56	96 ± 17
Phaeocystis antarctica	41	0.013 ± 0.0055	0.91 ± 0.32	71 ± 24
Pseudonitzschia sp.	332	0.0047 ± 0.0032	0.78 ± 0.19	233 ± 160
Pseudonitzschia sp.	149	0.0090 ± 0.0040	0.67 ± 0.26	76 ± 5.9
Pseudonitzschia sp.	41	0.018 ± 0.0005	0.57 ± 0.10	32 ± 7.0

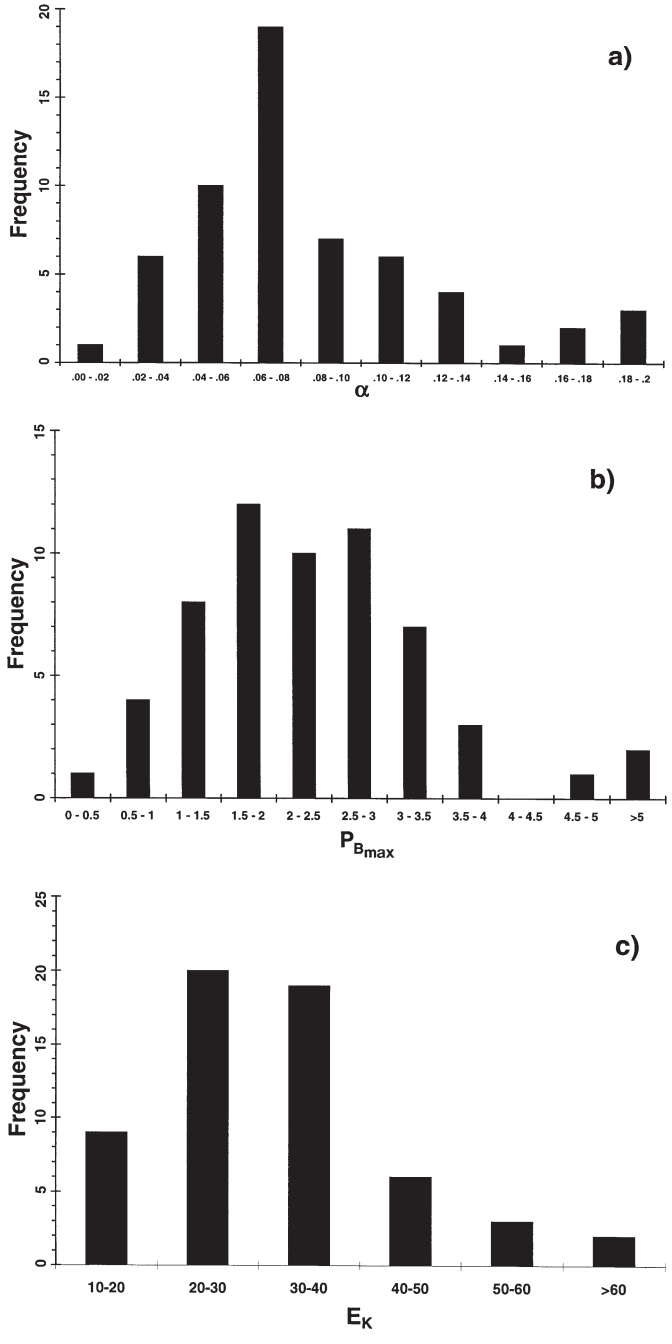

Fig. 4. Frequency distribution of observations relative to the total number of photosynthetic parameters: (a) Initial rate of photosynthesis per unit chlorophyll (α) as mg C (mg ch *a*)$^{-1}$ h^{-1} (µmol m^{-2} s^{-1})$^{-1}$; (b) theoretical maximum rate of production (P^B_{max}) as mg C (mg chl *a*)$^{-1}$ h^{-1}; (E_k) µmol photons m^{-2} s^{-1}

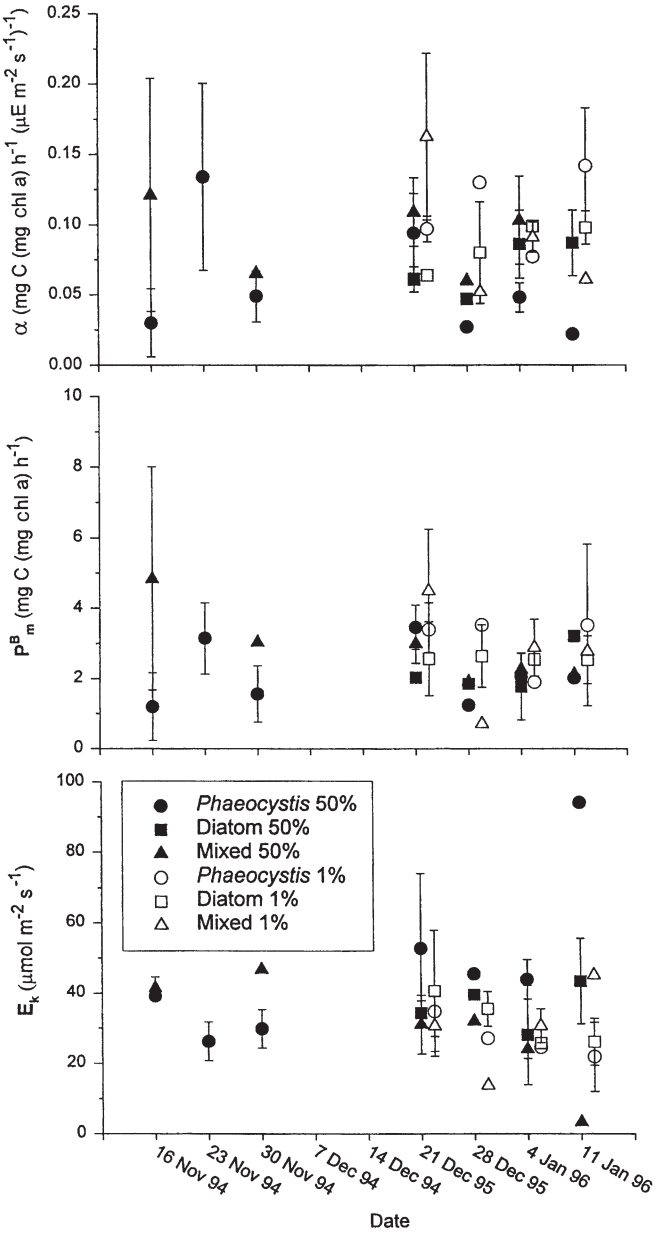

Fig. 5. Temporal progression of photosynthetic parameters (α, P^B_{max} and E_k) in the Ross Sea. Responses are separated by taxonomic affinity and irradiance sampled. *Phaeocystis* = *P. antarctica*; other details as in Fig. 4

multiple means comparison of the values at the different irradiance levels indicated that the response at 322 µmol m^{-2} s^{-1} was significantly different from the lower 2 levels, being nearly 2× the values at 149 and 41 µmol m^{-2} s^{-1} [1.32 vs 0.70 mg C (mg chl *a*)$^{-1}$ h^{-1}].

Differences in chl *a*, chls c1 and c2, 19′-hexanoyloxyfucoxanthin (*Phaeocystis antarctica* only), and fucoxanthin (*Pseudonitzschia* sp. only) concentrations due to irradiance and taxa within the cultures were assessed. Because differences in cellular sizes and therefore pigment concentrations occurred, all pigment concentrations were normalized to chl *a* (Table 4). Both irradiance level and taxa had an effect on chl c1 and c2 levels. When averaged by irradiance, the chlorophyll concentrations increased as irradi-

Table 4. *Phaeocystis antarctica* and *Pseudonitzschia* sp. pigment concentrations (absolute and normalized to chlorophyll *a*) under different irradiance levels when grown in the laboratory. Chl *a*: chlorophyll *a*; Chl c1, c2: chlorophylls c1 and c2; 19′-HEX: 19′hexanoyloxyfucoxanthin; FUCO: fucoxanthin. nd: not detectable; –: not calculated

Species	Irradiance ($\mu mol\ m^{-2}\ s^{-1}$)	Chl a ($\mu g\ l^{-1}$)	Chl c1, c2 ($\mu g\ l^{-1}$)	19′-HEX ($\mu g\ l^{-1}$)	FUCO ($\mu g\ l^{-1}$)	Chl c1, c2/ Chl *a*	19′-HEX/ Chl *a*	FUCO/ Chl *a*
P. antarctica	332	7.63	0.69	0.24	nd	0.09	0.032	–
P. antarctica	149	21.6	2.69	1.81	nd	0.12	0.084	–
P. antarctica	41	44.5	6.62	5.46	nd	0.15	0.123	–
Pseudonitzschia sp.	332	110.5	6.33	nd	0.12	0.057	–	0.0011
Pseudonitzschia sp.	149	186.9	13.7	nd	0.18	0.073	–	0.0010
Pseudonitzschia sp.	41	264.1	25.1	nd	0.26	0.095	–	0.0010

ance decreased. A Kruskal-Wallis test revealed significant differences among the mean concentrations of 19′-hexanoyloxyfucoxanthin at the 3 irradiance levels ($p < 0.05$), which increased with decreasing irradiance. However, there was no significant difference in fucoxanthin concentrations at the different irradiance levels. The POC: chlorophyll ratios were 387 and 53 for *P. antarctica* and *Pseudonitzschia* sp., respectively (significantly different), and the C:N ratios (5.64 ± 0.09 for *Phaeocystis antarctica* and 5.01 ± 0.24 for *Pseudonitzschia* sp.) were also significantly different (Student's *t*-test, $p < 0.001$).

DISCUSSION

The results from both the field and laboratory experiments demonstrate that irradiance is the major factor controlling photosynthetic parameters. Harrison & Platt (1986) stated that temperature and irradiance are the most important factors determining variation in P/E parameters for high latitude phytoplankton assemblages. Seasonal temperature variations in the Ross Sea are small (ca 4°C at most, and generally closer to 2.5°C) and therefore likely to have small influence (Sakshaug 1989). Photosynthetically available radiation and photoperiod, however, do change dramatically. 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; the presence of snow and ice also significantly attenuates the light. Even with these extremes, the integrated daily irradiance at the poles in spring can be higher than in temperate regions (Holm-Hansen et al. 1977, Smith & 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. 2000). The early onset of the spring bloom is unusual at this high latitude, and is most probably due to early stratification of the polynya.

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 adaptive mechanisms employed by these phytoplankton is not clear, the adaptation may not have been merely the result of a simple increase in chlorophyll content in the cells. Palmisano et al. (1986) found similar results when investigating the changes in photosynthetic parameters of an assemblage dominated by *P. antarctica* that had been advected under the sea ice in McMurdo Sound. Their study suggested increased cellular accessory pigments or possible enhancement of electron flow between photosystems as the possible causes for enhanced photosynthetic efficiency at lower irradiance levels. The HPLC data from both cultures in the present study demonstrated that the concentrations of accessory pigments increased with decreasing irradiance (Table 4), suggesting enhanced photosynthetic efficiencies at lower light levels. Brightman & Smith (1989) also found that Antarctic phytoplankton were well adapted to low irradiance. They measured photosynthetic efficiencies ranging from 0.01 to 0.06 $mg\,C\ (mg\,chl\ a)^{-1}\ (\mu mol\ m^{-2}\ s^{-1})^{-1}\ h^{-1}$ during the winter in the Bransfield Strait region when the mean daily irradiance was 0.795 $mol\ m^{-2}\ d^{-1}$. Our α values [0.006 to 0.193 $mg\,C\ (mg\,chl\ a)^{-1}\ h^{-1}\ (\mu mol\ m^{-2}\ s^{-1})^{-1}$] overlap those of the Bransfield Strait study, even though these cruises experienced different irradiance conditions, supporting the conclusion that Antarctic phytoplankton are well adapted to low irradiance regimes (Palmisano et al. 1986, Sakshaug & Holm-Hansen, 1986, Figueiras et al. 1998, Lazzara et al. 2000).

The E_k values of this study also support the conclusion that these species are well adapted to a low-irradiance regime. The field results show that at 1% E_0 the assemblages had low E_k (an estimate of the optimal

irradiance for maximal photosynthesis) values (27 µmol m^{-2} s^{-1} compared to 36 µmol m^{-2} s^{-1} at 50% E_0), indicating that maximal assimilation is still reached at lower irradiance. This is further supported by an absence of significant differences between the P^B_{max} values at the different irradiance levels in the field. The laboratory E_k values also corroborated this trend. For the cultures grown at the lower irradiance levels, the E_k values were lower than for the cultures grown at the highest irradiance. It is clear that these taxa are well adapted to the low-irradiance regime in their high-latitude environment and are able to maximize their photosynthetic potential at low irradiances (Lipizer et al. 2000). The E_k values were significantly different, suggesting that mixing within the euphotic zone was not rapid enough to remove biological differences that had been established. However, they are comparable to most other measurements made for polar phytoplankton (Smith & Sakshaug 1990, Lazzara et al. 2000). The results from the laboratory experiments also suggest that different irradiance regimes result in different states of acclimation. Saggiomo et al. (1998) hypothesized that light was the most important environmental factor controlling photoadaptive state in the Ross Sea. They measured E_k values between 23 and 24 µmol m^{-2} s^{-1} for assemblages from the fluorescence maximum, nearly the same as our values.

Chl *a* concentrations remained relatively constant throughout the spring and summer, but began to decline towards the end of the summer (Smith & Asper 2001). Although the difference is not statistically significant, the mean chl *a* concentration at the lowest 2 isolumes (1 and 0.1% E_0) was greater than the mean concentration at the upper isolumes, resulting in a subsurface chlorophyll maximum. The increased concentration may be a result of passive settling of phytoplankton at high irradiance levels and reduced sinking rates at the lower irradiance encountered deeper in the euphotic zone (e.g. Cullen & Eppley 1981, Bienfang et al. 1983). Conversely, it is also possible that the phytoplankton at the lower irradiance levels have a larger growth rate than those at the surface, and the increased chlorophyll reflects the differential growth patterns. In other regions it has been reported that the subsurface chlorophyll maximum results from a change in the chlorophyll content per cell due to enhanced nutrient availability at the nutricline, but this is unlikely in the Ross Sea because of the elevated macronutrient concentrations present throughout the water column. However, we do not have cellular abundance data to test for numerical responses. Because our results show few differences in photosynthetic parameters within the water column, we suggest that gravitational settling of cells and colonies was the major factor in the production of the sub-surface chlorophyll maximum.

An increase in P^B_{max} over time was detected (Fig. 5), suggesting that the assemblage became increasingly acclimated to the *in situ* irradiance field as the season progressed. This is opposite to the effect that would be expected to result from iron limitation. P^B_{max} values have been shown to be sensitive indicators of iron limitation, decreasing under iron stress (Lindley et al. 1995). If iron limitation was significant during early summer, we would have expected a decline in the maximum photosynthetic rate rather than an increase. Sedwick et al. (2000) reported results of iron-addition experiments from the same cruise that suggested a substantial limitation of phytoplankton growth by iron during summer. It is possible that such a response may have been present, but that because of the substantial spatial variability that our study included, the overall decline in P^B_{max} was not detected. It is also possible that the effects of irradiance were greater than any trace metal effects, at least through mid-January. Measurements of photosynthetic parameters from samples collected from the Ross Sea in February in bottles enriched with iron did show a marked increase in P^B_{max} (Hiscock et al. unpubl. data), and the fluorescence characteristics of individual cells in summer also suggested iron limitation (Olson et al. 2000). Therefore, our results cannot exclude the possibility of micronutrient limitation, and we speculate that had the study continued into February that such a decline in P^B_{max} would have been detected.

The field data showed no significant differences for any of the photosynthetic parameters among the taxonomic groups. That is, both *Phaeocystis antarctica*- and diatom-dominated stations showed equivalent photosynthetic responses with respect to α and P^B_{max} values (Table 2). The results differ from the suggestion of Arrigo et al. (1999), who hypothesized that *P. antarctica* dominated in more deeply mixed waters with lower irradiance levels because of its ability to maintain maximal photosynthetic rates at lower irradiance levels. In this study, both *P. antarctica* and diatoms were found at the base of the euphotic zone (1% E_0), and both maintained maximal photosynthetic rates. Hence, there was no evidence of a difference in photosynthetic capabilities as a function of taxonomic composition.

Phaeocystis antarctica dominated 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 other factors may have contributed to the characteristic taxonomic distribution. For example, the deeper mixed layers may support greater growth of *P. antarctica* because of higher concentrations of micronutrients supplied from depth. Because the south central region is often the site of Antarctic Circumpolar deep water

(ACDW) that has been upwelled onto the continental shelf, trace metal concentrations indeed might be spatially variable and influence phytoplankton composition. Unfortunately, at this time insufficient data on trace metal fluxes are available to test this hypothesis directly. Another possibility is that the ACDW, which is warmer than any shelf water, induces ice melting earlier and changes the pattern of ice algal seeding. Both *P. antarctica* and diatoms such as *Fragilariopsis curta* occur in the ice and are released into the water column upon ice melt. The composition of ice algae also changes with growth (Arrigo et al. 1996), and thus an earlier melting could potentially release different species into the waters of different regions.

The differences in P/E parameters between the culture and field experiments may have resulted from differences in taxonomic composition. While the stations sampled in the polynya were dominated by a single species, in no cases were the stations completely unialgal. In addition, several species of diatoms are present in the Ross Sea polynya, including *Pseudonitzschia subcurvata*, *Thalassiosira* sp., and *Fragilariopsis* sp., and the response of the diatom populations as a whole is unlikely to be exactly like that of a unialgal culture. Specifically, it is possible that 1 diatom species (or 1 clone of *Phaeocystis antarctica*) was much more active than the others, but our methods would not adequately characterize the response of the active population. In addition, the *P. antarctica* cultures formed large (up to 500 µm in diameter) colonies, similar to those found in the field (Mathot et al. 2000), and the higher P^B_{max} values may result from different chlorophyll concentrations in the cultures. The *P. antarctica* cultures did have lower concentrations of chlorophyll than the *Pseudonitzschia* sp. cultures at any irradiance level.

In conclusion, our results did not support the hypothesis that *Phaeocystis antarctica* and diatoms have different photosynthetic capabilities that allow *P. antarctica* to grow more rapidly and at lower irradiance levels within the Ross Sea polynya. The data showed detectable differences between irradiance levels but not between taxonomic groupings, and it is clear that all phytoplankton assemblages were well adapted to low irradiance conditions. 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 *P. antarctica* and diatoms exhibit a near-optimal response throughout the growing season.

The causes of *Phaeocystis antarctica*'s dominance in the south central region of the Ross Sea remain unclear, but it is likely that many environmental factors control phytoplankton bloom dynamics. Possible explanations for the differences in the distributions of diatoms and *P. antarctica* include different micronutrient (iron) distributions and limitations, spatial and temporal variations in the vertical mixing regime, and variable grazing by herbivores. In polar environments, where numerous processes exhibit substantial variability, it is unlikely that a single process controls the dynamics of phytoplankton.

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