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Photosynthetic parameters and empirical modelling of primary production: a case study on the Antarctic Peninsula shelf

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Abstract: Eight hundred photosynthesis-irradiance relationships were determined in the shelf waters adjacent to Palmer Station, Antarctica during the spring/summer periods of 1991–94. Biomass specific maximum photosynthetic rate, P^B_{max}, and the light limited photosynthetic efficiency, α^B, were poorly correlated to the physical forcing and nutrient regimes at the sampling stations. The two photosynthetic parameters, however, did strongly covary indicating the minimum irradiance required to saturate photosynthesis, I_k, was relatively constant in this highly variable environment. The variability in I_k could partially be attributed to both depth in the water column and time of the year, with the highest values occurring for surface samples during the summer period of peak incident irradiance. Given this and the significant dependence of P_{max} on phytoplankton biomass, a simple empirical model for primary productivity was developed. An independent test of the model was performed on data collected in a mesoscale offshore grid and predicted primary production was found to be within 13% of measured values. Although there are limitations to this approach (i.e. exclusion of diel periodicity in photosynthetic response), these results provide relatively robust estimates of daily primary production for the Southern Ocean.

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Introduction

Phytoplankton biomass and primary productivity show a great deal of temporal and spatial heterogeneity in the Southern Ocean (*cf.* Holm-Hansen *et al.* 1977, El-Sayed & Weber 1982, El-Sayed *et al.* 1983, Bodungen *et al.* 1986, Wilson *et al.* 1986, Holm-Hansen & Mitchell 1991, Helbling *et al.* 1995). In order to understand the environmental factors regulating the variability in phytoplankton productivity, sampling regimes must span the relevant spatial and temporal scales. This can be particularly difficult in the Southern Ocean where weather conditions limit sampling capabilities and phytoplankton biomass varies by an order of magnitude over short distances (Smith & Nelson 1985, Wilson *et al.* 1986, Estrada & Delgado 1990, Mitchell & Holm-Hansen 1991).

Remote sensing from space and mooring technologies have shown promise in resolving the spatial and temporal phytoplankton dynamics in temperate and tropical oceans (see Dickey 1991, Wiggert *et al.* 1994), but developing these approaches for the Southern Ocean has only recently received attention (Arrigo *et al.* 1995, 1997). While these technologies have the potential of defining the time and space variability in phytoplankton pigmentation and biomass, they require knowledge of the physiological state to derive rates of primary productivity. Recent efforts to develop remote sensing approaches to estimate primary production from space utilize algorithms which incorporate phytoplankton physiology (Lewis 1992) and are generally based upon a mechanistic understanding of the photosynthesis-irradiance (P-I) relationship (Morel 1991, Bidigare *et al.* 1992). Most often, optical modelling of phytoplankton productivity has focused on the variability and stability of the light utilization index (Ψ, Falkowski 1981) or water column photosynthetic cross section (Ψ^*, Morel 1978, 1991), which are the ratios of integrated productivity to the product of surface irradiance and areal chlorophyll *a*. Whilst Morel (1978) and Platt (1986) have shown Ψ^* to vary by ± 50% in temperate and tropical oceans, recent work in the Southern Ocean measured higher variability (Claustre *et al.* 1997). This increased variability in Ψ^* was shown to be partially dependent on significant photophysiological differences between algal groups (Claustre *et al.* 1997). These results illustrate the need for further assessment of photophysiological variability in the Southern Ocean and incorporation of this variability into primary productivity models.

As the majority of field studies sample at large spatial intervals, their ability to resolve the mechanisms underlying the observed productivity patterns is limited. This question of resolution also holds true for temporal work. Areas sampled

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* This manuscript is dedicated to Barbara Prézelin for her mentorship and support.

on time scales of weeks to months have shown seasonal changes in phytoplankton biomass (El-Sayed & Weber 1982, Fukuchi *et al.* 1985, Satoh *et al.* 1986, Lipski 1987), species composition (Krebs 1983, Krebs *et al.* 1987, Perrin & Marchant 1987), and productivity (El-Sayed 1971, Whitaker 1982, Domanov & Lipski 1990, Holm-Hansen & Mitchell 1991). However, the time scales of critical processes regulating phytoplankton dynamics (i.e. phytoplankton succession, photoadaptation, productivity, and growth) can range from hours to weeks. Weekly or monthly sampling schemes may, therefore, bias our understanding of the physiological ecology of phytoplankton.

As part of the Palmer Long-Term Ecological Research (LTER) program (Smith *et al.* 1995), nearshore stations were repeatedly sampled every 2–3 days during the spring/summer seasons from 1991–94 to examine the temporal dynamics and regulation of coastal Antarctic phytoplankton communities. Previous analyses of these data have examined the effects of sampling frequency and diel periodicity in photosynthetic parameters on estimating primary production (Moline & Prézelin 1997), the physical factors regulating phytoplankton biomass, productivity and taxonomic composition over seasonal and interannual time scales (Moline & Prézelin 1996, Moline *et al.* 1997) and the photoadaptive response of diatom pigments to rapidly changing light fields during the development of a bloom (Moline in press). Here, 800 photosynthesis-irradiance (P-I) relationships are used to describe the variability and temporal dynamics in photophysiology of natural phytoplankton communities. We derive a simple empirical model from the photosynthetic parameters measured at Palmer Station, apply the model over a large spatial grid along the Antarctic Peninsula to estimate primary productivity, and comment on the strengths and weaknesses of empirical approaches in the Southern Ocean.

Methods and materials

Sampling and Q_{par} measurements

Over the spring/summer period from November 1991, through January 1994, a total of 823 discrete water samples were collected at the LTER stations A–E (Fig. 1) for concurrent determinations of photosynthesis-irradiance relationships and phytoplankton pigmentation. Station A is the shallowest station (~40 m), while station E is a significantly deeper (~280 m) and more exposed station located on the northern edge of the Bismark Strait. Water column sampling was conducted from a Mark V Zodiac and, whenever possible, samples were collected within a few hours of solar noon. Whole water samples were collected in cleaned 5 l GoFlo bottles, transferred to acid-washed dark bottles and returned to Palmer Station within 30 min, where samples remained in a cold room (-2°C) until analysis. In addition to discrete water samples, surface and in-water Q_{par} (400–700 nm) profiles were collected at each station over the three year sampling period. In-water and reference light data were used to calculate the percent Q_{par} at each sampling depth, which was assumed not to change over the course of a day. For additional details of the measurements made and sampling equipment, see Moline & Prézelin (1996).

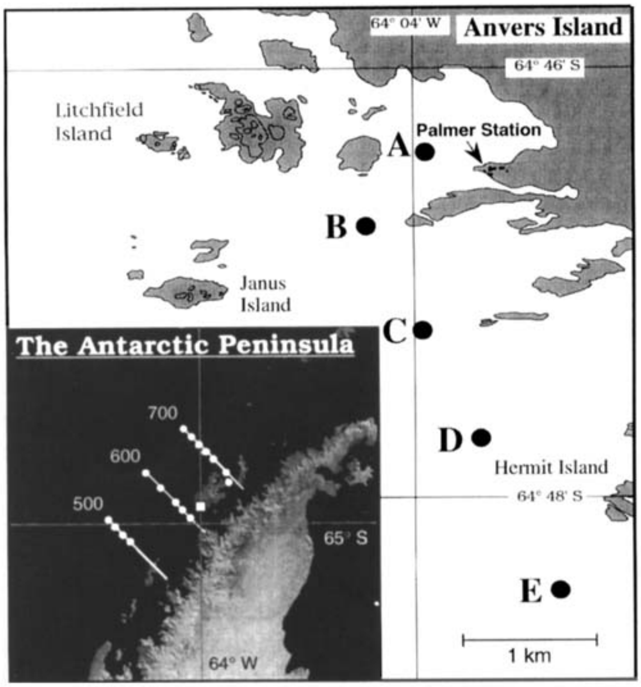

Fig. 1. Location of Long-Term Ecological Research (LTER) program nearshore sampling stations A–E with respect to Palmer Station and (inset; square) the Antarctic Peninsula (visual satellite image; DMSP-11 OLS). Superimposed on the inset are the 16 stations sampled from the LTER offshore sampling grid during November 1991.

Photosynthesis-irradiance relationships

Photosynthesis-irradiance (P-I) relationships were measured from each discrete water sample collected from stations A–E over the three year period. The P-I procedures are detailed in Moline & Prézelin (1996, 1997). In short, each discrete sample was inoculated with radiolabelled $H^{14}CO_3$ and exposed to 25 light levels up to 1500 µmol photons m^{-2} s^{-1}. Incubation times were kept to 90 min and incubation temperatures were controlled to within 0.2°C of *in situ* temperatures.

Non-linear curve fits for the volumetric P-I data were made with the Simplex method of Caceci & Cacheris (1984) using the hyperbolic tangent model of Neale & Richerson (1987). Curve fitting provided independent estimates of the photosynthetic parameters P_{max} (mg C m^{-3} h^{-1}), the light-saturated photosynthetic potential; I_k (µmol photons m^{-2} s^{-1}), an estimate of the minimum irradiance required to saturate photosynthesis and α (mg C $m^{-3}h^{-1}$ (µmol photons m^{-2} $s^{-1})^{-1}$), the light limited photosynthetic efficiency. Chlorophyll *a* (chl *a*) concentrations used to provide biomass-specific parameters (P^B_{max} and α^B) were measured with HPLC methods outlined in Moline & Prézelin (1996, 1997). Estimates of the standard deviations for the P-I parameters were calculated using the procedures described by Zimmerman *et al.* (1987). These standard deviations were used only for quality control of the P-I database. Discrete P-I samples with estimated standard deviations > 25% for P_{max} and/or > 30% for α were eliminated from this study. This reduced the size of the productivity data base from 823 to 800 samples.

Results and discussion

Variability in P_{max} and α

Both mean values and ranges of the photosynthetic parameters varied widely within seasons and between years (Table I). Much of the variability with respect to P_{max} and α was a direct result of the fluctuations in phytoplankton biomass, which were driven by physical processes in this nearshore environment. The influence of glacial meltwater, variable wind speeds, and advective forcing resulted in chl *a* biomass ranging from 0.01–29.21 mg chl *a* m^{-3}. The intermittent presence of ice algae and the seasonal range of incident light levels during sampling also contributed to the observed variability. Details of the factors driving the variability in the biomass and productivity on daily to interannual time scales are described in Moline & Prézelin (1996, 1997) and Moline *et al.* (1997). Figure 2a illustrates the linear relationship between chl *a* and P_{max} ($P_{max} = 2.81 \times \text{chl } a$, $r^2 = 0.75$, $n = 800$, $P < 0.001$). Similar significance between chl *a* and α was also found ($\alpha = 0.032 \times \text{chl } a$, $r^2 = 0.79$, $n = 800$, $P < 0.001$; data not shown).

Chlorophyll *a* normalized P-I parameters were highly variable (Table I) and did not follow either the dynamics in hydrography or the nutrient fields. Differences in P^B_{max} and α^B between stations (Fig. 1) at any given time were minimal. This observed variability is in contrast to the open ocean waters of the Sargasso Sea where P^B_{max} and α^B were found to vary little with season, and the observed variability in the photosynthetic parameters could largely be described by changes in nitrate availability (Platt *et al.* 1992). Our findings agree with other coastal waters where P^B_{max} and α^B can be highly variable and robust empirical models are difficult to derive (Schofield *et al.* 1993). Variability in these Chl-specific photosynthetic parameters for Antarctic water have been associated with changes in both temperature, light environment, nutrients and community composition. In contrast to Tilzer *et al.* (1986), temperature fluctuations from -1.2°C to +2°C in this study (Moline & Prézelin 1996) did not impact photosynthetic parameters. There were, however, decreases in both α^B and P^B_{max} during the mid summer periods each year, timed with the input of glacial meltwater into the area (data not shown). Associated with these periods of low salinity was a transition from diatom dominance to a water column dominated by cryptophytes (Moline & Prézelin 1996). Claustre *et al.* (1997) found a related two-fold decrease in the column photosynthetic cross section (Ψ^*, m^2 g chl*a*) associated with the presence of cryptophytes. These taxonomic differences in P^B_{max} and α^B have also been documented for other polar waters (Rivkin & Putt 1987, Lizotte & Priscu 1992, Cota *et al.* 1994).

There was a weak dependence of P^B_{max} on depth, with the highest P^B_{max} values at the surface (data not shown). This observation has been found in other polar locations (Lizotte & Sullivan 1991). It has been suggested that P^B_{max} is dependent on enzymatic activity, which in turn is regulated by temperature and nutrient availability and does not depend on adaptation to light (see Prézelin *et al.* 1991 for review). However, in addition to photoadaptive changes in pigment concentration and pigment packaging within a cell (Prézelin 1981, Prézelin *et al.* 1991, Richardson *et al.* 1983), assimilation numbers are dependent on the relative efficiency of the dark reaction to the light reaction (Osmond 1994). As in higher plants with shade and sun adaptation, algae exposed to higher irradiances

Table I. Mean values and ranges of chl *a* concentrations (mg m^{-3}), photosynthesis-irradiance (P-I) parameter estimates and derived biomass-specific P-I parameters for the LTER nearshore stations from 1991–94.

	Chl *a*	P_{max}	α	I_k	P^B_{max}	α^B
1991–92						
χ	2.95	8.44	0.101	84.66	2.7	0.035
sd[†]	3.88	13.17	0.142	43.94	2.16	0.025
min	0.08	0.01	0.000	14.89	0.04	0.000
max	29.21	76.95	0.739	389.18	13.17	0.174
n	404	307	307	307	307	307
1992–93						
χ	0.64	1.55	0.022	77.41	2.83	0.040
sd	0.54	1.19	0.018	43.52	1.79	0.026
min	0.01	0.07	0.002	17.31	0.20	0.004
max	4.16	7.79	0.117	373.45	19.98	0.334
n	547	306	306	306	306	306
1993–94						
χ	0.63	1.71	0.026	70.17	3.73	0.059
sd	0.79	1.4	0.023	33.61	1.9	0.033
min	0.03	0.06	0.001	25.81	0.84	0.010
max	4.37	8.34	0.132	289.28	13.59	0.252
n	414	187	187	187	187	187
Combined dataset 1991–94						
χ	1.52	4.23	0.053	78.44	2.99	0.043
sd	2.87	8.86	0.097	41.92	2.00	0.029
min	0.01	0.01	0.000	14.89	0.04	0.000
max	29.21	76.95	0.739	389.18	19.98	0.334
n	1365	800	800	800	800	800

[†] Standard deviations were calculated from the P-I parameter estimates and not from the estimated standard deviations of the parameters from the curve fitting procedures.

Units:
P_{max} - (mgC m^{-3} h^{-1})
α - (mgC m^{-3} h^{-1} (µmol photons m^{-2} s^{-1})$^{-1}$)
I_k - (µmol photons m^{-2} s^{-1})
P^b_{max} - (mgC chl a^{-1} h^{-1})
α^B - (mgC chl a^{-1} h^{-1} (µmol photons m^{-2} s^{-1})$^{-1}$)

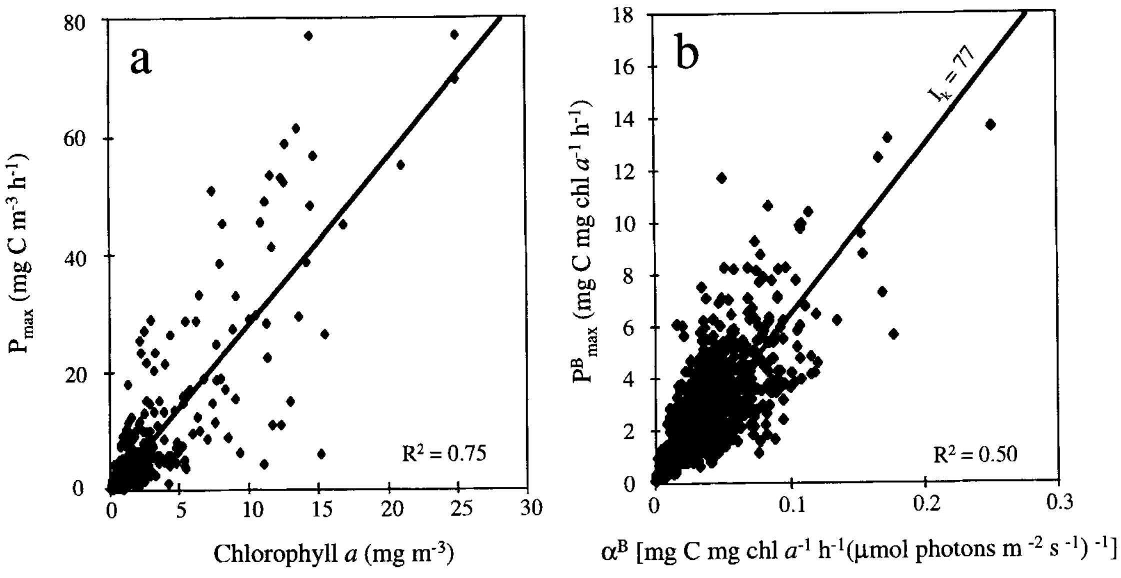

Fig. 2. Relationship between **a.** chl *a* concentration and maximum photosynthetic rate, P_{max}, and **b.** chl *a*-specific light-limited photosynthetic rate, α^B, and P^B_{max} for all data collected from stations A–E from 1991–94 (*n* = 800). Best-fit regression lines were forced through the origin. For **a**, $P_{max} = 2.81$*chl *a*. For **b**, $\alpha^B = 0.013 * P^B_{max}$, equivalent to a minimum irradiance required to saturate photosynthesis, I_k, of 77 µmol photons m^{-2} s^{-1}.

exhibit higher saturated rates of photosynthesis per chl *a* and are less susceptible to photoinhibition (Osmond 1994).

Interestingly, α^B, which displayed some of the highest recorded values for polar phytoplankton (Cota *et al.* 1994), did not show any trend with depth. This parameter has been shown to be light-dependent and should be dependent on vertical mixing rates (Lewis *et al.* 1984, Cullen & Lewis 1988, Cota *et al.* 1994). However, during protracted periods (more than one month) of water column stratification (Moline *et al.* 1997), limited mixing, and photoadaptation of photoprotective pigments to *in situ* irradiance (Moline in press), there were no depth-related differences in α. These results are similar to other work (Lizotte & Priscu 1992, Lizotte & Sullivan 1991, Priscu *et al.* 1987) and support the conclusion that the phytoplankton in this study were generally adapting to irradiances by altering photosynthetic capacity (dark reactions) and not photosynthetic efficiency (light reactions). As phytoplankton adapted to incident light levels, changes in cellular absorption capabilities were offset by inverse changes in the maximum quantum yield of photosynthesis resulting in no depth-dependence in α.

Variability in I_k

Photosynthetic parameters α^B and P^B_{max} significantly covaried (Fig. 2b). Because these parameters are derivations from a shared function, the two are necessarily correlated, not necessarily linearly (Platt & Jassby 1976, Malone & Neale 1981). The regression slope, equivalent to the mean minimum irradiance required to saturate photosynthesis (I_k) for the entire database, was 77 µmol photons m^{-2} s^{-1} with a range in I_k from 14–389 µmol photons m^{-2} s^{-1} (Table I). The variability in I_k was much less than the four orders of magnitude variability in either α^B or P^B_{max} (Table I). Figure 3 illustrates the dynamics of I_k and its relationship to the attenuation of light in the water column at station B over the three year study period. During the development of a large diatom bloom in December 1991, when the water column was stabilized by the input of glacial meltwater (Moline & Prézelin 1996), I_k was high in the surface waters. As the bloom developed, the attenuation of light increased and higher I_k values (> 100µmol photons m^{-2} s^{-1}) were restricted to the surface waters. With the advection of the bloom out of the area in mid January and increased average daily wind speeds (>20 m s^{-1}; Moline *et al.* 1997), high I_k values were found deeper in the water column. In 1992, high winds dominated the season with no measured periods of stratification (Moline & Prézelin 1996) and I_k was generally not stratified with depth. In 1993, the water column was covered by fast ice during the first two months of the season, limiting exposure to high irradiances. I_k values for this period were consistently the lowest measured during the study. With the break up of the ice in early November 1993, there was a dramatic increase in I_k in the surface waters from 20 to >125 µmol photons m^{-2} s^{-1} (Fig. 3). As in 1991, the attenuation increased with increasing biomass (Moline & Prézelin 1996) and high I_k values were restricted to the surface waters. These interannual dynamics illustrate the correspondence between I_k and the *in situ* light levels, which are a function of both surface irradiance and attenuation of light within the water column. Figure 4 shows all I_k values with respect to time of year and as a function of depth. Trends in I_k generally corresponded to changes in incident surface irradiance, with peak values centered around the summer solstice (Fig. 4a). I_k values were also highest in surface waters

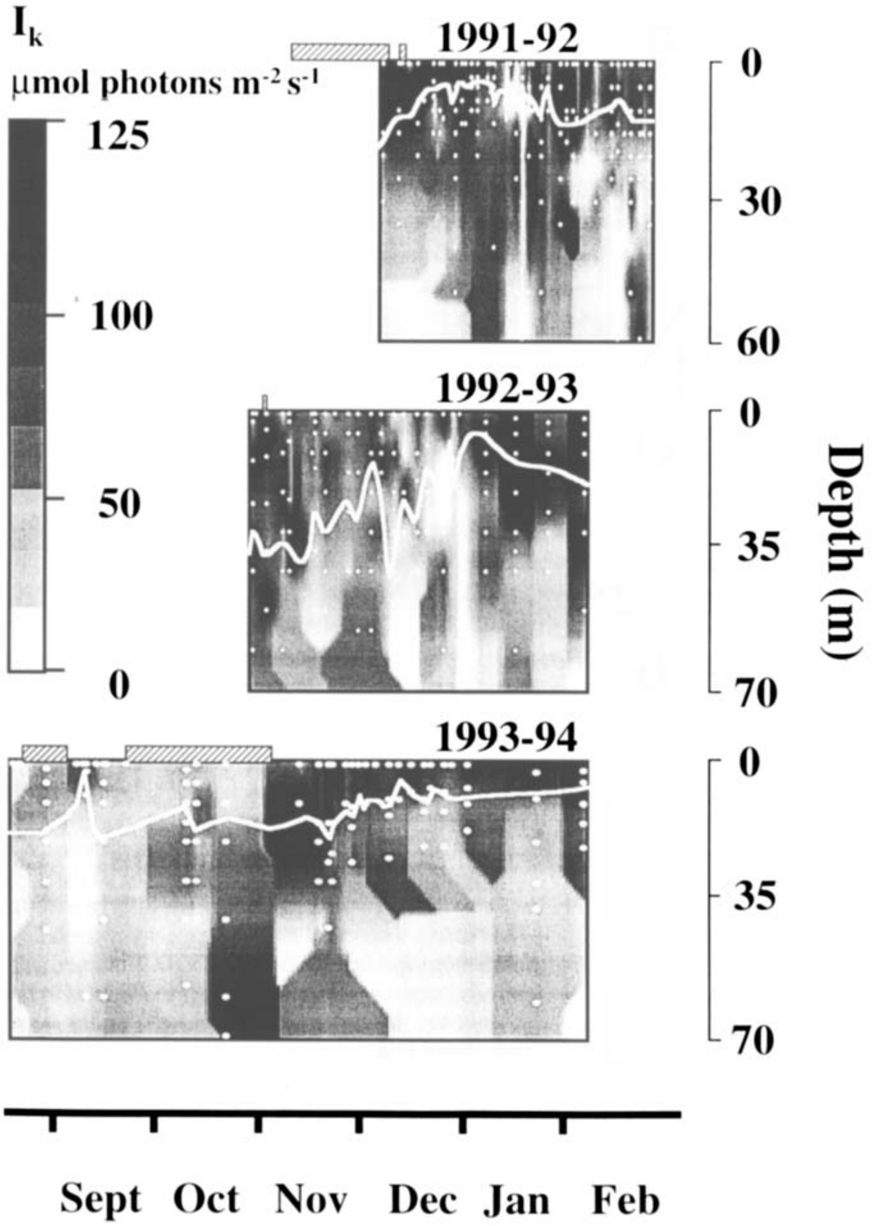

Fig. 3. Seasonal change at station B in the depth distribution of the minimum irradiance required to saturate photosynthesis, I_k, over the three field seasons from 1991–94. The presence of significant pack ice (> 50% coverage) is indicated by hatched bars. The white line represents the depth of the 10% Q_{par} light level. Contours are shown for irradiances ranging from 0–125 µmol photons m^{-2} s^{-1} for comparative purposes between years. Note the difference in the depth scales. The seasonal depth distribution of discrete samples are shown as filled circles. Contours for 1991 (*n* = 179), 1992 (*n* = 134) and 1993 (*n* = 108) were generated using exponential kriging interpolation techniques (Fortner Research LLC Transform, Sterling, VA).

and decreased with increasing depth (Fig. 4b). The response of I_k with depth appeared to be primarily dependent on changes in P^B_{max} and not α^B, which was relatively constant with depth.

The dependence of I_k on *in situ* light fields is consistent with other studies which have shown similar results with respect to depth (Cullen 1991, Schofield *et al.* 1993), advection under the ice (Palmisano *et al.* 1986), and varying light environments (Rivkin & Putt 1987, Lizotte & Sullivan 1991). Few, however, have illustrated the seasonal dependence of I_k. Rivkin & Putt (1988, table I) found a significant increasing trend in I_k for individual diatom species, with I_k increasing from ~27–48 µmol photons m^{-2} s^{-1} from September to early December. These results are similar to results of this study, but were limited to the autumn period and do not show the full seasonal dynamics.

Model formulation

Given the dependence of I_k with both depth and season (Fig. 4), and the significant relationship between P_{max} on chl *a* (Fig. 2a), a simple empirical model was developed to predict instantaneous productivity (P; mg C m^{-3} h^{-1}) at any given depth (z) and time (t). The hyperbolic tangent model of Platt & Gallegos (1980) was used as a basis for the formulation, such that

$$P(z,t) = 2.81 \bullet Chl(z) \bullet \tanh\left(\frac{Q_{par}(z,t)}{I_k(z,JD)}\right) \qquad \text{Eq. 1}$$

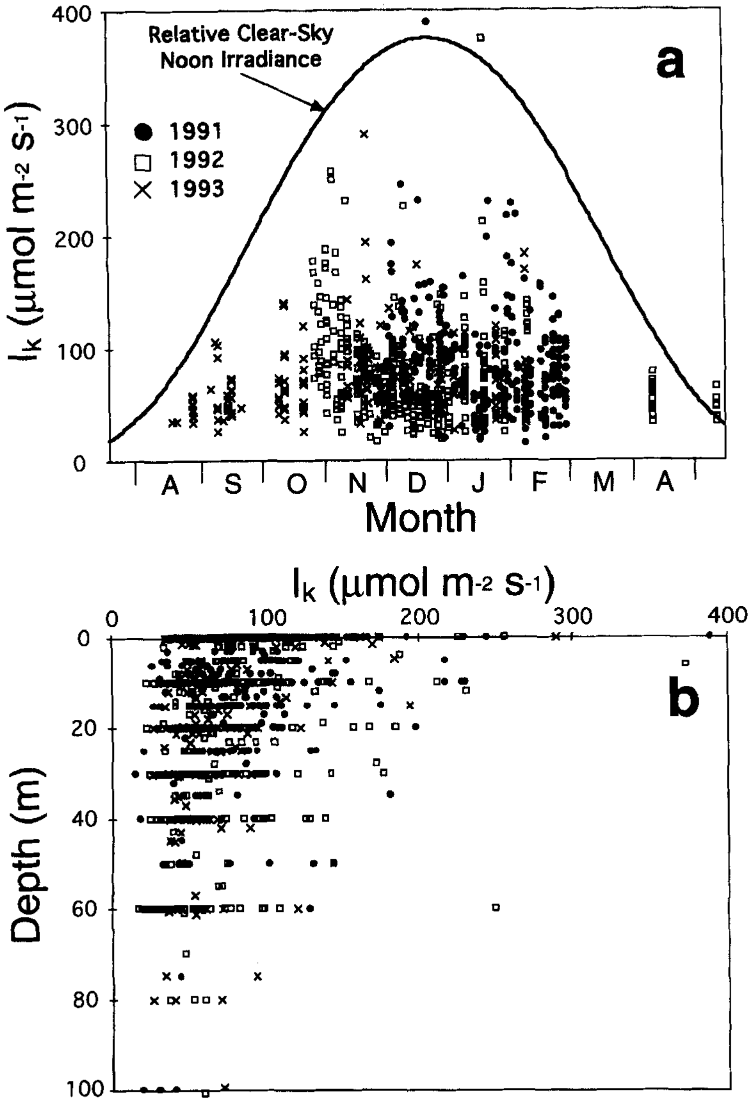

Fig. 4. a. Seasonal change in the minimum irradiance required to saturate photosynthesis, I_k, for all data collected from stations A–E from 1991–94 ($n = 800$). The relative theoretical maximum clear sky noon irradiance modelled for 64°46.45'S (D. Antoine personal communication) according to Morel (1991) is also shown. **b.** I_k as a function of depth for the same data shown in **a**.

where chl *a* is in mg m^{-3}, Q_{par} (µmol photons m^{-2} s^{-1}) is a function of depth and time and I_k is a function of both depth and julian date (JD) according to formulations in Fig. 5. The mean depth distribution of I_k was scaled to the surface I_k values over the time of year to produce an I_k on any day between August and May for any depth ≤100 m (Fig. 5). With the knowledge of the *in situ* light field, chl *a*, and I_k assumed to follow this function of season and depth, primary productivity, P (z, t), was estimated according to Eq. 1. The use of the Platt & Gallegos model was appropriate as no significant photoinhibition was observed within the database (Moline in press).

Independent test of empirical model

The empirical coefficients for the productivity model derived from the three year temporal nearshore dataset at Palmer (Eq. 1), were applied to an independent dataset collected over the LTER mesoscale spatial sampling grid along the Antarctic Peninsula. In November 1991 (one month prior to initiation of the nearshore study), discrete samples were taken at nine depths from 16 LTER offshore grid stations (Waters & Smith 1992) along the west coast of the Antarctic Peninsula (Fig. 1, inset). Details of the profiling systems and sampling equipment are given in Smith *et al.* (1992). P-I relationships were determined using protocols identical to this study.

Chlorophyll *a* concentrations and *in situ* light fields measured over the mesoscale grid in combination with the derived I_k relationships obtained from the three year nearshore database (see Fig. 5) were used in Eq. 1 to estimate primary productivity along the Antarctic Peninsula. Figure 6 shows the relationships between measured and predicted daily carbon fixation at both discrete depths and for the integrated water column. Predicted primary production was within 15 ± 7% of the measured values. If the average I_k from this study (77 µmol photons m^{-2} s^{-1}) was used in place of the I_k function in Fig. 5, the predictive accuracy of the model decreased by 20%, illustrating the utility in incorporating photophysiological variability. One nearshore station, associated with loose pack ice, showed the highest productivity. At this station, predicted

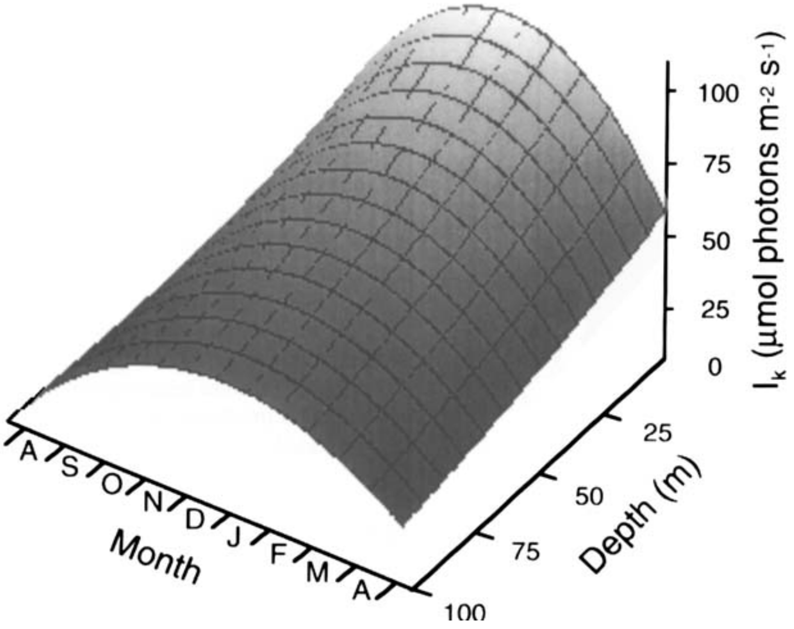

Fig. 5. Surface contour plot of the minimum irradiance required to saturate photosynthesis, I_k, with respect to depth over a period from July–May. Surface was generated by scaling the mean depth distribution of I_k from Fig. 4b to the mean surface I_k values in Fig. 4a using a 3rd order polynomial fit. The mean depth relationship was, $I_k = 87.24*e^{-0.0075z}$, and the surface polynomial was,

$I_k = -0.0032*(JD)^2+2.3558*(JD)-324.7$,

where JD = Julian Date.

daily productivity was significantly higher than measured values, with maximum deviations of 57% and 28% for discrete and integrated estimates, respectively.

Predicted instantaneous depth-integrated productivity rates also agreed well with measured rates for the majority of grid stations (see Fig. 7a). When diel variation in photosynthetic parameters was significant, however, the correspondence between the measured and predicted primary production decreased (see Fig. 7b). At discrete depths, measured P_{max} values were found to vary as much as 60% over the day (Boucher & Prézelin 1996). This resulted in underestimates of predicted instantaneous depth-integrated productivity by as much as 43% at local solar noon (data not shown). In addition to the measured diel variability in P_{max} impacting the predicted productivity, measured I_k values in the upper 10 m were occasionally 150–225 µmol photons m^{-2} s^{-1} or 50–125% higher than I_k values assumed by the function in Fig. 5. To summarize, the model worked well for estimating daily depth-integrated primary productivity in the offshore grid (Fig. 6b). The model was also robust, predicting primary productivity at discrete depths (Fig. 6a) and depth-integrated instantaneous productivity (Fig. 7a). There were, however, higher deviations from the measured values as the model was applied to specific depths at particular times over the day.

Concluding remarks

Increasing the temporal/spatial sampling capabilities for phytoplankton productivity has been a historical focus for biological oceanographers (Jenkins 1937, Ryther & Yentsch 1957, Dubinsky & Berman 1976, Platt & Jassby 1976). Most of these approaches have relied on empirical models, all of

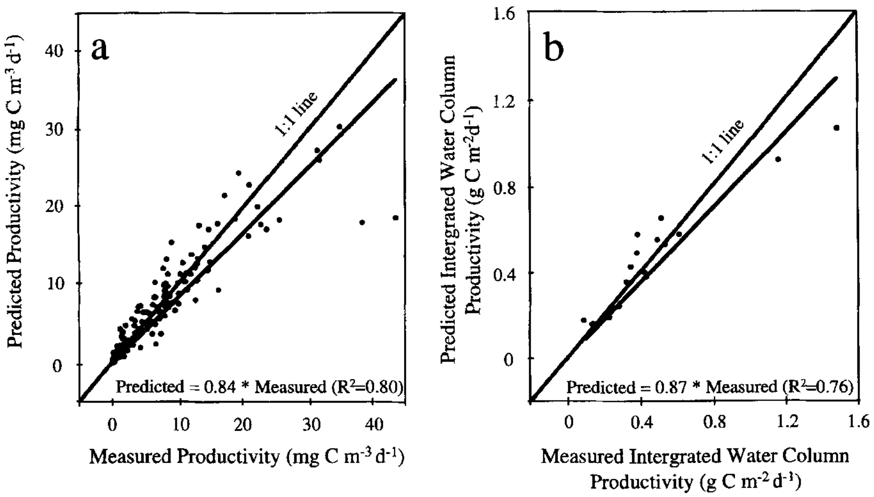

Fig. 6. Relationship between measured and modelled daily primary productivity for **a.** discrete samples (*n* = 144) and **b.** for the integrated water column for samples collected at the 16 stations (see Fig. 1) during November 1991.

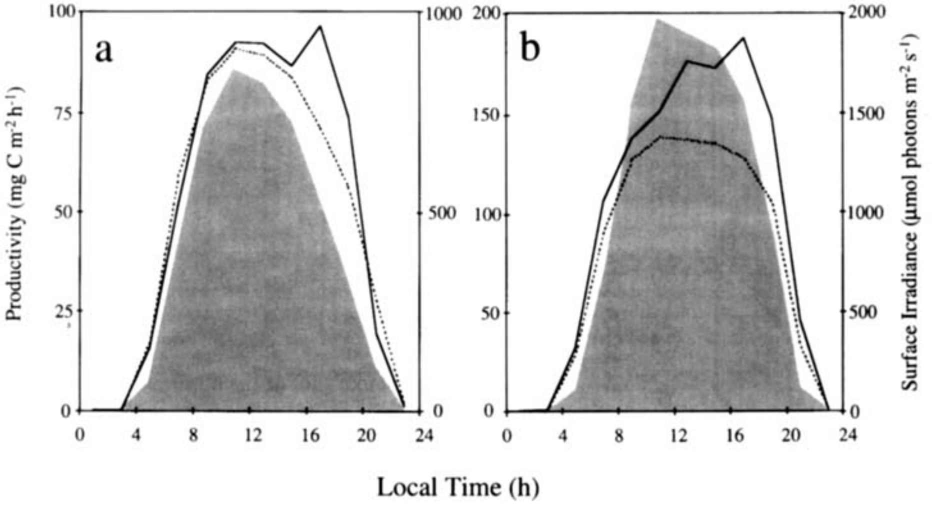

Fig. 7. Measured hourly depth-integrated primary productivity rates (solid line) and modelled rates (dashed lines) using the I_k function in Fig. 5 for **a.** an offshore station (500.160) and **b.** a nearshore station (700.040) from the Long-Term Ecological Research (LTER) November 1991 cruise. Daytime variations in photosynthetic parameters (P_{max}, α and I_k) are incorporated in measured values. Instantaneous irradiance over each day is shown shaded.

which depend on an estimate of phytoplankton biomass. These models can range in complexity by incorporating various environmental (Eppley *et al.* 1985, Balch *et al.* 1989) and physiological variables (Kiefer & Mitchell 1983, Bidigare *et al.* 1987, Platt & Sathyendranath 1988, Morel 1991). Incorporation of physiological variability into productivity models makes them less sensitive to temporal and spatial environmental changes (Platt & Sathyendranath 1988). Application of these models over the relevant space and time scales of phytoplankton dynamics, however, are constrained by biological parameters obtained by satellites (Morel 1978) and/or moorings (Smith *et al.* 1991). These are most often limited to bulk estimates of chl *a*, total particulate absorption, and the *in situ* light environment. The Palmer LTER database is ideal for developing physiologically-based productivity models for the coastal waters of the Southern Ocean, as it is comprehensive and this approach can be independently tested using datasets collected during the LTER cruises along the Antarctic Peninsula.

While empirical approaches can expand the temporal/spatial resolution of phytoplankton productivity in field studies, application of these models should be undertaken cautiously as they ignore biological phenomena known to be important in Antarctic phytoplankton. Numerous studies have demonstrated there is diel variability in photosynthetic parameters (see Prézelin 1992 for review). Our model currently does not incorporate diel variability in photosynthetic parameters and we believe this contributed to much of the error in the model estimates (Figs 6 & 7). The model also ignores phytoplankton community composition, which has been shown to significantly impact the photosynthetic efficiency of a phytoplankton population at a given site (Claustre *et al.* 1997). Furthermore, empirical approaches will be sensitive to nutrient limitation, which can occur during large phytoplankton blooms in Antarctic coastal regions (Perrin *et al.* 1987, Holm-Hansen *et al.* 1989, Moline & Prézelin 1994, McMinn *et al.* 1995, Moline *et al.* 1997). Despite these shortcomings, the model, which incorporates some aspects of phytoplankton photophysiology, accounted for 80% and 76% of the observed variability in both daily productivity at discrete depths and for the integrated water column, respectively. Given this, simple empirical models for phytoplankton productivity may be effective tools for the shelf waters of the Southern Ocean.

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