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Photosynthesis–irradiance responses in the Ross Sea, Antarctica: a meta-analysis

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Abstract

A meta-analysis of photosynthesis/irradiance measurements was completed using data from the Ross Sea, Antarctica. A total of 544 independent measurements were included. P_s^B, the maximum, chlorophyll-specific, irradiance-saturated rate of photosynthesis, averaged $1.07 \pm 0.060 \,\mu g C (\mu g chl)^{-1} h^{-1}$. Light-limited photosynthetic rates (α) averaged 0.03±0.023 µg C (µg chl)⁻¹ h⁻¹ (µmol photons m⁻² s⁻¹)⁻¹. Significant variations in $P_{\rm s}^{\rm B}$ and α were found as a function of season, with spring maximum photosynthetic rates being 59 % greater than those in summer. Similarly, α values were 48% greater in spring. There was no detectable effect of space on the photosynthetic parameters, and temperature and macronutrient (NO₃) concentrations also did not 10 exert a strong influence. However, irradiance, dissolved iron concentrations, and carbon dioxide concentrations when altered under controlled conditions exerted significant influences on photosynthetic parameters. Specifically, reduced irradiance resulted in decreased $P_{\rm s}^{\rm B}$ and α values, whereas reduced iron concentrations were associated with increased P_s^B and α values. Increased CO₂ concentrations also resulted in significantly increased P_s^B and α values. No significant difference was detected between stations dominated by diatoms and those dominated by the haptophyte Phaeocystis antarctica. The meta-analysis generally confirms the photosynthetic rates predicted from global analyses that are based solely on temperature and irradiance availability, but suggests that for more accurate predictions 20 of the productivity of polar systems a more detailed model that includes temporal effects of photosynthetic parameters will be required.

Introduction 1

The relationship of phytoplankton photosynthesis to irradiance is fundamental not only to our understanding of marine productivity, but also in predicting the response of 25 marine systems to climate change and other anthropogenic alterations (Brown and

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Arrigo, 2012; Huot et al., 2013). This is especially true in high-latitude systems, where modifications in ice cover will bring dramatic changes in available irradiance and hence productivity (e.g., Montes-Hugo et al., 2008; D. R. Arrigo et al., 2008a; Smith et al., 2014b), as well as changes in air–sea interactions and food-web dynamics (Smith et al.,

⁵ 2014a). Photosynthesis–irradiance (*P*–*E*) relationships are also essential components of estimating productivity from satellite remote sensing data, as productivity is generally modeled as a function of integrated chlorophyll concentrations, available irradiance, and the *P*–*E* response as a function of temperature (Behrenfeld and Falkowski, 1997; Platt et al., 2007). The temperature–photosynthesis relationship is assumed to be constant below 0°C (Behrenfeld and Falkowski, 1997), despite the fact that substantial oceanographic variability is known in other variables that influence photosynthesis in these waters.

P–E responses are generally described by a relatively simple equation that parameterizes the response as a function of irradiance: $P_{\rm S}^{\rm B}$, the maximum, biomassspecific rate of photosynthesis at saturating irradiances (where B indicates biomassnormalized and S is the maximum irradiance-saturated rate), α , the irradiance-limited, linear portion of the hyperbolic response, and β , the portion of the curve where photosynthesis decreases at high irradiances (photoinhibition) (Platt et al., 1980a). A parameter describing the irradiance at which saturation is initiated, E_k , is derived from the ratio of $P_{\rm S}^{\rm B}$ and α . Chlorophyll *a* concentrations are generally used as an index of biomass. Estimates of photoinhibition are often difficult to obtain and are thought to represent a non-steady state condition (Marra et al., 1985), and measurements often do not result in statistically significant estimates of β (van Hilst and Smith, 2002; Huot

et al., 2013); hence β is often assumed to be zero.

P-E responses from the Southern Ocean have been assessed from a number of regions (e.g., West Antarctic Peninsula: Brightman and Smith, 1989; Moline et al., 1994; Scotia Sea: Tilzer et al., 1986; Ross Sea: van Hilst and Smith, 2002; Robinson et al., 2003; Smyth et al., 2012), but unlike for the Arctic Ocean (Platt et al., 1980b; Huot et al., 2013), no synthesis of photosynthetic responses or their environmental



controls is available. Different investigators also have used slightly different methods, making a comparison more difficult; furthermore, because regions in the Southern Ocean change rapidly, it is challenging to interpret the results of changing P-E responses in the context of spatial and temporal variability of oceanographic conditions.

- ⁵ In general, phytoplankton in the Southern Ocean exhibit low maximum photosynthetic rates (between 1 and $2 \mu g C (\mu g chl)^{-1} h^{-1}$), and E_k values reflect the in situ irradiance environment from which the phytoplankton were sampled. That is, when phytoplankton are sampled from within a deeply mixed surface layer or from under the ice, E_k values are low, reflecting an acclimation to reduced available irradiance. Conversely,
- E_k values generally increase when phytoplankton are sampled from stratified, ice-free environments in summer that are characterized by higher irradiance values.

The Ross Sea is among the best studied areas in the Antarctic, and a great deal is known about its oceanography, productivity, temporal and spatial variability, and food web dynamics (Smith et al., 2012, 2014b). Despite a broad understanding of

- the system's characteristics, a full synthesis of the area's photosynthesis–irradiance relationships is lacking. It is known that the colonial haptophyte *Phaeocystis antarctica* typically blooms in austral spring and reaches high abundance (Tremblay and Smith, 2007; Smith et al., 2014a), and disappears rapidly from the water column after reaching its seasonal maximum (Smith et al., 2011a). Laboratory and field investigations have
- shown that *P. antarctica* is well adapted to growth at low and variable irradiances characteristic of deeply mixed surface layers and under ice (Kroupenske et al., 2009; Arrigo et al., 2010). In contrast, diatoms often bloom after *P. antarctica* is reduced in biomass, but the magnitude of the diatom growth is highly variable among years (Peloquin and Smith, 2007). Diatoms are in general capable of growth at higher photon
- flux densities, characteristic of stratified, summer conditions and in close proximity to melting sea ice (Arrigo et al., 2010). The general distributions of both functional groups suggest that the photosynthetic capacity of each is different and reflects the in situ habitat that each is found. Despite this, van Hilst and Smith (2002) and Robinson et al. (2003) were unable to show a statistically significant difference between the P-E



responses of samples dominated by one functional group or the other. This suggests that the distribution of functional groups may be controlled by factors other than just photosynthesis, despite photophysiological abilities and acclimations to different environments.

- ⁵ This study synthesizes the results from a large number of photosynthesis–irradiance measurements conducted at various times and locations in the Ross Sea. Given the generally predictable pattern of phytoplankton growth in the area (*Phaeocystis antarctica* blooms upon the removal of ice in relatively deeply mixed water columns, and drives the biomass maximum in late spring, which is followed by diatom growth; Smith et al. 2014b) we assessed the photosynthetic responses as a function of season. We
- et al., 2014b), we assessed the photosynthetic responses as a function of season. We also compared the various environmental controls (e.g., temperature, nitrate, and iron) on maximum and irradiance-saturated photosynthetic rates, as well as their relationship to assemblage composition.

2 Methods

15 2.1 Analytical procedures

Samples were collected during a number of cruises, most of which concentrated their sampling in the southern Ross Sea (Fig. 1). The first was IVARS (Interannual Variations in the Ross Sea; Smith et al., 2011a, b), which collected samples during short cruises twice each year, with the first cruise sampling ice-free periods in late December and the second sampling the end of summer (early February). The second

- December and the second sampling the end of summer (early February). The second project was CORSACS (Controls on Ross Sea Algal Community Structure), which had two cruises. The first cruise began was in January 2006, and the second was in November–December 2006 (Sedwick et al., 2011; Smith et al., 2013). Many of the *P–E* results from CORSACS involved experimental manipulations of irradiance, dissolved
- ²⁵ iron and CO₂ concentrations and used trace-metal clean procedures (Feng et al., 2010; Rose et al., 2010). The final project was PRISM (Processes Regulating Iron



Supply at the Mesoscale), which sampled in January–February 2012 (McGillicuddy Jr. et al., 2014; Smith Jr. and Jones, 2014). Figure 1 shows the locations of the stations analyzed for photosynthesis/irradiance relationships. Published measurements from other investigations are included in the meta-analysis (e.g., van Hilst and Smith, 2002; Robinson et al., 2003; Saggiomo et al., 2004; Hiscock, 2004; Smyth et al., 2012).

- Photosynthesis/irradiance (P-E) relationships of phytoplankton were determined by assessing uptake of ¹⁴C-bicarbonate in short incubations (Lewis and Smith, 1983). The largest difference among the different published reports was sample filtration; samples that were not filtered thus included any short-term DOC release (Table 1). Robinson et al. (2003) concluded that filtration of samples dominated by colonial *Phaeocystis antarctica* resulted in an underestimate of photosynthetic rates, but comparison within
- IVARS and CORSACS did not identify this systematic bias (Smith, unpublished). Samples (ca 160 mL) were generally collected from one or two depths (generally those of the 50 and 1 % isolumes) at each station, to which ca. $100 \,\mu$ Ci NaH¹⁴CO₃
- ¹⁵ were added. Incubations were conducted at a constant temperature from the depth of sampling (determined by the CTD cast and maintained by a circulating water bath). Samples were placed in glass scintillation vials in a photosynthetron that provided a wide range of irradiances, but ultraviolet radiation was excluded by the incubation design. Photosynthetically available radiation was modified from the maximum value
- ²⁰ by neutral density screening at irradiances ca. 70% of the full irradiance, and by a combination of neutral and blue screening at lower irradiances (Laws et al., 1990). Darkened vials served as controls. Irradiance was measured for each sample; the total number of irradiances used ranged from 16 to 32. Incubations lasted approximately 2 h. All samples were counted on liquid scintillation counters, and total available inorganic
- ²⁵ ¹⁴C-bicarbonate was assessed by counting aliquots directly in scintillation fluor. While details of the methods of each study varied somewhat, we did not find that the methods introduced error to obscure the overall patterns.



Data were fitted to the rectilinear hyperbolic model of Platt et al. (1980a):

$$P^{\rm B} = P_{\rm s}^{\rm B} \left[1 - e^{-\alpha E/P_{\rm s}^{\rm B}} \right] \tag{1}$$

where P^{B} = the rate of photosynthesis normalized to chlorophyll а $(mg C (mg chl a)^{-1} h^{-1}), P_s^B =$ the maximum, irradiance-saturated rate of photosynthesis in the absence of photoinhibition, α = the initial, light-limited, linear photosynthetic rate (mg C (mg chl a)⁻¹ h⁻¹ (µmol photons m⁻² s⁻¹)), and E =irradiance (µmol photons m⁻² s⁻¹). Some of the published analyses included β , the photoinhibition parameter, but for consistency these were omitted in this meta-analysis, since β appears to represent a non-equilibrium conditions and in our samples was not consistently evident (Denman and Marra, 1986; MacIntyre et al., 2002). The 10 derived parameter E_{k} (the irradiance at which photosynthesis becomes saturated) is calculated by:

 $E_k = P_s^{\rm B} / \alpha$

 E_k provides a measure by which the acclimation to irradiance can be compared. If the observations did not result in a significant determination of both α and P_{s}^{B} (p < 0.05), 15 then the entire sample was omitted from analysis.

Chlorophyll a concentrations were analyzed by fluorometry (JGOFS, 1996) on independent samples collected from the same depth. Nutrient (NO₃, NO₂, PO₄, $Si(OH)_4$, NH_4) analyses were performed at sea on a Lachat QuickChem Autanalyzer using standard automated techniques. Mixed layer depths were determined from 20 density profiles determined from CTD casts using a change in density of 0.01 kg m⁻³ from a stable surface value (Thomson and Fine, 2003; Smith et al., 2013). Spring and summer were arbitrarily delineated on 1 January. Seawater samples for dissolved iron analysis were collected in custom-modified 5-L Teflon-lined, external-closure Niskin-

X samplers (General Oceanics Inc.) or 10-L teflon-lined GO-FLO samplers, all of 25 which were deployed on a non-metallic line (Sedwick et al., 2011). Filtered samples

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were acidified to pH 1.7 with ultrapure hydrochloric acid and stored for at least 24 h prior to the analysis of dissolved iron. Dissolved iron was determined by flow injection analysis with colorimetric detection after in-line pre-concentration on resin-immobilized 8-hydroxyquinoline (Sedwick et al., 2008).

5 2.2 Statistical analyses

All responses were fit to a 2-parameter exponential increase to maxima in SigmaPlot 12.3, which provided estimates of P_s^B and α and their significance, as determined by a *t* test. An a priori limit of significance was set as p < 0.05. Data were tested for normality and homogeneity of variance, and ANOVAs were performed using R (v2.13.2).

3 Results

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3.1 IVARS, CORSACS and PRISM photosynthesis/irradiance determinations

P–E determinations in IVARS were conducted during the peak of the spring bloom (generally late December) and at the end of summer (early February) (Smith et al., 2011a). Ice concentrations were < 15% at all stations. Average α , P_s^B and E_k values for December and February were 0.040 ± 0.035 and 0.53 ± 0.035 µgC (µgchl)⁻¹ h⁻¹ (µmol photons m⁻² s⁻¹)⁻¹, 1.25 ± 0.75 and 0.68 ± 0.34 µgC (µgchl)⁻¹ h⁻¹, and 41.9 ± 28.7 and 23.3 ± 30.2 µmol photons m⁻² s⁻¹, respectively (Table 2). P_s^B values of the two seasons were significantly different (p < 0.05), but α and E_k values were not.

²⁰ CORSACS measurements were largely conducted as part of experiments that manipulated irradiance (7 and 33 % of surface irradiance), iron concentrations (ambient and +1 nM), and CO₂ concentrations (380 and 750 μ atm) (Feng et al., 2010). Natural populations were used as inocula in semi-continuous cultures (Hutchins et al., 2003), and *P*–*E* determinations were made through time on all treatments to assess



the impact of each variable (and their interactions) on short-term photosynthetic responses. Irradiance variations generated changes in P_s^B , α and E_k values, which increased significantly (p < 0.05) at low irradiances (Fig. 2). Increased CO_2 concentrations also resulted in significantly (p < 0.05) increased α and P_s^B values, although little net change was noted in E_k values. Finally, increased iron concentrations did not impact either α or P_s^B values significantly in these experiments (Fig. 2). P_s^B values were greater than those representing sub-optimal, in situ conditions such as in IVARS and PRISM.

PRISM samples investigated the broad spatial patterns of P-E responses (Table 2). The mean α and P_s^B values were $0.035 \pm 0.020 \ (\mu g C (\mu g chl)^{-1} h^{-1} (\mu mol photons m^{-2} s^{-1})^{-1})$ and $1.14 \pm 0.50 \ \mu g C (\mu g chl)^{-1} h^{-1}$, respectively. The average E_k value was $52.2 \pm 48.1 \ \mu mol photons m^{-2} s^{-1}$. There was no significant difference between PRISM P-E parameters and those collected during IVARS (December, February, or the total data set), and again no spatial pattern was observed. There was no significant difference in the combined IVARS, PRISM and CORSACS field data when the depth of sampling (50 vs. 1% of surface irradiance) in any photosynthetic parameter.

Iron and nitrate concentrations were measured at a number of stations where P-E measurements were conducted during PRISM (McGillicuddy Jr. et al., 2014). Dissolved

- ²⁰ Fe levels ranged from 0.066 to 0.69 nM, and nitrate ranged from 9.05 to 30.6 μ M. No significant difference in the mean α , P_s^B or E_k values was observed between the stations with nitrate concentrations less than 20 μ M and those with concentrations > 20 μ M (Table 3). In contrast, at stations with Fe concentrations below and above 0.10 nM (a level that approximates the onset of Fe limitation in Antarctic phytoplankton;
- ²⁵ Timmermans et al., 2004), P_s^B values were significantly (p < 0.01) greater (1.58 ± 0.55 vs. 0.95 ± 0.45) at lower iron concentrations (Table 3). α and E_k values, however, were not significantly different, suggesting that iron largely impacts irradiance-saturated photosynthetic rates, which in turn are largely controlled by carbon fixation processes.



3.2 Comparison with previous *P*–*E* determinations

Because P-E determinations have been conducted during the past two decades with a similar methodology, we merged all data from the Ross Sea to assess the average photosynthetic response by season (Table 4). There is a significant difference between austral spring and summer averages for P_s^B and α values, with spring having a greater P_s^B (1.37 vs. 0.86) and α values (0.034 vs. 0.023). However, no significant difference was observed between spring and summer E_k values. Values of α and P_s^B were correlated ($P_s^B = 10.91\alpha + 0.070$; $R^2 = 0.383$; p < 0.001; Fig. 3), as has been found previously (van Hilst and Smith, 2002; Behrenfeld et al., 2004), but the large amount of variability in the relationship suggests that each is being influenced by numerous independent factors as well. No interannual temporal trend was obvious, and interannual variability was substantial (Table 4). The overall P_s^B , α , and E_k averages for all samples (n = 544) equaled 1.07 ± 0.77 µgC (µg chl)⁻¹ h⁻¹, 0.030 ± 0.023 µgC (µg chl)⁻¹ h⁻¹ (µmol photons m⁻² s⁻¹)⁻¹ and 43.7 ± 26.9 µmol photons m⁻² s⁻¹.

3.3 Controls by environmental factors and phytoplankton composition

photosynthesis is largely independent of these environmental controls.

We tested for the effects of nitrate and temperature from the depth of sampling on *P*-*E* parameters from all cruises. The data were arbitrarily divided above and below 20 µMNO₃ and above and below 0°C, and the *P*-*E* parameters compared.
Nitrate concentrations at the time of sampling ranged from 9.5–31.0 µM, and 54 *P*-*E* measurements were conducted with NO₃ concentrations greater than 20 µM. 58 analyses were conducted with NO₃ levels less than 20 µM. Sample temperatures ranged from -1.6 to 2.58 °C; 58 of the 102 *P*-*E* determinations were below 0°C, and 44 were above. No significant differences were noted for any of the three photosynthetic
parameters within the nitrate or temperature data subsets, suggesting that short-term



The two dominant functional groups in the Ross Sea, diatoms and haptophytes (largely *Phaeocystis antarctica*), have different temporal and spatial distributions, with *P. antarctica* generally dominating in spring in water columns with deeper vertical mixing, and diatoms dominating in more stratified, summer conditions (Smith et al., 2014a). *P. antarctica* largely occurs in cold waters (< 0 °C) and is responsible for the spring reduction in micro- and macronutrients (Liu and Smith Jr., 2012). To investigate if the two taxa have different photosynthesis–irradiance responses, we selected 40 stations that were identified by chemical or microscopic means as being overwhelmingly dominated by one of these groups, and assessed their *P*–*E* characteristics (Table 5). We found no statistical difference between the two groups with respect to α , P_s^B or E_k values.

4 Discussion

4.1 Overall patterns of photosynthetic parameters

One major finding of this meta-analysis is that the average maximum, light-saturated rate of photosynthesis equals 1.07 μgC (μgchl)⁻¹ h⁻¹ (Table 4). This is similar to the P^B_{opt} value determined from Behrenfeld and Falkowski's (1997) polynomial equation (1.29 μgC (μgchl)⁻¹ h⁻¹) at 0 °C, despite the difference between P^B_{opt} and P^B_s as well as the range of temperatures at which the *P*–*E* determinations were conducted. It therefore strongly reinforces the validity of using their equation to estimate maximum photosynthetic rates and primary productivity within the waters of the Ross Sea, and presumably the entire Southern Ocean. This average can also be used in other bio-optical models of production to constrain the rates of carbon fixation over broad areas (e.g., K. R. Arrigo et al., 2003, 2008). However, given the seasonal variability observed, more detailed models that incorporate seasonal and environmental impacts
²⁵ may require inclusion of other oceanographic variables to more accurately predict production.



We found relatively minor spatial differences in photosynthetic parameters, but significant seasonal differences. Specifically, α and P_s^B values of the entire metaanalysis data set were significantly greater during spring than summer (both p < 0.001), which is consistent with the large seasonal changes found in nearly all biological variables. The macro-environment of the Ross Sea continental shelf changes markedly from spring to summer, with increased temperatures and vertical stratification, decreased macro- and micronutrient concentrations, and an altered assemblage composition (Smith et al., 2012). As such, it is not surprising that the P-E parameters also changed. Clearly the growth environment usually found in summer in the Ross Sea is not favorable to high photosynthetic rates, a conclusion that have been consistently corroborated by direct measurements of productivity (e.g., Long et al., 2011). It was impossible to accurately assess interannual variations, given the relatively

low numbers of samples in some years, but in view of the large variations observed from 1995 through 2010, any interannual trend is likely obscured by the substantial seasonal variability.

4.2 Controls of photosynthesis–irradiance parameters

While not all data sets had complete macro- and micronutrient data available for inclusion, we were unable to detect any controls of short-term photosynthetic rates by temperature or nitrate. The temperature range was modest (ca. 4 °C), so the direct impact may have been limited and obscured by other factors. Liu and Smith Jr. (2012) demonstrated that the environmental factor that had the strongest impact on phytoplankton biomass was temperature. They found that that diatoms were more likely to be found in waters above 0 °C, and in sub-zero waters assemblage composition was more often dominated by *Phaeocystis antarctica*. Waters with temperatures less
than 0 °C also tend to have deeper mixed layers, which also favor the growth of *P. antarctica* (Tremblay and Smith, 2007). Nitrate concentrations varied more widely (from 9.3 to 31 µM), but still remained above those thought to limit nitrogen uptake (Cochlan et al., 2002). Reduced iron, concentrations, however, resulted in lower



 $P_{\rm s}^{\rm B}$ values, despite the relatively limited number of measurements at concentrations greater than 0.1 nM. In contrast, we did not detect a change at the end of the controlled experiments (CORSACS) in which iron concentrations were measured, but all but one of those experiments had dissolved Fe concentrations > 0.13 nM (Feng et al., 2010), concentrations which are substantially greater than those found in situ (Sedwick et al., 2011). Iron can influence growth rates of Antarctic diatoms (Timmermans et al., 2004; Mosby and Smith, 2014), but growth rate responses are integrated over many days, whereas P-E responses are not immediately influenced by iron additions (Hiscock et al., 2008). Furthermore, it is tempting to suggest that the reduced summer P-E parameters may have resulted from iron limitation, but iron 10 availability is rarely determined in parallel with P-E parameters. We suggest that the impacts of iron we observed – significantly reduced P_s^{B} values – were mediated by a long-term assemblage response rather than on short-term photosynthesis rates. Iron limitation can impact chlorophyll synthesis (in a manner similar to irradiance), and under co-limitation by iron and irradiance chlorophyll levels can be elevated (Sunda 15 and Huntsman, 1997), which would result in lowered P_s^B values. Determination of the exact cause of the iron effect on $P_{\rm s}^{\rm B}$, however, is impossible with the present data set.

The CORSACS experiments showed a clear impact of both irradiance and (CO_2) on photosynthetic responses. Under low irradiance conditions (ca. 7 % that of surface irradiance), there was an increase in the light-limited rates of photosynthesis (α) and light-saturated (P_s^B) values (Fig. 2). Low irradiance conditions often generate increased chlorophyll concentrations per cell, but can also generate increased photosynthetic efficiencies (via changes in photosynthetic units), which can result in elevation of both parameters (Prézelin, 1981; Dubinsky and Stambler, 2009). P_s^B reflects the light-saturated rates, and presumably is set by the amount of carbon that can be reduced by the cells, which in turn is thought to be limited by the amount of chemical energy generated by the cells' photosystems. Increasing carbon dioxide concentrations resulted in a marked and significant increase in P_s^B and α values, reinforcing the classical view of the limitation of short-term photosynthesis by carbon availability under



high irradiance conditions. Enhanced α values may reflect the interaction between lightlimited and light-saturated rates described by Behrenfeld et al. (2004). Interestingly, increased CO₂ levels had little impact on phytoplankton composition (Tortell et al., 2002), and independent measurements suggest that most Antarctic phytoplankton have a relatively broad capability to use a wide range of carbon dioxide concentrations

- (Tortell et al., 2006). Although it is tempting to suggest that future increases in oceanic CO_2 concentrations might increase maximum photosynthetic rates, such changes need to be assessed using long-term experiments that allow for acclimation and adaptation over many generations (e.g., Lohbeck et al., 2012).
- ¹⁰ The influence of phytoplankton composition was insignificant (Table 5). This is consistent with the previous results of van Hilst and Smith (2002) using a less extensive data set, but in contrast to the extensive laboratory results of Arrigo et al. (2010), who found that α and P_s^B values of *P. antarctica* grown at constant irradiances (from 5 to 125 µmol photons m⁻² s⁻¹) and saturating nutrients were always greater ¹⁵ than those of the diatom *Fragilariopsis cylindrus*. The diatom had low P_s^B (from 0.46 to 0.54 µg C (µg chl)⁻¹ h⁻¹) and α values (from 0.014 to 0.043 (µg C (µg chl)⁻¹ h⁻¹) (µmol photons m⁻² s⁻¹)⁻¹)) when compared to those of the haptophyte (from 1.4 to 6.4, and from 0.038 to 0.11, respectively). The diatom parameters determined in culture were lower than our data subset, and the haptophyte values higher; these differences likely reflect the parameters of the individual species cultured and/or the influence of constant growth conditions. The in situ data also had substantial variability, which likely resulted from the environmental conditions that allowed one particular functional

group to dominate. Appearance of taxa in situ reflects a long-term process involving both growth and losses, and both field and laboratory data suggest that the P-Eparameters of the dominant forms in spring and summer reflect the importance of selected environmental features (irradiance, iron) on their long-term success with the water column.

In summary, the broad photosynthetic responses of Ross Sea phytoplankton are consistent with the patterns used in global production estimates from satellite biomass



estimates. However, significant seasonal differences occur, as do differences driven by irradiance, iron concentrations, and carbon dioxide levels. Such significant differences may need to be included in regional models of productivity and carbon flux. While these results may suggest that future changes in photosynthetic capacity and production in the Ross Sea as a result of climate change could be substantial, confirmation of this

awaits future analyses of these parameters.

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Table 1. Listing of photosynthesis–irradiance responses used in this meta-analysis. N = number of determinations; V_{inc} = volume incubated; F/NF = filtered/not filtered.

Cruise Name	Dates of Sampling	Ν	V _{inc} (mL)	F/NF	Reference
RSP ²	16 Nov 1994–30 Nov 1995	10	2	NF	van Hilst and Smith (2002)
	21 Dec 1995–13 Jan 1996	54	2	NF	
JGOFS	16 Nov 1996–11 Dec 2006	70	10	F	Hiscock (2004)
	12 Jan 1997–8 Feb 2007	87	10	F	
	17 Apr 2007–26 Apr 2007	5	10	F	
ROSSMIZ	11 Jan 1996–10 Feb 1996	72	50	F	Saggiomo et al. (2002)
ROAVERRS	10 Nov 1998–10 Dec 1998	15	2	F*	Robinson et al. (2003)
NBP05-08	8 Nov 2005–30 Nov 2005	10	5	NF	Smyth et al. (2012)
IVARS 1	19 Dec 2001–2 Feb 2002	6	2	NF	This report
IVARS 3	26 Dec 2003–6 Feb 2004	9	2	NF	This report
IVARS 4	19 Dec 2004–31 Jan 2005	16	2	NF	This report
IVARS 5	26 Dec 2005–2 Jan 2006	7	2	NF	This report
CORSACS 1	27 Dec 2005–31 Jan 2006	83	2	NF	This report
CORSACS 2	16 Nov 2006–11 Dec 2006	23	2	NF	This report
PRISM	8 Jan 2012–2 Feb 2012	77	2	NF	This report

* Gravity filtration.

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Table 2. Mean, standard deviation, and range of photosynthesis-irradiance pa	arameters c	
determined during IVARS and PRISM cruises.		100.00

Year	α	P _s ^B	E _k
	$(\mu g C (\mu g chl)^{-1} h^{-1}$	$(\mu g C (\mu g chl)^{-1} h^{-1})$	$(\mu mol photons m^{-2} s^{-1})$
	(µmolphotonsm ⁻ s ⁻) ⁻)		
2001	0.060 ± 0.015 (4)	2.33 ± 0.605	42.0 ± 18.1
2002	0.0077 (1)	0.845	110
2002	0.033 ± 0.012 (4)	0.972 ± 0.319	34.4 ± 23.6
2003	0.019 ± 0.0046 (5)	0.611 ± 0.356	36.9 ± 28.0
2004	0.067 ± 0.047 (4)	0.800 ± 0.57	16.3 ± 15.3
2004	0.022 ± 0.0087 (10)	1.10 ± 0.418	61.5 ± 38.3
2005	0.051 ± 0.023 (6)	0.577 ± 0.048	13.6 ± 6.13
2005	0.070 ± 0.055 (7)	1.61 ± 0.80	27.6 ± 11.2
_	0.040 ± 0.035 (27)	1.25 ± 0.72	41.9 ± 28.7
_	0.053 ± 0.035 (11)	0.68 ± 0.34	23.3 ± 30.2
2010	0.035 ± 0.020 (77)	1.13 ± 0.500	52.2 ± 48.1
	Year 2001 2002 2002 2003 2004 2004 2004 2005 2005 2010	Year α $(\mu g C (\mu g chl)^{-1} h^{-1} (\mu mol photons m^{-2} s^{-1})^{-1})$ 2001 0.060 \pm 0.015 (4) 2002 0.033 \pm 0.012 (4) 2002 0.033 \pm 0.012 (4) 2003 0.019 \pm 0.0046 (5) 2004 0.067 \pm 0.047 (4) 2004 0.022 \pm 0.0087 (10) 2005 0.051 \pm 0.023 (6) 2005 0.070 \pm 0.055 (7) $-$ 0.040 \pm 0.035 (27) $-$ 0.053 \pm 0.035 (11) 2010 0.035 \pm 0.020 (77)	Year α P_s^B $(\mu g C (\mu g chl)^{-1} h^{-1})$ $(\mu mol photons m^{-2} s^{-1})^{-1})$ $(\mu g C (\mu g chl)^{-1} h^{-1})$ $(\mu g c (\mu g chl)^{-1} h^{-1})$ 20010.060 \pm 0.015 (4)2.33 \pm 0.60520020.0077 (1)0.84520020.033 \pm 0.012 (4)0.972 \pm 0.31920030.019 \pm 0.0046 (5)0.611 \pm 0.35620040.067 \pm 0.047 (4)0.800 \pm 0.5720040.022 \pm 0.0087 (10)1.10 \pm 0.41820050.051 \pm 0.023 (6)0.577 \pm 0.04820050.070 \pm 0.055 (7)1.61 \pm 0.80-0.040 \pm 0.035 (27)1.25 \pm 0.72-0.053 \pm 0.020 (77)1.13 \pm 0.500



Table 3. Comparison of PRISM photosynthetic parameters as a function of nitrate and temperature (means and standard deviations). Range of data listed in parentheses. The available data were divided into those stations that had nitrate concentrations above and below 20 μ M, and sea temperatures above and below 0 °C. No significant differences occurred between low- vs. high-nutrient and low- vs. high-temperature parameters.

Variable Group	N	α (µg C (µg chl) ⁻¹ h ⁻¹ (µmol photons m ⁻² s ⁻¹) ⁻¹)	$P_{\rm s}^{\rm B}$ (µg C (µg chl) ⁻¹ h ⁻¹)	E_k (µmol photons m ⁻² s ⁻¹)
[NO ₃] < 20 μM [NO ₃] > 20 μM <i>T</i> > 0 °C <i>T</i> < 0 °C	58 56 44 58	$\begin{array}{c} 0.035 \pm 0.020 \; (0.012 - 0.095) \\ 0.043 \pm 0.039 \; (0.0077 - 0.183) \\ 0.040 \pm 0.036 \; (0.015 - 0.183) \\ 0.032 \pm 0.021 \; (0.011 - 0.095) \end{array}$	$1.15 \pm 0.64 (0.29-3.09)$ $1.16 \pm 0.58 (0.21-2.79)$ $1.15 \pm 0.66 (0.29-3.09)$ $1.15 \pm 0.53 (0.21-2.66)$	$43.3 \pm 34.2 (6.58-193) 48.0 \pm 47.1 (3.79-238) 44.6 \pm 39.6 (6.58-193) 49.7 \pm 44.4 (7.75-238)$



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Table 4. Seasonal comparison of photosynthetic parameters from the Ross Sea.

Season	$P_{\rm s}^{\rm B}$	α	E_k	Ν	Reference
	$(\mu g C (\mu g chl)^{-1} h^{-1})$	$(\mu g C (\mu g chl)^{-1} h^{-1}$	$(\mu mol photons m^{-2} s^{-1})$		
		$(\mu mol photons m^{-2} s^{-1})^{-1})$			
Spring	1.77 ± 0.97	0.047 ± 0.023	37.0 ± 7.50	37	van Hilst and Smith
Summer	2.48 ± 1.29	0.087 ± 0.043	31.0 ± 16.0	31	(2002)
Spring	1.22 ± 0.54	0.036 ± 0.015	37.1 ± 13.4	70	Hiscock (2004)
Summer	0.64 ± 0.26	0.016 ± 0.0068	42.9 ± 18.4	98	
Autumn	0.70 ± 0.13	0.040 ± 0.017	20.7 ± 9.00	5	
Summer	1.34 ± 0.39	0.073 ± 0.088	23 ± 8	51	Saggiomo et al. (2002)
Spring	1.78 ± 0.68	0.020 ± 00043	88.7 ± 23.1	15	Robinson et al. (2003)
Spring ^b	2.11 ± 0.48	0.072 ± 0.027	31.1 ± 8.04	10	Smyth et al. (2012)
Spring	1.25 ± 0.72	0.040 ± 0.035	41.9 ± 28.7	27	IVARS: This report
Summer	0.68 ± 0.34	0.053 ± 0.035	23.3 ± 30.2	11	IVARS: This report
Summer	1.13 ± 0.500	0.035 ± 0.020	52.2 ± 48.1	77	PRISM: This report
Mean spring ^a	1.37 ± 0.63	0.034 ± 0.024	44.0 ± 25.2	159	_
Mean summer ^a	0.86 ± 0.45	0.023 ± 0.018	43.4 ± 28.3	268	-
Overall mean ^a	1.07 ± 0.60	0.030 ± 0.023	43.7 ± 26.9	417	-

 a Weighted mean of all samples. b α and E_k values calculated from data using factor described in original paper.

Table 5. Comparison of the mean photosynthesis–irradiance parameters as a function of phytoplankton composition (means and standard deviations). Dominance was determined by either chemical or microscopic analyses. Twenty stations from the entire data set were selected for inclusion in this comparison. No significant difference in any photosynthetic parameter was detected.

Functional Group	$P_{\rm s}^{\rm B}$	α	E_k
	$(\mu g C (\mu g chl)^{-1} h^{-1})$	$(\mu g C (\mu g chl)^{-1} h^{-1}$	$(\mu mol photons m^{-2} s^{-1})$
		$(\mu mol photons m^{-2} s^{-1})^{-1})$	
Phaeocystis antarctica	1.36 ± 0.76	0.067 ± 0.060	33.2 ± 22.7
Diatoms	1.11 ± 0.63	0.050 ± 0.045	32.0 ± 18.7





Figure 1. Map showing the location of the stations were photosynthesis-irradiance determinations were conducted.

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Figure 2. Photosynthesis–irradiance parameters determined from experimental manipulations of natural populations. Samples had either high or low (33 or 7% of surface value) irradiance, high or low (750 or 380 ppm) CO_2 , and high or low (+1 nM and ambient; ca. 0.1 nm) iron concentrations. Asterisks indicate a significant difference between the high and low treatments within each variable.







