

TO: Dr. Carol Robinson, Editor
Biogeosciences

FROM: Dr. Walker Smith

DATE: April 21, 2015

RE: Manuscript bg-2014-573 revision

Within this electronic resubmission you will find a) a revised manuscript that has answered all comments, and b) a list of changes that details the responses to all reviews. At the end of the comment section (this pdf) you will find the version of the manuscript with the changes made in response to the last review.

I want to apologize for the often poor construction of this manuscript. As senior author, I cannot offer any compelling "excuse", but realize that the previous versions were far too filled with errors and mis-statements. We appreciate the thoroughness of all reviewers, and apologize for the errors that led to confusion. We believe the manuscript is now substantially improved and hope you concur.

Although the manuscript has been improved, it still exhibits two important inconsistencies related to the effects of irradiance and iron. These imprecisions had already been identified in some way by the three reviewers in their previous reviews.

Concerning light, the figure 2 clearly shows that P_m^B was significantly lower at low irradiance than at high irradiance. This figure also shows the opposite response for α^B , which was significantly higher at low irradiance than at high irradiance. However, the manuscript comment the results in this figure 2 on page 10 (lines 204-206) writing “Irradiance variations generated changes in P_m^B , α^B and E_k values, **which increased significantly ($p < 0.05$) at the low and constant irradiances** (Fig. 2)”. Surprising, the contrary was written in the abstract, where is possible to read (lines 33-35) “Specifically, **reduced irradiance resulted in decreased P_m^B and α^B values**, whereas reduced iron...” but the effect of light in the CORSACS experiments is discussed (page 16, lines 342-350) assuming the opposite response, increases in both P_m^B and α^B and invoking Fig. 2.

This comment is absolutely correct. As the abstract now says, reduced irradiance resulted in decreased P_m^B and increased α^B values, which is shown in Figure 2. The description near line 205 was incorrect and resulted from a carry-over from a previous version. Not excusable, and we greatly appreciate bringing that error to our attention.

About iron, table 3 shows significant higher values of P_m^B in waters with iron concentrations < 0.1 nM during PRISM cruise and this was the only significant difference in photosynthetic variables related to iron variability. However, in the abstract is possible to read “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_m^B and α^B values, **whereas reduced iron concentrations were associated with increased P_m^B and α^B values**”. But altered controlled conditions are only shown in Fig. 2, where the effect of iron is not significant. In the discussion it is also possible to read (page 15, lines 325 and 326) “Reduced iron concentrations, however, resulted in lower P_m^B values, despite the relatively limited number of measurements at concentrations less than 0.1 nM”

I can understand why there was confusion over this. The CORSACS results (Fig. 2), run under controlled conditions, had iron concentrations that were elevated above those in situ (noted in the original line 329 - all but one Fe value was > 0.13). Indeed, the mean concentrations on the final day of sampling ranged from 0.09 to 0.98 nM. Hence the data could not be divided into the same “low” and “high” categories like the PRISM data. The significant iron effect is derived from the PRISM data set, which showed the significant differences in photosynthetic parameters.

To clarify this greatly (since it is one of the more important points of the paper), I have emphasized the difference in the two data sets, and have altered

the wording to make it clear why there is an apparent difference between the two. I believe the altered wording makes the distinction clearer, and the importance of this conclusion stronger.

Specific comments

Abstract

Page 2, line 29. should read . 64% should read 48% according to the values given in table 4.

Corrected

Introduction

Page 3, lines 58-59. Modify this sentence because P_s^B is the chlorophyll (or biomass)- specific light saturated of photosynthesis in the absence of photoinhibition. *Altered as suggested.*

Page 3, lines 61-62. Modify this sentence because P_m^B is the chlorophyll (or biomass)-specific light saturated (realized) rate of photosynthesis. *Altered as suggested.*

Page 3, line 63. Ek is derived from the ratio of P_m^B (not P_s^B) and α^B *Corrected*

Page 5, line 109. Remove maximum or irradiance-saturated, because the meaning is the same. *Modified as suggested.*

Methods

Page 6. Line 119. December, 2006 should read December, 2005. *Corrected*

Page 7, line 147. I suggest including “original solution”. Then, the sentence could be: and total available inorganic ¹⁴C-bicarbonate was assessed by counting aliquots of the original solution directly in scintillation fluor. *Changed as suggested.*

Page 7, line 154. P_m^B is the maximum realized (or irradiance-saturated) rate of photosynthesis. The irradiance-saturated rate of photosynthesis in the absence of photoinhibition is P_s^B and $P_s^B \geq P_m^B$. *Changed as suggested.*

Page 9, lines 180 and 181. This sentence should be relocated on page 7, lines 151 and 152.

Moved as suggested.

Page 10, lines 216-226. This paragraph is apparently better connected to the paragraph in the next section (page 12, lines 250-259) where the influence of nutrients and temperature is again analysed. May be the two paragraphs can be combined to analyse the 3 environmental variables (temperature, nitrate and iron) together. *Changed as suggested.*

Page 11, line 229. I think it is unclear what lack of correlation means. I understand lack of relationship between photosynthetic parameters and % of surface irradiance. If I am right it could be specified. *Changed as suggested*

Page 12, line 247. 1.1 ± 0.77 is 1.1 ± 0.60 in table 4 *Corrected*

Page 12, line 253. The values of the range of nitrate concentration here are close but different to the values given before on page 10, line 218. 54 P-E measurements should read 56 P-E measurements according to table 3. *Corrected*

Discussion

Page 15, lines 332-334. But CORSACS experiments lasted for several days or at least this is deduced from what was written at the bottom of page 9 and at the top of page 10. According to this, phytoplankton could acclimate to iron additions and modify the photosynthetic response to these new conditions, as was the case for the two levels of irradiance and the two levels of CO₂.

This is correct - the CORSACS experiment lasted for 18 days (now explicitly mentioned). But as we now state, concentrations at the end of the experiment ranged from 0.09 - 0.98 nM. Fe concentrations were measured only at the start and end of the experiment, but it is reasonable to expect that concentrations prior to the experiment's end were greater than 0.1 nM, given the rapidly increasing biomass Feng et al. observed. We now mention this (line 345) in our revised discussion and comparison of CORSACS and PRISM Fe results.

Page 16, lines 353-354. The sentence “Enhanced values may reflect the interaction between light-limited and light-saturated rates described by Behrenfeld et al. (2004)” needs further explanation. It is not directly evident for the audience. *The sentence has been expanded to incorporate Behrenfeld's original idea.*

Page 17, lines 366-368. I am not totally convinced about the idea that only environmental features determine the P-E response, I think species are also important because they integrate, in some way, the environmental variability. *I certainly do not disagree at all, and have modified this portion (lines 380-382) to reflect the potential (albeit largely unknown) of individual species.*

Figure legends

Figure 2. The level of probability must be specified. Typically, * p < 0.05; ** p < 0.01; *** p < 0.001. *Now specified in legend for Figure 2.*

Figure 3. Replace α^B by α in the text and in the equation, and replace P_s^B by P_m^B in the text. *Corrected*

Figures

Figure 2. Replace P_m^b by P_m^B and α by α^B in the 3 legends; photons should read quanta in the legend of the right axis. *Corrected*

Figure 3. Replace P_m^b by P_m^B and α by α^B in the 2 legends. *Corrected.*

Tables

Table 2. Honestly, I do not think that Zmix and Z1% were determined with such exactitude. One meter of precision (without decimal figures) should be enough. *So altered, although it could*

easily be argued that while individual mixed layer depths are measured to 1 m, but means generally are given one additional significant digit.

Table 3, Footnote. For this level of probability two asterisks are needed. *So altered.*

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

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Running Head: Ross Sea photosynthesis

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Abstract

A meta-analysis of photosynthesis/irradiance measurements was completed using data from the Ross Sea, Antarctica using a total of 417 Antaretica. A total of 417 independent measurements ~~were included~~. P_m^B , the maximum, chlorophyll-specific, irradiance-saturated rate of photosynthesis, averaged $1.1 \pm 0.06 \mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$. Light-limited, chlorophyll-specific photosynthetic rates (α^B) averaged $0.030 \pm 0.023 \mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$ ($\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$)⁻¹. Significant variations in P_m^B and α^B were found as a function of season, with spring maximum photosynthetic rates being 60% greater than those in summer. Similarly, α values were 4864% greater in spring. There was no detectable effect of space-sampling location on the photosynthetic parameters, and temperature and macronutrient (NO_3) concentrations also did not exert a strong have an 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 significantly decreased P_m^B and increased α^B values; ~~whereas reduced iron concentrations were associated with increased P_m^B and α^B values, and~~ ~~increased CO_2 concentrations also~~ resulted in significantly increased P_m^B and α^B values. Comparison of photosynthetic parameters derived at stations where iron concentrations were above and below 0.1 nM indicated that reduced iron levels were associated with significantly increased P_m^B values, confirming the importance of iron within the photosynthetic process. 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

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predictions of ~~the~~ productivity ~~of~~ in polar systems. a more detailed model that includes temporal effects of photosynthetic parameters will be required.

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1. Introduction

The relationship of phytoplankton photosynthesis to irradiance is fundamental not only to our understanding of marine productivity, but also in predicting the response of marine systems to climate change and other anthropogenic alterations (Brown and 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; Arrigo et al., 2013; Smith et al., 2014b), as well as changes in air-sea interactions and food-web dynamics (Smith et al., 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 generally 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 low temperature seas~~ ~~in these waters~~.

P-E responses are generally described by a relatively simple equation that parameterizes the response as a function of irradiance: P_s^B , the ~~maximum~~-biomass-specific rate of photosynthesis at saturating irradiances ~~in the absence of photoinhibition~~, α^B , the irradiance-limited, biomass-specific linear portion of the hyperbolic response, and β^B , the portion of the curve where photosynthesis decreases at high irradiances (photoinhibition) (Platt et al., 1980a). P_m^B is the ~~maximum-biomass-specific, realized~~ rate of photosynthesis at saturating irradiances ~~in the absence of photoinhibition~~. A parameter describing the irradiance at which saturation is initiated, E_k , is derived from the ratio of $\frac{P_m^B}{P_s^B}$ and α^B . Chlorophyll *a* concentrations are

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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^B (van Hilst and Smith, 2002; Huot et al., 2013); hence β^B 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., 1998; 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. In general, phytoplankton in the Southern Ocean exhibit low maximum photosynthetic rates (between 1 and 2 $\mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$), 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 [mean](#) 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 grow at low and variable irradiances characteristic of deeply mixed surface layers and under [variable ice cover](#) (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 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 strongly influenced by factors other than just photosynthesis, despite photophysiological abilities and acclimations to different environments.

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 deep water columns, and drive the biomass maximum in late spring, and are followed by diatom growth; Smith 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

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 project was CORSACS (Controls on Ross Sea Algal Community Structure), which had two cruises. The first cruise began in late December, 2005~~6~~ and the second was in November-December, 2006 (Sedwick et al., 2011; Smith et al., 2013). P-E results from CORSACS involved controlled experimental manipulations of irradiance, dissolved 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 (Smith and Jones, 2014; McGillicuddy et al., in press). Figure 1 shows the locations of the stations analyzed for photosynthesis/irradiance relationships. Published measurements from other investigations are also 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 were generally collected from one or two depths (generally that of the 50 and 1% isolumes) at each station (50% depths were generally from 1-4 m, and 1% depths from 15-50 m), to which ca. 100-150 $\mu\text{Ci NaH}^{14}\text{CO}_3$ 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 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 ^{14}C -bicarbonate was assessed by counting aliquots of the original solution directly in scintillation fluor. While details of the methods of each study varied somewhat, we were unable to detect a significant difference between filtered and unfiltered results, and concluded that the methods did not introduce a significant source of error to obscure the overall patterns. All responses were fit to a 2-parameter exponential increase to maxima in SigmaPlot 12.3, which provided estimates of P_m^B and α^B and their significance, as determined by a t test.

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All data were fitted to the rectilinear hyperbolic model of Platt et al. (1980**b**):

$$PB = P_m^B \left[1 - e^{-\alpha^B E / P_m^B} \right] \quad (\text{Eq. 1})$$

where P^B = the rate of photosynthesis normalized to chlorophyll a [$\text{mg C (mg chl } a)^{-1} \text{ h}^{-1}$], P_m^B = the ~~maximum, maximum realized~~, irradiance-saturated rate of photosynthesis ~~in the absence of photoinhibition~~, α^B = the initial, light-limited, linear photosynthetic rate normalized to chlorophyll- [$\text{mg C (mg chl } a)^{-1} \text{ h}^{-1}$ ($\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$)], and E = irradiance ($\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$). All responses were fit to a 2-parameter exponential increase to maxima in SigmaPlot 12.3, which provided estimates of P_m^B and α^B and their significance, as determined by a t-test. Some of the published analyses included β^B , the photoinhibition parameter, but for consistency these were omitted in this meta-analysis, since β^B appears to represent a non-equilibrium conditions and in our samples was not consistently evident (Denman and Marra, 1986; MacIntyre et al., 2002). Photoinhibitory data from stations where photoinhibition occurred were not removed, as the impact on photosynthetic parameters was generally minor. The derived parameter E_k (the irradiance at which photosynthesis becomes saturated) is calculated by:

$$E_k = P_m^B / \alpha^B \quad (\text{Eq. 2})$$

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^B and P_m^B ($p < 0.05$), then the entire sample was omitted from the meta-analysis.

Chlorophyll a concentrations were analyzed by fluorometry (JGOFS, 1996) on independent samples collected from the same depth. Nutrient (NO_3 , NO_2 , PO_4 , Si(OH)_4 , NH_4) analyses were performed at sea on a Lachat QuickChem Autanalyzer using standard automated techniques, or on frozen samples after return to the laboratory. Mixed layer depths were determined from 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). Seawater samples for

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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 which were deployed on a non-metal line (Sedwick et al., 2011). Filtered samples 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).

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_m^B and α^B and their significance, as determined by a t test.~~

Comparisons between data sets were made using analyses of variance. 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). Stations selected for a comparison of the effects of assemblage composition were chosen based on HPLC analysis of pigments and the contribution of each functional group to total chlorophyll (Mackey et al., 1996). When pigment data were not included in the published reports, taxonomic discrimination was made by reported microscopic results.

3. Results

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^B , P_m^B and E_k values for the IVARS spring and summer cruises were 0.040 ± 0.035 and $0.053 \pm 0.035 \mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$ ($\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$)⁻¹, 1.3 ± 0.72 and $0.68 \pm 0.34 \mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$, and 42 ± 29 and $23 \pm 30 \mu\text{mol quanta m}^{-2}$

s^{-1} , respectively (Table 2). P_m^B values of the two seasons were significantly different ($p < 0.05$), but α^B and E_k values were not.

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 μatm) (Feng et al., 2010). Natural populations were used as inocula in semi-continuous cultures grown at constant irradiances (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 resulted in significantly ($p < 0.05$) decreased P_m^B and increased α^B values at the low and constant irradiances used (Fig. 2). No net changes were noted in E_k means. ~~generated changes in P_m^B , α^B and E_k values, which increased significantly ($p < 0.05$) at the low and constant irradiances (Fig. 2).~~—Increased CO₂ concentrations also resulted in significantly ($p < 0.05$) increased α^B and P_m^B values, although again little net change was noted in E_k values. Finally, increased iron concentrations in these experiments did not impact either α^B or P_m^B values significantly in these experiments (Fig. 2). However, iron concentrations at the end of the 18-day experiment ranged from 0.09 – 0.98 nM and were largely above concentrations that are considered to be limiting (Timmermans et al., 2004). Therefore, any effect of iron on photosynthetic parameters was not well tested in this experiment. Observed mean P_m^B -values were greater than those representing sub-optimal, in situ conditions such as in IVARS and PRISM.

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PRISM samples investigated the broad spatial patterns of P-E responses (Table 2). The mean α^B and P_m^B values were 0.035 ± 0.020 ($\mu\text{g C} (\mu\text{g chl})^{-1} \text{h}^{-1} (\mu\text{mol quanta m}^{-2} \text{s}^{-1})^{-1}$) and 1.1 ± 0.50 $\mu\text{g C} (\mu\text{g chl})^{-1} \text{h}^{-1}$, respectively. The average E_k value was 52 ± 48 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$. 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.

Temperature. Iron and nitrate concentrations were measured during PRISM at a number of stations where P-E measurements were conducted (McGillicuddy et al., in press). The data were arbitrarily divided above and below 20 μM NO_3 and above and below 0°C, and the P-E parameters compared. Dissolved Fe ~~levels~~ concentrations ranged from 0.066 to 0.69 nM, and nitrate ranged from 9.105 to 30.6 μM . Sample temperatures ranged from -1.6 to 2.6°C; 58 of the 102 P-E determinations were below 0°C, and 44 were above. No significant difference in the mean α^B , P_m^B or E_k values were observed between the stations with nitrate concentrations less than 20 μM and those with concentrations $> 20 \mu\text{M}$ (Table 3), which is not unexpected as these concentrations are considered to be ~~non-~~ far above levels thought to be limiting. 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; Timmermans et al., 2004), P_m^B values were significantly ($p < 0.01$) greater (1.6 ± 0.55 vs. 0.95 ± 0.44) at lower iron concentrations (Table 3). α^B 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. No significant differences were noted for any of the three photosynthetic parameters within the temperature data subset, corroborating the PRISM results (Table 3). This result suggests that photosynthetic responses are largely independent of temperature over short time scales.

There was no significant ~~difference-relationship~~ in the combined IVARS, JGOFS and PRISM ~~data-data between in any photosynthetic parameter when the depth of sampling (from samples collected at 50 vs. 1% of surface irradiance) in any photosynthetic parameter.~~ This lack of

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correlation differs from the CORSACS results (Fig. 2), which were conducted under constant irradiance using natural assemblages (but which changed appreciably during the experiments). Available irradiances at the time of sampling do not necessarily reflect the irradiance that influenced growth over times scales of days to weeks, which are unknown and likely highly variable. This suggests-indicates that there is no substantial photoacclimation within water columns of the Ross Sea, which in turn may suggest that the time needed for acclimation at these temperatures is longer than the time scales of water column perturbation.

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_m^B and α^B values, with spring having a greater P_m^B (1.4 vs. 0.86) and α^B values (0.034 vs. 0.023). However, no significant difference was observed between spring and summer E_k values. Values of α^B and P_m^B were linearly correlated ($P_m^B = 10.9\alpha^B + 0.070$; $R^2 = 0.15$; $p < 0.001$; Fig. 3), as has been found previously (Harrison and Platt, 1980; 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 multiple independent factors as well. No interannual temporal trend was obvious, and interannual variability was substantial (Table 4). The overall P_m^B average for all samples ($N = 417$) equaled $1.1 \pm 0.6077 \mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$, $\alpha^B = 0.030 \pm 0.023 \mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1} (\mu\text{mol quanta m}^{-2} \text{ s}^{-1})^{-1}$ and $E_k = 44 \pm 27 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$.

3.3. Controls by Environmental Factors and Phytoplankton Composition

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 $20 \mu\text{M NO}_3$ and

above and below 0°C, and the P-E parameters compared. Nitrate concentrations at the time of sampling ranged from ~~9.15~~ – ~~304.60~~ μM , and ~~564~~ P-E measurements were conducted with NO_3 concentrations greater than 20 μM . 58 analyses were conducted with NO_3 levels less than 20 μM . Sample temperatures ranged from -1.6 – 2.6°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, corroborating the PRISM results (Table 3). This suggests that photosynthetic responses are largely independent of these environmental controls over short time scales.

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, 2012). To investigate if the two taxa have different photosynthesis-irradiance responses, we selected 20 stations for each group that were identified by chemical or microscopic means as being 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^B , P_m^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 1.1 $\mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$ (Table 4). This is similar to the P_{opt}^B value determined from Behrenfeld and Falkowski's (1997) polynomial equation ($1.3 \mu\text{g C } (\mu\text{g chl})^{-1}$

h^{-1}) at 0°C , despite the difference between P_{opt}^B and P_m^B as well as the range of temperatures at which the P-E determinations were conducted. Our results reinforce 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., Arrigo et al., 2003, 2008). However, given the seasonal variability observed, more detailed models that incorporate seasonal and environmental impacts on photosynthetic parameters may require inclusion of other oceanographic variables- (especially iron concentrations) to more accurately predict production.

We found relatively minor spatial differences in photosynthetic parameters, but significant seasonal differences. Specifically, α^B and P_m^B values of the entire meta-analysis 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 oceanographic and biological variables. The macro-environment of the Ross Sea continental shelf changes markedly from spring to summer, with increased temperatures, stronger vertical stratification, shallower mixed layers, decreased macro- and micronutrient concentrations, and an altered assemblage composition (Smith et al., 2012). All of these variables have been shown to influence P-E responses in laboratory and field studies (e.g., MacIntyre et al., 2002; Xie et al., 2015), and as such, it is not surprising that the P-E parameters also changed. It is tempting to suggest that the seasonal changes were driven by changes in phytoplankton composition, but we believe that the seasonal changes in oceanographic conditions led to changes in P-E parameters as well as in composition, and that both oceanographic changes and phytoplankton composition contributed to the seasonal differences in P-E parameters we observed. An experiment which isolates natural assemblages

(perhaps a Lagrangian tracking of a parcel of water that is dominated by one taxa or a large-volume mesocosm experiment such as has been conducted in the Baltic Sea; Riebesell et al., 2013) would be more definitive test of the impacts of composition and the seasonal changes in P-E parameters. 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 in P-E parameters, given the relatively low numbers of samples in some years, but in view of the large variations observed in biomass and productivity from 1995 through 2010 (Smith and Comiso, 2008; Smith et al., 2011a), 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 within the seasonal data sets. The temperature range was modest (ca. 4°C), so the direct impact of temperature may have been limited and obscured by other factors. Liu and Smith (2012) demonstrated that the environmental factor that had the strongest impact on phytoplankton biomass anc composition 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, reducing mean irradiance available for growth, which also favors 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). Xie et al. (2015) also did not find a correlation between nutrients and

P_m^B , and suggested that this reflected the lag time between nutrient inputs and phytoplankton growth in the English Channel. They also found a complicated relationship between photosynthetic parameters and temperature and suggested that each functional group had temperature optima that were characterized by specific photosynthetic responses.

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Reduced in situ iron concentrations in PRISM, however, resulted in ~~lower-elevated~~ P_m^B values, despite the relatively limited number of measurements at concentrations less than 0.1 nM (Table 3). In contrast, we did not detect a change at the end of the controlled experiments (CORSACS) in which iron concentrations were measured, ~~but~~ However, all but one of those ~~experiments-conditions~~ had dissolved Fe concentrations > 0.13 nM at the end of the 18-day experiment (Feng et al., 2010), concentrations which are greater than those generally found in situ (Sedwick et al., 2011). Furthermore, given that the lowest Fe concentration at the experiment's termination was 0.09 nM, it would be expected that preceding levels were even greater and may have obscured any Fe effect. Because ~~because~~ the experiments were completed in a constant irradiance environment, the impact of iron also may have been lessened. Iron influences growth rates of Antarctic diatoms (Timmermans et al., 2004), but growth rate responses are integrated over many days, whereas P-E responses are not immediately influenced by iron additions (Hiscock et al., 2008). It is tempting to suggest that the reduced summer P-E parameters may have resulted from iron limitation, but iron availability is rarely determined in parallel with P-E parameters. We suggest that the impacts of iron we observed – significantly ~~reduced-increased~~ P_m^B values under low Fe concentrations – were mediated by a long-term assemblage response rather than an impact on short-term photosynthetic rates. Iron limitation can impact chlorophyll synthesis (in a manner similar to irradiance), and under ~~co-limitation by~~ iron and irradiance co-limitation, chlorophyll levels can be elevated (Sunda and Huntsman,

1997), which would result in ~~lowered~~altered P_m^B values. Determination of the exact cause of the iron effect on P_m^B , however, is impossible with the present data set.

The CORSACS experiments showed a clear impact of both irradiance and $[\text{CO}_2]$ on photosynthetic responses. Under low and constant irradiance conditions (ca. 7% that of surface irradiance), there was an increase in the light-limited rates of photosynthesis (α^B) and light-saturated (P_m^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 (Prezelin, 1981; Dubinsky and Stambler, 2009). P_m^B reflects the light-saturated rate, 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_m^B and α^B values, reinforcing the classical view of the limitation of short-term photosynthesis by carbon availability under high irradiance conditions. Enhanced ~~α^B~~ α values may reflect the interaction between light-limited and light-saturated rates described by Behrenfeld et al. (2004), in which the two co-vary and result in the maintenance of a relatively constant E_k . Interestingly, increased CO_2 levels had little impact on phytoplankton composition (Tortell et al., 2008b), 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., 2008a). 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).

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The influence of phytoplankton composition was insignificant (Table 5). This is consistent with the previous results of van Hilst and Smith (2002) and Robinson et al. (2003), using a less extensive data set, but in contrast to the extensive laboratory results of Arrigo et al. (2010), who found that α^B and P_m^B values of *P. antarctica* grown at constant irradiances (from 5 – 125 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$) and saturating nutrients were always greater than those of the diatom *Fragilariopsis cylindrus*. The diatom had low P_m^B [from 0.46 to 0.54 $\mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$] and α^B values [0.014 to 0.043 $(\mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1} (\mu\text{mol quanta m}^{-2} \text{s}^{-1})^{-1})$] when compared to those of the haptophyte (from 1.4 to 6.4, and 0.038 to 0.11, respectively). The diatom parameters determined in culture were lower than in our data subset, and the haptophyte values higher; these differences likely reflect the parameters of the individual species cultured and/or the acclimation to influence of constant culturing conditions. The in situ data also had substantial variability, which likely resulted at least in part from the environmental conditions that allowed one particular functional group to dominate. In addition to the influence of environmental conditions, individual species likely have evolved mechanisms to permit adaptation within a wide environmental range. 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-E parameters of the dominant forms in spring and summer reflect the importance of selected environmental features (irradiance, iron) on their long-term success within 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, strong and significant seasonal differences occur, as do variations 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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Figure Legends

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

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) CO₂, 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 (*: p < 0.05; **: p < 0.01; ***: p < 0.001).

Figure 3. Relationship of α^B (light-limited photosynthesis) and P_m^B (irradiance-saturated photosynthesis) in samples from the Ross Sea. Solid line is the linear regression ($P_m^B = 10.9\alpha^B + 0.70$; $r^2 = 0.15$; $p < 0.001$).

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

*: Gravity filtration

Table 2. Mean and standard deviations of photosynthesis-irradiance parameters, mixed layer depths (Z_{mix}) and euphotic zone depths ($Z_{1\%}$) determined during IVARS and PRISM cruises. Units: α^B : $\mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$ ($\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$) $^{-1}$; P_m^B : $\mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$; E_k : $\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$; Z_{mix} : m; $Z_{1\%}$: m. Number of observations in parentheses.

Month	Year	α^B	P_m^B	E_k	Z_{mix}	$Z_{1\%}$
December	2001	$0.060 \pm$	$2.3 \pm$	$42 \pm$	$37.1 \pm$	$9.38 \pm$
		0.015 (4)	0.61	18	13.3 $-(17)$	1.06 (8)
February	2002	0.008 (1)	0.85	110	$35.1 \pm$	$14.3 \pm$
					9 8.96 (16)	2.74 (9)
December	2002	$0.033 \pm$	$0.97 \pm$	$34 \pm$	$298.5 \pm$	$36.0 \pm$
		0.012 (4)	0.32	24	7 0.09 (8)	14.5 (3)
December	2003	$0.019 \pm$	$0.61 \pm$	$37 \pm$	$232.7 \pm$	$27.8 \pm$
		0.005 (5)	0.36	28	10 1 (12)	11.4 (9)
February	2004	$0.067 \pm$	$0.80 \pm$	$16 \pm$	$25.2 \pm$	$25.8 \pm$
		0.047 (4)	0.57	15	9 8.67 (25)	6.57 (12)
December	2004	$0.022 \pm$	$1.1 \pm$	$62 \pm$	$21.0 \pm$	$23.8 \pm$
		0.009 (10)	0.42	38	6 0.47 (23)	7.66 (23)
February	2005	$0.051 \pm$	$0.57 \pm$	$14 \pm$	$20.1 \pm$	$24.6 \pm$
		0.023 (6)	0.048	6.1	7 0.44 (24)	8.20 (25)
December	2005	$0.070 \pm$	$1.6 \pm$	$28 \pm$	$20.0 \pm$	$24.0 \pm$
		0.055 (7)	0.80	11	11	1.91 (7)

					0.5 (12)	
Mean:	---	0.040 ±	1.3 ±	42 ±	265.7 ±	23.0 ±
December		0.035 (27)	0.72	29	12	10.1 (50)
					1.7 (72)	
Mean:	---	0.053 ±	0.68 ±	23 ±	265.7 ±	22.9 ±
February		0.035 (11)	0.34	30	10	8.13 (45)
					-0 (65)	
PRISM,	2010	0.035 ±	1.1 ±	52 ±	27.8 ±	42.2 ± 22.8
January		0.020 (77)	0.50	48	23	(116)
					2.7 (116)	

Table 3. Comparison of PRISM photosynthetic parameters as a function of nitrate, temperature and iron (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 μM , in situ temperatures above and below 0°C , and iron concentrations greater than or less than 0.1 nM. No significant differences were noted between the two sets of parameters except where noted.

Variable Group	N	α^B ($\mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$ ($\mu\text{mol quanta m}^{-2} \text{ s}^{-1})^{-1}$)	P_m^B ($\mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$)	E_k ($\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$)
[NO ₃] < 20 μM	58	0.035 \pm 0.020 (0.012 – 0.095)	1.2 \pm 0.64 (0.29 – 3.1)	43 \pm 34 (7 – 193)
[NO ₃] > 20 μM	56	0.043 \pm 0.039 (0.008 – 0.183)	1.2 \pm 0.58 (0.21 – 2.8)	48 \pm 47 (4 – 238)
T > 0°C	44	0.040 \pm 0.036 (0.015 – 0.183)	1.2 \pm 0.66 (0.29 – 3.1)	44 \pm 40 (7 – 193)
T < 0°C	58	0.032 \pm 0.021 (0.011 – 0.095)	1.2 \pm 0.53 (0.21 – 2.7)	50 \pm 44 (8 – 238)
[Fe] < 0.1 nM	6	0.03875 \pm 0.023 (0.021 – 0.053)	1.6 \pm 0.55** (1.1 – 2.7)	41 \pm 18 (28 – 54)
[Fe] > 0.1 nM	33	0.029 \pm 0.017 (0.011 – 0.066)	0.951 \pm 0.44 (0.21 – 1.7)	48 \pm 36 (8 – 131)

** : t-test indicated a significant difference (p<0.01)

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

Season	P_m^B ($\mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$)	α^B ($\mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$) ($\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$) ⁻¹)	E_k ($\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$)	N	Reference
Spring	1.7 ± 0.97	0.047 ± 0.023	37 ± 7.5	37	van Hilst and Smith (2002)
Summer	2.5 ± 1.3	0.087 ± 0.043	31 ± 16	31	
Spring	1.2 ± 0.54	0.036 ± 0.015	37 ± 13	70	Hiscock (2004)
Summer	0.64 ± 0.26	0.016 ± 0.007	44 ± 18	98	
Autumn	0.70 ± 0.13	0.040 ± 0.017	21 ± 9	5	
Summer	1.3 ± 0.39	0.073 ± 0.088	23 ± 8	51	Saggiomo et al. (2002)
Spring	1.8 ± 0.68	0.020 ± 0.004	89 ± 23	15	Robinson et al. (2003)
Spring ²	2.1 ± 0.48	0.072 ± 0.027	31 ± 8.0	10	Smyth et al. (2012)
Spring	1.3 ± 0.72	0.040 ± 0.035	42 ± 29	27	IVARS: This report
Summer	0.68 ± 0.34	0.053 ± 0.035	23 ± 30	11	IVARS: This report
Summer	1.1 ± 0.500	0.035 ± 0.020	52 ± 48	77	PRISM: This report
Mean Spring ¹	1.4 ± 0.63	0.034 ± 0.024	44 ± 25	159	---
Mean Summer ¹	0.86 ± 0.45	0.023 ± 0.018	43 ± 28	268	---
Overall Mean ¹	1.1 ± 0.60	0.030 ± 0.023	44 ± 27	417	---

¹: Weighted mean of all samples

²: α^B 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 for each functional group (N) from the entire data set were selected for inclusion in this comparison. No significant difference in any photosynthetic parameter was detected.

Functional Group	P_m^B ($\mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$)	α^B ($\mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$) ($\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$) ⁻¹)	E_k ($\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$)
<i>Phaeocystis antarctica</i> (N=20)	1.4 ± 0.76	0.067 ± 0.060	33 ± 23
Diatoms (N=20)	1.1 ± 0.63	0.050 ± 0.045	32 ± 19

Fig. 1.

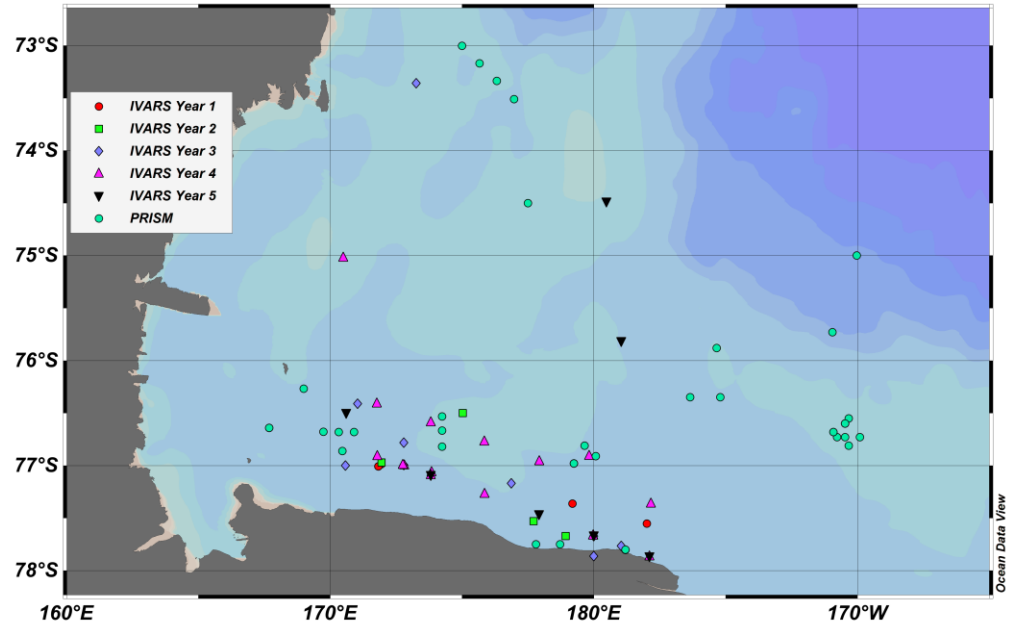
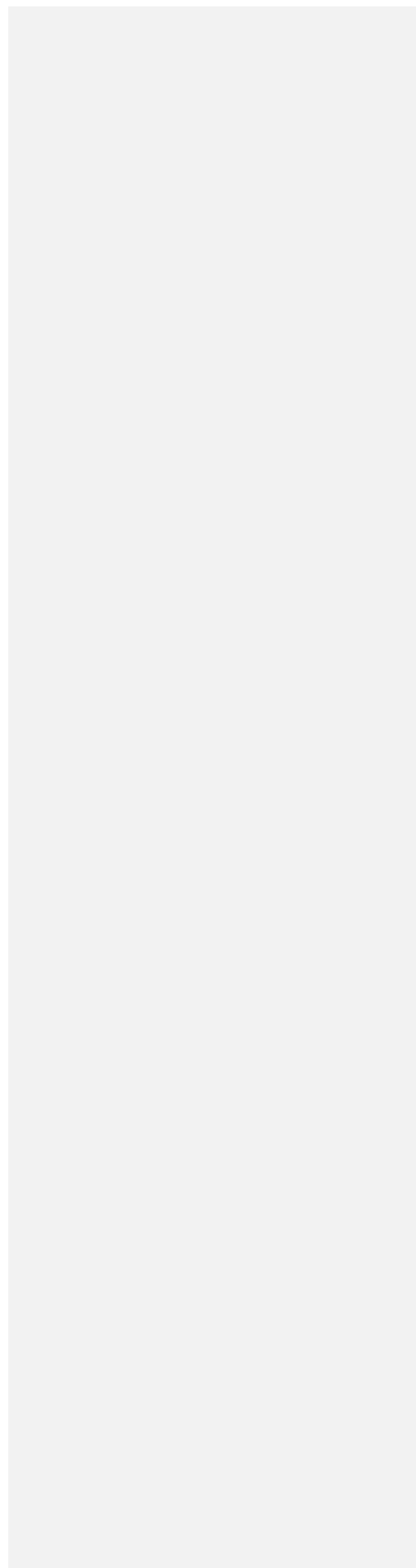


Fig. 2



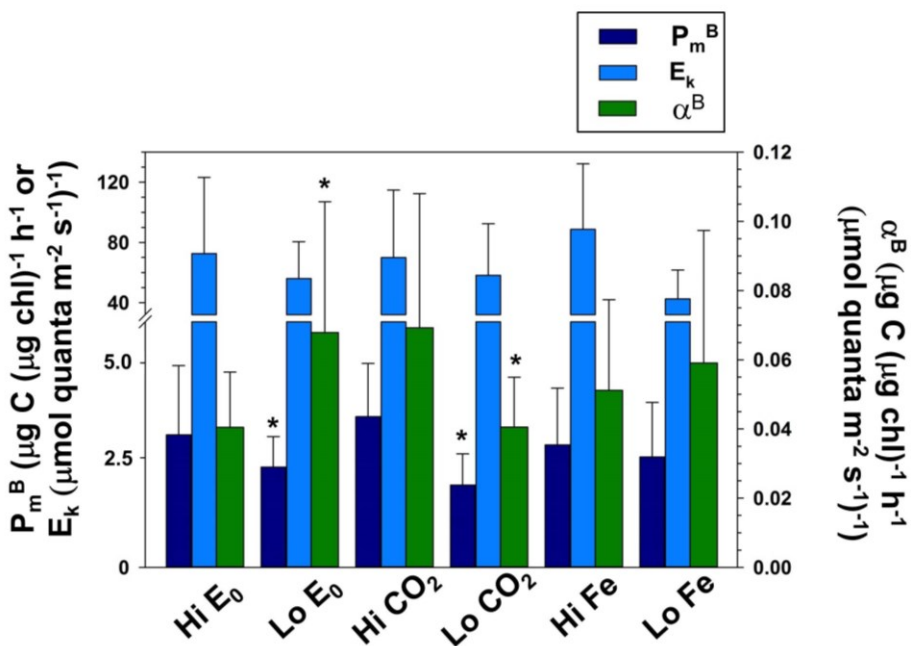
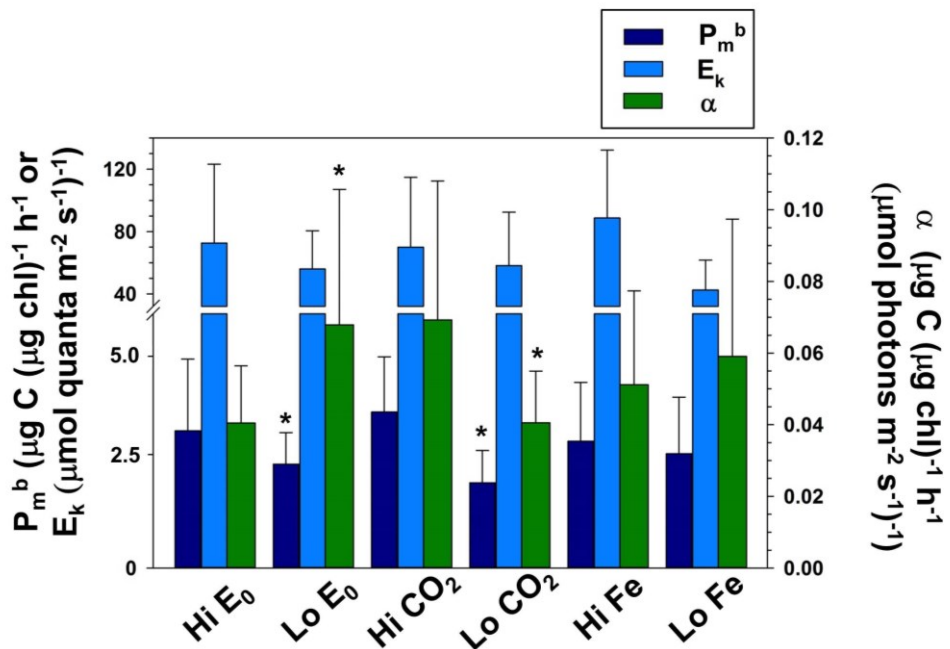


Figure 3.

