TO: Dr. Carol Robinson, Editor  
   *Biogeosciences*

FROM: Dr. Walker Smith

DATE: March 2, 2015

RE: Manuscript bg-2014-573 revision

Within this electronic resubmission you will find a) a revised manuscript that has answered all reviews and comments, and b) a list of changes that details the responses to all reviews. I will admit that one change that I made throughout based on the insistence of Reviewer 8089 makes me a bit uncomfortable – reducing the significant digits on $P_m$ values to 2. Nearly all the papers we used and are familiar with use 3 significant digits, which does not necessarily make it right, but does make it convention. In one sense I understand the reviewer’s comment, but I still remain uncomfortable with that change. Perhaps you can weigh in on this concern.

We appreciate the thoroughness of all reviewers, and apologize for the initial errors that led to confusion for all. We believe their inputs have resulted in a substantially improved manuscript. We hope you concur, and look forward to your response.
Responses to Review bgd-11-C8361-2015

We appreciate the constructive comments of the reviewer, and have changed the ms. throughout as suggested. Specifically,

1. The reviewer pointed out the difference between \( P_s^B \) and \( P_m^B \), and is correct in his notation of the difference. We have converted from using \( P_s^B \) and explained in the methods why this was used. We have also used the suggested notation for \( \alpha^B \) throughout.

2. The reviewer noted the ambiguity in the methods with regard to the treatment of data with either a 2- or 4-parameter model. We have clarified this (lines 150 and 159-160), and have noted that no data were removed in the analyses, as that would be an arbitrary removal that potentially might introduce a bias. However, the removal of points generally resulted in only a minor change in the estimated \( P_m^B \) value, and considering the variability inherent in the entire data set, was not considered significant.

3. Depth as a variable was not explicitly treated, but the range of depths sampled is now included in the methods (lines 137-8). Mixed layers in most (ca. 80%) of the stations exceeded euphotic depths.

4. The reviewer asked why irradiance was not included in our analyses, and how mixed layer depths were analyzed. We considered irradiance to be a critical feature in the phytoplankton response; however, irradiance also varies substantially on a number of scales: seasonal, diel, and “randomly” (weather/cloud impacts and vertical mixing). Hence we believe the irradiance at the time of sampling has little bearing on the photosynthetic responses measured. We do not disagree that irradiance on some scale does indeed modulate the P-E responses. That is why we did the seasonal comparison, since mean seasonal irradiance can be broadly defined as “low” and “high” in a relative sense, and why we emphasized the large difference. We initially did not want to confuse the issue by looking at irradiance on shorter scales, simply because we were not comfortable in defining the scale which is important to the phytoplankton response from our results.

   However, to address this issue, we have compared all samples from the 50% and the 1% isolumes. The cruises that had the most samples from the 50 and 1% isolumes were the JGOFS and PRISM cruises. JGOFS was conducted in a more restricted spatial domain, but had far fewer stations. PRISM had more samples, but had much greater spatial variability. Both, however, were in January so that the comparison was within summer when we would expect any difference to be greatest. JGOFS data did indeed show a significant difference in \( P_m^B \) values, but not \( \alpha \) or \( E_k \) values. PRISM data showed no significant difference in any parameter, and when we merged the two data sets, no significant difference remained. To be honest, the analysis is far from perfect, but based on these results we cannot conclude that the irradiance environment sampled resulted in a significantly adapted assemblage.

   We have added a short comment to this effect in the results (Line 230), but did not emphasize this to a great extent. We hope our analysis satisfies the reviewer.

   The reviewer also noted that mixed layer depths were not included anyway, and we have done so now in Table 2. We also included data on the euphotic zone depths to provide some insight into the relative depths of the two.

5. The reviewer is correct in catching this difference, and it was our error in describing the results. What we did is select 40 independent stations, or 20 of each functional group. We have clarified this confusion. As the reviewer no doubt realizes, nearly all stations had a
mixture of the two groups; we endeavored to select those that were substantially dominated by one or the other. Our means of doing so was pigment-based, and we have enhanced the description of our station selection in the methods (line 184).

Specific Comments
1. We added material in the methods (line 149) to clarify this statement.
2. We have tempered this statement (line 278), but still believe that the results do indeed suggest a broad support for their conclusions.
3. We added a statement in the caption of Table 5 to clarify the number of stations used.
4. Changed.
5. Corrected.
7. This was a serious error, and we have now included the statistical summary in Table 3. The figure has also been corrected.
8. Correct. The range was not provided because the table became too complex in our view.

Responses to Review bgd-11-C8014-2015

The reviewer offered a number of suggestions that prompted us to alter the manuscript substantially to improve its clarity.
1. The reviewer pointed out an apparent contradiction listed in Tables 3-5 and the statistics, in that we found a strong seasonal comparison yet none within the data sets selected for analyses for temperature, iron and nitrate impacts. We have altered our discussion of the results to clarify and explain why we believe the results are consistent. In essence, the seasonal changes appeared to be robust, whereas many of the other factors had little impact when assessed within one season or between seasons. Clearly many of the oceanographic factors do indeed vary with season (mixed layers become shallower, nutrients are reduced through growth, irradiance increases seasonally), but these effects are manifested collectively to generate the seasonal affect.
   We have altered the discussion of these effects to clarify the differences (and consistencies) (see lines 292, 303, and 311).
2. The reviewer was correct in that the iron data were inadvertently omitted from Table 3, and they now are included (as is a more thorough discussion of these data). We have also altered our discussion of the CORSACS data to clarify the difference between the field observations (Table 5) and the controlled experimental data (Fig. 2) (lines 321)
3. The reviewer is correct in stating that type I errors may be associated with t tests. We indeed did investigate the normality of distribution of the parameters, and tried various transformations to improve the normality of the distribution, but none of our attempts enhanced the normality. After numerous attempts at this, we concluded that the large ranges of parameter values, especially for α and E_k, reduced the statistical power of the tests and resulted in a lack of significance in our comparisons of α and E_k.
4. The reviewer was concerned with the lack of difference we found between P. antarctica and diatoms (Table 5). As with the previous reviewer, there was confusion in the manner we stated the number of stations used in the analysis. We used 20 stations for each functional group, and so number of degrees of freedom that the reviewer assumed is an underestimate. We did not understand the exercise in artificially reducing the sample size, nor do we understand where he got the number of replicates of N=61.
We apologize for the misunderstanding of our description of the data used in the functional group comparison, but are confident that the analysis is correct. It also is consistent with results of Robinson et al. (2003) and van Hilst and Smith (2002). We also note that the selection of data using pigments involves selecting stations that were largely dominated by one form or the other, and that both data sets had contributions from different taxa. Expanding the numbers of stations included would result in increasing the taxonomic variability in the selected data and, in our view, decreasing the power of the comparison.

5. We were again a bit confused by the reviewers comment that “The algorithms that use integrated chl, irradiance, and P-E response as a function of temperature actually do a reasonable job in the Ross Sea because in fact there are not big differences between spring and summer in the P-E response.” We are unaware of any publications other than those from Kevin Arrigo’s group that have modeled Ross Sea productivity. We agree that Arrigo’s algorithms do a reasonable job in estimating productivity, but suggest that if a better seasonal analysis of P-E responses were included, that estimate would be improved. Most of Arrigo’s models are bio-optical and depend on satellite estimates of chlorophyll. Since very few regional values are available (they are largely composites over one month), that variability will mask any generated by the P-E response. Again, the data we present are a synthesis of a large number of measurements, and we strongly believe the seasonal difference is real and a major feature of the temporal variations of photosynthetic parameters in the region.

6. We agree with the reviewer that emphasizing nitrate concentrations relative to P-E responses (and growth limitation) was unlikely to reveal a significant difference. However, other studies have included this variable, and we would have been remiss to include it. It certainly is not a major point of the paper, and we have left it in to be consistent with other studies and to be complete. We in no way suggested that nitrate was expected to have a significant impact.

7. The reviewer was correct in stating that Table 2 included values that were unclear, and those have all been clarified.

Responses to Review bgd-11-C8089-2015
We appreciate the comments of the reviewer, and have worked hard to improve the clarity and logic throughout. In response to his comments, we made the following changes:

1. The reviewer commented that the data in Figure 2 were inconsistent with the manuscript’s comments. We have emphasized in the results that the irradiance effects observed in this controlled experiment were in fact very different from any observed in situ. The irradiances in Fig. 2 were in fact constant as well as different, whereas the irradiance in situ is obviously much more variable on a wide range of time scales. We have tried to emphasize this difference throughout (lines 205, 230, 321, 335).

2. The reviewer is correct (like the other two reviewers) that we inadvertently omitted the Fe data, and we have now done so. As we commented in our responses to the other reviews, we have attempted to clarify why the PRISM results appear to differ from the CORSACS results, and hope we have resolved this lack of clarity.

3. This reviewer commented, as did Reviewer 8014, that there was confusion about the statistical power of our conclusions from Table 5. We strongly believe that simply attributing the seasonal changes to solely phytoplankton composition is inappropriate, simply because all environmental variables (Fe concentrations, mixed layer depths, strength of stratification, temperatures) vary seasonally, in addition to composition. Indeed, we feel that
it is the sum of all seasonal changes that induce compositional changes, and the differences in
P-E parameters reflect all of these changes.

However, based on both reviewers’ comments, we have tried to clarify our logic and
support our conclusions with additional literature references. Substantial changes have been
made in the discussion (lines 291, 295) to reinforce this logic.

Specific comments
1. We have corrected this inconsistency. Actually, we left port in late December but initiated
sampling in January.
2. We understand the confusion, and to be honest, it has been confusing to others. An initial
part of CORSACS was devoted to IVARS Year 5, although they were part of the same
cruise. Internally we differentiated between them, and did so in this paper. We altered the
statement on line 122 to accurately state that the analyses in this paper involved
manipulations with natural assemblages. Changes are also made later (line 217).
3. The comparisons were indeed done by ANOVA tests, which is now specified (line 183).
4. We have checked all of these values throughout and believe any errors have been found.
5. The changes suggested have been made throughout. We are curious, however, at the
insistence of using whole numbers for E_k values; is that based on the accuracy of
measurement?
6. The values for R^2 have been checked and modified to reflect two significant digits.
7. Table 2 has been corrected as noted above.
8. Now provided.
9. Corrected as suggested.
10. Corrected as suggested.
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 417 independent measurements were included. \( P_m^\# \), the maximum, chlorophyll-specific, irradiance-saturated rate of photosynthesis, averaged 1.07 ± 0.060 µg C (µg chl)\(^{-1}\) h\(^{-1}\). Light-limited, chlorophyll-specific photosynthetic rates (\( \alpha_B^\# \)) averaged 0.03 ± 0.023 µg C (µg chl)\(^{-1}\) h\(^{-1}\) (µmol photons m\(^{-2}\) s\(^{-1}\))\(^{-1}\). Significant variations in \( P_m^\# \), \( \alpha_B^\# \), and \( \alpha_B^\# \) were found as a function of season, with spring maximum photosynthetic rates being 59% greater than those in summer. Similarly, \( \alpha \) values were 48% greater in spring. There was no detectable effect of space on the photosynthetic parameters, and temperature and macronutrient (NO\(_3\)) concentrations also did not 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 \( P_m^\# \), \( \alpha_B^\# \) and \( \alpha_B^\# \) values, whereas reduced iron concentrations were associated with increased \( P_m^\# \), \( \alpha_B^\# \) and \( \alpha_B^\# \) values. Increased CO\(_2\) concentrations also resulted in significantly increased \( P_m^\# \), \( \alpha_B^\# \) and \( \alpha_B^\# \) 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 of the productivity of polar systems a more detailed model that includes temporal effects of photosynthetic parameters will be required.
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 and Sathyendranath, 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 waters.

P-E responses are generally described by a relatively simple equation that parameterizes the response as a function of irradiance: \( P^* \), the maximum, biomass-specific rate of photosynthesis at saturating irradiances, \( \alpha_B \), the irradiance-limited, biomass-specific linear portion of the hyperbolic response, and \( \beta_B \), the portion of the curve where photosynthesis decreases at high irradiances (photoinhibition) (Platt et al., 1980). \( P^* \) is the maximum rate of photosynthesis at saturating irradiances in the absence of photoinhibition. A parameter describing the irradiance at which saturation is initiated, \( E_{sa} \), is derived from the ratio of \( P^* \) and \( \alpha_B \). 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 $\beta^B$ (van Hilst and Smith, 2002; Huot et al., 2013); hence $\beta^B$ 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., 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., 1980; 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 $\mu$g C ($\mu$g chl)$^{-1}$ h$^{-1}$), and $E_R$ 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, $E_R$ values are low, reflecting an acclimation to reduced available irradiance. Conversely, $E_R$ 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., 2011). 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 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 January late December, 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 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 review press; Smith and Jones, 2014). 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, to which ca. 100 μCi NaH¹⁴CO₃ 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 ᵃ¹⁴C-bicarbonate was assessed by counting aliquots directly in scintillation fluor. While details of the methods of each study varied somewhat, we did not find 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 data were fitted to the rectilinear hyperbolic model of Platt et al. (1980):

\[ P_{B} = P_{Bm} \left[ 1 - e^{-\alpha P_{B} E / P_{Bm}} \right] \]  

(Eq. 1)

where \( P_{B} \) = the rate of photosynthesis normalized to chlorophyll \( a \) [mg C (mg chl \( a \))⁻¹ h⁻¹], \( P_{Bm} \) = the maximum, irradiance-saturated rate of photosynthesis in the absence of photoinhibition, \( \alpha \) = the initial, light-limited, linear photosynthetic rate normalized to chlorophyll \( a \) [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 $\beta^B$, the photoinhibition parameter, but for consistency these were omitted in this meta-analysis, since $\beta^B$ 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:

$$E_k = \frac{P^B_m}{\alpha^B}$$  

(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 $\alpha^B$ and $P^B_m$ ($p < 0.05$), 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 (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. 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 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 $P^b_m$, $P^b_b$ and $\alpha^b$ 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 $\alpha^b$, $P^b_m$, $P^b_b$ and $E_k$ values for December and February were 0.040 ± 0.035 and 0.053 ± 0.035 µg C (µg chl)$^{-1}$ h$^{-1}$ (µmol photons m$^{-2}$ s$^{-1}$)$^{-1}$, 1.25 ± 0.72 and 0.68 ± 0.34 µg C (µg chl)$^{-1}$ h$^{-1}$, and 424.9 ± 298.7 and 23.3 ± 30.2 µmol photons m$^{-2}$ s$^{-1}$, respectively (Table 2). $P^b_m$ and $P^b_b$ values of the two seasons were significantly different ($p < 0.05$), but $\alpha^b$ 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 CO$_2$ concentrations (380 and 750 µatm) (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 $P_m$, $P_n$, $\alpha_B$, and $E_k$
values, which increased significantly ($p < 0.05$) at the low and constant irradiances (Figure 2).
Increased CO$_2$ concentrations also resulted in significantly ($p < 0.05$) increased $\alpha_B$ and $P_n$
values, although little net change was noted in $E_k$ values. Finally, increased iron concentrations
did not impact either $\alpha_B$ or $P_n$ values significantly in these experiments (Figure 2). $P_m$ and $P_n$
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
$\alpha_B$ and $P_n$ values were $0.035 \pm 0.020 \, \mu$g C (µg chl)$^{-1}$ h$^{-1}$ (µmol photons m$^{-2}$ s$^{-1}$)$^{-1}$ and
$1.143 \pm 0.50 \, \mu$g C (µg chl)$^{-1}$ h$^{-1}$, respectively. The average $E_k$ value was $52.2 \pm 48.4 \, \mu$mol
photons m$^{-2}$ s$^{-1}$. There was no significant different 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 during PRISM at a number of stations where
P-E measurements were conducted during PRISM (McGillicuddy et al., in review press).
Dissolved Fe levels ranged from 0.066 to 0.69 nM, and nitrate ranged from 9.05 to 30.6 µM. No
significant difference in the mean $\alpha_B$, $P_n$ or $E_k$ values were observed between the stations
with nitrate concentrations less than 20 µM and those with concentrations > 20 µM (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; Timmermans et al., 2004), $P_m^{B} \cdot \alpha^{B}$ values were significantly ($p < 0.01$) greater (1.58 ± 0.55 vs. 0.95 ± 0.45) at lower iron concentrations (Table 3). $\alpha^{B}$ 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.

There was no significant difference in the combined IVARS, JGOFS and PRISM data when the depth of sampling (50 vs. 1% of surface irradiance) in any photosynthetic parameter. This lack of correlation is different from the CORSACS results (Fig. 2), which were conducted under constant irradiance using natural assemblages. Available irradiances at the time of sampling do not necessarily reflect the irradiance that influenced growth over timescales of days to weeks, which are unknown. This suggests that there is no substantial photoacclimation within the water column, which in turn may suggest that the time needed for acclimation at these temperatures may be 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 $P_m^{B} \cdot \alpha^{B}$ and $\alpha^{B}$ values, with spring having a greater $P_m^{B} \cdot \alpha^{B}$ (1.37 vs. 0.86) and $\alpha^{B}$ values (0.034 vs. 0.023). However, no significant difference was observed between spring and summer $E_k$ values. Values of $\alpha^{B}$ and $P_m^{B} \cdot \alpha^{B}$ were correlated ($P_m^{B} \cdot \alpha^{B} = 10.91 \cdot \alpha^{B} + 0.070; R^2 = 0.383; p < 0.001; Fig. 3$), 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 $pB_{\alpha}a$ average for all samples ($n = 4157$) equaled $1.07 \pm 0.77 \mu g \text{C (µg chl)}^{-1} \text{h}^{-1}$. 

\[ \alpha_{\text{in}} = 0.030 \pm 0.023 \mu g \text{C (µg chl)}^{-1} \text{h}^{-1} (\mu\text{mol photons m}^{-2} \text{s}^{-1})^{-1} \] and \[ E_k = 443.7 \pm 276.9 \mu\text{mol photons m}^{-2} \text{s}^{-1}. \]

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 µM NO$_3$ 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 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 – 2.58°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 photosynthesis is largely independent of these environmental controls.

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 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 $\alpha_B$, $P_{\text{sn}}^B$, $P_{\text{st}}^B$, 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 $\mu$g C ($\mu$g chl)$^{-1}$ h$^{-1}$ (Table 4). This is similar to the $P_{\text{opt}}^B$ value determined from Behrenfeld and Falkowski’s (1997) polynomial equation (1.29 $\mu$g C ($\mu$g chl)$^{-1}$ h$^{-1}$) at 0°C, despite the difference between $P_{\text{opt}}^B$ and $P_{\text{to}}^B$ 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., Arrigo et al., 2003, 2008). However, given the seasonal variability observed, more detailed models that incorporate seasonal and environmental impacts 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, $\alpha_B$, $P_{\text{sn}}^B$, $P_{\text{st}}^B$, and $E_k$ 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 and 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 resulted in both changes in P-E parameters as well as in composition. 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 a clear 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., 2012). 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 within the seasonal data sets. The temperature range was modest (ca. 4°C), so the direct impact 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 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). Xie et al. (2015) also did not find a correlation between nutrients and \( P_E \), and suggested that reflected the lag time between nutrient inputs and phytoplankton growth in the English Chanel. 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. Reduced iron concentrations, however, resulted in lower \( P_E \) 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). Furthermore, because the experiments were completed in a constant irradiance environment, the impact of iron may have been lessened. Iron can influence growth rates of Antarctic diatoms (Timmermans et al., 2004; Mosby, 2013), 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 availability is rarely determined in parallel with P-E parameters. We suggest that the impacts of iron we observed – significantly reduced \( P_E \) 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 and Huntsman, 1996), which would result in lowered $P_{m}^{b}$ and $P_{s}^{b}$ values.

Determination of the exact cause of the iron effect on $P_{m}^{b}$ and $P_{s}^{b}$, 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 and constant irradiance conditions (ca. 7% that of surface irradiance), there was an increase in the light-limited rates of photosynthesis ($\alpha^{b}$) and light-saturated ($P_{m}^{b}$ and $P_{s}^{b}$) 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 (Prezelin, 1984; Dubinsky and Stambler, 2009). $P_{m}^{b}$ and $P_{s}^{b}$ 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 $P_{m}^{b}$, $P_{s}^{b}$ and $\alpha^{b}$ values, reinforcing the classical view of the limitation of short-term photosynthesis by carbon availability under high irradiance conditions. Enhanced $\alpha$ values may reflect the interaction between light-limited and light-saturated rates described by Behrenfeld et al. (2004). Interestingly, increased CO$_2$ levels had little impact on phytoplankton composition (Tortell et al., 2009), 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).

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 $\alpha^B_a$ and $P^B$ values of *P. antarctica* grown at constant irradiances (from 5 – 125 µmol photons m$^{-2}$ s$^{-1}$) and saturating nutrients were always greater than those of the diatom *Fragilariopsis cylindrus*. The diatom had low $P^B_a$, $P^B_s$ (from 0.46 to 0.54 µg C (µg chl)$^{-1}$ h$^{-1}$) and $\alpha^B_a$ values [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 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-E parameters of the dominant forms in spring and summer reflect the importance of selected environmental features (irradiance, iron) on their long-term success in 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 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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Figure 1. Map showing the location of the stations were 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.

Figure 3. Relationship of $\alpha$ (light-limited photosynthesis) and $P^\theta_s$ (irradiance-saturated photosynthesis) in samples from the Ross Sea. Solid line is the linear regression ($P^\theta_s = 10.9\alpha + 0.70; r^2 = 0.246; p < 0.001$).
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.

<table>
<thead>
<tr>
<th>Cruise Name</th>
<th>Dates of Sampling</th>
<th>N</th>
<th>$V_{inc}$ (mL)</th>
<th>F/NF</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>12/21/1995 – 1/13/1996</td>
<td>54</td>
<td>2</td>
<td>NF</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1/12/1997 – 2/8/2007</td>
<td>87</td>
<td>10</td>
<td>F</td>
<td></td>
</tr>
<tr>
<td>IVARS 1</td>
<td>12/19/2001 – 2/2/2002</td>
<td>6</td>
<td>2</td>
<td>NF</td>
<td>This report</td>
</tr>
<tr>
<td>IVARS 3</td>
<td>12/26/2003 – 2/6/2004</td>
<td>9</td>
<td>2</td>
<td>NF</td>
<td>This report</td>
</tr>
<tr>
<td>IVARS 4</td>
<td>12/19/2004 – 1/31/2005</td>
<td>16</td>
<td>2</td>
<td>NF</td>
<td>This report</td>
</tr>
<tr>
<td>IVARS 5</td>
<td>12/26/2005 – 1/2/2006</td>
<td>7</td>
<td>2</td>
<td>NF</td>
<td>This report</td>
</tr>
<tr>
<td>CORSACS 1</td>
<td>12/27/2005 – 1/31/2006</td>
<td>83</td>
<td>2</td>
<td>NF</td>
<td>This report</td>
</tr>
<tr>
<td>CORSACS 2</td>
<td>11/16/2006 – 12/11/2006</td>
<td>23</td>
<td>2</td>
<td>NF</td>
<td>This report</td>
</tr>
<tr>
<td>PRISM</td>
<td>1/8/2012 – 2/2/2012</td>
<td>77</td>
<td>2</td>
<td>NF</td>
<td>This report</td>
</tr>
</tbody>
</table>

*: Gravity filtration
Table 2. Mean, and standard deviations, and range of photosynthesis-irradiance parameters, mixed layer depths ($Z_{mix}$) and euphotic zone depths ($Z_{1\%}$) determined during IVARS and PRISM cruises. Units: $\alpha^B$: µg C (µg chl)$^{-1}$ h$^{-1}$ (µmol quanta m$^{-2}$ s$^{-1}$); $P_{sP}$: µg C (µg chl)$^{-1}$ h$^{-1}$; $E_k$: µmol photons m$^{-2}$ s$^{-1}$; $Z_{mix}$: m; $Z_{1\%}$: m. Number of observations in parentheses.

<table>
<thead>
<tr>
<th>Month</th>
<th>Year</th>
<th>$\alpha^B$</th>
<th>$P_{sP}$</th>
<th>$E_k$</th>
<th>$Z_{mix}$</th>
<th>$Z_{1%}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>December 2001</td>
<td>0.060 ± 0.015 (4)</td>
<td>2.3 ± 0.6</td>
<td>42.0 ± 10.5</td>
<td>37.1 ± 11.3</td>
<td>9.38 ± 8.9</td>
<td></td>
</tr>
<tr>
<td>February 2002</td>
<td>0.0087 (1)</td>
<td>0.845</td>
<td>110</td>
<td>35.1 ± 8.9</td>
<td>14.3 ± 14.5</td>
<td></td>
</tr>
<tr>
<td>December 2002</td>
<td>0.033 ± 0.012 (4)</td>
<td>0.972 ± 0.3</td>
<td>34.4 ± 11.6</td>
<td>28.5 ± 11.3</td>
<td>36.0 ± 15.8</td>
<td></td>
</tr>
<tr>
<td>December 2003</td>
<td>0.019 ± 0.0054 (5)</td>
<td>0.614 ± 0.356</td>
<td>37.6 ± 28.8</td>
<td>22.7 ± 10.1</td>
<td>27.8 ± 11.4</td>
<td></td>
</tr>
<tr>
<td>February 2004</td>
<td>0.067 ± 0.047 (4)</td>
<td>0.800 ± 0.57</td>
<td>16.3 ± 15.4</td>
<td>25.2 ± 8.6</td>
<td>25.8 ± 6.57</td>
<td></td>
</tr>
<tr>
<td>December 2004</td>
<td>0.022 ± 0.0098 (10)</td>
<td>1.10 ± 0.4248</td>
<td>62.4 ± 38.3</td>
<td>21.0 ± 6.47</td>
<td>23.8 ± 7.66</td>
<td></td>
</tr>
<tr>
<td>February 2005</td>
<td>0.051 ± 0.023 (6)</td>
<td>0.572 ± 0.048</td>
<td>14.4 ± 6.13</td>
<td>20.1 ± 7.44</td>
<td>24.6 ± 8.2</td>
<td></td>
</tr>
<tr>
<td>December 2005</td>
<td>0.070 ± 0.055 (7)</td>
<td>1.61 ± 0.80</td>
<td>28.7 ± 11.2</td>
<td>20.0 ± 10.5</td>
<td>24.0 ± 1.91</td>
<td></td>
</tr>
<tr>
<td>Mean: December</td>
<td>---</td>
<td>0.040 ± 0.325 (27)</td>
<td>42.19 ± 11.7 (72)</td>
<td>25.7 ± 10.1</td>
<td>23.0 ± 10.1 (50)</td>
<td></td>
</tr>
</tbody>
</table>
| Mean: --- | 0.053 ± 0.68 ± 23.3 ± 25.7 ± 22.9 ±
<table>
<thead>
<tr>
<th></th>
<th>February</th>
<th>PRISM, 2010</th>
<th>January</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>0.035 (11)</td>
<td>0.34</td>
<td>0.020 (77)</td>
<td>0.500</td>
<td>48.4</td>
</tr>
<tr>
<td>309.2</td>
<td>10.0 (65)</td>
<td>42.2 (116)</td>
<td>22.7 (116)</td>
<td>(116)</td>
</tr>
<tr>
<td>8.13 (45)</td>
<td>27.8 ±</td>
<td>42.2 ± 22.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.035 ±</td>
<td>1.14 ±</td>
<td>52.2 ±</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.020 ±</td>
<td>0.500 ±</td>
<td>48.4 ±</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Formatted:** Line spacing: 1.5 lines
Table 3. Comparison of PRISM photosynthetic parameters as a function of nitrate, and 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, and sea in situ temperatures above and below 0°C, and iron concentrations greater than or less than 0.1 nM. No significant differences occurred were noted between low vs. high-nutrient and low vs. high-temperature the two sets of parameters except where noted.

<table>
<thead>
<tr>
<th>Variable Group</th>
<th>N</th>
<th>$\alpha^B$</th>
<th>$P^B$</th>
<th>$E_k$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>($\mu$g C ($\mu$g chl)$^{-1}$ h$^{-1}$)</td>
<td>($\mu$g C ($\mu$g chl)$^{-1}$ h$^{-1}$)</td>
<td>($\mu$mol photons quanta m$^{-2}$ s$^{-1}$)</td>
</tr>
<tr>
<td>$[\text{NO}_3^-] &lt; 20$ µM</td>
<td>58</td>
<td>0.035 ± 0.020</td>
<td>1.245 ± 0.64</td>
<td>43.3 ± 34.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.012 – 0.095)</td>
<td>(0.29 – 3.109)</td>
<td>(76.58 – 193)</td>
</tr>
<tr>
<td>$[\text{NO}_3^-] &gt; 20$ µM</td>
<td>56</td>
<td>0.043 ± 0.039</td>
<td>1.246 ± 0.58</td>
<td>48.0 ± 47.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.0077 – 0.183)</td>
<td>(0.21 – 2.879)</td>
<td>(43.79 – 238)</td>
</tr>
<tr>
<td>$T &gt; 0$°C</td>
<td>44</td>
<td>0.040 ± 0.036</td>
<td>1.245 ± 0.66</td>
<td>44.6 ± 4049.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.015 – 0.183)</td>
<td>(0.29 – 3.109)</td>
<td>(76.58 – 193)</td>
</tr>
<tr>
<td>$T &lt; 0$°C</td>
<td>58</td>
<td>0.032 ± 0.021</td>
<td>1.245 ± 0.53</td>
<td>5049.7 ± 44.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.011 – 0.095)</td>
<td>(0.21 – 2.766)</td>
<td>(7825 – 238)</td>
</tr>
<tr>
<td>$[\text{Fe}] &lt; 0.1$ nM</td>
<td>6</td>
<td>0.375 ± 0.023</td>
<td>1.6 ± 0.55*</td>
<td>41 ± 18</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.021 – 0.053)</td>
<td>(1.1 – 2.7)</td>
<td>(28 – 54)</td>
</tr>
<tr>
<td>$[\text{Fe}] &gt; 0.1$ nM</td>
<td>33</td>
<td>0.029 ± 0.017</td>
<td>1.0 ± 0.44</td>
<td>48 ± 36</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.011 – 0.066)</td>
<td>(0.21 – 1.7)</td>
<td>(8 – 131)</td>
</tr>
</tbody>
</table>

*: t-test indicated a significant difference (p<0.01)
Table 4. Seasonal comparison of photosynthetic parameters from the Ross Sea.

<table>
<thead>
<tr>
<th>Season</th>
<th>$P_{\text{m}}$ ($\mu$g C ($\mu$g chl)$^{-1}$ h$^{-1}$)</th>
<th>$P_{\text{x}}$ ($\mu$g C ($\mu$g chl)$^{-1}$ h$^{-1}$)</th>
<th>$\alpha P_{\text{f}}$ ($\mu$mol photons quanta m$^{-2}$ s$^{-1}$)$^{-1}$</th>
<th>$E_{\text{k}}$ ($\mu$mol photons quanta m$^{-2}$ s$^{-1}$)</th>
<th>N</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>SPRING</td>
<td>1.72 ± 0.97</td>
<td>0.047 ± 0.023</td>
<td>37.0 ± 7.50</td>
<td>37</td>
<td>van Hilst and Smith (2002)</td>
<td></td>
</tr>
<tr>
<td>SUMMER</td>
<td>2.548 ± 1.329</td>
<td>0.087 ± 0.043</td>
<td>31.0 ± 16.0</td>
<td>31</td>
<td>Hiscock (2004)</td>
<td></td>
</tr>
<tr>
<td>SPRING</td>
<td>1.22 ± 0.54</td>
<td>0.036 ± 0.015</td>
<td>37.1 ± 13.4</td>
<td>70</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SUMMER</td>
<td>0.64 ± 0.26</td>
<td>0.016 ± 0.0068</td>
<td>442.9 ± 18.4</td>
<td>98</td>
<td></td>
<td></td>
</tr>
<tr>
<td>AUTUMN</td>
<td>0.70 ± 0.13</td>
<td>0.040 ± 0.017</td>
<td>210.7 ± 9.00</td>
<td>5</td>
<td>Saggiomo et al. (2002)</td>
<td></td>
</tr>
<tr>
<td>SUMMER</td>
<td>1.34 ± 0.39</td>
<td>0.073 ± 0.088</td>
<td>23 ± 8</td>
<td>51</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SPRING</td>
<td>1.878 ± 0.68</td>
<td>0.020 ± 0.0043</td>
<td>898.7 ± 23.1</td>
<td>15</td>
<td>Robinson et al. (2003)</td>
<td></td>
</tr>
<tr>
<td>SPRING$^2$</td>
<td>2.14 ± 0.48</td>
<td>0.072 ± 0.027</td>
<td>31.4 ± 8.04</td>
<td>10</td>
<td>Smyth et al. (2012)</td>
<td></td>
</tr>
<tr>
<td>SPRING</td>
<td>1.325 ± 0.72</td>
<td>0.040 ± 0.035</td>
<td>421.9 ± 298.7</td>
<td>27</td>
<td>IVARS: This report</td>
<td></td>
</tr>
<tr>
<td>SUMMER</td>
<td>0.68 ± 0.34</td>
<td>0.053 ± 0.035</td>
<td>23.3 ± 30.2</td>
<td>11</td>
<td>IVARS: This report</td>
<td></td>
</tr>
<tr>
<td>SUMMER</td>
<td>1.13 ± 0.500</td>
<td>0.035 ± 0.020</td>
<td>52.2 ± 48.4</td>
<td>77</td>
<td>PRISM: This report</td>
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</tr>
<tr>
<td>MEAN</td>
<td>1.437 ± 0.63</td>
<td>0.034 ± 0.024</td>
<td>44.0 ± 25.2</td>
<td>159</td>
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</tr>
<tr>
<td>MEAN</td>
<td>0.86 ± 0.45</td>
<td>0.023 ± 0.018</td>
<td>43.4 ± 28.3</td>
<td>268</td>
<td>---</td>
<td></td>
</tr>
<tr>
<td>OVERALL</td>
<td>1.167 ± 0.60</td>
<td>0.030 ± 0.023</td>
<td>443.7 ± 276.9</td>
<td>417</td>
<td>---</td>
<td></td>
</tr>
</tbody>
</table>

1: Weighted mean of all samples

2: $\alpha P_{\text{f}}$ and $E_{\text{k}}$ 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.

<table>
<thead>
<tr>
<th>Functional Group</th>
<th>$p_s^B$</th>
<th>$q_B$</th>
<th>$E_k$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phaeocystis</td>
<td>1.436 ± 0.76</td>
<td>0.067 ± 0.060</td>
<td>33.2 ± 3.2</td>
</tr>
<tr>
<td>(N=20)</td>
<td>Phaeocystis</td>
<td>Antarctica</td>
<td></td>
</tr>
<tr>
<td>Diatoms (N=20)</td>
<td>1.14 ± 0.63</td>
<td>0.050 ± 0.045</td>
<td>32.0 ± 19.0</td>
</tr>
</tbody>
</table>

33
Fig. 2
Figure 3.

![Graph showing data points for spring and summer labeled as 'Spring' and 'Summer'. The graph plots $P_b$ [\(\mu g C (\mu g \text{chl})^{-1} \text{h}^{-1}\)] against $\alpha$ [\(\mu g C (\mu g \text{chl})^{-1} \text{h}^{-1} \mu \text{mol photons m}^{-2} \text{s}^{-1}^{-1}\)].]