



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  $P_m^B$  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  $\alpha$  ( $\alpha^B$ ) 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.
6. Corrected to 1.13.
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  $\alpha$  and  $E_k$ , reduced the statistical power of the tests and resulted in a lack of significance in our comparisons of  $\alpha$  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.

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

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Running Head: Ross Sea photosynthesis

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22 **Abstract**

23 A meta-analysis of photosynthesis/irradiance measurements was completed using data from  
24 the Ross Sea, Antarctica. A total of 417 independent measurements were included.  $P_m^B$ , the  
25 maximum, chlorophyll-specific, irradiance-saturated rate of photosynthesis, averaged  $1.07 \pm$   
26  $0.060 \mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$ . Light-limited, [chlorophyll-specific](#) photosynthetic rates ( $\alpha^B$ ) averaged  
27  $0.03 \pm 0.023 \mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1} (\mu\text{mol photons m}^{-2} \text{ s}^{-1})^{-1}$ . Significant variations in  $P_m^B/P_s^B$  and  
28  $\alpha^B/\alpha$  were found as a function of season, with spring maximum photosynthetic rates being 59%  
29 greater than those in summer. Similarly,  $\alpha$  values were 48% greater in spring. There was no  
30 detectable effect of space on the photosynthetic parameters, and temperature and macronutrient  
31 ( $\text{NO}_3$ ) concentrations also did not exert a strong influence. However, irradiance, dissolved iron  
32 concentrations, and carbon dioxide concentrations when altered under controlled conditions  
33 exerted significant influences on photosynthetic parameters. Specifically, reduced irradiance  
34 resulted in decreased  $P_m^B/P_s^B$  and  $\alpha^B/\alpha$  values, whereas reduced iron concentrations were  
35 associated with increased  $P_m^B/P_s^B$  and  $\alpha^B/\alpha$  values. Increased  $\text{CO}_2$  concentrations also resulted in  
36 significantly increased  $P_m^B/P_s^B$  and  $\alpha^B/\alpha$  values. No significant difference was detected between  
37 stations dominated by diatoms and those dominated by the haptophyte *Phaeocystis antarctica*.  
38 The meta-analysis generally confirms the photosynthetic rates predicted from global analyses  
39 that are based solely on temperature and irradiance availability, but suggests that for more  
40 accurate predictions of the productivity of polar systems a more detailed model that includes  
41 temporal effects of photosynthetic parameters will be required.

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43 **1. Introduction**

44 The relationship of phytoplankton photosynthesis to irradiance is fundamental not only to our  
45 understanding of marine productivity, but also in predicting the response of marine systems to  
46 climate change and other anthropogenic alterations (Brown and Arrigo, 2012; Huot et al., 2013).  
47 This is especially true in high-latitude systems, where modifications in ice cover will bring  
48 dramatic changes in available irradiance and hence productivity (e.g., Montes-Hugo et al., 2008;  
49 Arrigo et al., 2013; Smith et al., 2014b), as well as changes in air-sea interactions and food-web  
50 dynamics (Smith et al., 2014a). Photosynthesis-irradiance (P-E) relationships are also essential  
51 components of estimating productivity from satellite remote sensing data, as productivity is  
52 generally modeled as a function of integrated chlorophyll concentrations, available irradiance,  
53 and the P-E response as a function of temperature (Behrenfeld and Falkowski, 1997; Platt and  
54 Sathyendranath, 2007). The temperature-photosynthesis relationship is generally assumed to be  
55 constant below 0°C (Behrenfeld and Falkowski, 1997), despite the fact that substantial  
56 oceanographic variability is known in other variables that influence photosynthesis in these  
57 waters.

58 P-E responses are generally described by a relatively simple equation that parameterizes the  
59 response as a function of irradiance:  $P_s^B$ , the maximum, biomass-specific rate of photosynthesis  
60 at saturating irradiances,  $\alpha^B$ , the irradiance-limited, biomass-specific linear portion of the  
61 hyperbolic response, and  $\beta^B$ , the portion of the curve where photosynthesis decreases at high  
62 irradiances (photoinhibition) (Platt et al., 1980).  $P_m^B$  is the maximum rate of photosynthesis at  
63 saturating irradiances in the absence of photoinhibition. A parameter describing the irradiance at  
64 which saturation is initiated,  $E_R$ , is derived from the ratio of  $P_s^B$  and  $\alpha^B$ . Chlorophyll *a*  
65 concentrations are generally used as an index of biomass. Estimates of photoinhibition are often

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66 difficult to obtain and are thought to represent a non-steady state condition (Marra et al., 1985),  
67 and measurements often do not result in statistically significant estimates of  $\beta^B$  (van Hilst and  
68 Smith, 2002; Huot et al., 2013); hence  $\beta^B$  is often assumed to be zero.

69 P-E responses from the Southern Ocean have been assessed from a number of regions (e.g.,  
70 West Antarctic Peninsula: Brightman and Smith, 1989; Moline et al., 1994; Scotia Sea: Tilzer et  
71 al., 1986; Ross Sea: van Hilst and Smith, 2002; Robinson et al., 2003; Smyth et al., 2012), but  
72 unlike for the Arctic Ocean (Platt et al., 1980; Huot et al., 2013), no synthesis of photosynthetic  
73 responses or their environmental controls is available. Different investigators also have used  
74 slightly different methods, making a comparison more difficult; furthermore, because regions in  
75 the Southern Ocean change rapidly, it is challenging to interpret the results of changing P-E  
76 responses in the context of spatial and temporal variability of oceanographic conditions. In  
77 general, phytoplankton in the Southern Ocean exhibit low maximum photosynthetic rates  
78 (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  
79 from which the phytoplankton were sampled. That is, when phytoplankton are sampled from  
80 within a deeply mixed surface layer or from under the ice,  $E_K$  values are low, reflecting an  
81 acclimation to reduced available irradiance. Conversely,  $E_K$  values generally increase when  
82 phytoplankton are sampled from stratified, ice-free environments in summer that are  
83 characterized by higher irradiance values.

84 The Ross Sea is among the best studied areas in the Antarctic, and a great deal is known  
85 about its oceanography, productivity, temporal and spatial variability, and food web dynamics  
86 (Smith et al., 2012. 2014b). Despite a broad understanding of the system's characteristics, a full  
87 synthesis of the area's photosynthesis-irradiance relationships is lacking. It is known that the  
88 colonial haptophyte *Phaeocystis antarctica* typically blooms in austral spring and reaches high

89 abundance (Tremblay and Smith, 2007; Smith et al., 2014a), and disappears rapidly from the  
90 water column after reaching its seasonal maximum (Smith et al., 2011). Laboratory and field  
91 investigations have shown that *P. antarctica* is well adapted to growth at low and variable  
92 irradiances characteristic of deeply mixed surface layers and under ice (Kroupenske et al., 2009;  
93 Arrigo et al., 2010). In contrast, diatoms often bloom after *P. antarctica* is reduced in biomass,  
94 but the magnitude of the diatom growth is highly variable among years (Peloquin and Smith,  
95 2007). Diatoms are in general capable of growth at higher photon flux densities, characteristic of  
96 stratified, summer conditions and close proximity to melting sea ice (Arrigo et al., 2010). The  
97 general distributions of both functional groups suggest that the photosynthetic capacity of each is  
98 different and reflects the in situ habitat that each is found. Despite this, van Hilst and Smith  
99 (2002) and Robinson et al. (2003) were unable to show a statistically significant difference  
100 between the P-E responses of samples dominated by one functional group or the other. This  
101 suggests that the distribution of functional groups may be strongly influenced by factors other  
102 than just photosynthesis, despite photophysiological abilities and acclimations to different  
103 environments.

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

112

## 113 **2. Methods**

### 114 *2.1. Analytical Procedures*

115 Samples were collected during a number of cruises, most of which concentrated their  
116 sampling in the southern Ross Sea (Fig. 1). The first was IVARS (Interannual Variations in the  
117 Ross Sea; Smith et al., 2011a,b), which collected samples during short cruises twice each year,  
118 with the first cruise sampling ice-free periods in late December and the second sampling the end  
119 of summer (early February). The second project was CORSACS (Controls on Ross Sea Algal  
120 Community Structure), which had two cruises. The first cruise began in ~~January~~[late December](#),  
121 2006 and the second was in November-December, 2006 (Sedwick et al., 2011; Smith et al.,  
122 2013). ~~Many of the~~ P-E results from CORSACS involved experimental manipulations of  
123 irradiance, dissolved iron and CO<sub>2</sub> concentrations and used trace-metal clean procedures (Feng et  
124 al., 2010; Rose et al., 2010). The final project was PRISM (Processes Regulating Iron Supply at  
125 the Mesoscale), which sampled in January-February, 2012 ([Smith and Jones, 2014](#);  
126 [McGillicuddy et al., in review](#)~~press~~; ~~Smith and Jones, 2014~~). Figure 1 shows the locations of the  
127 stations analyzed for photosynthesis/irradiance relationships. Published measurements from  
128 other investigations are [also](#) included in the meta-analysis (e.g., van Hilst and Smith , 2002;  
129 Robinson et al., 2003; Saggiomo et al., 2004; Hiscock, 2004; Smyth et al., 2012).

130 Photosynthesis-irradiance (P-E) relationships of phytoplankton were determined by assessing  
131 uptake of <sup>14</sup>C-bicarbonate in short incubations (Lewis and Smith, 1983). The largest difference  
132 among the different published reports was sample filtration; samples that were not filtered thus  
133 included any short-term DOC release (Table 1). Robinson et al. (2003) concluded that filtration  
134 of samples dominated by colonial *Phaeocystis antarctica* resulted in an underestimate of  
135 photosynthetic rates, but comparison within IVARS and CORSACS did not identify this

136 systematic bias (Smith, unpublished). Samples were generally collected from one or two depths  
 137 (generally that of the 50 and 1% isolumes) at each station [\(50% depths were generally from 1-4](#)  
 138 [m, and 1% depths from 15-50 m\)](#), to which ca. 100  $\mu\text{Ci NaH}^{14}\text{CO}_3$  were added. Incubations  
 139 were conducted at a constant temperature from the depth of sampling (determined by the CTD  
 140 cast and maintained by a circulating water bath). Samples were placed in glass scintillation vials  
 141 in a photosynthetron that provided a wide range of irradiances, but ultraviolet radiation was  
 142 excluded by the incubation design. Photosynthetically available radiation was modified from the  
 143 maximum value by neutral density screening at irradiances ca. 70% of the full irradiance, and by  
 144 a combination of neutral and blue screening at lower irradiances (Laws et al., 1990). Darkened  
 145 vials served as controls. Irradiance was measured for each sample; the total number of  
 146 irradiances used ranged from 16 to 32. Incubations lasted approximately 2 h. All samples were  
 147 counted on liquid scintillation counters, and total available inorganic  $^{14}\text{C}$ -bicarbonate was  
 148 assessed by counting aliquots directly in scintillation fluor. While details of the methods of each  
 149 study varied somewhat, we ~~did not find~~ [were unable to detect a significant difference between](#)  
 150 [filtered and unfiltered results, and concluded](#) that the methods ~~did not~~ introduced [a significant](#)  
 151 [source of](#) error to obscure the overall patterns.

152 ~~All d~~Data were fitted to the rectilinear hyperbolic model of Platt et al. (1980):

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

154 where  $P^B$  = the rate of photosynthesis normalized to chlorophyll  $a$  [ $\text{mg C (mg chl } a)^{-1} \text{ h}^{-1}$ ],  $P_m^B$   
 155  ~~$P_s^B$~~  = the maximum, irradiance-saturated rate of photosynthesis in the absence of photoinhibition,  
 156  ~~$\alpha^B$~~  = the initial, light-limited, linear photosynthetic rate [normalized to chlorophyll](#) [ $\text{mg C (mg}$   
 157  $\text{chl } a)^{-1} \text{ h}^{-1}$  ( $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ )], and  $E$  = irradiance ( $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ). Some of the

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158 published analyses included  $\beta^B$ , the photoinhibition parameter, but for consistency these were  
159 omitted in this meta-analysis, since  $\beta^B$  appears to represent a non-equilibrium conditions and in  
160 our samples was not consistently evident (Denman and Marra, 1986; MacIntyre et al., 2002).

161 [Photoinhibitory data from stations where photoinhibition occurred were not removed, as the](#)  
162 [impact on photosynthetic parameters was generally minor.](#) The derived parameter  $E_k$  (the  
163 irradiance at which photosynthesis becomes saturated) is calculated by:

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

164  
165  $E_k$  provides a measure by which the acclimation to irradiance can be compared. If the  
166 observations did not result in a significant determination of both  $\alpha^B$  and  $P_m^B - P_s^B$  ( $p < 0.05$ ),  
167 then the entire sample was omitted from analysis.

168 Chlorophyll *a* concentrations were analyzed by fluorometry (JGOFS, 1996) on independent  
169 samples collected from the same depth. Nutrient ( $\text{NO}_3$ ,  $\text{NO}_2$ ,  $\text{PO}_4$ ,  $\text{Si}(\text{OH})_4$ ,  $\text{NH}_4$ ) analyses were  
170 performed at sea on a Lachat QuickChem Autanalyzer using standard automated techniques.  
171 Mixed layer depths were determined from density profiles determined from CTD casts using a  
172 change in density of  $0.01 \text{ kg m}^{-3}$  from a stable surface value (Thomson and Fine, 2003; Smith et  
173 al., 2013). Seawater samples for dissolved iron analysis were collected in custom-modified 5-L  
174 Teflon-lined, external-closure Niskin-X samplers (General Oceanics Inc.) or 10-L teflon-lined  
175 GO-FLO samplers, all of which were deployed on a non-metal line (Sedwick et al., 2011).  
176 Filtered samples were acidified to pH 1.7 with ultrapure hydrochloric acid and stored for at least  
177 24 h prior to the analysis of dissolved iron. Dissolved iron was determined by flow injection  
178 analysis with colorimetric detection after in-line pre-concentration on resin-immobilized 8-  
179 hydroxyquinoline (Sedwick et al., 2008).

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180 2.2. *Statistical analyses*

181 All responses were fit to a 2-parameter exponential increase to maxima in SigmaPlot 12.3,  
182 which provided estimates of  $P_m^B/P_s^B$  and  $\alpha^B$  and their significance, as determined by a t-test.

183 [Comparisons between data sets were made using analyses of variance.](#) An *a priori* limit of  
184 significance was set as  $p < 0.05$ . Data were tested for normality and homogeneity of variance,  
185 and ANOVAs were performed using R (v2.13.2). [Stations selected for a comparison of the](#)  
186 [effects of assemblage composition were chosen based on HPLC analysis of pigments and the](#)  
187 [contribution of each functional group to total chlorophyll \(Mackey et al., 1996\). When pigment](#)  
188 [data were not included in the published reports, taxonomic discrimination was made by reported](#)  
189 [microscopic results.](#)

190  
191 **3. Results**

192 3.1. *IVARS, CORSACS and PRISM Photosynthesis/Irradiance Determinations*

193 P-E determinations in IVARS were conducted during the peak of the spring bloom (generally  
194 late December) and at the end of summer (early February) (Smith et al., 2011a). Ice  
195 concentrations were  $< 15\%$  at all stations. Average  $\alpha^B$ ,  $P_m^B/P_s^B$  and  $E_k$  values for December  
196 and February were  $0.040 \pm 0.035$  and  $0.053 \pm 0.035 \mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$  ( $\mu\text{mol photons m}^{-2} \text{ s}^{-1})^{-1}$ ,  
197  $1.25 \pm 0.725$  and  $0.68 \pm 0.34 \mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$ , and  $424.9 \pm 298.7$  and  $23.3 \pm 30.2 \mu\text{mol}$   
198  $\text{photons m}^{-2} \text{ s}^{-1}$ , respectively (Table 2).  $P_m^B/P_s^B$  values of the two seasons were significantly  
199 different ( $p < 0.05$ ), but  $\alpha^B$  and  $E_k$  values were not.

200 CORSACS measurements were largely conducted as part of experiments that manipulated  
201 irradiance (7 and 33% of surface irradiance), iron concentrations (ambient and +1 nM), and CO<sub>2</sub>  
202 concentrations (380 and 750  $\mu\text{atm}$ ) (Feng et al., 2010). Natural populations were used as inocula

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203 in semi-continuous cultures (Hutchins et al., 2003), and P-E determinations were made through  
204 time on all treatments to assess the impact of each variable (and their interactions) on short-term  
205 photosynthetic responses. Irradiance variations generated changes in  $P_m^B/P_s^B$ ,  $\alpha^B$  and  $E_k$   
206 values, which increased significantly ( $p < 0.05$ ) at the low and constant irradiances (Figure 2).  
207 Increased CO<sub>2</sub> concentrations also resulted in significantly ( $p < 0.05$ ) increased  $\alpha^B$  and  $P_m^B/P_s^B$   
208 values, although little net change was noted in  $E_k$  values. Finally, increased iron concentrations  
209 did not impact either  $\alpha^B$  or  $P_m^B/P_s^B$  values significantly in these experiments (Figure 2).  $P_m^B/P_s^B$   
210 values were greater than those representing sub-optimal, in situ conditions such as in IVARS and  
211 PRISM.

212 PRISM samples investigated the broad spatial patterns of P-E responses (Table 2). The mean  
213  $\alpha^B$  and  $P_m^B/P_s^B$  values were  $0.035 \pm 0.020$  ( $\mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$  ( $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ )<sup>-1</sup>) and  
214  $1.143 \pm 0.50$   $\mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$ , respectively. The average  $E_k$  value was  $52.2 \pm 48.4$   $\mu\text{mol}$   
215  $\text{photons m}^{-2} \text{ s}^{-1}$ . There was no significant different between PRISM P-E parameters and those  
216 collected during IVARS (December, February, or the total data set), and again no spatial pattern  
217 was observed. ~~There was no significant difference in the combined IVARS, PRISM and~~  
218 ~~CORSACS field data when the depth of sampling (50 vs. 1% of surface irradiance) in any~~  
219 ~~photosynthetic parameter.~~

220 Iron and nitrate concentrations were measured during PRISM at a number of stations where  
221 P-E measurements were conducted during PRISM (McGillicuddy et al., in review press).  
222 Dissolved Fe levels ranged from 0.066 to 0.69 nM, and nitrate ranged from 9.05 to 30.6  $\mu\text{M}$ . No  
223 significant difference in the mean  $\alpha^B$ ,  $P_m^B/P_s^B$  or  $E_k$  values were observed between the stations  
224 with nitrate concentrations less than 20  $\mu\text{M}$  and those with concentrations  $> 20$   $\mu\text{M}$  (Table 3). In

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225 contrast, at stations with Fe concentrations below and above 0.10 nM (a level that approximates  
226 the onset of Fe limitation in Antarctic phytoplankton; Timmermans et al., 2004),  $P_m^B/P_s^B$  values  
227 were significantly ( $p < 0.01$ ) greater ( $1.58 \pm 0.55$  vs.  $0.95 \pm 0.45$ ) at lower iron concentrations  
228 (Table 3).  $\alpha^B$  and  $E_k$  values, however, were not significantly different, suggesting that iron  
229 largely impacts irradiance-saturated photosynthetic rates, which in turn are largely controlled by  
230 carbon fixation processes.

231 There was no significant difference in the combined IVARS, JGOFS and PRISM data when  
232 the depth of sampling (50 vs. 1% of surface irradiance) in any photosynthetic parameter. This  
233 lack of correlation is different from the CORSACS results (Fig. 2), which were conducted under  
234 constant irradiance using natural assemblages. Available irradiances at the time of sampling do  
235 not necessarily reflect the irradiance that influenced growth over times scales of days to weeks,  
236 which are unknown. This suggests that there is no substantial photoacclimation within the water  
237 column, which in turn may suggest that the time needed for acclimation at these temperatures  
238 may be longer than the time scales of water column perturbation.

### 239 3.2. Comparison with Previous P-E Determinations

240 Because P-E determinations have been conducted during the past two decades with a similar  
241 methodology, we merged all data from the Ross Sea to assess the average photosynthetic  
242 response by season (Table 4). There is a significant difference between austral spring and  
243 summer averages for  $P_m^B/P_s^B$  and  $\alpha^B$  values, with spring having a greater  $P_m^B/P_s^B$  (1.37 vs.  
244 0.86) and  $\alpha^B$  values (0.034 vs. 0.023). However, no significant difference was observed  
245 between spring and summer  $E_k$  values. Values of  $\alpha^B$  and  $P_m^B/P_s^B$  were correlated ( $P_m^B/P_s^B =$   
246  $10.91\alpha^B + 0.070$ ;  $R^2 = 0.383$ ;  $p < 0.001$ ; Fig. 3), as has been found previously (van Hilst and  
247 Smith, 2002; Behrenfeld et al., 2004), but the large amount of variability in the relationship

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248 suggests that each is being influenced by ~~numerous~~ multiple independent factors as well. No  
249 interannual temporal trend was obvious, and interannual variability was substantial (Table 4).

250 The overall  $\frac{P_m^B}{P_s^B}$  average for all samples (n = 4157) equaled  $1.07 \pm 0.77 \mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$ ,  
251  $\alpha^B = 0.030 \pm 0.023 \mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1} (\mu\text{mol photons m}^{-2} \text{ s}^{-1})^{-1}$  and  $E_k = 443.7 \pm 276.9 \mu\text{mol}$   
252  $\text{photons m}^{-2} \text{ s}^{-1}$ .

### 253 3.3. Controls by Environmental Factors and Phytoplankton Composition

254 We tested for the effects of nitrate and temperature from the depth of sampling on P-E  
255 parameters from all cruises. The data were arbitrarily divided above and below  $20 \mu\text{M NO}_3$  and  
256 above and below  $0^\circ\text{C}$ , and the P-E parameters compared. Nitrate concentrations at the time of  
257 sampling ranged from  $9.5 - 31.0 \mu\text{M}$ , and 54 P-E measurements were conducted with  $\text{NO}_3$   
258 concentrations greater than  $20 \mu\text{M}$ . 58 analyses were conducted with  $\text{NO}_3$  levels less than  $20$   
259  $\mu\text{M}$ . Sample temperatures ranged from  $-1.6 - 2.58^\circ\text{C}$ ; 58 of the 102 P-E determinations were  
260 below  $0^\circ\text{C}$ , and 44 were above. No significant differences were noted for any of the three  
261 photosynthetic parameters within the nitrate or temperature data subsets, suggesting that short-  
262 term photosynthesis is largely independent of these environmental controls.

263 The two dominant functional groups in the Ross Sea, diatoms and haptophytes (largely  
264 *Phaeocystis antarctica*), have different temporal and spatial distributions, with *P. antarctica*  
265 generally dominating in spring in water columns with deeper vertical mixing, and diatoms  
266 dominating in more stratified, summer conditions (Smith et al., 2014a). *P. antarctica* largely  
267 occurs in cold waters ( $< 0^\circ\text{C}$ ) and is responsible for the spring reduction in micro- and  
268 macronutrients (Liu and Smith, 2012). To investigate if the two taxa have different  
269 photosynthesis-irradiance responses, we selected 40 stations that were identified by chemical or  
270 microscopic means as being overwhelmingly dominated by one of these groups, and assessed

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271 their P-E characteristics (Table 5). We found no statistical difference between the two groups  
272 with respect to  $\alpha^B$ ,  $P_m^B$  or  $P_s^B$  or  $E_k$  values.

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## 274 4. Discussion

### 275 4.1. Overall Patterns of Photosynthetic Parameters

276 One major finding of this meta-analysis is that the average maximum, light-saturated rate of  
277 photosynthesis equals  $1.07 \mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$  (Table 4). This is similar to the  $P_{opt}^B$  value  
278 determined from Behrenfeld and Falkowski's (1997) polynomial equation ( $1.29 \mu\text{g C } (\mu\text{g chl})^{-1}$   
279  $\text{h}^{-1}$ ) at  $0^\circ\text{C}$ , despite the difference between  $P_{opt}^B$  and  $P_m^B$  or  $P_s^B$  as well as the range of temperatures at  
280 which the P-E determinations were conducted. ~~It therefore strongly~~ Our results reinforces the  
281 validity of using their equation to estimate maximum photosynthetic rates and primary  
282 productivity within the waters of the Ross Sea, and presumably the entire Southern Ocean. This  
283 average can also be used in other bio-optical models of production to constrain the rates of  
284 carbon fixation over broad areas (e.g., Arrigo et al., 2003, 2008). However, given the seasonal  
285 variability observed, more detailed models that incorporate seasonal and environmental impacts  
286 may require inclusion of other oceanographic variables to more accurately predict production.

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287 We found relatively minor spatial differences in photosynthetic parameters, but significant  
288 seasonal differences. Specifically,  $\alpha^B$  and  $P_m^B$  or  $P_s^B$  values of the entire meta-analysis data set  
289 were significantly greater during spring than summer (both  $p < 0.001$ ), which is consistent with  
290 the large seasonal changes found in nearly all oceanographic and biological variables. The  
291 macro-environment of the Ross Sea continental shelf changes markedly from spring to summer,  
292 with increased temperatures, ~~stronger and~~ vertical stratification, shallower mixed layers,  
293 decreased macro- and micronutrient concentrations, and an altered assemblage composition

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294 (Smith et al., 2012). [All of these variables have been shown to influence P-E responses in](#)  
295 [laboratory and field studies \(e.g., MacIntyre et al., 2002; Xie et al., 2015\), and](#) As such, it is not  
296 surprising that the P-E parameters also changed. [It is tempting to suggest that the seasonal](#)  
297 [changes were driven by changes in phytoplankton composition, but we believe that the seasonal](#)  
298 [changes in oceanographic conditions resulted in both changes in P-E parameters as well as in](#)  
299 [composition. An experiment which isolates natural assemblages \(perhaps a Lagrangian tracking](#)  
300 [of a parcel of water that is dominated by one taxa or a large-volume mesocosm experiment such](#)  
301 [as has been conducted in the Baltic Sea; Riebesell et al., 2013\) would be a clear test of the](#)  
302 [impacts of composition and the seasonal changes in P-E parameters.](#) Clearly the growth  
303 environment usually found in summer in the Ross Sea is not favorable to high photosynthetic  
304 rates, a conclusion that have been consistently corroborated by direct measurements of  
305 productivity (e.g., Long et al., 2012). It was impossible to accurately assess interannual  
306 variations, given the relatively low numbers of samples in some years, but in view of the large  
307 variations observed from 1995 through 2010, any interannual trend is likely obscured by the  
308 substantial seasonal variability.

#### 309 *4.2. Controls of Photosynthesis-Irradiance Parameters*

310 While not all data sets had complete macro- and micronutrient data available for inclusion,  
311 we were unable to detect any controls of short-term photosynthetic rates by temperature or  
312 nitrate [within the seasonal data sets](#). The temperature range was modest (ca. 4°C), so the direct  
313 impact may have been limited and obscured by other factors. Liu and Smith (2012)  
314 demonstrated that the environmental factor that had the strongest impact on phytoplankton  
315 biomass was temperature. They found that that diatoms were more likely to be found in waters  
316 above 0°C, and in sub-zero waters assemblage composition was more often dominated by

317 *Phaeocystis antarctica*. Waters with temperatures less than 0°C also tend to have deeper mixed  
318 layers, which also favor the growth of *P. antarctica* (Tremblay and Smith, 2007). Nitrate  
319 concentrations varied more widely (from 9.3 to 31 µM), but still remained above those thought  
320 to limit nitrogen uptake (Cochlan et al., 2002). [Xie et al. \(2015\) also did not find a correlation](#)  
321 [between nutrients and  \$P\_m^B\$ , and suggested that reflected the lag time between nutrient inputs and](#)  
322 [phytoplankton growth in the English Chanel. They also found a complicated relationship](#)  
323 [between photosynthetic parameters and temperature and suggested that each functional group](#)  
324 [had temperature optima that were characterized by specific photosynthetic responses.](#) Reduced  
325 iron concentrations, however, resulted in lower  $P_m^B$  values, despite the relatively limited number  
326 of measurements at concentrations ~~greater~~ less than 0.1 nM. In contrast, we did not detect a  
327 change at the end of the controlled experiments (CORSACS) in which iron concentrations were  
328 measured, but all but one of those experiments had dissolved Fe concentrations > 0.13 nM (Feng  
329 et al., 2010), concentrations which are substantially greater than those found in situ (Sedwick et  
330 al., 2011). [Furthermore, because the experiments were completed in a constant irradiance](#)  
331 [environment, the impact of iron may have been lessened.](#) Iron can influence growth rates of  
332 Antarctic diatoms (Timmermans et al., 2004; Mosby, 2013), but growth rate responses are  
333 integrated over many days, whereas P-E responses are not immediately influenced by iron  
334 additions (Hiscock et al., 2008). ~~Furthermore, it~~ is tempting to suggest that the reduced summer  
335 P-E parameters may have resulted from iron limitation, but iron availability is rarely determined  
336 in parallel with P-E parameters. We suggest that the impacts of iron we observed – significantly  
337 reduced  $\frac{P_m^B}{P_s^B}$  values – were mediated by a long-term assemblage response rather than on  
338 short-term photosynthesis rates. Iron limitation can impact chlorophyll synthesis (in a manner  
339 similar to irradiance), and under co-limitation by iron and irradiance chlorophyll levels can be

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340 elevated (Sunda and Huntsman, 1996), which would result in lowered  $\frac{P_m^B}{P_s^B}$  values.

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341 Determination of the exact cause of the iron effect on  $\frac{P_m^B}{P_s^B}$ , however, is impossible with the  
342 present data set.

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343 The CORSACS experiments showed a clear impact of both irradiance and [CO<sub>2</sub>] on  
344 photosynthetic responses. Under low and constant irradiance conditions (ca. 7% that of surface  
345 irradiance), there was an increase in the light-limited rates of photosynthesis ( $\alpha^B$ ) and light-  
346 saturated ( $\frac{P_m^B}{P_s^B}$ ) values (Fig. 2). Low irradiance conditions often generate increased

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347 chlorophyll concentrations per cell, but can also generate increased photosynthetic efficiencies  
348 (via changes in photosynthetic units), which can result in elevation of both parameters (Prezelin,  
349 1984; Dubinsky and Stambler, 2009).  $\frac{P_m^B}{P_s^B}$  reflects the light-saturated rate, and presumably is

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350 set by the amount of carbon that can be reduced by the cells, which in turn is thought to be  
351 limited by the amount of chemical energy generated by the cells' photosystems. Increasing

352 carbon dioxide concentrations resulted in a marked and significant increase in  $\frac{P_m^B}{P_s^B}$  and  $\alpha^B$

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353 values, reinforcing the classical view of the limitation of short-term photosynthesis by carbon  
354 availability under high irradiance conditions. Enhanced  $\alpha$  values may reflect the interaction  
355 between light-limited and light-saturated rates described by Behrenfeld et al. (2004).

356 Interestingly, increased CO<sub>2</sub> levels had little impact on phytoplankton composition (Tortell et al.,  
357 2009), and independent measurements suggest that most Antarctic phytoplankton have a  
358 relatively broad capability to use a wide range of carbon dioxide concentrations (Tortell et al.,  
359 2006). Although it is tempting to suggest that future increases in oceanic CO<sub>2</sub> concentrations  
360 might increase maximum photosynthetic rates, such changes need to be assessed using long-term

361 experiments that allow for acclimation and adaptation over many generations (e.g., Lohbeck et  
362 al., 2012).

363 The influence of phytoplankton composition was insignificant (Table 5). This is consistent  
364 with the previous results of van Hilst and Smith (2002) using a less extensive data set, but in  
365 contrast to the extensive laboratory results of Arrigo et al. (2010), who found that  $\alpha^B$  and  $P_m^B$   
366  $P_s^B$  values of *P. antarctica* grown at constant irradiances (from 5 – 125  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) and  
367 saturating nutrients were always greater than those of the diatom *Fragilariopsis cylindrus*. The  
368 diatom had low  $P_m^B P_s^B$  [from 0.46 to 0.54  $\mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$ ] and  $\alpha^B$  values [0.014 to 0.043  
369 ( $\mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1} (\mu\text{mol photons m}^{-2} \text{s}^{-1})^{-1}$ )] when compared to those of the haptophyte (from  
370 1.4 to 6.4, and 0.038 to 0.11, respectively). The diatom parameters determined in culture were  
371 lower than our data subset, and the haptophyte values higher; these differences likely reflect the  
372 parameters of the individual species cultured and/or the influence of constant growth conditions.  
373 The in situ data also had substantial variability, which likely resulted from the environmental  
374 conditions that allowed one particular functional group to dominate. Appearance of taxa in situ  
375 reflects a long-term process involving both growth and losses, and both field and laboratory data  
376 suggest that the P-E parameters of the dominant forms in spring and summer reflect the  
377 importance of selected environmental features (irradiance, iron) on their long-term success in the  
378 water column.

379 In summary, the broad photosynthetic responses of Ross Sea phytoplankton are consistent  
380 with the patterns used in global production estimates from satellite biomass estimates. However,  
381 strong and significant seasonal differences occur, as do differences driven by irradiance, iron  
382 concentrations, and carbon dioxide levels. Such significant differences may need to be included  
383 in regional models of productivity and carbon flux. While these results may suggest that future

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384 changes in photosynthetic capacity and production in the Ross Sea as a result of climate change  
385 could be substantial, confirmation of this awaits future analyses of these parameters.

386

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391

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534 | **Figure Legends**

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

538 Figure 2. Photosynthesis-irradiance parameters determined from experimental manipulations of  
539 natural populations. Samples had either high or low (33 or 7% of surface value)  
540 irradiance, high or low (750 or 380 ppm) CO<sub>2</sub>, and high or low (+1 nM and ambient; ca.  
541 0.1 nM) iron concentrations. Asterisks indicate a significant difference between the  
542 high and low treatments within each variable.

543 Figure 3. Relationship of  $\alpha$  (light-limited photosynthesis) and  $P_s^B$  (irradiance-saturated  
544 photosynthesis) in samples from the Ross Sea. Solid line is the linear regression ( $P_s^B =$   
545  $10.9\alpha + 0.70$ ;  $r^2 = 0.246$ ;  $p < 0.001$ ).

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

<b>Cruise Name</b>	<b>Dates of Sampling</b>	<b>N</b>	<b><math>V_{inc}</math> (mL)</b>	<b>F/NF</b>	<b>Reference</b>
RSP <sup>2</sup>	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

549 \*: Gravity filtration

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

Month	Year	$\alpha^B$ ( $\mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$ ) ( $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ) $^{-1}$ )	$P_m^B$ ( $\mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$ )	$E_k$ ( $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ )	$Z_{mix}$	$Z_{1\%}$
December	2001	0.060 ± 0.015 (4)	2.33 ± 0.6105	42.0 ± 18.1	37.1 ± 13.3 (17)	9.38 ± 1.06 (8)
February	2002	0.00877 (1)	0.845	110	35.1 ± 8.96 (16)	14.3 ± 2.74 (9)
December	2002	0.033 ± 0.012 (4)	0.972 ± 0.3219	34.4 ± 243.6	28.5 ± 7.09 (8)	36.0 ± 14.5 (3)
December	2003	0.019 ± 0.00546 (5)	0.611 ± 0.356	376.9 ± 288.0	22.7 ± 10.1 (12)	27.8 ± 11.4 (9)
February	2004	0.067 ± 0.047 (4)	0.800 ± 0.57	16.3 ± 15.3	25.2 ± 8.67 (25)	25.8 ± 6.57 (12)
December	2004	0.022 ± 0.00987 (10)	1.10 ± 0.4218	621.5 ± 38.3	21.0 ± 6.47 (23)	23.8 ± 7.66 (23)
February	2005	0.051 ± 0.023 (6)	0.577 ± 0.048	143.6 ± 6.13	20.1 ± 7.44 (24)	24.6 ± 8.20 (25)
December	2005	0.070 ± 0.055 (7)	1.61 ± 0.80	287.6 ± 11.2	20.0 ± 10.5 (12)	24.0 ± 1.91 (7)
Mean:	---	0.040 ±	1.325 ±	421.9 ±	25.7 ±	23.0 ±
December		0.035 (27)	0.72	298.7	11.7 (72)	10.1 (50)
Mean:	---	0.053 ±	0.68 ±	23.3 ±	25.7 ±	22.9 ±

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February		0.035 (11)	0.34	<del>300.2</del>	<u>10.0 (65)</u>	<u>8.13 (45)</u>
PRISM,	2010	0.035 ±	1.13 ±	52.2 ±	<u>27.8 ±</u>	<u>42.2 ± 22.8</u>
January		0.020 (77)	0.500	48.4	<u>22.7 (116)</u>	<u>(116)</u>

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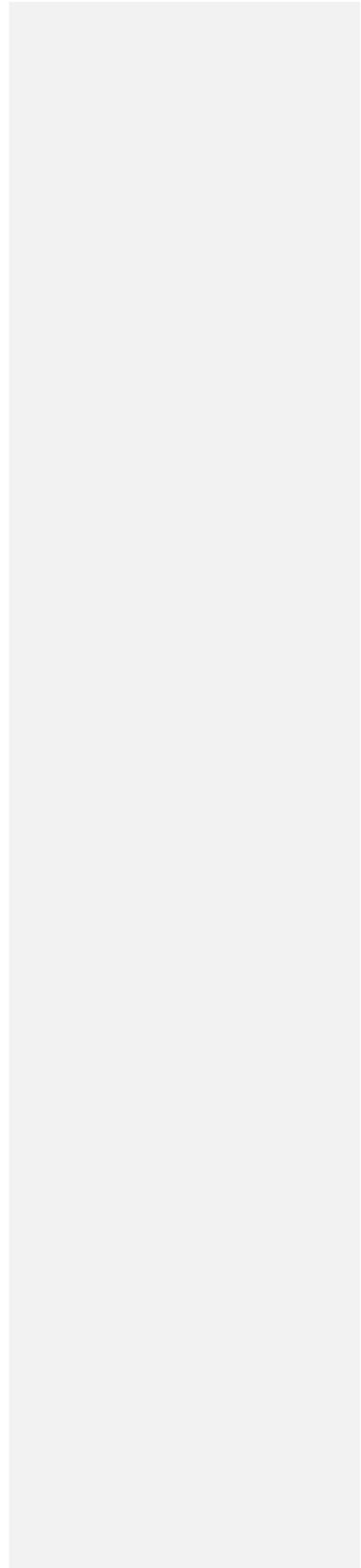
556 Table 3. Comparison of PRISM photosynthetic parameters as a function of nitrate, ~~and~~  
 557 temperature ~~and iron~~ (means and standard deviations). Range of data listed in parentheses. The  
 558 available data were divided into those stations that had nitrate concentrations above and below  
 559 20  $\mu\text{M}$ , ~~and sea in situ~~ temperatures above and below  $0^\circ\text{C}$ , ~~and iron concentrations greater than or~~  
 560 ~~less than 0.1 nM~~. No significant differences ~~occurred were noted~~ between ~~low vs. high nutrient~~  
 561 ~~and low vs. high temperature~~ the two sets of parameters ~~except where noted~~.  
 562

Variable Group	N	$r^B$ ( $\mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$ ( $\mu\text{mol photons quanta}$ $\text{m}^{-2} \text{ s}^{-1})^{-1}$ )	$\frac{P^B}{P_m} - \frac{P^B}{P_s}$ ( $\mu\text{g C } (\mu\text{g chl})^{-1}$ $\text{h}^{-1}$ )	$E_k$ ( $\mu\text{mol photons}$ $\text{quanta}$ $\text{m}^{-2} \text{ s}^{-1}$ )
[NO <sub>3</sub> ] < 20 $\mu\text{M}$	58	0.035 $\pm$ 0.020 (0.012 – 0.095)	1.215 $\pm$ 0.64 (0.29 – 3.109)	43.3 $\pm$ 34.2 (76.58 – 193)
[NO <sub>3</sub> ] > 20 $\mu\text{M}$	56	0.043 $\pm$ 0.039 (0.0077 – 0.183)	1.246 $\pm$ 0.58 (0.21 – 2.879)	48.0 $\pm$ 47.1 (43.79 – 238)
T > 0°C	44	0.040 $\pm$ 0.036 (0.015 – 0.183)	1.215 $\pm$ 0.66 (0.29 – 3.109)	44.6 $\pm$ 40.39.6 (76.58 – 193)
T < 0°C	58	0.032 $\pm$ 0.021 (0.011 – 0.095)	1.215 $\pm$ 0.53 (0.21 – 2.766)	50.49.7 $\pm$ 44.4 (7.875 – 238)
[Fe] < 0.1 nM	6	0.375 $\pm$ 0.023 (0.021 – 0.053)	1.6 $\pm$ 0.55*	41 $\pm$ 18 (28 – 54)
[Fe] > 0.1 nM	33	0.029 $\pm$ 0.017 (0.011 – 0.066)	1.0 $\pm$ 0.44 (0.21 – 1.7)	48 $\pm$ 36 (8 – 131)

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

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

Season	$\frac{P_m^B - P_s^B}{P_m^B - P_s^B}$ ( $\mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$ )	$r^B$ ( $\mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$ ) ( $\mu\text{mol photons quanta m}^{-2} \text{ s}^{-1}$ ) <sup>-1</sup> )	$E_k$ ( $\mu\text{mol photons quanta m}^{-2} \text{ s}^{-1}$ )	N	Reference
Spring	1.77 ± 0.97	0.047 ± 0.023	37.0 ± 7.50	37	van Hilst and Smith (2002)
Summer	2.548 ± 1.329	0.087 ± 0.043	31.0 ± 16.0	31	
Spring	1.22 ± 0.54	0.036 ± 0.015	37.1 ± 13.4	70	Hiscock (2004)
Summer	0.64 ± 0.26	0.016 ± 0.0068	44.2.9 ± 18.4	98	
Autumn	0.70 ± 0.13	0.040 ± 0.017	210.7 ± 9.00	5	
Summer	1.34 ± 0.39	0.073 ± 0.088	23 ± 8	51	Saggiomo et al. (2002)
Spring	1.878 ± 0.68	0.020 ± 0.0043	898.7 ± 23.1	15	Robinson et al. (2003)
Spring <sup>2</sup>	2.11 ± 0.48	0.072 ± 0.027	31.1 ± 8.04	10	Smyth et al. (2012)
Spring	1.325 ± 0.72	0.040 ± 0.035	421.9 ± 298.7	27	IVARS: This report
Summer	0.68 ± 0.34	0.053 ± 0.035	23.3 ± 30.2	11	IVARS: This report
Summer	1.13 ± 0.500	0.035 ± 0.020	52.2 ± 48.1	77	PRISM: This report
Mean Spring <sup>1</sup>	1.437 ± 0.63	0.034 ± 0.024	44.0 ± 25.2	159	---
Mean Summer <sup>1</sup>	0.86 ± 0.45	0.023 ± 0.018	43.4 ± 28.3	268	---
Overall Mean <sup>1</sup>	1.107 ± 0.60	0.030 ± 0.023	443.7 ± 276.9	417	---

566 <sup>1</sup>: Weighted mean of all samples

567 <sup>2</sup>:  $\alpha^B$  and  $E_k$  values calculated from data using factor described in original paper

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

573

Functional Group	$\frac{P_m^B - P_s^B}{h^{-1}}$ ( $\mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$ )	$\Gamma^B$ ( $\mu\text{g C } (\mu\text{g chl})^{-1} \text{ h}^{-1}$ ) ( $\mu\text{mol photons-quantum}^{-1} \text{ m}^{-2} \text{ s}^{-1}$ )	$E_k$ ( $\mu\text{mol photons-quantum}^{-1} \text{ m}^{-2} \text{ s}^{-1}$ )
<i>Phaeocystis</i> <i>—Antarctica</i> (N=20)	1.436 ± 0.76	0.067 ± 0.060	33.2 ± 232.7
Diatoms (N=20)	1.14 ± 0.63	0.050 ± 0.045	32.0 ± 198.7

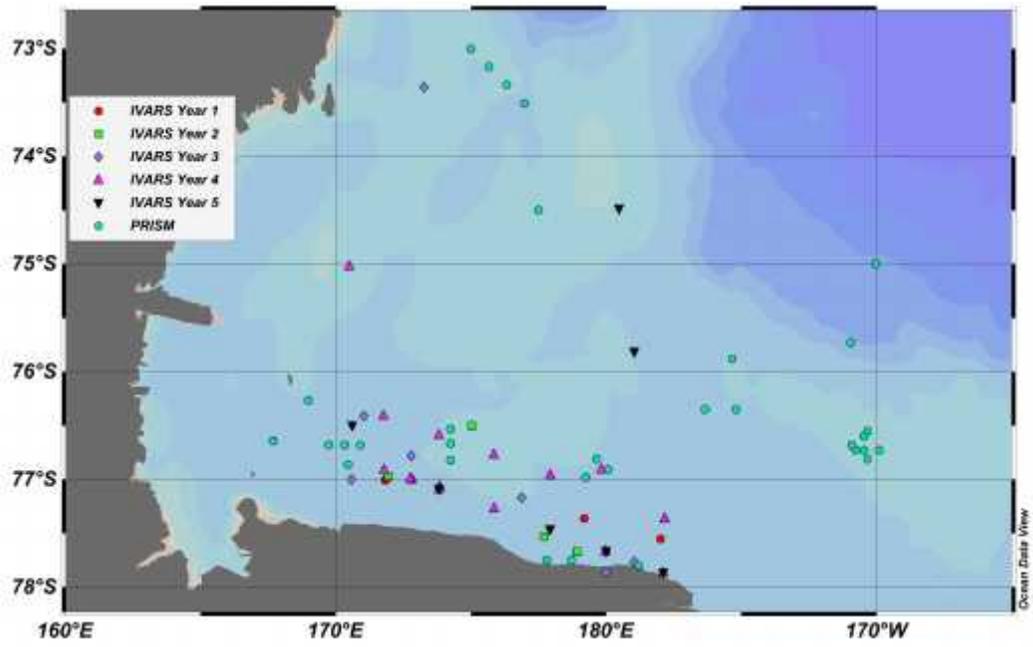
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577 Fig. 1.

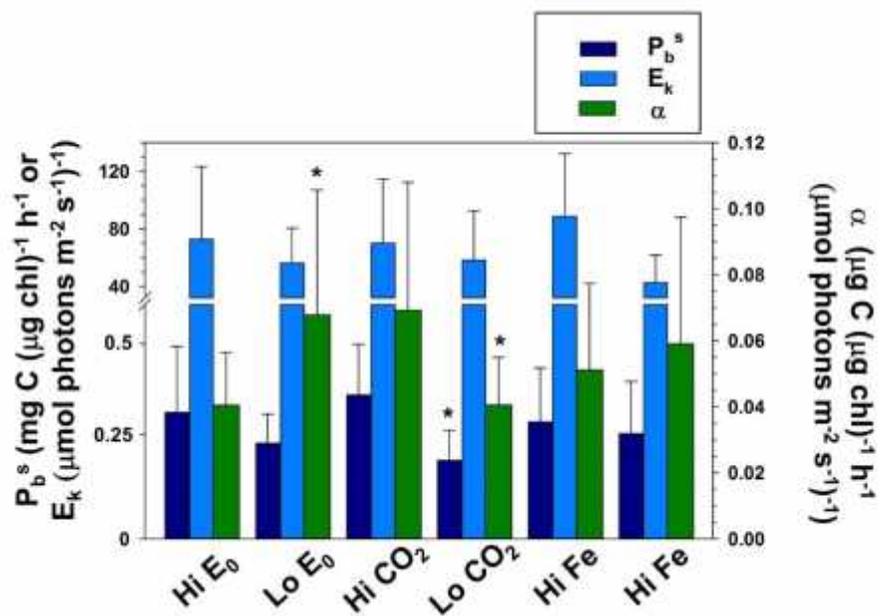


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581 Fig. 2

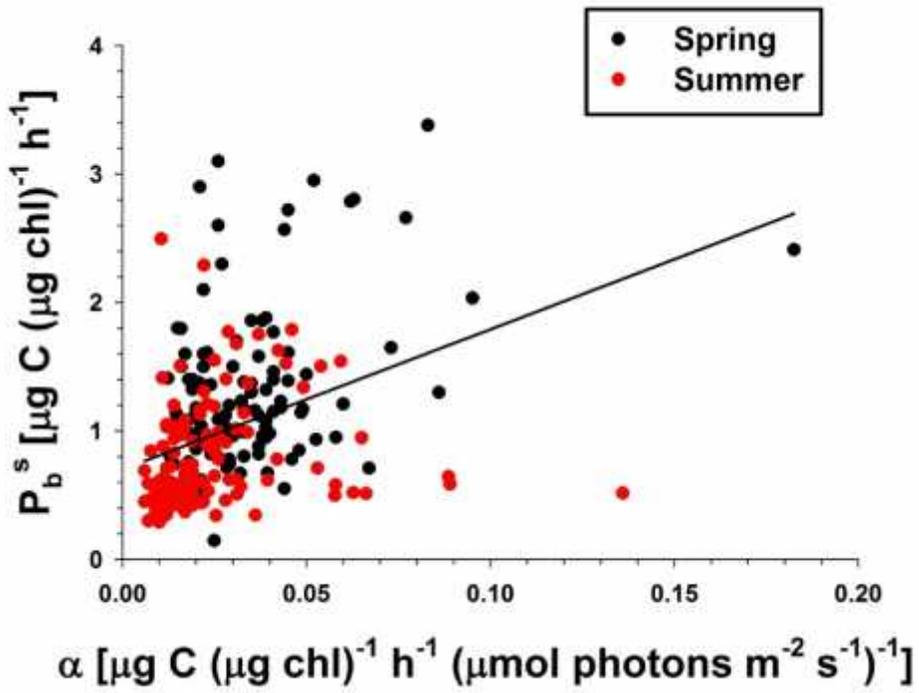


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584 Figure 3.

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