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3	Photosynthesis-irradiance responses in the Ross Sea, Antarctica: a meta-analysis
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### 22 Abstract

A meta-analysis of photosynthesis/irradiance measurements was completed using data from 23 the Ross Sea, Antarctica. A total of 417 independent measurements were included.  $P_m^B$ , the 24 maximum, chlorophyll-specific, irradiance-saturated rate of photosynthesis, averaged  $1.1 \pm 0.06$ 25  $\mu$ g C ( $\mu$ g chl)<sup>-1</sup> h<sup>-1</sup>. Light-limited, chlorophyll-specific photosynthetic rates ( $\alpha$ <sup>B</sup>) averaged 0.030 26  $\pm 0.023 \ \mu g \ C \ (\mu g \ chl)^{-1} \ h^{-1} \ (\mu mol \ quanta \ m^{-2} \ s^{-1})^{-1}$ . Significant variations in  $P_m^B$  and  $\alpha^B$  were 27 found as a function of season, with spring maximum photosynthetic rates being 60% greater than 28 those in summer. Similarly,  $\alpha$  values were 64% greater in spring. There was no detectable 29 effect of space on the photosynthetic parameters, and temperature and macronutrient (NO<sub>3</sub>) 30 concentrations also did not exert a strong influence. However, irradiance, dissolved iron 31 concentrations, and carbon dioxide concentrations when altered under controlled conditions 32 exerted significant influences on photosynthetic parameters. Specifically, reduced irradiance 33 resulted in decreased  $P_m^B$  and  $\alpha^B$  values, whereas reduced iron concentrations were associated 34 with increased  $P_m^B$  and  $\alpha^B$  values. Increased CO<sub>2</sub> concentrations also resulted in significantly 35 increased  $P_m^B$  and  $\alpha^B$  values. No significant difference was detected between stations dominated 36 by diatoms and those dominated by the haptophyte Phaeocystis antarctica. The meta-analysis 37 generally confirms the photosynthetic rates predicted from global analyses that are based solely 38 on temperature and irradiance availability, but suggests that for more accurate predictions of the 39 productivity of polar systems a more detailed model that includes temporal effects of 40 photosynthetic parameters will be required. 41

### 43 1. Introduction

The relationship of phytoplankton photosynthesis to irradiance is fundamental not only to our 44 understanding of marine productivity, but also in predicting the response of marine systems to 45 climate change and other anthropogenic alterations (Brown and Arrigo, 2012; Huot et al., 2013). 46 47 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; 48 Arrigo et al., 2013; Smith et al., 2014b), as well as changes in air-sea interactions and food-web 49 50 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 51 generally modeled as a function of integrated chlorophyll concentrations, available irradiance, 52 and the P-E response as a function of temperature (Behrenfeld and Falkowski, 1997; Platt et al., 53 2007). The temperature-photosynthesis relationship is generally assumed to be constant below 54 0°C (Behrenfeld and Falkowski, 1997), despite the fact that substantial oceanographic variability 55 is known in other variables that influence photosynthesis in these waters. 56 P-E responses are generally described by a relatively simple equation that parameterizes the 57 response as a function of irradiance:  $P_s^B$ , the maximum, biomass-specific rate of photosynthesis 58 at saturating irradiances,  $\alpha^{B}$ , the irradiance-limited, biomass-specific linear portion of the 59 hyperbolic response, and  $\beta^{B}$ , the portion of the curve where photosynthesis decreases at high 60 irradiances (photoinhibition) (Platt et al., 1980a).  $P_m^B$  is the maximum rate of photosynthesis at 61 saturating irradiances in the absence of photoinhibition. A parameter describing the irradiance at 62 which saturation is initiated,  $E_k$ , is derived from the ratio of  $P_s^B$  and  $\alpha^B$ . Chlorophyll *a* 63 concentrations are generally used as an index of biomass. Estimates of photoinhibition are often 64

difficult to obtain and are thought to represent a non-steady state condition (Marra et al., 1985),

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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. 67

P-E responses from the Southern Ocean have been assessed from a number of regions (e.g., 68 West Antarctic Peninsula: Brightman and Smith, 1989; Moline et al., 1998; Scotia Sea: Tilzer et 69 al., 1986; Ross Sea: van Hilst and Smith, 2002; Robinson et al., 2003; Smyth et al., 2012), but 70 unlike for the Arctic Ocean (Platt et al., 1980b; Huot et al., 2013), no synthesis of photosynthetic 71 72 responses or their environmental controls is available. Different investigators also have used slightly different methods, making a comparison more difficult; furthermore, because regions in 73 the Southern Ocean change rapidly, it is challenging to interpret the results of changing P-E 74 responses in the context of spatial and temporal variability of oceanographic conditions. In 75 general, phytoplankton in the Southern Ocean exhibit low maximum photosynthetic rates 76 (between 1 and 2  $\mu$ g C ( $\mu$ g chl)<sup>-1</sup> h<sup>-1</sup>), and  $E_k$  values reflect the in situ irradiance environment 77 from which the phytoplankton were sampled. That is, when phytoplankton are sampled from 78 within a deeply mixed surface layer or from under the ice,  $E_k$  values are low, reflecting an 79 acclimation to reduced available irradiance. Conversely,  $E_k$  values generally increase when 80 phytoplankton are sampled from stratified, ice-free environments in summer that are 81 characterized by higher irradiance values. 82

The Ross Sea is among the best studied areas in the Antarctic, and a great deal is known 83 84 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 85 synthesis of the area's photosynthesis-irradiance relationships is lacking. It is known that the 86 87 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 88

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

103 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 104 105 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, 106 and are followed by diatom growth; Smith et al., 2014b), we assessed the photosynthetic 107 responses as a function of season. We also compared the various environmental controls (e.g., 108 temperature, nitrate, and iron) on maximum and irradiance-saturated photosynthetic rates, as well 109 as their relationship to assemblage composition. 110

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#### 112 **2.** Methods

# 113 2.1. Analytical Procedures

Samples were collected during a number of cruises, most of which concentrated their 114 sampling in the southern Ross Sea (Fig. 1). The first was IVARS (Interannual Variations in the 115 Ross Sea; Smith et al., 2011a,b), which collected samples during short cruises twice each year, 116 117 with the first cruise sampling ice-free periods in late December and the second sampling the end 118 of summer (early February). The second project was CORSACS (Controls on Ross Sea Algal Community Structure), which had two cruises. The first cruise began in late December, 2006 119 120 and the second was in November-December, 2006 (Sedwick et al., 2011; Smith et al., 2013). P-121 E results from CORSACS involved experimental manipulations of irradiance, dissolved iron and CO<sub>2</sub> concentrations and used trace-metal clean procedures (Feng et al., 2010; Rose et al., 2010). 122 123 The final project was PRISM (Processes Regulating Iron Supply at the Mesoscale), which sampled in January-February, 2012 (Smith and Jones, 2014; McGillicuddy et al., in press). 124 Figure 1 shows the locations of the stations analyzed for photosynthesis/irradiance relationships. 125 126 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 127 et al., 2012). 128

Photosynthesis-irradiance (P-E) relationships of phytoplankton were determined by assessing uptake of <sup>14</sup>C-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

136 (generally that of the 50 and 1% isolumes) at each station (50% depths were generally from 1-4 m, and 1% depths from 15-50 m), to which ca. 100 µCi NaH<sup>14</sup>CO<sub>3</sub> were added. Incubations 137 were conducted at a constant temperature from the depth of sampling (determined by the CTD 138 cast and maintained by a circulating water bath). Samples were placed in glass scintillation vials 139 140 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 141 maximum value by neutral density screening at irradiances ca. 70% of the full irradiance, and by 142 143 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 144 145 irradiances used ranged from 16 to 32. Incubations lasted approximately 2 h. All samples were counted on liquid scintillation counters, and total available inorganic <sup>14</sup>C-bicarbonate was 146 assessed by counting aliquots directly in scintillation fluor. While details of the methods of each 147 study varied somewhat, we were unable to detect a significant difference between filtered and 148 149 unfiltered results, and concluded that the methods did not introduce a significant source of error 150 to obscure the overall patterns.

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

$$P^{B} = P^{B}_{m} \left[ 1 - e^{-\alpha^{B} E / P^{B}_{m}} \right]$$
(Eq. 1)

where  $P^B$  = the rate of photosynthesis normalized to chlorophyll *a* [mg C (mg chl *a*)<sup>-1</sup> h<sup>-1</sup>],  $P_m^B$  = the maximum, irradiance-saturated rate of photosynthesis in the absence of photoinhibition,  $\alpha^B$ = the initial, light-limited, linear photosynthetic rate normalized to chlorophyll [mg C (mg chl *a*)<sup>-1</sup> h<sup>-1</sup> (µmol quanta m<sup>-2</sup> s<sup>-1</sup>)], and E = irradiance (µmol quanta m<sup>-2</sup> s<sup>-1</sup>). 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:

$$E_k = P_m^B / \alpha^B \tag{Eq. 2}$$

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

Chlorophyll *a* concentrations were analyzed by fluorometry (JGOFS, 1996) on independent 167 samples collected from the same depth. Nutrient (NO<sub>3</sub>, NO<sub>2</sub>, PO<sub>4</sub>, Si(OH)<sub>4</sub>, NH<sub>4</sub>) analyses were 168 performed at sea on a Lachat QuickChem Autanalyzer using standard automated techniques. 169 Mixed layer depths were determined from density profiles determined from CTD casts using a 170 change in density of 0.01 kg m<sup>-3</sup> from a stable surface value (Thomson and Fine, 2003; Smith et 171 al., 2013). Seawater samples for dissolved iron analysis were collected in custom-modified 5-L 172 Teflon-lined, external-closure Niskin-X samplers (General Oceanics Inc.) or 10-L teflon-lined 173 GO-FLO samplers, all of which were deployed on a non-metal line (Sedwick et al., 2011). 174 Filtered samples were acidified to pH 1.7 with ultrapure hydrochloric acid and stored for at least 175 24 h prior to the analysis of dissolved iron. Dissolved iron was determined by flow injection 176 analysis with colorimetric detection after in-line pre-concentration on resin-immobilized 8-177 hydroxyquinoline (Sedwick et al., 2008). 178

179 *2.2. Statistical analyses* 

180	All responses were fit to a 2-parameter exponential increase to maxima in SigmaPlot 12.3,
181	which provided estimates of $P_m^B$ and $\alpha^B$ and their significance, as determined by a t-test.
182	Comparisons between data sets were made using analyses of variance. An a priori limit of
183	significance was set as $p < 0.05$ . Data were tested for normality and homogeneity of variance,
184	and ANOVAs were performed using R (v2.13.2). Stations selected for a comparison of the
185	effects of assemblage composition were chosen based on HPLC analysis of pigments and the
186	contribution of each functional group to total chlorophyll (Mackey et al., 1996). When pigment
187	data were not included in the published reports, taxonomic discrimination was made by reported
188	microscopic results.
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190	3. Results
191	3.1. IVARS, CORSACS and PRISM Photosynthesis/Irradiance Determinations
192	P-E determinations in IVARS were conducted during the peak of the spring bloom (generally
193	late December) and at the end of summer (early February) (Smith et al., 2011a). Ice
194	concentrations were < 15% at all stations. Average $\alpha^{B}$ , $P_{m}^{B}$ and $E_{k}$ values for the IVARS spring
195	and summer cruises were 0.040 $\pm$ 0.035 and 0.053 $\pm$ 0.035 µg C (µg chl) <sup>-1</sup> h <sup>-1</sup> (µmol quanta m <sup>-2</sup>

196  $s^{-1}$ )<sup>-1</sup>, 1.3 ± 0.72 and 0.68 ± 0.34 µg C (µg chl)<sup>-1</sup> h<sup>-1</sup>, and 42 ± 29 and 23 ± 30 µmol quanta m<sup>-2</sup>

197 s<sup>-1</sup>, respectively (Table 2).  $P_m^B$  values of the two seasons were significantly different (p < 0.05),

198 but  $\alpha^{B}$  and  $E_{k}$  values were not.

199	CORSACS measurements were largely conducted as part of experiments that manipulated
200	irradiance (7 and 33% of surface irradiance), iron concentrations (ambient and +1 nM), and $CO_2$
201	concentrations (380 and 750 µatm) (Feng et al., 2010). Natural populations were used as inocula
202	in semi-continuous cultures grown at constant irradiances (Hutchins et al., 2003), and P-E

203 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 204 changes in  $P_m^B$ ,  $\alpha^B$  and  $E_k$  values, which increased significantly (p < 0.05) at the low and 205 constant irradiances (Fig. 2). Increased  $CO_2$  concentrations also resulted in significantly (p < p206 0.05) increased  $\alpha^{B}$  and  $P_{m}^{B}$  values, although little net change was noted in E<sub>k</sub> values. Finally, 207 increased iron concentrations did not impact either  $\alpha^{B}$  or  $P_{m}^{B}$  values significantly in these 208 experiments (Fig. 2).  $P_m^B$  values were greater than those representing sub-optimal, in situ 209 conditions such as in IVARS and PRISM. 210 211 PRISM samples investigated the broad spatial patterns of P-E responses (Table 2). The mean  $\alpha^{\rm B}$  and  $P_m^{\rm B}$  values were 0.035 ± 0.020 (µg C (µg chl)<sup>-1</sup> h<sup>-1</sup> (µmol quanta m<sup>-2</sup> s<sup>-1</sup>)<sup>-1</sup>) and 1.1 ± 0.50 212  $\mu$ g C ( $\mu$ g chl)<sup>-1</sup> h<sup>-1</sup>, respectively. The average E<sub>k</sub> value was 52 ± 48  $\mu$ mol quanta m<sup>-2</sup> s<sup>-1</sup>. There 213 was no significant different between PRISM P-E parameters and those collected during IVARS 214 (December, February, or the total data set), and again no spatial pattern was observed. 215 Iron and nitrate concentrations were measured during PRISM at a number of stations where 216 P-E measurements were conducted (McGillicuddy et al., in press). Dissolved Fe levels ranged 217 from 0.066 to 0.69 nM, and nitrate ranged from 9.05 to 30.6 µM. No significant difference in 218 the mean  $\alpha^{\rm B}$ ,  $P_m^{\rm B}$  or  $E_k$  values were observed between the stations with nitrate concentrations less 219 than 20  $\mu$ M and those with concentrations > 20  $\mu$ M (Table 3), which is not unexpected as these 220 concentrations are considered to be non-limiting. In contrast, at stations with Fe concentrations 221 below and above 0.10 nM (a level that approximates the onset of Fe limitation in Antarctic 222 phytoplankton; Timmermans et al., 2004),  $P_m^B$  values were significantly (p < 0.01) greater (1.6 ± 223 0.55 vs. 0.95  $\pm$  0.44) at lower iron concentrations (Table 3).  $\alpha^{B}$  and E<sub>k</sub> values, however, were 224

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 227 the depth of sampling (50 vs. 1% of surface irradiance) in any photosynthetic parameter. This 228 lack of correlation differs from the CORSACS results (Fig. 2), which were conducted under 229 constant irradiance using natural assemblages (but which changed appreciably during the 230 experiments). Available irradiances at the time of sampling do not necessarily reflect the 231 irradiance that influenced growth over times scales of days to weeks, which are unknown. This 232 suggests that there is no substantial photoacclimation within water column of the Ross Sea, 233 which in turn may suggest that the time needed for acclimation at these temperatures is longer 234 than the time scales of water column perturbation. 235

236 *3.2.* Comparison with Previous P-E Determinations

Because P-E determinations have been conducted during the past two decades with a similar 237 methodology, we merged all data from the Ross Sea to assess the average photosynthetic 238 239 response by season (Table 4). There is a significant difference between austral spring and summer averages for  $P_m^B$  and  $\alpha^B$  values, with spring having a greater  $P_m^B$  (1.4 vs. 0.86) and  $\alpha^B$ 240 values (0.034 vs. 0.023). However, no significant difference was observed between spring and 241 summer E<sub>k</sub> values. Values of  $\alpha^{\rm B}$  and  $P_m^{\rm B}$  were linearly correlated ( $P_m^{\rm B} = 10.9\alpha^{\rm B} + 0.070$ ; R<sup>2</sup> = 242 0.15; p < 0.001; Fig. 3), as has been found previously (Harrison and Platt, 1980; van Hilst and 243 Smith, 2002; Behrenfeld et al., 2004), but the large amount of variability in the relationship 244 suggests that each is being influenced by multiple independent factors as well. No interannual 245 temporal trend was obvious, and interannual variability was substantial (Table 4). The overall 246

- 247  $P_m^B$  average for all samples (N = 417) equaled  $1.1 \pm 0.77 \ \mu g \ C \ (\mu g \ chl)^{-1} \ h^{-1}, \ \alpha^B = 0.030 \pm 0.023$
- 248  $\mu g C (\mu g chl)^{-1} h^{-1} (\mu mol quanta m^{-2} s^{-1})^{-1}$  and  $E_k = 44 \pm 27 \mu mol quanta m^{-2} s^{-1}$ .

## 249 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 250 parameters from all cruises. The data were arbitrarily divided above and below 20  $\mu$ M NO<sub>3</sub> and 251 above and below 0°C, and the P-E parameters compared. Nitrate concentrations at the time of 252 sampling ranged from  $9.5 - 31.0 \mu$ M, and 54 P-E measurements were conducted with NO<sub>3</sub> 253 254 concentrations greater than 20  $\mu$ M. 58 analyses were conducted with NO<sub>3</sub> levels less than 20  $\mu$ M. Sample temperatures ranged from -1.6 – 2.6°C; 58 of the 102 P-E determinations were 255 below 0°C, and 44 were above. No significant differences were noted for any of the three 256 257 photosynthetic parameters within the nitrate or temperature data subsets, corroborating the PRISM results (Table 3). This suggests that photosynthetic responses are largely independent of 258 these environmental controls over short time scales. 259

The two dominant functional groups in the Ross Sea, diatoms and haptophytes (largely 260 *Phaeocystis antarctica*), have different temporal and spatial distributions, with *P. antarctica* 261 generally dominating in spring in water columns with deeper vertical mixing, and diatoms 262 dominating in more stratified, summer conditions (Smith et al., 2014a). P. antarctica largely 263 occurs in cold waters ( $< 0^{\circ}$ C) and is responsible for the spring reduction in micro- and 264 265 macronutrients (Liu and Smith, 2012). To investigate if the two taxa have different photosynthesis-irradiance responses, we selected 20 stations for each group that were identified 266 by chemical or microscopic means as being dominated by one of these groups, and assessed their 267 268 P-E characteristics (Table 5). We found no statistical difference between the two groups with respect to  $\alpha^{\rm B}$ ,  $P_m^{\rm B}$  or  $E_k$  values. 269

270

## 271 **4. Discussion**

272 4.1. Overall Patterns of Photosynthetic Parameters

One major finding of this meta-analysis is that the average maximum, light-saturated rate of 273 photosynthesis equals 1.1  $\mu$ g C ( $\mu$ g chl)<sup>-1</sup> h<sup>-1</sup> (Table 4). This is similar to the  $P_{opt}^{B}$  value 274 determined from Behrenfeld and Falkowski's (1997) polynomial equation (1.3 µg C (µg chl)<sup>-1</sup> 275 h<sup>-1</sup>) at 0°C, despite the difference between  $P_{opt}^{B}$  and  $P_{m}^{B}$  as well as the range of temperatures at 276 which the P-E determinations were conducted. Our results reinforce the validity of using their 277 equation to estimate maximum photosynthetic rates and primary productivity within the waters 278 of the Ross Sea, and presumably the entire Southern Ocean. This average can also be used in 279 other bio-optical models of production to constrain the rates of carbon fixation over broad areas 280 (e.g., Arrigo et al., 2003, 2008). However, given the seasonal variability observed, more detailed 281 models that incorporate seasonal and environmental impacts may require inclusion of other 282 oceanographic variables to more accurately predict production. 283

We found relatively minor spatial differences in photosynthetic parameters, but significant 284 seasonal differences. Specifically,  $\alpha^{B}$  and  $P_{m}^{B}$  values of the entire meta-analysis data set were 285 significantly greater during spring than summer (both p < 0.001), which is consistent with the 286 large seasonal changes found in nearly all oceanographic and biological variables. The macro-287 environment of the Ross Sea continental shelf changes markedly from spring to summer, with 288 increased temperatures, strongervertical stratification, shallower mixed layers, decreased macro-289 and micronutrient concentrations, and an altered assemblage composition (Smith et al., 2012). 290 All of these variables have been shown to influence P-E responses in laboratory and field studies 291 (e.g., MacIntyre et al., 2002; Xie et al., 2015), and as such, it is not surprising that the P-E 292

293 parameters also changed. It is tempting to suggest that the seasonal changes were driven by 294 changes in phytoplankton composition, but we believe that the seasonal changes in oceanographic conditions led to in changes in P-E parameters as well as in composition, and that 295 296 both oceanographic changes and phytoplankton composition contributed to the seasonal differences in P-E parameters we observed. An experiment which isolates natural assemblages 297 (perhaps a Lagrangian tracking of a parcel of water that is dominated by one taxa or a large-298 299 volume mesocosm experiment such as has been conducted in the Baltic Sea; Riebesell et al., 2013) would be more definitive test of the impacts of composition and the seasonal changes in P-300 301 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 302 direct measurements of productivity (e.g., Long et al., 2011). It was impossible to accurately 303 304 assess interannual variations in P E parameters, given the relatively low numbers of samples in some years, but in view of the large variations observed in biomass and productivity from 1995 305 through 2010 (Smith and Comiso, 2008; Smith et al., 2011a), any interannual trend is likely 306 307 obscured by the substantial seasonal variability.

308 *4.2.* Controls of Photosynthesis-Irradiance Parameters

While not all data sets had complete macro- and micronutrient data available for inclusion, we were unable to detect any controls of short-term photosynthetic rates by temperature or nitrate within the seasonal data sets. The temperature range was modest (ca. 4°C), so the direct impact of temperature may have been limited and obscured by other factors. Liu and Smith (2012) demonstrated that the environmental factor that had the strongest impact on phytoplankton biomass 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

316 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). 317 Nitrate concentrations varied more widely (from 9.3 to 31 µM), but still remained above those 318 thought to limit nitrogen uptake (Cochlan et al., 2002). Xie et al. (2015) also did not find a 319 correlation between nutrients and  $P_m^B$ , and suggested that reflected the lag time between nutrient 320 inputs and phytoplankton growth in the English Chanel. They also found a complicated 321 relationship between photosynthetic parameters and temperature and suggested that each 322 functional group had temperature optima that were characterized by specific photosynthetic 323 324 responses.

Reduced iron concentrations, however, resulted in lower  $P_m^B$  values, despite the relatively 325 limited number of measurements at concentrations less than 0.1 nM. In contrast, we did not 326 327 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 328 concentrations > 0.13 nM (Feng et al., 2010), concentrations which are greater than those 329 330 generally 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 331 influences growth rates of Antarctic diatoms (Timmermans et al., 2004), but growth rate 332 responses are integrated over many days, whereas P-E responses are not immediately influenced 333 by iron additions (Hiscock et al., 2008). It is tempting to suggest that the reduced summer P-E 334 parameters may have resulted from iron limitation, but iron availability is rarely determined in 335 parallel with P-E parameters. We suggest that the impacts of iron we observed – significantly 336 reduced  $P_m^B$  values – were mediated by a long-term assemblage response rather than an impact 337 on short-term photosynthetic rates. Iron limitation can impact chlorophyll synthesis (in a manner 338

339 similar to irradiance), and under co-limitation by iron and irradiance chlorophyll levels can be elevated (Sunda and Huntsman, 1997), which would result in lowered  $P_m^B$  values. Determination 340 of the exact cause of the iron effect on  $P_m^B$ , however, is impossible with the present data set. 341 The CORSACS experiments showed a clear impact of both irradiance and [CO<sub>2</sub>] on 342 photosynthetic responses. Under low and constant irradiance conditions (ca. 7% that of surface 343 irradiance), there was an increase in the light-limited rates of photosynthesis ( $\alpha^B$ ) and light-344 saturated  $(P_m^B)$  values (Fig. 2). Low irradiance conditions often generate increased chlorophyll 345 346 concentrations per cell, but can also generate increased photosynthetic efficiencies (via changes in photosynthetic units), which can result in elevation of both parameters (Prezelin, 1981; 347 Dubinsky and Stambler, 2009).  $P_m^B$  reflects the light-saturated rate, and presumably is set by the 348 amount of carbon that can be reduced by the cells, which in turn is thought to be limited by the 349 amount of chemical energy generated by the cells' photosystems. Increasing carbon dioxide 350 concentrations resulted in a marked and significant increase in  $P_m^B$  and  $\alpha^B$  values, reinforcing the 351 classical view of the limitation of short-term photosynthesis by carbon availability under high 352 353 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<sub>2</sub> levels 354 had little impact on phytoplankton composition (Tortell et al., 2008b), and independent 355 measurements suggest that most Antarctic phytoplankton have a relatively broad capability to 356 use a wide range of carbon dioxide concentrations (Tortell et al., 2008a). Although it is tempting 357 to suggest that future increases in oceanic CO<sub>2</sub> concentrations might increase maximum 358 photosynthetic rates, such changes need to be assessed using long-term experiments that allow 359 for acclimation and adaptation over many generations (e.g., Lohbeck et al., 2012). 360

361 The influence of phytoplankton composition was insignificant (Table 5). This is consistent 362 with the previous results of van Hilst and Smith (2002) and Robinson et al. (2003), using a less extensive data set, but in contrast to the extensive laboratory results of Arrigo et al. (2010), who 363 found that  $\alpha^{B}$  and  $P_{m}^{B}$  values of *P. antarctica* grown at constant irradiances (from 5 – 125 µmol 364 quanta  $m^{-2} s^{-1}$ ) and saturating nutrients were always greater than those of the diatom 365 *Fragilariopsis cylindrus*. The diatom had low  $P_m^B$  [from 0.46 to 0.54 µg C (µg chl)<sup>-1</sup> h<sup>-1</sup>)] and 366  $\alpha^{\rm B}$  values [0.014 to 0.043 (µg C (µg chl)<sup>-1</sup> h<sup>-1</sup> (µmol quanta m<sup>-2</sup> s<sup>-1</sup>)<sup>-1</sup>)] when compared to those 367 of the haptophyte (from 1.4 to 6.4, and 0.038 to 0.11, respectively). The diatom parameters 368 determined in culture were lower than our data subset, and the haptophyte values higher; these 369 370 differences likely reflect the parameters of the individual species cultured and/or the influence of constant culturing conditions. The in situ data also had substantial variability, which likely 371 resulted from the environmental conditions that allowed one particular functional group to 372 dominate. Appearance of taxa in situ reflects a long-term process involving both growth and 373 losses, and both field and laboratory data suggest that the P-E parameters of the dominant forms 374 375 in spring and summer reflect the importance of selected environmental features (irradiance, iron) on their long-term success in the water column. 376

In summary, the broad photosynthetic responses of Ross Sea phytoplankton are consistent with the patterns used in global production estimates from satellite biomass estimates. However, strong and significant seasonal differences occur, as do variations driven by irradiance, iron concentrations, and carbon dioxide levels. Such significant differences may need to be included in regional models of productivity and carbon flux. While these results may suggest that future changes in photosynthetic capacity and production in the Ross Sea as a result of climate change could be substantial, confirmation of this awaits future analyses of these parameters.

384

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389

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# 561 Figure Legends

562

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

565 Figure 2. Photosynthesis-irradiance parameters determined from experimental manipulations of

natural populations. Samples had either high or low (33 or 7% of surface value)

567 irradiance, high or low (750 or 380 ppm) CO<sub>2</sub>, and high or low (+1 nM and ambient; ca.

568 0.1 nm) iron concentrations. Asterisks indicate a significant difference between the

- 569 high and low treatments within each variable.
- 570 Figure 3. Relationship of  $\alpha$  (light-limited photosynthesis) and  $P_s^B$  (irradiance-saturated
- 571 photosynthesis) in samples from the Ross Sea. Solid line is the linear regression ( $P_m^B =$

572  $10.9\alpha + 0.70; r^2 = 0.15; p < 0.001).$ 

Cruise Name	Dates of Sampling	Ν	V <sub>inc</sub> (mL)	F/NF	Reference
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	$\frac{12/26/2005 - }{1/2/2006}$	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

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.

576 \*: Gravity filtration

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

Month	Year	$\alpha^{\mathrm{B}}$	$P_m^B$	$E_k$	Z <sub>mix</sub>	Z <sub>1%</sub>
December	2001	$0.060 \pm$	2.3 ±	42 ±	37.1 ±	9.38 ±
		0.015 (4)	0.61	18	13.3 (17)	1.06 (8)
February	2002	0.008 (1)	0.85	110	35.1 ±	14.3 ±
					8.96 (16)	2.74 (9)
December	2002	0.033 ±	$0.97 \pm$	34 ±	28.5 ±	$36.0 \pm$
		0.012 (4)	0.32	24	7.09 (8)	14.5 (3)
December	2003	$0.019 \pm$	0.61 ±	37 ±	22.7 ±	27.8 ±
		0.005 (5)	0.36	28	10.1 (12)	11.4 (9)
February	2004	$0.067 \pm$	$0.80 \pm$	16 ±	25.2 ±	25.8 ±
		0.047 (4)	0.57	15	8.67 (25)	6.57 (12)
December	2004	$0.022 \pm$	1.1 ±	62 ±	21.0 ±	23.8±
		0.009 (10)	0.42	38	6.47 (23)	7.66 (23)
February	2005	$0.051 \pm$	0.57 ±	14 ±	20.1 ±	24.6 ±
		0.023 (6)	0.048	6.1	7.44 (24)	8.20 (25)
December	2005	$0.070 \pm$	1.6 ±	28 ±	$20.0 \pm$	$24.0 \pm$
		0.055 (7)	0.80	11	10.5 (12)	1.91 (7)
Mean:		$0.040 \pm$	1.3 ±	42 ±	25.7 ±	23.0 ±
December		0.035 (27)	0.72	29	11.7 (72)	10.1 (50)
Mean:		0.053 ±	$0.68 \pm$	23 ±	25.7 ±	22.9 ±
February		0.035 (11)	0.34	30	10.0 (65)	8.13 (45)
PRISM,	2010	0.035 ±	1.1 ±	52 ±	27.8 ±	42.2 ± 22.8
January		0.020 (77)	0.50	48	22.7 (116)	(116)

582	Table 3. Comparison of PRISM photosynthetic parameters as a function of nitrate, temperature
583	and iron (means and standard deviations). Range of data listed in parentheses. The available data
584	were divided into those stations that had nitrate concentrations above and below 20 $\mu$ M, in situ
585	temperatures above and below 0°C, and iron concentrations greater than or less than 0.1 nM. No
586	significant differences were noted between the two sets of parameters except where noted.

Variable Group	Ν	$\alpha^{\rm B}$	$P_m^B$	$\mathbf{E}_{\mathbf{k}}$
		(μg C (μg chl) <sup>-1</sup> h <sup>-1</sup>	(µg C (µg chl) <sup>-1</sup>	(µmol quanta
		(μmol quanta m <sup>-2</sup> s <sup>-1</sup> ) <sup>-1</sup> )	<b>h</b> <sup>-1</sup> )	$m^{-2} s^{-1}$ )
$[NO_3] < 20 \ \mu M$	58	$0.035 \pm 0.020$	$1.2 \pm 0.64$	$43 \pm 34$
		(0.012 - 0.095)	(0.29 – 3.1)	(7 – 193)
$[NO_3] > 20 \ \mu M$	56	$0.043\pm0.039$	$1.2 \pm 0.58$	$48 \pm 47$
		(0.008 - 0.183)	(0.21 - 2.8)	(4 - 238)
T > 0°C	44	$0.040\pm0.036$	$1.2 \pm 0.66$	$44 \pm 40$
		(0.015 – 0.183)	(0.29 - 3.1)	(7 – 193)
T < 0°C	58	$0.032\pm0.021$	$1.2 \pm 0.53$	$50 \pm 44$
		(0.011 – 0.095)	(0.21 - 2.7)	(8 – 238)
[Fe] < 0.1 nM	6	$0.375 \pm 0.023$	$1.6 \pm 0.55*$	$41 \pm 18$
		(0.021 – 0. 053)	(1.1 - 2.7)	(28 - 54)
[Fe] > 0.1 nM	33	$0.029 \pm 0.017$	$1.0 \pm 0.44$	$48 \pm 36$
		(0.011 – 0.066)	(0.21 – 1.7)	(8 – 131)

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

Season	$P_m^B$	$\alpha^{B}$	$\mathbf{E}_{\mathbf{k}}$	Ν	Reference
	(μg C (μg chl) <sup>-1</sup> h <sup>-1</sup> )	(μg C (μg chl) <sup>-1</sup> h <sup>-1</sup> ) (μmol quanta m <sup>-2</sup> s <sup>-1</sup> ) <sup>-1</sup> )	(µmol quanta m <sup>-2</sup> s <sup>-1</sup> )		
Spring	$1.7\pm0.97$	$0.047\pm0.023$	$37 \pm 7.5$	37	van Hilst and
Summer	$2.5 \pm 1.3$	$0.087\pm0.043$	$31 \pm 16$	31	Smith (2002)
Spring	$1.2 \pm 0.54$	$0.036\pm0.015$	$37 \pm 13$	70	Hiscock (2004)
Summer	$0.64\pm0.26$	$0.016\pm0.007$	$44 \pm 18$	98	
Autumn	$0.70 \pm 0.13$	$0.040 \pm 0.017$	$21 \pm 9$	5	
Summer	$1.3 \pm 0.39$	$0.073 \pm 0.088$	23 ± 8	51	Saggiomo et al. (2002)
Spring	$1.8 \pm 0.68$	$0.020 \pm 0.004$	89 ± 23	15	Robinson et al. (2003)
Spring <sup>2</sup>	$2.1 \pm 0.48$	$0.072 \pm 0.027$	31 ± 8.0	10	Smyth et al. (2012)
Spring	$1.3 \pm 0.72$	$0.040 \pm 0.035$	$42 \pm 29$	27	IVARS: This report
Summer	$0.68 \pm 0.34$	$0.053 \pm 0.035$	$23 \pm 30$	11	IVARS: This report
Summer	$1.1 \pm 0.500$	$0.035 \pm 0.020$	$52 \pm 48$	77	PRISM: This report
Mean Spring <sup>1</sup>	$1.4 \pm 0.63$	$0.034 \pm 0.024$	$44 \pm 25$	159	
Mean Summer <sup>1</sup>	$0.86 \pm 0.45$	$0.023 \pm 0.018$	43 ± 28	268	
Overall Mean <sup>1</sup>	$1.1 \pm 0.60$	$0.030 \pm 0.023$	44 ± 27	417	

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

<sup>590</sup> <sup>1</sup>: Weighted mean of all samples

591 <sup>2</sup>:  $\alpha^{B}$  and  $E_{k}$  values calculated from data using factor described in original paper

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

	Functional Group	$P_m^B$	$\alpha^{\mathrm{B}}$	$\mathbf{E}_{\mathbf{k}}$
		(µg C (µg chl) <sup>-1</sup> h <sup>-1</sup> )	(μg C (μg chl) <sup>-1</sup> h <sup>-1</sup> ) (μmol quanta m <sup>-2</sup> s <sup>-1</sup> ) <sup>-1</sup> )	(µmol quanta m <sup>-2</sup> s <sup>-1</sup> )
	Phaeocystis	$1.4 \pm 0.76$	$0.067 \pm 0.060$	33 ± 23
	antarctica (N=20)			
	Diatoms (N=20)	$1.1 \pm 0.63$	$0.050 \pm 0.045$	$32 \pm 19$
598				
599				

Fig. 1. 



605 Fig. 2



