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Photosynthetic maximum quantum yield increases are an essential component of the Southern Ocean phytoplankton response to iron


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It is well established that an increase in iron supply causes an increase in total oceanic primary production in many regions, but the physiological mechanism driving the observed increases has not been clearly identified. The Southern Ocean iron enrichment experiment, an iron fertilization experiment in the waters closest to Antarctica, resulted in a 9-fold increase in chlorophyll (Chl) concentration and a 5-fold increase in integrated primary production. Upon iron addition, the maximum quantum yield of photosynthesis (Φmax) rapidly doubled, from 0.011 to 0.025 mol C mol−1 quanta−1. Paradoxically, this increase in light-limited productivity was not accompanied by a significant increase in light-saturated productivity (Pmax). Φmax, maximum Chl normalized productivity, was 1.34 mg C mg Chl−1 h−1 outside and 1.49 mg C mg Chl−1 h−1 inside the iron-enriched patch. The importance of Φmax as compared with Pmax in controlling the biological response to iron addition has vast implications for understanding the ecological response to iron. We show that an iron-driven increase in Φm is the proximate physiological mechanism affected by iron addition and can account for most of the increases in primary production. The relative importance of Φm over Pmax in this iron-fertilized bloom highlights the limitations of often-used primary productivity algorithms that are driven by estimates of Pmax but largely ignore variability in Φm and light-limited productivity. To use primary productivity models that include variability in iron supply in prediction or forecasting, the variability of light-limited productivity must be resolved.

A dozen iron enrichment experiments in high-nutrient low-chlorophyll (Chl) regions of the world ocean have unequivocally shown that iron limits primary production and that the addition of iron has significant biogeochemical consequences (1, 2). Although it has been shown that enhanced iron supply increases biomass, photosynthetic efficiency and primary production within the entire phytoplankton assemblage (3–6), the photophysiological mechanism driving the increased productivity has not been analytically linked to the observed changes in protein expression and photochemistry (7). On the most basic level, phytoplankton photophysiology can be categorized as either light-limited photosynthesis or light-saturated photosynthesis (8). At low irradiances, the rate of phytoplankton photosynthesis is light limited and proportional to the supply of irradiance. As irradiance increases, photosynthesis increases proportionally until the photosynthetic capabilities of the phytoplankton begin to become saturated. Light-saturated photosynthetic rates then remain constant as irradiance levels increase.

Here, we show that iron addition results in a doubling of light-limited photosynthesis rates but has no statistically significant impact on light-saturated photosynthesis rates. These results shed light on the mechanistic response to iron addition. Iron limitation decreases light-limited photosynthesis primarily by reducing the ability of phytoplankton to synthesize functional proteins for de novo creation or repair of damaged reaction centers (7). In particular, photosynthetic reaction center core and electron transport chain proteins that require iron cannot be formed or repaired, resulting in a reduced ability to process absorbed light energy into chemical energy. Under iron limitation, damaged photosystem II reaction centers manifest as decreased variable fluorescence, and a lesioned electron transport results in a decreased reaction center turnover rate (7, 9). Both processes directly reduce light-limited photosynthesis, ultimately resulting in a reduction in the quantum yield of photosynthesis (10).

In this context we explore (i) the strong ecological importance of light-limited photosynthesis, (ii) the implications of these results for primary production models that are primarily modulated by parameters that describe light-saturated photosynthesis, and (iii) the need for models to have the ability to represent changes in light-limited photosynthesis. We briefly describe the Southern Ocean iron enrichment experiment (SOFeX). We then introduce standard primary production models, the photosynthetic efficiency results from SOFeX, and an example of a primary production model that has the capacity to resolve increases in primary productivity caused by iron-dependent changes in the efficiency of light-limited photosynthesis.

Results and Discussion

SOFeX. The SOFeX group conducted an in situ iron fertilization in January and February 2002 in the Pacific Sector of the Southern Ocean, one of a series of experiments designed to test the Martin Iron Hypothesis (11). The southern of the two SOFeX patches (1) was in the waters nearer Antarctica and poleward of the southern boundary of the Antarctic circumpolar current (~66°S, 172°W). One of three major high-nutrient, low-Chl regions of the world ocean, these waters were characterized by high levels of macronutrients (~28 μM nitrate, 60 μM silicic acid) (12), extremely low iron concentrations (13, 14), iron-limited production (15), well defined mixed layers (45 m), and cold surface temperatures (~0.5°C) (1). Acidified iron sulfate was mixed with ambient seawater and introduced just

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and Falkowski (16) described a standard depth-integrated model reconciling numerous aliases for similar parameters and differences past four decades (16). Recent reviews conclude that after appeared in the literature on average once every 2 years over the derived Chl (\(P_{\text{opt}}\)) fertilization. Physiological units are as in Table 1:

\[
\text{Popt} = \frac{E_{\text{d}}(0^*)}{E_{\text{d}}(0^*)} + 4.1 \quad \text{(2)}
\]

where \(F\) is dimensionless and ranges between 0.45 and 0.61 for \(E_{\text{d}}(0^*)\). daily irradiance just above the surface of the ocean, values from 9 to 60 mol quanta m\(^{-2}\) d\(^{-1}\). With this empirical representation of \(F\) and observed measures of \(\text{Chl}_{b}\), \(Z_{\text{eu}}\), and \(F_{\text{opt}}\), the correlation between modeled and measured productivity was 86%. Furthermore, model performance decreased by only 3% \((r^2 = 0.83)\) when \(F\) was held constant at an average value of 0.55 (16).

This robust analysis marginalizes the use of light-limited photosynthesis parameters within productivity algorithms. Behrenfeld and Falkowski (16, 17) argued that productivity algorithm performance primarily depends on the accuracy to which \(P_{\text{opt}}\) can be modeled. Furthermore, they argued that adding computational overhead in the form of complex light propagation models adds limited, if any, increase in model performance. In a recent primary-productivity-algorithm-testing round robin there were 23 of 24 algorithms within the study that included variable phytoplankton physiology (19). Only six of those 23 algorithms included a light-limitation term that was based on physiology rather than scaled to daily mean irradiance (i.e., Eq. 2). In 13 of the algorithms, variations in phytoplankton physiology were limited to variations in \(P_{\text{opt}}\) or \(P_{\text{max}}\). It was also noted that one of the most widely used algorithms is the vertically generalized production model (17), a combination of Eqs. 1 and 2, in which \(P_{\text{opt}}\) is obtained as a seventh-order polynomial of sea surface temperature.

In this article we revisit the importance of light-limited productivity. We show that in this Southern Ocean iron enrichment 5-fold integrated primary productivity and 9-fold Chl concentration increases (4) were not accompanied by a significant increase in \(P_{\text{max}}\). Instead, productivity and biomass increases were driven by 2-fold increases in \(\alpha_b\) and \(\phi_{\text{opt}}\), measures of the efficiency of light-limited productivity and components of the productivity model variable \(F\). The standard DIM proposed by Behrenfeld and Falkowski (16, 17), a combination of Eqs. 1 and 2, would fail to model the development of an iron-enriched bloom because the proximal physiological drivers of the productivity increase (\(\alpha_b\), \(\phi_{\text{opt}}\)) are not model inputs. By showing that
productivity increases observed during SOFeX were driven by increases in \( \alpha^b \) and \( \phi_m \), we underscore the limitations of using light-saturated (\( P_{\text{max}}^b \) or \( P_{\text{opt}}^b \)-based) production models and the importance of using the family of models that resolve light-limited production (e.g., refs. 20–22). Models that account for variability in light-limited photosynthesis will better reproduce the effects of natural background and episodic iron input.

**SOFeX Results.** There was an immediate and sustained increase in the maximum quantum yield (\( \phi_m \)) of total phytoplankton in response to iron addition (Fig. 1A). \( \phi_m \) is the fundamental quotient of the moles of carbon incorporated in the phytoplankton cell divided by the moles of light that the phytoplankton cell absorbs and is a key indicator of the photosynthetic efficiency of phytoplankton. The >2-fold mean increase in \( \phi_m \) (Table 1) was driven by a nearly 2-fold increase in the maximum light utilization coefficient, \( \alpha^b \) (Table 1 and Fig. 1B), and a 28% decrease in the mean absorption normalized to incubator irradiance, \( (a_{\text{inc}}^b) \) (Table 1). The increases in photosynthetic efficiency of light-limited production, \( \alpha^b \) and \( \phi_m \), were not accompanied by a statistically significant increase in \( P_{\text{max}}^b \) (Fig. 1C and Table 1).

Throughout the iron enrichment experiment, Chl accumulated and primary productivity increased (Fig. 1 D and E). It is important to note that the increases in Chl resulted from a proportionally similar increase within the pico-, nano-, and micro-phytoplankton size classes (Fig. 2A). Iron addition did not markedly change the proportional makeup of the phytoplankton size-fraction assemblage. Likewise, whereas the absolute concentrations of the photosynthetic carotenoids (PCs) peridinin, 19′-butanoyloxyfucoxanthin, fucoxanthin, and 19′-hexanoyloxyfucoxanthin increased ~2-fold with iron addition, the PC:Chl quotients were similar inside and outside the iron-enriched patch (Fig. 2B). Fucoxanthin, a marker for diatoms, was the dominant PC inside and outside the iron-enriched patch, and the Chl-normalized relationships among the PCs changed very little (Fig. 2B).

Because there was no significant increase in the performance of light-saturated maximum productivity (\( P_{\text{max}}^b \)) and the proportion of pigments and size classes within the phytoplankton assemblage changed very little, we argue that the observed increases in Chl and productivity were primarily the result of increased photosynthetic efficiency in light-limited productivity (\( \alpha^b \)). Primary productivity models that do not include light-limited photosynthesis parameters such as \( \alpha^b \) and \( \phi_m \) cannot model this productivity response to iron addition. The following light-limited-photosynthesis-resolving productivity model demonstrates that, by primarily increasing the efficiency of light-limited photosynthesis, significant increases in primary productivity can be achieved.

**Productivity Model Using SOFeX Results.** There is a diversity of primary productivity models that build in complexity on the standard DIM presented in Eq. 1. With some minor exceptions (i.e., changes in Chl and \( P_{\text{opt}}^b \), with depth) the overriding difference between the DIM presented in Eq. 1 and more complicated depth-, time- and wavelength-resolved models is the treatment of the propagation of light through the water column and the expression of the efficiency of light-limited productivity (\( \phi_m \), \( \alpha^b \)). In Eq. 1 the treatment of irradiance, \( \alpha^b \) and \( \phi_m \) is expressed within the dimensionless variable \( F \). Because it is thought that \( F \) plays a relatively minor role in the overall global variability of \( PP_{\text{opt}} \), most models of primary productivity use an average value of \( F \).
of F or vary F as a function of light, as in Eq. 2. However, to resolve the observed iron-dependent 2-fold changes in $\alpha_b$ and $\phi_{in}$ it is necessary to use a productivity model that expresses F and light-limited primary productivity more fully.

A typical light-limited, photosynthesis-resolving productivity model resolves the quantity and quality of irradiance throughout the water column and throughout the day (see review in ref. 18). In this case the resolution is 1 m and $\sim$30 s:

$$PP_{eu} = \int_{0}^{Z_{eu}} \int_{\text{sunrise}}^{\text{set}} P_{\text{max}}^b \text{Chl}(z) \text{d}t \times \text{d}z,$$

where $PP_{eu}$ is the daily primary productivity integrated to the depth of the euphotic zone (mg C m$^{-2}$ d$^{-1}$); $P_{\text{max}}^b$ is the maximum Chl-specific productivity (mg C mg Chl h$^{-1}$); Chl(z) is the depth-dependent Chl concentration (mg Chl m$^{-3}$); $\phi_{in}$ is the maximum quantum yield (mol C mol quanta$^{-1}$); $E_0(z, t)$ are 30-s and 1-m intervals of irradiance (mol quanta m$^{-2}$ s$^{-1}$); 43.2 converts micromol and milligrams to moles and hours to seconds; and $\tilde{a}_{\text{PUR}}^b(z)$ is the mean Chl-specific absorption coefficient (m$^2$ mg Chl$^{-1}$) defined in relation to the actual spectral composition of in situ light, photosynthetically usable radiation (PUR):

$$\tilde{a}_{\text{PUR}}^b(z) = \int_{700 \text{nm}}^{400 \text{nm}} \frac{a_b^\alpha(\lambda) - E_0(\lambda, z) \text{d}\lambda}{\int_{700 \text{nm}}^{400 \text{nm}} E_0(\lambda, z) \text{d}\lambda},$$

where $a_b^\alpha(\lambda)$ (m$^2$ mg Chl$^{-1}$) is lipid-soluble absorption by phytoplankton pigments (Fig. 3A), and $E_0(\lambda, z)$ (mol quanta m$^{-2}$ s$^{-1}$) is modeled depth- and spectrally dependent scalar in situ irradiance (Fig. 3B, black lines). Scalar irradiance is calculated from downwelling photosynthetically active radiation (PAR) that is measured above the surface of the ocean [E$_{inc}$ (0$^\circ$), mol quanta m$^{-2}$ s$^{-1}$] and propagated through the water column by using spectrally resolved light attenuation models dependent on date, location, and Chl concentration (23–25). This productivity model (Eq. 3) performed well in comparisons with 24-h simulated in situ $^{14}$C primary productivity measurements in which 24-h productivity, $\phi_{in}$, $P_{\text{max}}^b$, and $\tilde{a}_{\text{PUR}}^b(z)$ were measured from identical sample bottles ($r^2 = 0.95$, slope = 0.92).

We use the light-limited, photosynthesis-resolving primary productivity model in Eq. 3 to demonstrate the importance of light-limited productivity in response to enhanced iron supply. Approximately 30-s intervals of measured surface PAR from sunrise to sunset on a typical day during the SOFeX cruise were propagated through a 50-m water column (approximate mixed layer depth) at 1-m intervals using light attenuation models (23–25) to produce the family of 100,000 discrete PAR occurrences shown in the histogram in Fig. 4A. Using Eq. 3, the mean values in Table 1, and the histogram of PAR occurrences (Fig. 4A), the absolute amount of primary productivity (mmol C m$^{-2}$ d$^{-1}$) were calculated for each discrete PAR wavelength (Fig. 4D). The same variables were used to plot primary productivity versus depth (Fig. 4E). Fig. 4B shows the mean PvsE curve inside and outside the iron-enriched patch for the mean values in Table 1. The difference between the light-limited vs. light-saturated portion of the PvsE curve is clear in Fig. 4B; light-saturated photosynthesis begins at irradiances of $\sim$100 mmol quanta m$^{-2}$ s$^{-1}$ outside the iron-enriched patch. Approximately 83% of the family of PAR occurrences in Fig. 4A occur at light levels $<100$ mmol quanta m$^{-2}$ s$^{-1}$. As a result, the majority of $PP_{eu}$ occurs at low-light intensities (Fig. 4D). For example, $\sim$58% of the $PP_{eu}$ outside of the iron-enriched patch (total = 19.8 mmol C m$^{-2}$ d$^{-1}$) and 66% of the $PP_{eu}$ inside the patch (total = 27.7 mmol C m$^{-2}$ d$^{-1}$) occur at light intensities $<100$ mmol quanta m$^{-2}$ s$^{-1}$ (Fig. 4D). More importantly, the large majority of the difference in primary productivity outside and inside the iron-enriched patch occurs at very low light intensities; 50% of the difference occurs at irradiances $<37$ mmol quanta m$^{-2}$ s$^{-1}$ and 84% of the difference occurs at irradiances $<100$ mmol quanta m$^{-2}$ s$^{-1}$ (Fig. 4D).

The relative importance of light-limited productivity only weakly depends on daily irradiance. In Fig. 4, productivity is modeled by using an integrated daily surface irradiance of 16 mol quanta m$^{-2}$ d$^{-1}$, which represents a typical irradiance for the SOFeX cruise (range = 9 to 44 mol quanta m$^{-2}$ d$^{-1}$). Modeled with the cruise maximum of 44 mol quanta m$^{-2}$ d$^{-1}$, 50% of the productivity outside of the iron-enriched patch and 57% of the productivity inside the patch would occur at light intensities $<100$ mmol quanta m$^{-2}$ s$^{-1}$. Fully 50% of the difference in productivity from inside the patch to outside the patch would occur at light intensities $<48$ mmol quanta m$^{-2}$ s$^{-1}$. Regardless of the quantity of total daily irradiance, most photosynthesis in the water column occurs at light-limited irradiances.

Although maximum quantum yield, $\phi_{in}$, has not previously been reported in Southern Ocean iron experiments, all five Southern Ocean bloom-forming mesoscale iron additions conducted between 1999 and 2004 resulted in increased photosynthetic competency as measured by variable fluorescence (1, 2, 26–28). The PvsE experiment results reported here are similar to those made during a 2000 mesoscale iron enrichment experi-
iminent in the Atlantic sector of the Southern Ocean (EisenEx; ref., 28). “During EisenEx, we observed no general inside/outside difference in $P_{\text{phy}}$ whereas $a^h$ was slightly higher inside the Fe-enriched patch” (28). Also, one of the first iron-enrichment experiments conducted in the equatorial Pacific saw similar results; iron-induced increases in $\phi_{\text{phy}}$ were not accompanied by significant increases in $P_{\text{phy}}$. Chl-normalized primary production (mmol C mg Chl$^{-1}$ d$^{-1}$) (29).

The 5-fold increases in $PP_{\text{eu}}$ and 9-fold increases in Chl measured during the SOFeX iron addition were not accompanied by a significant increase in $P_{\text{phy}}$. Instead, biomass and productivity increases were driven by 2-fold increases in $\phi_{\text{phy}}$ and $a^h$. Any primary productivity model that does not incorporate variability in light-limited production will fail to reproduce the development of an iron-induced bloom because the physiological driver of the productivity increase ($\phi_{\text{phy}}$ and $a^h$) in such a model is a constant rather than a variable. Primary productivity algorithms that resolve the variability of light-limited photosynthesis are necessary to model iron effects in the Southern Ocean and, we hypothesize, other iron-regulated regions of the world ocean. Primary productivity models that account for variability in light-limited photosynthesis will better reproduce the effects of natural background and episodic iron inputs.

Materials and Methods

Chl was determined by fluorometric methods and HPLC. Water samples were filtered in parallel onto 25-mm Whatman glass fiber filters (GF/F, nominally a 0.7-$\mu$m size fraction) and 5- and 20-$\mu$m Poretics polycarbonate filters. Fresh samples were extracted in 90% acetone at –20°C for 24–30 h (30) and quantified by using a Turner Designs fluorometer (31, 32). A complete suite of phytoplankton pigments were also analyzed from frozen samples following the procedures described by Bidigare et al. (33).

Maximum quantum yield was determined with measurements of phytoplankton absorption and PoE experiments. Particulate matter was collected by filtering 0.5–4 liters of upper mixed layer sample water through 25-mm GF/F glass fiber filters, with greater volumes filtered for low biomass waters. Spectral absorption coefficients were measured with a dual beam spectrophotometer. Diffuse coefficients for total particulate matter were calculated by using the equations described in the National Aeronautics and Space Administration Ocean Optics Protocols (34) and by Mitchell (35). Methanol was used to extract pigments from the filtered sample, and the depigmented filter was then measured to estimate detrital absorption (36). The difference between the two measurements nominally represents lipid-soluble absorption by phytoplankton pigments [$\Delta(\alpha)$] (Fig. 3A). The mean Chl-specific absorption coefficient normalized to incubation irradiance ($\alpha_{\text{INC}}$) (m$^2$mg Chl$^{-1}$) is calculated as in Eq. 4 with the exception that $E_0$, the global irradiance, is replaced with $E_{\text{inc}}$ (see Spectral absorption coefficients were measured with a dual beam spectrophotometer. Diffuse coefficients for total particulate matter were calculated by using the equations described in the National Aeronautics and Space Administration Ocean Optics Protocols (34) and by Mitchell (35). Methanol was used to extract pigments from the filtered sample, and the depigmented filter was then measured to estimate detrital absorption (36). The difference between the two measurements nominally represents lipid-soluble absorption by phytoplankton pigments [$\Delta(\alpha)$] (Fig. 3A). The mean Chl-specific absorption coefficient normalized to incubation irradiance ($\alpha_{\text{INC}}$) (m$^2$mg Chl$^{-1}$) is calculated as in Eq. 4 with the exception that $E_0$, the global irradiance, is replaced with $E_{\text{inc}}$ (see Spectral absorption coefficients). The Chl-specific maximal photosynthetic rate ($P_{\text{max}}$) was estimated by using a nonlinear, least-squares routine (39). The maximum Chl-specific light utilization coefficient [$\alpha b$, mg Chl$^{-1}$ h$^{-1}$ (mol quantum$^{-2}$ s$^{-1}$)] was determined following Johnson and Barber (40). The light-saturation index ($E_{\text{inc}}$, mol quantum$^{-2}$ s$^{-1}$) is the quotient of $P_{\text{max}}$ and $\alpha b$. Maximum quantum yield of carbon uptake ($\phi_{\text{phy}}$, mol C mol quanta$^{-1}$) was calculated from $\alpha b$ and $\alpha_{\text{INC}}$:

$$\phi_{\text{phy}} = \frac{\alpha b}{43.2 \alpha_{\text{INC}}}$$

where 43.2 converts seconds to hours, milligrams to moles, and micromols to moles. It is important to note that $\phi_{\text{phy}}$ can be used to describe the $\phi_{\text{in situ}}$ of a single phytoplankton cell, in which case the theoretical $\phi_{\text{in situ}}$ is 0.125. Here, we use $\phi_{\text{phy}}$ to describe the $\phi_{\text{in situ}}$ of the in situ mixed phytoplankton assemblage that depends on irradiance, nutrients, and temperature and is unlikely to approach the theoretical maximum of 0.125 mol C mol quanta$^{-1}$. The range of $\phi_{\text{phy}}$ in this

![Figure 4](image-url)
study (0.006 to 0.040 mol C mol quanta⁻¹; Table 1) is in line with near surface
measurements made in the Atlantic Sector of the Southern Ocean (0.006–
0.027 mol C mol quanta⁻¹) (41).

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