# Modeling Photosynthesis and Exudation of DOM in Subtropical Oceans

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November 24, 2022

#### Abstract

Parameterizations of algal photosynthesis commonly employed in global biogeochemical simulations generally fail to capture the observed vertical structure of primary production. Here we examined the consequences of decoupling photosynthesis (carbon fixation) and biosynthesis (biomass building) with accumulation or exudation of excess photosynthate under energy rich conditions in both regional and global models. The results show that the decoupling of these two processes improved the simulated vertical profile of primary production, increased modeled global primary production up to ~35%, improved simulated meridional patterns of particulate C:N:P and increased modeled surface pool of semi-labile DOC.

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#### Key Points:

11	•	Decoupling of photosynthesis and biosynthesis improved simulations of primary
12		production
13	•	Predicted global primary production increased by $35\%$
14	•	Model results suggest exudation could contribute $\sim 20\%$ to total DOC source in
15		euphotic layer

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#### 17 Abstract

Parameterizations of algal photosynthesis commonly employed in global biogeochemical sim-18 ulations generally fail to capture the observed vertical structure of primary production. Here 19 we examined the consequences of decoupling photosynthesis (carbon fixation) and biosyn-20 thesis (biomass building) with accumulation or exudation of excess photosynthate under 21 energy rich conditions in both regional and global models. The results show that the decou-22 pling of these two processes improved the simulated vertical profile of primary production, 23 increased modeled global primary production up to  $\sim 35\%$ , improved simulated meridional 24 patterns of particulate C:N:P and increased modeled surface pool of semi-labile DOC. 25

#### <sup>26</sup> 1 Introduction

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The structure and rates of photosynthesis and biosynthesis by primary producers in the 27 ocean's subtropical gyres reflect the balance between photons delivered from above, macro-28 nutrients delivered largely from below, and essential trace metals such as iron which has both 29 oceanic and atmospheric sources. The observed vertical profiles in Fig.1 from North Pacific 30 and North Atlantic subtropical gyres (Karl & Church, 2014; White et al., 2015; Steinberg 31 et al., 2001; Letelier et al., 1996) reveal the transition from nutrient to light limitation 32 over a relatively short distance (less than 100m). Primary production is often highest 33 at the surface, decreasing with depth (Fig.1) while Chlorophyll-a concentrations (Chla) 34 are elevated in a region termed the Deep Chlorophyll Maximum (DCM), characterized by 35 persistent light limitation and proximity to the nitracline (Letelier et al., 2004). In contrast, 36 particulate organic carbon (POC; including living biomass) is more uniform over the upper 37 75 m leading to a vertical gradient in mass normalized primary production. These vertical 38 contrasts suggest a decoupling of photosynthesis (the fixation of  $CO_2$  into carbohydrates) 39 and biosynthesis (production of a suite of functional macromolecules including proteins) over 40 the light gradient. Yet commonly employed biogeochemical models treat photosynthesis 41 and biosynthesis as tightly coupled processes limited by light, temperature, and nutrients 42 (e.g. Dutkiewicz et al. (2015); Dunne et al. (2013); Aumont et al. (2015)). These models 43 typically represent the carbon-specific photosynthesis rate for phytoplankton type j,  $P_{C,i}$ 44  $(mmol \ C \ (mmol \ C)^{-1} \ d^{-1})$ , as a function of irradiance, and a flexible Chla:C ratio following 45 Geider et al. (1997): 46

$$P_{C,j} = P_{C,j}^{Sat} \left[ 1 - exp\left( -\frac{\alpha I \ \theta_j}{P_{C,j}^{Sat}} \right) \right]$$
(1)

where,  $\alpha$  is the initial slope of the photosynthesis-irradiance curve normalized to Chla  $(m^2 \ (mg \ Chla)^{-1} \ mmol \ C \ (\mu mol \ photons)^{-1}), I$  is the flux of photosynthetically active radiation (PAR,  $\mu mol \ photons \ m^{-2} \ s^{-1}), \theta_j$  is the Chla:C ratio of phytoplankton type  $j \ (mg \ Chla \ (mmol \ C)^{-1})$ . The light-saturated photosynthetic rate for type  $j, P_{C,j}^{Sat}$   $(mmol \ C \ (mmol \ C)^{-1} \ d^{-1})$ , is typically modeled as dependent on both temperature and nutrient availability:

$$P_{C,j}^{Sat} = P_{C,j}^{max} \frac{Nut}{Nut + K_{Nut,j}} \cdot T_{func}$$

$$\tag{2}$$

Following Geider et al. (1997), temperature dependence is introduced through a multiplica-55 tive function  $T_{func}$  (e.g. Arrhenius equation), and there is an explicit accounting of nutrient 56 limitation through a multiplicative, hyperbolic function of Nut, the limiting nutrient con-57 centration. The latter throttles back photosynthesis in low nutrient environments with the 58 consequence of tightly coupling photosynthesis and biosynthesis. However, the two pro-59 cesses may not be so tightly coupled. For example, photosynthesis can be limited by the 60 availability of light or photosynthetic apparatus (Mackey et al., 2008; Letelier et al., 2017), 61 while biosynthesis is limited by the cellular reserves and external availability of nitrogen 62 (N), phosphorus (P), or iron (Fe) (Marañón et al., 2013; Halsey & Jones, 2015) as well as 63 the necessary self-replicating apparatus. 64



Figure 1. Observed climatological average of photosynthesis rate, Chla, nitrate, particulate organic carbon (POC), and photosynthetically active radiation (PAR) at HOT and BATS. The data were obtained from the observations from 1988 to 2018 at both stations.

Phytoplankton may balance the supply and demand of photosynthesis and biosynthesis 65 by the regulation of nutrient uptake (Flynn, 2003), "luxury storage" of resources in excess 66 of demand (Martin et al., 2014) or the exudation of excess photosynthate (Halsey & Jones, 67 2015). The excretion of DOM in nutrient replete, exponentially growing cultures phyto-68 plankton is low,  $\sim 2\%$  of total gross carbon fixation (López-Sandoval et al., 2013). How-69 ever, recent studies show that *Prochlorococcus*, an abundant pico-cyanobacterium found in 70 oligotrophic ocean regions and which only have a moderate ability for photoacclimation, 71 can excrete a large fraction of fixed C under nutrient-limited conditions (Thompson et al., 72 2018; Cailliau et al., 1996; Szul et al., 2019; Kulk et al., 2011; Bertlisson et al., 2005; Roth-73 Rosenberg et al., 2021). Thus exudation is more likely significant in the oligotrophic surface 74 ocean where there is persistent nutrient limitation and light-saturating conditions. The 75 exudates may be a source of carbon for heterotrophic bacteria (Berman & Holm-Hansen, 76 77 1974; Bjørrisen, 1988), which increase remineralization and total ecosystem biomass, hence promoting the co-evolution of phototrophic and heterotrophic populations (Braakman et 78 al., 2017; Sarmento et al., 2016). 79

Here we use numerical models to investigate the consequences of decoupling photosyn-80 thesis and biosynthesis on the simulation of primary production in the oligotrophic gyres. 81 as well as the global rates of photosynthesis and potential exudation of DOC. First, we 82 briefly describe the 1D and 3D models with particular emphasis on the treatment of pho-83 tosynthesis and its coupling to biosynthesis (Methods, 2). We demonstrate, using a high 84 vertical-resolution, 1D model that the "standard" photosynthesis parameterization does not 85 capture the observed vertical profile of primary production. In particular, it strongly under-86 predicts photosynthesis in the nutrient depleted surface layer. We find that removing direct 87 macronutrient limitation on photosynthesis, but retaining the indirect cost of maintaining 88 photosynthetic machinery, significantly improves the vertical structure and vertically inte-89 grated rates of primary production in 1D water column simulations. It also increases global 90 primary production and DOC production by about 30% in a 3D global model (See Section 91 3).92

#### 93 2 Methods

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#### 2.1 Environmental Modeling Framework

The biogeochemical-ecosystem model describes the cycling of carbon, nitrogen, phosphorus, iron, silica and oxygen in both living and non-living forms as discussed in Follows et al. (2007) and Dutkiewicz et al. (2015). We employ one-dimensional (1D) and threedimensional (3D) physical configurations with identical biogeochemistry and ecology. We first examine the qualitative impact of decoupling carbon and nutrient flows in vertically well-resolved 1D simulations and then quantitatively evaluate the impact in 3D global simulations.

The 1D simulations were configured to resolve only the vertical dimension in space. 102 The 6000 m deep column has a vertical resolution of 10 m from sea surface to 120 m depth 103 and with gradually increasing thickness thereafter. Nutrient distributions and plankton 104 biomass were initialized according to World Ocean Atlas (Garcia et al., 2018) and previous 105 3D simulations relevant to HOT (Hawaii Ocean Time-series) in the North Pacific Subtrop-106 ical Gyre and BATS (Bermuda Atlantic Time-Series) in the North Atlantic (Dutkiewicz et 107 al., 2015). In this configuration, a seasonal mixed layer was driven by restoring to clima-108 tological, seasonal sea surface temperatures which drives winter-time convection following 109 Hickman et al. (2010). The 1D framework does not resolve the contributions of isopyc-110 nal nutrient transport nor the effect of mesoscale motions, tides, and internal waves which 111 drive intermittent nutrient transfer into the euphotic zone (McGillicuddy, 2016). Hence, 112 the vertical, diapycnal diffusivity for HOT and BATS were modified to parameterize these 113 processes. The time step of 1D configuration is 1h and we integrate the 1D configuration for 114 30 years with a repeating generic "year" of external forcings. The model results establish a 115 repeating pattern after several years spin-up leading to a "quasi-steady state" by year 10. 116 In the analysis presented below we consider the climatology of the last 15 years of 30 year 117 simulations. 118

The 3D configuration of the MIT general circulation model (MITgcm) (Marshall et al., 119 (1997) has a horizontal resolution of  $1^{\circ} \times 1^{\circ}$ . There are 23 vertical levels, 10m for the top two 120 levels, and then graduated in thickness to 500m at depth. The physical fields are constrained 121 by satellite and in-situ observations (Wunsch & Heimbach, 2007) (the ECCO-GODAE state 122 estimate), which is used by many previous biogeochemical-ecosystem studies (Follows et al., 123 2007; Ward et al., 2012; Dutkiewicz et al., 2015; Ward & Follows, 2016). The 3D simulations 124 were initialized by World Ocean Atlas (Garcia et al., 2018) for nitrate, phosphate, and silicic 125 acid and previous model output for iron, ammonium, nitrite, dissolved and particulate 126 matter, and plankton biomass. We integrate the system forward in time for 10 years from 127 initial conditions provided by an earlier simulation. The simulated phytoplankton establish 128 a repeating pattern after about 4 years after which the system represents a "quasi-steady 129

state" with a slow, longer term adjustment in nutrient fields not affecting the results that
 we discuss here. We show results from the tenth year of the simulation.

We resolve two size classes of phytoplankton (picophytoplankton and all others) as 132 well as two types of grazers. The biogeochemical and biological tracers interact through 133 the formation, transformation, and remineralization of organic matter. Mortality, sloppy 134 feeding, and exudation transfer living organic material into sinking particulate and dissolved 135 organic detritus which are respired back to inorganic form with simple parameterizations of 136 the activity of heterotrophic decomposers. Iron cycling includes scavenging by particles and 137 explicit complexation with an organic ligand following Dutkiewicz et al. (2015). Aeolian 138 iron fluxes to the ocean surface are provided by Luo et al. (2008). The complete model 139 equations and descriptions are provided in the Supporting Information. 140

#### <sup>141</sup> 2.2 Cellular Stoichiometry and Photosynthesis



Figure 2. Schematic representations of cellular C flow. (a) represents the model in which C and N flow are tightly coupled. (b) represents the model in which C and N flow are decoupled.

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In this study, we examine the biogeochemical implications of decoupling carbon and nutrient flow by comparing two physiological parameterizations (see Fig.2). In the "standard model" (depicted in Fig.2a) following Eq.2 (Geider et al., 1997), photosynthesis is directly influenced by the external concentration of fixed nitrogen (proportional to  $[NO_3^-]/([NO_3^-] + K_{NO_3}))$ ). In the "decoupled model", (depicted in Fig.2b) carbon and nitrogen flows are buffered by independent reserves (following, for example, Talmy et al. (2014), Bruggeman and Kooijman (2007)) and the light-saturated photosynthesis rate is not directly dependent on the external fixed-nitrogen availability (compare to Eq.2):

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$$P_{C,j}^{Sat} = P_{C,j}^{max} \cdot T_{func} \tag{3}$$

Here photosynthesis is sensitive to nitrogen availability only indirectly through Chla which is controlled by the rate of biosynthesis. Biosynthesis is controlled by the availability of reserves of both photosynthate and other nutrient elements. In the decoupled model, the rate of photosynthesis continues to be controlled by the light environment even when biosynthesis is nitrogen limited. In that case, excess photosynthate is stored in the reserve or exuded. The mathematical details of these parameterizations are described below.

#### 2.3 Details of physiological parameterizations.

In Eq.1 and Eq.2,  $P_{C,j}^{max}$  is the maximum carbon-normalized photosynthesis rate of phytoplankton  $j \pmod{C \pmod{C^{-1} d^{-1}}}$ ,  $T_{func}$  represents the temperature limitation

Parameter	Symbol	Type I	Type II	Unit
Maximum photosynthesis rate	$P_C^{max}$	0.76	3.15	$mmol \ C \ (mmol \ C)^{-1} \ d^{-1}$
Maximum uptake rate	$V_{NO_3}^{max}$	0.49	0.14	$mmol \ N \ (mmol \ C)^{-1} \ d^{-1}$
	$V_{NO_2}^{max}$	0.49	0.14	$mmol \ N \ (mmol \ C)^{-1} \ d^{-1}$
	$V_{NH_4}^{max}$	0.24	0.07	$mmol \ N \ (mmol \ C)^{-1} \ d^{-1}$
	$V_{PO_4}^{max}$	0.014	0.01	$mmol \ P \ (mmol \ C)^{-1} \ d^{-1}$
	$V_{Fe}^{max}$	$1.83 \times 10^{-5}$	$9.92 \times 10^{-6}$	$mmol\;Fe\;(mmol\;C)^{-1}\;d^{-1}$
Half-saturation concentration	$K_{NO_3}$	$2.76\times10^{-3}$	0.41	$mmol \ N \ m^{-3}$
	$K_{NO_2}$	$2.76\times 10^{-3}$	0.41	$mmol \ N \ m^{-3}$
	$K_{NH_4}$	$1.38 \times 10^{-3}$	0.21	$mmol \ N \ m^{-3}$
	$K_{PO_4}$	$1.73 \times 10^{-4}$	0.026	$mmol \ P \ m^{-3}$
	$K_{FeT}$	$1.73 \times 10^{-7}$	$2.59\times10^{-5}$	$mmol \ Fe \ m^{-3}$
Celluar stoichiometric ratios	$R_{C:N}$	7.5	7.5	$mmol \ C \ (mmol \ N)^{-1}$
	$R_{C:P}$	120.0	120.0	$mmol \ C \ (mmol \ P)^{-1}$
	$R_{C:Fe}$	$1.2\times 10^5$	$1.2\times 10^5$	$mmol \ C \ (mmol \ Fe)^{-1}$

Table 1. Biological parameters of different phytoplankton functional types.

160 on photosynthesis:

$$T_{func} = \tau \cdot exp \left[ A_E \left( \frac{1}{T + 273.15} - \frac{1}{T_0} \right) \right]$$
(4)

where  $\tau$  is Arrhenius coefficient,  $A_E$  is the slope of the linear region of the Arrhenius plot,  $T_0$  is the reference temperature of phytoplankton j (K), and T is water column temperature (°C).

Photosynthate is delivered to a "reserve" (carbohydrate or lipid) from where it may be used for biosynthesis or exuded. The potential rates of uptake of nutrients other than carbon (nitrogen, phosphorus, iron) are evaluated with Michaelis-Menten kinetics and an Arrhenius temperature dependence, following Eq.5 and Eq.6.

$$V_{R,j} = V_{R,j}^{max} \cdot \gamma_{R,j} \cdot T_{func} \tag{5}$$

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$$\gamma_{R,j} = \frac{R}{R + K_{R,j}} \tag{6}$$

where  $V_{R,j}^{max}$  is the maximum carbon-normalized uptake rate for resource R of phytoplankton j (mmol R (mmol C)<sup>-1</sup>  $d^{-1}$ ),  $\gamma_{R,j}$  is the nutrient limitation based on Michaelis-Menten kinetics,  $K_{R,j}$  is the half-saturation concentration of resource R of phytoplankton j(mmol  $R m^{-3}$ ). The total potential uptake of nitrogen is defined as the sum of the uptake of each species in Eq.7.

$$V_{N,j} = V_{NH_4,j} + V_{NO_3,j} + V_{NO_2,j}$$
<sup>(7)</sup>

The carbon demand to build biomass,  $D_{i,j}$  (mmol C (mmol C)<sup>-1</sup>  $d^{-1}$ ), for each nutrient element *i* and each phytoplankton type *j*, is evaluated based on an assumed, fixed stoichiometry of functional biomass (e.g. protein, nucleic acids, etc) in Eq.8.

$$D_{i,j} = V_{i,j} \cdot R_j^{C:i} \tag{8}$$

where *i* denotes  $N, P, Fe, R_j^{C:i}$  is the C: i ratio in phytoplankton  $j \pmod{C \pmod{i}^{-1}}$ . The carbon-specific production of functional biomass (biosynthesis) is then determined as the minimum of the photosynthesis rate and the carbon demand of the most limiting nutrient in Eq.9 and Eq.10.

$$BS_{C,j} = min[D_{min,j}, P_{C,j}] \tag{9}$$

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$$D_{min,j} = min[D_{N,j}, D_{P,j}, D_{Fe,j}]$$
(10)

Previously published models of exudation in laboratory cultures (Grossowicz, Roth-187 Rosenberg, et al., 2017; Grossowicz, Marques, & van Voorn, 2017; Vallino, 2000; Flynn et 188 al., 2008) have parameterized exudation as a simple, imposed fraction of primary produc-189 tion or with more complex approaches linked to nutrient limitation, biomass, and nutrient 190 stoichiometry (see the review of Livanou et al. (2019)). Here we assume that if the photo-191 synthesis rate is greater than growth rate (which means biosynthesis is limited by nutrients 192 rather than light energy), a fraction of the excess photosynthate accumulates in the carbon reserve and the remainder  $f_{e,j}$  is assumed exuded into the environment at the rate of  $E_{C,j}$ 194  $(mmol \ C \ (mmol \ C)^{-1} \ d^{-1})$  as described in Eq.11. In the results we assume  $f_{e,j}=0.7$  in 195 Fig.4-6. We examine this choice later in this manuscript. 196

$$E_{C,j} = max[0.0, P_{C,j} - BS_{C,j}] \cdot f_{e,j}$$
(11)

We parameterize the two classes of phytoplankton as pico-phytoplankton (type I) with high nutrient affinity, but low growth rates, and the larger phytoplankton (type II) with lower nutrient affinity and higher growth (Follows et al., 2007). Values of the parameters (Table 1) are similar to the cyanobacteria and diatom values used in Dutkiewicz et al. (2020).

#### <sup>202</sup> **3** Results and Discussion.

First we examine the qualitative impact of decoupling carbon and nutrient flows on the vertical structure of modeled primary production in a 1D framework, referencing observed profiles at HOT and BATS. Then we examine the quantitative impact on integrated primary production in 3D global simulations. For this discussion, we will refer to the simulations in which N and C flow are tightly coupled as the "standard" simulations and those in which N and C flow are decoupled as the "decoupled" simulations.

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#### 3.1 Vertical Profiles of Subtropical Productivity

We first examine qualitative differences between 1D simulations where photosynthesis 210 211 is explicitly limited by nutrient concentrations following Eq.2 ("standard" model, Fig.2a) to simulations where photosynthesis depends on nutrients only indirectly through the rate 212 of biosynthesis for photosynthetic pigments ("decoupled" model, Fig.2b, also see Eq.S20-21 213 in Supporting Information). The climatologies of the last 15 years of the simulations are 214 compared with climatological data from HOT (1988-2018) and BATS (1989-2016). Some 215 general features of the two sites were qualitatively captured in both simulations (Fig.3) 216 including the late winter bloom at BATS and the DCM at both sites (during the summer 217 at BATS and year-round at HOT). As observed, simulated seasonality at HOT was much 218 weaker than at BATS due to the difference in seasonal physical forcing (Malmstrom et al., 219 2010; Karl & Church, 2014; Steinberg et al., 2001; Cavender-Bares et al., 2001). 220

However, the standard and decoupled simulations also show some significant differ-221 ences with one-another which we highlight in Fig.4. Due to the explicit throttling back of 222 photosynthesis in the highly oligotrophic surface waters caused by nutrient limitation, the 223 standard model fails to capture the increase of photosynthesis towards the surface both at 224 HOT and, more strikingly, at BATS. The standard model consistently predicts extremely 225 low photosynthesis rates near the surface relative to the observed climatologies. In con-226 trast, the solid blue lines in Fig.4 indicate the simulations of the decoupled model. Here 227 photosynthesis was not throttled back under low nitrogen conditions however nitrogen lim-228



Figure 3. One-dimensional model simulations: seasonal variation and biases of photosynthesis rate and Chla at HOT and BATS. (a) photosynthesis rate of decoupled simulation at station ALOHA (mmol  $C m^{-3} d^{-1}$ ); (b) photosynthesis rate of standard simulation at station ALOHA (mmol  $C m^{-3} d^{-1}$ ); (c) observed photosynthesis rate at station ALOHA (mmol  $C m^{-3} d^{-1}$ ); (d) photosynthesis rate of decoupled simulation at station Bermuda (mmol  $C m^{-3} d^{-1}$ ); (e) photosynthesis rate of standard simulation at station Bermuda (mmol  $C m^{-3} d^{-1}$ ); (e) photosynthesis rate of standard simulation at station Bermuda (mmol  $C m^{-3} d^{-1}$ ); (f) observed photosynthesis rate at station Bermuda (mmol  $C m^{-3} d^{-1}$ ); (g) Chla concentration of decoupled simulation at station ALOHA (mg  $Chla m^{-3}$ ); (h) Chla concentration at station ALOHA (mg  $Chla m^{-3}$ ); (i) observed Chla concentration at station Bermuda (mg  $Chla m^{-3}$ ); (j) Chla concentration of decoupled simulation at station Bermuda (mg  $Chla m^{-3}$ ); (k) Chla concentration of standard simulation at station for  $m^{-3} (m^{-3})$ ; (k) Chla concentration of standard simulation at station Bermuda (mg  $Chla m^{-3}$ ); (k) Chla concentration of standard simulation at station Bermuda (mg  $Chla m^{-3}$ ); (k) Chla concentration of standard simulation at station Bermuda (mg  $Chla m^{-3}$ ); (k) Chla concentration of standard simulation at station Bermuda (mg  $Chla m^{-3}$ ); (k) Chla concentration of standard simulation at station Bermuda (mg  $Chla m^{-3}$ ).

itation does control biosynthesis of pigments. The vertical profiles of primary production
 increase towards the surface, both qualitatively and quantitatively more consistent with the
 observations.

The vertically integrated rate of photosynthesis (0-200m) in the decoupled experiments is increased by  $\sim 21.1\%$  at HOT and more than 170% at BATS compared to the standard simulation. In the upper 200m of the decoupled simulations, photosynthesis exceeded biosynthesis rate by  $\sim 25\%$  at HOT and  $\sim 58\%$  at BATS. Excess photosynthate in the decoupled simulations accumulates as storage in the cells or is exuded, consistent with numerous laboratory and field studies (Thornton, 2014; Szul et al., 2019; Bjørrisen, 1988). However,



**Figure 4.** Annual averaged vertical profiles of primary production at (a) HOT and (b) BATS. Model results are annual averages from the last 15 years of 30 year integrations. The green solid lines indicate observed primary production from 1988 to 2016 and the horizontal green bars represent deviation of the inter-annual variations. The red dashed lines indicate the standard simulation, where photosynthesis is directly regulated by local nutrient concentration. The blue solid lines represent simulations of photosynthesis rate in the decoupled simulation.

due to the complexity of DOC composition, we do not address the fate of excess photosynthate in detail in the decoupled simulation, but instead examine the general consequences
of the balance between storage and exudation for the C:N:P ratio of phytoplankton biomass
and production of DOC in the following 3D study.

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#### **3.2** Global Biomass and Productivity

In the previous section we demonstrated that the decoupling of N and C flow in the physiological model leads to a significant qualitative improvement in simulations of the vertical profile of primary production. We now examine the implications for the prediction of global-scale primary productivity and elemental composition of phytoplankton (and particulate matter) by comparing global 3D standard and decoupled simulations.

Both standard and uncoupled simulations capture the high surface Chla, primary production, and nutrient concentrations in the subpolar and equatorial regimes, as well as low surface Chla, primary production, and nutrient concentrations in subtropical gyres (Fig.5, also see Fig.S1). Typical for such coarse resolution simulations, the dynamics and biogeochemistry of continental shelves and coastal regions are not resolved or well represented.

We asked what is the sensitivity of globally integrated primary production to the decoupling of nutrient and C at the cellular scale? Modeled global primary production of the standard and decoupled simulations were 34.0  $Pg C \cdot yr^{-1}$  and 45.8  $Pg C \cdot yr^{-1}$  respectively - an increase of 34%. Satellite-derived estimates range between 44 - 57  $Pg C \cdot yr^{-1}$  with the mean of 50.7  $Pg C \cdot yr^{-1}$  (Carr et al., 2006; Field et al., 1998; Silsbe et al., 2016) suggesting that the decoupled estimate is potentially more plausible. However, there are large uncer-



Figure 5. Comparison of standard and decoupled simulations of Chla and primary production(PP). (a) simulated primary production of standard model (0-55 m depth integrated,  $gC m^{-2} yr^{-1}$ ), (b) simulated primary production of decoupled model (0-55 m depth integrated,  $gC m^{-2} yr^{-1}$ ), (c) difference of primary production between standard and decoupled simulations (%), (d) simulated Chla of standard model (mean 0-55 m,  $mg \ Chla \ m^{-3}$ ), (e) simulated Chla of decoupled model (mean 0-55 m,  $mg \ Chla \ m^{-3}$ ), (f) difference of Chla between standard and decoupled simulations (%).

tainties underlying in both ocean color based and general circulation model based estimates of global primary production ranging from ~ 35 to ~ 70 Pg  $C \cdot yr^{-1}$  (Carr et al., 2006).

The 1D simulations indicated a significant improvement in the simulation of the vertical profile of primary production. We have used a Taylor diagram (Taylor, 2001) to compare the spatial variations of primary production in the two 3D simulations (standard and decoupled) against a suite of remote-sensing derived estimates of global-scale patterns and rates of primary production (Behrenfeld & Falkowski, 1997; Westberry et al., 2008; Silsbe et al., 2016) (Fig.6; also Fig.S2). We focused on open ocean regimes having bottom depths greater than 500 m since the global model does not resolve coastal systems and remote sensing algorithms are typically modified.

A comparison of the decoupled simulation with various remote sensing primary pro-269 duction products revealed similar variability (standard deviation) but a range of poor to 270 weak spatial correlation. However, the correlations of spatial variations between the various 271 remote sensing products themselves was just as broad ranging and also as weak as simu-272 lations. The satellite-derived products also have large error margins associated with them 273 that are not spatially homogeneous (Szeto et al., 2011). Thus we could not quantitatively 274 distinguish whether either standard or decoupled simulation has more skill by comparing 275 patterns of primary production. 276

The difference in primary production between decoupled and standard simulations how-277 ever mainly lies in oligotrophic gyres where there is a low nutrient nutrient supply rate rel-278 ative to the incoming light energy, as illustrated in Fig.5. The difference is most notable in 279 the Atlantic subtropical gyres where macro-nutrients were most depleted in the simulations 280  $(NO_3 \text{ fields showed Fig.S1(a)})$ . The standard simulation of primary production in sub-281 tropical gyres is too low relative to all the satellite-based products (Fig.S2). The increased 282 primary production in these regions in the decoupled simulation (Fig.5, Fig.S2) suggests 283 that the decoupling of carbon and nitrogen flow does indeed improve modelled primary 284 production. 285

The difference in Chla between decoupled and standard simulations is also most pro-286 nounced in the oligotrophic subtropical gyres. Chla decreases in the decoupled model relative 287 to the standard model because Chla synthesis is regulated by the ratio of photosynthesis 288 rate and light harvesting rate resulting in a negative relationship with  $P_{C,i}^{Sat}$  (see Eq.S20-21 289 in Supporting Information). On a point-by-point basis, the simulations of Chla are modestly 290 correlated with the climatology based on remote sensing (Fig.6, correlation coefficient 0.45) 291 and has a much weaker variation (standard deviation less than half that) of the observed 292 field. The two simulations are almost identical in this regard (Fig.6) so Chla comparisons 293 do not discriminate. 294



**Figure 6.** Taylor diagram showing correlations and normalized standard deviations of annual averaged Chla, primary production(PP), nitrate(NO3), and phosphate(PO4) between model simulations (55m depth integrated) and satellited-derived products (Chla and PP) or nutrients from World Ocean Atlas. The circles represent the comparisons between standard simulation and the products, the dots represent the comparisons between decoupled simulation and the products, the square, triangle and diamond represent the comparisons between different satellited-derived primary production. The best match would be a correlation of 1 (on the x axis) and normalized standard deviation of 1 showed as a circle on x axis.

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#### 3.3 Global-scale Signatures of Excess Carbon Exudation

The mechanisms and controls on phytoplankton exudation still remain an open ques-296 tion. In these explorations we have assumed that excess photosynthate is produced when 297 photon capture is in excess of growth potential and either accumulates in a "reserve", up 298 to a maximum capacity, or is exuded. The fraction of excess photosynthesis that is ex-200 uded  $f_{e,i}$ , cannot be determined a priori (Eq.11) but in theory can vary between 0 and 1. 300 Different species may also have different  $f_{e,j}$ . In the results we have shown to this point 301 we set  $f_{e,j}=0.7$ . Here we examine the sensitivity of, and explain, this choice by running 302 5 simulations with the decoupled model varying  $f_{e,j}$  from 0.1, 0.3, 0.5, 0.7, and 0.9 (Ta-303 ble 2). The global exuation rate increased in proportion to  $f_{e,j}$  while the standing stock 304

of surface DOC increased by 21% in response to a 9-fold increase of  $f_{e,j}$ . The differences between standard and decoupled simulations here are not only caused by  $f_{e,j}$  but also the decoupling of carbon and nutrient flows in primary production (by removing the explicit nutrient limitation, difference of Eq.2 and Eq.3).

$f_{e,j}$	Standard	0.1	0.3	0.5	0.7	0.9
Exudation (Pg C/yr)	0.0	1.06	3.31	5.78	8.54	11.78
DOC (Pg C)	1.86	2.48	2.58	2.70	2.83	3.00
Percentage of	0.0	2.97%	9.13%	15.65%	22.66%	30.40%
C:N	6.62	10.03	9.43	8.79	8.10	7.33
$\mathbf{C}:\mathbf{P}$	106.0	160.49	150.88	140.67	129.63	117.27

Table 2. Surface exudation, DOC, PER, and phytoplankton stoichiometry (55m depth integrated) in different  $f_{e,j}$  scenarios.

By decoupling photosynthesis and biosynthesis and allowing extra C storage in cells, 309 the decoupled model (Fig.2b) also resolves a dynamic phytoplankton stoichiometry instead 310 of a fixed one, which leads to a more dynamic and realistic global pattern of particulate C:N 311 and C:P ratios (Fig.7 and S3). The global patterns of particulate (plankton and detrital 312 matter) C:N and C:P ratios could also serve as an indicator of the model performance when 313 comparing with observations. The regions where C:N:P ratios are most affected by  $f_{e,i}$ 314 are oligotrophic gyres where photosynthetic rate is usually higher than biosynthesis rate 315 (Fig.S3) and the extra carbon will be either exuded into the environment or retained in the 316 cells. Compared with observations, our decoupled simulations capture the general patterns 317 of global particulate C:N:P ratio (Martiny et al., 2014; Martiny, Pham, et al., 2013; Martiny, 318 Vrugt, et al., 2013): high C:N and C:P ratios in oligotrophic gyres and low C:N and C:P 319 ratios in cold, nutrient rich high latitude regions. 320

However, the simulation with  $f_{e,j} = 0.5$  has higher within region variation than observations especially in subtropical gyres while the simulation of  $f_{e,j} = 0.9$  has a much lower variation than observations across the whole global ocean. The results most consistent with the observed C:N:P ratio has  $f_{e,j} = 0.7$  (implying that 70% of extra fixed C is exuded and 30% of the extra C is stored in C reserve). And as such, this is the main simulation we have shown in this manuscript.

In the decoupled simulations of  $f_{e,i} = 0.7$ , the predicted surface exudation rate (0-55m 327 integral) is shown in Fig.8a and the predicted percentage of total C in the C reserve is 328 shown is Fig.8b. As would be expected, the percentage of total phytoplankton carbon in 329 the reserve pool shares a similar spatial pattern with surface exudation, reflecting regions 330 where strong nutrient limitation and high photon fluxes coincide and in accord with previous 331 experimental and modeling studies (Livanou et al., 2019; Flynn et al., 2008; Szul et al., 2019; 332 Braakman, 2019). We quantified the percentage of extracellular release (PER), defined as 333 the percentage of total net photosynthesis released as exudate (shown in Fig.8c). In the 334 model PER is less than 15% in high latitude regions and greater than 50% in subtropical 335 gyres. This pattern is broadly consistent with field studies that reported that PER less 336 than 10% in productive regions with high nutrient concentration and up to 46% in less 337 productive regions like oligotrophic subtropical gyres (Teira, Pazó, et al., 2001; Teira, Serret, 338 & Fernández, 2001; Lagaria et al., 2013). Similarly, in laboratory cultures, PER has been 339 observed to vary between 2% to 10% under nutrient-replete conditions and increase up to 340 60% in nutrient-deplete conditions (Myklestad, 2000). The global exudation accounted for 341 about 19% of the total global DOC source with the rest originating from death and sloppy 342 feeding. None of these rates are well constrained in the model, reflecting both the simplicity 343



Figure 7. Particulate C:N and C:P ratios in Martiny et al. (2014) (red) and decoupled simulations (blue) with different  $f_{e,j}$ . The red bars of observations only contain a limited number of observation points while the blue bars of the simulations include all the grid points within each range. (a) to (c) are C:N ratios with  $f_{e,j} = 0.5, 0.7, 0.9$ , (d) to (f) are C:P ratios with  $f_{e,j} = 0.5, 0.7, 0.9$ .

of the parameterizations, but also the challenge of a clear and quantitative interpretation of the mechanisms at laboratory work.

#### <sup>346</sup> 4 Summary and Outlook

We have examined the consequences of the tight coupling of nutrient availability and 347 photosynthesis in a commonly employed parameterization (Geider et al., 1997) for regional 348 and global-scale carbon cycle simulations. The decoupling of these two processes signifi-349 cantly improved simulations of the vertical profile of subtropical primary productivity when 350 compared to in situ observations. In global simulations, it increased integrated primary pro-351 duction by about one-third with the most impact in oligotrophic subtropical gyres where 352 the original formulation with coupled processes consistently underestimated primary pro-353 duction relative to many satellite-based estimates. However, we note the large uncertainty 354 in the large scale satellite based estimates (see e.g. Fig 6, Carr et al. (2006)). 355

In order to explore the sensitivity of regional and global-scale simulations we have assumed either complete coupling or decoupling of photosynthesis/biosynthesis. It is likely that neither extreme is fully realistic and Geider et al. (1997) were clear about the uncertainty associated with the coupled assumption. There are numerous ways in which phytoplankton can accommodate light intensities greater than required to satisfy biosynthesis constraints, including the production of photo-protective pigments and photo-respiration (Halsey & Jones, 2015) which have not been considered here. This study provides a clear



Figure 8. Global exudation rate, C reserve, and percentage of extracellular release patterns (55m depth integrated). (a) simulated exudation rate  $(day^{-1})$ , (b) Percentage of total C in C reserve (%), (c) Percentage extracellular release (%).

indication of the sensitivity to two extreme possibilities and shows that they do have ma-363 jor implications for the simulation of global-scale productivity and the production of DOC. 364 Most compellingly, the simulations demonstrate that the vertical profile of primary produc-365 tion in oligotrophic environments is significantly improved in the decoupled case, bringing 366 the simulations into agreement with observed profiles of primary production and Chla at 367 HOT and BATS. As a consequence we suggest that the decoupled approach is the better 368 candidate for global carbon cycle simulations at present. In the global 3D simulation this new parameterization increased globally-integrated, annual primary production by about 370 a third. Such changes could have significant impact on how models capture the cycling 371 of carbon in the upper ocean, and such processes may have an impact on their ability to 372 capture inter-annual and longer term changes in the carbon cycle. 373

As a point of discussion, we found that the improvement in the vertical profile of 374 simulations was more significant in the 1D simulation when vertically resolution is higher. In 375 other words, if the euphotic layer is represented coarsely (i.e. greater than 10m resolution), 376 the low surface productivity associated with the standard approach is not easily apparent 377 because the profile is not resolved. As climate and carbon cycle models increase in both 378 horizontal and vertical resolution with increasing computational resources, the issue will be 379 more apparent. That said, even at coarse vertical resolution in the 3D simulations, the lower 380 global primary production of the standard approach could represent a problem. Moreover, 381

if models using the standard approach have been tuned to have reasonable global primary
 productions, they may in fact overestimate biosynthetic rates (if simulated).

Allocation of excess photosynthate to the reserve increases simulated C:N and C:P 384 ratios of particulate matter, particularly in the subtropics. Depending on the choice of 385 parameter values for the amount of carbon exuded versus stored, these increases in the sub-386 tropics brought the model more into line with observations (Martiny et al., 2014), and thus 387 may provide an empirical, large-scale calibration. Allocation of all excess photosynthate to 388 exuation would imply an additional source of DOC of more than 12  $Pg \ C \ yr^{-1}$ . Alloca-389 tion of all excess photosynthate to reserves would imply a global increase in C:N from 6.6:1 390 (Redfield Ratio) to greater than 10:1. A systematic and quantitative data-model synthesis 301 might be employed to better constrain this allocation at the community level, though the 392 complexities and uncertainties of DOC dynamics still clouds the development of suitable 303 parameterizations. Additionally, here we used a uniform parameter  $f_{e,i}$  for both types of 394 phytoplankton to control the allocation of excess photosynthate which could be species spe-395 cific in future simulations. It is likely that different species would have different values, and 396 that these may be altered under different environmental conditions. 397

In summary, we examined the consequence of decoupling photosynthesis and biosynthe-398 sis in the parameterization of photosynthesis employed in global biogeochemical models. We 399 found that removing direct nutrient limitation to photosynthesis significantly improved the 400 simulations of vertical profiles of primary production in the subtropical gyres and increased 401 predicted global primary production by more than 30% relative to the case where photo-402 synthesis and biosynthesis were tightly coupled. We explored the consequences of retention 403 versus exudation of the excess photosynthate in the global simulations which allowed this 404 405 new model to have reasonable global patterns of C:N and C:P ratios in phytoplankton.

#### 406 Acknowledgments

We are grateful for the support by the Simons Collaboration on Ocean Processes and Ecology 407 (SCOPE, 329108 to MJF and AW) and Simons Collaboration on Computational Biogeo-408 chemical Modeling of Marine Ecosystems (CBIOMES, 549931 to MJF). Additional support 409 is provided by the NSF to the HOT program (OCE-1756517 to AW), the Human Fron-410 tiers Science Program (RGP0020/2016 to DS). We also thank the dedicated efforts of the 411 HOT and BATS teams who facilitated in situ sample collection. The code and config-412 urations of the models used in this paper can be found at https://doi.org/10.6084/ 413 m9.figshare.13564229. 414

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Figure 1.



Figure 2.





Figure 3.



Figure 4.



0.6

Figure 5.



Figure 6.



- VGPM-PP(decoupled)
  - VGPM-Eppley



Figure 7.



Figure 8.



## Supporting Information for "Modeling Photosynthesis and Exudation of DOM in Subtropical Oceans"

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- 1. Text S1
- 2. Figures S1 to S3

#### Text S1. Ecosystem and biogeochemical model equations

The model equations are based on Dutkiewicz et al. (2015) and Dutkiewicz et al. (2020). We consider the cycling of carbon, nitrogen, phosphorus, and iron. We also resolve explicit dynamic Chl-a (Geider et al., 1998). We resolve tow types of phytoplankton,  $PC_j$ , which uptake several nutrients,  $N_i$ , and are grazed by two types of zooplankton,  $ZC_k$ . Mortality and exudation from plankton and sloppy feeding by zooplankton contribute to a dissolved organic matter pool,  $DOM_i$ , and a particulate organic matter pool,  $POM_i$ . Subscript *i* refers to a nutrient/element, *j* to a phytoplankton type, and *k* to a zooplankton type. All tracers, *X*, are advected and diffused by three-dimensional flow fields. The complete set of equations are provided below.

$$\frac{\partial X}{\partial t} = -\nabla \cdot (\boldsymbol{u}X) + \nabla \cdot (\boldsymbol{K}\nabla X) + S_X \tag{S1}$$

Where  $\boldsymbol{u} = (u, v, w)$ , velocity in physical model,  $\boldsymbol{K}$  is the mixing coefficient in physical model, and  $S_X$  is the source and sink term of tracer X.

Nutrients

$$S_{DIC} = -\sum_{j} P_{C,j} \cdot c_{P,j} + r_{DOC} \cdot DOC + F_C$$
(S2)

$$S_{PO_4} = -\sum_j R_j^{P:C} \cdot BS_{C,j} \cdot c_{P,j} + r_{DOP} \cdot DOP$$
(S3)

$$S_{HN_4} = -\sum_j \Gamma_{NH_4,j} \cdot R_j^{N:C} \cdot BS_{C,j} \cdot c_{P,j} + r_{DON} \cdot DON - k_{NH_4} \cdot NH_4$$
(S4)

$$S_{NO_2} = -\sum_{j} \Gamma_{NO_2,j} \cdot R_j^{N:C} \cdot BS_{C,j} \cdot c_{P,j} + k_{NH_4} \cdot NH_4 - k_{NO_2} \cdot NO_2$$
(S5)

$$S_{NO_3} = -\sum_{j} \Gamma_{NO_3,j} \cdot R_j^{N:C} \cdot BS_{C,j} \cdot c_{P,j} + k_{NO_2} \cdot NO_2 - k_{NO_3} \cdot NO_3$$
(S6)

$$S_{FeT} = -\sum_{j} R_{j}^{Fe:C} \cdot BS_{C,j} \cdot c_{P,j} + r_{DOFe} \cdot DOFe + F_{atmos} + F_{sed} - c_{scav} \cdot Fe'$$
(S7)

Plankton

 $S_{Chl_j}$ 

$$S_{c_{P,j}} = BS_{C,j} \cdot c_{P,j} - m_{P,j} \cdot c_{P,j} - \sum_{k} g_{j,k} \cdot c_{Z,k} - \frac{\partial(w_{P,j} \cdot c_{P,j})}{\partial z}$$
(S8)

$$S_{c_{R,j}} = P_{C,j} \cdot c_{P,j} - BS_{C,j} \cdot c_{P,j} - E_{C,j} \cdot c_{P,j} - m_{P,j} \cdot c_{P,j} \cdot Q_j^{RC}$$
(S9)

$$-\sum_{k} g_{j,k} \cdot c_{Z,k} \cdot Q_{j}^{RC} - \frac{\partial (w_{P,j} \cdot c_{P,j} \cdot Q_{j}^{RC})}{\partial z}$$
$$= \rho_{j} \cdot BS_{C,j} \cdot c_{P,j} - m_{P,j} \cdot c_{P,j} \cdot Q_{j}^{Chl} - g_{j,k} \cdot c_{Z,k} \cdot Q_{j}^{Chl}$$
(S10)

$$-rac{\partial (w_{P,j} \cdot c_{P,j} \cdot Q_j^{Chl})}{\partial z}$$

$$S_{c_{Z,k}} = \sum_{j} \xi_{j,k} \cdot g_{j,k} \cdot c_{Z,k} \cdot (1 + Q_j^{RC}) - m_{Z,k} \cdot c_{Z,k}$$
(S11)

 $Particulate\ and\ dissolved\ organic\ matter$ 

$$S_{DOM_{i}} = r_{POM_{i}} \cdot POM_{i} \sum_{j} \varphi_{mp_{i,j}} m_{P,j} \cdot c_{P,j} + \sum_{k} \varphi_{mz_{i,k}} m_{Z,k} \cdot c_{Z,k}$$

$$+ \sum_{j} \sum_{k} \varphi_{i,j,k} (1 - \xi_{j,k}) \cdot g_{j,k} \cdot c_{Z,k} - r_{DOM_{i}} \cdot DOM_{i}$$

$$S_{POM_{i}} = \sum_{j} (1 - \varphi_{mp_{i,j}}) m_{P,j} \cdot c_{P,j} + \sum_{k} (1 - \varphi_{mz_{i,k}}) m_{Z,k} \cdot c_{Z,k}$$

$$+ \sum_{j} \sum_{k} (1 - \varphi_{i,j,k}) (1 - \xi_{j,k}) \cdot g_{j,k} \cdot c_{Z,k} - r_{POM_{i}} \cdot POM_{i}$$

$$- \frac{\partial (w_{POM_{i}} \cdot POM_{i})}{\partial z}$$

$$(S12)$$

Nutrient limitations

$$\gamma_{i,j} = \frac{N_i}{N_i + K_{N_i,j}} \quad i = NH_4, PO_4, FeT \tag{S14}$$

$$\gamma_{NO_2,j} = \frac{NO_2}{NO_2 + K_{NO_2,j}} e^{-\psi NH_4}$$
(S15)

$$\gamma_{NO_3,j} = \frac{NO_3}{NO_3 + K_{NO_3,j}} e^{-\psi_N H_4}$$
(S16)

$$\Gamma_{NH_{4},j} = \frac{\gamma_{NH_{4},j}}{\gamma_{NH_{4},j} + \gamma_{NO_{2},j} + \gamma_{NO_{3},j}}$$
(S17)

$$\Gamma_{NO_2,j} = \frac{\gamma_{NO_2,j}}{\gamma_{NH_4,j} + \gamma_{NO_2,j} + \gamma_{NO_3,j}}$$
(S18)
$$\Gamma_{NO_3,j}$$
(S19)

$$\Gamma_{NO_3,j} = \frac{\gamma_{NO_3,j}}{\gamma_{NH_4,j} + \gamma_{NO_2,j} + \gamma_{NO_3,j}}$$
(S19)

Chl-a synthesis

$$\rho_{j} = \theta_{j}^{max} \frac{P_{C,j}}{\alpha I \theta_{oj}}$$

$$\theta_{oj} = \frac{\theta_{j}^{max}}{1 + \frac{\alpha I \theta_{j}^{max}}{2P_{C,i}^{Sat}}}$$
(S20)
(S21)

Where 
$$P_{C,j}$$
 is the photosynthesis rate of phytoplankton j (function in main text),

- $P_{C,j}^{Sat}$  is light saturated photosynthesis rate of phytoplankton j (function in main text),
- $BS_{C,j}$  is the biosynthesis rate of phytoplankton j (function in main text),

 $E_{C,j}$  is the exclusion rate of phytoplankton j (function in main text),

- $r_{DOM_i}$  is remineralization rate of DOM for element *i*, here C, N, P, Fe,
- $r_{POM_i}$  is remineralization rate of POM for element *i*, here C, N, P, Fe,
- $R_{i}^{N_{i}:C}$  is  $N_{i}:C$  ratio in phytoplankton j, here N, P, Fe,
- $k_N H_4$  is oxidation rate of  $NH_4$  to  $NO_2$ ,
- $k_N O_2$  is oxidation rate of  $NO_2$  to  $NO_3$ ,
- $k_N O_3$  is denitrification rate of  $NO_3$ ,
- $c_{scav}$  is scavenging rate for free iorn Fe',
- $F_{atmos}$  is atmospheric deposition of iron dust on ocean surface,
- $F_{sed}$  is the sedimentral source of iron,
- $F_C$  is air-sea flux of carbon dioxide,
- $Q_{i}^{RC}$  is the ratio of carbon reserve to functional carbon pool  $c_{P,j}$  in phytoplankton j,
- $Q_j^{Chl}$  is the ratio of Chl-a to functional carbon pool  $c_{P,j}$  in phytoplankton j,
- $m_{P,j}$  is mortality rate for phytoplankton j,
- $m_{Z,j}$  is mortality rate for zooplankton k,

 $g_{j,k}$  is grazing rate of zooplankton k on phytoplankton j,

- $\xi_{j,k}$  is grazing efficiency of zooplankton k on phytoplankton j,
- $\varphi_{mp_{i,j}}$  is fraction of dead phytoplankton organic matter that goes to  $DOM_i$ ,
- $\varphi_{mz_{i,j}}$  is fraction of dead zooplankton organic matter that goes to  $DOM_i$ ,
- $\varphi_{m_{i,i,k}}$  is fraction of sloppy grazing that goes to  $DOM_i$ ,
- $w_{P,j}$  is sinking rate of phytoplankton j,
- $w_{POM_i}$  is sinking rate of  $POM_i$ ,
- $K_{N_{i},j}$  is the half-saturation constant of nutrient *i* for phytoplankton *j*, here i =  $NH_4$ ,  $NO_2$ ,  $NO_3$ ,  $PO_4$ , FeT,

 $\psi$  is the fixed nitrogen uptake inhibition coefficient by ammonia,

 $\theta_{i}^{max}$  is the maximum Chl-a:C ratio in phytoplankton  $j\mathbf{a},$ 

I is the flux of photosynthetically active radiation (PAR),

 $\alpha$  is the initial slope of the photosynthesis-irradiance (PI) curve normalized to Chl-a.

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Figure S1. Simulated annual mean of nitrate, iron, and phosphate in decoupled model. (a) modeled nitrate (mean 0-50 m, mmol N  $m^{-3}$ ), (b) modeled iron (mean 0-50 m,  $\mu mol \ Fe \ m^{-3}$ ), (c) modeled phosphate (mean 0-50 m, mmol P  $m^{-3}$ ).



Figure S2. Comparison of model simulations and satellite-derived products of Chl-a and primary production. (a) to (d) are different satellite-derived products, namely VGPM (Vertically Generalized Production Model), Eppley-VGPM, CbPM (Carbon-based Productivity Model), and CAFE (Carbon, Absorption, and Fluorescence Euphotic-resolving model) ( $gC m^{-2} yr^{-1}$ ), (e) to (h) are differences between primary production in decoupled simulation and satellite-derived products ( $gC m^{-2} yr^{-1}$ ), (i) to (l) are differences between primary production in standard simulation and satellite-derived products ( $gC m^{-2} yr^{-1}$ ).



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Figure S3. Simulated C:N and C:P ratios with different  $f_{e,j}$ . (a) to (e) are C:N ratios with  $f_{e,j} = 0.1$  to 0.9, (g) to (k) are C:P ratios with  $f_{e,j} = 0.1$  to 0.9. (f) and (l) are C:N and C:P ratios in coupled simulation. Opposite patterns of C:N and C:P ratios are observed between decoupled simulations and coupled simulation. In the decoupled simulations, C:N and C:P ratios are also sensitive to  $f_{e,j}$ .