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Pico-phytoplankton contribute half of global marine carbon export

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Key Points:

- Explicitly simulated *Prochlorococcus*, *Synechococcus*, and pico-eukaryotes contribute ~60% of global net primary productivity
- Pico-phytoplankton contribute half of global marine sinking particle export production
- Carbon export is elevated poleward of western boundary currents, dominated by pico-eukaryotes and diatoms with elevated C:P stoichiometry

24 **Abstract**

25 Earth System Models generally predict increasing upper ocean stratification from 21st century
26 planetary warming, which will cause a decrease in the vertical nutrient flux resulting in declining
27 marine net primary productivity (NPP) and carbon export fluxes. Recent advances in quantifying
28 marine ecosystem carbon to nutrient stoichiometry have identified large latitudinal and biome
29 variability, with low-latitude oligotrophic systems harboring pico-sized phytoplankton exhibiting
30 large phosphorus to carbon cellular plasticity. Climate forced changes in nutrient flux
31 stoichiometry and phytoplankton community composition is thus likely to alter the ocean's
32 biogeochemical response and feedback with the carbon-climate system. We have added three pico-
33 phytoplankton functional types within the Biogeochemical Elemental Cycling component of the
34 Community Earth System Model while incorporating variable cellular phosphorus to carbon
35 stoichiometry for all represented phytoplankton types. The model simulates *Prochlorococcus* and
36 *Synechococcus* populations that dominate the productivity and sinking carbon export of the
37 tropical and subtropical ocean, and pico-eukaryote populations that contribute significantly to
38 productivity and export within the subtropical to mid-latitude transition zone, contributing a
39 combined 50 – 70% of these fluxes. Pico-phytoplankton cellular stoichiometry and resulting
40 sinking export patterns inversely track the distribution of surface phosphate, with the western
41 subtropical regions of each basin supporting the most P-poor stoichiometries. Collectively, pico-
42 phytoplankton contribute ~58% of global NPP and ~46% of global particulate organic carbon
43 export below 100 meters. Subtropical gyre recirculation regions along the poleward flanks of
44 surface western boundary currents are identified as regional hotspots of enhanced carbon export
45 exhibiting C-rich/P-poor stoichiometry, preferentially inhabited by pico-eukaryotes and diatoms.

46

47 **1. Introduction**

48 Ocean biogeochemical (OBGC) models operating within larger Earth System Models
49 (ESMs) have been developed for the purpose of quantifying the feedbacks between ocean
50 biology, chemistry, and the climate system as well as to provide predictions of ocean
51 biogeochemistry fluxes and tracer concentrations decades to centuries into the future (Le Quéré
52 et al., 2005; Friedlingstein et al., 2006; Bopp et al., 2013; Cabré et al., 2015; Moore et al., 2013;
53 2018). ESM output from the Coupled Model Intercomparison Project Phase 5 (CMIP5) and
54 Phase 6 (CMIP6) has predicted ocean acidification, deoxygenation, and decreasing primary
55 productivity during the 21st century (Bopp et al., 2013; Cabré et al., 2015, Moore et al., 2013;
56 Kwiatkowski et al., 2020) and beyond (Moore et al., 2018) under a business-as-usual scenario,
57 primarily as a result of changes in ocean circulation and stratification in response to warming
58 ocean temperatures. Enhanced upper ocean stratification leads to a reduction in vertical nutrient
59 flux to the sunlight surface layer, decreasing net primary productivity (NPP) by phytoplankton,
60 with a concomitant reduction in carbon export to the ocean interior (Cabré et al., 2015; Wilson et
61 al., 2022), resulting in a positive feedback with the climate system as ocean carbon uptake is
62 diminished with sustained warming. These declines are nearly universal among CMIP5 models,
63 most of which feature fixed C:N:P:-O₂ stoichiometry (i.e. the Redfield ratio; Redfield et al.,
64 1934; 1958) to describe phytoplankton nutrient uptake, production of organic matter, and its
65 subsequent remineralization (Bopp et al., 2013). Further, declines in key carbon cycle features
66 persist in the latest generation CMIP6 models despite an increasingly prevalent switch to
67 variable nutrient to carbon quotas within the marine biogeochemistry modules (Séférián et al.,
68 2020; Wilson et al., 2022).

69 Common to nearly all OBGC models is the representation of one or more ‘groups’ of
70 phytoplankton that consume inorganic nutrients, resulting in photosynthesis, net primary
71 production, and production of autotrophic biomass. Autotrophy is most often distributed among
72 ≥ 2 phytoplankton functional types (PFTs), that are chosen to represent differing growth
73 strategies, e.g., slower-growing small pico- and nano-phytoplankton vs. fast-growing large
74 diatoms, to capture biogeographic latitudinal trends in nutrient uptake rates, cell size, and export
75 efficiency. Phytoplankton growth experiences top-down control due to grazing by one or more
76 zooplankton groups, also resulting in the production of particulate and dissolved organic detrital
77 pools. Bottom-up controls on phytoplankton growth include multiple nutrient limitations, light
78 limitation, and optimum temperature effects. Generally, nutrient uptake affinity is inversely
79 correlated with cell size with smaller PFTs better able to acquire nutrients at low *in situ*
80 concentrations. Each PFT acquires nutrients to satisfy their particular cellular N:C, P:C, and/or
81 Fe:C quota, depending on the simulated inorganic nutrient fields. These cellular nutrient quotas
82 are invariant for fixed stoichiometry models (i.e., at Redfield proportions; Moore et al., 2004;
83 Dunne et al., 2010; Ilyina et al., 2013; Aumont et al., 2015) or can be variable, dependent on *in*
84 *situ* environmental parameters such as nutrient concentration (Galbraith & Martiny, 2015) or
85 optimal resource allocation theory describing phytoplankton cellular functions (Klausmeier et al.,
86 2004; Dunne, 2013; Kwiatkowski et al., 2018). Many culture and field observations have
87 documented variability in cellular nutrient quotas that vary both with ambient nutrient
88 concentrations (Tanioka et al., 2022; Karl et al., 2001; Rhee, 1978) and/or across PFTs (Martiny
89 et al., 2013a; Baer et al., 2017; Geider & La Roche, 2002; Quigg et al., 2003). Additionally, with
90 the emergence of flow cytometry for the study of marine microbes (Lomas et al., 2011), a large
91 literature of field and culture based studies has accumulated in recent decades describing the

92 physiology, biogeography, and phylogeny of marine pico-phytoplankton, more specifically the
93 cyanobacterial lineages *Prochlorococcus* and *Synechococcus* and pico-eukaryotic phytoplankton,
94 which now allows for their representation in numerical marine ecosystem models (e.g. Moore et
95 al., 1998; Partensky et al., 1998; DuRand et al., 2001; Martiny et al., 2009; Buitenhuis et al.,
96 2012; Pasulka et al., 2013; Flombaum et al., 2013; 2020; Sohm et al., 2016; Baer et al., 2017).
97 Given the need to balance model complexity against limiting computational resources,
98 representation of additional pico-phytoplankton groups is perhaps of first order importance with
99 respect to introduction of variable elemental stoichiometry within OBGC models, since pico-
100 phytoplankton are known to exhibit the largest carbon to nutrient cellular plasticity (Quigg et al.,
101 2003; Klausmeier et al., 2004; Martiny et al., 2013a; Baer et al., 2017). In light of these
102 advances, representing the pico-phytoplankton and variable carbon to nutrient content of all
103 phytoplankton in OBGC models has become a pressing goal to better capture the ocean
104 ecosystem response to the changing 21st century climate and its associated feedbacks with the
105 climate system.

106 Many recent studies have identified and quantified the non-Redfield, variable carbon to
107 nutrient stoichiometry that permeates most ocean biogeochemical fluxes and tracer pools
108 including dissolved nutrients (Weber & Deutsch, 2010), biomass (Tanioka & Matsumoto, 2020),
109 particulate organic matter (Martiny et al., 2013a), dissolved organic matter (Letscher & Moore,
110 2015), export production (Teng et al., 2014), and organic matter remineralization (DeVries &
111 Deutsch, 2014). The emergent pattern from these studies is one of carbon-rich (nutrient-poor)
112 stoichiometry that describes biogeochemical functioning in the lower latitude, nutrient-poor
113 biomes of the subtropics, while the nutrient-replete upwelling and subpolar biomes exhibit
114 stoichiometries at or slightly below Redfield carbon to nutrient proportions. Two mechanisms

115 have been suggested to contribute to the observed biogeography of marine ecosystem
116 stoichiometry including phosphorus and/or nitrogen plasticity by the extant phytoplankton
117 community (e.g. Galbraith & Martiny, 2015; Van Mooy et al., 2009) as well as shifts in
118 phytoplankton community composition across biomes with relatively nutrient-deficient
119 cyanobacteria dominating the subtropics and more nutrient-rich diatoms and other larger
120 phytoplankton dominating elsewhere (e.g. Arrigo et al., 1999; Weber & Deutsch, 2010; Sharoni
121 & Halevy, 2020). Cell-sorted field populations of cyanobacteria (*Prochlorococcus* and
122 *Synechococcus*) and pico-eukaryotes from the Sargasso Sea, eastern Pacific, and Indian Ocean
123 suggest both mechanisms may be at play as cyanobacteria exhibited lower cellular P content as
124 compared to eukaryotes, while all groups exhibited cellular P plasticity in response to latitudinal
125 gradients in inorganic phosphorus availability, albeit at varying degrees across taxonomic groups
126 (Martiny et al., 2013a; Baer et al., 2017; Lomas et al., 2021).

127 Does representation of variable carbon to nutrient stoichiometry within OBGCM models
128 potentially buffer the well-documented positive ocean carbon cycle feedback to future climate
129 warming? A number of ESM's that have included representation of variable carbon to
130 phosphorus stoichiometry within the ocean ecosystem component generally predict a more
131 resilient response for future marine NPP and carbon export fluxes, with modest $\sim 0 - <5\%$
132 declines by year 2100 (Bopp et al., 2013; Cabré et al., 2015; Tanioka & Matsumoto, 2017;
133 Kwiatkowski et al., 2018; Buchanan et al., 2018; Matsumoto et al., 2020; Kwon et al., 2022).
134 Inclusion of variable phosphorus to carbon stoichiometry within the marine ecosystem
135 component permits flexibility in phytoplankton phosphorus quotas. Such frugal use of nutrients
136 allows phytoplankton to maintain similar growth rates under decreasing P flux as well as a shift
137 towards increasing biomass C:P that partially compensates for warming induced changes to

138 ocean circulation and stratification. Galbraith and Martiny (2015) demonstrated with a simple
139 box model that changes to the preformed phosphate concentration on the order of 100 nM within
140 low latitude surface waters can produce up to 20 ppm shifts in atmospheric CO₂ concentrations,
141 assuming P is the primary growth limiting nutrient. An OBGC modeling study incorporating
142 representation of variable marine elemental stoichiometry found that adding this sensitivity
143 buffered against a predicted decrease in global carbon export production on the order of ~3% for
144 the 21st century (Tanioka & Matsumoto, 2017). Similarly, results from the recent inclusion of
145 this process within the Pelagic Interactions Scheme for Carbon and Ecosystem Studies Quota
146 (PISCES-QUOTA) model, suggest its effects on 21st century ocean carbon uptake are modest
147 with up to a 3.5% underestimation as compared to fixed stoichiometry ESMs (Kwiatkowski et
148 al., 2018). However, larger regional changes of up to 50% reductions or stimulations of marine
149 NPP and carbon export were predicted which could have significant local to regional impacts on
150 marine ecosystems and fisheries. The above studies have thus far considered adaptive nutrient
151 quotas, while other phytoplankton adaptive strategies including altered physiological rates, trait-
152 based evolution, and changes in grazing pressure could all potentially influence phytoplankton
153 fitness and resilience with important controls on marine NPP and carbon export trends (Martiny
154 et al., 2021).

155 As the next generation of OBGC models mature to better represent variable carbon to
156 nutrient stoichiometry with the goal to study how this variability impacts the marine NPP and
157 carbon export fluxes, an important missing element to this question is the role for changes in
158 marine phytoplankton biodiversity to modulate the response. Most of the current generation of
159 OBGC models represent the marine phytoplankton community with 1 – 3 PFTs, with the notable
160 exception of the ECCO-Darwin OBGC model which simulates 35 up to 350 PFTs (e.g.,

161 Dutkiewicz et al., 2020; Juranek et al., 2020). This higher biodiversity model has been shown to
162 more accurately represent the marine phytoplankton diversity regionally to globally, as gauged
163 by such metrics as phytoplankton size distribution, biomass, size-fractionated NPP rates, and
164 species richness. How does marine phytoplankton diversity and associated carbon to nutrient
165 stoichiometric variability impact the regional to global patterns of carbon export? Based on
166 current understanding, enhanced thermal stratification of the water column depresses the vertical
167 nutrient input, favoring a shift to smaller sized pico-phytoplankton dominated by cyanobacteria
168 possessing higher plasticity in cellular nutrient quotas. Thus, in a future warmer ocean with
169 expanding stratification, the marine biodiversity response might be hypothesized to favor marine
170 cyanobacteria such as *Prochlorococcus* and *Synechococcus* with elevated C:P cellular
171 stoichiometry. While the shift to smaller phytoplankton may depress marine NPP rates, export of
172 a portion of the resultant biomass with high C:P may partially buffer against reductions in marine
173 carbon export and mitigate the expected positive feedback to warming by maintaining the
174 strength of the ocean's biological carbon pump. In support of this hypothesis, observations from
175 the Bermuda Atlantic Time-series station in the Sargasso Sea document a recent decline in
176 marine NPP due to enhanced stratification, without a concomitant decline in carbon export,
177 explained by a shift in the phytoplankton community composition in favor of cyanobacteria with
178 higher cellular C:P stoichiometry (Lomas et al., 2022).

179 This paper describes the addition of three new pico-phytoplankton functional types,
180 *Prochlorococcus*, *Synechococcus*, and pico-eukaryotes, to the OBGC component of the
181 Community Earth System Model, with the goal to better characterize the role for marine
182 phytoplankton biodiversity and associated variable cellular carbon to phosphorus stoichiometry
183 in controlling marine carbon export patterns. The implementation builds from recent advances in

184 this OBGC model to incorporate variable C:P stoichiometry within all pertinent tracers of the
185 marine ecosystem (Letscher et al., 2015; Wang et al., 2019) including phytoplankton, dissolved
186 organic matter, and sinking particulate organic matter, to now include representation of six PFTs:
187 *Prochlorococcus*, *Synechococcus*, pico-eukaryotes, nano-phytoplankton (including implicit
188 coccolithophores), diatoms, and diazotrophs.

189

190 **2. Model and Validation Data**

191 The model is the Biogeochemical Elemental Cycling (BEC) model, which is the
192 biogeochemistry and ecosystem component operating within the ocean circulation model (POP2)
193 of the Community Earth System Model (CESM) v.1.2.2 ([http://www.cesm.ucar.edu/models/](http://www.cesm.ucar.edu/models/cesm1.2/)
194 [cesm1.2/](http://www.cesm.ucar.edu/models/cesm1.2/)). The model resolution employed here is nominally 3° x 3° horizontally with 60 vertical
195 layers (gx3v7 grid) that increase in thickness with depth in the water column. The ocean
196 circulation is the output of the Parallel Ocean Program 2 (POP2) ocean circulation model using
197 the final thirty-year forcing from years 1980 – 2009 of the CORE-II forcing (Smith et al., 2010)
198 and includes parameter value changes to the isopycnal diffusivity (κ_{isop}) to partially account for
199 the transport of unresolved equatorial jets (Getzlaff & Dietze, 2013).

200 The BEC tracks the cycling of key biogeochemical tracers (e.g., C, N, P, Fe, and O₂)
201 amongst dissolved inorganic, dissolved organic, sinking particulate, and four plankton biomass
202 pools (Moore et al., 2004). Net primary production in the model is partitioned amongst three
203 PFTs—small phytoplankton (with implicit calcifiers), diatoms, and diazotrophs, which differ in
204 their relative competitiveness for limiting nutrients (N, P, Si, and Fe). In addition to bottom-up
205 nutrient and light control, phytoplankton mortality is controlled top-down by grazing from one
206 zooplankton group. Version 1.2.2 of the BEC contains significant improvements to the cycling of

207 marine dissolved organic matter (Letscher et al., 2015). More recent model development for
208 BEC v1.2.2 has incorporated variable phosphorus quotas for the three phytoplankton types
209 (Wang et al., 2019) that depend on *in situ* simulated inorganic phosphate concentration following
210 the linear relationship in Galbraith & Martiny (2015) but with an imposed minimum (110:1) and
211 maximum (210:1) C:P value for all PFTs. This current work describes the addition of three new
212 pico-phytoplankton groups with variable carbon to nutrient (P and Fe) stoichiometry to the BEC
213 model, building from the code base for the variable 3 PFT phosphorus quota model of Wang et
214 al., (2019). The ‘small phytoplankton’ group from the 3 PFT BEC model which jointly
215 represented pico- and nano-sized phytoplankton has been reparameterized to more closely
216 represent larger nano-phytoplankton. The newly named nano-phytoplankton along with the
217 diatom and diazotroph groups are updated to represent variable C:P and C:Fe stoichiometry. The
218 model retains one zooplankton group with Redfieldian stoichiometry. The marine ecosystem in
219 the BEC model is thus represented by 6 phytoplankton and 1 zooplankton groups, or 6p1z.

220 Output of the pico-phytoplankton BEC model is validated for the simulation of
221 chlorophyll a and NPP against the Sea-Viewing Wide Field-of-View Sensor (SeaWiFS) satellite
222 mission climatology products (1997 – 2010) related to chlorophyll a concentration (NASA
223 GSFC, 2018) and a model of carbon-based net primary productivity estimated from SeaWiFS
224 data products (Behrenfeld et al., 2005; Westberry et al., 2008). Simulated nutrient concentrations
225 from the pico-phytoplankton BEC model are compared against the World Ocean Atlas 2013
226 climatologies of nitrate, phosphate, and silicate (Garcia et al., 2013) and a global compilation of
227 dissolved Fe concentrations (Tagliabue et al., 2012). Simulated pico-phytoplankton biomass are
228 validated against the data assimilative niche modeling of Flombaum et al. (2013; 2020) that
229 predicts field observed *Prochlorococcus*, *Synechococcus* from inputs of temperature and

230 irradiance (Flombaum et al., 2013) and pico-eukaryote biomass from inputs of temperature,
231 irradiance, and dissolved nitrate (Flombaum et al., 2020). Simulated pico-phytoplankton C:P
232 stoichiometry and biomass are compared against observations of populations from the North
233 Atlantic, eastern Pacific, and eastern Indian Oceans of *Prochlorococcus*, *Synechococcus*, and
234 pico-eukaryotes measured for C and P content (Baer et al., 2017; Lomas et al., 2021). Simulated
235 total phytoplankton biomass C:P stoichiometry is compared against a global compilation of bulk
236 particulate organic matter C, N, and P content (Martiny et al., 2014).

237

238 **3. Methods**

239 The addition of three pico-phytoplankton groups with variable carbon to nutrient
240 stoichiometry introduces 12 additional tracers to the BEC model code: biomass carbon (C),
241 chlorophyll (Chl), iron (Fe), and phosphorus (P) for each of the 3 pico-phytoplankton groups,
242 termed ‘Prochlorococcus’ (pro), ‘Synechococcus’ (syn), and ‘Pico-eukaryotes’ (peuk). The
243 ‘small phytoplankton’ group from BEC v1.2.2 and earlier versions has been renamed ‘nano-
244 phytoplankton’ (nano) and retains the implicit calcifiers. Nano-phytoplankton as well as the
245 diatoms (diat) and diazotroph (diaz) phytoplankton groups carry the same four biomass tracers
246 (C, Chl, Fe, P) as the newly added pico-phytoplankton, with the addition of biomass silicon for
247 diatoms. Variable biomass nitrogen (N) content is not considered at this time and phytoplankton
248 biomass N:C is fixed for all six phytoplankton groups at a value of 0.1333 (C:N = 7.5) near the
249 mean of open ocean suspended particles (Martiny et al., 2013b) and nutrient replete versus
250 deplete cells across a range of phyla (Geider & La Roche, 2002).

251 Growth and mortality of each phytoplankton type is modeled with more than two dozen
252 parameter values specific to each group including half saturation constants for nutrient uptake,

253 photosynthesis vs irradiance curves, Fe and P quotas, temperature thresholds for growth,
 254 contributions to detrital pools, and zooplankton grazing rates among others. Table 1 lists these
 255 parameter values for each phytoplankton group including the relevant literature sources. Where
 256 literature sources are lacking to inform the value for a particular parameter, the principle of
 257 allometric scaling is employed to assign values corresponding with cell size with the order of
 258 increasing cell size following: pro/syn/peuk < nano/diaz < diat.
 259

Parameter	Description	Units	pro	syn	peuk	nano	diat	diaz	Reference
kFe	half sat. const. diss. iron	mmol/m ³	0.030e-3	0.040e-3	0.043e-3	0.055e-3	0.06e-3	0.04e-3	Shire & Kustka, 2015; Timmermans et al., 2005; Hutchins et al., 2002
kPO4	half sat. const. phosphate	mmol/m ³	0.008	0.01	0.015	0.04	0.07	0.025	Lomas et al., 2014; Stukel et al., 2014; Garcia et al., 2015
kDOP	half sat. const. diss. organic P	mmol/m ³	0.8	0.9	0.15	0.2	0.1	0.25	Casey et al., 2009; Orchard et al., 2010; Sohm & Capone, 2006; Dyhrman & Ruttnerberg, 2006
kNO3	half sat. const. nitrate	mmol/m ³	0.3	0.18	0.15	0.25	0.35	4.0	
kNH4	half sat. const. ammonium	mmol/m ³	0.005	0.008	0.011	0.02	0.035	0.4	
gQFe_0	initial Fe:C	ratio	80e-6	80e-6	90e-6	90e-6	90e-6	180e-6	Boyd et al., 2015
gQFe_min	minimum Fe:C	ratio	10.0e-6	10.0e-6	3.0e-6	3.0e-6	3.0e-6	6.0e-6	Boyd et al., 2015
FeOpt	threshold for reducing Fe quota	mmol/m ³	0.8e-3	0.8e-3	1.0e-3	1.6e-3	1.75e-3	1.5e-3	Boyd et al., 2015
gQp_0	initial P:C	ratio	1.042e-2	1.042e-2	1.111e-2	1.111e-2	1.111e-2	6.667e-3	Galbraith & Martiny, 2015; Martiny et al., 2013
gQp_min	minimum P:C	ratio	3.704e-3	5.208e-3	8.333e-3	8.333e-3	8.333e-3	3.333e-3	Galbraith & Martiny, 2015; Martiny et al., 2013
POpt	threshold for reducing P quota	mmol/m ³	0.5	0.5	0.75	1.0	1.0	0.5	Galbraith & Martiny, 2015; Martiny et al., 2013
	resulting max C:P	ratio	270	192	120	120	120	300	
	resulting max N:P	ratio	45	32	20	20	20	50	
alphaPI	initial slope of Photo-Irr curve	mmolC ² /mgChl W s	1.00	1.09	0.7	0.83	0.88	0.2	Stawiarski et al., 2017
PCref	maximum C-spec. growth rate	d ⁻¹	3.6	3.6	3.8	3.8	4.0	1.9	Stawiarski et al., 2017
thetaN_max	maximum Chl:N	ratio	3.33	2.20	3.55	3.00	4.00	2.00	Stawiarski et al., 2017
loss_thres	biomass where losses go to 0	mmolC/m ³	0.02	0.02	0.02	0.025	0.025	0.02	
temp_thres	temp. where Photo rates drop	°C	13.0	4.0	-1.5	-10.0	-10.0	18.0	Flombaum et al., 2013; 2020
mort	mortality rate	d ⁻¹	0.1	0.1	0.1	0.1	0.1	0.1	
agg_rate_max	maximum aggregation rate	d ⁻¹	0.5	0.5	0.5	0.5	0.8	0.5	
agg_rate_min	minimum aggregation rate	d ⁻¹	0.005	0.005	0.01	0.01	0.015	0.005	
z_umax_0	maximum zoopl. growth rate	d ⁻¹	2.66	2.60	2.97	2.80	2.70	2.80	
z_grz	grazing coefficient	mmolC/m ³	1.3	1.6	1.95	1.8	1.58	1.3	
graze_zoo	routing of grazing to zoopl.	fraction	0.3	0.3	0.3	0.3	0.3	0.3	
graze_poc	routing of grazing to POC	fraction	0.07	0.09	0.13	0.28	0.40	0.03	Lomas & Moran, 2011
graze_doc	routing of grazing to DOC	fraction	0.06	0.06	0.06	0.06	0.06	0.06	Leischer et al., 2015
f_zoo_detr	fract. zoopl. losses to detrital	fraction	0.33	0.32	0.3	0.2	0.2	0.36	

260
 261 **Table 1.** Description of phytoplankton parameters and values from the PICO simulation of the
 262 BEC model.

263
 264 Phytoplankton iron uptake half saturation constants are prescribed with cyanobacteria
 265 having the lowest values (pro = 30 pM; syn+diaz = 40 pM), followed by pico-eukaryotes (43
 266 pM), nano-eukaryotes (55 pM), and the large celled diatoms (60 pM) following the culture
 267 studies of Shire and Kustka, (2015) and Timmermans et al., (2005) and the field study of
 268 Hutchins et al., (2002) (Table 1). Phosphate half saturation constants are selected based on the

269 field study from the Sargasso Sea of Lomas et al., (2014), the culture study of Garcia et al.,
270 (2015), and the Amazon River plume ecosystem modeling work of Stukel et al., (2014) with
271 k_{PO4} values increasing from a value of 8 nM for pro, 10 nM for syn, 15 nM for peuk, 25 nM for
272 diaz, 40 nM for nano, and 70 nM for diatoms. Semilabile dissolved organic phosphorus (DOP) is
273 bioavailable for phytoplankton to utilize as a P source when phosphate levels are low in the BEC
274 model (Letscher et al., 2015) with the half saturation constants for its uptake selected based on
275 several field studies from the Sargasso Sea and eastern North Pacific (Dyhrman & Ruttenberg,
276 2006; Sohm & Capone, 2006; Casey et al., 2009; Orchard et al., 2010). Following these studies,
277 eukaryotes and diazotrophs are assigned the lowest half saturation values for DOP uptake
278 ranging from 100 – 250 nM, with higher k_{DOP} values ranging from 800 – 900 nM for the two
279 cyanobacteria groups. Half saturation constants for ammonium are assigned following allometric
280 scaling in the range 5 – 35 nM. Nitrate uptake half saturation constants are similarly assigned
281 following allometric scaling in the range 150 – 350 nM, with exceptions for syn and peuk which
282 are assigned the lowest values of 180 and 150 nM respectively, owing to their demonstrated
283 increased affinity for nitrate relative to pro in the Sargasso Sea (e.g., Glover et al., 1988; Fawcett
284 et al., 2013) and observed correlations between peuk abundance and *in situ* nitrate (Flombaum et
285 al., 2020). Diazotroph k_{NH4} and k_{NO3} are set to the highest value across the 6 PFTs to reflect
286 its reliance on internally fixed N for a significant but not exclusive fraction of its N quota
287 (Knapp, 2012).

288 Phytoplankton iron quotas in the BEC model allow for flexibility in phytoplankton
289 biomass Fe:C based on *in situ* dissolved iron concentrations, varying in the range of 3 $\mu\text{mol}:\text{mol}$
290 to 180 $\mu\text{mol}:\text{mol}$ (Table 1). Following the field study of Boyd et al., (2015), eukaryotes are
291 assigned the lowest minimum iron quotas followed by diazotrophs and non-N-fixing

292 cyanobacteria (*Prochlorococcus* and *Synechococcus*). The diazotroph group is assigned the
 293 highest maximum iron quotas based on the high iron requirement of the nitrogen-fixing enzyme
 294 nitrogenase (Berman-Frank et al., 2007). Phytoplankton iron quotas are reduced linearly when *in*
 295 *situ* dissolved Fe concentrations fall below a prescribed threshold (FeOpt), set to 1.75 nM for
 296 diatoms, 1.6 nM for nano, 1.5 nM for diaz, 1.0 nM for peuk, and 0.8 nM for pro and syn
 297 (Wisemann et al., under review).

298 Variable phosphorus quotas are implemented here for the six phytoplankton group BEC
 299 model following the approach introduced in Wang et al. (2019) and similar to the variable Fe:C
 300 approach described above. Variable phytoplankton biomass P:C is modeled as a function of *in*
 301 *situ* dissolved phosphate concentration using the linear relation detailed in Galbraith & Martiny
 302 (2015) diagnosed from a global compilation of suspended particulate organic phosphorus and
 303 carbon concentrations. Each PFT P:C quota (gQp) is computed from:

$$304 \quad gQp = \left[\left(\frac{gQp_0 - gQp_{min}}{PO_{opt}} \right) \times PO4 \right] + gQp_{min} \quad PO4 < PO_{opt} \quad (\text{Eq. 1})$$

$$305 \quad gQp = gQp_0 \quad PO4 \geq PO_{opt}$$

306 where PO4 is the *in situ* dissolved inorganic phosphate concentration (μM) and gQp_0 and
 307 gQp_min describe the minimum and maximum P:C quota (see Table 1). Equation 1 linearly
 308 decreases the phytoplankton P:C quota (increases its C:P ratio) below a prescribed threshold
 309 (PO_{opt}; range 0.5 – 1.0 μM across PFTs), from its initial maximum value, currently prescribed at
 310 gQp_0 = 0.01111; C:P = 90:1 for the eukaryotes (peuk+nano+diat), gQp_0 = 0.01042; C:P =
 311 96:1 for the cyanobacteria, and gQp_0 = 0.006667; C:P = 150:1 for diazotrophs, towards a
 312 minimum P:C quota that varies for each PFT (Table 1). This formulation is similar in approach
 313 to that presented in Galbraith & Martiny (2015). Here, field observations of surface ocean
 314 particulate organic carbon and phosphorus (of which autotrophic biomass is a significant

315 contributor) were found to fit a linear function of *in situ* phosphate concentration. The
316 formulation presented here prescribes differing P:C versus PO₄ slopes and y-intercepts for each
317 PFT set by the choice of gQp_{min}. Field-based estimates of cell-sorted biomass C:P and N:P for
318 *Prochlorococcus*, *Synechococcus*, and pico-eukaryotes from the Sargasso Sea (Martiny et al.,
319 2013a) and elsewhere (Baer et al., 2017; Lomas et al., 2021) are used to assign values of
320 gQp_{min} with a maximum C:P of 300:1 for diazotrophs, a C:P of 270:1 for *Prochlorococcus* and
321 192:1 for *Synechococcus*, and a maximum C:P of 120:1 for peuk, nano, and diat (retained from
322 the variable C:P BEC model; Wang et al., 2019).

323 Based on the phytoplankton niche modeling of Flombaum et al. (2013; 2020), each
324 phytoplankton group in the BEC is assigned a temperature threshold below which photosynthesis
325 rates and thus growth rates are depressed, with *Prochlorococcus* and diazotroph niches favoring
326 warmer temperatures above 13°C and 18°C, respectively. *Synechococcus* and pico-eukaryote
327 growth decreases as temperatures fall below 4°C and -1.5°C, respectively, while nano-
328 phytoplankton and diatom growth rates are not depressed as a function of temperature
329 (temp_{thres} value set to -10°C in Table 1).

330 Physiological response to light parameters describing the pico-phytoplankton are
331 assigned based on the culture study of Stawiarski et al. (2017) in which two strains of
332 *Prochlorococcus* (HL RCC 296, LL RCC 162), one *Synechococcus* strain (RCC 30), and four
333 pico-eukaryote species *Triparma eleuthera* (RCC 212), *Micromonas pusilla* (RCC 1677),
334 *Picochlorum* sp. (TCC 289), and *Nannochloropsis granulata* (RCC 438) from the Roscoff
335 culture collection (Vaulot et al., 2004) were studied. Following this study, cyanobacteria are
336 assigned slower maximum growth rates compared with eukaryotes, in the range 1.9 – 4 d⁻¹ (based
337 on a 24-hour light period). Stawiarski et al. (2017) found that light affinity is inversely related to

338 the maximum growth rate. *Prochlorococcus* and *Synechococcus* are assigned the highest light
339 affinities, as encoded within the ‘alphaPI’ model parameter which describes the initial slope of
340 the photosynthesis-irradiance curve, with decreasing affinities for the faster growing eukaryotes
341 (Table 1). The maximum Chl:N, the ‘thetaN_max’ model parameter, is assigned inversely
342 proportional to maximum growth rate with the exception of *Synechococcus* which exhibits lower
343 Chl:C in line with the results of Stawiarski et al. (2017).

344 Grazing on each of the six phytoplankton groups in the updated BEC model is carried out
345 by one adaptive zooplankton group. Grazing rates are largely unconstrained by field data. In the
346 BEC model, maximum grazing rates, ‘z_umax_0’ parameter, are adjusted to achieve satisfactory
347 biomass distributions and C:P stoichiometry for each phytoplankton group as validated against
348 phytoplankton niche modeling and flow-sorted biomass stoichiometry distributions. Variable
349 fractions of phytoplankton biomass are routed to zooplankton losses to detritus (e.g., fecal
350 pellets) and particulate organic matter pools resulting from zooplankton grazing (Table 1). Each
351 PFT’s contribution to the sinking export flux following grazing varies from a minimum of 3%
352 for diazotrophs to a maximum of 40% for diatoms (‘graze_poc’; Table 1) informed in part by
353 pigment biomarker analyses of the sediment trap flux in the Sargasso Sea (Lomas & Moran,
354 2011). Zooplankton contribute varying proportions of grazed phytoplankton biomass to detritus
355 (POC) based on the PFT grazed, ranging from a minimum of 20% for nano-phytoplankton and
356 diatoms to a maximum of 36% when grazing diazotrophs (‘f_zoo_detr’; Table 1). Grazing of
357 phytoplankton biomass also contributes 6% to the dissolved organic matter pool following the
358 inverse model diagnosed rate from our previous work (Letscher et al., 2015). In the BEC model,
359 combinations of two or more phytoplankton types can be grouped together in ‘grazee’ classes,
360 for which zooplankton grazing rates are computed jointly based on the total amount of biomass

361 in each simulated *in situ* ‘grazee’ class. Experimentation was carried out to decide which
362 combinations of phytoplankton groups in each ‘grazee’ class achieved distributions of
363 phytoplankton biomass, NPP, and dissolved nutrients that best matched observations. A model
364 configuration in which all six PFTs were ungrouped, i.e., parameter `grazee_ind` was set equal to
365 `auto_ind`, the unique index of each of the six PFTs, was chosen.

366 BEC simulations were carried out for sixty model years from initial conditions, allowing
367 the upper ocean ecosystem to achieve tracer equilibrium. After selection of the set of parameter
368 values that best matched observational constraints, a longer 300 model year simulation was
369 performed, repeating the 30-year (1980 – 2009) CORE-II forcing for a total of ten repetitions.
370 The annually averaged output from the final twenty years of this simulation were averaged and is
371 presented in all results to follow. Reported flux variability represents ± 1 S.D. of the mean from
372 the twenty years of output. The BEC simulation containing the additional pico-phytoplankton
373 groups for a total of 6 PFTs is termed PICO. In Section 4, this simulation is compared against
374 two similarly forced previous versions of the BEC model: a variable C:P stoichiometry version
375 with 3 PFTs herein termed VAR-3 (Wang et al., 2019) and a 3 PFT version with Redfield
376 stoichiometry governing phytoplankton dynamics herein termed RED-3 (Letscher et al., 2015).

377

378 **4. Results**

379 *Chlorophyll a & NPP*– Sea surface chlorophyll a (chl a) concentrations [mg m^{-3}] from the
380 PICO simulation and the SeaWiFS satellite climatology are shown in Figure 1a-b. BEC
381 simulated chl a captures the overall pattern of lowest concentrations within the subtropical ocean
382 gyres, highest concentrations within coastal and subpolar zones, and intermediate concentrations
383 in upwelling regions and subtropical to mid-latitude transitions zones (Fig. 1). The PICO

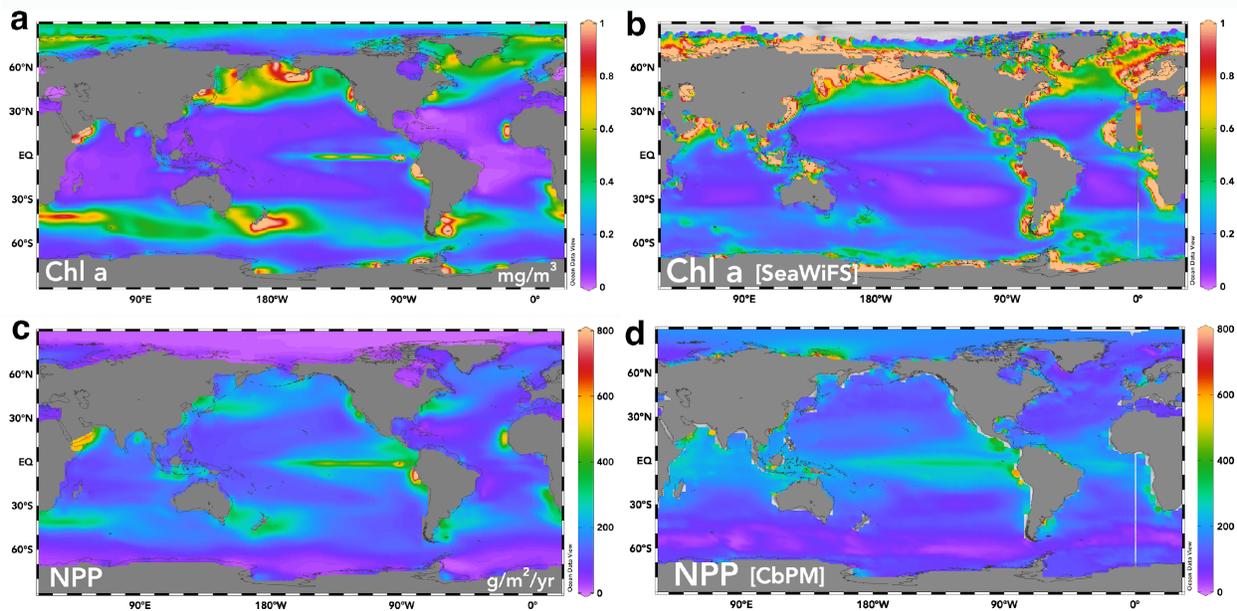
384 simulation exhibits an overall global negative mean bias in chl a (-6%; Table 2) relative to the
 385 SeaWiFS climatology, reducing by a factor of ~3 compared with the 3 PFT variable C:P
 386 stoichiometry BEC model (VAR-3) and an earlier version containing 3 PFTs and Redfield
 387 stoichiometry (RED-3) (Table 2).
 388

	PICO		VAR-3		RED-3	
	r-correlation	mean bias	r-correlation	mean bias	r-correlation	mean bias
Chl a	0.087	-6%	0.218	-19%	0.167	-17%
CbPM NPP	0.241	+3%	0.108	+0.5%	0.153	-3.0%
[NO ₃ ⁻]	0.938	0.01 μM	0.940	0.01 μM	0.920	0.01 μM
[PO ₄ ³⁻]	0.940	0.02 μM	0.932	-0.01 μM	0.944	0.03 μM
[SiO ₄ ⁴⁻]	0.935	0.01 μM	0.936	1.14 μM	0.932	-0.01 μM
[dFe]	0.398	0.18 nM	0.332	-0.14 nM	0.374	0.04 nM

389
 390 **Table 2.** Comparison metrics for PICO, VAR-3, and RED-3 simulated chlorophyll a and NPP
 391 versus satellite (SeaWiFS) climatology estimates using the CbPM model. Metrics for dissolved
 392 nutrients from the same three simulations are compared versus the World Ocean Atlas 2013
 393 (NO₃⁻, PO₄³⁻, SiO₄⁴⁻) and Tagliabue et al. (2012) Fe data compilation.

394
 395 Vertically integrated annual net primary productivity (NPP) [g C m⁻² yr⁻¹] from the PICO
 396 simulation is provided along with the Carbon-based Productivity Model estimate of NPP from
 397 the SeaWiFS climatology (Westberry et al., 2008) (Figure 1c-d). The globally integrated annual
 398 NPP from PICO is 51.4 ± 0.75 Pg C yr⁻¹, within the range of satellite-based estimates – 60-67 Pg
 399 C yr⁻¹ (Behrenfeld et al., 2005), 52 Pg C yr⁻¹ (Westberry et al., 2008; Silsbe et al., 2016), 58 ± 7
 400 Pg C yr⁻¹ (Buitenhuis et al., 2013). Highest rates of annual NPP are simulated in the equatorial
 401 Pacific, Arabian Sea, and the South Pacific and North Atlantic eastern boundary upwelling
 402 zones, reaching rates of ~400 – 600 g C m⁻² yr⁻¹ in the PICO simulation, which is approximately

403 25 – 75% greater than those estimated by the CbPM. The lowest rates of NPP simulated by PICO
 404 are found within the Arctic Ocean, which are approximately one-quarter of those estimated by
 405 CbPM. The PICO simulation also simulates higher rates of NPP as compared to CbPM within
 406 the mid-latitudes of both hemispheres, especially near the western boundary of each ocean basin.
 407 Overall, the PICO simulation exhibits a small positive mean bias of +3% in estimated global
 408 annual NPP rates when comparing binned $3^{\circ}\times 3^{\circ}$ pixels with the CbPM SeaWiFS climatology
 409 (Table 2).
 410

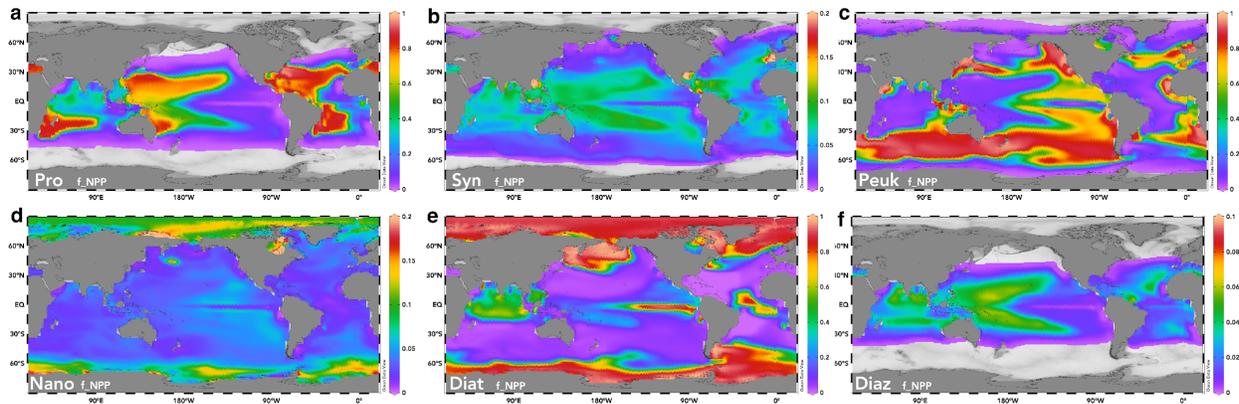


411
 412 **Figure 1.** PICO simulated 20-yr averaged sea surface chlorophyll a [mg m^{-3}] (a), climatological
 413 average sea surface chlorophyll a from the SeaWiFS satellite during 1997-2010 (b), PICO
 414 simulated 20-yr averaged NPP [$\text{g C m}^{-2} \text{yr}^{-1}$] (c), and from the CbPM model using SeaWiFS
 415 satellite data from the same era (d) (Westberry et al., 2008).

416
 417 *PFT contributions to spatial NPP patterns* – The fractional contribution of each of the six
 418 PFTs to simulated NPP rates within the PICO simulation is shown in Figure 2. The majority of

419 NPP within the five subtropical gyre regions is contributed by *Prochlorococcus* (fraction of NPP
420 $\sim 0.50 - 0.90$), with a general western intensification (Fig. 2a). *Synechococcus* NPP is similarly
421 elevated within the subtropics, albeit at lower fractional contributions in the range $\sim 0.06 - 0.12$
422 (Fig. 2b). *Prochlorococcus* and *Synechococcus* are mostly absent from the polar oceans due to
423 their imposed temperature threshold of 13°C and 4°C for positive growth rates (Flombaum et al.,
424 2013; Table 1). Pico-eukaryotes dominate NPP (fraction of NPP > 0.80) in many of the eastern
425 boundary and mid-latitude regions of the world ocean in PICO (Fig. 2c). Elsewhere, pico-
426 eukaryote contribution to simulated NPP is much reduced, in the range $\sim 0.02 - 0.10$. Nano-
427 phytoplankton contribute variably to NPP rates within a range of $0.02 - 0.20$ throughout the
428 world ocean in PICO (Fig. 2d). Lowest simulated contributions are found in the eastern and
429 equatorial upwelling regions; highest contributions are located in the polar oceans. Diatoms
430 dominate simulated NPP rates (fraction > 0.80) within the subpolar and polar oceans as well as
431 the equatorial Pacific (Fig. 2e), with lowest fractional contributions to NPP ($\sim 0.01 - 0.05$)
432 located within the subtropical gyres. Diazotrophs contribute < 0.07 to simulated NPP rates and
433 are absent from the subpolar and polar oceans, due to the imposed minimum temperature of 18°C
434 for positive growth rates (Table 1). Highest diazotroph contributions to NPP rates are found
435 within the western tropical to subtropical North and South Pacific Oceans ($\sim 0.04 - 0.07$) (Fig.
436 2f), similar to other OBGC model simulations that incorporate variable nutrient stoichiometry
437 (e.g., Wang et al., 2019).

438



439
 440 **Figure 2.** Fraction of vertically integrated, annual marine NPP attributable to each PFT from the
 441 PICO simulation. (a) *Prochlorococcus*, (b) *Synechococcus*, (c) pico-eukaryotes, (d) nano-
 442 phytoplankton, (e) diatoms, (f) diazotrophs. Note change in range in panels a,c,e from panels b,d,
 443 and panel f.

444
 445 *Nutrients* – Upper ocean (0 – 500 m) simulated dissolved nutrient concentrations from
 446 PICO have been compared against the World Ocean Atlas (WOA) 2013 climatology (Garcia et
 447 al., 2013) for nitrate (NO_3^-), phosphate (PO_4^{3-}), and silicate (SiO_4^{4-}) and a global compilation of
 448 dissolved Fe (dFe) measurements (Tagliabue et al., 2012). Table 2 provides the r-correlation
 449 parameter and mean bias (μM) from a regression of log-transformed model-observation pairs.
 450 Dissolved NO_3^- , PO_4^{3-} , and SiO_4^{4-} are equally well correlated with WOA nutrients, exhibiting r-
 451 correlation coefficients of ~ 0.94 and mean biases of $+0.01 \mu\text{M NO}_3^-$, $+0.02 \mu\text{M PO}_4^{3-}$, and $+0.01$
 452 $\mu\text{M SiO}_4^{4-}$. PICO simulated dFe is the most weakly correlated nutrient with observational data, r
 453 $= 0.40$, with a mean bias of $+0.18 \text{ nM}$. The PICO upper ocean dissolved nutrient mean biases are
 454 similar to those of the other variable C:P stoichiometry simulation, VAR-3, and the Redfield
 455 simulation, RED-3, with a notable improvement to the mean bias of SiO_4^{4-} from VAR-3 (Table
 456 2).

457 *Biomass* – PICO simulated biomass ($\mu\text{g C L}^{-1}$) is compared against the data assimilative
 458 niche model output for *Prochlorococcus* and *Synechococcus* (Flombaum et al., 2013) and pico-
 459 eukaryotes (Flombaum et al., 2020) binned by $3^\circ \times 3^\circ$ pixels. Simulated pico-phytoplankton
 460 biomass correlation coefficients with the niche model output range from 0.485 (pico-eukaryotes)
 461 to 0.637 (*Prochlorococcus*) (Table 3). However, significant negative biases are present within
 462 PICO simulated *Prochlorococcus* biomass (−56%), *Synechococcus* biomass (−85%), and pico-
 463 eukaryotes biomass (−76%) (Table 3). PICO pico-phytoplankton biomass has also been
 464 compared against a globally compiled field-based dataset of flow-sorted populations (Baer et al.,
 465 2017; Lomas et al., 2021), yielding metrics of: *Prochlorococcus* biomass (+76%, $r = 0.199$),
 466 *Synechococcus* biomass (−72%, $r = 0.245$), and pico-eukaryotes biomass (−72%, $r = 0.142$)
 467 (Table 3).

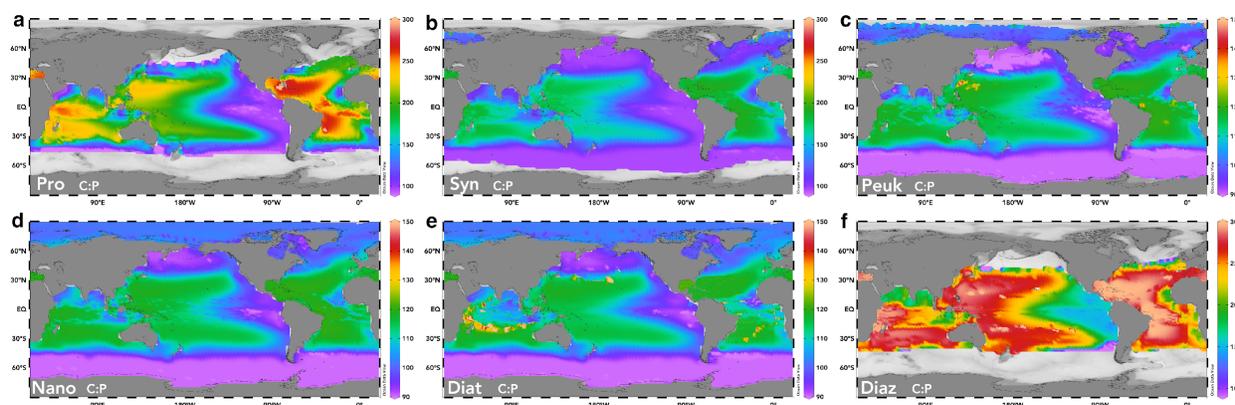
468

	r-correlation	mean bias	n
Pro C niche	0.637	 -56%	24,447
Syn C niche	0.459	 -85%	33,101
Peuk C niche	0.485	 -76%	39,244
Pro C:P	0.120	 -5.6%	55
Syn C:P	0.229	 -17.1%	44
Peuk C:P	0.021	 +11.1%	50
POC:POP	0.245	 +20%	4651
Pro C	0.199	 +76%	2188
Syn C	0.245	 -72%	4120
Peuk C	0.142	 -72%	4158

469

470 **Table 3.** Comparison metrics for PICO simulated pico-phytoplankton biomass versus the data
 471 assimilative niche models of Flombaum et al. (2013; 2020) (Pro C niche, Syn C niche, Peuk C
 472 niche); versus pico-phytoplankton biomass C:P stoichiometry (Baer et al., 2017; Lomas et al.,
 473 2021) (Pro C:P, Syn C:P, Peuk C:P) and biomass C (Pro C, Syn C, Peuk C); and versus bulk
 474 particulate organic matter C:P stoichiometry (Martiny et al., 2014) (POC:POP).

475
 476 *Phytoplankton Stoichiometry* – Euphotic zone-averaged PFT C:P stoichiometry from the
 477 PICO simulation is shown in Figure 3. *Prochlorococcus* (Fig. 3a) and diazotrophs (Fig. 3f)
 478 exhibit the greatest range in cellular C:P stoichiometry, with the minimum stoichiometry found
 479 within the eastern equatorial Pacific Ocean, C:P = ~90 for pro; C:P = ~150 for diaz, increasing to
 480 maximum cellular C:P = ~250 – 300 within the North and South Atlantic subtropical gyres.
 481 Elevated C:P stoichiometry for *Prochlorococcus* and diazotrophs is also found within the other
 482 three subtropical gyre regions, with typical values in the range ~180 – 300. *Synechococcus* (Fig.
 483 3b), pico-eukaryotes (Fig. 3c), nano-phytoplankton (Fig. 3d), and diatoms (Fig. 3e) all exhibit
 484 similar geographical variability in cellular C:P stoichiometry to *Prochlorococcus* and
 485 diazotrophs, with elevated values typical of the five subtropical ocean gyre regions, syn C:P =
 486 ~150 – 210; peuk + nano + diat C:P = ~110 – 125. Phytoplankton C:P stoichiometry is ~25 –
 487 80% more elevated within the western half of each subtropical gyre relative to the eastern half.
 488



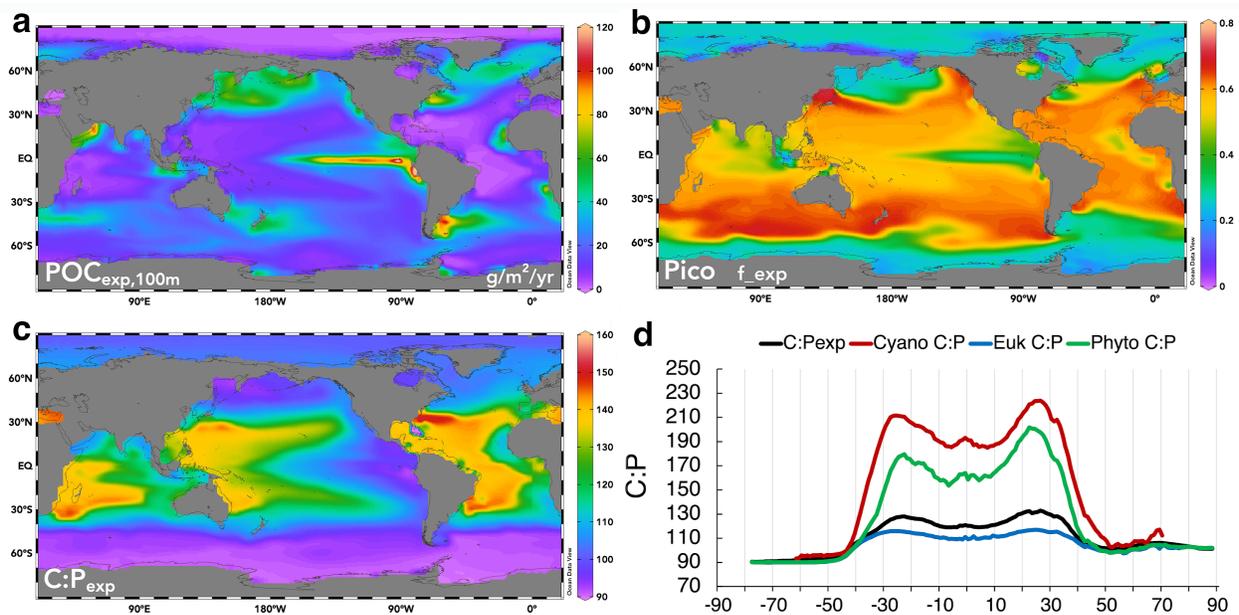
489
 490 **Figure 3.** Euphotic zone averaged cellular C:P stoichiometry for each PFT from the PICO
 491 simulation. (a) *Prochlorococcus*, (b) *Synechococcus*, (c) pico-eukaryotes, (d) nano-
 492 phytoplankton, (e) diatoms, (f) diazotrophs.

493

494 PICO simulated *Prochlorococcus*, *Synechococcus*, and pico-eukaryotes cellular C:P
495 stoichiometry has been compared against a subset of the cell-sorted population dataset for which
496 biomass P was measured (Baer et al., 2017; Lomas et al., 2021). PICO simulated
497 *Prochlorococcus* C:P exhibits the smallest mean bias of -6% below the average field-based
498 estimate of C:P = 221 (Table 3). PICO simulated *Synechococcus* C:P has a negative mean bias of
499 -17% below the field estimate of 187. PICO simulated pico-eukaryotes exhibited a positive
500 mean bias compared to field estimates at $+11\%$ above the field estimate of 103. PICO simulated
501 total autotrophic biomass C:P stoichiometry is compared with a global compilation of surface
502 ocean suspended organic matter C:P stoichiometry (Martiny et al., 2014), exhibiting a positive
503 mean bias of $+20\%$ above the field-based estimate of POC : POP = 171 : 1 (Table 3).

504 *Sinking carbon export* – The sinking particulate organic carbon flux through the 100
505 meter depth horizon ($\text{POC}_{\text{exp},100\text{m}}$) from the PICO simulation is plotted in Figure 4a. $\text{POC}_{\text{exp},100\text{m}}$
506 exhibits a similar geographical distribution as simulated NPP (Fig. 1c), with maximum rates of
507 $\sim 90 - 120 \text{ g C m}^{-2} \text{ yr}^{-1}$ found within the eastern equatorial Pacific, Peruvian, and Arabian Sea
508 upwelling regions as well as the SW Atlantic Ocean and minimum rates, $< 20 \text{ g C m}^{-2} \text{ yr}^{-1}$,
509 within the five subtropical ocean gyres and their bordering tropical regions, the Southern Ocean,
510 and the Arctic Ocean. Other regions exhibiting elevated $\text{POC}_{\text{exp},100\text{m}}$ include the eastern boundary
511 upwelling zones and the subtropical to mid-latitude transition zones with rates in the range $\sim 40 -$
512 $70 \text{ g C m}^{-2} \text{ yr}^{-1}$. The pico-phytoplankton contribution to $\text{POC}_{\text{exp},100\text{m}}$ is greatest across the tropics,
513 subtropics, and mid-latitudes (Fig. 4b), with a fractional contribution in the range $\sim 0.50 - 0.70$.
514 In both hemispheres, pico-phytoplankton make their largest contribution to sinking POC export
515 in the mid-latitudes ($\sim 40 - 50^\circ \text{N}$ and $^\circ \text{S}$), approaching $65 - 70\%$ of $\text{POC}_{\text{exp},100\text{m}}$, with minima

516 (~0.10 – 0.30) estimated for the subpolar, polar, and equatorial Pacific Oceans. The globally
 517 integrated $\text{POC}_{\text{exp},100\text{m}}$ flux below 100 m from PICO is $7.0 \pm 0.1 \text{ Pg C yr}^{-1}$; within the range of
 518 observational-, satellite-, and model-based estimates of global marine export production, e.g., 4 –
 519 14 Pg C yr^{-1} (summarized in Emerson, 2014; Britten & Primeau, 2016; Siegel et al., 2014;
 520 Henson et al., 2011). It should be noted when comparing the PICO carbon export flux to other
 521 estimates from the literature that DOC export below 100 m contributes an additional $\sim 2.1 \text{ Pg C}$
 522 yr^{-1} of carbon export production in the BEC model (Letscher et al., 2015; Letscher & Moore,
 523 2015) bringing estimated total organic carbon export below 100 m to $\sim 9.1 \text{ Pg C yr}^{-1}$.
 524



525
 526 **Figure 4.** PICO simulated 20-yr averaged sinking particulate organic carbon export below 100 m
 527 $\text{POC}_{\text{exp},100\text{m}}$ [$\text{g C m}^{-2} \text{ yr}^{-1}$] (a), the fraction of total $\text{POC}_{\text{exp},100\text{m}}$ attributable to pico-phytoplankton
 528 (pro + syn + peuk) (b), the C:P stoichiometry of sinking organic particles C:P_{exp} at 100 m (c),
 529 and the zonal mean C:P_{exp} at 100 m (black line), C:P of cyanobacteria (pro + syn + diaz; red
 530 line), C:P of eukaryotic phytoplankton biomass (peuk + nano + diat; blue line), and C:P of total
 531 phytoplankton (green line) within the upper 100 m (d).

532

533 The C:P stoichiometry of the sinking organic particulate flux at 100 m ($C:P_{exp}$) from the
534 PICO simulation is shown in Fig. 4c. Carbon rich/P-poor stoichiometry for $C:P_{exp}$ is found in the
535 ocean tropics and subtropics, being a function of both the large contribution of pico-
536 phytoplankton productivity (Fig. 2) in these regions as well as the elevated C:P stoichiometry of
537 the cyanobacteria (pro + syn + diaz) PFTs inhabiting these regions (Fig. 4d). Sinking particulate
538 export C:P stoichiometry exhibits global maxima within the western subtropical gyres of each
539 basin, reaching values of $\sim 140 - 150$ (Fig. 4c). C:P export stoichiometry is elevated elsewhere
540 within the subtropics, $\sim 120 - 140$, near Redfieldian in the mid-latitudes and the Arctic Ocean,
541 and depressed within the eastern equatorial Pacific, subpolar North Pacific, and the Southern
542 Ocean, exhibiting values in the range $\sim 90 - 105$. The zonal mean $C:P_{exp}$ is near the minimum
543 imposed value of 90 for eukaryotic phytoplankton groups south of $50^\circ S$ and near ~ 100 north of
544 $50^\circ N$ where the phytoplankton community is dominated by diatoms and other eukaryote groups
545 (Fig. 2). Maximal zonal mean $C:P_{exp}$ is found at subtropical latitudes exhibiting values of ~ 128 at
546 $23^\circ S$ and a slightly higher value of ~ 133 at $26^\circ N$ in the northern hemisphere (Fig. 4d).
547 Cyanobacteria phytoplankton (pro + syn + diaz), eukaryotic phytoplankton (peuk + nano + diat),
548 and the total phytoplankton community C:P stoichiometry all exhibit similar latitudinal patterns
549 with high latitude minima and subtropical maxima (Fig. 4d). Cyanobacteria phytoplankton C:P
550 varies between $\sim 96 - 223$, eukaryotic phytoplankton C:P varies between $\sim 90 - 117$, with total
551 phytoplankton C:P varying between $\sim 90 - 202$.

552

553 **5. Discussion**

554 Pico-phytoplankton were found to make their largest contribution to marine NPP within
555 the tropical and subtropical ocean, reaching contributions of ~50 – 90% within the latitudinal
556 range 45°N – 45°S (Fig. 2). In general, *Prochlorococcus* dominates NPP within the subtropical
557 gyre regions, transitioning to dominance by pico-eukaryotes both equatorward and poleward of
558 ~30° latitude to ~45°. *Synechococcus* follows a similar spatial pattern as *Prochlorococcus* but
559 never dominates the phytoplankton community, with fractional contributions peaking at ~10 –
560 12% in the subtropical gyres. Diazotrophs, which are parameterized to represent the
561 cyanobacteria lineages of *Trichodesmium* and *Crocospaera* in the BEC model, make a smaller
562 yet important additional contribution in these same low-latitude regions. The pico-phytoplankton
563 and diazotroph groups within the PICO simulation were assigned the largest cellular C:P
564 plasticity and higher minimum temperature thresholds for growth (Table 1) than the larger nano-
565 phytoplankton and diatoms, with the pico-phytoplankton niche being realized within the nutrient-
566 poor, high temperature waters of the low latitudes. The three pico-phytoplankton PFTs in PICO
567 contributed to globally integrated NPP at a percentage of $16.6 \pm 0.4\%$ for *Prochlorococcus*, $3.9 \pm$
568 0.5% for *Synechococcus*, and $37.1 \pm 0.6\%$ for pico-eukaryotes, for a total pico-phytoplankton
569 contribution of $57.6 \pm 0.8\%$ to marine NPP (Table 4). These estimates for global NPP
570 attributable to *Prochlorococcus* and *Synechococcus* within PICO are approximately double and
571 one-quarter, respectively, compared to an independent estimate based on data assimilative
572 modeling of niche partitioning, (pro = 8.5%, syn = 16.7%, Flombaum et al., 2013), however both
573 model estimates converge on a combined pro + syn contribution to marine NPP of ~20 – 25%.
574 Nano-phytoplankton contribute $3.6 \pm 0.7\%$ of global NPP in PICO (likely an underestimate, e.g.,
575 Brewin et al., 2010; Juranek et al., 2020), concentrated in the Southern Ocean, the subpolar and
576 Arctic Ocean, as well as the eastern tropical Pacific Ocean (Fig. 2d). Diatoms are the largest

577 contributor to global marine NPP in PICO, contributing $37.5 \pm 0.5\%$, concentrated in the
 578 subpolar and polar oceans as well as the equatorial Pacific upwelling (Table 4; Figure 2d). This
 579 rate of diatom contribution to global NPP is consistent with the $\sim 38\text{-}43\%$ contribution estimated
 580 from marine biogenic silica budgets (Nelson et al., 1995). Diazotrophs contribute $1.2 \pm 0.04\%$ to
 581 marine NPP in PICO (Table 4), concentrated in the same tropical and subtropical regions as
 582 pico-phytoplankton, especially the western tropical and subtropical Pacific Ocean (Fig. 2e).
 583

PFT	% of NPP	% of POC _{exp}
<i>Prochlorococcus</i>	16.6	14.9
<i>Synechococcus</i>	3.9	12.6
Pico-eukaryotes	37.1	18.1
Nano-phytoplankton	3.6	9.9
Diatoms	37.5	31.2
Diazotrophs	1.2	13.4
Σ Pico-phytoplankton	57.6	45.6

584
 585 **Table 4.** Percentages of globally integrated marine NPP and POC_{exp,100m} attributable to each
 586 PFT.

587
 588 Ecosystem processing of the newly fixed organic matter by each phytoplankton PFT
 589 contributes to the detrital particulate organic matter pools, which constitute the source terms to
 590 the sinking export fluxes of POC_{exp} and particulate organic phosphorus (POP_{exp}) in the BEC
 591 model. These processes include losses to the detrital pool upon grazing by zooplankton,
 592 zooplankton contributions to the detrital pool as a result of grazing (e.g., fecal pellet production),
 593 and aggregation and sinking of phytoplankton biomass upon cell mortality within the BEC
 594 model (Moore et al., 2004). The parameter values governing these processes were prescribed in a
 595 size-scaling manner across the six PFTs in PICO (Table 1), with the pico-phytoplankton

596 contributing the smallest to the particulate sinking fluxes, increasing with diazotrophs and nano-
597 plankton, to the largest contribution from diatoms. The fractions of pico-phytoplankton grazing
598 and zooplankton losses that accumulate within the particulate fluxes were prescribed in the range
599 0.07 – 0.33 (Table 1), at the upper end of estimates based on pigment biomarker analyses of the
600 sediment trap flux collected from the Sargasso Sea (Lomas & Moran, 2011). The higher
601 estimates for pico-phytoplankton detrital contributions were needed to export enough N and P
602 below the euphotic zone to prevent spurious accumulation of NO_3^- and PO_4^{3-} concentrations in
603 the upper layers of the subtropics. The nano-phytoplankton and diatom contributions to NPP are
604 <5% each over much of the subtropical regions in PICO (Fig. 2), which are biased low compared
605 to field observations (e.g., Nelson & Brzezinski, 1997; Brzezinski et al., 2011; Juranek et al.,
606 2020) and may potentially explain the low N and P export efficiency, partially satisfied by
607 prescribed elevated pico-phytoplankton detrital contributions in PICO. PFT-specific parameters
608 linked to the detrital contributions are held constant in PICO, however future formulations of the
609 BEC model could include parameterizations that are dependent on *in situ* temperature, PFT
610 growth rate, grazing rate, or nutrient limitation status among others.

611 Within PICO, pico-phytoplankton contribute nearly half ($45.6 \pm 0.3\%$) of the globally
612 integrated $\text{POC}_{\text{exp},100\text{m}}$ flux through 100 meters when accounting for both direct (e.g.,
613 aggregation) and indirect (e.g., zooplankton processing of pico-produced organic matter)
614 contributions. Approximately 40% of the pico-phytoplankton total is contributed by pico-
615 eukaryotes ($18.1 \pm 0.2\%$), an additional third contributed by *Prochlorococcus* ($14.9 \pm 0.1\%$), and
616 a quarter contributed by *Synechococcus* ($12.6 \pm 0.1\%$) (Table 4). Pico-phytoplankton dominate
617 the phytoplankton contribution to carbon export across large areas of the tropics, subtropics, and
618 mid-latitudes (Fig. 4b), which is an emergent result from the added phytoplankton biodiversity,

619 representation of variable carbon to phosphorus cellular stoichiometry, and ecosystem processing
620 of the detrital pool mediated by zooplankton grazing. Perhaps counterintuitively, pico-
621 phytoplankton contribution to carbon export peaks in importance ($\sim 0.65 - 0.7$), not where their
622 greatest environmental niche is realized, i.e., the high light, low nutrient waters of the
623 oligotrophic subtropical gyres, but at mid-latitudes, $\sim 35 - 45^\circ$, driven largely by regional maxima
624 in C:P stoichiometry (Fig. 4c).

625 The estimate of pico-phytoplankton contribution to sinking carbon export in PICO
626 ($\sim 46\%$) is approximately 80% their combined contributions to global NPP ($\sim 58\%$), in partial
627 agreement with inversions of PFT-specific observational data from the equatorial Pacific and
628 Arabian Sea suggesting that pico-phytoplankton contribute to carbon export at rates comparable
629 to their contribution to NPP (Richardson & Jackson, 2007). Group specific C export fraction to
630 NPP fraction ratios, computed from Table 4, range from a minimum of ~ 0.5 to ~ 3.2 , within the
631 range of the available group-specific estimates diagnosed from a range of field data, ~ 0.1 to ~ 4.5
632 (Richardson & Jackson, 2011; Stukel & Landry, 2010; Lomas & Moran, 2011; Fawcett et al.,
633 2011; Stukel et al., 2013), albeit at the higher end especially for Pro and Syn which are 0.9 and
634 3.2 in PICO and ~ 0.1 and ~ 0.1 to ~ 0.4 from the literature (Lomas & Moran, 2011; Fawcett et al.,
635 2011; Stukel et al., 2013), respectively. A notable outlier is the C export fraction to NPP fraction
636 ratio for diaz which is ~ 11 in PICO. Dissolved organic matter (DOM) contributes $\sim 20-25\%$ of
637 total organic carbon export production in the CESM (Letscher et al., 2015). We are unable to
638 provide an estimate of each PFT contribution to the DOM export flux, as DOM export is
639 spatially and temporally offset from its region of production, and the model does not track DOM
640 sourced from individual PFTs. Each PFT contributes a constant fraction of its newly produced

641 organic matter to the DOM pool; therefore, PFT contributions to DOM export should generally
642 track the proportions of PFT contributions to NPP (e.g., Table 4).

643 The regions located immediately along the poleward and western edges of the surface
644 western boundary currents of the subtropical gyre regions of each ocean basin exhibit elevated
645 $\text{POC}_{\text{exp},100\text{m}}$ fluxes on the order of $\sim 50 - 90 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Fig. 4a), approximately $\sim 2-3$ fold higher
646 as compared to the adjacent regions. These so-called ‘gyre recirculation regions’ of the surface
647 western boundary currents are characterized by strong eddying flow and enhanced lateral
648 nutrient concentration gradients that stand out as important regions for the delivery of a lateral
649 nutrient flux that dominates nutrient resupply to the subtropical gyres (Williams & Follows,
650 1998; Oschlies, 2002; Jenkins & Doney, 2003; Torres-Valdés et al., 2009; Palter et al., 2013;
651 Letscher et al., 2016; Yamamoto et al., 2019). The resolution of the BEC model employed in
652 PICO is non-eddy resolving, however it is able to simulate somewhat elevated rates of NPP (Fig.
653 1a) and associated $\text{POC}_{\text{exp},100\text{m}}$ (Fig 4a) along these subtropical to subpolar gyre flanks at the
654 western side. These gyre recirculation region biogeochemical features are driven by a larger
655 contribution of pico-eukaryotes and diatoms to simulated NPP (Fig. 2). These regions are also
656 where PFT cellular C:P stoichiometry transitions from C-rich/P-poor stoichiometry within the
657 subtropical gyres, to more Redfield-like C:P stoichiometry poleward (Fig. 3; Fig. 4c,d). Thus, the
658 magnitude of $\text{POC}_{\text{exp},100\text{m}}$ within the subtropical gyre recirculation regions identified as ‘ POC_{exp}
659 hotspots’ by PICO may be sensitive to small changes to the nutrient flux stoichiometry which
660 drive cellular C:P stoichiometry. Further field-based study of the *in situ* phytoplankton
661 community composition and associated biomass C:P stoichiometry within these regions could
662 help confirm their regional ‘ POC_{exp} hotspot’ status.

663 The PICO simulation builds from recent advances in a BEC model formulation that
664 added variable C:P stoichiometry within the three traditionally simulated PFTs (small
665 phytoplankton, diatoms, diazotrophs; Wang et al., 2019), by adding three pico-phytoplankton
666 PFTs with variable C:P stoichiometry. As compared to the variable C:P, three PFT version of the
667 BEC model (VAR-3; Wang et al., 2019), the PICO simulation exhibits ~1% higher globally
668 integrated NPP (51.4 Pg C yr⁻¹ vs. 50.8 Pg C yr⁻¹) and ~18% lower POC_{exp,100m} (7.0 Pg C yr⁻¹ vs.
669 8.5 Pg C yr⁻¹). Thus, given that both the three and six PFT, variable C:P formulations of the BEC
670 model reproduce similarly-well, the surface to deep ocean spatial gradients in dissolved nutrient
671 concentrations (Table 2), the pico-phytoplankton enabled (6p1z) BEC model predicts similar
672 rates of NPP, with lower rates of POC_{exp,100m}, and lower C:P_{exp} per unit of phosphorus utilized
673 within the euphotic zone as compared with the three PFT BEC model version (VAR-3; Wang et
674 al., 2019). The geographical distribution of POC_{exp,100m} is similar between the PICO and VAR-3
675 simulations, however VAR-3 simulated POC_{exp,100m} is approximately double to triple that
676 estimated by PICO within the subtropics to mid-latitudes (not shown), contributing to its overall
677 ~18% higher estimate of global POC_{exp,100m}. The lower POC_{exp,100m} estimate by the PICO model
678 is likely attributable to the lower prescribed values of zooplankton grazing routed to the
679 particulate organic pool, 'graze_poc' parameter, for the pico PFTs (graze_poc = 0.07 – 0.13;
680 Table 1) versus the small phytoplankton PFT in Wang et al. (2019) (graze_poc = 0.3). Maximum
681 C:P_{exp} is estimated within the ocean's subtropical gyres (Fig. 4c) in both simulations, with PICO
682 predicting slightly lower maximum C:P_{exp} within the Indo-Pacific subtropics, ~140 – 145 vs.
683 ~180 in VAR-3 (not shown). PICO simulated C:P_{exp} generally agrees with the spatial pattern
684 estimated from an inversion of dissolved inorganic carbon and phosphate data (Teng et al.,
685 2014), with notable differences in C:P_{exp} magnitude. PICO minimum PFT C:P is set at 90 while

686 the Teng et al. (2014) inversion estimates minimum C:P_{exp} of ~60 – 100 for the equatorial and
687 subpolar regions. Maximal C:P_{exp} in the subtropical North Atlantic is ~155 in PICO compared to
688 ~355 by Teng et al. (2014). These comparisons demonstrate that estimates of the globally
689 important fluxes of marine NPP and carbon export including its C:P stoichiometry vary on the
690 order of ~10 – 50% between OBGC model formulations, highlighting the continued need for
691 observational datasets to further constrain and validate model simulations of ocean
692 biogeochemistry.

693 We are aware of two other ESMs to which addition of variable phosphorus to carbon
694 ratios within the OBGC model has been performed as well as an additional global ocean
695 biogeochemistry model. While nearly all ESMs participating in the CMIP5 suite predict
696 declining marine NPP during the 21st century (Bopp et al., 2013), the GFDL-ESM2 which runs
697 the variable C:P enabled TOPAZ2 OBGC model (Dunne, 2013), was the only ESM to predict a
698 resilient rate of marine NPP throughout this century. Presumably the mechanism at play is one in
699 which declining nutrient fluxes to the surface ocean with increasing upper ocean stratification are
700 countered by a switch in phytoplankton community composition towards smaller, more nutrient
701 plastic types and/or an increase in phytoplankton C:P that allows for maintenance of carbon
702 based NPP rates at depressed phosphorus supply fluxes. The PICO simulation presented here
703 supports this interpretation, exhibiting a marginally ~1% higher overall rate of marine NPP than
704 its analogous three PFT, Redfield C:P sister simulation (RED-3; Letscher & Moore, 2015).
705 Results from a variable C:P OBGC model that added representation of pico-phytoplankton have
706 been published (the PISCES-QUOTA model; Kwiatkowski et al., 2018). The model predicts
707 similar 21st century declines in marine NPP (–8%) and POC_{exp} (–14%) as the fixed (Redfield)
708 stoichiometry ESMs that participated in CMIP5 (Bopp et al., 2013), while noting an increase in

709 carbon export efficiency per unit phosphorus, which increases by 4.5%. Both the TOPAZ2
710 OBGC model and PISCES-QUOTA parameterize variable C:P in the phytoplankton following
711 the optimal resource cell allocation model of Klausmeier et al., (2004), so it is surprising that the
712 two models yield divergent predictions for 21st century marine NPP (no decline in GFDL-ESM2
713 using TOPAZ2, decreasing in PISCES-QUOTA), that may be due to differences in model
714 physics and the simulated nutrient supply to the surface. The global ocean biogeochemistry
715 modeling study of Tanioka & Matsumoto (2017) in which variable C:P stoichiometry was
716 represented in a two phytoplankton marine ecosystem model, found that predicted declines in
717 global export production could be mitigated by ~3% relative to a Redfield stoichiometry model
718 over the 21st century that the authors attributed to combined mechanisms of flexible cellular
719 nutrient to carbon ratios and regional shifts in phytoplankton community composition.

720

721 **6. Future Directions**

722 A next step with the CESM-BEC model is to perform a future climate forced simulation
723 using PICO parameterizations to investigate changes in 21st century marine NPP and export in
724 the context of marine phytoplankton diversity and cellular nutrient plasticity. We also wish to
725 point out that during development of the PICO simulation it was found that the model solution
726 was very sensitive to the choice of the grazing rates for each of the six PFTs by the single
727 zooplankton group. This single zooplankton group formulation was not well suited to act as the
728 top-down control on the growth of six PFTs, with the model exhibiting behavior in which it was
729 difficult to obtain mixed communities of phytoplankton everywhere in the ocean. Future
730 improvement of the BEC model, now carried out within the Marine Biogeochemistry Library
731 (MARBL) in CESM v2, should include the addition of explicit nanophytoplankton groups (e.g.,

732 coccolithophores) and additional zooplankton groups representing multiple size classes and
733 grazing formulations that will likely result in a more robust simulation of plankton growth,
734 grazing, and export dynamics. Currently, a version with four zooplankton and eight
735 phytoplankton functional types is in development (8p4z).

736

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745

746 **Open Research**

747 The modified BEC model source code used to generate the PICO simulation can be found on
748 GitHub here: https://github.com/rletscher/GBC_PICO. The 20-year annually averaged output file
749 for PICO presented in this work is available by request from the corresponding author.

750

751 **References**

752 Arrigo, K. R., Robinson, D. H., Worthen, D. L., Dunbar, R. B., DiTullio, G. R., VanWoert, M.,
753 & Lizotte, M. P. (1999). Phytoplankton community structure and the drawdown of nutrients and
754 CO₂ in the Southern Ocean. *Science*, 283(5400), 365-367.

755

- 756 Aumont, O., Éthé, C., Tagliabue, A., Bopp, L., & Gehlen, M. (2015). PISCES-v2: an ocean
757 biogeochemical model for carbon and ecosystem studies. *Geoscientific Model Development*
758 *Discussions*, 8(2).
759
- 760 Baer, S. E., Lomas, M. W., Terpis, K. X., Mouginot, C., & Martiny, A. C. (2017). Stoichiometry
761 of Prochlorococcus, Synechococcus, and small eukaryotic populations in the western North
762 Atlantic Ocean. *Environmental microbiology*, 19(4), 1568-1583.
763
- 764 Behrenfeld, M. J., Boss, E., Siegel, D. A., & Shea, D. M. (2005). Carbon-based ocean
765 productivity and phytoplankton physiology from space. *Global biogeochemical cycles*, 19(1).
766
- 767 Berman-Frank, I., Quigg, A., Finkel, Z. V., Irwin, A. J., & Haramaty, L. (2007). Nitrogen-
768 fixation strategies and Fe requirements in cyanobacteria. *Limnology and Oceanography*, 52(5),
769 2260-2269.
770
- 771 Bopp, L., Resplandy, L., Orr, J. C., Doney, S. C., Dunne, J. P., Gehlen, M., ... & Tjiputra, J.
772 (2013). Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5
773 models. *Biogeosciences*, 10, 6225-6245.
774
- 775 Boyd, P. W., Strzepek, R. F., Ellwood, M. J., Hutchins, D. A., Nodder, S. D., Twining, B. S., &
776 Wilhelm, S. W. (2015). Why are biotic iron pools uniform across high-and low-iron pelagic
777 ecosystems?. *Global Biogeochemical Cycles*, 29(7), 1028-1043.
778
- 779 Brewin, R. J., Lavender, S. J., Hardman-Mountford, N. J., & Hirata, T. (2010). A spectral
780 response approach for detecting dominant phytoplankton size class from satellite remote
781 sensing. *Acta Oceanol. Sin*, 29(2), 14-32.
782
- 783 Britten, G. L., & Primeau, F. W. (2016). Biome-specific scaling of ocean productivity,
784 temperature, and carbon export efficiency. *Geophysical Research Letters*, 43(10), 5210-5216.
785
- 786 Brzezinski, M. A., Krause, J. W., Church, M. J., Karl, D. M., Li, B., Jones, J. L., & Updyke, B.
787 (2011). The annual silica cycle of the North Pacific subtropical gyre. *Deep Sea Research Part I:
788 Oceanographic Research Papers*, 58(10), 988-1001.
789
- 790 Buchanan, P. J., Matear, R. J., Chase, Z., Phipps, S. J., & Bindoff, N. L. (2018). Dynamic
791 biological functioning important for simulating and stabilizing ocean biogeochemistry. *Global
792 Biogeochemical Cycles*, 32(4), 565-593.
793
- 794 Buitenhuis, E. T., Hashioka, T., & Le Quéré, C. (2013). Combined constraints on global ocean
795 primary production using observations and models. *Global Biogeochemical Cycles*, 27(3), 847-
796 858.
797
- 798 Buitenhuis, E. T., Li, W. K., Vaultot, D., Lomas, M. W., Landry, M. R., Partensky, F., ... &
799 McManus, G. B. (2012). Picophytoplankton biomass distribution in the global ocean. *Earth
800 System Science Data*, 4(1), 37-46.
801

- 802 Cabré, A., Marinov, I., & Leung, S. (2015). Consistent global responses of marine ecosystems to
803 future climate change across the IPCC AR5 earth system models. *Climate Dynamics*, 45(5-6),
804 1253-1280.
- 805
- 806 Casey, J. R., Lomas, M. W., Michelou, V. K., Dyrman, S. T., Orchard, E. D., Ammerman, J.
807 W., & Sylvan, J. B. (2009). Phytoplankton taxon-specific orthophosphate (Pi) and ATP
808 utilization in the western subtropical North Atlantic. *Aquatic Microbial Ecology*, 58(1), 31-44.
809
- 810 DeVries, T., & Deutsch, C. (2014). Large-scale variations in the stoichiometry of marine organic
811 matter respiration. *Nature Geoscience*, 7(12), 890.
812
- 813 Dunne, J. P. (2013). Technical description of Tracers of Ocean Phytoplankton with Allometric
814 Zooplankton version 2 (TOPAZ2) used in GFDL's ESM2M and ESM2G submitted as part of the
815 Coupled Model Intercomparison Project phase 5. *J Clim.* <https://doi.org/10.1175/JCLI-D-12-00150.s1>.
816
- 817
- 818 Dunne, J. P., Gnanadesikan, A., Sarmiento, J. L., & Slater, R. D. (2010). Technical description of
819 the prototype version (v0) of tracers of phytoplankton with allometric zooplankton (TOPAZ)
820 ocean biogeochemical model as used in the Princeton IFMIP model. *Biogeosciences*, 7(Suppl),
821 3593.
822
- 823 DuRand, M. D., Olson, R. J., & Chisholm, S. W. (2001). Phytoplankton population dynamics at
824 the Bermuda Atlantic Time-series station in the Sargasso Sea. *Deep Sea Research Part II:
825 Topical Studies in Oceanography*, 48(8-9), 1983-2003.
826
- 827 Dutkiewicz, S., Cermeno, P., Jahn, O., Follows, M. J., Hickman, A. E., Taniguchi, D. A., &
828 Ward, B. A. (2020). Dimensions of marine phytoplankton diversity. *Biogeosciences*, 17(3), 609-
829 634.
830
- 831 Dyrman, S. T., & Ruttenberg, K. C. (2006). Presence and regulation of alkaline phosphatase
832 activity in eukaryotic phytoplankton from the coastal ocean: Implications for dissolved organic
833 phosphorus remineralization. *Limnology and Oceanography*, 51(3), 1381-1390.
834
- 835 Emerson, S. (2014). Annual net community production and the biological carbon flux in the
836 ocean. *Global Biogeochemical Cycles*, 28(1), 14-28.
837
- 838 Fawcett, S. E., Lomas, M. W., Casey, J. R., Ward, B. B., & Sigman, D. M. (2011). Assimilation
839 of upwelled nitrate by small eukaryotes in the Sargasso Sea. *Nature Geoscience*, 4(10), 717-722.
840
- 841 Flombaum, P., Gallegos, J. L., Gordillo, R. A., Rincón, J., Zabala, L. L., Jiao, N., ... & Vera, C.
842 S. (2013). Present and future global distributions of the marine Cyanobacteria *Prochlorococcus*
843 and *Synechococcus*. *Proceedings of the National Academy of Sciences*, 110(24), 9824-9829.
844
- 845 Flombaum, P., Wang, W. L., Primeau, F. W., & Martiny, A. C. (2020). Global
846 picophytoplankton niche partitioning predicts overall positive response to ocean
847 warming. *Nature Geoscience*, 13(2), 116-120.

848
849 Friedlingstein, P., Cox, P., Betts, R., Bopp, L., von Bloh, W., Brovkin, V., ... & Bala, G. (2006).
850 Climate-carbon cycle feedback analysis: results from the C4MIP model
851 intercomparison. *Journal of climate*, 19(14), 3337-3353.
852
853 Galbraith, E. D., & Martiny, A. C. (2015). A simple nutrient-dependence mechanism for
854 predicting the stoichiometry of marine ecosystems. *Proceedings of the National Academy of*
855 *Sciences*, 112(27), 8199-8204.
856
857 Garcia, H. E., Locarnini, R. A., Boyer, T. P., Antonov, J. I., Baranova, O. K., Zweng, M. M.,
858 Reagan, J. R., & Johnson, D. R. (2013). World Ocean Atlas 2013, Volume 4: Dissolved
859 inorganic nutrients (phosphate, nitrate, silicate). S. Levitus, Ed., A. Mishonov Technical Ed.,
860 NOAA Atlas NESDIS 76, 25 pp.
861
862 Garcia, N. S., Fu, F., Sedwick, P. N., & Hutchins, D. A. (2015). Iron deficiency increases growth
863 and nitrogen-fixation rates of phosphorus-deficient marine cyanobacteria. *The ISME*
864 *journal*, 9(1), 238.
865
866 Henson, S. A., Sanders, R., Madsen, E., Morris, P. J., Le Moigne, F., & Quartly, G. D. (2011). A
867 reduced estimate of the strength of the ocean's biological carbon pump. *Geophysical Research*
868 *Letters*, 38(4).
869
870 Geider, R. J., & La Roche, J. (2002). Redfield revisited: variability of C [ratio] N [ratio] P in
871 marine microalgae and its biochemical basis. *European Journal of Phycology*, 37(1), 1-17.
872
873 Getzlaff, J., & Dietze, H. (2013). Effects of increased isopycnal diffusivity mimicking the
874 unresolved equatorial intermediate current system in an earth system climate model. *Geophysical*
875 *Research Letters*, 40(10), 2166-2170.
876
877 Gregg, W. W., & Casey, N. W. (2004). Global and regional evaluation of the SeaWiFS
878 chlorophyll data set. *Remote Sensing of Environment*, 93(4), 463-479.
879
880 Hutchins, D. A., Hare, C. E., Weaver, R. S., Zhang, Y., Firme, G. F., DiTullio, G. R., ... & Trick,
881 C. G. (2002). Phytoplankton iron limitation in the Humboldt Current and Peru
882 Upwelling. *Limnology and Oceanography*, 47(4), 997-1011.
883
884 Ilyina, T., Six, K. D., Segschneider, J., Maier-Reimer, E., Li, H., & Núñez-Riboni, I. (2013).
885 Global ocean biogeochemistry model HAMOCC: Model architecture and performance as
886 component of the MPI-Earth system model in different CMIP5 experimental
887 realizations. *Journal of Advances in Modeling Earth Systems*, 5(2), 287-315.
888
889 Jenkins, W. J., & Doney, S. C. (2003). The subtropical nutrient spiral. *Global Biogeochemical*
890 *Cycles*, 17(4).
891

- 892 Juranek, L. W., White, A. E., Dugenne, M., Henderikx Freitas, F., Dutkiewicz, S., Ribalet, F., ...
 893 & Karl, D. M. (2020). The importance of the phytoplankton “middle class” to ocean net
 894 community production. *Global Biogeochemical Cycles*, *34*(12), e2020GB006702.
 895
- 896 Karl, D. M., Björkman, K. M., Dore, J. E., Fujieki, L., Hebel, D. V., Houlihan, T., ... & Tupas, L.
 897 M. (2001). Ecological nitrogen-to-phosphorus stoichiometry at station ALOHA. *Deep Sea*
 898 *Research Part II: Topical Studies in Oceanography*, *48*(8-9), 1529-1566.
 899
- 900 Klausmeier, C. A., Litchman, E., Daufresne, T., & Levin, S. A. (2004). Optimal nitrogen-to-
 901 phosphorus stoichiometry of phytoplankton. *Nature*, *429*(6988), 171.
 902
- 903 Knapp, A. (2012). The sensitivity of marine N₂ fixation to dissolved inorganic
 904 nitrogen. *Frontiers in microbiology*, *3*, 374.
 905
- 906 Kwiatkowski, L., Aumont, O., Bopp, L., & Ciais, P. (2018). The impact of variable
 907 phytoplankton stoichiometry on projections of primary production, food quality, and carbon
 908 uptake in the global ocean. *Global Biogeochemical Cycles*, *32*(4), 516-528.
 909
- 910 Kwiatkowski, L., Torres, O., Bopp, L., Aumont, O., Chamberlain, M., Christian, J. R., ... &
 911 Ziehn, T. (2020). Twenty-first century ocean warming, acidification, deoxygenation, and upper-
 912 ocean nutrient and primary production decline from CMIP6 model
 913 projections. *Biogeosciences*, *17*(13), 3439-3470.
 914
- 915 Kwon, E. Y., Sreesh, M. G., Timmermann, A., Karl, D. M., Church, M. J., Lee, S. S., &
 916 Yamaguchi, R. (2022). Nutrient uptake plasticity in phytoplankton sustains future ocean net
 917 primary production. *Science Advances*, *8*(51), eadd2475.
 918
- 919 Le Quéré, C. L., Harrison, S. P., Colin Prentice, I., Buitenhuis, E. T., Aumont, O., Bopp, L., ... &
 920 Wolf-Gladrow, D. (2005). Ecosystem dynamics based on plankton functional types for global
 921 ocean biogeochemistry models. *Global Change Biology*, *11*(11), 2016-2040.
 922
- 923 Letscher, R. T., & Moore, J. K. (2015). Preferential remineralization of dissolved organic
 924 phosphorus and non-Redfield DOM dynamics in the global ocean: Impacts on marine
 925 productivity, nitrogen fixation, and carbon export. *Global Biogeochemical Cycles*, *29*(3), 325-
 926 340.
 927
- 928 Letscher, R. T., Moore, J. K., Teng, Y. C., & Primeau, F. (2015). Variable C: N: P stoichiometry
 929 of dissolved organic matter cycling in the Community Earth System
 930 Model. *Biogeosciences*, *12*(1), 209-221.
 931
- 932 Letscher, R. T., Primeau, F., & Moore, J. K. (2016). Nutrient budgets in the subtropical ocean
 933 gyres dominated by lateral transport. *Nature Geoscience*, *9*(11), 815.
 934
- 935 Lomas, M. W., Baer, S. E., Mouginit, C., Terpis, K. X., Lomas, D. A., Altabet, M. A., &
 936 Martiny, A. C. (2021). Varying influence of phytoplankton biodiversity and stoichiometric

- 937 plasticity on bulk particulate stoichiometry across ocean basins. *Communications Earth &*
 938 *Environment*, 2(1), 1-10.
- 939
- 940 Lomas, M. W., Bates, N. R., Johnson, R. J., Steinberg, D. K., & Tanioka, T. (2022). Adaptive
 941 carbon export response to warming in the Sargasso Sea. *Nature Communications*, 13(1), 1211.
 942
- 943 Lomas, M. W., Bonachela, J. A., Levin, S. A., & Martiny, A. C. (2014). Impact of ocean
 944 phytoplankton diversity on phosphate uptake. *Proceedings of the National Academy of*
 945 *Sciences*, 111(49), 17540-17545.
 946
- 947 Lomas, M. W., Bronk, D. A., & van den Engh, G. (2011). Use of flow cytometry to measure
 948 biogeochemical rates and processes in the ocean. *Annual review of marine science*, 3, 537-566.
 949
- 950 Lomas, M. W., & Moran, S. B. (2011). Evidence for aggregation and export of cyanobacteria
 951 and nano-eukaryotes from the Sargasso Sea euphotic zone. *Biogeosciences*, 8(1), 203-216.
 952
- 953 Martiny, A. C., Hagstrom, G. I., DeVries, T., Letscher, R. T., Britten, G. L., Garcia, C. A., ... &
 954 Matsumoto, K. (2022). Marine phytoplankton resilience may moderate oligotrophic ecosystem
 955 responses and biogeochemical feedbacks to climate change. *Limnology and Oceanography*, 67,
 956 S378-S389.
 957
- 958 Martiny, A. C., Kathuria, S., & Berube, P. M. (2009). Widespread metabolic potential for nitrite
 959 and nitrate assimilation among Prochlorococcus ecotypes. *Proceedings of the National Academy*
 960 *of Sciences*, 106(26), 10787-10792.
 961
- 962 Martiny, A. C., Pham, C. T., Primeau, F. W., Vrugt, J. A., Moore, J. K., Levin, S. A., & Lomas,
 963 M. W. (2013a). Strong latitudinal patterns in the elemental ratios of marine plankton and organic
 964 matter. *Nature Geoscience*, 6(4), 279.
 965
- 966 Martiny, A. C., Vrugt, J. A., & Lomas, M. W. (2014). Concentrations and ratios of particulate
 967 organic carbon, nitrogen, and phosphorus in the global ocean. *Scientific data*, 1(1), 1-7.
 968
- 969 Martiny, A. C., Vrugt, J. A., Primeau, F. W., & Lomas, M. W. (2013b). Regional variation in the
 970 particulate organic carbon to nitrogen ratio in the surface ocean. *Global Biogeochemical*
 971 *Cycles*, 27(3), 723-731.
 972
- 973 Matsumoto, K., Tanioka, T., & Rickaby, R. (2020). Linkages between dynamic phytoplankton
 974 C: N: P and the ocean carbon cycle under climate change. *Oceanography*, 33(2), 44-52.
 975
- 976 Moore, J. K., Doney, S. C., & Lindsay, K. (2004). Upper ocean ecosystem dynamics and iron
 977 cycling in a global three-dimensional model. *Global Biogeochemical Cycles*, 18(4).
 978
- 979 Moore, J. K., Fu, W., Primeau, F., Britten, G. L., Lindsay, K., Long, M., ... & Randerson, J. T.
 980 (2018). Sustained climate warming drives declining marine biological
 981 productivity. *Science*, 359(6380), 1139-1143.
 982

- 983 Moore, J. K., Lindsay, K., Doney, S. C., Long, M. C., & Misumi, K. (2013). Marine ecosystem
984 dynamics and biogeochemical cycling in the Community Earth System Model [CESM1 (BGC)]:
985 Comparison of the 1990s with the 2090s under the RCP4.5 and RCP8.5 scenarios. *Journal of*
986 *Climate*, 26(23), 9291-9312.
- 987
988 Moore, L. R., Rocap, G., & Chisholm, S. W. (1998). Physiology and molecular phylogeny of
989 coexisting *Prochlorococcus* ecotypes. *Nature*, 393(6684), 464-467.
- 990
991 NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing
992 Group, 2018. Sea-viewing Wide Field-of-View Sensor (SeaWiFS) Ocean Color Data,
993 https://oceandata.sci.gsfc.nasa.gov/cgi/getfile/S19972472010334.L3b_CU_CHL.nc. Accessed on
994 Jun 5 2018.
- 995
996 Nelson, D. M., & Brzezinski, M. A. (1997). Diatom growth and productivity in an oligo-trophic
997 midocean gyre: A 3-yr record from the Sargasso Sea near Bermuda. *Limnology and*
998 *Oceanography*, 42(3), 473-486.
- 999
1000 Nelson, D. M., Tréguer, P., Brzezinski, M. A., Leynaert, A., & Quéguiner, B. (1995). Production
1001 and dissolution of biogenic silica in the ocean: revised global estimates, comparison with
1002 regional data and relationship to biogenic sedimentation. *Global Biogeochemical Cycles*, 9(3),
1003 359-372.
- 1004
1005 Orchard, E. D., Ammerman, J. W., Lomas, M. W., & Dyrman, S. T. (2010). Dissolved
1006 inorganic and organic phosphorus uptake in *Trichodesmium* and the microbial community: The
1007 importance of phosphorus ester in the Sargasso Sea. *Limnology and Oceanography*, 55(3), 1390-
1008 1399.
- 1009
1010 Oschlies, A. (2002). Nutrient supply to the surface waters of the North Atlantic: A model
1011 study. *Journal of Geophysical Research: Oceans*, 107(C5), 14-1.
- 1012
1013 Palter, J. B., Marinov, I., Sarmiento, J. L., & Gruber, N. (2013). Large-scale, persistent nutrient
1014 fronts of the World Ocean: Impacts on biogeochemistry in Chemical Oceanography of Frontal
1015 Zones, p. 1-38 Springer.
- 1016
1017 Partensky, F., Blanchot, J., & Vaultot, D. (1999). Differential distribution and ecology of
1018 *Prochlorococcus* and *Synechococcus* in oceanic waters: a review. *Bulletin-Institut*
1019 *Océanographique Monaco-Numero Special*-, 457-476.
- 1020
1021 Pasulka, A. L., Landry, M. R., Taniguchi, D. A., Taylor, A. G., & Church, M. J. (2013).
1022 Temporal dynamics of phytoplankton and heterotrophic protists at station ALOHA. *Deep Sea*
1023 *Research Part II: Topical Studies in Oceanography*, 93, 44-57.
- 1024
1025 Quigg, A., Finkel, Z. V., Irwin, A. J., Rosenthal, Y., Ho, T. Y., Reinfelder, J. R., ... & Falkowski,
1026 P. G. (2003). The evolutionary inheritance of elemental stoichiometry in marine
1027 phytoplankton. *Nature*, 425(6955), 291.
- 1028

- 1029 Rhee, G. Y. (1978). Effects of N: P atomic ratios and nitrate limitation on algal growth, cell
1030 composition, and nitrate uptake. *Limnology and oceanography*, 23(1), 10-25.
1031
- 1032 Richardson, T. L., & Jackson, G. A. (2007). Small phytoplankton and carbon export from the
1033 surface ocean. *Science*, 315(5813), 838-840.
1034
- 1035 S  ferian, R., Berthet, S., Yool, A., Palmieri, J., Bopp, L., Tagliabue, A., ... & Yamamoto, A.
1036 (2020). Tracking improvement in simulated marine biogeochemistry between CMIP5 and
1037 CMIP6. *Current Climate Change Reports*, 6(3), 95-119.
1038
- 1039 Sharoni, S., & Halevy, I. (2020). Nutrient ratios in marine particulate organic matter are
1040 predicted by the population structure of well-adapted phytoplankton. *Science Advances*, 6(29),
1041 eaaw9371.
1042
- 1043 Shire, D. M., & Kustka, A. B. (2015). Luxury uptake, iron storage and ferritin abundance in
1044 *Prochlorococcus marinus* (Synechococcales) strain MED4. *Phycologia*, 54(4), 398-406.
1045
- 1046 Siegel, D. A., Buesseler, K. O., Doney, S. C., Saille, S. F., Behrenfeld, M. J., & Boyd, P. W.
1047 (2014). Global assessment of ocean carbon export by combining satellite observations and food-
1048 web models. *Global Biogeochemical Cycles*, 28(3), 181-196.
1049
- 1050 Silsbe, G. M., Behrenfeld, M. J., Halsey, K. H., Milligan, A. J., & Westberry, T. K. (2016). The
1051 CAFE model: A net production model for global ocean phytoplankton. *Global Biogeochemical*
1052 *Cycles*, 30(12), 1756-1777.
1053
- 1054 Smith, R., Jones, P., Briegleb, B., Bryan, F., Danabasoglu, G., Dennis, J., ... & Hecht, M. (2010).
1055 The parallel ocean program (POP) reference manual: ocean component of the community
1056 climate system model (CCSM) and community earth system model (CESM). *Rep. LAUR-*
1057 *01853*, 141, 1-140.
1058
- 1059 Sohm, J. A., Ahlgren, N. A., Thomson, Z. J., Williams, C., Moffett, J. W., Saito, M. A., ... &
1060 Rocap, G. (2016). Co-occurring *Synechococcus* ecotypes occupy four major oceanic regimes
1061 defined by temperature, macronutrients and iron. *The ISME journal*, 10(2), 333-345.
1062
- 1063 Sohm, J. A., & Capone, D. G. (2006). Phosphorus dynamics of the tropical and subtropical north
1064 Atlantic: *Trichodesmium* spp. versus bulk plankton. *Marine Ecology Progress Series*, 317, 21-
1065 28.
1066
- 1067 Stawiarski, B., Buitenhuis, E. T., & Fallens, M. (2018). The physiological response of seven
1068 strains of picophytoplankton to light, and its representation in a dynamic photosynthesis
1069 model. *Limnology and Oceanography*, 63(S1), S367-S380.
1070
- 1071 Stukel, M., Coles, V., Brooks, M., & Hood, R. (2014). Top-down, bottom-up and physical
1072 controls on diatom-diazotroph assemblage growth in the Amazon River
1073 plume. *Biogeosciences*, 11(12).
1074

- 1075 Stukel, M. R., Décima, M., Selph, K. E., Taniguchi, D. A., & Landry, M. R. (2013). The role of
1076 *Synechococcus* in vertical flux in the Costa Rica upwelling dome. *Progress in*
1077 *Oceanography*, 112, 49-59.
- 1078
1079 Stukel, M. R., & Landry, M. R. (2010). Contribution of picophytoplankton to carbon export in
1080 the equatorial Pacific: A reassessment of food web flux inferences from inverse
1081 models. *Limnology and Oceanography*, 55(6), 2669-2685.
- 1082
1083 Tagliabue, A., Mtshali, T., Aumont, O., Bowie, A. R., Klunder, M. B., Roychoudhury, A. N., &
1084 Swart, S. (2012). A global compilation of dissolved iron measurements: focus on distributions
1085 and processes in the Southern Ocean. *Biogeosciences*, 9(6).
- 1086
1087 Tanioka, T., & Matsumoto, K. (2017). Buffering of ocean export production by flexible
1088 elemental stoichiometry of particulate organic matter. *Global Biogeochemical Cycles*, 31(10),
1089 1528-1542.
- 1090
1091 Tanioka, T., & Matsumoto, K. (2020). A meta-analysis on environmental drivers of marine
1092 phytoplankton C: N: P. *Biogeosciences*, 17(11), 2939-2954.
- 1093
1094 Teng, Y. C., Primeau, F. W., Moore, J. K., Lomas, M. W., & Martiny, A. C. (2014). Global-scale
1095 variations of the ratios of carbon to phosphorus in exported marine organic matter. *Nature*
1096 *Geoscience*, 7(12), 895.
- 1097
1098 Timmermans, K. R., Van der Wagt, B., Veldhuis, M. J. W., Maatman, A., & De Baar, H. J. W.
1099 (2005). Physiological responses of three species of marine pico-phytoplankton to ammonium,
1100 phosphate, iron and light limitation. *Journal of sea research*, 53(1-2), 109-120.
- 1101
1102 Torres-Valdés, S., Roussenov, V. M., Sanders, R., Reynolds, S., Pan, X., Mather, R., ... &
1103 Williams, R. G. (2009). Distribution of dissolved organic nutrients and their effect on export
1104 production over the Atlantic Ocean. *Global Biogeochemical Cycles*, 23(4).
- 1105
1106 Van Mooy, B. A., Fredricks, H. F., Pedler, B. E., Dyhrman, S. T., Karl, D. M., Koblížek, M., ...
1107 & Webb, E. A. (2009). Phytoplankton in the ocean use non-phosphorus lipids in response to
1108 phosphorus scarcity. *Nature*, 458(7234), 69-72.
- 1109
1110 Vaultot, D., Gall, F. L., Marie, D., Guillou, L., & Partensky, F. (2004). The Roscoff Culture
1111 Collection (RCC): a collection dedicated to marine picoplankton. *Nova Hedwigia*, 79(1-2), 49-
1112 70.
- 1113
1114 Wang, W. L., Moore, J. K., Martiny, A. C., & Primeau, F. W. (2019). Convergent estimates of
1115 marine nitrogen fixation. *Nature*, 566(7743), 205-211.
- 1116
1117 Weber, T. S., & Deutsch, C. (2010). Ocean nutrient ratios governed by plankton
1118 biogeography. *Nature*, 467(7315), 550.
- 1119

- 1120 Westberry, T., Behrenfeld, M. J., Siegel, D. A., & Boss, E. (2008). Carbon-based primary
1121 productivity modeling with vertically resolved photoacclimation. *Global Biogeochemical*
1122 *Cycles*, 22(2).
1123
- 1124 Williams, R. G., & Follows, M. J. (1998). The Ekman transfer of nutrients and maintenance of
1125 new production over the North Atlantic. *Deep Sea Research Part I: Oceanographic Research*
1126 *Papers*, 45(2-3), 461-489.
1127
- 1128 Wilson, J. D., Andrews, O., Katavouta, A., de Melo Virissimo, F., Death, R. M., Adloff, M., ... &
1129 Ying, R. (2022). The biological carbon pump in CMIP6 models: 21st century trends and
1130 uncertainties. *Proceedings of the National Academy of Sciences*, 119(29), e2204369119.
1131
- 1132 Yamamoto, A., Palter, J. B., Dufour, C. O., Griffies, S. M., Bianchi, D., Claret, M., ... &
1133 Galbraith, E. D. (2018). Roles of the Ocean Mesoscale in the Horizontal Supply of Mass, Heat,
1134 Carbon, and Nutrients to the Northern Hemisphere Subtropical Gyres. *Journal of Geophysical*
1135 *Research: Oceans*, 123(10), 7016-7036.