

1 **Complexity in Biogeochemical Models: Consequences** 2 **for the Biological Carbon Pump**

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14 15 **Abstract**

16
17 Ocean biogeochemical models underpin projections of future marine ecosystem change, including
18 anticipated shifts in the biological carbon pump (BCP) and broader biogeochemical cycles.
19 However, their outputs remain highly sensitive to model complexity and parameterisation choices.
20 Here, we evaluate five configurations of the Pelagic Interaction Scheme for Carbon and Ecosystem
21 Studies (PISCES) to quantify intramodel variability in net primary productivity (NPP), carbon
22 export (C_{exp}), and export efficiency (e-ratio) over the 21st century under the high emissions RCP8.5
23 scenario. The tested PISCES configurations differed from the standard model through distinct
24 modifications to phytoplankton growth processes, but are forced by identical physical variables,
25 representing an ensemble opportunity. All configurations resolve NPP and C_{exp} within the range of
26 remote-sensing variability. The more complex Quota-based configurations produce 15-21 (10-18) Pg
27 C yr^{-1} more NPP than the simpler Monod-quota models in the reference (future) period, but this
28 increase, driven by elevated small phytoplankton biomass, does not enhance C_{exp} , yielding lower
29 e-ratios (0.14-0.17) than in the Monod-quota configurations (~0.25). The introduction of a
30 picophytoplankton functional type (PFT) emerges as one of the most influential parameterisation
31 choices. It drives opposing future NPP responses between 30-60° N/S, an increase in the
32 Monod-quota configurations versus a decline in the Quota-based ones, as well as contrasting
33 latitudinal trends in C_{exp} within the same region. Other parameterisations, such as a low-iron scheme,
34 an added diazotroph PFT, and explicit manganese cycling, exert more modest, regionally confined
35 effects under high emissions scenarios, influencing NPP and C_{exp} primarily at biome scales rather
36 than driving large-scale divergence in model behaviour.

37 38 **Plain language summary**

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40 We use five different versions of a biogeochemical model to show that how phytoplankton growth
41 processes are represented strongly shapes projections of future ocean productivity and carbon
42 export. Added model complexity does not have a uniform global effect as some new processes
43 mainly influence specific ocean regions, while others, such as an additional small phytoplankton
44 type, lead to large intramodel differences in future trends and latitudinal patterns of productivity and
45 carbon export.

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47 Key words: biogeochemical modelling, parameterisations, biological carbon pump, export

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51 1. Introduction

52
53 The biological carbon pump (BCP) plays a critical role in regulating Earth's climate by facilitating
54 the vertical transport of carbon from the surface to the deep ocean, thereby helping to remove
55 atmospheric CO₂ on centennial to millennial timescales (Falkowski et al., 1998, 2000; Buesseler et
56 al., 2007; Visser, 2025). Since pre-industrial times (~280 ppm), global atmospheric CO₂
57 concentrations have risen by 51%, reaching 419 ppm as of 2023 (Friedlingstein et al., 2023). This
58 increase has contributed to a ~1.5 °C rise in average global surface temperatures, with the previous
59 decade (2014-2024) marking the warmest on record (Ripple et al., 2024; WMO, 2025). The ocean
60 has absorbed 20-30% of anthropogenic CO₂ emissions since the mid-1980s (Sabine et al., 2004;
61 Bindoff et al., 2019), equivalent to 2.1–2.4 Pg C yr⁻¹ (DeVries et al., 2023). Stand-alone ocean model
62 studies suggest that, at equilibrium, BCP-mediated processes result in baseline atmospheric CO₂
63 concentrations being 150-200 ppm lower than they would be otherwise in their absence
64 (Maier-Reimer et al., 1996; Falkowski et al., 2000). A fully interactive Earth System Model (ESM)
65 refines this estimate, showing a 163 ppm increase in pre-industrial CO₂ when marine ecosystems are
66 removed (Tjiputra et al., 2025). The BCP therefore represents a substantial ecosystem service,
67 valued at \$0.8-1.1 trillion per year globally (Berzaghi et al., 2025). Understanding how the
68 biological processes that underpin the BCP, and its efficiency, will respond to climate change
69 remains an important and active area of research (Jin et al., 2020).

70
71 Through air-sea gas exchange, atmospheric CO₂ dissolves into the surface ocean, increasing the
72 dissolved inorganic carbon (DIC) pool. In the ocean, this DIC is absorbed and sequestered through
73 two mechanisms, the solubility pump and BCP. The solubility pump is driven by the combination of
74 thermodynamic and physical processes that slowly transport DIC from the surface ocean into the
75 interior via mode and deep water formation. It is the dominant mechanism for the uptake and
76 transport of anthropogenic CO₂ from the surface ocean to below the mixed layer (Bindoff et al.,
77 2019). The BCP further facilitates this vertical transport of carbon through the export of particulate
78 organic carbon (POC), synthesised via phytoplankton net primary productivity (NPP) in the sunlit
79 surface ocean. The subsequent sinking and export (C_{exp}) of POC out of the euphotic zone and into
80 the deep ocean (> 1000 m) contributes to the long-term removal of carbon on timescales of hundreds
81 to thousands of years (Falkowski et al., 1998, 2000; Buesseler et al., 2007; Visser, 2025).
82 Phytoplankton photosynthesis lowers the partial pressure of CO₂ in the surface ocean while export
83 production sustains the vertical gradients in DIC necessary to promote the absorption of CO₂ from
84 the atmosphere. Therefore, the BCP emerges as a critical, climate-relevant pathway in the ocean's
85 role as a long-term carbon sink (Falkowski et al., 2000; Sigman and Boyle, 2000).

86
87 In the upper ocean, most of the produced POC is rapidly remineralised, with only a small fraction
88 (~20%) being exported below 100 m (Falkowski et al., 2000; Laws et al., 2000; Ducklow et al.,
89 2001; Henson et al., 2012; Siegel et al., 2014; Nowicki et al., 2022). The efficiency of the BCP,
90 commonly denoted as the e-ratio ($= C_{\text{exp}}/\text{NPP}$), principally determines how much fixed carbon is
91 exported from the surface ocean to depth, indirectly influencing the long-term sequestration of
92 atmospheric CO₂. A consensus emerging from multi-model intercomparison studies is that global
93 warming will lead to higher sea surface temperatures (SSTs), increased stratification, ocean
94 acidification, and reduced oxygen solubility by the end of the 21st century (Steinacher et al., 2010;
95 Bopp et al., 2013; Bindoff et al., 2019; Kwiatkowski et al., 2020). In response to these changing
96 physical environmental conditions, marine ecosystems (Frémont et al., 2022) and phytoplankton
97 community composition (Bopp et al., 2005; Basu and Mackey, 2018; Tréguer et al., 2018; Benedetti
98 et al., 2021; Henson et al., 2021; Fisher et al., 2025) are expected to be impacted, which will have
99 consequences for ocean productivity and export production.

100

101 Capturing the complexity of the BCP remains a major challenge in ESMs (Doney et al. 2024).
102 Across successive generations of Carbon Model Intercomparison Project(s) (CMIP), there is
103 substantial intermodel variability in projected 21st century NPP and C_{exp} (Bopp et al., 2013;
104 Laufkötter et al., 2015, 2016; Kwiatkowski et al., 2020; Tagliabue et al., 2021; Wilson et al., 2022),
105 reflecting large differences in how models represent key biogeochemical processes and marine
106 ecosystem complexity (Séférian et al., 2020; Henson et al., 2022). Under the high-emissions
107 scenario SSP5-8.5, CMIP6 models project export production to change by -41% to +1.8% relative to
108 the historical period (Henson et al., 2022) and relative to present-day conditions, global NPP is
109 projected to decline by 1.76%, with a model standard deviation of 8.06% (Tagliabue et al., 2021).
110 Furthermore, future declines in NPP are likely underestimated within the CMIP6 ensemble,
111 considering their contemporary trends relative to remote-sensing (Ryan-Keogh et al., 2025).

112
113 Within the CMIP ensemble, a wide range of biogeochemical models is represented (e.g. BEC –
114 Moore et al., 2001, 2004; BFM – Vichi et al., 2007; PISCES – Aumont et al., 2015; REcoM2 –
115 Hauck et al., 2013; TOPAZ – Dunne et al., 2012), each differing in its complexity and
116 parameterisation of key biogeochemical processes. Although model intercomparison projects have
117 provided valuable insights into the global BCP, it remains unclear how differences in these
118 biogeochemical parameterisations, and complexity thereof, contribute to the divergence among
119 CMIP models in their projections of the BCP over the 21st century. Most model intercomparison
120 studies evaluate different architectures against common criteria to identify model shortcomings and
121 ensemble-wide patterns (Fennel et al., 2022). However, pinpointing sources of divergence and the
122 role of individual parameterisations is challenging within this context. An alternative is to compare
123 different parameterisations within the same biogeochemical model under identical physical forcing,
124 enabling variability arising solely from biogeochemical differences to be isolated.

125
126 This study employs the PISCES ocean biogeochemical model (Aumont et al., 2015) in a suite of
127 distinct configurations under high emissions RCP8.5 scenario to isolate how differences in
128 biogeochemical parameterisations and complexity drive variability in the BCP over the 21st century.
129 The methodology details the various PISCES configurations and their nuances while the results are
130 presented in two parts. In the first, we compare present-day PISCES outputs with remote-sensing
131 data to evaluate whether variations in biogeochemical parameterisations and complexity lead to
132 discernible differences in NPP and export production at global and biome scales. The second
133 examines how these variables evolve between present/reference (1986–2005) and future
134 (2091–2100) projections, highlighting how differences in top-down processes propagate through
135 NPP and C_{exp} . Ultimately, the study identifies key biogeochemical parameterisations that strongly
136 shape ecosystem dynamics, driving differences in NPP and export production, and contributing to
137 intramodel variability in projections of the BCP.

138 139 **2. Methodology**

140 141 *2.1 PISCES configurations*

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143 Tab. (1) presents a summary of the five PISCES configurations used in this study, which differ
144 primarily in their parameterisation of phytoplankton growth processes. The standard PISCES (PST)
145 model of Aumont et al. (2015) served as the foundation for all configurations. The PST model
146 simulates the lower trophic levels of marine ecosystems and resolves the biogeochemical cycles of
147 carbon and the main nutrients of P, N, Si and Fe. The model has four living compartments, two
148 phytoplankton functional types (PFTs; diatoms and nanophytoplankton) and two zooplankton size
149 classes (microzooplankton and mesozooplankton). Particulate detritus, produced through
150 phytoplankton–zooplankton–nutrient interactions, is partitioned into small and large particles. Both

size classes arise from multiple processes, including zooplankton grazing, phytoplankton and zooplankton mortality, and aggregation. However, their dominant sources differ as small particles are primarily linked to nanophytoplankton–microzooplankton interactions, whereas large particles are mainly associated with those of diatom-mesozooplankton. The PST model employs a hybrid of Monod-quota formulations in representing the cycling of major nutrients. Phytoplankton C:N:P stoichiometry is fixed, with N and P limitations governed by a Monod parameterisation. As a result, growth rates follow a rectangular hyperbolic function of the limiting external nutrient concentration (Monod, 1949; Flynn, 2003). In contrast, Fe limitation is represented with a quota-based approach (Aumont et al., 2015), where growth depends on the internal nutrient quota of a cell, which itself is regulated by the external nutrient concentration (Droop, 1968).

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162 Table 1: List of PISCES configurations

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Configuration name	Short name	Nutrients	Phytoplankton types	Phytoplankton growth	Additional parameterisations relative to PST	References
PISCES standard	PST	P, N, Fe, Si	Nano-, diatom	Monod & quota (Fe)	Standard	Aumont et al. (2015); Tagliabue et al. (2020)
PISCES low-Fe	PSF	P, N, Fe, Si	Nano-, diatom	Monod & quota (Fe)	$\theta^{Fe,I}; \theta_{max}^{Fe,I}$ The biological ($\theta^{Fe,I}$) and maximum ($\theta_{max}^{Fe,I}$) iron quotas (umol Fe/mol C) for the two phytoplankton groups are adjusted for low iron conditions.	Tagliabue et al. (2020)
PISCES-QUOTA	P5Z	P, N, Fe, Si	Nano-, pico-, diatom	Quota	$f^n = 1 - \frac{Q_o^n}{Q^n}$ f^n is the effect of a given nutrient on phytoplankton growth rate, Q^n is the internal ratio of nutrient n to carbon biomass, and Q_o^n is the subsistence or minimum quota of the respective nutrients.	Kwiatkowski et al. (2018); Wrightson et al. (2022)
PISCES diazotroph (tricho)	P6Z	P, N, Fe, Si	Nano-, pico-, diatom, diazotroph	Quota	The addition of a diazotroph PFT to represent <i>Trichodesmium</i> . Thermal performance curves modulate diazotroph maximum growth rate and the elemental use efficiency (EUE) of P and Fe.	Wrightson et al. (2022)
PISCES Manganese	P5M	P, N, Fe, Mn, Zn, Si	Nano-, pico-, diatom	Quota	The inclusion of the biogeochemical Mn cycle and phytoplankton Mn limitation. The limiting nutrients for diatoms include: N, P, Si, Fe, Zn and Mn.	Anugerahanti and Tagliabue (2023, 2024)

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165 The PST and low-Fe PISCES (PSF) configurations are those described in Tagliabue et al. (2020).
166 The PSF configuration modified PST by adjusting biological and maximum iron quotas for
167 phytoplankton growth to better reflect low-iron conditions and their implications under climate
168 change. Iron availability plays a key role in regulating phytoplankton growth and global NPP
169 (Tagliabue et al., 2017); however, ESMs often show large uncertainties in representing the ocean
170 iron cycle and its effect on productivity (Tagliabue et al., 2016). Unlike PST and PSF, the
171 PISCES-QUOTA (P5Z) model allows for variable C:N:P stoichiometry (Kwiatkowski et al., 2018),

172 with growth exclusively governed by quota-based formulations (Tab. 1). P5Z resolves 39 prognostic
173 variables, compared to 24 in PST, and importantly includes three phytoplankton groups:
174 picophytoplankton, nanophytoplankton, and diatoms.

175
176 Wrightson et al. (2022) further developed the model by introducing an explicit diazotroph PFT
177 (*Crocospaera* and *Trichodesmium*), along with temperature-dependent nutrient uptake
178 parameterised via elemental use efficiencies (EUEs), resulting in the P6Z configuration. These
179 additions addressed a key limitation in P5Z, which represented nitrogen fixation as an implicit flux
180 of ammonia, preventing mechanistic investigation of diazotroph dynamics. Given that marine
181 nitrogen fixation plays a critical role in shaping the response of NPP to climate change (Wrightson
182 and Tagliabue, 2020; Bopp et al., 2022), explicitly resolving diazotrophs in P6Z allowed responses
183 to environmental drivers, especially rising ocean temperatures, to be investigated. Preliminary work
184 conducted in this study showed little difference in global C_{exp} or NPP patterns across the various P6Z
185 versions in Wrightson et al. (2022). Therefore, in this study, we used only the configuration that
186 included temperature dependent EUEs for Fe and P for the generic N-fixing PFT (Tab. 1).

187
188 Anugerahanti and Tagliabue (2024) built upon the base P5Z model by incorporating manganese
189 (Mn), following Hawco et al. (2022), which included its role in limiting phytoplankton productivity
190 in the Southern Ocean, where observations show Mn as either a primary or co-limiting micronutrient
191 alongside Fe (Wu et al., 2019; Browning et al., 2021; Hawco et al., 2022). The resulting P5M
192 configuration explicitly simulates coupled Mn and zinc (Zn) cycles (Richon and Tagliabue, 2021),
193 including biological uptake, scavenging, and regeneration for Mn and Zn.

194
195 The various PISCES configurations (Tab. 1) were identically forced with physical outputs from the
196 [IPSL-CM5A-LR](#) climate model on the ORCA tripolar grid with 2° horizontal spatial resolution. Two
197 model runs were conducted for each configuration. The first simulation was forced by outputs
198 derived from historical (1851-2005) climate forcing and the second with the high emission
199 Representative Concentration Pathway 8.5 (RCP8.5) scenario (2006-2100). For this study, we
200 conducted our analysis of the BCP using averaged model outputs over two time windows, the
201 ‘reference’ (1986-2005) and ‘future’ (2091-2100).

202 203 2.2 Remote-sensing products

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205 The five PISCES configurations were assessed for the reference period against an ensemble of
206 satellite-derived NPP and C_{exp} products, averaged over 1998-2005. This period was chosen to align
207 with the model simulations while accommodating the earliest availability of satellite observations.
208 **Although the averaging periods differ between the model outputs and remote-sensing products, the**
209 **use of multi-year means reduces the influence of interannual variability and allows for a consistent**
210 **comparison of large-scale patterns.** Model outputs and remote-sensing products were compared
211 globally as well as across RECCAP2 biomes (Fig. S1) by ocean basin (Fay and McKinley, 2014;
212 Doney et al., 2024).

213
214 Several algorithms have been described to estimate primary production based on ocean-colour
215 remote-sensing observations, each differing in complexity and formulation and exhibiting
216 substantial variability across regions such as the subtropical gyres and the Southern Ocean
217 (Ryan-Keogh et al., 2023; Westberry et al., 2023). Common algorithms include the: Vertically
218 Generalised Production Model (VPGM), Carbon-based Production Model (CbPM), and Carbon
219 Absorption Fluorescence Euphotic-resolving (CAFE) model. This study used six different NPP
220 datasets (Fig. S2), all of which are derived from ESA Ocean Colour Climate Change Initiative
221 (OC-CCI) remotely-sensed chlorophyll concentrations (Sathyendranath et al., 2019). Five were from

222 the regular 25 km gridded NPP datasets at 8-day resolution of Ryan-Keogh et al. (2023), who
223 considered the Eppley-VGPM (Eppley, 1972), Behrenfeld-VGPM (Behrenfeld and Falkowski,
224 1997), Behrenfeld-CbPM (Behrenfeld et al., 2005), Westberry-CbPM (Westberry et al., 2008), and
225 the Silsbe-CAFE model (Silsbe et al., 2016). The sixth NPP dataset was the 9 km monthly resolution
226 product from the Biological Pump and Carbon Exchange Processes (BICEP) project (Kulk et al.,
227 2020, 2021) which used a modified version of the base algorithm of Longhurst et al. (1995).

228
229 Similar to NPP, a number of algorithms exist to compute C_{exp} from remotely-sensed observations
230 (Jönsson et al., 2023). Export production can be related to NPP through a simple scaling factor
231 (Eppley and Peterson, 1979) or include multiple relationships, such as mixed-layer depth (MLD),
232 chlorophyll and SST (Jönsson et al., 2023). For simplicity, we restricted our analysis to export
233 algorithms that estimate C_{exp} from empirical relationships between NPP and SST. We applied five
234 commonly used formulations (Fig. S3, Tab. S1): Laws et al. (2000), Henson et al. (2011), two
235 equations from Laws et al. (2011), and Li and Cassar (2016). These algorithms have been evaluated
236 against *in situ* observations (e.g. Dunne et al., 2005; Mouw et al., 2016; Bisson et al., 2018), with
237 reported skill scores of $R^2 = 0.64-0.70$ (Li and Cassar, 2016; Jönsson et al., 2023). It is important to
238 note that they estimate export at different depth horizons such as Henson et al. (2011) at 100 m and
239 Li and Cassar (2016) at the climatological MLD, meaning biases in subtropical gyres and polar
240 regions may differ slightly across algorithms. We used SST from the 0.05° Operational Sea Surface
241 Temperature and Sea Ice Analysis (OSTIA) product, which is a Level 4 product that combines
242 multi-sensor satellite and *in situ* data (Good et al., 2020). From the daily fields for 1998-2005,
243 monthly SST averages were computed for OSTIA. Thereafter, C_{exp} was computed using the five
244 algorithms applied to the monthly SST and six NPP fields (interpolated to the 2° model grid),
245 resulting in 30 individual C_{exp} estimates. For each algorithm, outputs from the six datasets were then
246 averaged to produce a single representative C_{exp} field, yielding five ensemble algorithm outputs (Fig.
247 S3).

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249 3. Results

250

251 3.1 Model and remote-sensing variability

252

253 At both the global (Tab. 2) and biome scales (Fig. 1), differences in the complexity of phytoplankton
254 processes and parameterisations (Tab. 1) among the five PISCES configurations leads to substantial
255 intramodel variability in both the reference and future states (Figs. 2-3), particularly for NPP. For the
256 reference period (Tab. 2), the coefficient of variation (CV) for global NPP across the five
257 configurations is ~20%, indicating substantial divergence among models.

258

259 The two Monod-quota configurations, PST and PSF, simulate 15-21 Pg C yr⁻¹ less NPP than the
260 purely Quota-based configurations (P5Z, P6Z and P5M). In contrast, the relative range of C_{exp} is
261 much lower (CV ≈ 5%), showing export production is far more consistent across configurations and
262 reflecting the fact that no direct adjustments were made to the equations or parameterisations
263 explicitly controlling carbon export across the different configurations. Variability arises as an
264 indirect outcome, emerging primarily from upstream differences in primary productivity patterns,
265 which cascade down to influence export. Collectively, this results in the Monod-quota configurations
266 resolving a more efficient BCP than the purely Quota-based ones. However, despite these intramodel
267 differences, all the PISCES configurations largely fall within the range of remote-sensing estimates
268 for both NPP and C_{exp} (Tab. 2). Compared to the CMIP5 ensemble, NPP for the PISCES
269 configurations lies within the range of variability, whereas C_{exp} exceeds the upper bound.

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272 Table 2: Reference and future projections of NPP, C_{exp} , and e-ratio for the five PISCES configurations. C_{exp}
 273 is defined as the mass of POC sinking through the 100 m depth horizon, consistent with CMIP conventions
 274 (Palevsky and Doney, 2018). The e-ratio (C_{exp}/NPP) reflects the efficiency of the BCP as governed by
 275 particle formation and sinking processes. NPP is integrated over the upper 100 m when calculating the
 276 e-ratio. NPP and C_{exp} are reported as globally integrated values ($Pg\ C\ yr^{-1}$), and the e-ratio as an
 277 area-weighted global mean. Relative changes (%) from the reference to future period are shown, alongside
 278 CMIP5 estimates from Fu et al. (2016) and remote-sensing (RMT) values from this study's ensemble and
 279 Doney et al. (2024).

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	Reference			Future			Relative change		
	NPP	Cexp	e-ratio	NPP	Cexp	e-ratio	NPP	Cexp	e-ratio
PST	40.78	7.92	0.26	39.44	7.03	0.26	-3.29	-11.23	~ 0
PSF	42.3	7.85	0.24	40.93	6.97	0.24	-3.24	-11.21	~ 0
P5Z	61.15	6.91	0.14	54.92	5.88	0.14	-10.19	-14.91	~ 0
P6Z	63.29	7.12	0.14	58.69	6.13	0.13	-7.27	-13.90	-7.14
P5M	57.11	7.88	0.17	52.81	6.82	0.17	-7.53	-13.36	~ 0
Mean	52.93±10.64	7.54±0.48	0.19±0.057	49.36±8.65	6.57±0.53	0.19±0.059	-6.30±3.00	-12.94±1.65	-1.43±3.19
CMIP5 - Fu et al. (2016)	46.33±13.74	6.17±0.87	0.14±0.041	43.73±14.84	5.40±0.77	0.13±0.037	-6.55±4.19	-12.50±3.78	-6.33±3.64
RMT - study ensemble	55.99±9.95	10.43±3.74	-	-	-	-	-	-	-
RMT - Doney et al. (2024)	52.9±9.1	8.20±2.78	0.196±0.106	-	-	-	-	-	-

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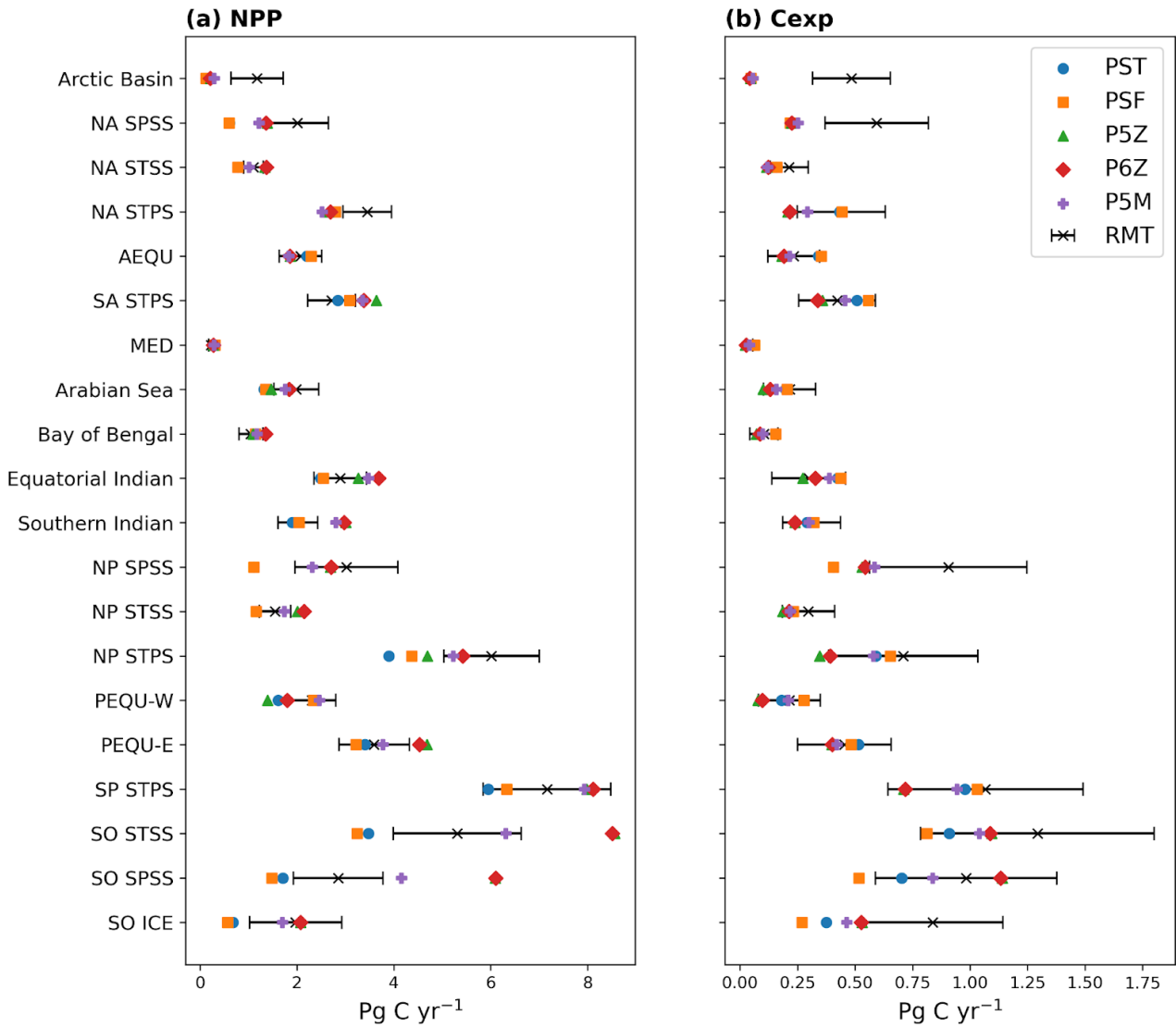
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At the biome scale (Fig. 1), no single configuration consistently reproduces all regions, with intramodel variability in NPP (Fig. 1a) and C_{exp} (Fig. 1b) varying considerably. A similar state of variability exists for remote-sensing derived estimates. The Southern Ocean shows the strongest intramodel variability ($CV \geq 30\%$; Fig. S4). P5Z and P6Z yield the highest NPP and C_{exp} , while the Monod-quota models give the lowest. P5M stands apart from both groups, with the inclusion of the manganese cycle dampening phytoplankton growth in this region, resulting in lower NPP than the other Quota-based configurations. This reduction in productivity propagates downstream, ultimately leading to lower C_{exp} .

In the equatorial and subtropical gyres, the Quota-based configurations simulate higher NPP, yet the simpler Monod-quota models produce slightly higher C_{exp} , indicating that greater primary production does not directly translate into greater export in these regions (see also Fig. 2). The inclusion of a diazotroph PFT in P6Z introduces regional differences relative to P5Z within these biomes, most notably in the South Atlantic and North Pacific subtropical gyres; however, C_{exp} remains broadly similar between the two configurations (Fig. 1b). The absence of a uniform NPP response to the added diazotroph group reflects basin-specific nutrient limitation regimes, particularly differences in Fe and P availability that constrain diazotroph growth across ocean basins (Wrightson et al., 2022). For PSF, the low-iron biological parameterisation results in slightly higher NPP in the equatorial biomes and subtropical gyres, but marginally lower productivity in the Southern Ocean compared to PST. This occurs because PSF prescribes smaller Fe:C quotas for phytoplankton, enabling growth under lower iron supply. As a result, productivity in low latitude biomes responds more strongly to assumptions about biological iron uptake, where Fe and N limitation play a larger role, whereas productivity in the Southern Ocean is less affected due to its already pervasive iron limitation (Tagliabue et al., 2020).



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 325 Figure 1: Model and remote-sensing (RMT) estimates of (a) NPP and (b) C_{exp} , integrated over each
 326 RECCAP2 biome (refer to Fig. S1). Black bars indicate ± 1 standard deviation across the remote-sensing
 327 ensemble.

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329 3.2 Future projections of the BCP

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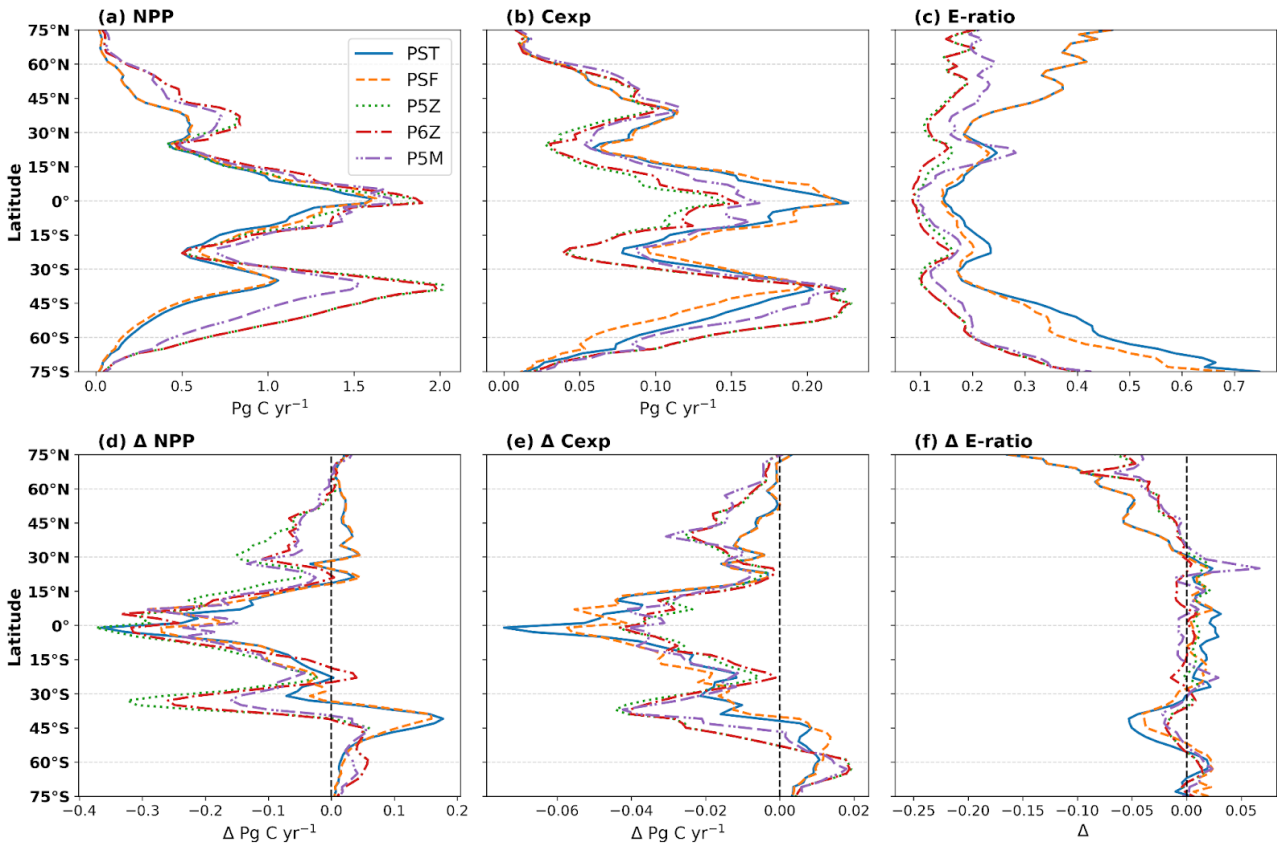
331 From Tab. (2), all configurations project future global declines in both NPP and C_{exp} by 2100, with
 332 NPP decreasing by $6.30 \pm 3.00\%$ and C_{exp} by $12.94 \pm 1.65\%$; however, the e-ratio remains largely
 333 unchanged. For NPP and C_{exp} , the largest absolute and relative declines are observed in the
 334 Quota-based configurations but all configurations fall within the variability of the CMIP5 ensemble
 335 (Tab. 2).

336

337 Fig. (2) expounds on the biome scale assessment in Fig. (1), presenting zonally integrated NPP and
 338 C_{exp} , and area-weighted e-ratios for the reference period, along with their projected future changes.
 339 For the reference period (Fig. 2a-c), all configurations reproduce the expected pattern of elevated
 340 NPP and C_{exp} in the equatorial region and at high latitudes, including the Southern Ocean and the
 341 subpolar to polar regions of the Northern Hemisphere, with lower values in the subtropical gyres.
 342 Differences arise mainly in magnitude, with the Quota-based configurations simulating higher NPP
 343 than the simpler Monod-quota ones (Fig. 2a); however, this does not translate into uniformly higher

344 C_{exp} (Fig. 2b), resulting in a less efficient BCP (Fig. 2c). Intramodel variability in C_{exp} is less than
 345 NPP, with PST and PSF producing slightly higher export production between $\sim 20^\circ$ N/S but notably
 346 lower C_{exp} than the Quota-based configurations in the Southern Ocean ($40\text{-}75^\circ$ S).

347
 348 For future projections (Fig. 2d-f), all configurations simulate declining NPP between 30° N/S (Fig.
 349 2d). Beyond this band, the models diverge. Around 45° S, PST and PSF show an increase in NPP of
 350 $\sim 25\%$, whereas the Quota-based configurations show only a 4-5% rise. North of 30° N, the
 351 Monod-quota configurations exhibit increasing NPP (from $\sim 1\%$ to 20% by 60° N), while the
 352 Quota-based configurations instead show a sharp decline of 15-25% at 30° N, which gradually
 353 weakens poleward. All configurations eventually project higher NPP in the northern polar region
 354 (Fig. 2d). In contrast, future changes in C_{exp} (Fig. 2e) follow a broadly consistent pattern across
 355 configurations, differing mainly in magnitude rather than trajectory. All configurations show
 356 declining export production over most latitudes, with a regional exception in the Southern Ocean,
 357 where C_{exp} increases. This increase occurs farther north ($\sim 45^\circ$ S) in PST and PSF, reflecting their
 358 distinct NPP response, while the Quota-based models show a similar feature centred farther south.
 359 North of 30° N, all configurations show declining C_{exp} , though the strength of the reduction varies
 360 Collectively, the e-ratio remains relatively stable across latitudes, with no clear model-specific
 361 pattern between 30° N/S (Fig. 2f). All models show a 10-20% decline in the e-ratio near 45° S, an
 362 increase of $\sim 5\text{-}10\%$ south of 60° S, and a consistent decrease north of 30° N (Fig. 2f).

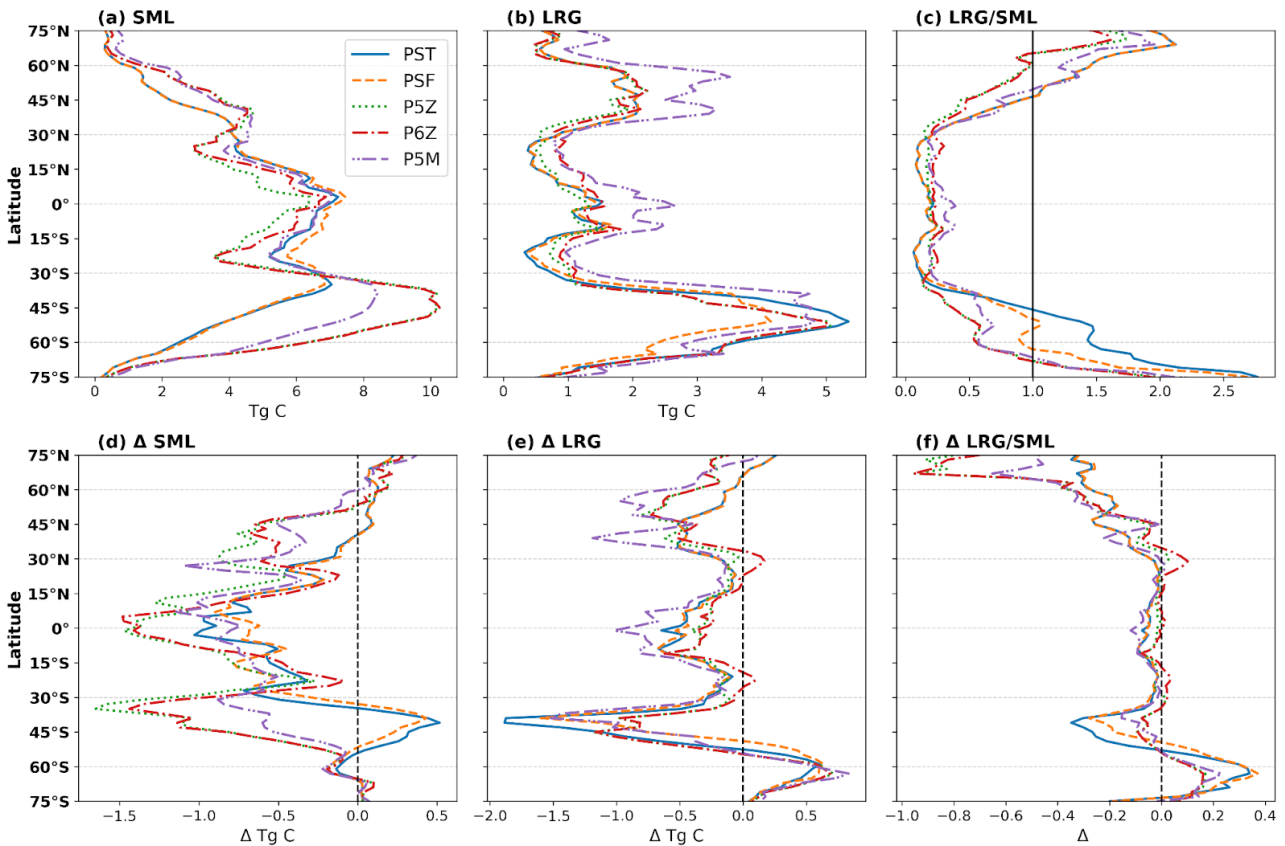


363
 364 Figure 2: Top row shows zonally integrated (a) NPP and (b) C_{exp} , and the area-weighted mean (c) e-ratio for
 365 the reference period. The lower row (d-f) shows the respective changes in the future relative to the reference
 366 period.

367 Intramodel variability in NPP, C_{exp} , and e-ratio across the reference and future periods reflects both
 368 the direct effects of differing phytoplankton parameterisations (Tab. 1) and the cascading, top-down
 369 consequences of these choices. To interpret the latitudinal patterns in Fig. (2), it is necessary to

370 examine how phytoplankton biomass responds within each configuration. Accordingly, Fig. (3)
 371 shows the reference and relative future changes in total phytoplankton biomass, grouped into small
 372 (SML) and large (LRG) phytoplankton to accommodate differences in PFT structure across
 373 configurations.

374
 375 For the reference period (Fig. 3a-c), the spatial patterns and intramodel differences in small (Fig. 3a)
 376 and large (Fig. 3b) phytoplankton biomass closely parallel those of NPP (Fig. 2a) and C_{exp} (Fig. 2b).
 377 These patterns are expected and stem from the differing ecological functions and environmental
 378 sensitivities of small versus large phytoplankton in the model. Small phytoplankton dominate most
 379 of the ocean (LRG/SML < 1; Fig. 3c) but contribute little to export because they remain in the
 380 surface layer, whereas large phytoplankton form larger, faster-sinking particles that
 381 disproportionately drive carbon export (Aumont et al., 2015). A striking feature is the substantially
 382 higher biomass of large phytoplankton (Fig. 3b) in P5M relative to the other configurations,
 383 particularly in the equatorial region and north of 30° N. Because P5M was specifically tuned to
 384 represent Mn and other co-limiting trace-metal effects in the Southern Ocean, its divergence
 385 elsewhere likely reflects model-specific tuning that produces unrealistic behaviour outside that
 386 region. This may also explain why P5M yields slightly higher global C_{exp} (Tab. 2) than the other
 387 Quota-based configurations.



388
 389 Figure 3: Top row shows zonally integrated (a) Small (SML) and (b) Large (LRG) phytoplankton biomass,
 390 and the area-weighted mean (c) LRG/SML ratio for the reference period. Across the different PISCES
 391 configurations, PST and PSF have two PFTs, whereas the Quota-based configurations incorporate three
 392 (P5Z and P5M) and four (P6Z). To enable a comparison of phytoplankton biomasses, PFTs were grouped
 393 into ‘small’ (nano-, pico- and N-fixers) and ‘large’ (diatoms) categories. The lower row (d-f) shows the
 394 respective changes in the future relative to the reference period.

395
 396 Responding to future changes in marine environmental conditions, small and large phytoplankton
 397 show global declines of $7.88 \pm 2.97\%$ and $14.24 \pm 1.82\%$, respectively by 2100. Across configurations,

398 the latitudinal patterns of future changes in small (Fig. 3d) and large (Fig. 3e) phytoplankton
399 biomass broadly follow those of NPP and C_{exp} (Fig. 2d, e). Intramodel divergence is most
400 pronounced for small phytoplankton (Fig. 3d). South of 30° S, PST and PSF show increasing small
401 phytoplankton biomass toward higher latitudes, whereas the Quota-based configurations simulate
402 the opposite trend. Around $\sim 40^{\circ}$ S this contrast is strongest, marking the clearest separation between
403 the two model frameworks. North of 30° N, the configurations also diverge, with opposing
404 latitudinal trends between 30 - 60° N. These differences likely stem from the contrasting
405 phytoplankton complexity (i.e. the number of PFTs) and growth formulations across the
406 Monod-quota and Quota-based configurations, which strongly shape how small phytoplankton, and
407 therefore NPP, respond to future environmental change. **This top-down interpretation is further
408 supported by the broadly consistent spatial patterns and projected changes in N and P inventories
409 across configurations (Fig. S5).**

410 Large phytoplankton show comparatively little intramodel variability (Fig. 3e), with all
411 configurations exhibiting similar spatial patterns and future changes, differing mainly in magnitude.
412 The largest deviations occur again in P5M outside the Southern Ocean, reflecting its anomalously
413 high large phytoplankton biomass in the reference state (Fig. 3b). Overall, the LRG/SML ratio is
414 projected to decline globally by $6.83 \pm 3.33\%$, with the largest absolute and relative changes
415 occurring for PST and PSF, especially near $\sim 45^{\circ}$ and 60° S (Fig. 3f). A declining ratio indicates a
416 shift towards proportionally more small phytoplankton at the global scale, although regional
417 exceptions occur, most notably in parts of the Southern Ocean, where large phytoplankton become
418 locally more dominant (Fig. 3f). Nevertheless, the concurrent global declines in both small and large
419 phytoplankton biomass ultimately reduces future NPP and C_{exp} .

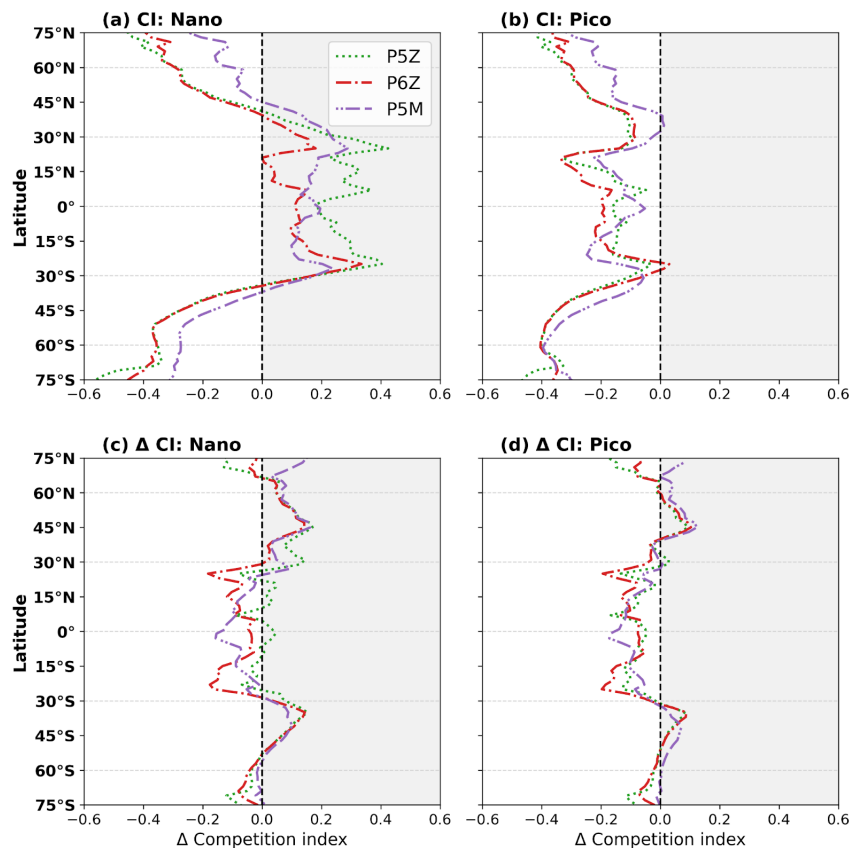
420 4. Discussion

421 4.1 *Differences in phytoplankton parameterisations driving intramodel variability*

422 Our results show that the more complex Quota-based configurations, which each include some
423 combination of additional PFTs, a more detailed growth formulation, and expanded nutrient cycling,
424 simulate a less efficient BCP than the simpler Monod-quota configurations for both the reference
425 and future periods. For the reference period, the added complexity across the five PISCES
426 configurations produces notable differences at both global (Tab. 2) and biome (Fig. 1) scales, most
427 clearly in NPP. Intramodel variability in C_{exp} is smaller and appears mainly as an indirect
428 consequence of differences in NPP rather than from explicit changes to export related
429 parameterisations. Despite these differences, all configurations reproduce broadly similar large-scale
430 patterns in NPP, C_{exp} , and the distribution of small and large phytoplankton for the reference period,
431 with intramodel differences arising in the magnitude of these respective fields.

432 The more complex Quota-based configurations simulate higher global NPP than the Monod-quota
433 configurations, but this increase does not translate uniformly into higher C_{exp} because the additional
434 productivity is carried by small phytoplankton, which enhance upper-ocean biomass but contribute
435 little to export. From Fig. (2b), export production is greater in PST and PSF between $\sim 20^{\circ}$ N/S,
436 whereas outside these latitudes, particularly in the Southern Ocean, C_{exp} is highest in the
437 Quota-based models. These contrasting, and in some regions contradictory, patterns in NPP and C_{exp}
438 behaviour for the reference period between the configurations likely arise from top-down controls
439 linked to the greater PFT complexity in the Quota-based configurations and its influence on
440 zooplankton dynamics. These interactions also likely underpin the intramodel differences seen in the
441 future projections of NPP and the BCP.

442 Between the standard model (Aumont et al., 2015) and PISCES-QUOTA, the two biggest updates
 443 are the representation of phytoplankton growth processes to use a quota-formulation and the addition
 444 of a dedicated picophytoplankton PFT (Kwiatkowski et al., 2018). Furthermore, the zooplankton
 445 feeding parameterisations are also adjusted. In the standard PST and PSF configurations,
 446 mesozooplankton feed on nanophytoplankton and diatoms, generating large sinking particles via
 447 faecal pellet production. In PISCES-QUOTA, however, picophytoplankton are grazed exclusively by
 448 microzooplankton rather than mesozooplankton. From this study, it is not possible to fully
 449 disentangle the respective contributions of the quota-based growth formulation and the inclusion of
 450 additional PFTs to variability in NPP and C_{exp} within the Quota-based configurations. The higher
 451 NPP simulated by these configurations (Tab. 2) is partly attributable to their explicit treatment of
 452 nitrogen assimilation costs as flexible stoichiometry reduces respiratory losses when ammonium
 453 (NH_4^+) is available. This then yields higher effective growth rates than in the Monod-quota
 454 configurations, particularly in low latitudes and during summer at high latitudes. However, NPP
 455 differences between the Monod-quota and Quota-based configurations remain modest in low
 456 latitudes (Fig. 2a), whereas in polar regions, a clearer association emerges between elevated small
 457 phytoplankton biomass and enhanced NPP in the Quota-based configurations. Kwiatkowski et al.
 458 (2018) concluded that accounting for variable phytoplankton stoichiometry has a limited impact on
 459 the global carbon cycle such that the added PFT complexity is likely the primary parameterisation
 460 driving the divergence in behaviour between the Monod-quota and Quota-based configurations in
 461 our study.



462
 463 Figure 4: The competition index (CI) quantifies where the standard nanophytoplankton PFT (mean of PST
 464 and PSF) outperforms the nano- and picophytoplankton PFTs of the Quota-based configurations. CI is
 465 computed from the mean realised growth rates (μ) over the upper 100 m and defined as $CI = (\mu_1 - \mu_2) / (|\mu_1| + |\mu_2|)$,
 466 where μ_1 is the mean Monod-quota nano- PFT and μ_2 is either the nano- or picophytoplankton PFT
 467 from the Quota-based configurations. Positive values showcase regions where the nanophytoplankton PFT
 468 of the Monod-quota configurations outcompetes the nano- and/or picophytoplankton PFT of the
 469 Quota-based models. Panels show CI for the reference (a, b) period and future shifts (c, d).

470 The competition index (CI; Fig. 4a) shows that the single small nanophytoplankton PFT in the
471 Monod-quota configurations outcompetes the nanophytoplankton PFT in the Quota-based
472 configurations across the equatorial and lower-latitude regions, although it is consistently
473 outcompeted by the picophytoplankton group across all regions (Fig. 4b). Splitting the small
474 phytoplankton PFT of the standard model into two distinct PFTs in PISCES-QUOTA allows for
475 greater ecosystem complexity and differentiation across environmental niches. For the open-ocean
476 regions of the lower latitudes (0-30° N/S), picophytoplankton dominate, comprising 50-70% of total
477 phytoplankton biomass for the reference period (Fig. S6). Consequently, relative to the Monod-quota
478 configurations, nanophytoplankton biomass is smaller in the Quota-based configurations, but this
479 reduction is offset by picophytoplankton biomass, leading to similar overall NPP in the region.
480 However, because mesozooplankton feed exclusively on nanophytoplankton and diatoms, the
481 reduced nanophytoplankton biomass in the Quota-based configurations limits their food supply. This
482 leads to lower mesozooplankton grazing rates (Fig. S7d) and a reduced production of large sinking
483 particles. This mechanistically explains why export production is higher in the equatorial region in
484 PST and PSF compared with the Quota-based configurations (Fig. 2b).

485 Outside of 30° N/S, the CI shows a shift in competitive behaviour, with the nanophytoplankton PFT
486 for the Quota-based configurations now outcompeting the single nanophytoplankton PFT of the
487 Monod-quota models (Fig. 4a). Because picophytoplankton already outcompete the Monod-quota
488 nano- PFT everywhere (Fig. 4b), this means that small phytoplankton as a whole can proliferate
489 more effectively in the Quota-based configurations beyond the tropics. This explains the higher
490 small phytoplankton biomass (Fig. 3a) and elevated NPP (Fig. 2a) in these regions. This pattern is
491 strongest in the Southern Ocean, where the Quota-based configurations show substantially higher
492 NPP and export production compared to PST and PSF. The elevated small phytoplankton biomass
493 fuels enhanced micro- and mesozooplankton grazing rates (Fig. S7c, d), enhancing export
494 production in the Southern Ocean (Fig. 2b) and this mechanism is consistent with the findings of
495 Laufkötter et al. (2013).

496 The mechanistic patterns identified in the reference period provide a critical foundation for
497 understanding why certain regions show stronger divergence than others in the future projections of
498 NPP and the BCP across the PISCES configurations. By 2100, our results show global NPP and C_{exp}
499 are projected to decline by $6.30 \pm 3.00\%$ and $12.94 \pm 1.65\%$, respectively, accompanied by a shift
500 towards dominance of small phytoplankton species. **These findings align with previous modelling
501 studies (Bindoff et al., 2019), and fall within the variability of the CMIP5 ensemble (Bopp et al.,
502 2013; Fu et al., 2016). The comparable magnitude of variability in NPP and C_{exp} (Tab. 2) indicates
503 that differences in parameterisations among the selected PISCES configurations can generate a
504 spread in results of similar order to that found across CMIP5 models (Séférian et al., 2020). While
505 this does not imply that the present ensemble captures the full diversity of CMIP model structural
506 differences, it nevertheless highlights the sensitivity of biogeochemical outputs to relatively subtle
507 differences in the representation of phytoplankton growth processes and ecosystem complexity
508 which do contribute to intermodel variability.**

509
510 **Global future reductions in NPP and C_{exp} likely reflect reduced nutrient supply to the surface
511 associated with enhanced stratification and increased interior residence times (Dunne, 2023);
512 however, the e-ratio shows little to no significant change for the five PISCES configurations,
513 indicating that BCP efficiency is maintained relative to the reference period.** In Fig. (4c, d), the CI
514 shows little change between the reference and future periods, indicating that the relative competitive
515 balance among PFTs remains largely unchanged. Consequently, the Quota-based configurations
516 continue to sustain higher absolute NPP in the future (Tab. 2) than the Monod-quota configurations.
517 However, they also maintain lower C_{exp} , reflecting persistent regional differences in
518 phytoplankton-zooplankton interactions (Fig. S7) that stem from the contrasting levels of PFT

519 complexity, particularly within the small phytoplankton community, across the PISCES
520 configurations.

521
522 Intramodel variability is greatest between 30-60° N/S for future projections of NPP and C_{exp} . Small
523 phytoplankton biomass increases from 30° S to a peak near ~40° S in the Monod-quota
524 configurations before weakening toward 60° S, whereas the Quota-based configurations show the
525 opposite latitudinal pattern, with both model families converging at ~60° S (Fig. 3d). NPP responds
526 accordingly, though the impact on C_{exp} is more muted. Under future changes in marine
527 environmental conditions, such as warmer SSTs and enhanced stratification, the simpler
528 Monod-quota models project an increase in small phytoplankton biomass, whereas the Quota-based
529 configurations project a decline in this region. This divergence arises from the added phytoplankton
530 complexity in the Quota-based configurations. By explicitly representing picophytoplankton, P5Z,
531 P6Z, and P5M resolve a broader range of ecological niches. As marine environmental conditions
532 shift, the response of picophytoplankton dominates the overall behaviour of the small phytoplankton
533 community, leading to a decrease in biomass (Fig. 3d). In contrast, the single nanophytoplankton
534 PFT in the Monod-quota models, being more generalised and arguably over-parameterised, responds
535 differently and shows an increase for 30-60° S. A similar pattern emerges in the Northern
536 Hemisphere, where both model families project an overall decline in small phytoplankton biomass
537 but the latitude-dependent trends differ (Fig. 3d). Again, this reflects the distinct niche sensitivities
538 of the picophytoplankton PFT in the Quota-based configurations versus the more simplified single
539 nanophytoplankton PFT present in the Monod-quota configurations.

540

541 4.2 *Complexity and the persistence of uncertainty*

542
543 For both the reference and future periods, our results show that differences in biogeochemical
544 parameterisations constitute a major axis of divergence across the five PISCES configurations.
545 Importantly, not all parameterisations exert influence at the same scale. Some, such as the
546 introduction of the picophytoplankton PFT in PISCES-QUOTA, generates substantial shifts in
547 global NPP, which in turn leads to moderate but consistent differences in C_{exp} , for both the reference
548 and future periods relative to the Monod-quota configurations. Other parameterisations exert more
549 limited effects, such as low-iron parameterisation in PSF, added diazotroph PFT in P6Z, and explicit
550 manganese cycling for P5M, impacting phytoplankton growth rates or expanding phytoplankton
551 complexity in ways that manifest significant differences in NPP and C_{exp} behaviour at the biome
552 scale rather than globally. Together, our findings highlight that certain parameterisations
553 fundamentally reshape model behaviour, whereas others provide more subtle or regionally confined
554 refinements.

555
556 Added complexity in biogeochemical models is intended to improve the representation of marine
557 ecosystem functioning. However, the current uncertainty ranges in remote-sensing estimates of
558 global NPP and C_{exp} remain extremely large at 46.3% and 109.8%, respectively (Doney et al., 2024).
559 As shown in Fig. (1), all five PISCES configurations fall well within the spectrum of remote-sensing
560 estimates at the biome scale such that understanding whether the added complexity is improving
561 representation of the marine system is difficult to discern. **Although not the focus of the study, a skill
562 assessment of the different configurations relative to the ensemble mean of the various
563 remote-sensing NPP and C_{exp} datasets showed increased complexity may improve global NPP
564 magnitude without improving, and possibly worsening, spatial pattern fidelity, while for C_{exp} , there
565 is little difference in skill across configurations (Fig. S8).** This raises an important point, one that is
566 actively discussed within the modelling community, determining the optimal balance of model
567 complexity, and the most effective combination of parameterisations, when utilising biogeochemical
568 models for future projections of the carbon cycle and the BCP.

569 One may argue that more complex biogeochemical models permit more sources of error and degrees
570 of freedom; however, Flynn (2010) makes the bold statement that models that ignore key
571 biogeochemical processes are inherently dysfunctional. Especially for future projections beyond the
572 extent of observations as the absence of process driven biogeochemical feedback will lead to
573 compensating errors and large future uncertainties. Furthermore, one also needs to consider the
574 computational expenses that accompany greater complexity as PISCES-QUOTA is far more costly
575 to operate than the simpler standard model (Kwiatkowski et al., 2018). These *quid pro quos* preclude
576 a single ‘best’ configuration, but they illuminate the key considerations when choosing among
577 PISCES configurations of differing complexity. Finally, we tested these different configurations
578 under the very strong climate forcing of the RCP8.5 scenario. Results may be different under weaker
579 levels of global warming currently expected or strongly mitigated scenarios.

580

581 **5. Conclusion**

582

583 In this study, we used five distinct PISCES configurations of varying complexity that differ in their
584 number of PFTs, growth formulations, imposed nutrient limitations, and the representation of
585 nutrient cycling. We showed that these parameterisation differences alone can generate substantial
586 divergence and intramodel variability under the high emissions RCP8.5 scenario in projections of
587 the BCP, with NPP responding more sensitively than C_{exp} . Yet, despite these contrasts, all
588 configurations produce for the reference period NPP and C_{exp} magnitudes that fall within the broad
589 range of remote-sensing estimates, making it difficult to assess whether added complexity
590 unequivocally improves model realism. Moreover, the spread in future NPP and C_{exp} projections
591 across the PISCES configurations is comparable to that seen in the CMIP5 ensemble, suggesting that
592 relatively subtle differences in phytoplankton processes and their parameterisation may underpin a
593 substantial fraction of the intermodel variability in ESM projections.

594

595 The introduction of a picophytoplankton PFT in PISCES-QUOTA, and its presence in the other
596 Quota-based configurations, emerges as one of the most influential parameterisation choices,
597 producing higher global NPP yet slightly lower C_{exp} , and driving opposing future NPP responses and
598 latitudinal trends in C_{exp} between 30-60° N/S compared with the Monod-quota configurations. Other
599 parameterisations, such as the low-iron scheme in PSF, the added diazotroph PFT in P6Z, and
600 explicit manganese cycling in P5M, exert more modest, regionally confined effects, influencing NPP
601 and C_{exp} primarily at biome scales rather than driving large-scale divergence in model behaviour.
602 Finding that differing parameterisations produce contrasting model outputs is unsurprising, but the
603 nature of our study allowed us to identify which parameterisations generate substantial intramodel
604 variability and which exert only minimal influence. The discrete number of configurations inevitably
605 constrains our conclusions to parameterisations centred on phytoplankton processes. Nevertheless,
606 within the PISCES and broader ESM modelling community, this study represents a novel
607 contribution, highlighting how different configurations of a biogeochemical model behave in
608 projecting contemporary and future states of NPP and C_{exp} .

609

610

611 **Code availability**

612

613 The code to do the calculations and generate the main manuscript figures can be found at
614 https://github.com/RGRJON002/Complexity_in_Biogeochemical_Models_BCP_Rogerson.git

615

616 **Data availability**

617

618 The remote-sensing data products used in this study are publicly available. The BICEP NPP (<https://doi.org/10.3390/rs12050826>),
619 datasets of Ryan-Keogh et al. (2023) (<https://doi.org/10.5281/ZENODO.8314348>), and OSTIA SST
620 (<https://doi.org/10.48670/moi-00168>) can be sourced from the links provided. Model outputs from the different PISCES
621 configurations are available either through direct correspondence with the respective lead authors or via the repository links provided
622 in their associated publications.

623 Author contributions

624
625 **Conceptualization:** JR, AT, MV, MG **Methodology:** JR, AT, AN, AO, MG **Formal analysis:** JR, AN **Writing-Original Draft:** JR
626 **Data curation:** JR, AT, LW, PA **Writing-Review & Editing:** JR, AT, MV, LW, PA, AO, MG **Funding acquisition:** MG

628 Competing interests

629
630 The authors declare that they have no conflicts of interest

632 Declaration of AI

633
634 No generative AI was used in the writing of this manuscript.

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