Earth System
Dynamics
Discussions

Resolving ecological feedbacks on the ocean carbon sink in Earth system models

David I. Armstrong McKay*[1,2], Sarah E. Cornell[1,2], Katherine Richardson[3], Johan Rockström[1,4]

[1]Stockholm Resilience Centre, Stockholm University, Stockholm, 106 91, Sweden
5 [2]Bolin Centre for Climate Research, Stockholm University, Stockholm, 106 91, Sweden
[3]Globe Institute, Center for Macroecology, Evolution and Climate, University of Copenhagen, Copenhagen, 2100, Denmark
[4]Potsdam Institute for Climate Impact Research, Potsdam, 14473, Germany

Correspondence to: David I. Armstrong McKay (david.armstrongmckay@su.se)

Abstract. The Earth's oceans are one of the largest sinks in the Earth system for anthropogenic CO2 emissions, acting as a
10 negative feedback on climate change. Earth system models predict, though, that climate change will lead to a weakening ocean carbon uptake rate as warm water holds less dissolved CO2 and biological productivity declines. However, most Earth system models do not incorporate the impact of warming on bacterial remineralisation and rely on simplified representations of plankton ecology that do not resolve the potential impact of climate change on ecosystem structure or elemental stoichiometry. Here we use a recently-developed extension of the cGEnIE Earth system model (ecoGEnIE) featuring a trait-based scheme for
15 plankton ecology (ECOGEM), and also incorporate cGEnIE's temperature-dependent remineralisation (TDR) scheme. This enables evaluation of the impact of both ecological dynamics and temperature-dependent remineralisation on the soft-tissue biological pump in response to climate change. We find that including TDR strengthens the biological pump relative to default runs due to increased nutrient recycling, while ECOGEM weakens the biological pump by enabling a shift to smaller plankton classes. However, interactions with concurrent ocean acidification cause opposite sign responses for the carbon sink in both
20 cases: TDR leads to a smaller sink relative to default runs whereas ECOGEM leads to a larger sink. Combining TDR and ECOGEM results in a net strengthening of the biological pump and a small net reduction in carbon sink relative to default. These results clearly illustrate the substantial degree to which ecological dynamics and biodiversity modulate the strength of climate-biosphere feedbacks, and demonstrate that Earth system models need to incorporate more ecological complexity in order to resolve carbon sink weakening.

25 **1.   Introduction**

Oceans absorb about a quarter of anthropogenic carbon dioxide emissions, drawing down around 2-3 GtCyr[-1] in recent decades (Ciais et al., 2013; Friedlingstein et al., 2019; Gruber et al., 2019). The mechanisms are well understood: solubility (dissolution) and biological (soft tissue and carbonate) pumps gradually transfer carbon to the deep ocean where it remains on timescales of several centuries to millennia (Broecker and Peng, 1982). However, increasing ocean temperature as a result of global
30 warming could potentially lead to a weakening of this ocean carbon sink (Arora et al., 2013; Ciais et al., 2013). The global

Earth System
Dynamics
Discussions

Open Access

EGU

carbon sink uptake rate was observed to decline by ~0.91%yr^{-1} between 1959 and 2012, of which approximately 40% is estimated to be due to sink feedbacks with the oceans playing a large role (Raupach et al., 2014). The combined effect of future feedbacks on both land and ocean carbon sinks reduce the RCP4p5-compatible anthropogenic carbon budget by ~157 ± 76 GtC (Ciais et al., 2013).

35

This sink weakening might therefore act as a positive feedback on anthropogenic warming (Steffen et al., 2018). However, many of the Earth system models (ESMs) used to make these carbon sink projections do not incorporate sufficient ecological complexity to fully resolve these feedbacks, including for the ocean the impact of both warming and acidification on metabolic dynamics, ecosystem structure, and changing nutrient stoichiometry (Ciais et al., 2013). Of the ten ESMs used for carbon sink

40 projections in IPCC AR5, only one resolves the impact of warming on organic carbon remineralisation, three resolve different plankton sizes, and three resolve changing nutrient usage ratios (discussed in Background below), all of which critically influence the biological pump in a warming ocean.

In this study we investigate changes in the biological pump in response to climate change and ocean acidification using

45 ecoGEnIE, an ESM of intermediate complexity (EMIC) with more complex biogeochemistry and ecosystem dynamics than present in most CMIP5 ESMs. The ecoGEnIE model allows temperature-dependent remineralisation (TDR), greater biodiversity via size trait-based plankton ecology, and flexible elemental stoichiometry. This combination allows the impact of metabolic and ecological dynamics on the biological pump and the ocean carbon sink in response to climate change to emerge, while the choice of an EMIC makes such additional complexity computationally tractable. We simulate a suite of

50 historical and future climate change scenarios and assess the impact on the ocean carbon sink of replacing the default Fixed Profile Remineralisation (FPR) parameterisation with the TDR scheme and/or replacing the original NPZD-based biogeochemistry module with ecoGEnIE's new trait-based plankton ecology scheme.

2.   Background

The primary driver of a weakening ocean carbon sink is the reduced dissolution capacity of warmer water (i.e. a weaker

55 solubility pump), but a reduction in the efficacy of the biological pump due to an increase in marine bacterial respiration has also been suggested as an important factor in past warm episodes (Boscolo-Galazzo et al., 2018; John et al., 2014a; Olivarez Lyle and Lyle, 2006). The biological pump describes the fixation and export of carbon from the surface to deep ocean by biological activity (Figure 1). The formation and export of calcium carbonate shells (Particulate Inorganic Carbon; PIC) also forms part of the biological pump, but hereafter we focus on the soft-tissue biological pump as it is the dominant driver of

60 surface carbon export (Dunne et al., 2007). Despite this, the ecological dynamics affecting the soft-tissue pump has had less attention in plankton model development than resolving calcifier and silicifier plankton shells (Ward et al., 2018).

[Figure 1]

65   After organic carbon is fixed in the surface euphotic layer by phytoplankton and some is consumed by zooplankton, Particulate

Organic Carbon (POC) begins to be remineralised by detritivorous bacteria as it falls through the water column as POC rain.

Most POC is remineralised near the surface layer where the nutrients released are rapidly recycled into 'regenerated'

production (Dugdale and Goering, 1967), but up to 4-12 GtCy^{-1} of POC reaches the deep ocean where it becomes part of the

long-term carbon sink on centennial-to-millennial timescales (Ciais et al., 2013; Dunne et al., 2007; Henson et al., 2011, 2012).

70   This simplified representation of plankton ecology forms the basis of many marine biogeochemical models, such as the one-

size fixed-trait phyto- and zooplankton classes in the common NPZD (Nutrient-Phytoplankton-Zooplankton-Detritus) scheme

(Kwiatkowski et al., 2014). This approach misses many important biogeochemical processes though, prompting the

development of 'dynamic green ocean models' which introduce multiple Plankton Functional Types (PFTs) with differentiated

biogeochemical roles (Aumont et al., 2003; Quere et al., 2005). However, this class of plankton model is limited by a profusion

75   of poorly constrained parameters, taxonomic overspecificity, and still-limited biodiversity (Anderson, 2005; Boscolo-Galazzo

et al., 2018; Friedrichs et al., 2007; Shimoda and Arhonditsis, 2016; Ward et al., 2018).

Critically, both NPZD and dynamic green ocean models also fail to fully account for allometric effects in biogeochemistry,

despite cell size distribution and elemental stoichiometry being the dominant traits controlling plankton ecosystem function

80   and total production (Finkel et al., 2010; Guidi et al., 2009) and the fraction of large phytoplankton projected to increase with

nutrient availability and decrease with warming (Mousing et al., 2014). Trait-based plankton models have been proposed,

based on simulating generic ecosystem rules using key functional traits such as size rather than specific taxonomic identity,

allowing ecosystem structure, biodiversity, and biogeography to emerge without being parameterised (Bruggeman and

Kooijman, 2007; Follows et al., 2007; Harfoot et al., 2014; McGill et al., 2006). These models still do not enable better

85   understanding of Earth system feedbacks though because they do not capture biogeochemical and large-scale physical

dynamics.

Metabolic processes are also temperature-dependent, and so ocean temperature partly determines many marine biogeochemical

patterns (Hoppe et al., 2002; Laws et al., 2000; Regaudie-De-Gioux and Duarte, 2012). For every 10ºC increase in temperature,

90   gross primary production in any location is expected to increase by up to 100% (represented by a Q10 factor of 1-2), while

average community respiration is expected to increase by between 100 and 200% (Q10 = 2-3) (Bendtsen et al., 2015; Boscolo-

Galazzo et al., 2018; Eppley, 1972; Pomeroy and Wiebe, 2001; Regaudie-de-Gioux and Duarte, 2012; Sarmento et al., 2010).

If warming-induced increases in respiration rates rise faster than production rates, organic matter will be remineralised more

quickly, raising the remineralisation depth (the point at which most POC is remineralised) higher up in the water column

95   (Boscolo-Galazzo et al., 2018; John et al., 2014a). One might expect this to reduce carbon export overall as less carbon makes

it out of the surface ocean, but increased remineralisation also allows more nutrients to be recycled back into the surface,

Earth System
Dynamics
Discussions
EGU
Open Access

potentially resulting in more regenerated production (Segschneider and Bendtsen, 2013; Taucher and Oschlies, 2011). Even only a small shift in the remineralisation depth has a significant potential impact on atmospheric CO_2, with a global deepening of 24m reducing CO_2 by 10-27 ppm in one model (Kwon et al., 2009), and so can potentially act as a climate feedback

100 mechanism.

Other processes that affect the biological pump and remineralisation will also be impacted by climate change. Ocean stratification is projected to increase, as surface warming increases the temperature gradient (Ciais et al., 2013; Riebesell et al., 2009). This reduces the nutrient flux from deep to surface waters, potentially leading to an expansion of low-nutrient

105 oligotrophic zones (hereafter referred to as 'oligotrophication') in subpolar surface waters (Bopp et al., 2005; Sarmiento et al., 2004). Oligotrophication is normally assumed to lead to lower overall productivity, but there is also evidence that warming will not substantially affect productivity in existing oligotrophic regions (Richardson and Bendtsen, 2017) and that the depth rather than intensity of stratification determines productivity (Richardson and Bendtsen, 2019). The reduction in nutrient supply may also favour smaller plankton that can better cope with warmer and oligotrophic conditions, resulting in a shift in

110 ecosystem dynamics and function (Beaugrand et al., 2010; Bopp et al., 2005; Finkel et al., 2010). Reduced mixing rates also result in ocean interior deoxygenation, leading to an expansion of oxygen minimum zones, reduced nitrogen availability, and increased phosphate release from affected sediments (Ciais et al., 2013; Keeling et al., 2010; Stramma et al., 2008).

The organic biological pump may also be affected by ocean acidification through shifting ecosystem composition, altered

115 nutrient availability and stoichiometry (Ciais et al., 2013; Nagelkerken and Connell, 2015; Riebesell et al., 2009; Tagliabue et al., 2011), and reduced particle ballasting – the hypothesised process by which POC sticks to denser falling PIC and so increases POC export (Armstrong et al., 2001; Klaas and Archer, 2002). Furthermore, the human-driven loss of organisms higher up the food chain as a result of overharvesting and habitat degradation has a considerable yet poorly quantified effect on the biological pump (Pershing et al., 2010). Many of these factors influence and/or are influenced by both the magnitude

120 of primary production and the remineralisation depth.

[Table 1]

Despite these known influences on the biological pump, many of the CMIP5 Earth system models (ESMs) used for the IPCC

125 AR5's ocean carbon sink projections did not incorporate many or any of these biogeochemical processes (Ciais et al., 2013; Schwinger et al., 2014). One study (Segschneider and Bendtsen, 2013) quantified the impact of including TDR, modifying the CMIP5 model MPI-ESM and its marine biogeochemistry model HAMOCC5.2, and projected an ~18 GtC reduction in ocean carbon uptake by 2100 under high emission scenario RCP8p5. However, only one out of ten CMIP5 ESMs featured non-fixed POC remineralisation profiles by enabling TDR (CanESM2) (Table 1), with most instead prescribing a fixed attenuating

130 remineralisation profile (Bendtsen et al., 2015; Dunne et al., 2007; Martin et al., 1987). Additionally, NPZD-type models

cannot fully resolve the potential impact of climate change or ocean acidification on ecosystem structure, biodiversity, and plankton size shifts. Only four of the ten CMIP5 ESMs featured multiple PFTs with different ecosystem functions beyond a simple NPZD scheme. Of these, only three account for plankton size in some way, and only three featured at least partially flexible stoichiometry (e.g. nutrient quotas and optimal allocation) that allow potential changes in nutrient utilisation in

135   response to changing environmental conditions to be resolved (Kwiatkowski et al., 2018; Moreno and Martiny, 2018). Investigating changes in the biological pump in response to the physical and chemical perturbations of climate change and ocean acidification therefore requires an ESM with more complex biogeochemistry and ecosystem dynamics than present in the CMIP5 ESMs.

3.   Methods

140   ### 3.1.   The ecoGEnIE model

ecoGEnIE is an extension of cGEnIE – the carbon-centric Grid Enabled Integrated Earth system model, an EMIC featuring modules for 3D ocean circulation, 2D energy-moisture balance atmosphere, simplified thermo-dynamic sea ice, optional ocean sediments, and a comprehensive ocean biogeochemistry module with phosphorus (in the form of phosphate, PO_4) as the main limiting nutrient (Ridgwell et al., 2007; Ridgwell and Schmidt, 2010). cGEnIE has been used in many previous studies of

145   climate-carbon cycle interactions in both modern (Tagliabue et al., 2016) and palaeo applications (Gibbs et al., 2016; John et al., 2014a; Meyer et al., 2016; Monteiro et al., 2012; Norris et al., 2013; Ridgwell and Schmidt, 2010). The default cGEnIE configuration uses a fixed remineralisation profile similar to the Martin curve (Martin et al., 1987; Ridgwell et al., 2007), but includes an optional temperature-dependent remineralisation scheme which has previously been used to explore the biological pump in warm palaeo oceans (John et al., 2014b). An updated tuning of this scheme which also couples TDR with temperature-

150   dependent export production is currently being developed (Crichton et al., 2020), but was not available at the time of this study. EMICs such as cGEnIE have lower spatiotemporal resolution than more comprehensive ESMs based on atmosphere-ocean general circulation models, but they are also less computationally expensive and thus well-suited for investigating more complex biogeochemical dynamics and performing efficient simulations of longer timescales or multiple scenarios (Claussen et al., 2002; Ward et al., 2018).

155

The current cGEnIE version (*cGEnIE.muffin*) has been extended to ecoGEnIE by incorporating a new scheme for plankton ecology (ECOGEM), replacing cGEnIE's implicit, flux-based parameterisation with an explicitly resolved and temperature-sensitive trait-based ecosystem module (Ward et al., 2018). In this case, size is the dominant trait controlling plankton biogeochemical function and response to warming (Finkel et al., 2010; Mousing et al., 2014), and so each PFT (here only

160   phytoplankton and zooplankton, but further classes such as calcifiers and silicifiers will be available in future) is further split

into 8 size classes ranging from 0.6μm to 1900μm. This allows a better representation of biodiversity within the model, with the ecosystem capable of shifting to a different structure in response to environmental forcing. ECOGEM includes flexible stoichiometry rather than being fixed to the canonical Redfield Ratio (of C:N:P = 106:16:1 or similar (Martiny et al., 2014; Redfield, 1934)), allowing dynamic usage of nutrients in response to warming and nutrient availability to also be resolved
165 (Boscolo-Galazzo et al., 2018; Martiny et al., 2016; Moreno and Martiny, 2018). Dissolved Organic Matter (DOM) production is also explicit in ECOGEM and so allows a variable POM/DOM ratio, variations in which may have a significant impact on primary production in oligotrophic regions (Richardson and Bendtsen, 2017). However, cGEnIE/ecoGEnIE has relatively coarse ocean layer resolution (16 layers of variable thickness), and so is not able to sufficiently resolve the dynamics that potentially link stratification and deep chlorophyll maxima in oligotrophic regions (Richardson and Bendtsen, 2017, 2019).
170 ecoGEnIE has not yet been fully recalibrated to the modern ocean and does not perform quite as well against observational data as cGEnIE, but the results are still broadly similar (Ward et al., 2018) and are sufficient for analysis of the global biological pump response.

3.2.   Experimental setup

We assess the differing impacts of replacing cGEnIE's Fixed Profile Remineralisation (FPR) parameterisation with its
175 Temperature-Dependent Remineralisation (TDR) scheme (John et al., 2014b) and replacing cGEnIE's original NPZD-based biogeochemistry BIOGEM module (BIO) with ecoGEnIE's trait-based ECOGEM module (ECO) (Ward et al., 2018). We test each new element both separately and in combination, analysing four cGEnIE/ecoGEnIE configurations:

- **BIO+FPR** is cGEnIE with the default NPZD biogeochemistry module (BIO) and the default Fixed Profile
180   Remineralisation scheme (FPR)

- **BIO+TDR** is cGEnIE with the default NPZD biogeochemistry module (BIO) and the alternative Temperature-Dependent Remineralisation scheme (TDR)

- **ECO+FPR** is ecoGEnIE, incorporating the trait-based ECOGEM module (ECO), and the default Fixed Profile Remineralisation scheme (FPR)

185 - **ECO+TDR** is ecoGEnIE (ECO) and the alternative Temperature-Dependent Remineralisation scheme (TDR)

Each configuration is calibrated to result in the same global biological pump strength (POC export of ~7.5 GtCy^{-1} and PIC export of ~1 GtCy^{-1}) and similar global mean total Dissolved Inorganic Carbon (DIC) and Alkalinity (ALK) and surface DIC speciation relative to the cGEnIE/ecoGEnIE default configurations and data (see Supplementary Table S1 & Figures S1-18).

190   The main difference between them is a higher POC sedimentation rate in the ecoGEnIE configurations, but as POC rain in non-sediment enabled configurations of cGEnIE is returned as deep ocean DIC, this is acceptable on shorter sub-overturning timescales. Each model configuration is spun-up for 10,000 years and restarted at 0 CE (10000 HE), and then forced from 1765 CE with combined historical and future CMIP5 RCP total CO_2 emission scenarios (3PD, 4p5, 6p0, and 8p5, corresponding to low, moderate, high, and very high emission scenarios respectively) extended through to 2500 CE

195   (Meinshausen et al., 2011). We use the global POC export flux (GtCyr^{-1}) from the surface layer (fixed in cGEnIE/ecoGEnIE as the top 80.8m of the ocean) as our measure of biological pump strength and compare cumulative changes between the years 2000 and 2100 CE, and also quantify cumulative changes in the ocean carbon sink for each configuration through the air-to-sea CO_2 flux. We calculate cumulative changes in biological pump and ocean carbon sink capacity for the policy-relevant timescale of the 21st Century CE (Table 2), but the biological pump results are shown up to 2500 CE (Figure 2).

200   **4.**   **Results**

4.1.   **Biological Pump Strength**

[Figure 2]

Our results show that the biological pump weakens under all scenarios and configurations, but adding TDR and trait-based

205   plankton ecology has strong and opposite impacts on relative biological pump strength. Under the default cGEnIE configuration (BIO+FPR) anthropogenic climate change results in an overall weakening of the global biological pump, with global POC flux falling ~6.1% below preindustrial by 2100 under RCP4p5 (Figure 2; Table 2). In the model this is primarily driven by stratification resulting in reduced surface nutrient concentrations and decreased primary production in high-productivity subpolar waters (Figure 3) in line with previous model results (Bopp et al., 2005; Ciais et al., 2013; Crichton et

210   al., 2020; Riebesell et al., 2009; Sarmiento et al., 2004). In contrast, there is an increase in production in high-latitude waters, where mixing is already so deep that stratification and decreased mixing actually increases productivity by confining phytoplankton within the euphotic zone (matching theoretical expectations; Riebesell et al., 2009).

[Figure 3]

215

Adding TDR (BIO+TDR) leads to a substantially different result than the default cGEnIE configuration, with a far smaller biological pump weakening under RCP4p5 of only ~-0.3% by 2100, and eventually a net strengthening after 2100 (Figure 2). This occurs in the model because adding TDR results in an initial decrease in biological pump strength as more POC is remineralised with warming, but this also leads to a shallower remineralisation depth and an increase in nutrient recycling and

220   regenerated production. While a warming-induced shoaling of the remineralisation depth has been modelled to reduce POC export (Kwon et al., 2009), we find that a secondary effect is to increase PO_4 concentrations just below the mixed layer from remineralisation that would otherwise have occurred deeper in intermediate waters (Supporting Figure S19). This in turn leads to increased PO_4 input to the surface layer through mixing, which is sufficient to lead to an elevated baseline in new production and POC export in warmer subpolar waters (Figure 4a) and stimulate a relative increase in POC export with further warming.

225   This result is consistent with a previous TDR-enabled EMIC, which found that including TDR resulted in increased Net Primary Production and a marginally smaller decrease in POC export under RCP8p5 (Taucher and Oschlies, 2011). A recent update to cGEnIE's TDR scheme (Crichton et al., 2020) also found a similar result, with historical warming resulting in a ~0.3% decline in POC export with TDR activated versus ~2.9% without.

230   **[Figure 4]**

    Activating ecoGEnIE (ECO+FPR) instead of TDR results in a greater weakening of the biological pump than in BIO+FPR, with global POC flux falling by ~10.1% by 2100 under RCP4p5 (Figure 2). Adding ECOGEM allows an overall decrease in average plankton size in response to climate change, as warming and stratification leads to oligotrophication in subpolar waters

235   which favours smaller plankton size classes, and is in line with previous observational and modelling studies (Finkel et al., 2010; Riebesell et al., 2009). The shift to smaller plankton classes lower in the food chain in warmer regions increases the rapidity of carbon cycling within the surface ocean, reduces the productivity and biomass of the whole ecosystem, and so decreases overall POC export (Figure 4b). Adding both trait-based plankton ecology and TDR (ECO+TDR) produces a complex result, with the weakening effect of adding ECO on the biological pump partly counteracting the strengthening effect

240   of adding TDR. The overall effect is a moderate net weakening of the biological pump by ~7.8% by 2100 (Figure 2), as decreasing plankton size and POC export in subpolar waters due to adding ECO reduces the capacity for nutrient recycling to increase as a result of adding TDR (Figure 4c). The combined effect of ECO+TDR relative to BIO+FPR in this model is therefore an additional ~1.9% weakening of the biological pump relative to pre-industrial under RCP4p5 (Figure 5), resulting in ~8.2 GtC less POC being exported by the biological pump in this model during the 21st Century. In all configurations and

245   scenarios the changes in the biological pump continue past 2100, and in many cases only begin to stabilise after several hundred years (Figure 2).

    [Figure 5]

Earth System
Dynamics
Discussions

Open Access

EGU

4.2.   Ocean Carbon Sink Capacity

250   It has sometimes been implied in previous discussions of empirical and model results that a decrease in biological pump
strength directly leads to a corresponding decrease in the ocean carbon sink capacity, as less POC is exported from the surface
to deep ocean and so more CO_2 remains in surface waters and therefore the atmosphere (Boscolo-Galazzo et al., 2018; John et
al., 2014a; Olivarez Lyle and Lyle, 2006; Steffen et al., 2018). However, reduced POC export affects many other processes,
which results in a nonlinear relation between biological pump strength and the ocean carbon sink capacity that can lead to
255   counter-intuitive outcomes.

[Table 2]

In our simulations, the relative strengthening of the biological pump when TDR is included actually leads to a net decrease in
260   the ocean carbon sink capacity during the 21st century (Table 2). Conversely, the relative weakening of the biological pump
with ECOGEM activated instead (ECO+FPR) is associated with a net increase in the ocean carbon sink capacity. Combining
both ECOGEM and TDR (ECO+TDR) results in a smaller overall relative weakening of the biological pump compared to
default, and a marginal net decrease in the ocean carbon sink capacity of ~0.4 GtC (~2.4 GtC under RCP8p5) over the 21st
Century. Including trait-based ecology using size classes largely but not entirely offsets the impact on the ocean carbon sink
265   of also including TDR in this model. The model thus suggests that ecological dynamics increases the resilience of plankton
ecosystem functioning against the pressures of climate change.

A decrease in POC export does not automatically result in a decrease in the ocean carbon sink capacity in this model as a result
of interactions with carbonate chemistry and ocean acidification. Adding TDR results in greater production of both POC and
270   PIC in sub-polar regions. Along with increased respiration rates this results in an initial net decrease in surface DIC and ALK,
which through DIC speciation leads to a decrease in the concentration of dissolved carbonate ([CO_3]), an increase in the
concentration of surface dissolved CO_2 ([CO_2]), and decreased pH and carbonate saturation state (Ω) (as theoretically described
by Zeebe and Wolf-Gladrow, 2001). This increases the partial pressure of CO_2 in surface waters (pCO_2), therefore reducing
the capacity for additional CO_2 to dissolve from the atmosphere into the ocean. This effect on the air-to-sea CO_2 flux gradually
275   limits the total DIC content for the whole ocean and therefore the ocean carbon sink as a whole. Ocean acidification also
concurrently increases surface pCO_2 and decreases Ω, and so adding TDR results in a synergistic interaction with ocean
acidification. Conversely, adding ECOGEM reduces total ecosystem POC/PIC production, leading to higher surface DIC and
ALK, increased surface [CO_3] and Ω, decreased surface [CO_2] and pCO_2, and therefore increased air-to-sea CO_2 flux and total
ocean DIC in the long-term. ECOGEM and the resultant oligotrophication-induced plankton size shift therefore slightly
280   counters the ocean acidification trend.

Earth System
Dynamics
Discussions

Open Access

EGU

5.   Discussion

These initial results clearly illustrate the importance of incorporating multiple dimensions of ecological complexity within Earth system models in order to capture the impact of nonlinear climate-biosphere feedbacks, biodiversity, and ecological resilience on the future dynamics of carbon sinks. Our ecoGEnIE experiments simulate a modest decline in the ocean carbon

285   sink capacity of around ~5 GtC (~0.05 GtCy^{-1}) during the 21st Century under an RCP8p5 scenario when accounting for TDR, compared to a previous estimate of ~18 GtC (~0.18 GtCy^{-1}) using a much simpler NPZD-based ecosystem representation (Segschneider and Bendtsen, 2013) and the 2018 ocean carbon sink uptake rate of 2.6±0.6 GtCy^{-1} (Friedlingstein et al., 2019). This decline is partially countered when greater ecological complexity is introduced as well, with a shift to smaller plankton classes in response to oligotrophication leading to an ocean carbon sink reduction of only ~2.4 GtC. Other processes that are

290   not resolved in this configuration of ecoGEnIE could also substantially affect the biological pump though, such as ballasting, calcifier-silicifier trade-offs, and deep chlorophyll maxima (discussed more fully below), and further work is required to assess their impact on our estimates.

Few of the ESMs used in CMIP5 sufficiently resolve marine ecology, instead relying on simple plankton ecosystems with

295   minimal or non-existent ecological and metabolic dynamics (Table 1). This reduces computational expense and so allows higher resolution of important physical processes, but comes at the price of poorly resolving known biogeochemical and ecological feedbacks that could substantially affect carbon partitioning (Anderson, 2005; Ward et al., 2018). To date, gains in computational power have largely been allocated to improved resolution and physical process representation. This study suggests that it is timely for the research community to debate again where future gains should be focused, in order to enable

300   ESMs to include more complex marine biogeochemical modules without compromising the high resolution representation of physical processes. This would also allow more accurate representation of fine-scale biogeochemical processes such as the interaction of stratification, the nutricline, and deep chlorophyll maxima in oligotrophic regions (Richardson and Bendtsen, 2017, 2019), which has not been possible in this study. EMICs with lower physical resolution can more readily incorporate ecological complexity though, and remain a crucial tool for further exploring these feedbacks in the interim.

305

In this study we focus on the dominant soft-tissue biological pump, but the variable response of plankton classes with different shell types to climate change and ocean acidification will also have an impact on the biological pump. For instance, silicifiers with opal-based shells such as diatoms thrive in nutrient-rich waters. Segschneider and Bendtsen (2013) found that the increased nutrient recycling when TDR was introduced in their model initially drives an increase in diatom production and

310   opal export in response to climate change. This eventually leads to silicate-depleted surface waters and suppressed diatom production, allowing a subsequent increase in calcifying plankton and PIC export instead. This has the effect of reducing surface alkalinity and increasing surface pCO_2, which drives a substantial proportion of the large ocean carbon sink reduction in their analysis. However, the model of Segschneider and Bendtsen (2013) does not feature trait-based size classes or flexible

stoichiometry, which we have shown is critical for determining the soft-tissue biological pump response. In order to fully

315   compare our results it will be necessary to repeat our simulations with the silicifier-enabled ECOGEM currently under development. Together, resolving plankton size classes, TDR, flexible stoichiometry, and separate silicifier and calcifier functional types will allow the response of the marine biological pump to climate change to be more fully diagnosed. Further development will also allow the potential impact of ballasting to be assessed. Empirical observations have suggested that the ballasting effect is weaker than hypothesised (Wilson et al., 2012), making ballasting unlikely to substantially alter our

320   findings, but it would likely result in greater surface layer remineralisation in scenarios with reduced PIC production.

6.   Conclusions

The response of the biological pump to future climate change and its role in the ocean carbon sink is critical for projecting climate feedbacks, but many of the most influential Earth system models fail to incorporate sufficient metabolic or ecological complexity for this to be fully resolved. In this study, we investigate for the first time the impact of integrating both

325   temperature-dependent remineralisation, size-based biodiversity, and flexible nutrient usage on the biological pump and ocean carbon sink in response to climate change. We find that while adding temperature-dependent remineralisation to an Earth system model of intermediate complexity (ecoGEnIE) results in a greater weakening of the ocean carbon sink as a result of climate change as expected, this actually results from a relative strengthening of the biological pump itself as a result of shallower nutrient remineralisation. Conversely, adding trait-based ecosystem dynamics instead results in an even weaker

330   biological pump as a result of oligotrophication favouring smaller plankton, and in turn a larger ocean carbon sink. Finally, combining both of these features results in a smaller relative weakening of the biological pump and a modest reduction in the ocean carbon sink capacity. This implies that the biological pump positive feedback on climate change may be larger than CMIP5 models project, but is potentially less than some other post-CMIP5 projections. These complex relations require further analyses and validation. This study has primarily focused on the allometric aspects of dominant soft-tissue components of the

335   biological pump, and the results clearly illustrate the substantial degree to which ecological dynamics and biodiversity modulate the strength of climate-biosphere feedbacks. Going beyond simple biogeochemical traits and incorporating more ecological complexity in Earth system models will allow feedbacks such as the marine biological pump to be more fully resolved in future.

Author Contributions

340   DIAM, SEC, & KR conceived of the study; DIAM designed the study, configured and ran the model, and performed the analyses; DIAM wrote the paper with input from SEC, KR, & JR.

Earth System
Dynamics
Discussions

Data availability

cGEnIE.muffin is available for download from https://github.com/derpycode/cgenie.muffin, and a manual detailing code installation, model configuration, and extensive tutorials is available from https://github.com/derpycode/muffindoc. Modern
345 observational data for model-data comparison are available from http://www.seao2.info/mymuffin.html. CO_2 emission scenarios for forcing the model are available from http://www.pik-potsdam.de/~mmalte/rcps/ (Meinshausen et al., 2011).

Conflicts of Interest

The authors declare that they have no conflict of interest

References

Anderson, T. R.: Plankton functional type modelling: Running before we can walk?, J. Plankton Res., 27(11), 1073–1081,
355 doi:10.1093/plankt/fbi076, 2005.

Armstrong, R. A., Lee, C., Hedges, J. I., Honjo, S. and Wakeham, S. G.: A new, mechanistic model for organic carbon fluxes in the ocean based on the quantitative association of POC with ballast minerals, Deep Sea Res. Part II Top. Stud. Oceanogr., 49(1–3), 219–236, doi:10.1016/S0967-0645(01)00101-1, 2001.

Arora, V. K., Boer, G. J., Christian, J. R., Curry, C. L., Denman, K. L., Zahariev, K., Flato, G. M., Scinocca, J. F., Merryfield,
360 W. J. and Lee, W. G.: The Effect of terrestrial photosynthesis down regulation on the twentieth-century carbon budget simulated with the CCCma Earth System Model, J. Clim., 22(22), 6066–6088, doi:10.1175/2009JCLI3037.1, 2009.

Arora, V. K., Scinocca, J. F., Boer, G. J., Christian, J. R., Denman, K. L., Flato, G. M., Kharin, V. V, Lee, W. G. and Merryfield, W. J.: Carbon emission limits required to satisfy future representative concentration pathways of greenhouse gases, Geophys. Res. Lett., 38(5), n/a-n/a, doi:10.1029/2010GL046270, 2011.

365 Arora, V. K., Boer, G. J., Friedlingstein, P., Eby, M., Jones, C. D., Christian, J. R., Bonan, G., Bopp, L., Brovkin, V., Cadule, P., Hajima, T., Ilyina, T., Lindsay, K., Tjiputra, J. F. and Wu, T.: Carbon-concentration and carbon-climate feedbacks in CMIP5 earth system models, J. Clim., 26(15), 5289–5314, doi:10.1175/JCLI-D-12-00494.1, 2013.

Aumont, O. and Bopp, L.: Globalizing results from ocean in situ iron fertilization studies, Global Biogeochem. Cycles, 20(2), 1–15, doi:10.1029/2005GB002591, 2006.

Earth System
Dynamics
Discussions

370   Aumont, O., Maier-Reimer, E., Blain, S. and Monfray, P.: An ecosystem model of the global ocean including Fe, Si, P
      colimitations, Global Biogeochem. Cycles, 17(2), n/a-n/a, doi:10.1029/2001GB001745, 2003.

Beaugrand, G., Edwards, M. and Legendre, L.: Marine biodiversity, ecosystem functioning, and carbon cycles, Proc. Natl.
      Acad. Sci. U. S. A., 107(22), 10120–10124, doi:10.1073/pnas.0913855107, 2010.

Bendtsen, J., Hilligsøe, K. M., Hansen, J. L. S. and Richardson, K.: Analysis of remineralisation, lability, temperature
375   sensitivity and structural composition of organic matter from the upper ocean, Prog. Oceanogr., 130(October 2014), 125–
      145, doi:10.1016/j.pocean.2014.10.009, 2015.

Bopp, L., Aumont, O., Cadule, P., Alvain, S. and Gehlen, M.: Response of diatoms distribution to global warming and potential
      implications: A global model study, Geophys. Res. Lett., 32(19), 1–4, doi:10.1029/2005GL023653, 2005.

Boscolo-Galazzo, F., Crichton, K. A., Barker, S. and Pearson, P. N.: Temperature dependency of metabolic rates in the upper
380   ocean: A positive feedback to global climate change?, Glob. Planet. Change, 170(March), 201–212,
      doi:10.1016/j.gloplacha.2018.08.017, 2018.

Broecker, W. S. and Peng, T.-H.: Tracers in the sea, Lamont-Doherty Geological Observatory, Palisades, New York., 1982.

Bruggeman, J. and Kooijman, S. A. L. M.: A biodiversity-inspired approach to aquatic ecosystem modeling, Limnol.
      Oceanogr., 52(4), 1533–1544, doi:10.4319/lo.2007.52.4.1533, 2007.

385   Christian, J. R., Arora, V. K., Boer, G. J., Curry, C. L., Zahariev, K., Denman, K. L., Flato, G. M., Lee, W. G., Merryfield, W.
      J., Roulet, N. T. and Scinocca, J. F.: The global carbon cycle in the Canadian Earth system model (CanESM1): Preindustrial
      control simulation, J. Geophys. Res. Biogeosciences, 115(3), 1–20, doi:10.1029/2008JG000920, 2010.

Ciais, P., Sabine, C., Bala, G., Bopp, L., Brovkin, V., Canadell, J., Chhabra, A., DeFries, R., Galloway, J., Heimann, M., Jones,
      C., Quéré, C. Le, Myneni, R. B., Piao, S. and Thornton, P.: Carbon and Other Biogeochemical Cycles, in Climate Change
390   2013 - The Physical Science Basis, edited by Intergovernmental Panel on Climate Change, pp. 465–570, Cambridge
      University Press, Cambridge., 2013.

Claussen, M., Mysak, L., Weaver, A., Crucifix, M., Fichefet, T., Loutre, M. F., Weber, S., Alcamo, J., Alexeev, V., Berger,
      A., Calov, R., Ganopolski, A., Goosse, H., Lohmann, G., Lunkeit, F., Mokhov, I., Petoukhov, V., Stone, P. and Wang, Z.:
      Earth system models of intermediate complexity: Closing the gap in the spectrum of climate system models, Clim. Dyn.,
395   18(7), 579–586, doi:10.1007/s00382-001-0200-1, 2002.

Collins, W. J., Bellouin, N., Doutriaux-Boucher, M., Gedney, N., Halloran, P., Hinton, T., Hughes, J., Jones, C. D., Joshi, M.,
      Liddicoat, S., Martin, G., O'Connor, F., Rae, J., Senior, C., Sitch, S., Totterdell, I., Wiltshire, A. and Woodward,
      S.: Development and evaluation of an Earth-System model – HadGEM2, Geosci. Model Dev., 4(4), 1051–1075,
      doi:10.5194/gmd-4-1051-2011, 2011.

400   Crichton, K. A., Wilson, J. D., Ridgwell, A. and Pearson, P. N.: Calibration of key temperature-dependent ocean microbial
      processes in the cGENIE . muffin Earth system model, Geophys. Model Dev. Discuss., (February), 1–26, 2020.

Dufresne, J. L., Foujols, M. A., Denvil, S., Caubel, A., Marti, O., Aumont, O., Balkanski, Y., Bekki, S., Bellenger, H., Benshila,
      R., Bony, S., Bopp, L., Braconnot, P., Brockmann, P., Cadule, P., Cheruy, F., Codron, F., Cozic, A., Cugnet, D., de Noblet,

N., Duvel, J. P., Ethé, C., Fairhead, L., Fichefet, T., Flavoni, S., Friedlingstein, P., Grandpeix, J. Y., Guez, L., Guilyardi, E.,

405   Hauglustaine, D., Hourdin, F., Idelkadi, A., Ghattas, J., Joussaume, S., Kageyama, M., Krinner, G., Labetoulle, S., Lahellec, A., Lefebvre, M. P., Lefevre, F., Levy, C., Li, Z. X., Lloyd, J., Lott, F., Madec, G., Mancip, M., Marchand, M., Masson, S., Meurdesoif, Y., Mignot, J., Musat, I., Parouty, S., Polcher, J., Rio, C., Schulz, M., Swingedouw, D., Szopa, S., Talandier, C., Terray, P., Viovy, N. and Vuichard, N.: Climate change projections using the IPSL-CM5 Earth System Model: From CMIP3 to CMIP5., 2013.

410   Dugdale, R. C. and Goering, J. J.: Uptake of New and Regenerated Forms of Nitrogen in Primary Productivity, Limnol. Oceanogr., 12(2), 196–206, doi:10.4319/lo.1967.12.2.0196, 1967.

Dunne, J. P., Sarmiento, J. L. and Gnanadesikan, A.: A synthesis of global particle export from the surface ocean and cycling through the ocean interior and on the seafloor, Global Biogeochem. Cycles, 21(4), 1–16, doi:10.1029/2006GB002907, 2007.

Dunne, J. P., John, J. G., Adcroft, A. J., Griffies, S. M., Hallberg, R. W., Shevliakova, E., Stouffer, R. J., Cooke, W., Dunne,

415   K. A., Harrison, M. J., Krasting, J. P., Malyshev, S. L., Milly, P. C. D., Phillipps, P. J., Sentman, L. T., Samuels, B. L., Spelman, M. J., Winton, M., Wittenberg, A. T. and Zadeh, N.: GFDL's ESM2 Global Coupled Climate–Carbon Earth System Models. Part I: Physical Formulation and Baseline Simulation Characteristics, J. Clim., 25(19), 6646–6665, doi:10.1175/JCLI-D-11-00560.1, 2012.

Dunne, J. P., John, J. G., Shevliakova, E., Stouffer, R. J., Krasting, J. P., Malyshev, S. L., Milly, P. C. D., Sentman, L. T.,

420   Adcroft, A. J., Cooke, W., Dunne, K. A., Griffies, S. M., Hallberg, R. W., Harrison, M. J., Levy, H., Wittenberg, A. T., Phillips, P. J. and Zadeh, N.: GFDL's ESM2 Global Coupled Climate–Carbon Earth System Models. Part II: Carbon System Formulation and Baseline Simulation Characteristics*, J. Clim., 26(7), 2247–2267, doi:10.1175/JCLI-D-12-00150.1, 2013.

Eppley, R. W.: Fishery Bulletin Vol70 No4 1972.Pdf, Fish. Bull., 70(4), 1063–1085, 1972.

Finkel, Z. V., Beardall, J., Flynn, K. J., Quigg, A., Rees, T. A. V. and Raven, J. A.: Phytoplankton in a changing world: cell

425   size and elemental stoichiometry, J. Plankton Res., 32(1), 119–137, doi:10.1093/plankt/fbp098, 2010.

Follows, M. J., Dutkiewicz, S., Grant, S. and Chisholm, S. W.: Emergent biogeography of microbial communities in a model ocean, Science (80-.)., 315(5820), 1843–1846, doi:10.1126/science.1138544, 2007.

Friedlingstein, P., Jones, M. W., O'Sullivan, M., Andrew, R. M., Hauck, J., Peters, G. P., Peters, W., Pongratz, J., Sitch, S., Le Quéré, C., DBakker, O. C. E., Canadell1, J. G., Ciais1, P., Jackson, R. B., Anthoni1, P., Barbero, L., Bastos, A., Bastrikov,

430   V., Becker, M., Bopp, L., Buitenhuis, E., Chandra, N., Chevallier, F., Chini, L. P., Currie, K. I., Feely, R. A., Gehlen, M., Gilfillan, D., Gkritzalis, T., Goll, D. S., Gruber, N., Gutekunst, S., Harris, I., Haverd, V., Houghton, R. A., Hurtt, G., Ilyina, T., Jain, A. K., Joetzjer, E., Kaplan, J. O., Kato, E., Goldewijk, K. K., Korsbakken, J. I., Landschützer, P., Lauvset, S. K., Lefèvre, N., Lenton, A., Lienert, S., Lombardozzi, D., Marland, G., McGuire, P. C., Melton, J. R., Metzl, N., Munro, D. R., Nabel, J. E. M. S., Nakaoka, S. I., Neill, C., Omar, A. M., Ono, T., Peregon, A., Pierrot, D., Poulter, B., Rehder, G.,

435   Resplandy, L., Robertson, E., Rödenbeck, C., Séférian, R., Schwinger, J., Smith, N., Tans, P. P., Tian, H., Tilbrook, B., Tubiello, F. N., Van Der Werf, G. R., Wiltshire, A. J. and Zaehle, S.: Global carbon budget 2019, Earth Syst. Sci. Data, 11(4), 1783–1838, doi:10.5194/essd-11-1783-2019, 2019.

Earth System
Dynamics
Discussions

Friedrichs, M. A. M., Dusenberry, J. A., Anderson, L. A., Armstrong, R. A., Chai, F., Christian, J. R., Doney, S. C., Dunne, J., Fujii, M., Hood, R., McGillicuddy, D. J., Moore, J. K., Schartau, M., Spitz, Y. H. and Wiggert, J. D.: Assessment of skill

440   and portability in regional marine biogeochemical models: Role of multiple planktonic groups, J. Geophys. Res. Ocean., 112(8), 1–22, doi:10.1029/2006JC003852, 2007.

Gibbs, S. J., Bown, P. R., Ridgwell, A., Young, J. R., Poulton, A. J. and O'Dea, S. A.: Ocean warming, not acidification, controlled coccolithophore response during past greenhouse climate change, Geology, 44(1), 59–62, doi:10.1130/G37273.1, 2016.

445   Gruber, N., Clement, D., Carter, B. R., Feely, R. A., van Heuven, S., Hoppema, M., Ishii, M., Key, R. M., Kozyr, A., Lauvset, S. K., Lo Monaco, C., Mathis, J. T., Murata, A., Olsen, A., Perez, F. F., Sabine, C. L., Tanhua, T. and Wanninkhof, R.: The oceanic sink for anthropogenic CO_2 from 1994 to 2007, Science (80-.)., 363(6432), 1193–1199, doi:10.1126/science.aau5153, 2019.

Guidi, L., Stemmann, L., Jackson, G. A., Ibanez, F., Claustre, H., Legendre, L., Picheral, M. and Gorsky, G.: Effects of

450   phytoplankton community on production, size and export of large aggregates: A world-ocean analysis, Limnol. Oceanogr., 54(6), 1951–1963, doi:10.4319/lo.2009.54.6.1951, 2009.

Halloran, P. R.: Does atmospheric CO_2 seasonality play an important role in governing the air-sea flux of CO_2?, Biogeosciences, 9(6), 2311–2323, doi:10.5194/bg-9-2311-2012, 2012.

Harfoot, M. B. J., Newbold, T., Tittensor, D. P., Emmott, S., Hutton, J., Lyutsarev, V., Smith, M. J., Scharlemann, J. P. W.

455   and Purves, D. W.: Emergent Global Patterns of Ecosystem Structure and Function from a Mechanistic General Ecosystem Model, edited by M. Loreau, PLoS Biol., 12(4), e1001841, doi:10.1371/journal.pbio.1001841, 2014.

Henson, S. A., Dunne, J. P. and Sarmiento, J. L.: Decadal variability in North Atlantic phytoplankton blooms, J. Geophys. Res. Ocean., 114(4), 1–11, doi:10.1029/2008JC005139, 2009.

Henson, S. A., Sanders, R., Madsen, E., Morris, P. J., Le Moigne, F. and Quartly, G. D.: A reduced estimate of the strength of

460   the ocean's biological carbon pump, Geophys. Res. Lett., 38(4), 10–14, doi:10.1029/2011GL046735, 2011.

Henson, S. A., Sanders, R. and Madsen, E.: Global patterns in efficiency of particulate organic carbon export and transfer to the deep ocean, Global Biogeochem. Cycles, 26(1), n/a-n/a, doi:10.1029/2011GB004099, 2012.

Hoppe, H. G., Gocke, K., Koppe, R. and Begler, C.: Bacterial growth and primary production along a north-south transect of the Atlantic Ocean, Nature, 416(6877), 168–171, doi:10.1038/416168a, 2002.

465   Ilyina, T., Six, K. D., Segschneider, J., Maier-Reimer, E., Li, H. and Núñez-Riboni, I.: Global ocean biogeochemistry model HAMOCC: Model architecture and performance as component of the MPI-Earth system model in different CMIP5 experimental realizations, J. Adv. Model. Earth Syst., 5(2), 287–315, doi:10.1029/2012MS000178, 2013.

John, E. H., Wilson, J. D., Pearson, P. N. and Ridgwell, A.: Temperature-dependent remineralization and carbon cycling in the warm Eocene oceans, Palaeogeogr. Palaeoclimatol. Palaeoecol., 413, 158–166, doi:10.1016/j.palaeo.2014.05.019, 2014a.

470   John, E. H., Wilson, J. D., Pearson, P. N. and Ridgwell, A.: Temperature-dependent remineralization and carbon cycling in the warm Eocene oceans, Palaeogeogr. Palaeoclimatol. Palaeoecol., 413, 158–166, doi:10.1016/j.palaeo.2014.05.019,

2014b.

Jones, C. D., Hughes, J. K., Bellouin, N., Hardiman, S. C., Jones, G. S., Knight, J., Liddicoat, S., O'Connor, F. M., Andres, R. J., Bell, C., Boo, K. O., Bozzo, A., Butchart, N., Cadule, P., Corbin, K. D., Doutriaux-Boucher, M., Friedlingstein, P.,
475   Gornall, J., Gray, L., Halloran, P. R., Hurtt, G., Ingram, W. J., Lamarque, J. F., Law, R. M., Meinshausen, M., Osprey, S., Palin, E. J., Parsons Chini, L., Raddatz, T., Sanderson, M. G., Sellar, A. A., Schurer, A., Valdes, P., Wood, N., Woodward, S., Yoshioka, M. and Zerroukat, M.: The HadGEM2-ES implementation of CMIP5 centennial simulations, Geosci. Model Dev., 4(3), 543–570, doi:10.5194/gmd-4-543-2011, 2011.

Kawamiya, M., Kishi, M. J. and Suginohara, N.: An ecosystem model for the North Pacific embedded in a general circulation
480   model. Part I: Model description and characteristics of spatial distributions of biological variables, J. Mar. Syst., 25(2), 129–157, doi:10.1016/S0924-7963(00)00012-9, 2000.

Keeling, R. F., Körtzinger, A. and Gruber, N.: Ocean Deoxygenation in a Warming World, Ann. Rev. Mar. Sci., 2(1), 199–229, doi:10.1146/annurev.marine.010908.163855, 2010.

Klaas, C. and Archer, D. E.: Association of sinking organic matter with various types of mineral ballast in the deep sea:
485   Implications for the rain ratio, Global Biogeochem. Cycles, 16(4), 63-1-63–14, doi:10.1029/2001gb001765, 2002.

Kwiatkowski, L., Yool, A., Allen, J. I., Anderson, T. R., Barciela, R., Buitenhuis, E. T., Butenschön, M., Enright, C., Halloran, P. R., Le Quéré, C., De Mora, L., Racault, M. F., Sinha, B., Totterdell, I. J. and Cox, P. M.: IMarNet: An ocean biogeochemistry model intercomparison project within a common physical ocean modelling framework, Biogeosciences, 11(24), 7291–7304, doi:10.5194/bg-11-7291-2014, 2014.

490   Kwiatkowski, L., Aumont, O., Bopp, L. and Ciais, P.: The Impact of Variable Phytoplankton Stoichiometry on Projections of Primary Production, Food Quality, and Carbon Uptake in the Global Ocean, Global Biogeochem. Cycles, 32(4), 516–528, doi:10.1002/2017GB005799, 2018.

Kwon, E. Y., Primeau, F. and Sarmiento, J. L.: The impact of remineralization depth on the air-sea carbon balance, Nat. Geosci., 2(9), 630–635, doi:10.1038/ngeo612, 2009.

495   Laws, E. A., Falkowski, P. G., Smith, W. O., Ducklow, H. and McCarthy, J. J.: Temperature effects on export production in the open ocean, Global Biogeochem. Cycles, 14(4), 1231–1246, doi:10.1029/1999GB001229, 2000.

Long, M. C., Lindsay, K., Peacock, S., Moore, J. K. and Doney, S. C.: Twentieth-century oceanic carbon uptake and storage in CESM1(BGC), J. Clim., 26(18), 6775–6800, doi:10.1175/JCLI-D-12-00184.1, 2013.

Martin, J. H., Knauer, G. A., Karl, D. M. and Broenkow, W. W.: VERTEX: carbon cycling in the northeast Pacific, Deep Sea
500   Res. Part A, Oceanogr. Res. Pap., 34(2), 267–285, doi:10.1016/0198-0149(87)90086-0, 1987.

Martiny, A. C., Vrugt, J. A. and Lomas, M. W.: Concentrations and ratios of particulate organic carbon, nitrogen, and phosphorus in the global ocean, Sci. Data, 1, 1–7, doi:10.1038/sdata.2014.48, 2014.

Martiny, A. C., Ma, L., Mouginot, C., Chandler, J. W. and Zinser, E. R.: Interactions between thermal acclimation, growth rate, and phylogeny influence prochlorococcus elemental stoichiometry, PLoS One, 11(12), 1–12,
505   doi:10.1371/journal.pone.0168291, 2016.

McGill, B. J., Enquist, B. J., Weiher, E. and Westoby, M.: Rebuilding community ecology from functional traits, Trends Ecol. Evol., 21(4), 178–185, doi:10.1016/j.tree.2006.02.002, 2006.

Meinshausen, M., Smith, S. J., Calvin, K., Daniel, J. S., Kainuma, M. L. T., Lamarque, J.-F., Matsumoto, K., Montzka, S. A., Raper, S. C. B., Riahi, K., Thomson, A., Velders, G. J. M. and van Vuuren, D. P. P.: The RCP greenhouse gas concentrations

510   and their extensions from 1765 to 2300, Clim. Change, 109(1–2), 213–241, doi:10.1007/s10584-011-0156-z, 2011.

Meyer, K. M., Ridgwell, A. and Payne, J. L.: The influence of the biological pump on ocean chemistry: Implications for long-term trends in marine redox chemistry, the global carbon cycle, and marine animal ecosystems, Geobiology, 14(3), 207–219, doi:10.1111/gbi.12176, 2016.

Monteiro, F. M., Pancost, R. D., Ridgwell, A. and Donnadieu, Y.: Nutrients as the dominant control on the spread of anoxia

515   and euxinia across the Cenomanian-Turonian oceanic anoxic event (OAE2): Model-data comparison, Paleoceanography, 27(4), 1–17, doi:10.1029/2012PA002351, 2012.

Moore, J. K., Lindsay, K., Doney, S. C., Long, M. C. and Misumi, K.: Marine ecosystem dynamics and biogeochemical cycling in the community earth system model [CESM1(BGC)]: Comparison of the 1990s with the 2090s under the RCP4.5 and RCP8.5 scenarios, J. Clim., 26(23), 9291–9312, doi:10.1175/JCLI-D-12-00566.1, 2013.

520   Moreno, A. R. and Martiny, A. C.: Ecological Stoichiometry of Ocean Plankton, Ann. Rev. Mar. Sci., 10(1), 43–69, doi:10.1146/annurev-marine-121916-063126, 2018.

Mousing, E. A., Ellegaard, M. and Richardson, K.: Global patterns in phytoplankton community size structure -evidence for a direct temperature effect, Mar. Ecol. Prog. Ser., 497, 25–38, doi:10.3354/meps10583, 2014.

Nagelkerken, I. and Connell, S. D.: Global alteration of ocean ecosystem functioning due to increasing human CO2 emissions,

525   Proc. Natl. Acad. Sci. U. S. A., 112(43), 13272–13277, doi:10.1073/pnas.1510856112, 2015.

Najjar, R. G., Jin, X., Louanchi, F., Aumont, O., Caldeira, K., Doney, S. C., Dutay, J.-C., Follows, M., Gruber, N., Joos, F., Lindsay, K., Maier-Reimer, E., Matear, R. J., Matsumoto, K., Monfray, P., Mouchet, A., Orr, J. C., Plattner, G.-K., Sarmiento, J. L., Schlitzer, R., Slater, R. D., Weirig, M.-F., Yamanaka, Y. and Yool, A.: Impact of circulation on export production, dissolved organic matter, and dissolved oxygen in the ocean: Results from Phase II of the Ocean Carbon-cycle

530   Model Intercomparison Project (OCMIP-2), Global Biogeochem. Cycles, 21(3), n/a-n/a, doi:10.1029/2006GB002857, 2007.

Norris, R. D., Kirtland Turner, S., Hull, P. M. and Ridgwell, A.: Marine ecosystem responses to Cenozoic global change, Science (80-.)., 341(6145), 492–498, doi:10.1126/science.1240543, 2013.

Olivarez Lyle, A. and Lyle, M. W.: Missing organic carbon in Eocene marine sediments: Is metabolism the biological feedback that maintains end-member climates?, Paleoceanography, 21(PA2007), 1–13, doi:10.1029/2005PA001230, 2006.

535   Palmer, J. R. and Totterdell, I. J.: Production and export in a global ocean ecosystem model, Deep Sea Res. Part I Oceanogr. Res. Pap., 48(5), 1169–1198, doi:10.1016/S0967-0637(00)00080-7, 2001.

Pershing, A. J., Christensen, L. B., Record, N. R., Sherwood, G. D. and Stetson, P. B.: The impact of whaling on the ocean carbon cycle: Why bigger was better, PLoS One, 5(8), 1–9, doi:10.1371/journal.pone.0012444, 2010.

Pomeroy, L. R. and Wiebe, W. J.: Temperature and substrates as interactive limiting factors for marine heterotrophic bacteria,

Earth System
Dynamics
Discussions

540   Aquat. Microb. Ecol., 23(2), 187–204, doi:10.3354/ame023187, 2001.

Quere, C. Le, Harrison, S. P., Colin Prentice, I., Buitenhuis, E. T., Aumont, O., Bopp, L., Claustre, H., Cotrim Da Cunha, L., Geider, R., Giraud, X., Klaas, C., Kohfeld, K. E., Legendre, L., Manizza, M., Platt, T., Rivkin, R. B., Sathyendranath, S., Uitz, J., Watson, A. J. and Wolf-Gladrow, D.: Ecosystem dynamics based on plankton functional types for global ocean biogeochemistry models, Glob. Chang. Biol., (2005), 051013014052005-???, doi:10.1111/j.1365-2486.2005.1004.x, 2005.

545   Raupach, M. R., Gloor, M., Sarmiento, J. L., Canadell, J. G., Frölicher, T. L., Gasser, T., Houghton, R. A., Le Quéré, C. and Trudinger, C. M.: The declining uptake rate of atmospheric CO2 by land and ocean sinks, Biogeosciences, 11(13), 3453–3475, doi:10.5194/bg-11-3453-2014, 2014.

Redfield, A. C.: On the proportions of organic derivatives in sea water and their relation to the composition of plankton, James Johnstone Meml. Vol., 176, 176–192, 1934.

550   Regaudie-de-Gioux, A. and Duarte, C. M.: Temperature dependence of planktonic metabolism in the ocean, Global Biogeochem. Cycles, 26(1), n/a-n/a, doi:10.1029/2010GB003907, 2012.

Regaudie-De-Gioux, A. and Duarte, C. M.: Temperature dependence of planktonic metabolism in the ocean, Global Biogeochem. Cycles, 26(1), 1–10, doi:10.1029/2010GB003907, 2012.

Richardson, K. and Bendtsen, J.: Photosynthetic oxygen production in a warmer ocean: the Sargasso Sea as a case study, 555   Philos. Trans. R. Soc. A Math. Phys. Eng. Sci., 375(2102), 20160329, doi:10.1098/rsta.2016.0329, 2017.

Richardson, K. and Bendtsen, J.: Vertical distribution of phytoplankton and primary production in relation to nutricline depth in the open ocean, Mar. Ecol. Prog. Ser., 620, 33–46, doi:10.3354/meps12960, 2019.

Ridgwell, A. J. and Schmidt, D. N.: Past constraints on the vulnerability of marine calcifiers to massive carbon dioxide release, Nat. Geosci., 3(3), 196–200, doi:10.1038/ngeo755, 2010.

560   Ridgwell, A. J., Hargreaves, J. C., Edwards, N. R., Annan, J. D., Lenton, T. M., Marsh, R., Yool, A. and Watson, A.: Marine geochemical data assimilation in an efficient Earth System Model of global biogeochemical cycling, Biogeosciences, 4(1), 87–104, doi:10.5194/bg-4-87-2007, 2007.

Riebesell, U., Rtzinger, A. K. and Oschlies, A.: Sensitivities of marine carbon fluxes to ocean change, Proc. Natl. Acad. Sci. U. S. A., 106(49), 20602–20609, doi:10.1073/pnas.0813291106, 2009.

565   Sarmento, H., Montoya, J. M., Vázquez-Domínguez, E., Vaqué, D. and Gasol, J. M.: Warming effects on marine microbial food web processes: How far can we go when it comes to predictions?, Philos. Trans. R. Soc. B Biol. Sci., 365(1549), 2137–2149, doi:10.1098/rstb.2010.0045, 2010.

Sarmiento, J. L., Slater, R., Barber, R., Bopp, L., Doney, S. C., Hirst, A. C., Kleypas, J., Matear, R., Mikolajewicz, U., Monfray, P., Soldatov, V., Spall, S. A. and Stouffer, R.: Response of ocean ecosystems to climate warming, Global Biogeochem. 570   Cycles, 18(3), doi:10.1029/2003GB002134, 2004.

Schmittner, A., Oschlies, A., Giraud, X., Eby, M. and Simmons, H. L.: A global model of the marine ecosystem for long-term simulations: Sensitivity to ocean mixing, buoyancy forcing, particle sinking, and dissolved organic matter cycling, Global Biogeochem. Cycles, 19(3), 1–17, doi:10.1029/2004GB002283, 2005.

Schwinger, J., Tjiputra, J. F., Heinze, C., Bopp, L., Christian, J. R., Gehlen, M., Ilyina, T., Jones, C. D., Salas-Mélia, D.,
575   Segschneider, J., Séférian, R. and Totterdell, I.: Nonlinearity of ocean carbon cycle feedbacks in CMIP5 earth system models,
J. Clim., 27(11), 3869–3888, doi:10.1175/JCLI-D-13-00452.1, 2014.

Segschneider, J. and Bendtsen, J.: Temperature-dependent remineralization in a warming ocean increases surface pCO2
through changes in marine ecosystem composition, Global Biogeochem. Cycles, 27(4), 1214–1225,
doi:10.1002/2013GB004684, 2013.

580   Shimoda, Y. and Arhonditsis, G. B.: Phytoplankton functional type modelling: Running before we can walk? A critical
evaluation of the current state of knowledge, Ecol. Modell., 320, 29–43, doi:10.1016/j.ecolmodel.2015.08.029, 2016.

Steffen, W., Rockström, J., Richardson, K., Lenton, T. M., Folke, C., Liverman, D., Summerhayes, C. P., Barnosky, A. D.,
Cornell, S. E., Crucifix, M., Donges, J. F., Fetzer, I., Lade, S. J., Scheffer, M., Winkelmann, R. and Schellnhuber, H. J.:
Trajectories of the Earth System in the Anthropocene, Proc. Natl. Acad. Sci., 115(33), 8252–8259,
585   doi:10.1073/pnas.1810141115, 2018.

Stramma, L., Johnson, G. C., Sprintall, J. and Mohrholz, V.: Expanding oxygen-minimum zones in the tropical oceans, Science
(80-.)., 320(5876), 655–658, doi:10.1126/science.1153847, 2008.

Tagliabue, A., Bopp, L. and Gehlen, M.: The response of marine carbon and nutrient cycles to ocean acidification: Large
uncertainties related to phytoplankton physiological assumptions, Global Biogeochem. Cycles, 25(3), 1–13,
590   doi:10.1029/2010GB003929, 2011.

Tagliabue, A., Aumont, O., DeAth, R., Dunne, J. P., Dutkiewicz, S., Galbraith, E., Misumi, K., Moore, J. K., Ridgwell, A.,
Sherman, E., Stock, C., Vichi, M., Völker, C. and Yool, A.: How well do global ocean biogeochemistry models simulate
dissolved iron distributions?, Global Biogeochem. Cycles, 30(2), 149–174, doi:10.1002/2015GB005289, 2016.

Taucher, J. and Oschlies, A.: Can we predict the direction of marine primary production change under global warming?,
595   Geophys. Res. Lett., 38(2), 1–6, doi:10.1029/2010GL045934, 2011.

Tjiputra, J. F., Roelandt, C., Bentsen, M., Lawrence, D. M., Lorentzen, T., Schwinger, J., Seland and Heinze, C.: Evaluation
of the carbon cycle components in the Norwegian Earth System Model (NorESM), Geosci. Model Dev., 6(2), 301–325,
doi:10.5194/gmd-6-301-2013, 2013.

Volodin, E. M.: Atmosphere-ocean general circulation model with the carbon cycle, Izv. Atmos. Ocean. Phys., 43(3), 266–
600   280, doi:10.1134/S0001433807030024, 2007.

Ward, B. A., Wilson, J. D., Death, R. M., Monteiro, F. M., Yool, A. and Ridgwell, A.: EcoGEnIE 1.0: plankton ecology in the
cGEnIE Earth system model, Geosci. Model Dev., 11(10), 4241–4267, doi:10.5194/gmd-11-4241-2018, 2018.

Watanabe, S., Hajima, T., Sudo, K., Nagashima, T., Takemura, T., Okajima, H., Nozawa, T., Kawase, H., Abe, M., Yokohata,
T., Ise, T., Sato, H., Kato, E., Takata, K., Emori, S. and Kawamiya, M.: MIROC-ESM 2010: Model description and basic
605   results of CMIP5-20c3m experiments, Geosci. Model Dev., 4(4), 845–872, doi:10.5194/gmd-4-845-2011, 2011.

Wilson, J. D., Barker, S. and Ridgwell, A.: Assessment of the spatial variability in particulate organic matter and mineral
sinking fluxes in the ocean interior: Implications for the ballast hypothesis, Global Biogeochem. Cycles, 26(4), n/a-n/a,

doi:10.1029/2012GB004398, 2012.

Wu, T., Song, L., Li, W., Wang, Z., Zhang, H., Xin, X., Zhang, Y., Zhang, L., Li, J., Wu, F., Liu, Y., Zhang, F., Shi, X., Chu,
610   M., Zhang, J., Fang, Y., Wang, F., Lu, Y., Liu, X., Wei, M., Liu, Q., Zhou, W., Dong, M., Zhao, Q., Ji, J., Li, L. and Zhou,
      M.: An overview of BCC climate system model development and application for climate change studies, Acta Meteorol.
      Sin., 28(1), 34–56, doi:10.1007/s13351-014-3041-7, 2014.

Zeebe, R. E. and Wolf-Gladrow, D.: CO2 in Seawater: Equilibrium, Kinetics, Isotopes, Elsevier Oceanography Series (65).,
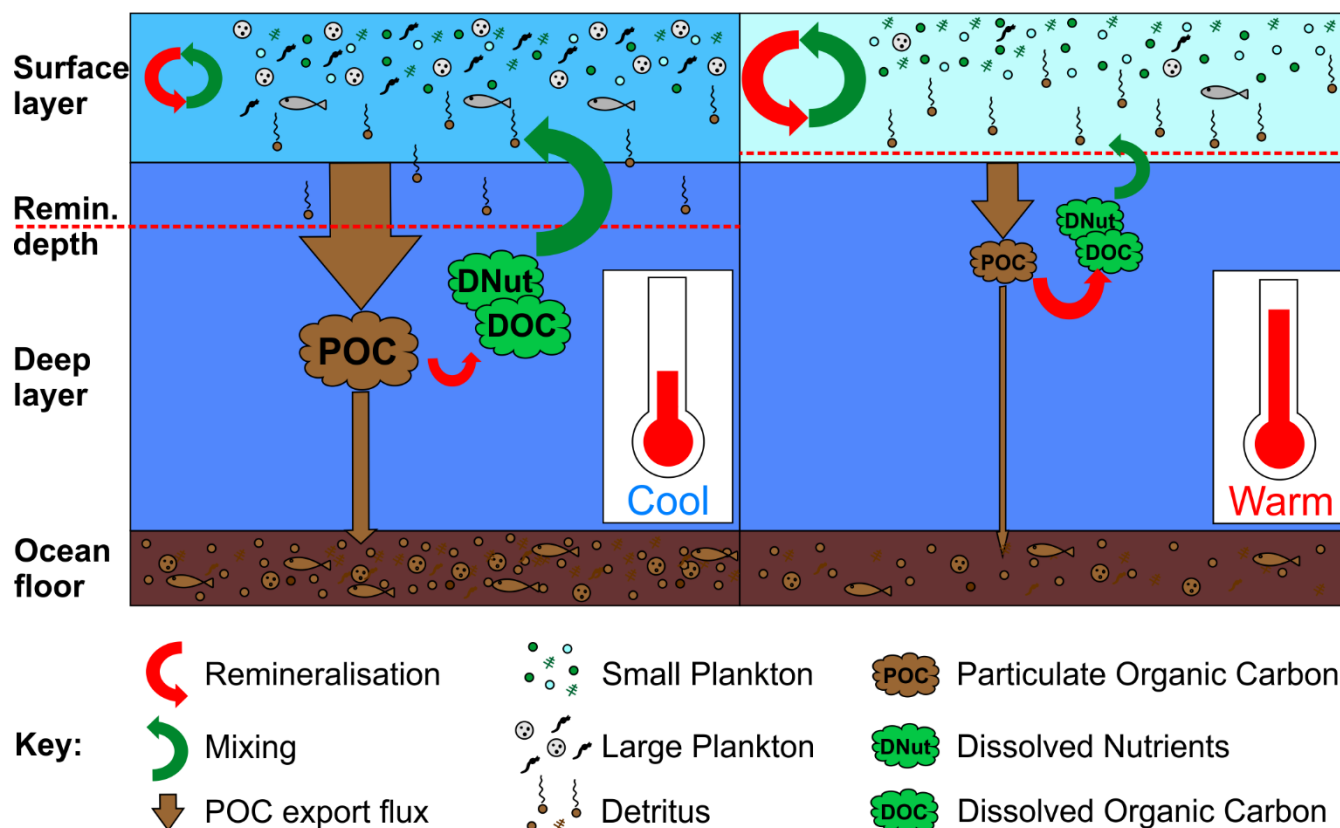   2001.

615

Figures and Tables

Figure 1: Schematic illustrating the impact of warming on the soft tissue biological pump. On the left-side, under cooler pre-industrial conditions the surface layer remains fairly well mixed with the deep ocean (green arrow), returning dissolved nutrients and carbon (DNut & DOC) from remineralisation of exported POC (red arrow), while some POC is remineralised above the remineralisation depth (surface red arrows) partly within the surface layer. On the right-side, warming leads to a shift to dominance by smaller plankton as well as stratification leading to less mixing between the shallow and deep ocean, while shoaling of the remineralisation depth leads to greater recycling of nutrients and carbon close to the surface layer, combining to result in an overall reduction in POC export and sedimentation.

620
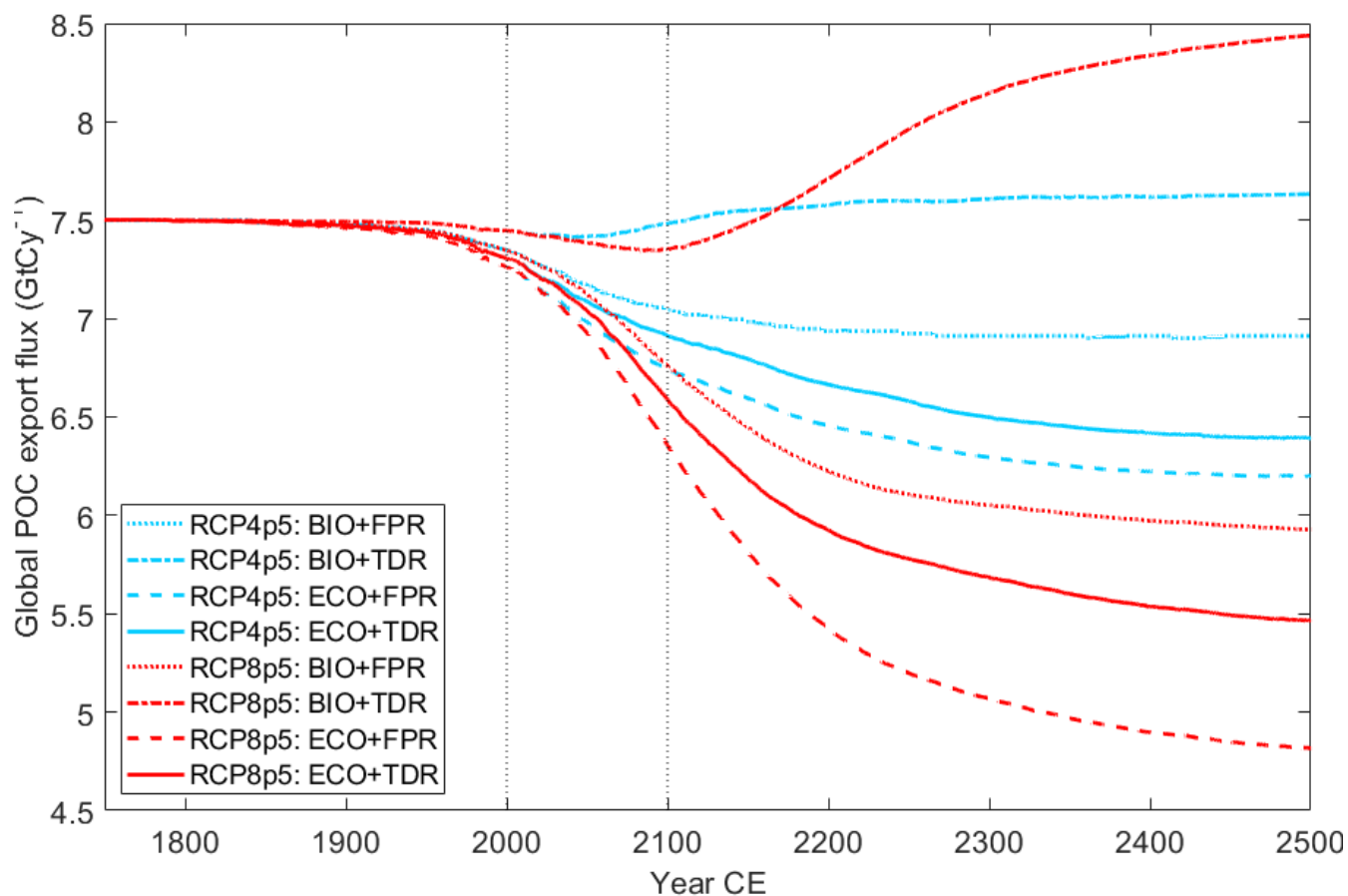
Figure 2:cGEnIE/ecoGEnIE simulation results for global POC export flux under different configurations and forcing scenarios. Results for RCP4p5 (pale blue) and RCP8p5 (dark red) are shown for each of the configurations (BIO+FPR – dotted; BIO+TDR – dot-dashed; ECO+FPR – dashed; ECO+TDR – solid), and the 21st Century (used for cumulative POC flux and ocean carbon sink capacity calculations in Table 2) marked by the vertical dotted lines.
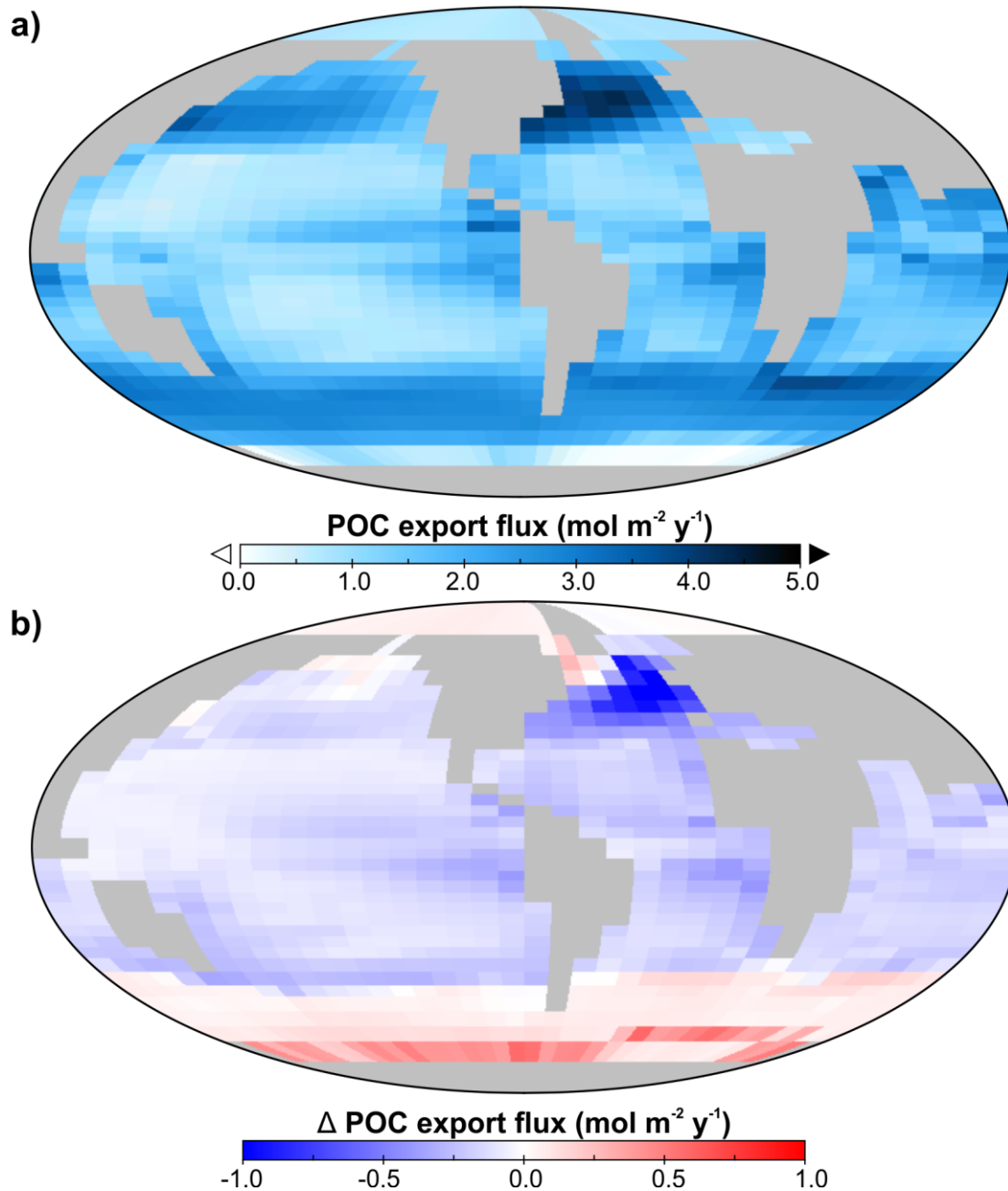
Figure 3: cGEnIE POC export maps for BIO+FPR, showing baseline patterns (a) and the change in POC export by 2100 relative to the 1765 pre-industrial baseline as a result of RCP4p5 (b).

Earth System
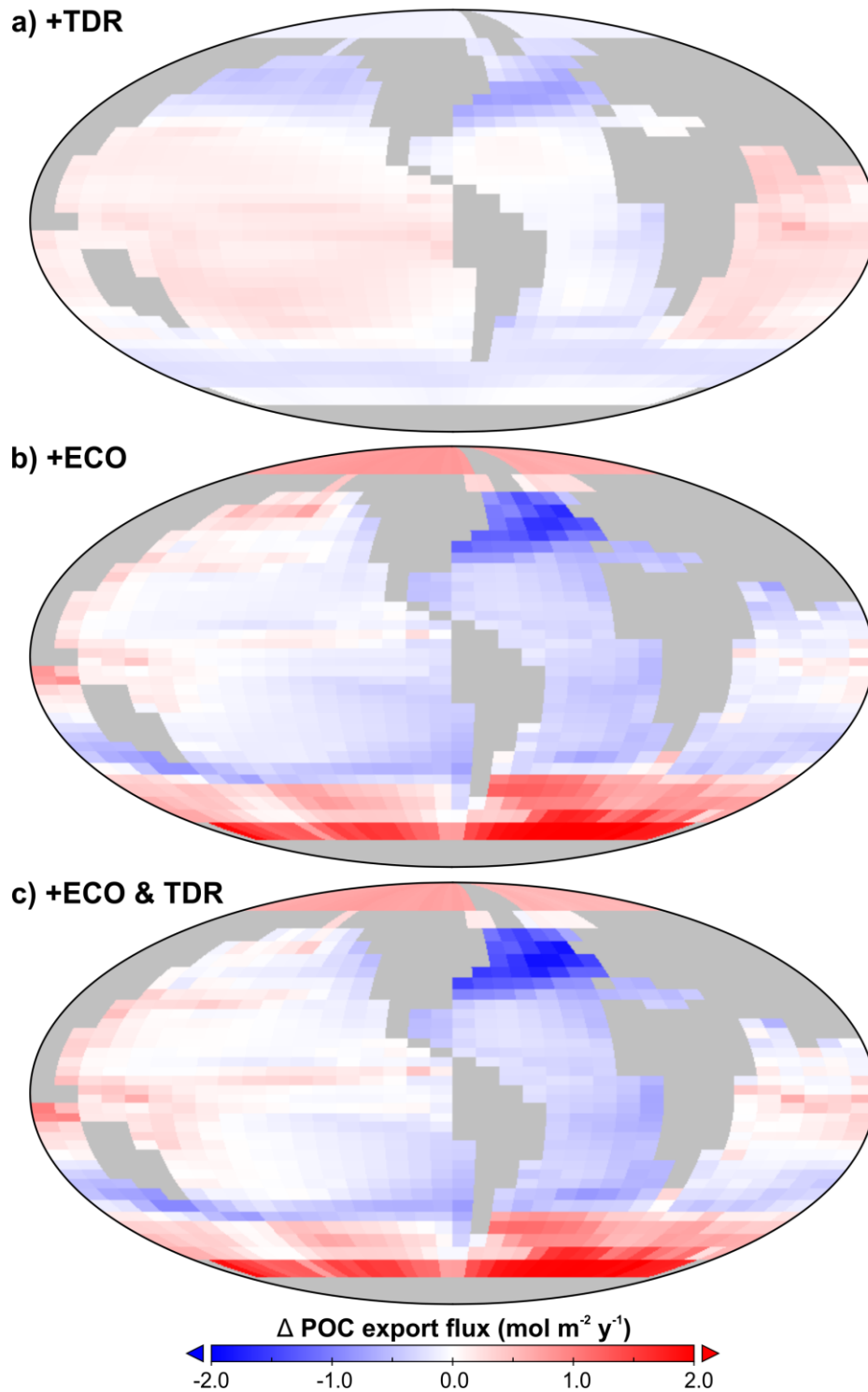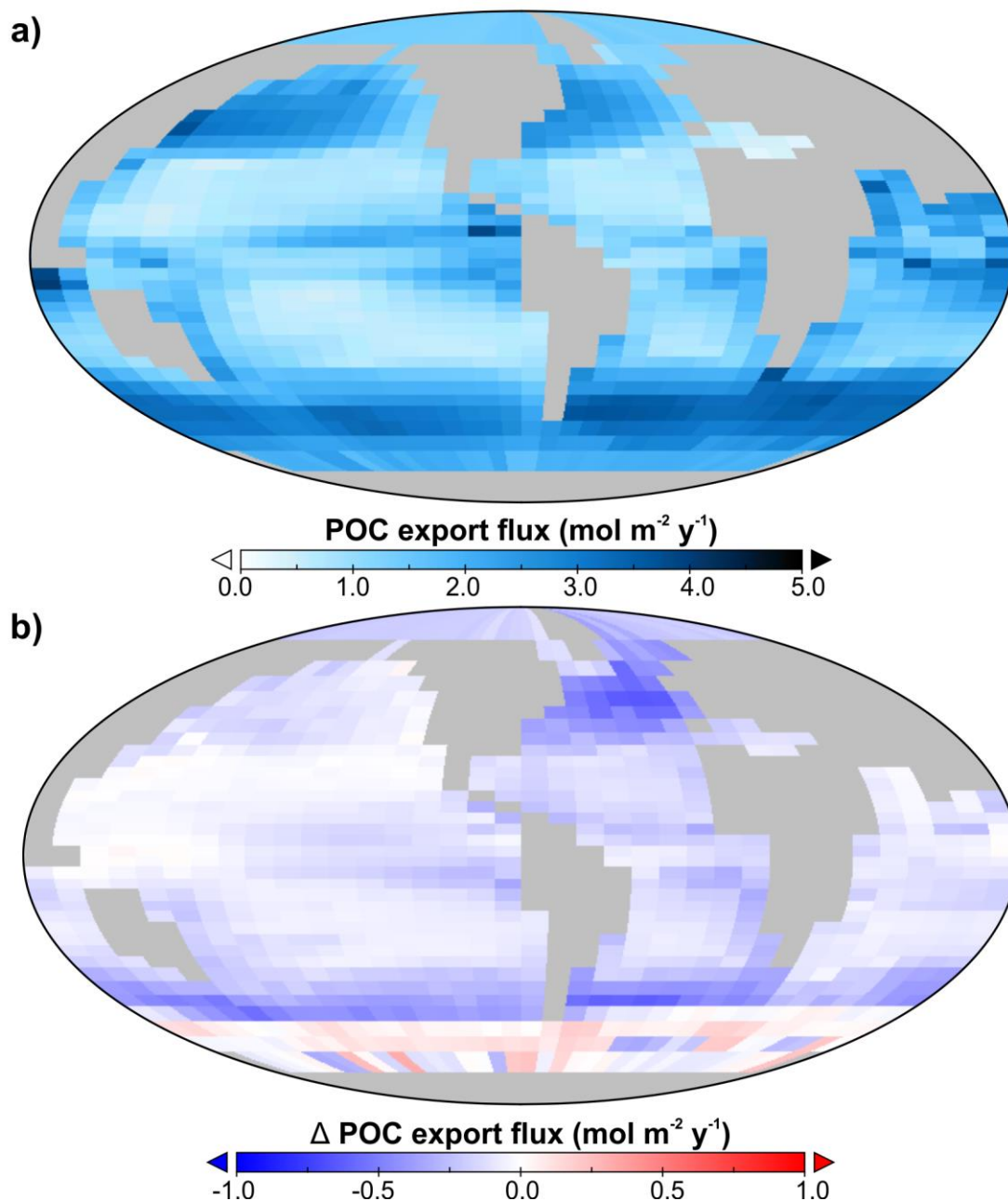Dynamics
Discussions

Open Access

Figure 4: cGEnIE/ecoGEnIE POC export maps, showing changes in baseline for BIO+TDR (a), ECO+FPR (b), and ECO+TDR (c) relative to the default BIO+FPR configuration (Figure 3).

Figure 5: ecoGEnIE POC export maps for ECO+TDR, showing baseline patterns (a) and the change in POC export by 2100 relative to the 1765 pre-industrial baseline as a result of RCP4p5 (b).

Table 1: **Features critical for resolving biological pump dynamics of CMIP5 ESMs used to simulate ocean carbon sink projections in IPCC AR5.** Details based on IPCC AR5 WG1 Table 6.11, Table 9.A.1, and cited literature. Note that there are some mismatches between number of functional groups reported in the literature and the IPCC description. Highlighted cells indicate the models with the most (green/darker) or moderately (orange/lighter) comprehensive – but not necessarily sufficient – representation of the relevant model feature.

ES Model (variant)	BGCM module	Key references	Type *	Functional Groups †	Reminerali-sation ‡	Element Cycles §	Elemental Stoichiometry		Limiting Nutrient	Shell Si/Ca ◇	Ballasting option ⸱
BCC-CSM1.1	(Inc.)	Based on OCMIP2 & MOM4; (Najjar et al., 2007; Wu et al., 2014)	Nutrient-restoring	0T: N/A [0]	Fixed rate	C, P, O	Fixed	P	N/A	N/A
CESM1 (BGC)	BEC	(Long et al., 2013; Moore et al., 2013)	PFTs	4.5T: 3.5P (diatom, diazo., small + cocco. fraction) 1Z [4]	Fixed rate (soft / ballast)	C, N, P, Fe, Si, O	Fixed quasi-Redfield (except diaz), Fe quota	N, P, Fe, Si	Diatoms (Si) & Coccos (Ca) separated by classes	Yes, part of fixed remin rate
CanESM2	CMOC	(Arora et al., 2009, 2011; Christian et al., 2010)	NPZD	2T: 1P 1Z [1X]	TDR	C, N	Fixed - Redfield	N, (Fe-param'd)	Temp-depend rain ratio for Ca, no Si	No mention
GFDL-ESM (2G & 2M)	TOPAZ2	(Dunne et al., 2012, 2013; Henson et al., 2009)	PFTs	3.5T: 3P (small, large, diazo.) 1Z implicit [6X]	Fixed rate (an/oxic)	C, N, P, Fe, Si, O	Variable N:P, optimal allocation, PFe quota	N+Am, P, Fe	No classes; opal (Si), calc., & arag.(Ca) "diagnosed"	Yes
HADGEM2 (CC & ES)	Diat-HadOCC	(Collins et al., 2011; Halloran, 2012; Jones et al., 2011; Palmer and Totterdell, 2001)	PFTs	3T: 2P (non/diatoms) 1Z [3]	Fixed rate	C, N, Fe, Si	Fixed - Redfield	N, Fe, Si (& DMS)	Si/Ca separated as diatom/non classes	No mention
INM-CM4	(Inc.)	(Volodin, 2007)	Parameterised POC flux	0T: N/A [0]	N/A	C	N/A	N/A	NA	N/A
IPSL-CM5 (A-LR, A-MR, & B-LR)	PISCES	(Aumont et al., 2003; Aumont and Bopp, 2006; Dufresne et al., 2013)	PFTs	4T: 2P (diatom, nano) 2Z (micro, meso) [2X]	Fixed rate (an/oxic)	C, N, P, Fe, Si	C,N,P Redfield; Fe,Si quota	N+Am, P, Fe, Si	Diatom Si class; ad hoc parametrised Rain Ratio for Ca	No
MIROC.ESM (- & CHEM)	(NPZD-type)	(Kawamiya et al., 2000; Schmittner et al., 2005; Watanabe et al. 2011)	NPZD	2T: 1P 1Z [2]	Fixed rate	C, N	Fixed - Redfield	N	N/A	No mention
MPI-ESM (LR)	HAMOC C5	(Ilyina et al., 2013)	NPZD	2T: 1P 1Z [2]	Fixed rate (an/oxic)	C, N, P, Fe, Si	Fixed - Redfield	N, P, Fe	Si/Ca fractionated by Si availability	No mention
NorESM1 (ME)	HAMOC C5	(Tjiputra et al., 2013)	NPZD	2T: 1P 1Z [2]	Fixed rate (an/oxic)	C, N, P, Fe, Si	Fixed - Redfield	N, P, Fe	Si/Ca fractionated by Si availability	No mention

Earth System
Dynamics
Open Access
Discussions
EGU

* NPZD = Nutrient Phytoplankton Zooplankton Detritus pools; PFTs = Plankton Functional Types (diatoms, coccolithopores, etc.)

† #T:=No. Total; #P=No. Phytoplankton types; #Z= No. Zooplankton types; [#]= IPCC AR5.1 table 6.11 No. plankton types; [#X]=

645 mismatch between cited literature and IPCC AR5.1 Table 6.11

‡ Fixed rate = prescribed remineralisation profile for sinking POC (sometimes split by class); TDR= temperature-dependent remineralisation

§ Major & minor nutrient cycles present

| Fixed= set ratio of C:N:P etc. (e.g. Redfield Ratio) in OM; Variable/quota= OM can take up / store differing ratios of nutrient relative to C

¶ One major limiting nutrient (P or N), co-limitation by both, and/or micronutrients (e.g. Fe) as well

650 ◊ Silicifiers & calcifiers differentiated (& by parameterisation or by functional classes)

⁇ Ballasting (OM sticks to sinking heavy PIC) available as an option

Table 2: Simulated changes in cumulative POC export and air-to-sea CO$_2$ flux during the 21st Century under different climate change scenarios (CMIP5 RCPs 3PD, 4p5, 6p0, and 8p5), illustrating the relative changes in biological pump strength and ocean carbon sink capacity respectively. Colours and shading designate strengthening (green/darker) or weakening (red/lighter) of the biological pump and ocean carbon sink relative to the default cGEnIE (the BIO+FPR configuration).

RCP	Model Configuration	Biological Pump Strength		Ocean Carbon Sink Capacity	
		Cumulative ΔPOC export 2000-2100 relative to preindustrial rates (GtC)	Cumulative ΔPOC export 2000-2100 relative to default cGEnIE (GtC)	Cumulative Air-to-Sea CO$_2$ transfer 2000-2100 (GtC)	Cumulative Air-to-Sea CO$_2$ transfer 2000-2100 relative to default cGEnIE (GtC)
3PD	BIO+FPR	-27.76	0	269.3	0
	BIO+TDR	-3.92	+23.84	266.6	-2.74
	ECO+FPR	-45.52	-17.76	271.4	+2.06
	ECO+TDR	-35.63	-7.87	270.2	+0.85
4p5	BIO+FPR	-32.88	0	387.6	0
	BIO+TDR	-6.64	+26.24	384.0	-3.65
	ECO+FPR	-51.97	-19.09	388.9	+1.32
	ECO+TDR	-41.12	-8.24	387.2	-0.43
6p0	BIO+FPR	-34.60	0	460.8	0
	BIO+TDR	-8.15	+26.45	456.7	-4.08
	ECO+FPR	-53.99	-19.39	461.1	+0.38
	ECO+TDR	-43.12	-8.52	459.3	-1.48
8p5	BIO+FPR	-41.23	0	585.5	0
	BIO+TDR	-11.54	+29.69	580.3	-5.12
	ECO+FPR	-62.92	-21.70	585.4	-0.09
	ECO+TDR	-50.64	-9.41	583.1	-2.39