

Ecosystem community structure shapes carbon dynamics in the ocean

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Abstract

Understanding how marine ecosystems influence air–sea CO₂ flux under climate change remains a major uncertainty in ocean carbon-cycle projections. Progress is hampered by insufficient representation of ecosystem complexity in climate models and insufficient observations for developing and calibrating complex marine ecosystem models. We present a novel three-branch ensemble of the PlankTOM12 global ocean biogeochemistry model, designed to isolate the influence of ecosystem community structure on carbon dynamics. PlankTOM12 represents ecosystem dynamics and their influence on carbon and other biogeochemical cycles through twelve interacting Plankton Functional Types (PFTs) spanning four trophic levels: heterotrophic bacteria/archaea, six phytoplankton PFTs, and five zooplankton PFTs. The branches share this ecosystem framework but differ in ecological parameterisations, producing distinct emergent communities. Branch 1 (GCB) is the historical configuration used in the Global Carbon Budget 2025. Branch 2 (OBio) focuses on reproducing observation-based global estimates of PFT carbon biomass, while Branch 3 (SMor) focuses on reproducing PFT vertical profiles. We evaluate each branch against ecosystem and biogeochemical observations and quantify differences in PFT biomass partitioning. The branches differ in total biomass, allocation among PFTs, and relative total phytoplankton and zooplankton biomass. These ecosystem differences propagate to primary production; sinking fluxes of organic carbon, calcium carbonate, and silica; carbon export and export efficiency. Ecosystem-driven differences also affect the latitudinal distribution of surface-ocean CO₂ flux in the tropics and Southern Ocean. We conclude that marine ecosystems have the potential to influence air–sea CO₂ flux under climate change and suggest priorities for future model–data development and integration.

1 Introduction

The increase of CO₂ concentration in the atmosphere and the associated climate change is weakening the ability of the oceans to take up further CO₂ (Canadell et al., 2021). This weakening effect is primarily due to the reduced chemical buffering of CO₂ under acidifying conditions, and to the reduced solubility of CO₂ in warm waters. The more complex effects of changes in ocean circulation and changes in marine ecosystems on the storage of natural CO₂ in the ocean are much less well known, both in direction and in amplitude. In particular, the feedback between climate change and marine ecosystems have been highlighted as a “known-unknown” in the past four Assessment Reports of the Intergovernmental Panel on Climate Change (IPCC; Le Quéré et al. in revision). The interactions between climate and marine ecosystems, as well as possible feedback mechanisms, are highly complex (Cooley et al., 2022), as most marine ecosystem processes are highly sensitive to rising temperatures (Doney et al., 2012; Poloczanska et al., 2016; Smale et al., 2019). Unlike for terrestrial ecosystems, marine ecosystems respond little to the direct effect of rising CO₂ concentrations in the ocean because CO₂ is already abundant (Riebesell et al., 2009). However, the effects of ocean acidification on organisms can be widespread, most directly through increasing energetic costs for calcifying organisms and thus reducing populations of key ecosystem habitats such as coral reefs and oyster beds (Doney et al., 2012), and organisms such as coccolithophores (Riebesell et al., 2017) and pteropods (Bednaršek et al., 2023). Climate change also has profound effects on ecosystem dynamics, including through changes in phenology, resulting in a mismatch between blooms of phytoplankton and energy needs of zooplankton (Cooley et al., 2022; Poloczanska et al., 2016). Climate change has already modified the niche of some critical organisms such as copepods (Beaugrand et al., 2014). Evidence from paleo-climate shows that changes in ecosystems are responsible for an increase in atmospheric CO₂ of around 30 ppm during the last glacial cycle (Kohfeld et al., 2005; Riebesell et al., 2009).

The ocean’s biological carbon pump (BCP) contributes to the regulation of atmospheric CO₂ over long time-scales by transporting carbon fixed by phytoplankton in the surface ocean to the ocean interior, where it can be stored for tens to thousands of years. Export occurs through three main pathways: the gravitational pump, involving the sinking of particulate organic carbon; the migrant pump, where vertically migrating organisms transport carbon to depth; and the mixing pump, which transports organic carbon via physical mixing (Nowicki et al., 2022). However, the strength of this connection between the BCP and the regulation of atmospheric CO₂ is uncertain due to poorly constrained export efficiencies, remineralisation depths, and circulation pathways (DeVries, 2022; Frenger et al., 2024; Siegel et al., 2023). Export efficiency – the fraction of organic carbon generated by photosynthesis in the surface ocean that sinks into the deep ocean – dictates how effectively the biological carbon pump removes atmospheric carbon dioxide, and is defined as export over primary production (Henson et al., 2019).

Progress in understanding of the linkages between climate and marine ecosystems is hampered by the lack of suitable ecosystem models that represent sufficient structure of ecosystems to account for shifts in ecosystem communities and quantify the associated carbon fluxes. Most models used by the IPCC have simplistic ecosystem structure representing only 1-3 phytoplankton and zooplankton PFTs (Rohr et al., 2022, 2023) and miss many key processes that influence export flux (Boyd et al., 2019; Henson et al., 2022). Increasingly detailed “Dynamic Green Ocean Models (DGOMs)” based on the representations of marine organisms as

plankton functional types (PFTs) have been developed to help understand the interactions between biogeochemical cycles, marine ecosystems, and their environment (Hood et al., 2006; Le Quéré et al., 2005, 2016). These more detailed models have provided insight into net primary production (Bopp et al., 2022; Buitenhuis, Hashioka, et al., 2013; Doléac et al., 2025), export (Henson et al., 2024), the role of oceans in the carbon pump (Dupont et al., 2023; Hauck et al., 2015) and the role of PFTs in ecosystem processes (Clerc et al., 2024; Hashioka et al., 2013; Le Quéré et al., 2016; Wright et al., 2021) and biogeochemical fluxes (Buitenhuis et al., 2006, 2010, 2019; Planchat et al., 2024).

DGOM development was inspired by terrestrial Dynamic Global Vegetation Models, which successfully applied the concept of plant functional types (Smith et al., 2001; Steffen, 1996) to reduce global biological complexity to a level manageable within the modelling context (Prentice et al., 1992). The criteria for defining functional types as PFTs in DGOMs detailed in Le Quéré et al. (2005) include that each PFT should (a) have an explicit biogeochemical role, (b) be defined by a distinct group of physiological, environmental, or nutrient requirements controlling its biomass and productivity, (c) have distinct effects on other PFTs e.g. through grazing, and (d) be of quantitative importance in at least some region of the ocean. The PlankTOM DGOM emerged from the PISCES model in 2003 (Aumont et al., 2003), which included two phytoplankton and two zooplankton PFTs at the time. PlankTOM has undergone multiple iterations, expanding initially to six phytoplankton PFTs (Le Quéré et al., 2005), two zooplankton and bacteria/archaea (Buitenhuis et al., 2006, 2010), and then crustacean macrozooplankton (Le Quéré et al., 2016), to then expand the zooplankton PFTs to five by adding jellyfish (Wright et al., 2021) and pteropods (Buitenhuis et al., 2019).

The main difficulty in the development of DGOMs has been the availability of observations to parameterise and calibrate the growing number of processes and interactions represented in the model, and to evaluate the outcome. To circumvent this difficulty, we build three branches of the PlankTOM12 model following three different logics of using available observations for model calibration. The three branches have identical ecosystem framework and identical physical environment, but each branch has its own set of ecosystem parameters allowing the emergence of distinct ecosystems. The three branches are based on the last published version of PlankTOM12 (here called GCB), which is the historical branch that underpinned much prior research on the carbon cycle using this model and contributed to the Global Carbon Budget 2023 (Friedlingstein et al., 2023). The two novel branches are (1) OBio, which was calibrated with a focus on reproducing global PFT biomass and ocean biogeochemistry fluxes (primary and export production), and (2) SMor, which was calibrated with a focus on reproducing the attenuation of PFTs with depth and minimising biases in surface ocean $f\text{CO}_2$ concentrations. We document the parameterisation and performance of the three PlankTOM branches here, and use this three-branch model setup to isolate and examine the effects of ecosystem composition on carbon dynamics.

2 Materials and Methods

2.1 General model description

The PlankTOM12 model version 2.1 presented here includes twelve PFTs, consisting of one heterotrophic bacteria/archaea, six phytoplankton (picophytoplankton, nitrogen fixers, coccolithophores, mixed phytoplankton, diatoms, and *Phaeocystis*), and five zooplankton (microzooplankton, mesozooplankton, pteropods, gelatinous macrozooplankton, and crustacean macrozooplankton). A description of each PFT and the size range covered by each type is provided in Table 1. The PFTs cover multiple trophic levels (Fig. 1a). All phytoplankton PFTs (pPFTs) contribute to net primary production (PP). Herbivores (PRO) and other zooplankton PFTs contribute to secondary production (SPP) when feeding on pPFTs. Carnivores, which include all zooplankton PFTs except protozooplankton, contribute to tertiary production (TPP) when feeding on zooplankton PFTs. Within carnivores, gelatinous and crustacean macrozooplankton consume all zooplankton PFTs (including each-other), while mesozooplankton and pteropods both consume protozooplankton. The grazing relationship between pteropods and mesozooplankton depends on the model branch. This trophic dynamic has been shown to be essential in reproducing the North-South ratio in surface chlorophyll that is present in the observations but not in most models (Le Quéré et al., 2016).

The evolution of PFTs are governed by equations of state which include a growth (or grazing) rate as a function of temperature (Fig. 2), and macronutrients and iron-light co-limitation (for phytoplankton PFTs) and food (for zooplankton PFTs). Loss rates include respiration, mortality for the top zooplankton (gelatinous and crustacean macrozooplankton), and grazing (Fig. 1).

Organic matter is represented with a dissolved organic carbon (DOC) pool, a small particulate organic carbon (POC) pool, a large POC pool, and in the most recent update a huge POC pool (see section 2.2.2). The allocation of carbon fluxes resulting from ecosystem processes among organic carbon (OC) pools is made according to the size of the PFTs feeding into each pool (Table 1; Fig. 1b). Small POC sinks at a constant speed (≤ 10 m/d; see Table 2). Large POC sinks between 50 and 150 m/d depending on the ballasting effect of calcite and silicate present in the particles (Buitenhuis et al., 2019). Huge POC sinks at a constant speed of 150 m/d. PlankTOM12 includes 39 tracers representing the full biogeochemical cycles of carbon, nitrate, phosphate, silicate, alkalinity, oxygen and chlorophyll and a simplified iron cycle. A full description of the PlankTOM12 model structure and equations is provided in the supplementary material (Buitenhuis et al., 2025).

PlankTOM12 is coupled to the global general circulation model Nucleus for European Modelling of the Ocean version 3.6 (NEMO v3.6). We use the global configuration with a horizontal resolution of 2° longitude by a mean resolution of 1.1° latitude using a tripolar orthogonal grid. The vertical resolution is 10m in the top 100m, gradually increasing to 500m at 5km depth, with a total of 30 vertical z-levels (Madec, 2013). The ocean is described as a fluid using the Navier–Stokes equations and a nonlinear equation of state (Madec, 2013). NEMO v3.6 explicitly calculates vertical mixing at all depths using a turbulent kinetic energy model and sub-grid eddy-induced mixing. The model is interactively coupled to a thermodynamic sea-ice model (LIM v2; Timmermann et al., 2005).

Table 1. Size range and descriptions of PFT groups used in PlankTOM12. Adapted from Wright et al. (2021).

Name	Abbreviation	Size Range (µm)	Description
Autotrophs			
Picophytoplankton	PIC	0.5 – 2	Pico-eukaryotes and non nitrogen fixing cyanobacteria such as <i>Synechococcus</i> and <i>Prochlorococcus</i>
Nitrogen fixers	FIX	0.7 – 2	<i>Trichodesmium</i> and nitrogen fixing unicellular cyanobacteria
Coccolithophores	COC	5 – 10	
Mixed-phytoplankton	MIX	2 – 200	Predominantly autotrophic dinoflagellates and chrysophytes
Diatoms	DIA	20 – 200	
<i>Phaeocystis</i>	PHA	120 – 360	Colonial <i>Phaeocystis</i>
Heterotrophs			
Bacteria	BAC	0.3 – 1	Here used to subsume both heterotrophic <i>Bacteria</i> and <i>Archaea</i>
Protozooplankton	PRO	5 – 200	Predominantly heterotrophic flagellates and ciliates
Mesozooplankton	MES	200 – 2000	Predominantly copepods
Pteropods	PTE	1000 – 3000	Pteropods
Crustacean macrozooplankton	CRU	>2000	Euphausiids, amphipods, and others
Gelatinous macrozooplankton	GEL	200 – >20,000	Cnidaria medusae, Ctenophores, and Tunicates

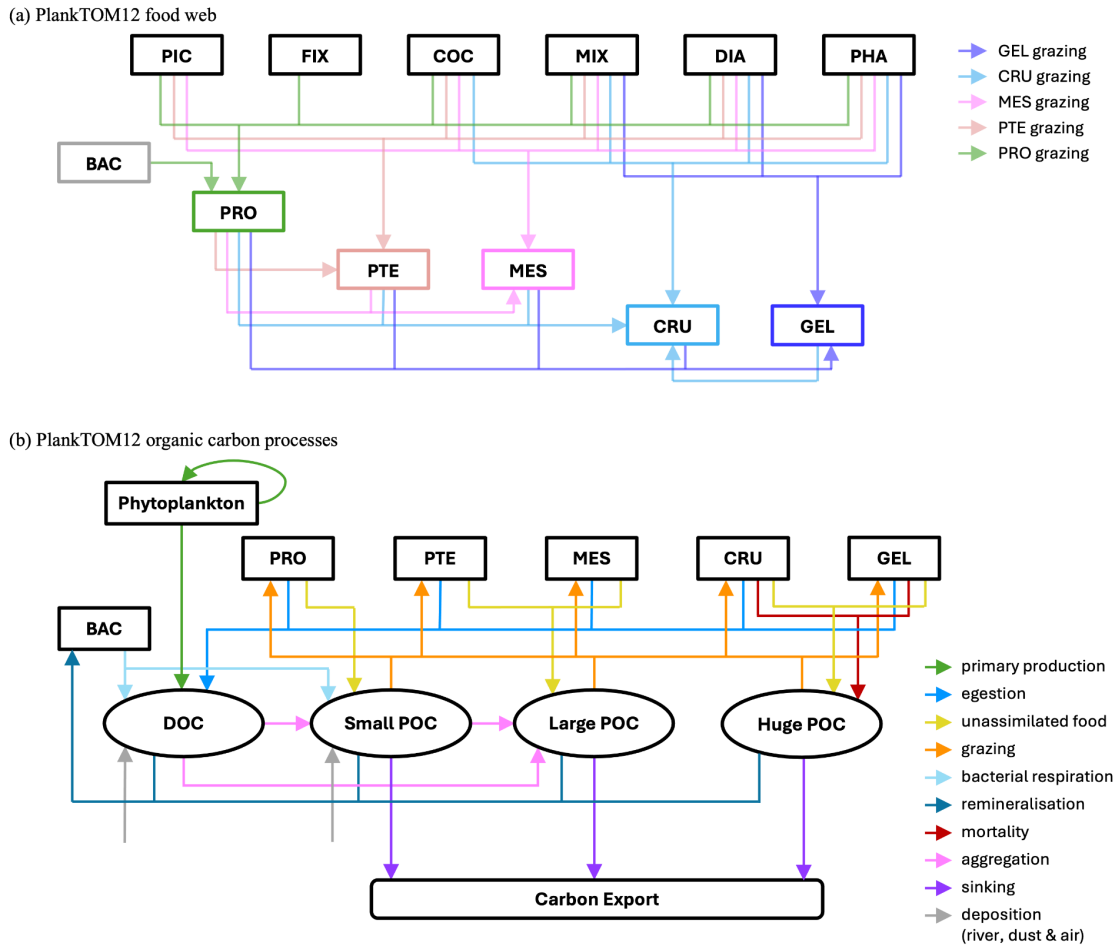


Figure 1. PlankTOM12 food web and organic carbon (OC) structure. Schematic representation of the main carbon fluxes between PFT and organic carbon components in PlankTOM12. (a) The food web structure of the PFT's showing zooplankton grazing on other plankton by directional arrows of the transfer of carbon. (b) The main carbon fluxes from PFTs to the organic carbon pools (dissolved (DOC), and three size classes of particulate organic carbon (POC)). The GCB branch has no huge POC pool, with fluxes from CRU and GEL going to the large POC pool. The corresponding processes are indicated in the legend, with full equations provided in the Supplementary Material. See Table 1 for PFT abbreviations.

2.2 Differences in branch set up

Processes have been revised since the last publication of PlankTOM12 (GCB branch). The key updates include the adoption of PFT growth equations based on optimal temperature, the addition of a third huge POC pool, the update of the dissolution of shells of calcite and aragonite (CaCO_3) and silicate (SiO_2), and the inclusion of a sediment module that accumulates and remobilises particulate organic matter reaching the ocean floor (Table 2). Branches OBio and SMor further differ through the closure mortality term for top predators and different calibration logics and associated parameter values (Table A1 and Fig. A1). A full documentation of the differences between the three branches is given in the appendix (Table A1 and Fig. A1), with key differences described below.

Table 2. Summary of differences in model formulations between the three PlankTOM12 branches. See text for details.

Difference	GCB	OBio	SMor
Temperature-dependence of PFT growth	Exponential growth with temperature, fit to 50th percentile	Bell shaped around optimal temperature, fit to 90th percentile	Bell shaped around optimal temperature, fit to 90th percentile
POC pools	Two POC pools Small POC sinks at 3m/d	Three POC pools Small POC sinks at 10m/d	Three POC pools Small POC sinks at 10m/d
Proxy biomass for top predation mortality	Total plankton biomass	Total plankton biomass	CRU biomass squared and GEL biomass squared
Dissolution of shells	SiO ₂ dissolution rate based on historic observations CaCO ₃ dissolution rate uses first order kinetics	SiO ₂ dissolution rate adjusted down based on recent observations CaCO ₃ dissolution rate uses second order kinetics	SiO ₂ dissolution rate adjusted down based on recent observations CaCO ₃ dissolution rate uses second order kinetics
Sedimentation process	Accumulates and remobilises particulate organic matter in the bottom water layer	Accumulates and remobilises particulate organic matter in a sediment layer	Accumulates and remobilises particulate organic matter in a sediment layer

2.2.1 PFT growth equation

Growth and grazing observations, upon which the model parameters are based, are from a compilation of multiple studies (Buitenhuis et al., 2006, 2010, 2019; Le Quéré et al., 2016; Stawiarski et al., 2016; Wright et al., 2021). In previous published versions of the PlankTOM model, and in the GCB branch here, growth as a function of temperature (μ^T) is represented using an exponential growth fitted with two parameters:

$$\mu^{T2} = \mu^0 \times Q_{10}^{\frac{T}{10}} \quad (Eq. 1)$$

where μ^0 is the growth at 0°C and Q_{10} is the temperature dependence of growth, both derived from observations, and T is the temperature (Le Quéré et al., 2016). The GCB branch fits the median of the normalised observations using the two-parameter formulation (Eq. 1; Fig. 2); for pteropods, the mesozooplankton fit to observational values is used because insufficient growth rate data in warm waters are available for pteropods (Buitenhuis et al., 2019). To better capture the observations given the multiple PFTs represented in PlankTOM12, the growth formulation has been updated to a bell-shaped curve centred around an optimal growth rate at a given temperature (Fig. 2). The three-parameter fit of the bell-shape curve is suitable for the global modelling of plankton because it can represent an exponential increase if the data support this (Schoemann et al., 2005). The three-parameter growth rate as a function of temperature (μ^{T3}) is defined by the maximum growth rate (μ_{max}) at the optimal temperature (T_{opt}) and the temperature interval (dT):

$$\mu^{T3} = \mu_{max} \times \exp\left[\frac{-(T-T_{opt})^2}{dT^2}\right] \quad (Eq. 2)$$

The bell curve is used in the OBio and SMor branches and was first introduced to the PlankTOM model by Wright et al. (2021). In Wright et al. (2021) the bell curve was fitted to the 50th percentile, whereas in the OBio and SMor branches the bell curve is fitted to the 90th percentile of observations to recognise that species with faster growth rates will dominate at a given temperature within each PFTs (Fig. 2). For pteropods in the OBio and SMor branches, the fit to the 90th percentile of observations was further calibrated to account for the skew in observations towards cold waters. Specifically, μ_{max} and dT were calibrated to provide the best spatial match to pteropod biomass observations in conjunction with the best match to spatial and seasonal observations of chlorophyll and pCO_2 .

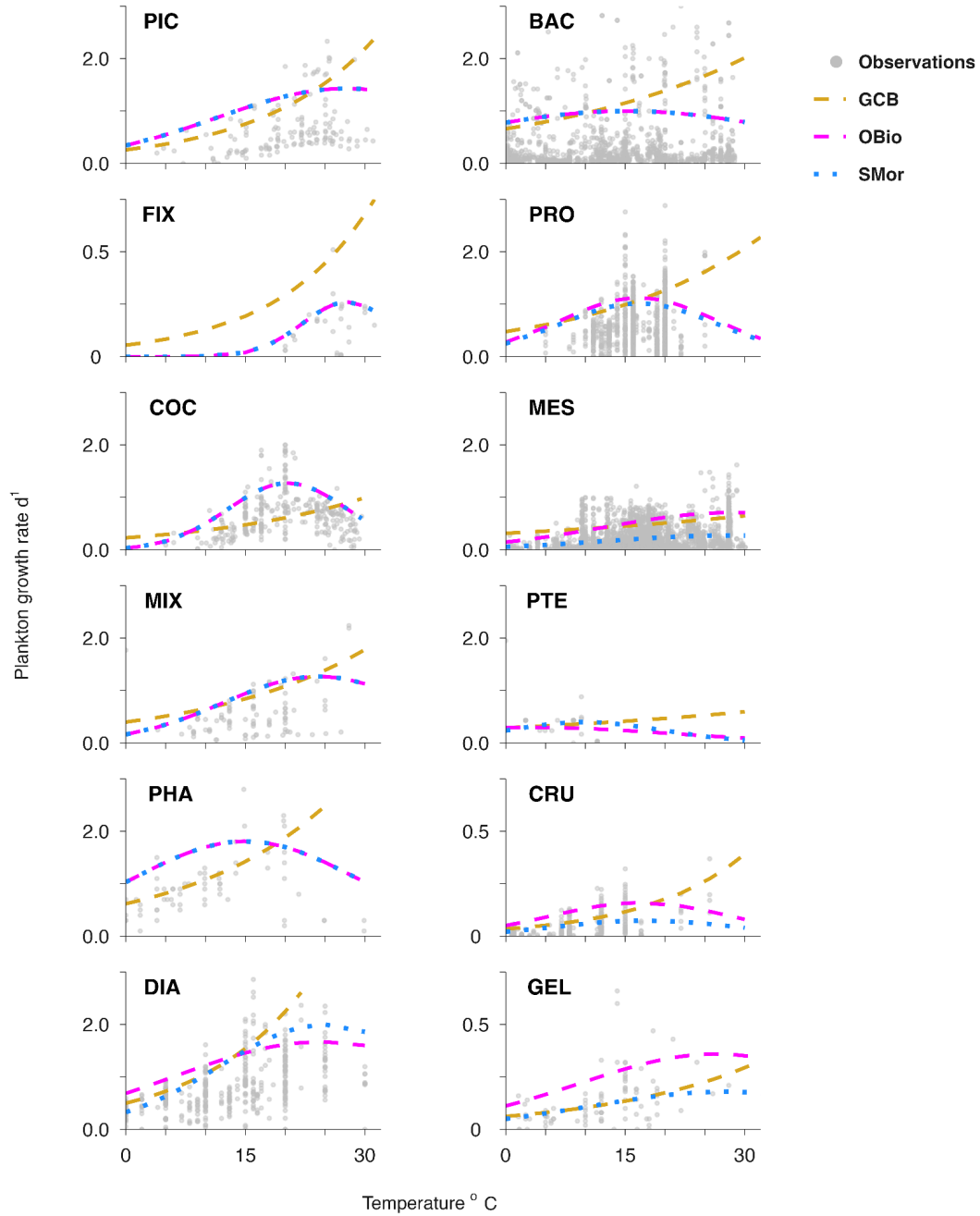


Figure 2. Growth rate as a function of temperature for the 12 PFTs represented in the PlankTOM12 model.

Observations are shown in grey. The fit to observations for each branch is shown; an exponential fit (Eq. 1) is used for GCB and a bell-shape fit (Eq. 2) is used for OBio and SMor.

2.2.2 Huge organic carbon pool

The OBio and SMor branches include a third, largest size class of POC (huge POC), which is produced by the egestion and mortality of macrozooplankton (crustacean and gelatinous). Huge POC sinks faster than the other two POC size classes at 150 m/d and has the same degradation rate, leading to a deeper remineralisation length scale and adding another pathway for ecosystem structure to influence export efficiency to the deep sea.

2.2.3 Dissolution of shells

The representation of particulate inorganic carbon export was updated by revising the parameterisation of calcite dissolution ($\beta_{CO_3} CAL$) as a function of saturation state (Ω_{sat}). A simplified log-linear formula,

$\beta_{CO_3} CAL = 0.253(1 - \Omega_{sat})^2$, was adopted based on CDiSK-IV observations, replacing earlier

parameterisations which overestimated dissolution rates. Field data suggest a potential step change in dissolution kinetic around $\Omega \approx 0.8$ (Naviaux et al., 2019), however this complexity was not implemented due to the risk of introducing model instability. In addition, the remineralisation of biogenic silica was reparameterised to produce a more realistic temperature dependence, resulting in a smoother increase in dissolution rates with temperature. This adjustment reduces silica remineralisation in the updated models relative to earlier versions and improves consistency with observed detrital silica export.

2.2.4 Sediment module

In some model simulations with the previous versions of PlankTOM, repeated cycles of resuspension of detritus that had accumulated in the bottom water layer followed by resedimentation led to numerical instability of the model. To address this, a simple 1-layer sediment was added to PlankTOM12 with only particulate detritus (carbon and iron in the three size classes of POC, $CaCO_3$ (calcite and aragonite) and SiO_2). The remineralisation rates of these pools of detritus is the same as in the overlying bottom water layer, and the dissolved remineralisation products are also added to the bottom water layer.

2.3 Calibration of model parameters

PlankTOM12 includes 280 ecosystem parameters. To limit the degrees of freedom, parameters for all pPFT and all zPFT are initially set at the same value by default, unless there is evidence from observations or from understanding of differences among PFTs. A wide range of observations are used to constrain model parameters as detailed in previous publications (Buitenhuis et al., 2006, 2010; Buitenhuis, Hashioka, et al., 2013; Buitenhuis et al., 2019; Le Quéré et al., 2016; Wright et al., 2021). Parameters are generally fixed at the median value of the observations, with the upper and lower quartiles (where they exist) used for calibration. Nevertheless, many parameters remain poorly constrained. To account for this limitation, we build three model branches calibrated individually following their own logic as detailed below. The parameter differences between the three branches are provided in the Appendices (Table A1). The full list of model parameters and their descriptions is given in the PlankTOM12 Manual, provided in the Supplementary Material.

The calibration of the OBio branch was conducted as follows. The well-measured parameters (e.g., thermal optima, maximum growth rate) are taken from experimental observation, while the more uncertain parameters (e.g., grazing preference matrix and half saturation concentration for zooplankton grazing) are adjusted freely to fit observed global PFT biomass from the MAREDAT database (Buitenhuis, Vogt, et al., 2013), chlorophyll distribution from satellite data (Sathyendranath et al., 2021), and nutrient vertical distribution from the World Ocean Atlas (Garcia, Bouchard, et al., 2024). Specifically, the model has pteropods consuming

mesozooplankton, but not mesozooplankton consuming pteropods (Hunt et al., 2008). In addition to the calibration above, this branch also uses the temperature-dependent and dissolution-dependent biogenic silica dissolution scheme of PISCESv2 (Aumont et al., 2015) to improve the dissolved silica distribution. For the iron cycle, the maximal iron-binding ligand concentration and the depth at which ligand reaches the maximum are prescribed as a latitude-dependent value. Maximum ligand concentration decreases from 0.8 nM north of 30°S to 0.5 nM south of 40°S, and the depth where the ligand field reaches its maximum deepens from 100 m in the north to 300 m south of 50°S. This enables the OBio branch to match the Huang *et al.* (2022) dissolved iron dataset.

The calibration of the SMor branch was conducted as follows. The growth parameters are also taken from observations as for OBio, with some further calibration (Figure 2). The first calibration focused on reproducing the vertical profiles of the PFTs reported in the MAREDAT observational database (Buitenhuis, Vogt, et al., 2013), which contains information on respiration and remineralisation processes not used in the OBio calibration. This necessitated the reduction of loss/respiration rates, which are less well constrained than growth rates. While this calibration improved the vertical structure of PFTs, it also made the model ecosystem less stable. This necessitated a secondary change, in which the mortality rates of the two top macrozooplankton PFTs were changed from a closure term using total biomass as a proxy for top predators not represented in PlankTOM, to square mortality closure terms for each of the two PFTs, giving the SMor branch its name. The model was then calibrated a second time to reduce biases in average PFT concentrations while also minimising the RMSE between the modeled and the observed fCO₂ from the SOCAT database (Bakker et al., 2024).

2.4 Model Simulations

The simulations are run from 1750 to 2023 forced by meteorological data including daily wind stress, cloud cover, precipitation and freshwater riverine input from ERA reanalysis fields (Kalnay et al., 1996; Soci et al., 2024). The simulations start with a 190-year spin up for 1750-1939 where the meteorological conditions for the year 1990 are used, looping over a single year. Year 1990 is used as a typical average year, as it has no strong El Nino/La Nina, and because of the greater availability of weather data (including by satellite) in 1990 compared to 1940, the dynamical fields are generally more representative of small-scale structures than the earlier years. The spin up is followed by daily forcing varying interannually for actual years from 1940-2023. All analysis is carried out on the average of the last 34-year period of 1990-2023. The simulations are initialised using a wide range of observations for physical and biogeochemical variables (nutrients: Garcia, Bouchard, et al., 2024; oxygen: Garcia, Wang, et al., 2024; temperature: Locarnini et al., 2024; salinity: Reagan et al., 2024), and the mean concentration from the MAREDAT carbon biomass database for PFTs (Buitenhuis, Vogt, et al., 2013).

2.5 Analysis

A benchmarking analysis was applied to each model branch, comparing 18 variables to observations. The relative ratio is calculated as the modelled value divided by the observed value. We use a log scale for the heatmap centered on 1 and ranging from 0.125x to 8x. A relative ratio of 2 indicates the model value is double

the observed value, and 0.5 that it is half the observed value. If the observation comparison has a range of data, we use the upper or lower limit for calculating the relative difference, depending on whether the model value is above or below the range, respectively. If the model value is within the observation range, we set the difference to one. Blank columns indicate no observation data is available for that variable. The North/South chlorophyll ratio (N/S ratio) is an emergent ecosystem metric developed by Le Quéré et al. (2016) as a simple method to quantify model performance for emergent properties, focusing on the Pacific Ocean, where this ratio is most pronounced in observations. The N/S ratio averages chlorophyll in two regions in the Pacific Ocean; between 30° and 55° latitude in both hemispheres and 140–240°E in the north and 140–290°E in the south.

Principal component analysis (PCA) was applied independently to each model branch using PFT biomass and ecosystem flux variables to identify the dominant patterns of covariance among model variables. Variables included in PCA analysis were the twelve PFTs, export and biogeochemical fluxes, and primary production. For the PCA analysis, PFT biomass was vertically integrated over the upper 200 m, which is close to observed zooplankton net sampling. Primary production was vertically integrated over the upper 100m (to capture the association with export fluxes), and carbon export and export efficiency were extracted directly from the 100 m depth level. Processed variables were flattened into a common sample dimension and z-standardised prior to PCA. PCA loadings were used to characterise ecosystem covariance structure across models. Loading spaces were aligned using orthogonal Procrustes rotation to facilitate inter-model comparison, and exploratory clustering of aligned loading vectors was performed using k-means clustering to identify groups of variables with similar covariance structure within PCA space. The optimal number of clusters for each model configuration was determined by selecting the clustering solution with the highest silhouette score across candidate solutions ranging from 2–5 clusters. Similarity between model loading structures was further quantified using permutation-based Procrustes analysis applied to aligned PCA loading matrices (PC1-PC3), where statistical significance was assessed from 9,999 random permutations of variable ordering following orthogonal Procrustes rotation.

3 Results

3.1 Branch Assessment

We evaluated the three branches using a suite of observational metrics. Our assessment focused on surface ocean observations with the broadest global coverage to minimize errors from spatial gaps in the data. We subsampled the model to match each observational metric before conducting statistical analysis. In the statistical comparison, no single branch emerged as clearly superior across multiple parameters. For example, OBio performs best for chlorophyll but least well for export, while SMor performs best for primary production but least well for Si concentration (Fig. 3). The spread in each metric between the branches in the Taylor distribution is greater than in previous PlankTOM updates (Le Quéré et al., 2016), highlighting the increasing complexity of the modelled system and associated feedbacks.

The benchmarking in Figure 4 demonstrates both the consistency and the differences between the branches. Most of the PFTs sit within the observational range, which were used for model calibration, but notably *Phaeocystis* and bacteria are consistently underestimated across the three branches. Coccolithophores are also notably overestimated in GCB by ~9 times and in SMor by ~1.3 times the upper end of the observations and are within the observed range in OBio. The ecosystem fluxes and chlorophyll metrics show more of a patchwork for the model relative differences to observations, again showing no single branch emerging as clearly superior across multiple parameters (Fig. 4).

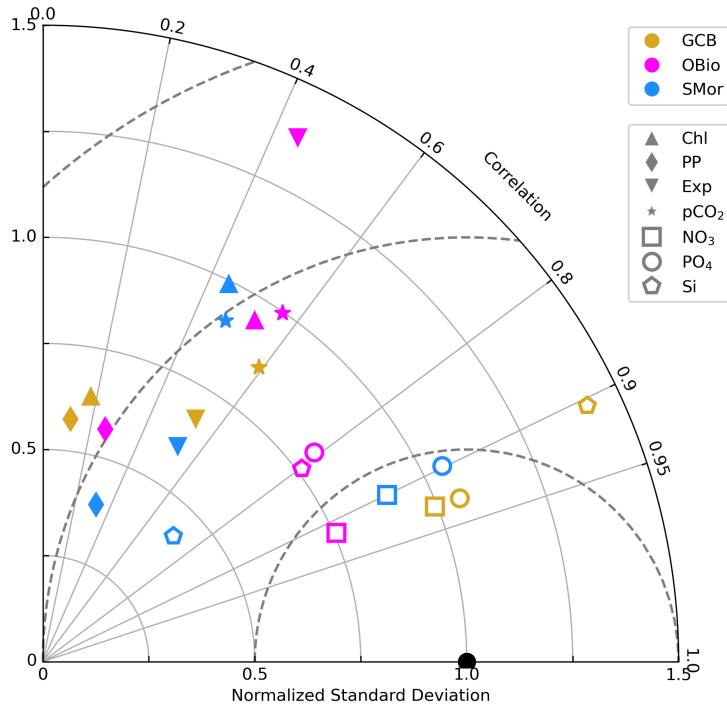


Figure 3. Taylor Diagram comparing the spatial distributions of surface concentration in annual mean chlorophyll, primary production (PP), export production (Exp), $p\text{CO}_2$, NO_3 , PO_4 and Si, of the three model branches with observations. Chlorophyll observations and model treatment are as in Figure 3.5 (Sathyendranath et al., 2019, 2021). Primary production observations are from Buitenhuis et al. (2013). Export observations are a gridded data product from Nowicki et al. (2022), using the gravitational pump. $p\text{CO}_2$ observations and model treatment are as in Figure 3.8. Nutrients are shown as open symbols to aid in visual clarity, nutrient observations are from WOA23 (Garcia, Bouchard, et al., 2024). The black dot shows the location where the model results should be if it was perfect and there were no errors in the observations. The distance from the black dot quantifies the performance of the model (Taylor, 2001).

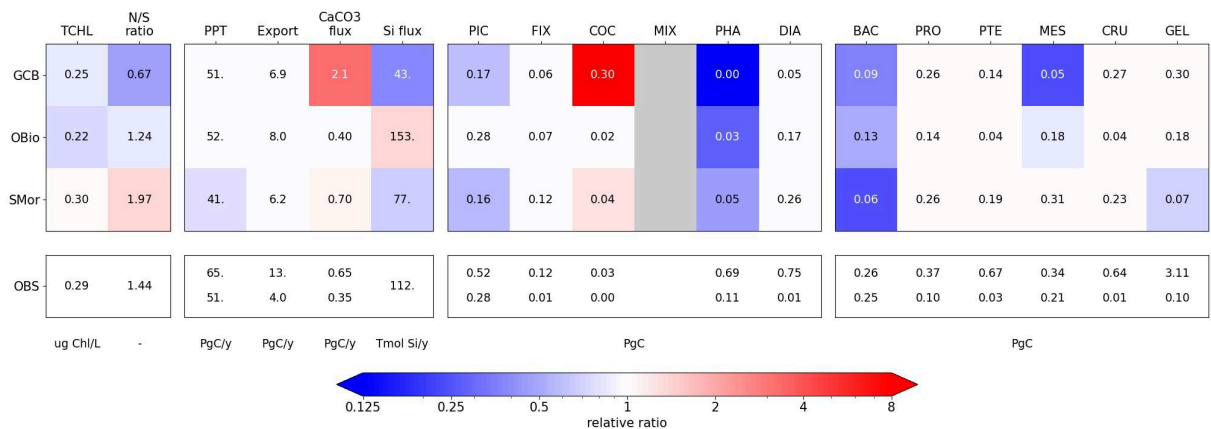


Figure 4. Benchmarking analysis to compare 18 variables to observations across three model branches. Relative ratio is computed as the model value divided by the observed value. The ratio is shown on a log scale centered on 1, so that a relative ratio of 2 indicates the model is double the observed value, and 0.5 indicates that the model is half the observed value. For observation ranges, we use the nearest bound (upper if the model is higher, lower if below); values within the range are set to 1. Blank columns indicate no observations.

3.2 Ecosystem Composition

Distinct ecosystem structures emerge from the three model branches, characterized by unique plankton assemblages at both global (Table 3, Fig. 5) and regional scales (Fig. 6-7). Each branch exhibited characteristic dominant PFTs. The GCB branch was characterized by the predominance of mid-sized phytoplankton (Coccolithophores) alongside small and large zooplankton (protozooplankton and gelatinous and macro-zooplankton). In contrast, the OBio branch was dominated globally by small and large phytoplankton (picophytoplankton and diatom), with region-specific dominance of nitrogen-fixers in the tropics and *Phaeocystis* in the polar north (Fig. 6-7). The OBio total zooplankton biomass was notably smaller (almost half) of that in GCB and SMor (Table 3), and was mostly distributed mainly among protozooplankton, mesozooplankton, and gelatinous macrozooplankton, but with dominance of pteropods and crustacean macrozooplankton in the high latitudes. The SMor branch also showed abundant picophytoplankton and diatom biomass, although with very different regional patterns in picophytoplankton compared to OBio, with also abundant mixed phytoplankton (Fig. 6-7). SMor produced high biomass across all zooplankton except gelatinous macrozooplankton, with dominance of pteropods and crustacean macrozooplankton in the high latitudes that extends further into the subpolar regions than in OBio (Fig. 7). There is distinct PFT regional distribution within and across branches (Fig. 6-7).

Table 3. Global PFT biomass (0-200m average in PgC) for 1990-2023. The observed phytoplankton and zooplankton totals are calculated as the sum of the min and max of the PFT's in each group.

	PlankTOM12 Branches			Observations	References
	GCB	OBio	SMor		
Autotroph biomass					
PIC	0.17	0.28	0.16	0.28 - 0.52	Luo et al. (2012)
FIX	0.06	0.07	0.12	0.008 - 0.12	Buitenhuis et al. (2013a)
COC	0.3	0.02	0.04	0.001 - 0.032	O'Brien et al. (2013)
MIX	0.09	<0.01	0.21	-	-
PHA	<0.01	0.03	0.05	0.11 - 0.69	Vogt et al. (2012)
DIA	0.05	0.17	0.26	0.013 - 0.75	Leblanc et al. (2012)
Heterotroph biomass					
BAC	0.09	0.13	0.06	0.25 - 0.26	Buitenhuis et al. (2012)
PRO	0.26	0.14	0.26	0.10 - 0.37	Buitenhuis et al. (2010)
PTE	0.14	0.04	0.19	0.026 - 0.67	Buitenhuis et al. (2013a)
MES	0.05	0.18	0.31	0.21 - 0.34	Moriarty & O'Brien (2013)
CRU	0.27	0.04	0.23	0.01 - 0.64	Moriarty et al. (2013)
GEL	0.3	0.18	0.07	0.10 - 3.11	Bar-On et al. (2018), Lucas et al. (2014), Wright et al. (2021)
Phytoplankton total	0.68	0.56	0.84	0.41 - 2.11	
Zooplankton total	1.01	0.57	1.06	0.45 - 5.13	

Finally, OBio produced the lowest total plankton biomass among the three branches, with nearly equal biomass among phytoplankton and zooplankton (0.56 and 0.57 PgC). Both GCB and SMor produced higher zooplankton than phytoplankton biomass, by 49% and 26%, respectively. SMor produced the highest phytoplankton and zooplankton biomass of the three branches (Table 3). All three branches sit comfortably within the observed ranges for total zooplankton and total phytoplankton biomasses (Table 3), although the biomass of bacteria appears underestimated in all three branches and all branches under or overestimate the biomass of at least one PFT.

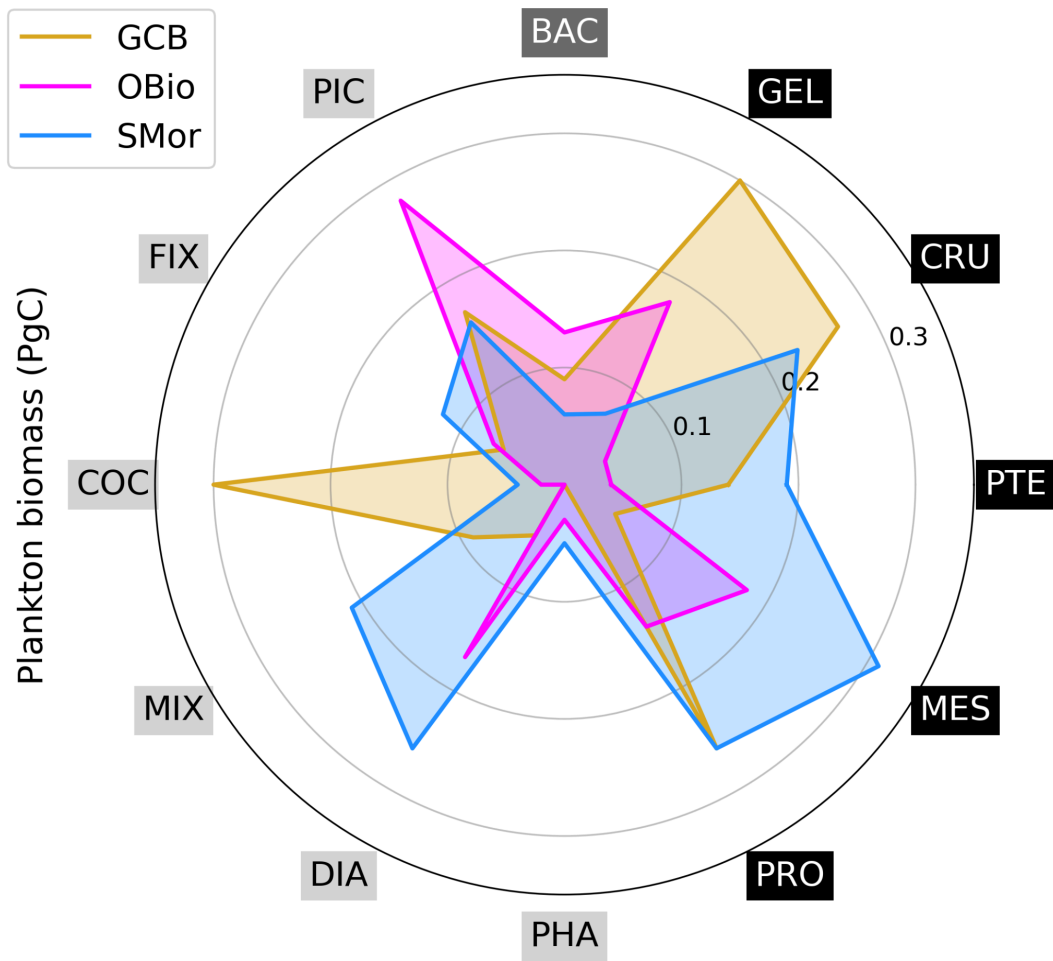


Figure 5. Global plankton carbon biomass for three model branches (PgC). Results are averaged over 1990-2023 and over 0-200m. The PFT's are presented clockwise in size order from largest (gelatinous zooplankton) to smallest (bacteria; Table 1). PFT labels are grouped by colour; zooplankton labels are black, phytoplankton labels are light grey and the bacteria label is dark grey.

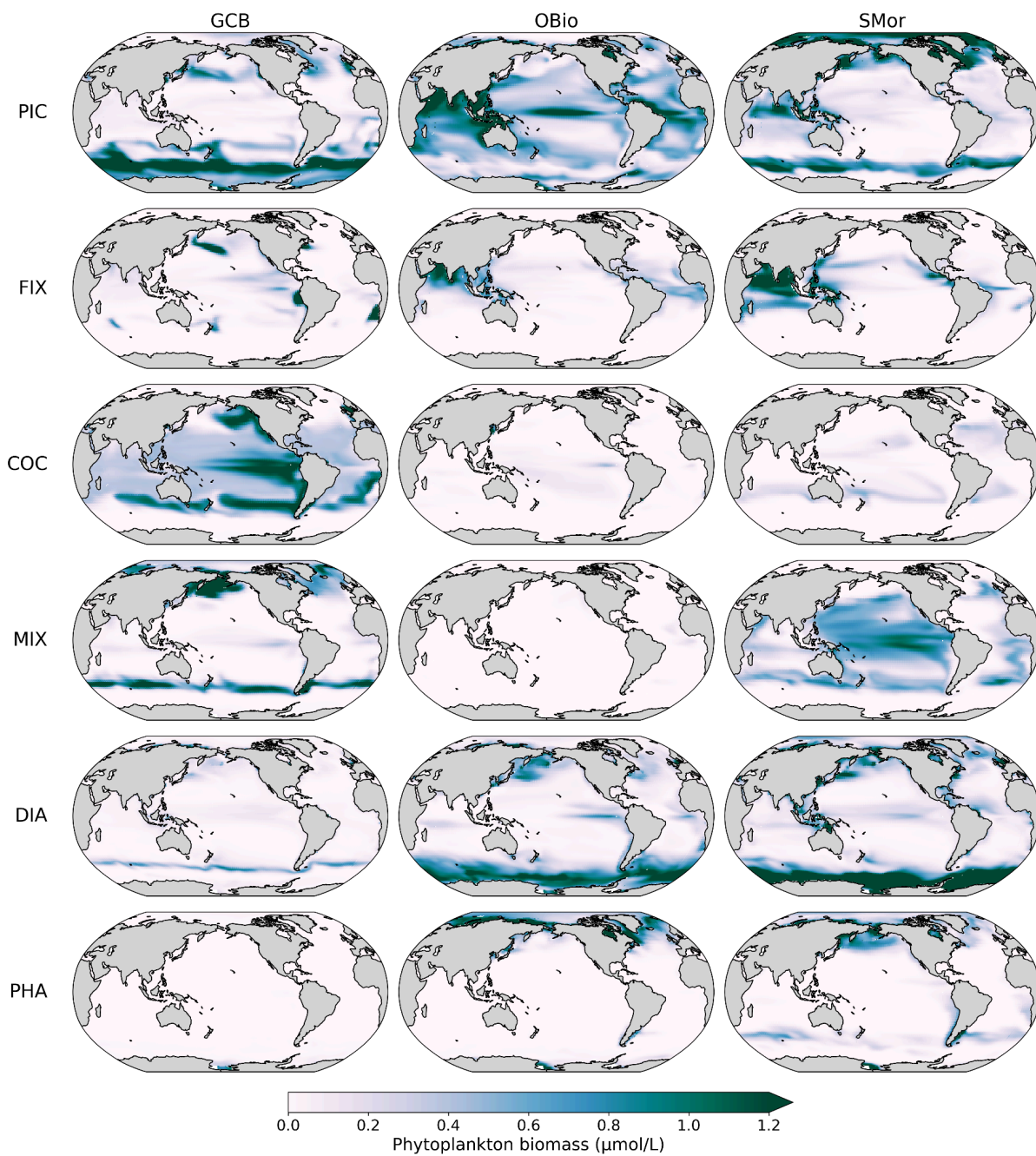


Figure 6. Annual mean phytoplankton carbon biomass ($\mu\text{mol C/L}$) for three model branches. The left-hand column is the GCB branch, the middle column is the OBio branch and the right-hand column is the SMor branch. Results are averaged over 1990-2023 and over 0-200m.

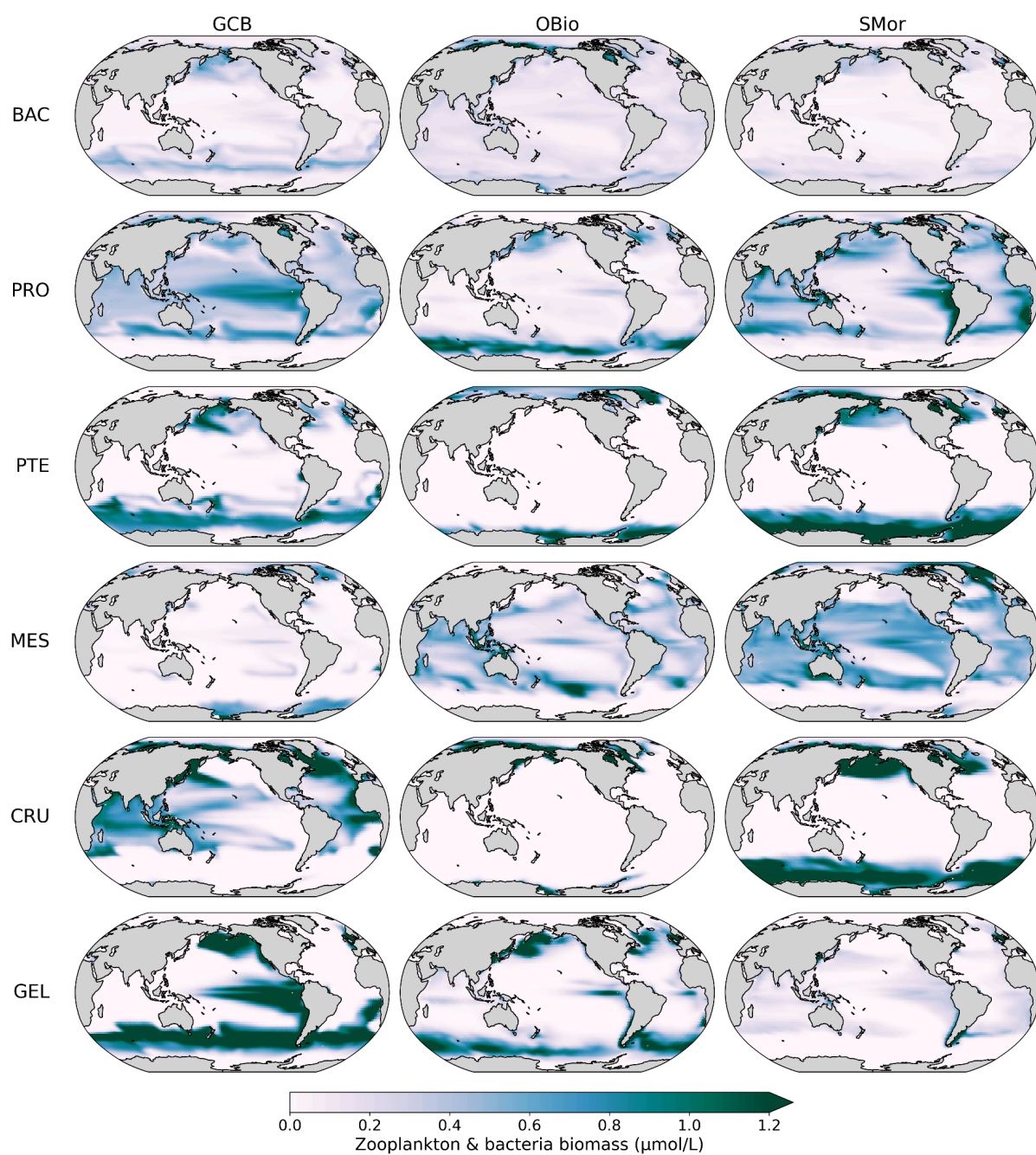


Figure 7. Annual mean zooplankton carbon biomass ($\mu\text{mol C/L}$) for three model branches. The left-hand column is the GCB branch, the middle column is the OBio branch and the right-hand column is the SMor branch. Results are averaged over 1990-2023 and over 0-200m.

3.3 Chlorophyll

The surface chlorophyll concentration and spatial distribution is distinct among the three model branches, reflecting the emergent phytoplankton composition (Fig. 8). OBio most closely matches the observations, with the shortest distance to the Taylor plot measure of model performance (Fig. 3). OBio shows peaks in the equatorial Atlantic and Pacific Oceans and in polar and subpolar regions, with low chlorophyll in the subtropical gyres and high chlorophyll primarily in coastal regions (Fig. 8). SMor is slightly further from observations in terms of model performance than OBio (Fig. 3). SMor closely matches observed chlorophyll concentration above 55°N but over-estimates chlorophyll at similar latitudes in the south. In the tropics, SMor has a skewed distribution away from the Pacific ocean towards the Indian ocean, opposing the observed distribution (Fig. 8). GCB underestimates the observed chlorophyll concentration at northern latitudes, particularly in the Atlantic Ocean, and overestimates across the central Southern Ocean. Both OBio and SMor improve on GCB estimates of chlorophyll, particularly in the high latitudes (Fig. 8).

While OBio shows the best overall spatial match to chlorophyll observations (Fig 3 and Fig. 8), SMor is closer to the global observed concentration of 0.29 $\mu\text{g Chl/L}$, with a slightly higher concentration of 0.3 $\mu\text{g Chl/L}$, compared to OBio's underestimate of 0.22 $\mu\text{g Chl/L}$ (Fig. 4). GCB also performs better than OBio for global chlorophyll, with a closer underestimation of 0.25 $\mu\text{g Chl/L}$ (Fig. 4). OBio performs best of the three branches for the North/South ratio metric, with OBio slightly underestimating the observed ratio of 1.44 with a ratio of 1.24, SMor performs the next best overestimating the observations with a ratio of 1.97, and both improve upon GCB which underestimates the observations with a ratio of 0.67 (Fig. 4). The North/South chlorophyll ratio metric was developed by Le Quéré et al. (2016) as a simple method to quantify model performance for emergent properties, focusing on the Pacific Ocean, where this ratio is most pronounced in observations. These differences in which model performs best for chlorophyll depending on which metric is used, highlights the importance of assessing models over multiple metrics, as well as highlighting the emergent complexity of the modelled ocean systems.

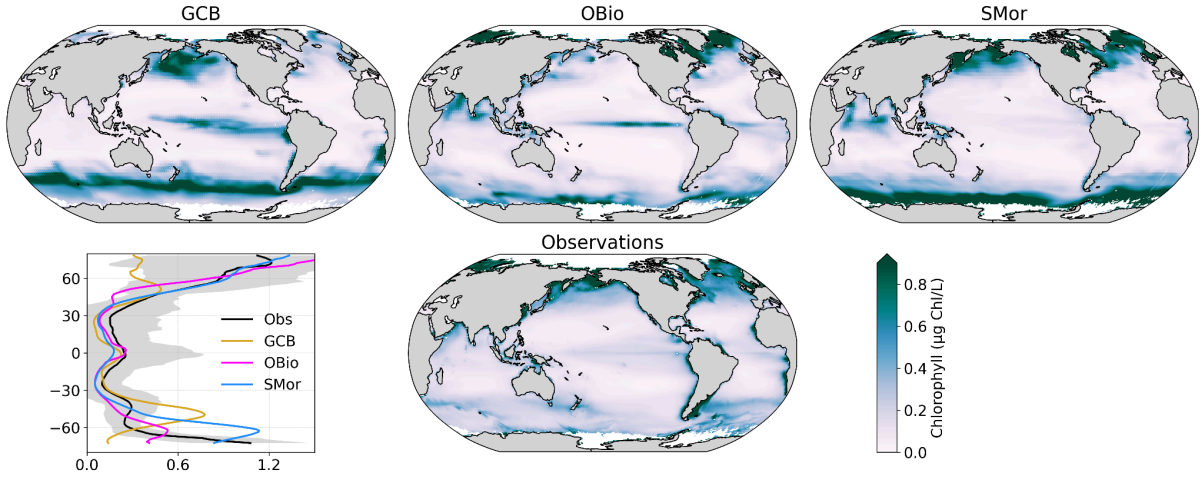


Figure 8. Annual mean surface ocean chlorophyll ($\mu\text{g Chl/L}$) for observations and three model branches. Observations are a climatology, filtered by removing grid cells where <6 months of data are available. Model results are converted to climatologies and then subsampled to the filtered observational locations. The top left-hand panel is the GCB branch, followed by the OBio and SMor branches. The centre bottom panel is the observations from OC-CCIv5 (**Sathyendranath et al., 2019, 2021**). The lower left panel shows the latitudinal average for each model branch and the observations, together with a ± 1 standard deviation for the observations. Results are averaged over 1998-2023.

3.4 Ecosystem Productivity & Fluxes

GCB and OBio have primary production of 51.3 and 51.5 PgC/y, respectively, within the range of observational estimates of 51-65 PgC/y. SMor has the lowest primary production of 40.5 PgC/y, despite having the highest phytoplankton biomass (Table 4 and Table 3). OBio has the highest carbon export flux at 100m of 8.0 PgC/y, within the range of observational estimates of 4-13 PgC/y, while GCB and SMor have lower carbon export still within the range of observations of 6.9 and 6.2 PgC/y respectively (Table 4).

GCB has high calcium carbonate production and flux, consistent with its overestimation of coccolithophores (Table 3) and well above the upper end of observational estimates of 0.5-1.6 PgC/y, with 4 times the production and 2 times the flux (Table 4). OBio has calcium carbonate production of 1.7 PgC/y, just above the top end of the observed range, while the CaCO_3 export flux is 0.41 PgC/y, at the low end of the observed range. SMor has a calcium carbonate production of 1.8 PgC/y, but its CaCO_3 export flux sits within the observed range at 0.7 PgC/y (Table 4). The higher flux in SMor than OBio is consistent with its higher biomass of coccolithophores and pteropods (Table 3).

Diatoms are the dominant driver of silicate production and flux, accumulating silica within their frustules as they grow (Tréguer et al., 2021; Yool & Tyrrell, 2003). OBio has the highest silicate production and export flux (216 and 153 Tmol Si/y), within and just above observational estimates, followed by SMor with silicate production and export flux of 114 and 77 Tmol Si/y, roughly half and two-thirds that of observations, respectively (Table 4). Both branches have diatom biomass within the observational range, however the diatom biomass in OBio is approximately two-thirds of the diatom biomass in SMor (Table 3), despite the higher silicate production and flux in OBio. This discrepancy likely reflects the distinction between silicate production as a rate and diatom biomass as a standing stock: a smaller diatom stock in OBio could sustain higher annual silica production if growth and loss occur more rapidly. Consistent with this interpretation, silica production per unit diatom biomass is ~2.6-fold higher in OBio, indicating substantially faster diatom turnover and/or an elevated Si:C ratio. The GCB branch is prior to the silica updates and does not include silica production, so is not appropriate for direct comparison to its silica flux here (see Table 2 and Sect. 2.2.3).

Oceanic nitrogen fixation is the process by which marine organisms (namely *Trichodesmium* and nitrogen fixing unicellular cyanobacteria) convert dissolved nitrogen gas into biologically available nitrogen compounds that help sustain marine primary production (Sun et al., 2026). OBio has the highest nitrogen fixation of the three branches (226 Tg N/y), followed by SMor (179 Tg N/y) and then GCB (159 Tg N/y). All three branches are substantially higher than the most recent observational estimates of 74 (59-86) Tg N/y (Table 4). However, SMor and GCB are consistent with the much higher budget-based estimate from Wang et al. (2019) of 163 Tg N/y and align with the higher end of Earth System Model estimates of 76-186 Tg N/y (Wrightson & Tagliabue, 2020). Counterintuitively OBio does not have the highest standing biomass of nitrogen fixers despite having the highest nitrogen fixation, with almost half the biomass of SMor (0.07 and 0.12 PgC respectively; Table 3). However, OBio has the highest protozooplankton grazing preference for nitrogen fixers of the three branches (Fig. A1) which prevents biomass accumulation through consumption.

Table 4. Global means for the carbonate system and ecosystem productivity and fluxes for 1990-2023 (Pg/y). Productivity is integrated over the full model depth, except where indicated. Fluxes are at 100m. Branches values are for the full model and not subsampled to observations.

*no silicate production in GCB because it is prior to the silica update.

	PlankTOM12			Observations	Reference
	GCB	OBio	SMor		
Ecosystem Productivity depth integrated					
Primary production (PgC/y)	51.3	51.5	40.5	51 - 65	Buitenhuis, Hashioka et al. (2013)
Calcium carbonate production (PgC/y)	6.3	1.7	1.8	0.5 - 1.6	Doney et al. (2009)
Silicate production (Tmol Si/y)	N/A*	215.5	113.6	255 ± 52	Tréguer et al. (2021)
Nitrogen fixation (Tg N/y)	158.8	226.3	178.5	74 (59 - 86)	Sun et al., (2026)
Ecosystem Fluxes at 100m					
Carbon export flux (PgC/y)	6.9	8.0	6.2	4 - 13	Doney et al. (2024)
Calcium carbonate flux (PgC/y)	2.1	0.4	0.7	0.5 ± 0.15	Dunne et al. (2007)
Silicate flux (Tmol Si/y)	43.0	153.0	76.7	112	Tréguer et al. (2021)
Carbonate System (PgC/y) surface ocean					
CO ₂ Sink	2.1	2.6	2.8	2.7 ± 0.4	Friedlingstein et al. (2026)

OBio and SMor have a CO₂ sinks of 2.6 and 2.8 PgC/y, respectively, matching the observed sink (Table 4). The CO₂ sink in GCB is just below the observed sink range, at 2.1 PgC/y.

3.4.1 CO₂ Flux and *p*CO₂ Distribution

All three branches show similar global patterns of *p*CO₂ that are within the range of observations (Fig. 9), although there are some inter-model differences. OBio performs better in the high-latitudes with values close to the annual longitudinal mean, while GCB and SMor overestimate *p*CO₂ in these regions. The observed peak in *p*CO₂ in the equatorial pacific is most closely estimated by GCB (Fig. 9).

For Δ*p*CO₂, all branches are within the observational range for the Subtropical North, Tropics and Subtropical South. In the Polar North all three branches slightly overestimate in the winter and underestimate in mid-summer. In the Polar South GCB and SMor show the inverse seasonal pattern to the observations, while the

pattern for OBio is better, the values are consistently too high (Fig. A2). In the tropics SMor shows the closest match to the observations (Fig. A2).

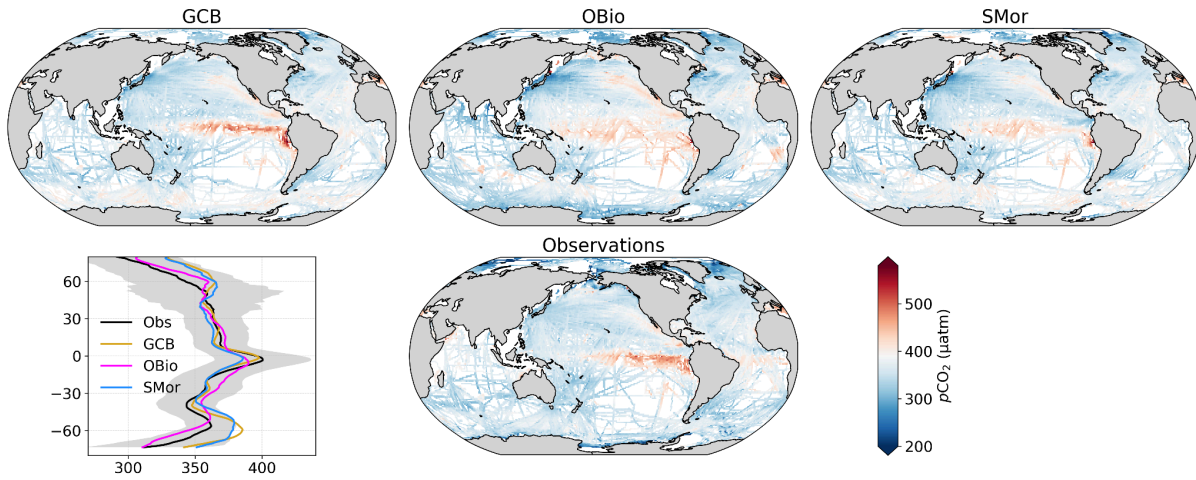


Figure 9. Annual mean $p\text{CO}_2$ (μatm) for the three model branches and observations. Observations are a gridded monthly data product from SOCATv2020 (Bakker et al., 2020), to which the model is subsampled. The bottom left panel shows the latitudinal average for the observations and each model branch, smoothed over 10 degrees.

3.4.2 Vertical Ecosystem Fluxes

Vertically, OBio has the closest carbon export depth profile compared to the observations, with higher values in the surface and greater attenuation with depth (Fig. 10). GCB and SMor have similar export depth profiles, slightly underestimating flux in the surface (above 500m), and over estimating below 500m, with a shallower attenuation curve (Fig. 10).

Calcium carbonate flux at 100m in the full model (unsampled) results in Table 4, show GCB has the highest flux (slightly above observations), followed by SMor which is within the observed range, and then OBio at the lower end of the observed range. When the model is subsampled to calcium carbonate flux observations and the vertical profile analysed (Fig. 10), the results are consistent in their magnitude ranking, although slightly different compared to observations. GCB performs the best of the three branches, OBio consistently underestimates the calcium carbonate flux across all depths, and SMor is in between (Fig. 10). However, the sparse nature of calcium carbonate flux observations makes the depth profiles hard to interpret and care must be taken not to read too much into the detail of them.

All three branches show a similar silicate flux depth profile to the observations overall, although GCB and SMor perform better in the surface (0-200m) where OBio underestimates, and OBio and SMor perform better in the subsurface (200-500m) where GCB underestimates compared to observations (Fig. 10). All three branches show a similar DOC depth profile to the observations, falling within the spread of the observations, although SMor underestimates and GCB overestimates the median from 0-1000m, while OBio matches the median from 0-300m and then slightly underestimates it to 1000m (Fig. 10).

The observed POC data (Kiko et al., 2022) were split into size ranges that best match the modelled components entering each POC pool. These are small POC 0.032-0.406 mm, large POC 0.406-3.25 mm and huge POC 3.25->26mm. All three branches have highest concentrations of POC in the small pool, followed by the large and huge pools, as observed (for the 50-300m depth band; Table 5), but their vertical distribution and attenuation differs both among branches and compared to observations. All three branches overestimate small POC in the surface compared to observations, OBio the least and GCB the most. By 300m small POC in all three branches has attenuated to a similar median to the observations (Fig. 10; Table 5).

All three branches estimate a median large POC which is within the spread of observations across the depth profile (Fig. 10), although the medians differ (Table 5). GCB consistently overestimates large POC median concentrations at all depths. OBio and SMor are close to observations at the surface, but overestimate in the subsurface and peak at ~100–150 m, similar to GCB. In contrast, the observed large POC maximum occurs closer to the surface. Large POC in OBio attenuates rapidly, reaching low concentration by 500m. In SMor large POC attenuates much more slowly, crossing the observed median at 1200m (Fig. 10).

The huge POC pool is a new update to the PlankTOM12 model and is not represented in the GCB branch. For OBio and SMor huge POC is within the spread of observations but show different depth profiles. Both branches peak around 100-150m, as in large POC, while the observations peak nearer the surface. OBio substantially overestimates the median of huge POC in the top 500m, but attenuates rapidly reaching a concentration close to the observed median by 1500m and below (Fig. 10; Table 5). Huge POC in SMor is closer to the observed median in the surface, but attenuates slower and its concentration remains higher than the observed median for all depths (Fig. 10; Table 5). The differences in huge POC between OBio and SMor can be attributed to the varying ecosystems biomass components which generate and remove huge POC. OBio has larger biomasses than SMor of both GEL (0.18 vs 0.16 PgC) and CRU (0.04 vs <0.01 PgC) which generate huge POC through messy-eating, fecal pellets and carcasses, and so a higher huge POC concentration in the top 200m is expected. The much faster attenuation over depth in OBio can be attributed to the larger BAC biomass than in SMor (0.13 vs 0.06 PgC), which remineralise huge POC. Although SMor has a greater total zooplankton biomass than OBio (0.91 vs 0.57 PgC) zooplankton grazing on huge POC is low and only has a small effect on the attenuation (Fig. 10, Table 3).

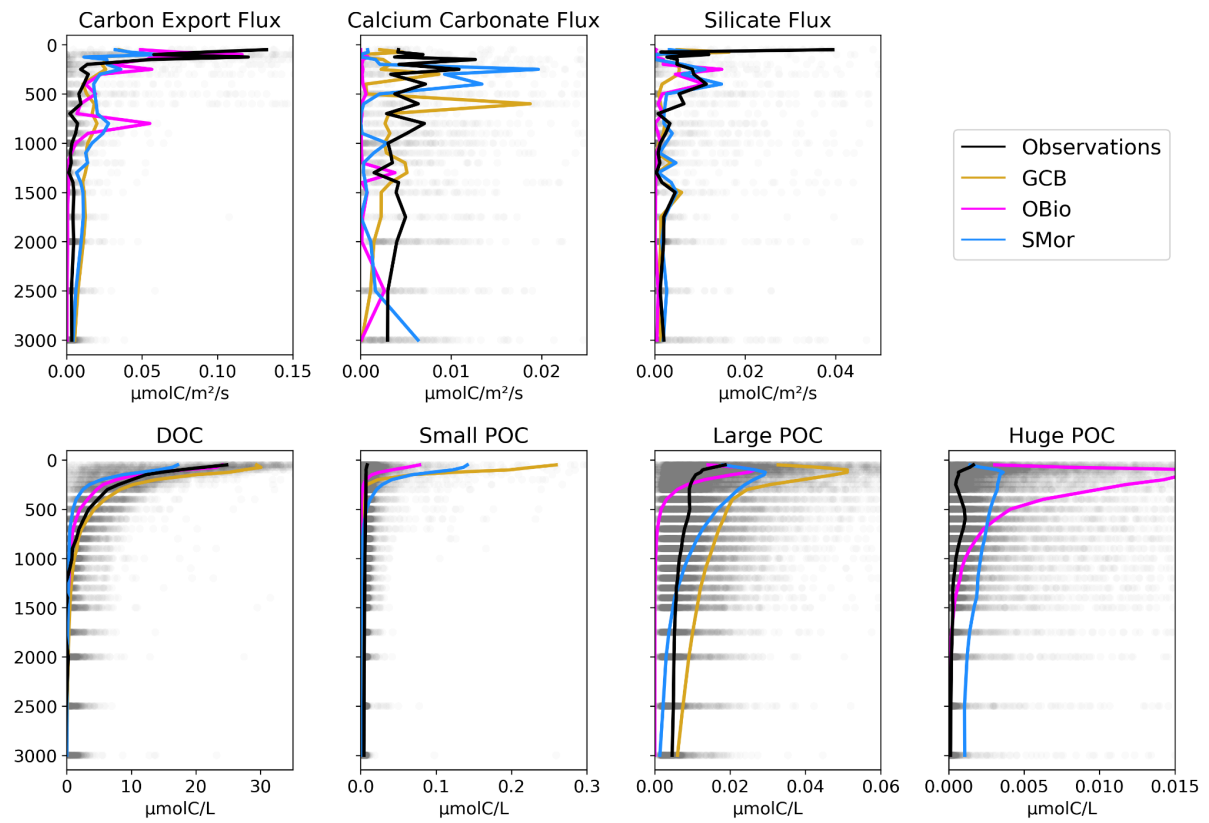


Figure 10. Ecosystem Fluxes. Global depth profiles for fluxes of organic carbon export, calcium carbonate, silicate, dissolved organic carbon (DOC), and small, large and huge particulate organic carbon (POC). Model results are subsampled to the observations. Observed POC data (Kiko et al., 2022) were split into size ranges that best match the modelled components entering each POC pool; small POC 0.032 - 0.406 mm, large POC 0.406 - 3.25 mm and huge POC 3.25 - >26mm. Lines show the median depth profiles for observations and subsampled models, starting from 50m depth.

Table 5. Median POC concentration ($\mu\text{molC/L}$) for the three model branches and the observations. Calculated over 50-300m, 300-1000m, and 1000-3000m. Observations are the same as described in Figure 10.

	PlankTOM12			Observations
	GCB	OBio	SMor	
Small POC				
50-300 m	0.096	0.020	0.081	0.007
300-1000 m	0.003	0.0004	0.005	0.006
1000-3000 m	0.001	0.000	0.001	0.005
Large POC				
50-300 m	0.041	0.017	0.025	0.010
300-1000 m	0.018	0.001	0.014	0.008
1000-3000 m	0.011	0.0001	0.005	0.005
Huge POC				
50-300 m	-	0.0130	0.0032	0.0007
300-1000 m	-	0.0027	0.0026	0.0008
1000-3000 m	-	0.0004	0.0018	0.0003

3.6 Ecosystem connectivity between export and carbon flux

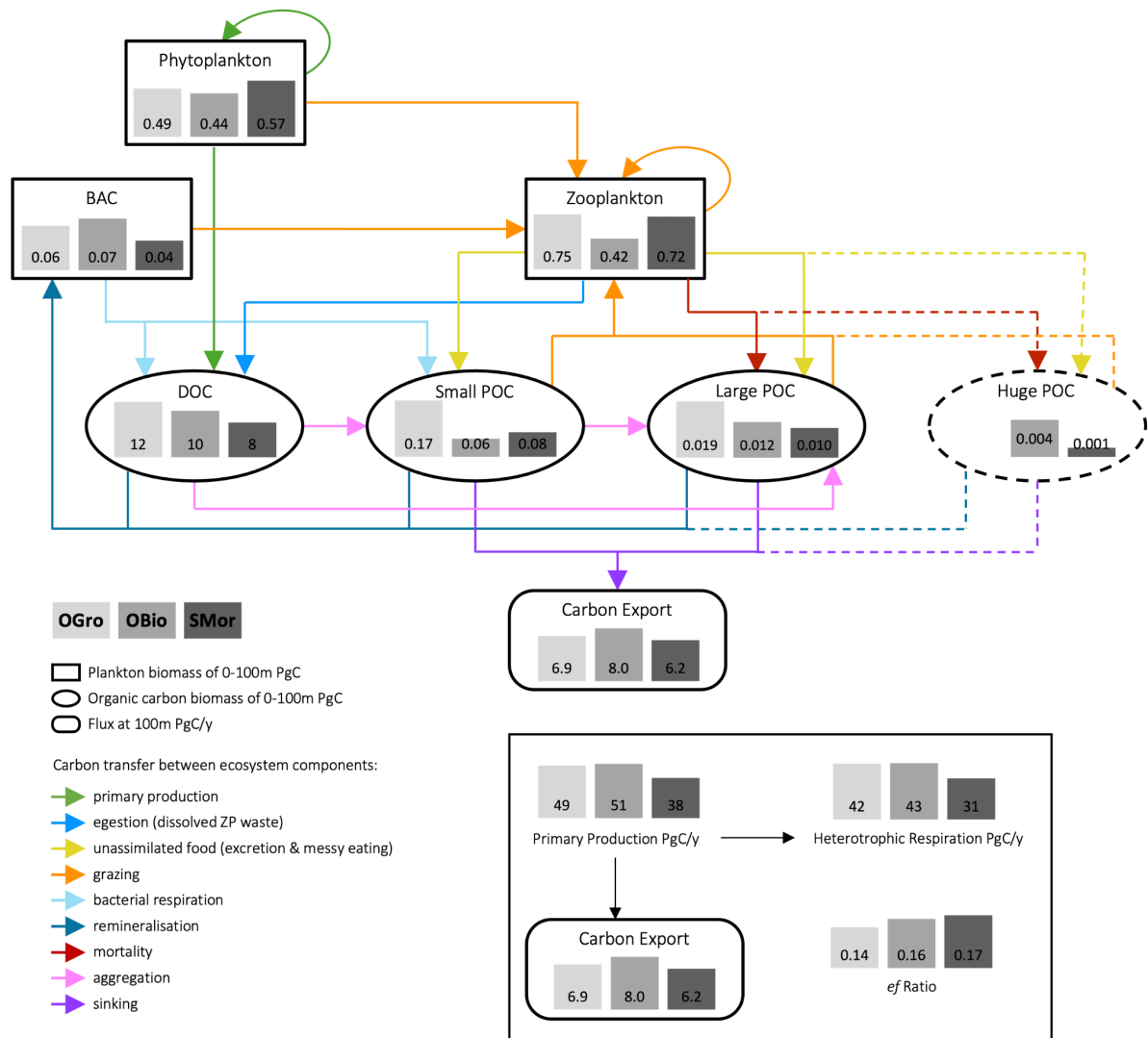


Figure 11. Transfer of carbon biomass through the model ecosystem. Schematic representation of the main carbon fluxes between PFTs and organic carbon components in PlankTOM12 by directional arrows of the transfer of carbon. Huge POC is a new component only present in OBio and SMor, and so the fluxes in and out are shown as dashed lines. All bars and values are the global average for 1990-2023, for the plankton and organic carbon biomass of 0-100m in PgC, and fluxes at 100m in PgC/y.

The transfer of carbon biomass through the ecosystem in PlankTOM12 (Fig. 11) begins with the phytoplankton biomass and associated primary production, which is partly transferred to DOC via autotrophic respiration, or, to zooplankton biomass via grazing. The DOC pool also gains mass from zooplankton egestion, bacterial respiration, plus a small input from river and dust deposition. DOC is either aggregated into small or large POC, or, remineralised by bacteria. The zooplankton gains biomass via grazing on bacteria and phytoplankton, between zooplankton PFTs (see Fig. 1a for a detailed view of the PFT grazing), and grazing on POC pools. Zooplankton unassimilated food transfers biomass to small POC from protozooplankton and to large POC from pteropods, mesozooplankton, crustaceans and gelatinous zooplankton. The small POC pool gains carbon via aggregation from DOC, and bacterial respiration and protozooplankton excretion, plus a small input from river

deposition. Small POC is aggregated into large POC, remineralised by bacteria and grazed by all zooplankton, with a small amount sinking to become part of carbon export. In GCB the large POC pool gains carbon via aggregation from DOC and small POC, and via unassimilated food from pteropods, mesozooplankton, crustaceans and gelatinous zooplankton, and mortality from crustaceans and gelatinous zooplankton. Carbon leaves the large POC pool through grazing by all zooplankton, bacterial remineralization, and sinking, which constitutes a significant portion of carbon export. In OBio and SMor the large POC pool gains carbon via aggregation from DOC and small POC, and from pteropods and mesozooplankton via unassimilated food, while the huge POC pool gains carbon from crustaceans and gelatinous zooplankton, via unassimilated food and mortality. Carbon leaves the large and huge POC pools through grazing by all zooplankton, bacterial remineralization, and sinking, which constitutes a significant portion of carbon export.

GCB, in comparison to the other branches, has mid-level phytoplankton, high zooplankton and mid-level bacteria biomass. This transfers to high DOC and high small and large POC, but mid-level export. GCB also shows mid-level primary production and heterotrophic respiration (Fig. 11). OBio has low phytoplankton and zooplankton and high bacteria biomass. This transfers to mid-level DOC, low small POC, mid-level large POC and high huge POC, which transfers to high export. OBio also has high primary production and heterotrophic respiration, despite low phytoplankton biomass, due to high turnover rates from bacterial respiration (Fig. 11). SMor meanwhile, has high phytoplankton, mid-level zooplankton and low bacteria biomass. This transfers to low DOC, mid-level/low small POC, and low large and huge POC, which then transfers to low carbon export. SMor also has low primary production and heterotrophic respiration (Fig. 11). The carbon export in OBio is higher than GCB by 1.1 PgC/y, despite having primary production only 2 PgC/y higher. The carbon export in SMor is lower than GCB by 0.7 PgC/y, while the primary production is 10 PgC/y lower. This results in an increased export efficiency for OBio and SMor of 0.16 and 0.17, respectively, compared to GCB's of 0.14 (Fig. 11), the three branches also show distinct spatial patterns in their export efficiency (Fig. A3).

An interesting question to pose and work through the results presented in Figure 11 is; why does OBio have low biomass and mostly low organic carbon pools, but the highest export and primary production? OBio phytoplankton biomass mostly comes from picophytoplankton and diatoms (Fig. 5). SMor has similar picophytoplankton biomass and higher diatom biomass, plus more of the other phyto-PFTs, but has very low primary production. However, SMor has high biomass of low- and mid-trophic-level zooplankton (Fig. 5), which graze more readily on phytoplankton and thus keep primary production low in this system. In OBio, low zooplankton biomass allows more phytoplankton activity, even though overall phytoplankton biomass is not especially high, and it also means less zooplankton grazing on POC pools in OBio compared to SMor, allowing for more POC to sink, transferring to greater export (Fig. 11). The answer to the question posed therefore is that low zooplankton grazing pressure in OBio supports higher phytoplankton activity and allows more POC to sink, resulting in higher primary production and export despite relatively low standing biomass.

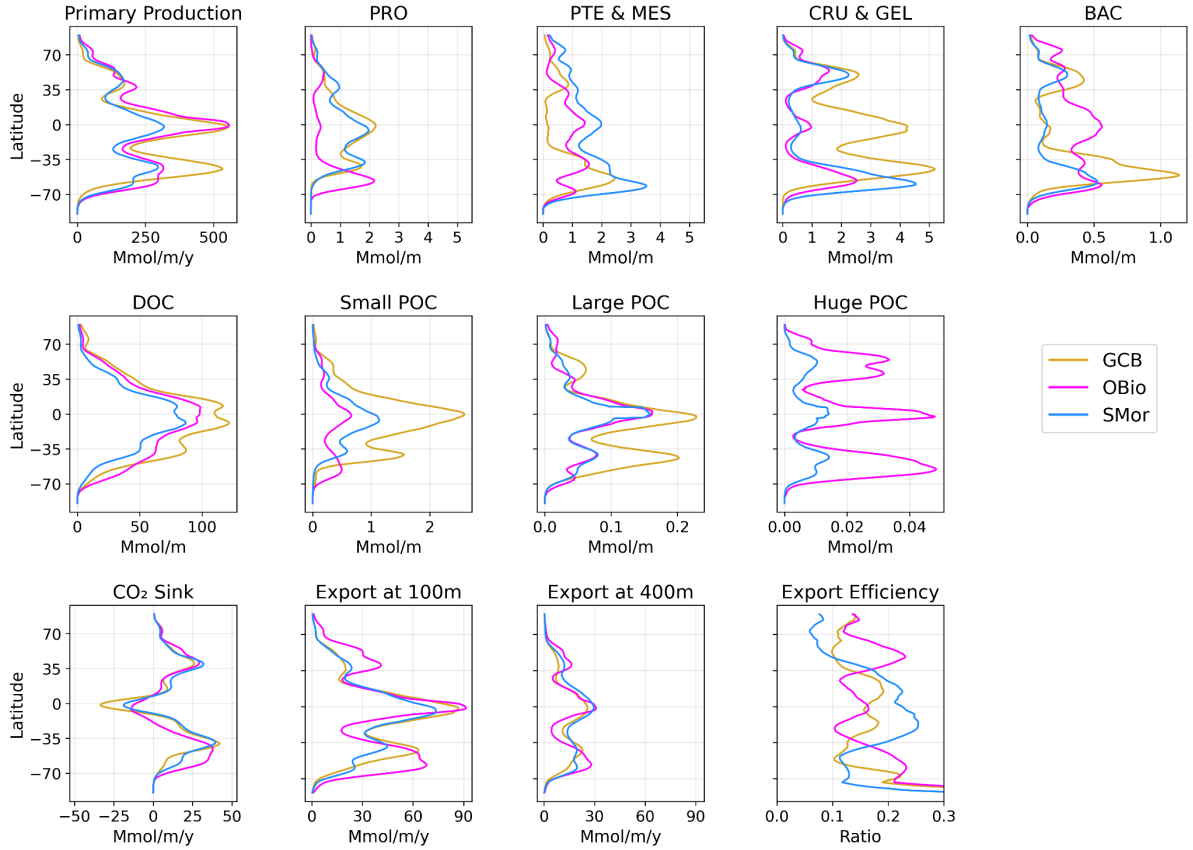


Figure 12. Latitude profiles of carbon biomass and fluxes for three model branches. The biological ecosystem components are grouped in the top row, the organic carbon pool components are grouped in the middle row and the direct carbon fluxes plus the export efficiency ratio (ef Ratio) are grouped in the bottom row. Model results are integrated over 0-100m and over longitude and averaged over 1990-2023. The latitude profile is then smoothed over 10 degrees to aid visual clarity.

All three PlankTOM12 branches show distinct latitudinal profiles across the carbon fluxes. Overall the most northerly latitudes ($>60^{\circ}\text{N}$) show the least variation between branches, while the equator and subpolar south ($35\text{--}70^{\circ}\text{S}$) show the greatest variation between branches (Fig. 12). Surface ocean CO_2 sink differs most between the model branches at the equator and in the Southern Ocean. In the tropical ocean, air-sea CO_2 flux is commonly directed from the ocean to the atmosphere because surface seawater $p\text{CO}_2$ often exceeds atmospheric $p\text{CO}_2$, making the region a net CO_2 source. This disequilibrium is largely driven by equatorial upwelling - particularly in the Pacific Ocean - which brings carbon-rich subsurface waters to the surface and elevates seawater $p\text{CO}_2$ despite concurrent biological uptake (Takahashi et al., 2009). Additionally, the warm tropical surface waters reduce CO_2 solubility, further enhancing oceanic CO_2 outgassing. All three model branches have the same underlying physical processes, and so any difference that presents between them can be attributed to ecosystem differences. At the equator, GCB surface ocean CO_2 sink is $\sim 20\text{--}25$ Mmol/m/yr lower than OBio and SMor (Fig. 12), so the ocean is absorbing more CO_2 from the atmosphere in GCB at this latitude. In the same region GCB has substantially higher large zooplankton (GEL & CRU) biomass and substantially lower mid-sized zooplankton (PTE & MES) than OBio and SMor. GCB also has high PRO biomass, along with SMor (Fig. 12). This pattern propagates to POC, where GCB has substantially higher small and large POC (mostly

produced by zooplankton processes, see Fig. 11) compared to OBio and SMor (Fig. 12). GCB's more productive ecosystem provides more carbon for export at 100m, but by 400m GCB export has reduced the most of the three branches, due to greater recycling of POC by the higher biomass of zooplankton (Fig. 12). This high recycling of carbon, keeps more carbon in surface waters, driving a stronger outgassing of carbon at the surface.

In the Southern Ocean, air-sea CO₂ flux is predominantly directed from the atmosphere into the ocean, making the region a major global CO₂ sink. Strong winds and deep winter mixing promote the uptake and subduction of anthropogenic CO₂ into intermediate and mode waters, efficiently transporting carbon into the ocean interior (Gruber et al., 2009, Takahashi et al., 2009). In addition, the relatively cold surface waters increase CO₂ solubility, further enhancing CO₂ uptake by the ocean. In the subpolar south, the surface ocean CO₂ sink in GCB and SMor peaks at 40°S at 38-40 Mmol/m/y and then steeply declines as latitude decreases. In contrast the OBio carbon flux peaks slightly lower and further south at 45°S and 37 Mmol/m/y and then remains elevated around 35 Mmol/m/y until 60°S, past which it then steeply declines. This indicates that the ocean is releasing more carbon into the atmosphere across the subpolar south in OBio (Fig. 12). This enhances CO₂ sink in the Southern Ocean (50°S-60°S) in OBio, which can be traced to enhanced export in the same region at both 100m and 400m (Fig. 12). Much higher biomass of protozooplankton in this region results in more small POC, without much recycling by larger zooplankton or bacteria. The enhanced protozooplankton biomass comes from low predation pressure from pteropods and mesoplankton, which have low biomass in this region.

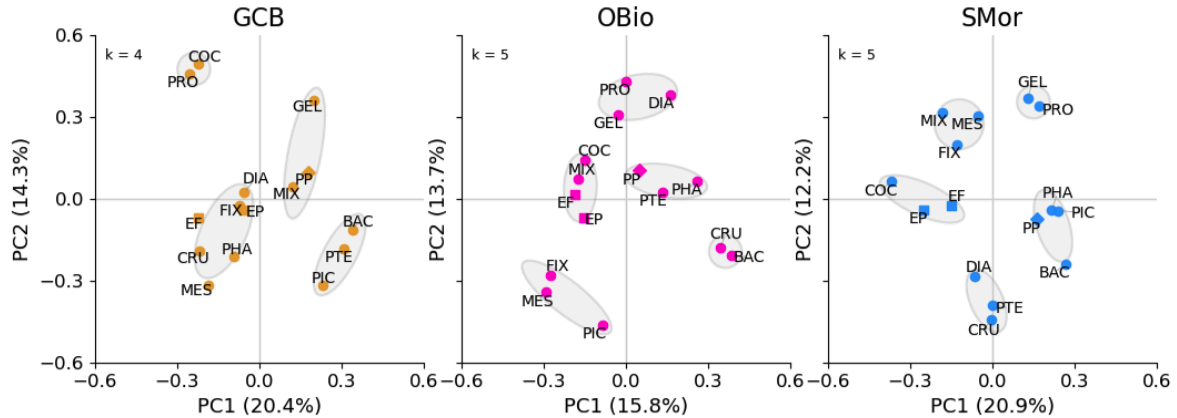


Figure 13. Comparison of aligned principle component analysis (PCA) loading structures across the three model branches. PCA was applied independently to each branch using PFT biomass and ecosystem flux variables. Points represent twelve PFTs, export production flux (EP), primary production (PP) and *ef*Ratio (EF). PFTs were averaged over the upper 200m, while flux variables extracted directly from the 100 m depth level. Shown in this figure is the PC1–PC2 loading space. PCA loading spaces were aligned using orthogonal Procrustes rotation prior to comparison. Grey ellipses indicate k-means clusters identified within each aligned loading space, with the optimal number of clusters selected by maximising silhouette score.

Principal component loading structures differed significantly across the three model configurations despite all simulations being derived from the same underlying ecosystem model framework (Fig. 13). Following

Procrustes alignment, which rotates and scales ordinations to maximise their similarity for comparison, all pairwise comparisons were significantly different ($p < 0.05$), indicating that differences in parameterisation and ecosystem representation produced a distinct multivariate covariance structure amongst PFTs, primary production, and export. Although moderate agreement remained between ordinations ($r = 0.58-0.67$), reflecting their common underlying ecosystem framework, the observed disparities ($0.55-0.67$) indicate that changes in ecosystem parameterisation and representation consistently altered the dominant relationships amongst variables. The strongest agreement occurred between OBio and SMor ($r = 0.58$, disparity = 0.67 , $p = 0.034$), whereas GCB exhibited similar but weaker agreement with both OBio ($r = 0.58$, disparity = 0.67 , $p = 0.034$) and SMor ($r = 0.58$, disparity = 0.67 , $p = 0.042$) suggesting greater divergence in ecosystem organisation (Fig. 13). Collectively, these results demonstrate that even within a shared base-model framework, structural and parameter differences can lead to distinct emergent ecosystem covariance patterns within PCA loading space.

Some similarities emerged consistently across the models. In all three configurations, export production and *ef* Ratio clustered closely together, indicating that both variables showed similar relationships with the dominant modes of ecosystem variability across the models, which follows logically as the two variables are linked, however primary production clustered separately and differently across the three models (Fig. 13). Coccolithophores are closely associated with export production and *ef* Ratio in OBio and SMor, forming a consistent export-associated covariance grouping (Fig. 13).

Despite these shared features, export-related variables exhibited markedly different relationships with the broader ecosystem structure across the models. In GCB, export production and *ef* Ratio clustered alongside diatoms, nitrogen fixers, *Phaeocystis*, mesozooplankton, and crustaceans, indicating that export-related variability shared loading relationships with a relatively broad range of phytoplankton and zooplankton functional groups (Fig. 13). In contrast, OBio exhibited stronger separation between export-associated variables and trophic organisation, with export production, *ef* Ratio, coccolithophores, and mixed phytoplankton forming a distinct cluster separate from most zooplankton-associated PFTs (Fig. 13). In addition, OBio grouped diatoms, gelatinous zooplankton, and protozooplankton together within a distinct covariance cluster, while nitrogen fixers, mesozooplankton, and picophytoplankton formed a separate cluster with similarly strong loading structure. SMor showed the strongest structural separation of export-related variables, with export production, *ef* Ratio and coccolithophores forming an isolated cluster distinct from both microbial-associated groups and larger zooplankton assemblages. In SMor, crustaceans, diatoms, and pteropods formed a coherent trophic grouping, whereas bacteria, *Phaeocystis*, picophytoplankton, and primary production clustered separately (Fig. 13).

Together, these results demonstrate that the three model branches produce distinctly different ecosystem structures, indicating that the parameterisation and structural modifications successfully generated divergent representations of plankton community organisation and export-related variability despite sharing the same underlying model framework (Fig. 11-13).

4 Discussion

The three model branches examined in this study reveal significant insights into how ecosystem structure influences carbon dynamics in the ocean. Our analysis demonstrates that the ecosystem composition differs considerably between the three model branches, which drives variations in primary production and leads to differences in carbon cycling, carbon export and, consequently, differences in surface ocean CO₂ fluxes. Ecosystem composition influencing the ocean carbon flux has widespread implications, for the current understanding of global carbon fluxes and for how future ecosystems will respond to, and influence in return, the global carbon cycle. Climate-driven changes in temperature and carbonate chemistry are already weakening the ocean CO₂ sink, while the magnitude—and even direction—of ecosystem feedback remains uncertain. The resulting spread in ecosystem metrics and carbon fluxes among the three PlankTOM12 models branches presented here demonstrate that plausible, observation-constrained ecosystem choices can materially alter carbon export pathways and regional air–sea CO₂ exchange, even when large-scale circulation and atmospheric climate forcing are identical.

4.1 Model skill depends on metric, reinforcing the need for multi-constraint evaluation

Consistent with the earlier discussion on poorly constrained ecosystem processes, no single branch is uniformly “best” across the observational benchmarks. OBio shows the strongest chlorophyll spatial agreement (and improved high-latitude patterns relative to GCB), yet performs least well for carbon export; SMor better matches global primary production but shows larger biases for silicate; and the historical GCB parameterisation strongly overestimates coccolithophores and therefore CaCO₃ flux, while remaining strong in the representation of N and P concentrations. This trade-off highlights that calibration based on single-variables can yield compensating errors in coupled fluxes: improving surface biomass patterns does not guarantee correct export magnitude or attenuation, and matching integrated production does not ensure correct partitioning among particulate pools.

4.2 Ecosystem structure regulates carbon routing and export efficiency through grazing and recycling

Differences among the model branches suggest that carbon export is governed less by total plankton standing stock than by the pathways through which organic matter is processed within the food web. Zooplankton exert a dual control on the biological carbon pump: grazing and egestion can enhance export through the production of rapidly sinking particles, while respiration, particle fragmentation, coprophagy and recycling can retain carbon within the upper ocean and increase its exposure to microbial remineralisation (Cavan, Henson, et al., 2017; Turner, 2015). Consequently, export efficiency depends not simply on the amount of zooplankton biomass present, but on how trophic interactions regulate the balance between particle production and recycling. The higher export across 100 m in OBio despite lower total biomass indicates a system characterised by high turnover and efficient transfer of newly produced particulate material out of the surface layer. In contrast, the combination of higher phytoplankton biomass and lower primary production in SMor is consistent with greater retention of carbon within the upper-ocean food web and enhanced recycling before particles can contribute substantially to export. These patterns are consistent with differences in the routing and recycling of organic

matter within the food web, whereby weaker trophic processing in OBio permits a greater fraction of particulate material to escape the surface layer, whereas stronger recycling in SMor retains carbon in the upper ocean.

The explicit representation of a huge POC pool in OBio and SMor provides a mechanism through which ecosystem structure can be translated into differences in carbon export. Large faecal pellets and carcasses have been identified as an important, and often underrepresented, pathway for carbon transfer to depth because their high sinking velocities can reduce exposure to remineralisation and recycling in surface waters (Lebrato et al., 2013; Turner, 2015; Wright et al., 2021). However, observations also show that the production of fast-sinking particles does not guarantee efficient sequestration because these particles can be fragmented, consumed or remineralised before reaching depth (Cavan et al., 2015; Cavan, Henson, et al., 2017; Pauli et al., 2021). The branch comparison demonstrates that simply adding a large and fast-sinking pool does not determine the outcome. Rather, the emergent balance between the production of huge POC through macrozooplankton processes and its subsequent removal through bacterial remineralisation and zooplankton grazing determines whether this material contributes to deep export or is recycled within the mesopelagic zone. The differing vertical export profiles among the branches therefore represent a mechanistic expression of ecosystem organisation, rather than a purely physical signal. OBio exhibits higher export across 100 m but stronger attenuation below the euphotic zone, whereas SMor retains proportionally more large and huge particulate material at depth despite its lower surface export. Because the three branches share the same physical circulation, these differences point to contrasting biological pathways of particle production and processing and highlight the importance of ecosystem structure in regulating the efficiency of carbon transfer.

PlankTOM12 does not explicitly represent active carbon transport by diel vertical migrants, an increasingly recognised component of the biological carbon pump (Archibald et al., 2019; Nowicki et al., 2022). Consequently, zooplankton influence export in the model only through grazing, egestion, mortality and detrital processing, and not through the active transport of carbon below the surface feeding layer via respiration, excretion and mortality at depth. Although this omission does not affect the relative differences among the model branches, it implies that the contribution of zooplankton-mediated export to total carbon sequestration is likely underestimated. Nevertheless, the branch comparison demonstrates that even within the gravitational pump alone, ecosystem structure exerts a strong control on carbon routing by regulating the balance between particle production and upper-ocean recycling.

4.3 Regional Variations in Carbon Flux

Our results highlight that substantial regional differences in carbon flux emerge despite identical physical circulation and atmospheric forcing across the three PlankTOM branches. The regional contrasts therefore arise from differences in ecosystem organisation and trophic interactions rather than from physical transport, demonstrating that ecosystem community structure is an important source of variability in regional carbon dynamics. This finding supports previous work identifying biological processes as a major source of uncertainty in projections of ocean carbon sequestration (Kwon et al., 2009; Laufkötter et al., 2015).

The equatorial oceans provide a particularly informative example because they are regions where intense upwelling continuously supplies dissolved inorganic carbon and nutrients to the surface. Air-sea CO₂ exchange

therefore depends on the balance between the physical resupply of carbon-rich waters and biological carbon fixation (Gruber et al., 2009; Takahashi et al., 2009). Under these identical physical conditions, GCB exhibits lower air–sea CO₂ flux than OBio and SMor, indicating that differences in ecosystem structure modify the efficiency with which biological production offsets the upwelled carbon. The larger macrozooplankton biomass and enhanced production of POC in GCB suggest that changes in grazing pathways and detrital production alter the partitioning between recycling and export. Such trophic controls on particle production and remineralisation have increasingly been recognised as key regulators of biological carbon sequestration, particularly in regions where high productivity coincides with rapid microbial recycling (Cavan, Henson, et al., 2017; Steinberg & Landry, 2017). Our results therefore support the emerging view that food-web structure can substantially modify the efficiency of the biological carbon pump independently of primary production alone.

The Southern Ocean represents a contrasting regime, where the biological carbon pump plays an important role in regulating global carbon uptake owing to the formation of intermediate and deep waters and the large exchange of carbon with the atmosphere (DeVries, 2014; Frölicher et al., 2015). Here, the persistence of elevated export in OBio farther poleward (to ~60°S) coincides with enhanced protozooplankton biomass and reduced grazing pressure from larger zooplankton groups. These ecosystem differences increase the production of small POC while simultaneously modifying its subsequent processing through the food web. Previous observational and modelling studies have shown that Southern Ocean carbon export is highly sensitive to grazing dynamics, food-web structure and particle transformation, particularly through the balance between microbial remineralisation and zooplankton-mediated export (Boyd et al., 2019; Cavan, Trimmer, et al., 2017; Smetacek et al., 2012). The present comparison reinforces these conclusions by demonstrating that relatively modest changes in trophic organisation can generate substantial differences in regional carbon uptake despite identical physical forcing.

4.4 Implications for projecting future ocean carbon uptake and priorities for future work

The original motivation for introducing PFTs into global ocean biogeochemical models was to represent the functional diversity of marine ecosystems while maintaining computational efficiency, thereby improving simulations of marine biogeochemical cycles (Le Quéré et al., 2005). The present comparison extends this concept by demonstrating that alternative representations of ecosystem community structure, implemented within an identical physical circulation and biogeochemical framework, produce substantially different pathways of carbon routing, export production and air-sea CO₂ exchange. These differences arise despite all three PlankTOM12 branches reproducing broadly realistic large-scale distributions of primary production and carbon uptake, indicating that similar large-scale carbon budgets can emerge from fundamentally different ecosystem organisations. Ecosystem community structure should therefore be regarded as an important source of uncertainty in projections of ocean carbon cycling alongside uncertainty associated with physical climate forcing (Kwiatkowski et al., 2020; Laufkötter et al., 2015).

This has important implications for projections under future climate change scenarios. Warming, ocean acidification, deoxygenation and changes in nutrient supply are expected to alter the composition, physiology and trophic interactions of marine plankton communities (Canadell et al., 2021; Cooley et al., 2022; Doney et

al., 2012). These ecosystem responses remain one of the major sources of uncertainty in projections of marine primary production, export production and carbon sequestration because different models represent plankton communities and trophic interactions in fundamentally different ways (Henson et al., 2022; Tagliabue et al., 2021; Wilson et al., 2022). Our results demonstrate that ecosystem reorganisation can substantially alter regional carbon dynamics even under identical physical forcing, suggesting that future projections of ocean carbon uptake will depend not only on how much primary production changes, but also on how carbon is partitioned between trophic pathways, organic matter pools and sinking particles. This conclusion is consistent with recent studies emphasising that more realistic representations of plankton ecology are required to improve projections of marine ecosystem responses to global change.

An equally important implication concerns model evaluation. Assessing marine ecosystem models against integrated quantities such as global primary production, export production or air-sea CO₂ flux alone is unlikely to provide a sufficiently rigorous test of model performance because these are emergent properties of complex food webs and may conceal compensating errors in ecosystem organisation. Recent studies have shown that the efficiency of the biological carbon pump depends strongly on trophic interactions, particle characteristics and remineralisation pathways rather than on primary production alone (Boyd et al., 2019; Henson et al., 2019; Steinberg & Landry, 2017). The branch comparison presented here reinforces this view by demonstrating that markedly different ecosystem structures can generate similar large-scale carbon budgets while producing contrasting regional carbon pathways and export efficiencies.

These findings highlight several priorities for future model development. Improved observational estimates of the carbon biomass across the major PFTs are needed to provide stronger constraints on ecosystem structure, while reducing the remaining uncertainties in regional and global estimates of primary production and export will improve confidence in model evaluation. More importantly, there is a need for systematic and community-based benchmarking of ecosystem variables that extends beyond traditional bulk biogeochemical diagnostics to include PFTs biomass, trophic interactions, particle-size distributions and export pathways. Such ambitious ecosystem model developments cannot be achieved by individual research groups alone and will require closer collaborations between observationalists and modellers to develop coordinated datasets, benchmark products and process-based model evaluation frameworks (Flynn et al., 2025).

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Availability Statement:

The model data, observational data and code used for the production of results figures in the study are available at Zenodo via doi: [10.5281/zenodo.21701279](https://doi.org/10.5281/zenodo.21701279) (Wright et al., 2026).

The authors declare there are no conflicts of interest for this manuscript.

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Appendices

Table A1. Ecosystem parameter differences between model branches. Note that gelatinous and crustacean zooplankton mortality rate for SMor uses a different calculation to GCB and OBio, so the values are not directly comparable.

Parameter description	PlankTOM12 Branches		
	GCB	OBio	SMor
POC sinking speed (m/d)	3	10	10
(1 - estuarine retention fraction) of river iron (no units)	0.05	0.25	0.25
scavenging rate of iron (no units)	0.001	0.003	0.0005
minimum scavenging rate of iron (no units)	0.001	0	0.0005
ligand concentration of iron in the north (nmol/L)	0.6	0.8	0.9
depth at which iron concentration starts to be restored to ligand concentration (m) in the North	50	100	25
bacteria preference for DOC (no units)	0.0105	0.088	0.088
bacteria preference for POC (no units)	9.13	8.76	8.76
bacteria preference for GOC (no units)	9.13	8.76	8.76
DSi degradation at infinite T (1/d)	179831	0.2	179831
T dependence DSi degradation (Kelvin)	-4366	-11200	-4366
optimum BAC uptake rate (1/d)	3.15	4.76	4.76
half saturation in DOC remineralisation by bacteria (umol/L)	8	45	4
half saturation for Fe in DOC remineralisation by bacteria (nmol/L)	0.025	2.5	0.025
gelatinous zooplankton mortality rate (1/d)	0.05	0.03	10000
crustacean zooplankton mortality rate (1/d)	0.015	0.015	1000
BAC respiration rate (1/d)	0.028	0.008	0.087
T dependence of BAC respiration rate (no units)	1.0244	1.1	1.0494
nutrient-replete Si:C (mol/mol)	0.13	0.13	0.07
ratio of calcification:photosynthesis coccolithophores (molCaCO3/molC)	0.1	1	0.1
max. additional Si:C in open-ocean (multiplier)	3	1	2
max. additional Si:C in HNLC (multiplier)	6	4	2
silicate half saturation constant for Si:C of DIA (umol/L)	20	100	20
subsaturated max calcite dissolution rate (1/d) (mol/L ^{1-m_lyoco3})	10.9	0.253	0.253
silicate half saturation constant diatoms (umol/L)	0.42	2	1
ubsaturated max aragonite dissolution rate (1/d) (mol/L ^{1-m_lyoco3})	10.9	0.253	0.253

use squared mortality (1) or total biomass as a proxy for top-predator (0)	-	0	1	
Zooplankton parameters	PFT	GCB	OBio	SMor
gross growth efficiency (no units)	PRO	0.3	0.29	0.29
	PTE	0.26	0.25	0.25
	MES	0.26	0.25	0.25
unassimilated fraction of grazing as fecal pellets (no units)	PRO	0.13	0.5	0.13
	PTE	0.3	0.5	0.3
	MES	0.3	0.5	0.3
	GEL	0.18	0.5	0.18
	CRU	0.18	0.5	0.18
zPFT optimal grazing rate (1/d)	PRO	1.59	3.86	3.5
	PTE	1.12	1.2	1.6
	MES	1.22	2.84	1.1
	GEL	0.207	1.2	0.6
	CRU	0.116	0.53	0.25
half saturation grazing (umol/L)	PRO	10	8	10
	PTE	10	20	15
	MES	10	10	15
	GEL	10	15	15
	CRU	10	15	15
respiration rate of zooplankton at 0C (1/d)	PRO	0.024	0.008	0.016
	PTE	0.041	0.015	0.008
	MES	0.026	0.008	0.008
	GEL	0.014	0.0293	0.0293
	CRU	0.009	0.0121	0.0121
T dependence of zooplankton respiration (no units)	PRO	1.0818	1.0897	1.0797
	PTE	1.0748	1.0748	1.0748
	MES	1.0837	1.0887	1.0887
	GEL	1.0704	1.0654	1.0654
	CRU	1.079	1.0942	1.0942
Phytoplankton parameters		GCB	OBio	SMor
phytoplankton respiration as a fraction of growth (no units)	DIA	0.01	0.12	0.01
	MIX	0.01	0.15	0.02
	COC	0.01	0.15	0.01

	PIC	0.01	0.15	0.01
	PHA	0.05	0.15	0.05
	FIX	0.1	0.15	0.05
half saturation concentration for nitrate (umolC-equivalent/L)	DIA	2	0.2	6
	MIX	2	0.2	2
	COC	1	0.2	2
	PIC	1.5	0.15	2
	PHA	15.0	0.2	3
	FIX	6.0	1.3	13
half saturation concentration for PO4 (umolC-equivalent/L)	DIA	15.9	0.06	24.4
	MIX	15.9	0.12	15.9
	COC	6.1	0.09	12.2
	PIC	9.15	0.06	7.6
	PHA	97.6	0.4	97.6
	FIX	24.4	0.25	24.4
optimum growth rate of phytoplankton PFTs (d1)	DIA	0.5	1.67	2
	MIX	0.4	1.27	1.27
	COC	0.23	1.27	1.27
	PIC	0.26	1.43	1.43
	PHA	0.62	1.81	1.81
	FIX	0.055	0.26	0.26
half saturation constant of iron (nmol/L)	DIA	40	10	40
	MIX	25	10	25
	COC	15	5	25
	PIC	10	5	25
	PHA	25	15	60
	FIX	40	15	40
maximum iron quota (umolFe/umolC)	DIA	20	20	47
	MIX	20	20	20
	COC	20	20	20
	PIC	20	20	10
	PHA	20	20	20
	FIX	20	20	45
minimum iron quota (umolFe/umolC)	DIA	4	4	6

	FIX	4	4	8
optimal iron quota ($\mu\text{molFe}/\mu\text{molC}$)	DIA	8.6	8.6	12.9
	FIX	8.6	8.6	17
maximum CHL:C ratio (gChl/molC)	DIA	0.7	0.6	0.7
	MIX	0.4	0.45	0.4
	COC	0.4	0.35	0.4
	PIC	0.4	0.2	0.4
	PHA	0.5	0.6	0.5
	FIX	0.3	0.2	0.3

Figure A1. Zooplankton grazing preferences for the three model branches. All grazing preferences are relative to diatoms which are fixed at 1.

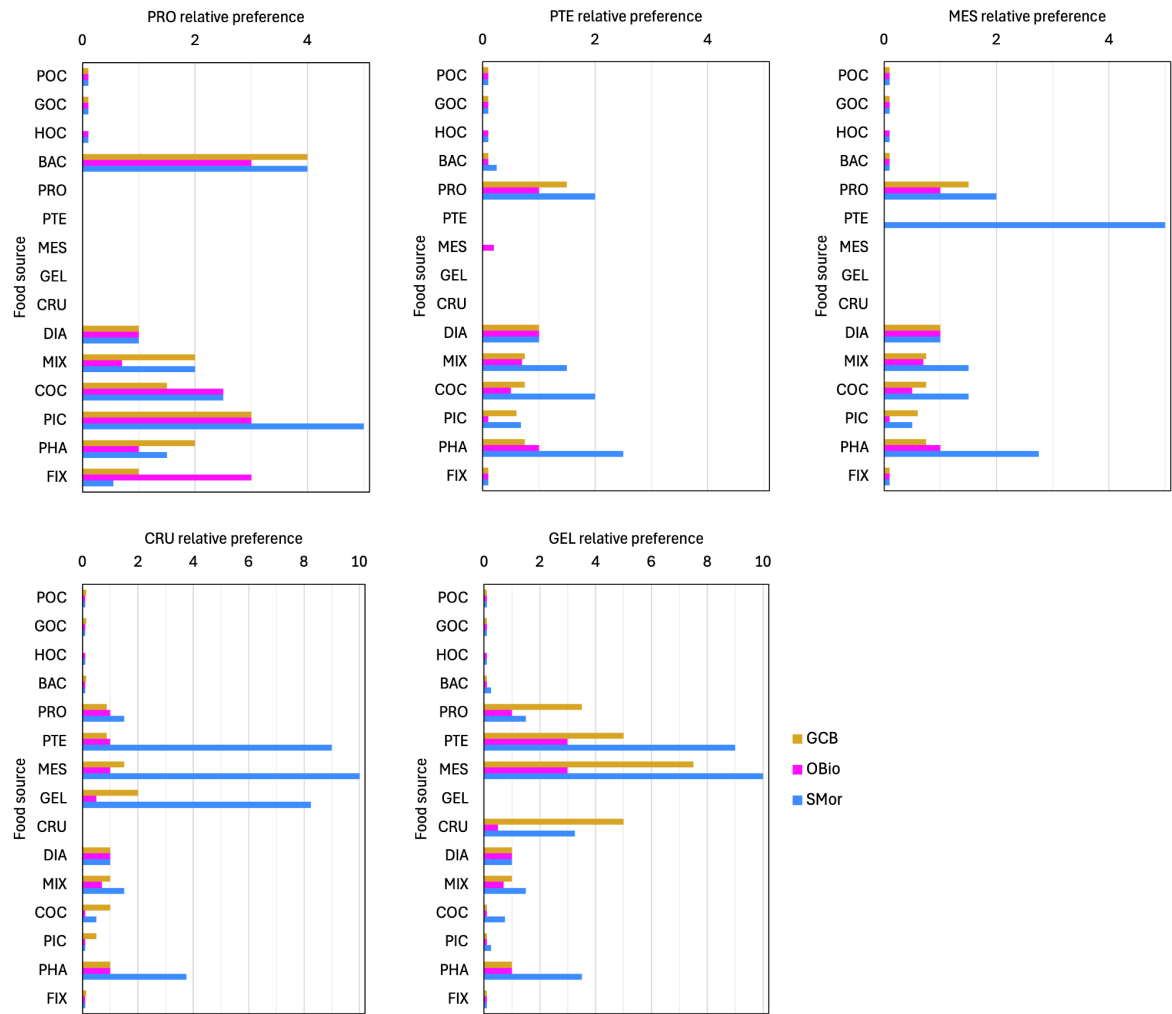


Figure A2. Seasonal cycle of Chlorophyll ($\mu\text{g Chl/L}$) and $\Delta p\text{CO}_2$ (μatm) for observations and three model branches. For surface ocean chlorophyll grid cells are removed from observations (from OC-CCIv5; Sathyendranath et al., 2019, 2021) where <6 months of data are available. Model results are then subsampled to the sampled observations. Results are shown as a climatology of 1998-2023 and for 0m. For $\Delta p\text{CO}_2$, models are subsampled to observations (from SOCATv2020; Bakker et al., 2020) and results are shown as a climatology of 2012-2021. Observations show the mean $\pm$ 1 standard deviation.

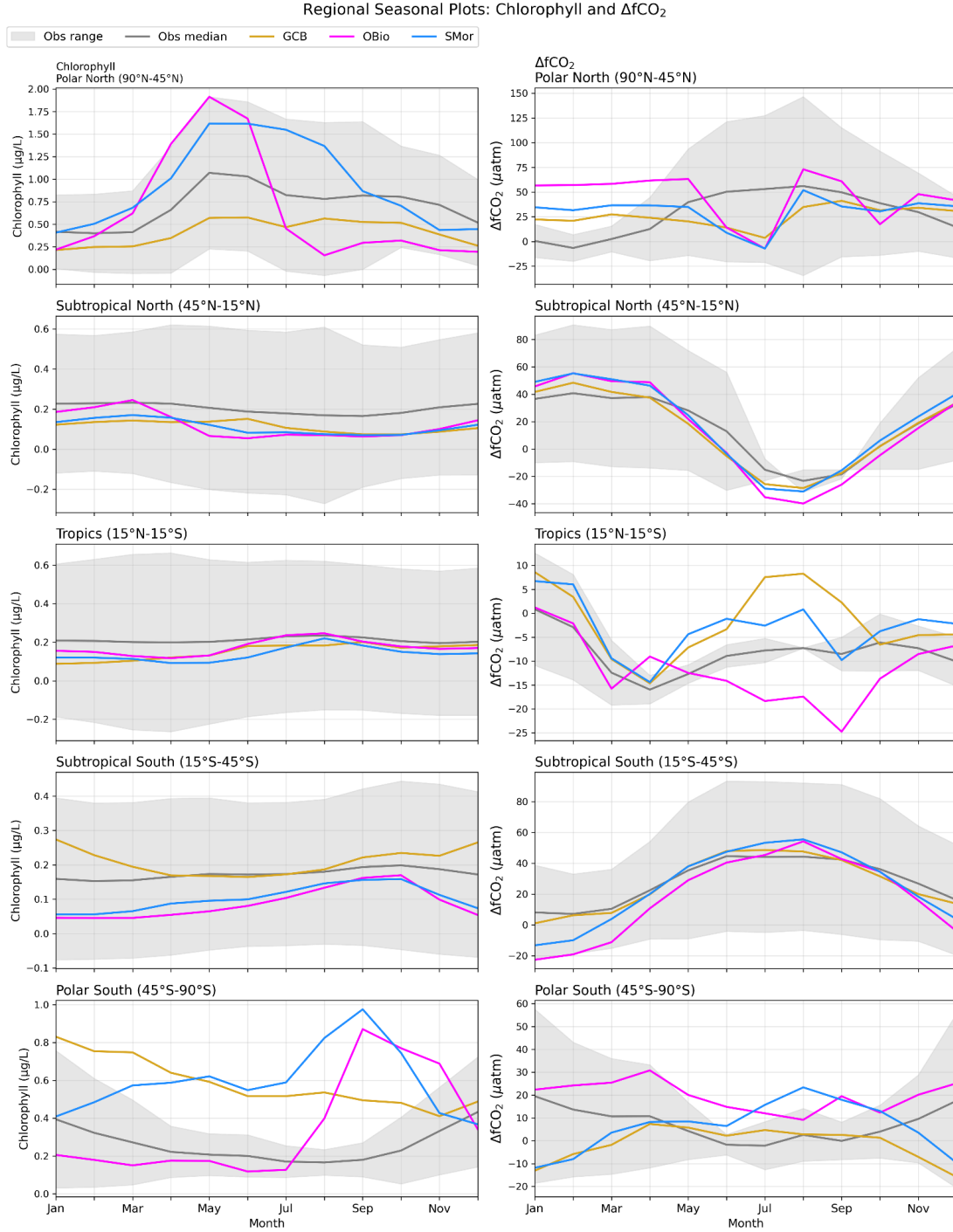


Figure A3. Annual mean ecosystem production and fluxes for three model branches. The left-hand column is the GCB branch, the middle column is the OBio branch and the right-hand column is the SMor branch. Results are averaged over 1990-2023, primary production is integrated over 0-100m and carbon export is at 100m.

