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Modelling primary production: multitude of theories, or multitude of languages?

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Abstract. Marine primary production, converting approximately 50 Gt of inorganic carbon into organic carbon per year, is an important component of the global carbon cycle, and a major determinant of past, present and future climate. Large-scale, long-term estimates of marine primary production rely primarily on two types of models: satellite-based models that make extensive use of remote-sensing data, and ecosystem models providing numerical simulation of ecological processes embedded in general ocean circulation models. Intercomparison exercises of model outputs (both within and across the two model types) have consistently revealed high discrepancies between estimated global ocean primary production, including divergent magnitudes and even opposite trends. Model-observation comparisons are also complex, because paucity of data, differences in measurement techniques, and evolving methodologies could all lead to dif-

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ficulties with the interpretation of results. These uncertainties limit the applications of primary production models (both satellite-based and ecosystem), especially in the climate context, where an important question is whether climate change will drive significant future changes in regional or global primary production. Both satellite-based and ecosystem models rely on a range of fixed model parameters, whose values need to be carefully estimated and tested. In this paper, we suggest that such model parameters represent an underappreciated but important source of inter-model differences. With the proliferation of both satellite and in situ observations of relevant variables at global scales, and the availability of powerful statistical tools such as data assimilation and machine learning, we argue that time is right to systematically examine model parameters, gaining both better insights into parameter values and how those values might vary in space and time. We argue that such spatio-temporal parameter variability can be theoretically justified for ecosystem models with complexity similar to those commonly used within Earth System Models (ESMs) in climate studies. The spatially and temporally varying parameter values could serve to unify models that are structurally different. An important aspect of this unification could be the ability to infer the spatio-temporal variability of parameters in the less complex models from the emergent behaviour of the more complex ones. This could include ecosystem model simulations of nutrients, temperature, phytoplankton classes, or vertical distributions informing satellite-based models. We conclude that better understanding of model parameter roles and integration (or inter-calibration) of different types of models could reduce discrepancies among the primary production models and improve the reliability of marine primary production projections.

1 Introduction

The climate problem is highly complex, the stakes are very high, and substantial knowledge gaps remain, especially in the ocean biogeochemistry domain (Kwiatkowski et al., 2020). More broadly, the need to address complex issues related to the carbon cycle, ecosystem services and biogeochemistry through Earth System Models (ESMs), e.g., in the context of climate adaptation and resilience, has been highlighted by expert groups (Hewitt et al., 2021). Similarly, Jones et al. (2024) evaluate modelling priorities to support international climate policy and emphasise the value of "a coordinated, internally consistent set of simulations, data, and knowledge to support Intergovernmental Panel on Climate Change (IPCC) assessments" and outline multiple applications of Coupled Model Intercomparison Project (CMIP) projections. These include investigations of threats to marine ecosystems (which have consequences for the ocean's ability to buffer climate change, Tjiputra et al., 2025) and downstream services under various climate scenarios and associated risks of tipping points. Jones et al. (2024) also state that improving confidence in future projections requires models to reproduce the observed historical period. Furthermore, they identify parameter uncertainty as one of the key elements of uncertainty in climate models.

Against this background and in line with the recommendations of expert bodies, we focus on the climate priority challenge associated with marine ecosystem and biogeochemistry modelling, and particularly on marine primary production. Phytoplankton primary production (PP), the process by which marine autotrophs convert CO_2 into organic matter through photosynthesis, is a major component of the ocean and planetary carbon cycle. Currently estimated at around $50\,\mathrm{Pg\,C\,yr^{-1}}$ (Kulk et al., 2020, 2021), the magnitude of marine PP is five times the estimated fossil fuel emissions of $10\,\mathrm{Pg\,C\,yr^{-1}}$ in 2022 and nearly 20 times the net ocean carbon sink (Friedlingstein et al., 2025). Its magnitude is comparable to that of terrestrial primary production (Lurin et al., 1994; Longhurst et al., 1995; Field et al., 1998; Friedlingstein et al., 2025). A key question in climate research is whether the current levels of marine PP can be maintained under climate change (Tagliabue et al., 2021), when marine ecosystems are increasingly threatened by a variety of processes, including ocean acidification (Jin et al., 2020; Dai et al., 2025), rising seawater temperatures (Kwiatkowski et al., 2020), intensified storminess over the oceans (Gastineau and Soden, 2009; Young and Ribal, 2019; Gentile et al., 2023; Liu et al., 2024), ocean deoxygenation (Schmidtko et al., 2017), modified current and stratification influencing surface nutrients (Maishal, 2024), changes in aerial nutrient supply (Bergas-Masso et al., 2025), biodiversity loss (Luypaert et al., 2020), and sea-ice loss (Myksvoll et al., 2023). In this review we consider PP estimated from two types of models: "satellite-based models" that utilise remote-sensing data together with physiological models, whose parameters are informed by in situ measurements, to calculate PP; and mechanistic "ecosystem models" which use numerical methods to solve a set of differential equations representing many ecological processes, with one of them being PP.

When discussing marine PP it is important to keep track of its different components. Theoretically, PP before any of the loss terms are considered is referred to as gross PP (GPP); once the respiration by marine autotrophs is subtracted from GPP we obtain net PP (NPP). GPP can also be partitioned according to whether only the organic carbon fixed into particulate material is considered (production of particulate organic carbon), or if the exudates (dissolved organic matter) are also included in the estimate (production of total organic carbon, Regaudie-de-Gioux et al., 2014). Models can make explicit distinction between these components, though this is not always done. When it comes to in situ observations, experimental methodologies and carefully assembled protocols exist for measurement of each of these components (IOCCG, 2022); however, practical constraints may limit the extent to which the components may be differentiated from each other. Furthermore, various observational methods of the same component could yield differing values. For example, multiple methods for measuring the same component could have different intrinsic timescales that are applicable to them, making direct comparisons difficult. Improving observational tools for PP, including developing reliable PP error models, is a priority for the scientific community, in addition to the modelling issues that are the primary focus of this paper.

Here, we focus mainly on GPP as computed in many ecosystem models. For satellite-based estimates, we treat PP derived from short (1–4 h) in situ incubations as GPP, and those derived from longer (12–24 h) incubations as NPP, while fully recognising that the distinction is not that clear cut (e.g., Halsey et al., 2011). Furthermore, estimates of the magnitude of losses due to respiration vary considerably. Some estimates place it at about 30 % of GPP (e.g., Platt and Sathyendranath, 1991), while some other estimates are higher (e.g., 60 % according to Halsey et al., 2011). Platt and Sathyendranath (1988) compared daily water-column PP computed on the basis of short incubations with those measured in situ over daily time scales, and showed the two sets of independent estimates to be comparable, which points to low respiration losses. Also, satellite-based estimates of NPP (Behrenfeld and Falkowski, 1997) tend to be roughly the same or higher than GPP estimates (Longhurst et al., 1995). Since, by definition, NPP cannot be greater than GPP, these comparisons reveal a great deal of uncertainty in respiration, or in PP computed using different approaches, when compared with each other.

2 Background

Considerable differences exist in model-based estimates (here and elsewhere, we use “models” without a qualifier, to mean both satellite-based and ecosystem models) of the current and past global PP in the ocean, and in ecosystem-model based projections into the future.

Satellite-based estimates of global marine PP are converging around 45–55 $\mathrm{Pg\,C\,yr^{-1}}$ (Fig. 1A). These estimates were obtained from both multi-sensor products of the Ocean Colour Climate Change Initiative (OC-CCI; version 6, Sathyendranath et al., 2019; Kulk et al., 2020, 2021), as well as from single-sensor products of the Oregon State University (http://orca.science.oregonstate.edu/, last access: 28 April 2026), which include the Carbon, Absorption, and Fluorescence Euphotic-resolving (CAFE) model (Silsbe et al., 2016, 2025), Carbon-Based Primary Productivity Model (CBPM; Westberry et al., 2008), the Vertically Generalised Production Model (VGPM; Behrenfeld and Falkowski, 1997) and the VGPM-Eppley model (which incorporates the Eppley (1972) temperature function). However, we note that much higher values (up to 67 $\mathrm{Pg\,C\,yr^{-1}}$) and lower values ($\leq 45\,\mathrm{Pg\,C\,yr^{-1}}$) have also been reported from satellite-based products (Antoine et al., 1996; Behrenfeld et al., 2005; Carr et al., 2006; Uitz et al., 2010) (here we recognise that satellite products may differ in the computed PP components, as noted earlier).

Large differences also emerge in the PP trends over the last decades estimated from both the CCI and Oregon State University products (Fig. 1B), as well as associated reanalyses (e.g., those of Gregg and Rousseaux, 2019). These differences are strongly impacted by the choice of historical period and the underlying characteristics of the satellite products (e.g., single sensor or multi-sensor), but the choice of satellite-based PP model does matter: in a recent comparison (Ryan-Keogh et al., 2025) of six satellite-based primary production models applied to a common satellite product (OC-CCI) and a common period (1998–2023), four of them showed declining trends, while the other two showed an increasing trend. Interestingly, the split is along the lines of whether the models incorporated temperature-dependent production parameters, or not. Ryan-Keogh et al. (2025) also compared satellite products with those of several ecosystem models from the Climate Model Intercomparison Project (CMIP-6), and concluded that, in general, the climate models underestimated the decreasing trends seen in some of the satellite-based models.

Differences in marine PP and its trends are not limited to satellite-based products. Earth System Model intercomparisons show considerably larger uncertainty than the satellite models for the annual NPP estimate during the (recent past) “historical” period (with values reported in the 17–83 $\mathrm{Pg\,C\,yr^{-1}}$ range; Bopp et al., 2013; Doney et al., 2014; Laufkötter et al., 2015; Tagliabue et al., 2021; see Fig. 2), whilst showing weak or no trends over the recent historical period (Kwiatkowski et al., 2020). Ecosystem model uncertainties are even higher in future projections where models disagree even on the sign of change up to the year 2100 under the high emission scenario, although most ecosystem models project a decline in global PP. While the uncertainty in annual NPP in the recent past has decreased in the CMIP6 (Coupled Model Intercomparison Project phase 6) ensemble compared with CMIP5, the uncertainty in projected PP trends has increased significantly in the CMIP6 ensemble compared with CMIP5 (Kwiatkowski et al., 2020). In particular, while the ensemble mean in CMIP5 suggested a significant decrease in PP at the global scale of $-8.06\,\% \pm 4.83\,\%$ (where the uncertainties are reported as the inter-model standard deviation), the CMIP6 ensemble has a much smaller mean and the larger standard deviation includes the null hypothesis of no trend ($-1.76\,\% \pm 9.01\,\%$). Frölicher et al. (2016) have noted that ecosystem model uncertainties (missing/mis-represented processes, parameter uncertainties) dominated the total uncertainty in the 21st-century projections of PP and their relative importance with respect to scenario uncertainty does not decrease with projection lead time. Recent studies have confirmed this, highlighting the role of uncertainty in the rep-

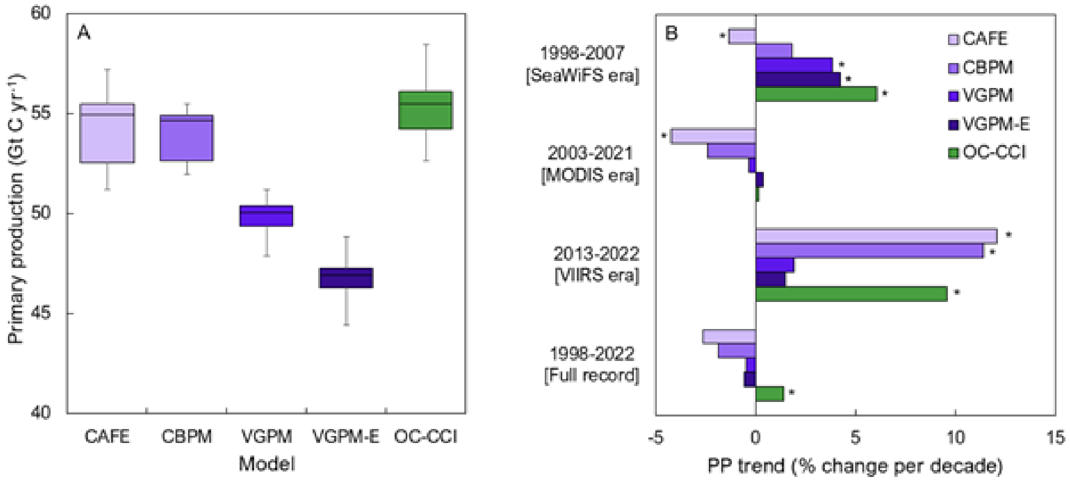


Figure 1. Global marine PP computed using the satellite-based model of Platt and Sathyendranath (1988) as updated by Sathyendranath et al. (2020) and Kulk et al. (2020, 2021) with version 6.0 of Ocean Colour Climate Change Initiative (OC-CCI) data as input (in green), compared with openly available time-series data from four other satellite-based primary production models from the Oregon State University Primary Production website (http://orca.science.oregonstate.edu/-npp_products.php, last access: 28 April 2026) based on single-sensors: Sea-viewing Wide Field-of-view Sensor (SeaWiFS; 1998–2007), Moderate Resolution Imaging Spectroradiometer Aqua (MODIS-Aqua; 2003–present), and Visible Infrared Imaging Radiometer Suite (VIIRS; 2013–present). The panels show the following: **(a)** Global ocean primary production for the five different satellite-based primary production models for the time period between 1998–2022 (i.e., full data record), for all sensors combined; and **(B)** trends in primary production for the full ocean colour data record and for subsets of the periods during which specific sensors were operational, with stars indicating significant trends ($p < 0.05$), for the five satellite-based primary production models. All latitudes were considered, but coverage at higher latitudes (> 70° N and S) is typically poor in satellite data.

resentation of key biogeochemical processes, including diazotrophy (Tagliabue et al., 2021; Bopp et al., 2022; Doléac et al., 2025), bacterial remineralisation (Kim et al., 2023) and parameter uncertainty (Jones et al., 2024), including in zooplankton grazing rates (Rohr et al., 2023). Laufkötter et al. (2015) concluded that the projected future changes in marine PP are driven by multiple processes, including changes in circulation or mixing, leading to a stronger lateral or vertical loss of biomass; increased aggregation or mortality of phytoplankton; or higher grazing pressure. Laufkötter et al. (2015) also noted that temperature-dependent functions of PP and loss terms can affect the direction of change of PP from marine ecosystem models in climate warming scenarios. Regional variations in PP are especially sensitive to how models represent this wide range of processes (Dutkiewicz et al., 2013), and given the high uncertainty in their model representation, very few of the models agree on the direction of the trend regionally. Furthermore, global models, with their coarse horizontal resolution, struggle to capture coastal and estuarine processes that enhance PP (coastal regions account for 14 %–33 % of global PP; Gattuso et al., 1998), which makes them also prone to underestimate global PP.

Several studies have also been carried out to compare estimates from ecosystem models with satellite-based products and in situ observations, both at global scale (Carr et al., 2006; Steinacher et al., 2010; Bopp et al., 2013; Laufkötter et al., 2015; Séférian et al., 2020; Ryan-Keogh et al., 2025) and at regional scales (Friedrichs et al., 2009; Saba et al., 2010; Lee and Yoo, 2016; Doléac et al., 2025). In some cases, these comparisons (e.g., between ecosystem and satellite-based models) led to better constrained PP projections, e.g., in the tropics, using an emergent constraint approach (Kwiatkowski et al., 2017). However, it is fair to say that, overall, these comparisons have not led to convergence of model outputs that would reduce the uncertainty of marine PP estimates. All previous works have highlighted large differences between estimates (e.g., varying from $< -60\,\%$ to $> 60\,\%$; Séférian et al., 2020), with highly variable spatial patterns (Bopp et al., 2013). Tagliabue et al. (2021) highlighted the need for stronger constraints on NPP using new approaches that include the growing observational coverage from Biogeochemical-Argo (BGC-Argo) floats (Claustre et al., 2020; for an example of this see Arteaga et al., 2022). Field-based observations of PP, typically treated as the "truth", are often compared with model outputs to evaluate model performance. However, this type of comparison is confounded by uncertainties in PP measurements, which can be quite high, as well as by the differences in the spatial and temporal scales of the in situ observations and the validated models. Furthermore, there are also questions around whether the PP is measured directly, or estimated indirectly. For example, BGC-Argo estimates PP indirectly, inferring it from other, more directly measured variables.

Given these challenges both in remote sensing and ecosystem modelling, the IPCC has assigned low confidence to current estimates of marine PP and its trends. The reasons

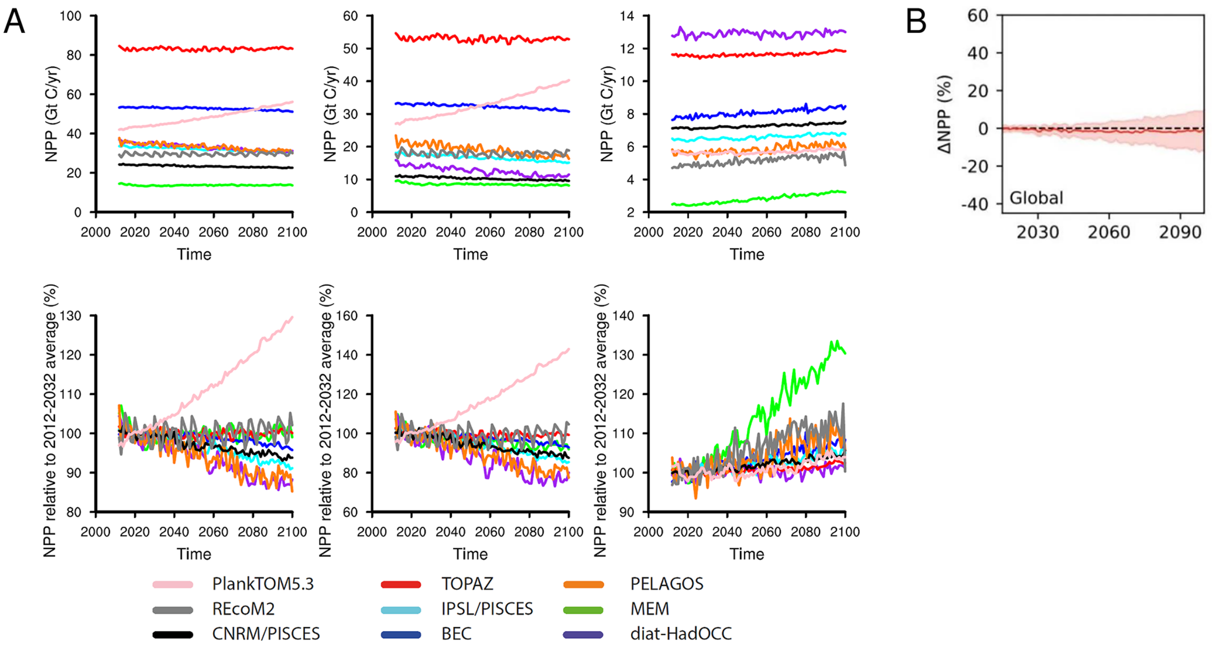


Figure 2. Comparison of NPP from marine ecosystem models in CMIP5 comparison projected to the end of this century under a high emission scenario. **(A)** From Laufkötter et al. (2015) – RCP8.5 (Representative Concentration Pathways 8.5 scenario), from left to right are global values, lower latitudes (30° S–30° N) and Southern Ocean (90–50° S) in $\mathrm{Gt\,C\,yr^{-1}}$ (top panels) and percent (bottom panels); and **(B)** global NPP projections from Tagliabue et al. (2021) – SSP5-8.5 (Shared Socio-economic Pathways 8.5 scenario). Note that the magnitude of contemporary annual NPP ranges from less than 20 to more than 80 $\mathrm{Pg\,C\,yr^{-1}}$ in the compilation from Laufkötter et al. (2015). Both analyses showed negative and positive global trends, though most ecosystem models predict decreasing trends towards the year 2100. The figures were reproduced from Laufkötter et al. (2015) and Tagliabue et al. (2021) papers, under the CC-BY licence.

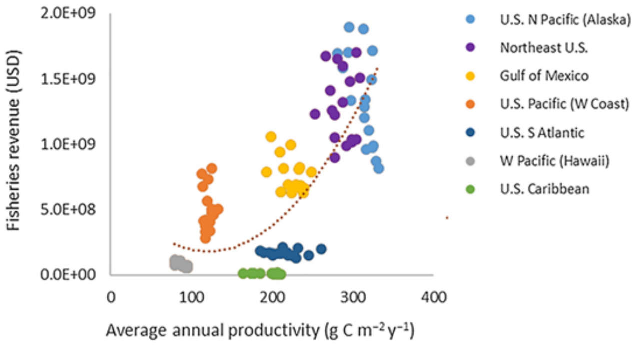


Figure 3. The impact of PP on fisheries. Figure reproduced from Marshak and Link (2021) paper under the CC-BY license. Individual observations from different coastal regions of the USA are indicated in different colours.

cited include uncertainties in production estimates and projections, the short duration of available time series data used in the analyses, and the lack of independent validation (IPCC, 2019, 2021; Gulev et al., 2021). This assessment is of particular concern as it has major implications for ecosystem service provision, mitigation planning, enhancing adaptation and building resilience to climate change (Hewitt et al., 2021). These applications often require regional to local information, as PP determines spatial variability in ecosystem services such as fisheries (Marshak and Link, 2021; see Fig. 3), but uncertainties increase at these scales compared with global estimates (Tagliabue et al., 2021). Both remote sensing and ecosystem models can, in principle, deliver such regional insights, when used with granularity and resolution needed at the appropriate scales. Reducing uncertainty in models, ideally through a coordinated and internally consistent set of simulations, data and knowledge, would then enable us to discuss downstream services under various climate scenarios and associated risks of tipping points (Jones et al., 2024). Such improvements would support climate policy, as well as management decisions pertaining to climate mitigation and adaptation strategies, at both international and regional levels.

We argue here that efforts to reduce uncertainty in estimates and projections of marine PP should include a focus on *investigating model structures and parametrisations*, with the goal of identifying genuine inter-model differences and reconciling apparent differences. In this review, we examine both the sources of differences between satellite-based and ecosystem models, as well as within these two types of models. We argue that there is strong scientific justification for considering how the current model parameterisations could be improved. A straightforward avenue to improvement is that parameters which are currently treated as constants (e.g., the A_i parameters from Table 1) are assigned the most appropriate values consistent with the model structure and with all the available information. A step further is to allow the currently constant parameter values to vary with spatial locations and times. Although variable parameters would increase the complexity of the functional forms used in PP models, we argue that, at least in the less complex PP models (e.g., within satellite models and ecosystem models used in ESMs for climate projections), there are good scientific reasons to expect such parameter variations to be realistic. We propose that absence of such variations is responsible for the many apparent differences between the current PP models. Parameter variability might be less important for the more complex models with large numbers of phytoplankton types and/or size-classes, but for those models it is still essential to focus on the best possible ways of optimising the existing constant parameters. Furthermore, these highly complex models could provide valuable information for estimating the spatio-temporal variability of parameters used in less complex ecosystem and satellite-based models. This would also help increase consistency among different models, making them more comparable. At the same time, caution must be applied to ensure that increased consistency and convergence is not confused with increased accuracy. For this, we would need to continue independent assessments of accuracy, for example by comparisons with in situ observations, with full recognition of the caveats that such comparisons entail, as discussed above.

In general, we highlight the importance of correct parameterisations that are valid across multiple spatial and temporal scales, and for multiple phytoplankton types. We also discuss the challenges posed by such PP model parametrisations, argue that this is the right time to rise to those challenges, and propose strategies to overcome them. Finally, we discuss uncertainties in marine PP that might persist even when improved model parametrisations are adopted.

3 Modelling primary production

In this section, we assess how marine PP is treated in satellite-based and ecosystem models, identifying inter-model differences.

It is useful to consider GPP as the product of a biomass-specific production, say P^M, where M is a measure of phytoplankton biomass, multiplied by the biomass itself. In other words:

$$P = P^M \times M, \tag{1}$$

such that P^M carries all the information on the physiological controls on PP, whereas M accounts for the role of varying phytoplankton concentrations. Since phytoplankton are complex organisms, many options exist for defining biomass, including concentrations of the phytoplankton pigment chlorophyll a (B), phytoplankton carbon (C), or nitrogen content. The choice of biomass often depends on practical considerations (such as data availability) or by the study objectives (for example, carbon is an obvious choice in models designed to investigate the biologically mediated carbon cycle in the ocean). Models can also be classified according to which measure of biomass they track as the main currency in the ecosystem.

Dimensional analysis suggests that, in its simplest form, P^M can be represented in a canonical form with two parts: a scale factor P_m^M that carries the same dimensions as P^M, and a dimensionless function f_I of the scaled irradiance I_* available for photosynthesis (Platt and Sathyendranath, 1993), where the scaling factor would be a model parameter with the same dimensions as light, such that I_* is dimensionless. Thus, in such a canonical form, P^M can be written as:

$$P^M = P_m^M \times f_I\left(I_*\right). \tag{2}$$

In this form, P_m^M is not strictly constant, but implicitly accounts for the effects of other environmental variables on primary production, such as temperature (T) and nutrients (N), or changes in species composition. Such dependencies can be made more explicit (removing T and N dependence from P_m^M), such that Eq. (1) becomes:

$$P^M = P_m^M \times F\left(f_T(T), f_N(N), f_I\left(I_*\right)\right). \tag{3}$$

The function $F(f_T, f_N, f_{I,})$ can be specified as a simple product $f_T \times f_N \times f_I$ (e.g., Laufkötter et al., 2015; Kishi et al., 2007; Vichi et al., 2007; Yool et al., 2013; Butenschön et al., 2016), representing co-limitation by each variable, or it can follow Liebig's law of the minimum (e.g., Grégoire et al., 2008; Daewel and Schrum, 2013; Radtke et al., 2019), where the most limiting resource dictates the growth rate. Note that in Eqs. (2) and (3), the functions f_i are dimensionless, and that all the dimensions are carried by the scaling factor P_m^M. When models resolve multiple phytoplankton groups or species, Equation 3 is specified for each group, and their contributions are added to get total PP.

Commonly-used functions in PP models that represent the modulating roles of temperature, nutrients and light are summarised in Table 1. When more than one nutrient is considered, additional terms have to be included for each nutrient. Thus, models (the combined functions F) differ depending on (i) how many environmental factors are included in the model, (ii) the explicit functional forms selected for each modulating function; and (iii) the parameter values A_i, D_i assigned to those modulating functions, and whether they are allowed to vary with region and time. Finally, the functions f_i would ideally have values within the [0, 1] interval; however, this is often not the case for some of the temperature f_T functions (as can be seen in Table 1).

In some cases, it is necessary to track multiple measures of phytoplankton biomass within a model. For example, a unit conversion between chlorophyll a and carbon might be

Table 1. The different f_T, f_N, f_I and θ functions used across variety of CMIP and operationally used ecosystem models, as well as satellite models (which however typically do not use an explicit nutrient-limitation function, see Westberry et al., 2008). The ecosystem models explicitly mentioned are Biogeochemical Model for Hypoxic and Benthic Influenced areas (BAHMBI; Grégoire and Soetaert, 2010), Biogeochemical Flux Model (BFM; Vichi et al., 2015), ECOSystem MOdel (ECOSMO; Daewel and Schrum, 2013), European Regional Seas Ecosystem Model (ERSEM; Butenschön et al., 2016), Hadley Centre Ocean Carbon Cycle (HadOCC; Totterdell, 2019), Model of Ecosystem Dynamics, Sequestration and Acidification (MEDUSA; Yool et al., 2013), Marine Ecosystem Model (MEM; Shigemitsu et al., 2012), North-Pacific Ecosystem Model for Understanding Regional Oceanography (NEMURO; Kishi et al., 2007), PELAgic biogeochemistry for Global Ocean Simulations (PELAGOS; Vichi et al., 2007), Pelagic Interactions Scheme for Carbon and Ecosystem Studies (PISCES; Aumont et al., 2015), Carbon, Ocean Biogeochemistry and Lower Trophics (COBALT; Stock et al., 2020, 2025), and DARWIN model (Ward et al., 2012). $\widehat{\mathrm{Ph}}$ and N represent the concentrations of phosphate and nitrogen, respectively. Carbon is represented as C, and A_i and D_i stand for the different model parameters. In photoacclimation models, θ is the chlorophyll-to-carbon ratio.

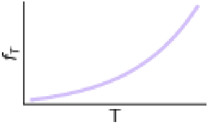
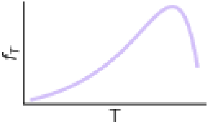
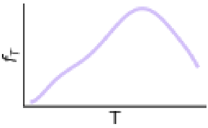
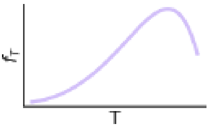
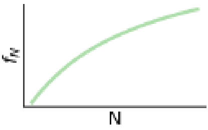
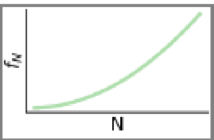
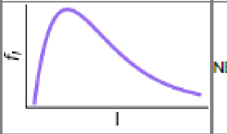
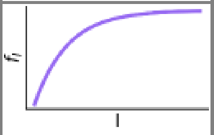
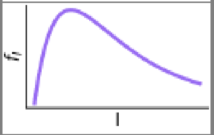
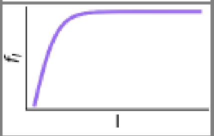
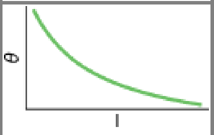
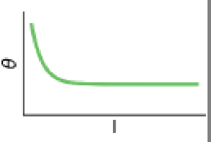
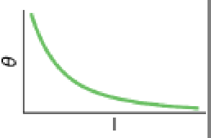
Process / Structure	Equation	Description & remarks	Graphical Representation	Examples	Key References
Temperature limitation on photosynthesis	$f_T = 0.59e^{0.0633T}$	Exponential temperature dependence on growth rate.		BAHMBI, MEDUSA, NEMURO, BFM, PISCES, PELAGOS, COBALT, DARWIN	Eppley (1972); Bissinger *et al.* (2008)
	$f_T = Q_{10}^{\frac{T-10}{10}} - Q_{10}^{\frac{T-32}{3}}$	Phytoplankton growth rate increases initially exponentially, with enzyme inhibition above optimal temperature.		ERSEM	Blackford *et al.* (2004)
	$f_T = \sum_{i=0}^{7} D_i T^i$	Phytoplankton growth rate is represented as an empirical seventh-order polynomial function, fit to observed data.		Vertically Generalised Production Model (VGPM)	Behrenfeld & Falkowski (1997)
	$f_T = 0.59e^{0.0633T} \times \left(1 - \frac{T-A_1}{A_2}\right)^2$	Function designed to model individual phytoplankton species or types according to their temperature traits, in multi-species models. It has yet to be used routinely in global-scale simulation models, except in a special case of DARWIN.		A version of DARWIN	Norberg (2004); Thomas *et al.* (2016); Sauterey *et al.* (2024); Krinos *et al.* (2025)
	N/A	No explicit temperature dependence is included in the model structure.	N/A	ECOSMO, HadOCC	Yumruktepe, Samuelsen, Daewel (2022)
	Empirical assignment	Indirect methods. An example is province-based assignment of parameters.	N/A	Satellite P&S, BICEP	Sathyendranath & Platt (1988); Longhurst *et al.* (1995); Sathyendranath *et al.* (2020); Kulk *et al.* (2020)
N-limitation	$f_N = \left(\frac{(\hat{N}/\hat{C})-A_3}{A_4-A_3} \times \frac{(\hat{P}/\hat{C})-A_5}{A_6-A_5}\right)^{0.5}$	Describes nutrient limitation based on internal nutrient quota for phytoplankton cells. Here, $0 \le f_N \le 1$ depends on internal cell N to C ($\hat{N}/\hat{C}$) and P to C ($\hat{P}/\hat{C}$) ratios and their maximum (A_4, A_6) and minimum (A_3, A_5) ratios.	N/A	ERSEM PISCES (for iron), DARWIN (quota version)	Droop (1974)
	$f_N = \frac{N}{N + A_7}$	Michaelis-Menton Equation. Describes N-limitation as a saturating function of external nutrient concentration, and the half saturation coefficient A_7 for that nutrient.		NEMURO, ECOSMO, BFM, MEDUSA, HadOCC PISCES (for all nutrients except iron), DARWIN (monod version)	Michaelis and Menton (1913); Kovarova-Kovar and Egli (1998); Lee *et al.* (2015)

Table 1.

	$f_N = \frac{(1-f_A)\times A_8\times N}{\left(\frac{(1-f_A)\times A_8}{f_A\times A_9}+N\right)}$, $f_A = \frac{1}{1+\sqrt{\frac{A_9\times N}{A_8}}}$	Optimal uptake kinetics.		MEM	Smith *et al.* (2009)
Light Limitation	$f_I = I \times e^{1-A_{10}\times I}$	Photosynthesis rate increases then declines at high light intensities due to photoinhibition.		NEMURO	Steele (1962)
	$f_I = (1-e^{-A_{11}\times I})$	Photosynthesis follows a light saturation curve with no inhibition at high light levels.		Satellite	Platt *et al.* (1980, 1990); Sathyendranath *et al.* (2020); Kulk *et al.* (2020)
	$f_I = (1-e^{-A_{12}\times I}) \times e^{-A_{13}\times I}$	Photosynthesis follows a light saturation curve with inhibition at high light levels.		BAHBI, MEM	Platt *et al.* (1980)
	$f_I = tanh(A_{14} \times I)$	Model with no photoinhibition. A hyperbolic tangent function is used to simulate light saturation curve.		ECOSMO	Jassby and Platt (1976)
Photo-acclamation	$\theta = \frac{A_{15}}{\left(1+\frac{A_{15}A_{16}I}{2A_{17}}\right)}$	Photo-acclimation model based on the concept of resource allocation, with maximum Chl-to-carbon ratio reached as light approaches zero.		ERSEM, BFM, PISCES, PELAGOS, COBALT, DARWIN	Geider *et al.* (1997, 1998)
	$\theta_{max} = 0.022 + (0.045-0.022)e^{-3I}$	Here, the maximum Chl-to-carbon ratio (θ_{max}) represent the Chl-to-carbon ratio (θ) in nutrient replete optimal growth conditions. The realised θ can be modulated by temperature and nutrients.		CBPM	Westberry *et al.* (2008)
	$\theta = \frac{A_{18}}{I\times {A_{19}}^{-1}} \times \left(1-e^{-\left(I\times {A_{19}}^{-1}\right)}\right)$	Based on an extended version of Geider *et al.* (1997,1998) photo-acclimation model. Uses exact analytic solution to Guider *et al.* (1997) model Jackson *et al.* (2017), extended to account for spectral light effects (Sathyendranath *et al.* 2020). It incorporates photo-acclimation effects on the Chl-to-carbon ratio.		Satellite	Sathyendranath *et al.* (2020); Jackson *et al.* (2019); Zheng *et al.* (2025)

needed to make the exponent in the light function (f_I) dimensionless, or it may be that the model tracks more than one currency. Such a conversion may also be needed to transform modelled phytoplankton carbon fields into chlorophyll *a* fields for comparison with satellite-based chlorophyll *a* products. This is typically achieved using a chlorophyll-to-carbon ratio (θ), which varies among phytoplankton and under different environmental conditions and is usually estimated using photo-acclimation models. Commonly used functions in photo-acclimation models are also shown in Table 1.

In the next two sections, we examine in more detail the variety of ways in which these concepts are implemented in satellite-based and ecosystem models.

3.1 Satellite-based models

In satellite-based PP models, daily water-column production is calculated as a function of phytoplankton biomass and light available at the sea surface, obtained from ocean-colour remote-sensing observations, coupled with models of photosynthetic response to light. Since the launch of the

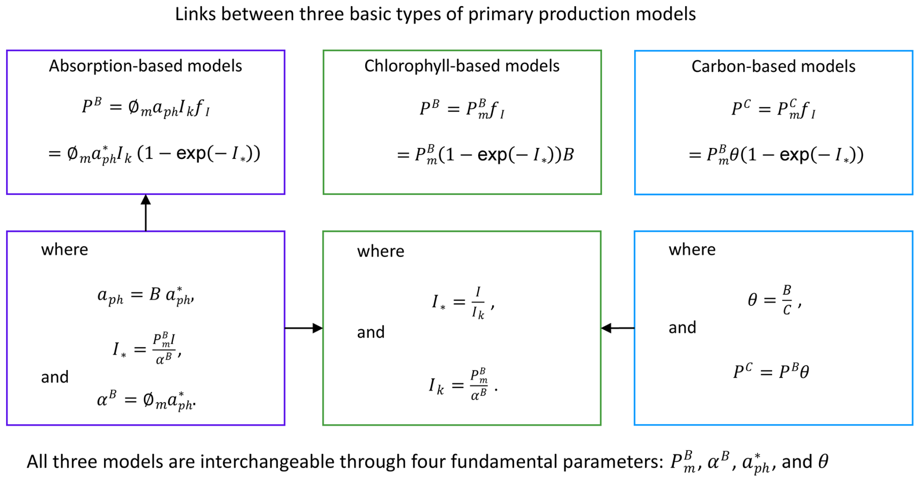


Figure 4. Phytoplankton absorption-, chlorophyll a- and carbon-based primary-production models commonly-used in satellite-based approaches, and the parameter transformations between them. Notations: primary production (P), light-limitation function (f_I), as in Table 1, assimilation number of the saturation-light curve, or the light saturation parameter (P^B_m), initial slope of the light-saturation curve (α^B), mean absorption coefficient of phytoplankton (a_{ph}), chlorophyll-to-carbon ratio (θ), chlorophyll-specific absorption coefficient of phytoplankton (a^*_{ph}), realised maximum quantum yield of photosynthesis (ϕ_{m}), photoacclimation parameter of the light-saturation curve (I_k), phytoplankton biomass in chlorophyll a units (B), normalised irradiance (I_*), irradiance (I), phytoplankton carbon biomass (C), time (t), and growth rate (g). One of the (f_I) functions from Table 1 was selected here for illustrative purposes, but other functions have also been used in the literature. As shown below (Fig. 7), numerically, most of the (f_I) functions are almost identical to each other, unless photo-inhibition is introduced. Currently, remote-sensing-based primary-production models do not incorporate the photo-inhibition term.

first ocean-colour satellite, the Coastal Zone Color Scanner (CZCS) in the 1970s, scientists have developed various satellite-based PP models that can be roughly categorised into three classes: (1) chlorophyll-based models, (2) absorption-based models, and (3) carbon-based models (Fig. 4). Each of these models could be further classified according to whether they are implemented as linear/nonlinear, spectral/non-spectral, vertically-uniform/vertically-non-uniform, or as a combination of these (Platt and Sathyendranath, 1993; Sathyendranath and Platt, 2007). Further bifurcations occur, depending on whether the models are depth-integrated, or not (Friedrichs et al., 2009). Most of the satellite-based models do not resolve PP by phytoplankton size classes, or functional types, with some exceptions, such as Uitz et al. (2010), Brewin et al. (2017) and Tao et al. (2017).

Satellite-based model outputs have been compared against in situ data, both globally and regionally (Friedrichs et al., 2009; Saba et al., 2010; Lee et al., 2015). No clear new directions have emerged from these intercomparisons. A contributing factor to this outcome could be the uncertainty in field measurements of PP and also to issues related to mismatches between the temporal and spatial resolutions of models and observations. These inter-comparisons did not examine closely the role of model parameters in the divergence of outputs. However, the assignment of model parameters remains one of the biggest sources of uncertainty in estimates of primary production from remote sensing observations (Platt and Sathyendranath, 1993; Sathyendranath and Platt, 2007; Sathyendranath et al., 2009; Kulk et al., 2020, 2021; Brewin et al., 2023).

Interestingly, the types of models described above all converge to the same principles and a common set of parameters (Sathyendranath and Platt, 2007; Fig. 4). Chlorophyll-based (or available-light or photosynthesis-irradiance) models typically use the parameters of the photosynthesis-irradiance curve, normalised to B, the concentration of chlorophyll a, i.e., the initial slope (α^B) and the assimilation number (P^B_m) of the light saturation curve, and the photoacclimation parameter ($I_k = P^B_m/\alpha^B$) derived from the other two (Platt et al., 1980; Sathyendranath and Platt, 2007; Fig. 4). Absorption-based (which are also called biomass-independent or inherent-optical-property) models use the realised maximum quantum yield (ϕ_{m}) and the absorption coefficient of phytoplankton (a_{ph}) (Kiefer and Mitchell, 1983, Lee et al., 2015). This model can be shown to be equivalent to the photosynthesis-irradiance models by using the identity $\phi_{\mathrm{m}} = \alpha^B/a_{\mathrm{ph}}$ (Platt and Sathyendranath, 1988; Sathyendranath and Platt, 2007; Fig. 4). The key parameter in carbon-based (or growth) models is the growth rate (g), i.e., the rate of change of carbon per unit time normalised to the initial phytoplankton carbon concentration. The chlorophyll-to-carbon ratio (θ) can be used to transform growth models to production models and vice versa (Sathyendranath and Platt, 2007; Sathyendranath et al., 2009). Thus, the different types of satellite-based primary production models are interchangeable through a common set of parameters: the initial slope (α^B) and assimilation number (P^B_m) of the light saturation curve, the mean specific absorption coefficient of phytoplankton (a^*_{ph}), and the chlorophyll-to-carbon ratio (θ) (Sathyendranath and Platt, 2007; Sathyendranath et al., 2009). When the light incident at the sea surface exceeds a threshold above which light can damage the photosystems, a photo-inhibition term has to be added to the photosynthesis-irradiance equation (Platt et al., 1980). This parameter is often not used in satellite-based models; a sensitivity analysis on a photosynthesis-irradiance model (Platt et al., 1990) showed that incorporation of realistic values of the photo-inhibition parameter into the model had only small to negligible effect on computed water-column primary production, which lends some justification to why this term is often ignored. But this is a simplification that can be readily dropped, if new evidence suggests that photo-inhibition could be important at large scales.

Spectral models of primary production are designed to capture the wavelength-dependent light penetration underwater, and wavelength-dependent photosynthesis (Sathyendranath and Platt, 1989). In fully-spectral models, the action spectrum of photosynthesis (which describes the wavelength-resolved values of the initial slope α^B) is coupled to the light available at corresponding wavelengths for photosynthesis (Sathyendranath and Platt, 1989; Kyewalyanga et al., 1992), such that the product $\alpha^B I$ that appears in non-spectral models has to be replaced by the wavelength integral $\int \alpha^B(\lambda) I(\lambda) d\lambda$, where λ represents the wavelength, and the integral is taken over the photosynthetically active range (400–700 nm). The spectral form of the action spectrum closely resembles that of the phytoplankton absorption spectrum (a_{ph}) (Sathyendranath et al., 1989; Kyewalyanga et al., 1997). Spectral effects are generally considered to be not relevant at saturating light levels. Under light-limiting conditions, if the light available is blue-rich, where the action spectrum has a maximum, the coupling between light and photosynthesis would be stronger than if the light were green-rich, where the action spectrum typically goes through a minimum. We know from previous studies that spectral and non-spectral models may differ from each other in a systematic manner (Sathyendranath and Platt, 2007), because non-spectral models are not able to account for the covariance (or the lack of it) between spectrally-resolved α^B and a_{ph}. To some extent, the impact of the spectral effects on water-column primary production could be accommodated into non-spectral models by suitably tuning the parameters of non-spectral models (Platt and Sathyendranath, 1991). Typically, therefore, one anticipates systematic differences between spectral and non-spectral models of marine primary production, unless model parameters are adjusted to compensate for the difference.

3.2 Ecosystem models

Ecosystem models differ greatly in their complexity, ranging from simple, three-component Nutrient-Phytoplankton-Zooplankton (NPZ) models (Fasham et al., 1990; Steele and Henderson, 1992; Franks, 2002; Gentleman, 2002) to highly complex ones with hundreds of ecosystem components (e.g., Dutkiewicz et al., 2020; Fennel et al., 2022). Some models use a single measure for biomass (e.g., carbon), and a single nutrient (usually nitrogen) as the model currency, assuming a fixed stoichiometry (relationship between biogeochemically-important elements), whereas other models allow for dynamically resolved stoichiometry within f_N. In this section, we focus primarily (but not exclusively) on marine ecosystem models (here used interchangeably with "‘marine biogeochemical models") that participate in the Climate Model Intercomparison Project (CMIP) (e.g., Laufkötter et al., 2015; Kwiatkowski et al., 2020), as well as regional ecosystem models that are run operationally by forecasting centres (e.g., Fennel et al., 2019) for regional climate projections. In these models, PP is usually estimated along the lines of Eqs. (2) and (3), where primary production (P) is calculated by multiplying the phytoplankton biomass (usually carbon) by its reference growth rate g), modulated typically by the three functions, f_T, f_N and f_I.

There are also many similarities across the ecosystem models that go beyond the functional form of Eq. (2), and a few common approaches can be identified in the equations used to express the functions f_T, f_N and f_I (Table 1). For instance, f_T is typically described through an exponential function (originating from Eppley, 1972; e.g., see Laufkötter et al., 2015), that was proposed as an outer envelope of temperature response functions of many single phytoplankton species (Eppley, 1972; Norberg, 2004). The response functions of individual phytoplankton species could include inhibition temperatures higher than what is optimal for growth of that specific species (e.g., Norberg, 2004; Butenschön et al., 2016; Dutkiewicz et al., 2020), which is linked to Q_{10}, a measure of the sensitivity of photosynthesis to temperature. This temperature inhibition of individual phytoplankton species is not captured by the exponential function representing the collective response. Furthermore, ecosystem models that resolve groups of phytoplankton (e.g., diatoms) do not have temperature inhibition, with the implicit assumption that there is a spectrum of diatoms that have temperature optima across the full temperature range (see e.g., Anderson et al., 2021). Furthermore, some models do not have explicit PP temperature dependence at all (e.g., Daewel and Schrum, 2013). When multiple nutrients are considered, the f_N function is typically formulated to use Liebig's law of minimum to combine their effects on PP, and is often based either on cell quota of nutrients within the cells (Droop, 1974), or on the concentrations of the nutrients in the medium (Michaelis and Menten, 1913). In some cases (e.g., Shigemitsu et al., 2012), f_N is based on the optimal nutrient uptake kinetics (Smith et al., 2009), which allows for parameters in the Michaelis–Menten equation to vary (Table 1). A variety of equations are currently in use to describe the light-dependence function (f_I, see Table 1) in ecosystem models, including those from Platt et al. (1980), Steele (1962), and Jassby and Platt (1976), some of which account for the effect of photo-inhibition at high light, whilst others do not. Furthermore, many of the ecosystem models also include photoacclimation, either as part of the f_I function, or as an additional term, mostly following the model of Geider et al. (1997, 1998).

Other significant differences across ecosystem photosynthesis models include the number of phytoplankton functional types and size-classes represented, the number of limiting nutrients included (and the types of equations selected to represent the role of each nutrient), and the number of wavebands considered in representation of irradiance (the level to which light is spectrally and directionally resolved, e.g., see Platt and Sathyendranath, 1991; Dutkiewicz et al., 2015; Gregg and Rousseaux, 2016). Practically all ecosystem models include nitrogen limitation. But iron limitation is also considered important, as is silica limitation, especially in those models that include diatoms as a phytoplankton class. Phosphate limitation becomes important as well, in particular when dealing with nitrogen-fixing organisms. Another fundamental difference lies in the representation of the production and remineralisation of particulate and dissolved organic matter which are included in the models as explicit or implicit processes, affecting the model parametrisations of GPP, which may or may not include exudation (e.g., Butenschön et al., 2016; Vichi et al., 2007; Wu et al., 2021).

3.3 Comparison of satellite-based and ecosystem models

Satellite-based and ecosystem models for estimating ocean PP have some similarities, but also key distinctions (Fig. 5; also see IOCCG, 2020). Model parameter assignment provides one clear perspective on a difference between the two types of models. For example, parameters associated with PP models in the satellite-based approach of Platt and Sathyendranath (1988), Kulk et al. (2020) and Sathyendranath et al. (2020) are established from field observations, whereas ecosystem model parameters are typically estimated using information from laboratory experiments conducted under controlled conditions, followed by tuning the model towards the available observations. But here also, the distinction is not clear cut: for example, the carbon-based production model of Behrenfeld et al. (2005) relies on culture measurements to establish growth rate and carbon-to-chlorophyll ratio. Some satellite-based models that do not have explicit nutrient and temperature dependencies implicitly incorporate those dependencies in the model parameter values, which are allowed to vary across biogeographical provinces (Longhurst, 2007) and seasons (e.g., see Fig. 6 for photosynthesis-irradiance parameter data partitioned according to Longhurst provinces), representing different nutrient and temperature environments. Ecosystem models typically represent the nutrient and temperature limitation explicitly, with different parameters assigned to each plankton group. Another difference in parameterisation is that many ecosystem models use maximum carbon or nitrogen-specific production rate under optimal conditions as a model parameter and the corresponding biomass is then used to scale PP to its absolute value (Fig. 5). While carbon-based satellite algorithms for PP are similar to ecosystem models in this respect, other satellite models rely on bio-optical properties such as chlorophyll *a* concentration or phytoplankton absorption coefficient as the state variable. Some ecosystem models also include a photo-inhibition term, to represent the reduction in photosynthesis under high light intensities, whereas satellite-based models typically account only for the saturating response to light without including photoinhibition. Photoacclimation is generally addressed by both approaches, with many of them relying on variations of the Geider et al. (1997, 1998), though there are exceptions (e.g., photoaccilimation model in Westberry et al., 2008).

Finally, the ecosystem models are able to compute depth-resolved PP, as is the case for the satellite-based method proposed by Platt and Sathyendranath (1988), whereas some other satellite-based models are designed to yield vertically integrated production (e.g., Behrenfeld and Falkowski, 1997).

All satellite-based models are data-rich, in the sense that they are designed to exploit satellite observations, typically with global coverage and nominal daily repeat frequency. Some use culture data as auxiliary information; others rely on in situ field observations. Ecosystem models, on the other hand, tend to be data-sparse; even when operated in data assimilation mode, only a fraction of the modelled ecosystem compartments or fluxes are usually constrained by assimilation. The constraints imposed by satellite data availability limit the processes and variables that can be estimated, whereas ecosystem models tend to be rich in outputs they provide.

Platt and Sathyendranath (1997) proposed a hierarchy of PP models (Fig. 7). Almost all the types of models in this hierarchical classification, other than purely statistical models, are represented in PP models under discussion in this paper. With the exception of absorbed-light models that are in use in satellite-based models, but not in ecosystem models, the different classes of models are found in both types of models. In this regard, the diversity of models within satellite-based or ecosystem-based approaches is no smaller than across those two groups of models, though, notably, models that use chlorophyll *a* as the state variable are unique to satellite-based approaches. (There are sound reasons for the choice of chlorophyll *a* concentration as the state variable, in addition to the obvious one that it is readily available from ocean-colour data (e.g., Sathyendranath et al., 2023).

When dealing with complex problems such as the one addressed here, it is always an advantage to look at the problem from multiple angles. Convergence of solutions add confidence, divergence helps identify sources of discrepancy. It

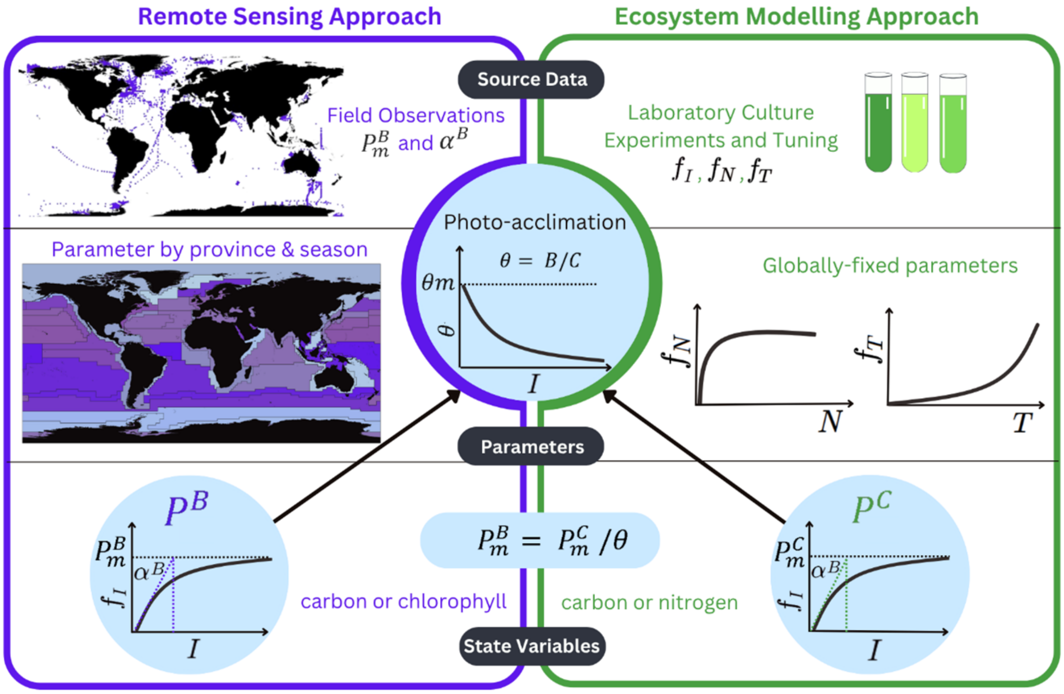


Figure 5. Comparison of satellite remote sensing (left) and ecosystem modelling (right) approaches to computing marine primary production, and where they interact (light blue) through the photo-acclimation model which is essential to enable comparison between the models. $I =$ Light, $N =$ Nutrient, $T =$ Temperature. It should be noted that although carbon, or nitrogen, are the most common currency used by the ecosystem models, there are also ecosystem models which use chlorophyll a as the currency.

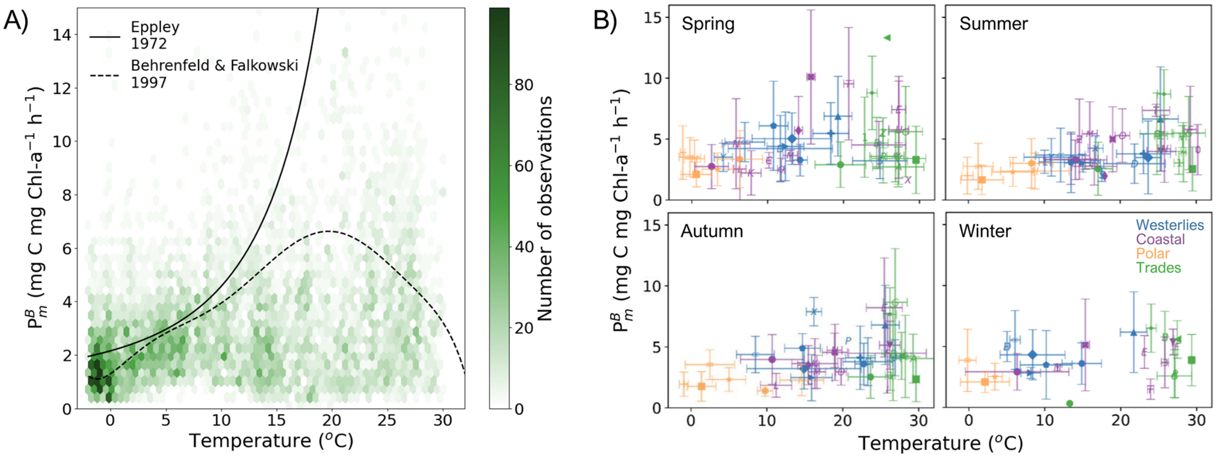


Figure 6. Variability in the photosynthesis-irradiance parameter P_m^B in the ocean. **(A)** Parameter values from a global in situ dataset (Bouman et al., 2018; Kulk et al., 2020) plotted as a function of temperature. Two commonly-used temperature-dependent equations (Eppley, 1972; Behrenfeld and Falkowski, 1997) of this parameter are also shown. **(B)** The same data sorted according to ecological provinces of Longhurst (2007) and according to season, with colours representing four different oceanic biomes (Longhurst, 2007), showing that some structure and pattern emerge when the data are organised according to oceanic biomes and to a smaller degree seasons.

is worth emphasising that the relative strengths and weaknesses of ecosystem and satellite-based models can be leveraged, once the two types of models become better integrated, as advocated in this paper. We provide concrete examples on how the two types of models could be of benefit to each other in the section outlining the way forward.

4 How similar are the different primary production models?

Platt and Sathyendranath (1993) showed that we can anticipate systematic biases between satellite-based models that are structured differently, and we can theoretically, or nu-

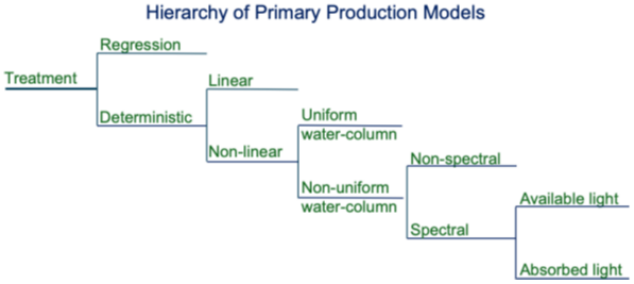


Figure 7. Hierarchy of primary production models. The models get more complete (and more complex), as we go from left to right, and from the upper to the lower limb of each branch.

merically predict under what conditions the biases relative to each other will manifest themselves. For example, linear and non-linear models are expected to behave similarly under low-light levels, but to diverge as light levels increase. The authors also showed that when PP models have similar structures, it is possible to reduce all of them to a common, canonical form, revealing that apparently-different model types (available light models, absorbed light models, chlorophyll-based or carbon-based models) become equivalent when implemented with comparable model parameter values (Platt and Sathyendranath, 1993; also see Sathyendranath and Platt, 2007; Sathyendranath et al., 2020). Such comparisons also reveal systematic biases between spectral and non-spectral models of PP, arising from spectral effects in both underwater light penetration and phytoplankton light utilisation. It has been demonstrated that biases between spectral and non-spectral PP models can be minimised by tuning the diffuse attenuation coefficient of downwelling irradiance, which determines the rate of change of available light with depth (Platt and Sathyendranath, 1991; Kyewalyanga et al., 1992). Similarly, Kovač et al. (2016a) demonstrated that a locally tuned non-spectral model, with adjusted values of photosynthesis parameters, can outperform a spectral model, without locally tuned values of photosynthesis parameters. Such comparisons bring to the fore the importance of parameter assessment, assignment, and evaluation to understand model performances, uncertainties and divergences, which is at the core of this review.

To illustrate the point, let us focus, for example, on the light function (f_I), which takes a wide range of forms in the literature (see Table 1). Even though the functional forms cannot be analytically transformed into each other (they are mathematically different), numerically they could still be very close to each other, in the sense that they can all fit the same observations similarly well when the parameters are chosen appropriately (Kovač et al., 2017). These different forms split into two classes: one that includes photo-inhibition and the other that does not (Amirian et al., 2025). Figure 8 shows that the f_I, models without photo-inhibition (Webb et al., 1974; Jassby and Platt, 1976; Smith, 1936) are all practically identical to each other for equivalent parameter values and are therefore basically indistinguishable from each other. It should also be noted that the Webb et al. (1974) model is a special case of the Platt et al. (1980) model for the case of zero photo-inhibition. The f_I, model that stands out is the one of Steele (1962), which struggles to match the other f_I, models under low-light conditions. However, when photo-inhibition is important, the f_I, model of Platt et al. (1980) can again nicely match the Steele (1962) model if their parameter values are chosen appropriately. What we learn from Fig. 8 is that a lot of the diversity in f_I models is only apparent, as the diversity can be eliminated via model parametrisation.

In general, PP models are designed to represent limitations to phytoplankton growth (whether from light, nutrients or temperature) under different environmental conditions and for different groups of phytoplankton, as appropriate. These models have the potential to be generalised to deal with additional external conditions (which may not be explicitly included in the model) by incorporating spatially and temporally variable parameter values. This flexibility allows models to account for the diversity of phytoplankton and the processes responsible for their dynamics, which are not explicitly represented in current models. Representing the full diversity of phytoplankton species is not feasible due to lack of understanding and computational demand, which is why models typically rely on the use of phytoplankton classes to represent aggregations of multiple species based on shared characteristics or traits, such as body size, biogeochemical functions, life strategies and behaviours. This approach captures at best the average or most typical behaviour of each class (e.g., Anderson et al., 2021; Ratnarajah et al., 2023). When aggregating species according to their physiological and functional traits and behavioural patterns into a pre-defined number of modelled classes, fixed values are assigned to model parameters within each aggregated class. For ecosystem models, many of these parameters have assigned values based on laboratory or mesocosm experiments (Geider et al., 1998; Schartau et al., 2017; Ratnarajah et al., 2023), often focusing on a small number of carefully-selected species, far from capturing the full diversity of organisms or their responses and behaviours that might be expected in the natural environment across large spatio-temporal scales (Geider et al., 1998; Schartau et al., 2017; Ratnarajah et al., 2023). In contrast, in the natural environment, we can expect parameters to vary in time and space, reflecting both changes in the governing conditions and in the unresolved functional diversity in the makeup of modelled planktonic communities (Schartau et al., 2017). Such parameter variability can be observed in model calibration experiments (e.g., Leeds et al., 2013; Mattern et al., 2012, 2014), including those using data assimilation to estimate model parameters jointly with the model state (e.g., Pastres et al., 2003; Tjiputra et al., 2007; Roy et al., 2012; Doron et al.,

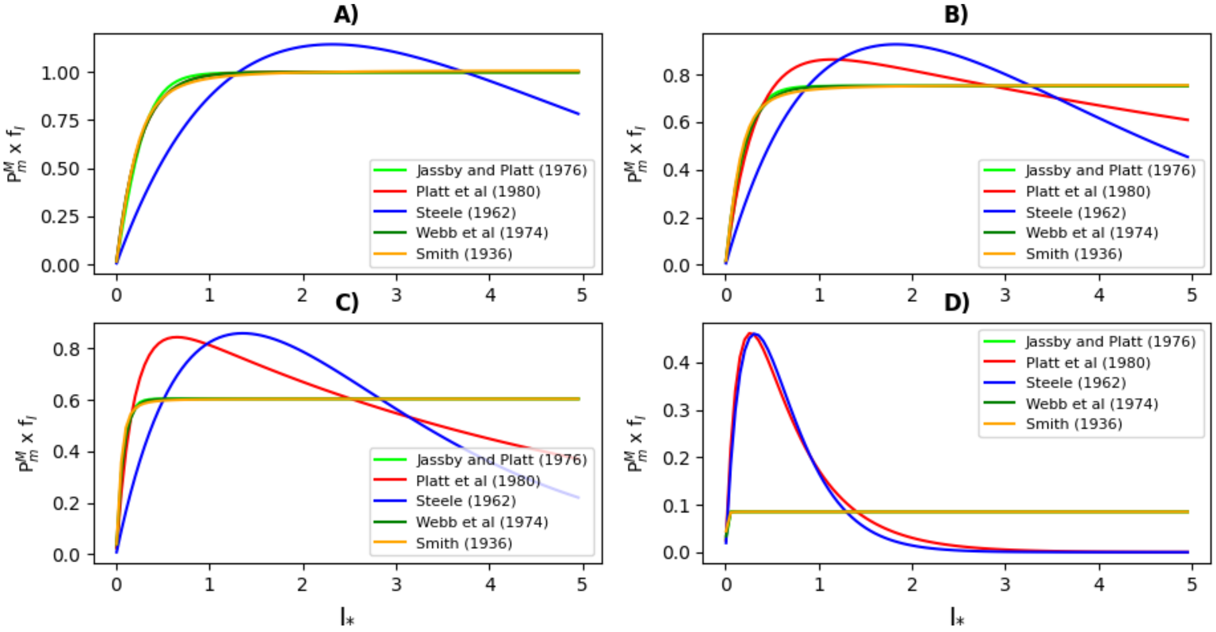


Figure 8. Comparing the functional forms of four f_I models in different regimes. Since only the functional forms are compared, the x and y axes do not necessarily represent realistic values of normalized irradiance (I_*) or f_I, and the units are arbitrary. The figure shows the degree to which the five different models can be "tuned" to each other through fitting their parameters in a suitable way. The functional forms for the f_I models presented in this figure are introduced in Table 1, except the model by Webb et al. (1974), which is a special case of Platt et al. (1980) for zero photoinhibition (setting $A_{14} = 0$, see Table 1). Furthermore, what is plotted in this figure is f_I multiplied by the scaling factor P_m^M in Eqs. (2) and (3). The panels **(A)**–**(D)** show cases of increasing photoinhibition as modelled by the most complex Platt et al. (1980) model (**A** is the lowest, **D** the highest), with the other models tuned to best fit the curve corresponding to Platt et al. (1980). We see that the five models essentially split into two families, each representing well a limiting case of either no photoinhibition (Jassby and Platt, 1976; Webb et al., 1974; Smith, 1936), or very high photoinhibition (Steele, 1962).

2013; Simon et al., 2015; Gharamti et al., 2017a, b; Skákala et al., 2024).

A simple illustration of how parameter variability emerges from aggregating species into classes is provided in Fig. 9. Although models differ from each other in the number of phytoplankton classes they resolve, for each phytoplankton class they typically use the same functional form to describe photosynthesis, with total phytoplankton PP corresponding to the sum of contributions across all classes. Figure 9 demonstrates that models with different numbers of classes become equivalent in their description of total PP, provided that the parameters in models with fewer classes are allowed to vary with space and time. In such a way, spatio-temporal parameter variations could effectively capture the influence of unresolved diversity in phytoplankton community structure, in models with only a few phytoplankton classes. The spatio-temporal model parameter variations would then be a consequence of the models' inability to sufficiently resolve phytoplankton species, which also means that such parameter variability would be expected to be especially relevant for the simpler models (e.g., ecosystem models typically used in ESMs). The more complex models currently in use (e.g., DARWIN; see Ward et al., 2012; Dutkiewicz et al., 2020) would have less reason to adopt spatio-temporally variable parameters; but these models are typically too computationally expensive to be run as part of ESMs in long-term ensemble-based climate projections. Furthermore, even as complex as they are, they still represent only a fraction of the real-world diversity. On the other hand, as the models get more complex by incorporating more ecosystem compartments, the challenge shifts to calibrating each of the large numbers of parameters to adequately capture the functions of each of the model components.

5 A way forward

Together, these considerations suggest that investigating parameter assignment and parameter variability may be an important route to understand and potentially reduce many of the apparent differences between marine PP models, and hence in the estimated magnitudes of production. Investigation into the role of parameters should be followed by a consistent calibration against observational data. To estimate spatially and temporally varying parameters in ecosystem models, data assimilation can provide a natural tool for model calibration (e.g., Tjiputra et al., 2007; Singh et al., 2025). However, introducing spatio-temporally variable (or

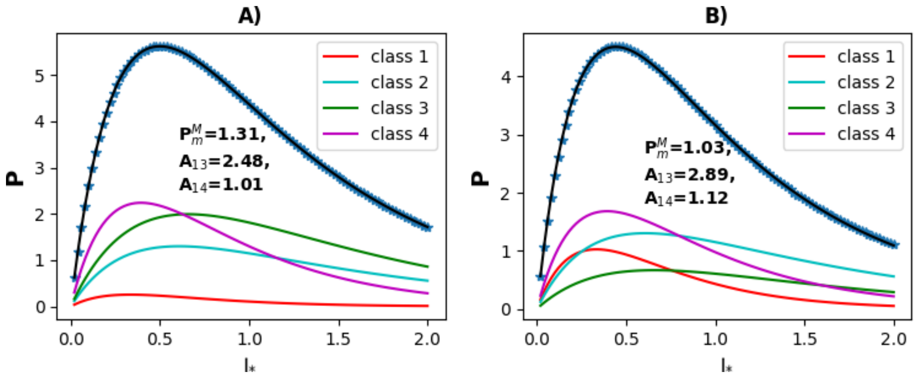


Figure 9. A simple illustration of how unresolved phytoplankton community structure can lead to parameter variability. In both panels, we plot PP expressed as $P = P_m^M f_I(I_*)M$ with functional form f_I corresponding to the Platt et al. (1980) model (see Table 1). As in Fig. 8, ranges of scaled irradiance, I_*, and PP values are arbitrary. Four phytoplankton classes are plotted, each with different $P_m^M A_{13} A_{14}$ parameters. The dark blue dots are obtained by summing up the PP across the four classes (this corresponds to PP of total phytoplankton) and the dark blue line is the fit of the points with the same functional form used for the four phytoplankton classes assuming the total phytoplankton concentration is the sum of the concentrations of the four classes. The two panels show two situations where the same total phytoplankton concentration is distributed into classes in different ways (the phytoplankton community structure changes). We can see that if we did not resolve the four classes, we could still use the Platt et al. (1980) model (including photoinhibition) for the total phytoplankton, but the parameters $P_m^M A_{13}$, and A_{14} would vary depending on the (unresolved) variations in the phytoplankton community structure.

too many constant) parameters comes with its own challenges. For example, allowing the (often many) model parameters to vary substantially increases model flexibility, but at the risk of overfitting to observations, particularly if the number of model parameters is large or observational data are insufficient. Overfitting may reduce the model ability in predicting new phenomena, including future climate-driven changes. It is therefore essential that the introduction of variable parameters takes into account such risks and ensures that reasonable assumptions are made to simplify the parameter calibration task. These assumptions would ensure that model calibration is sufficiently constrained, so that there are sufficient observations per each calibrated model parameter value. For example, only a carefully selected subset of parameters may be calibrated, based on their relevance for PP (established, for example, through sensitivity analysis, e.g., Ciavatta et al., 2025) and lack of correlations with other model parameters.

A key consideration when exploring variable parameters is the spatial and temporal scales at which they might vary. For example, it would be important to establish whether seasonal, climatological variability in parameters would be sufficient to capture observed patterns, implying that variability at shorter (sub-seasonal) and longer (inter-annual) time scales could be negligible. If so, this would relax the requirement on the volumes of observational data needed for the calibration, and also on the need to continually update parameter values from day to day or year to year. Hypotheses about temporal variability scales for model parameters can be tested using long time-series of measurements at specific stations, such as the Bermuda Atlantic Time-series Study and the Hawaii Ocean Time-series, both of which present seasonal cycles in photosynthesis parameters (Kovač et al., 2016b, 2018). Another key question is whether parameters vary over fine spatial scales or maintain coherence over large scales such as within ocean biomes or Longhurst provinces (Longhurst, 2007). Preliminary evidence suggests that, at least for the global-scale applications, ecological provinces according to Longhurst might provide an appropriate template for mapping parameters (see Fig. 6B), and that monthly or seasonal time scales might be appropriate for modelling variability in photosynthesis-irradiance parameters (Britten et al., 2025). If province-based approaches emerge as viable candidates, it would be desirable to avoid sharp discontinuities in parameter values at province boundaries, which might require incorporation of smoothing methods to make inter-province changes seamless. Moreover, it is essential that model parameter calibration does not compensate for unrelated spatio-temporally varying model biases, such as those arising from external forcings or other ecosystem model constraints (e.g., boundary conditions). For example, given the importance of underlying physical processes, caution should be applied when calibrating parameters in ecosystem models to avoid models better reproducing the observed PP, but for the wrong reasons. Singh et al. (2025) illustrate that ecosystem parameters in global ocean biogeochemical models are likely calibrated to compensate for biases in their physics (see also Löptien and Dietze, 2019). To avoid mixing different sources of ecosystem model errors, parameters should be ideally estimated jointly with the model state, e.g., using joint parameter-state data assimilation techniques (Schartau et al., 2017). Finally, existing knowledge of acceptable ranges of parameter values needs to be incorporated into the calibration process to prevent parameters from acquiring unrealistic values.

Since parameter spatio-temporal variability results from poorly resolved species types or ecosystem processes, interesting insights into its scale and patterns can be also obtained by comparing models of different complexity. For example, high-complexity ecosystem models (such as the DARWIN ecosystem model) could be used in some cases to deduce the degree of parameter variability of simpler ecosystem models or help inform spatio-temporally varying parameter calibration of those models (always keeping in mind that inter-model consistency does not automatically imply model quality). Comparison studies across models of different complexity would be desirable in this case (for some examples see Friedrichs et al., 2007; Xiao and Friedrichs, 2014). Similarly, emergent properties of ecosystem models can be leveraged to provide specific information for satellite-based models, such as vertical and class-distribution of phytoplankton (e.g., Stock, 2019), or information about nutrient distributions. Such inter-calibrations of models against each other could potentially improve satellite PP products and conversely make the satellite PP data more useful for ecosystem model development. However, one has to be cautious here: model-model intercomparisons and tuning would help models look more like each other, but independent information would be needed to ensure that the simulations are also getting closer to key features in the real world that the models are designed to reproduce.

Even after successfully overcoming the challenges associated with spatio-temporal parameter calibration, significant PP uncertainty is likely to remain in both historical estimates and future projections. For satellite-based models, residual uncertainties could be associated with inherent observational biases, e.g., gaps in data due to cloud cover or adverse viewing geometry, or inaccuracies in satellite products associated with bio-optical conditions in water, or biases inherited from calibration against in situ PP observations with their own inherent uncertainties. For ecosystem models, additional sources of uncertainty include the forcing data and the physical model driving biogeochemical processes, e.g., its vertical and horizontal resolution, and its ability to represent currents and mixing responsible for nutrient supply and export of organic material. For example, differences in how models treat external forcing, such as micro- and macronutrient depositions from the atmosphere, could still contribute to the growth of uncertainties as models become more complex. Furthermore, the spread in the underlying environmental changes such as warming, stratification, changes in irradiation, and ocean circulation among others, contributes significantly to uncertainties in the PP projection.

Further constraints are inherent to ecosystem models themselves. Traditionally, plankton are divided into phototrophic phytoplankton and phagotrophic zooplankton. However, recent research emphasises ubiquitous presence of mixotrophy in the global ocean (Mitra et al., 2023), which not only differs in its physiology and ecological role, but also in its complex interactions with other types of plankton (Flynn and Mitra, 2023). Despite certain commonality in their approach to modelling PP, as discussed above, models differ significantly in their approaches to representing various biogeochemical processes such as grazing and associated fluxes, deposition of organic matter and its remineralisation. For many of those processes (e.g., zooplankton grazing), lack of data, and variability and high uncertainty of available data, are major issues. Focusing on biological ocean carbon storage, Henson et al. (2024) identified key areas where improved understanding of processes is required to support future modelling efforts. For PP, the processes that were ranked highest were: resource limitation for growth, nitrogen fixation, zooplankton processes and phytoplankton loss processes. Current ecosystem models differ considerably in their formulation and parameterisation of these processes, contributing to uncertainties in model outcomes. Moreover, nitrogen-fixation is often not included in these models. Even when these key processes are included, spatial parameter estimation through assimilating observed state variables (such as water column nutrients and oxygen) in ocean biogeochemical models does not necessarily lead to an improved estimate of PP, suggesting that current ecosystem model parameterisations may still be oversimplified compared with the real world (Singh et al., 2025).

The time is right to address the problem of parameter estimation in PP models, both for ecosystem models and satellite-based models. Novel and rapidly expanding observations such as BGC Argo profiles, other types of autonomous data collected by in-water vehicles and also large marine mammals (Chai et al., 2020; Claustre et al., 2020) have been providing large volumes of biological and bio-optical data that complements in situ data from long time series stations, and could be harnessed for this purpose (Fig. 10). Complementary observations from satellite remote sensing, now available over multiple decades and merged into climate-quality, consistent data streams (e.g., Sathyendranath et al., 2019), is another rich data source, along with novel satellite products from emerging capabilities such as geostationary, lidar, cubesat and hyperspectral data. When these are combined with more traditional in situ platforms, including long-term gridded climatology from sources such as World Ocean Atlas (WOA, e.g., Garcia et al., 2019), and potentially complemented by the intercomparison of models with different complexity, there is in several cases already enough data to support a suitably-constrained spatio-temporally varying parameter calibration. This opportunity is further enhanced by new advances in artificial intelligence (AI) and machine learning (ML), giving us an historically unprecedented capability to exploit large and growing datasets to address long-standing questions about marine PP. AI can be used in a variety of different ways, either as a direct prediction approach to optimise model parameterisation and also to emulate models, allowing it to explore a range of

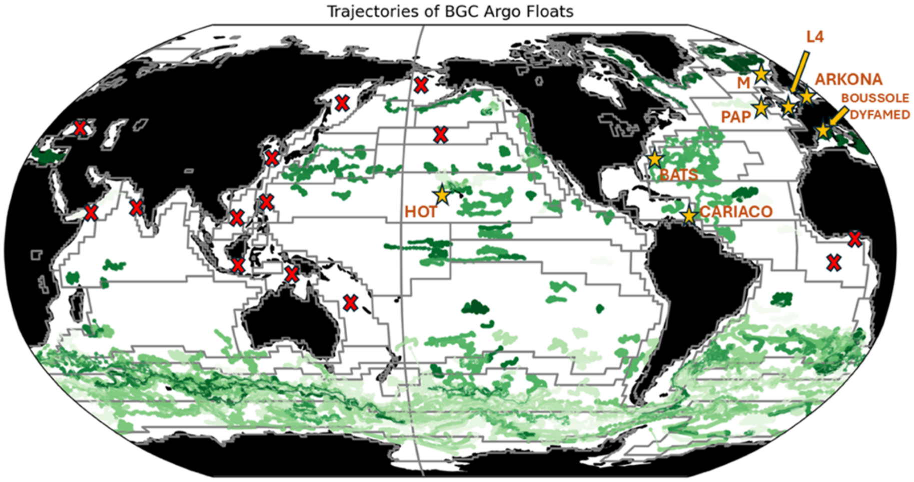


Figure 10. The global in situ data available for model calibration. The boundaries show ecological provinces according to Longhurst (2007). BGC-Argo float trajectories are shown in shades of green, providing sufficiently long time-series (since 2008) for calibration. Orange stars mark in situ time series stations with sufficiently long time-series records that can also be used for model calibration. The red crosses mark provinces without sufficient BGC-Argo data or in situ stations, where the models will need to rely solely on satellite records and compilations of in situ observations, such as the World Ocean Atlas.

model behaviours at reduced computational cost for parameter sensitivity analyses and model calibration (e.g., Mattern et al., 2012; Schartau et al., 2017). Furthermore, recent statistical approaches unique to the ML field enable insights into what the ML model has learned, for example, using Explainable AI, or physically constrained machine learning.

However, crucial to this endeavour would be a clear focus on data quality, and on data validation, following community-wide accepted protocols and reliable uncertainty characterisation. Moreover, some regions, such as sea-ice margins, coastal margins, and high latitudes in winter, which are often regions experiencing long-term rapid changes and include some of the most productive areas of the global ocean, also tend to be regions that are difficult to observe, and hence suffer from sparse data coverage. More observations are needed in such locations to understand the behaviour of model parameters in such regions, including their future changes. Even if constrained spatio-temporally varying calibration is possible in these regions with the available datasets, the importance of further investing in data quantity and quality cannot be overemphasised.

6 Conclusions

We have argued that, given the growing abundance of observations from diverse platforms, such as satellites and BGC-Argo, combined with rapidly advancing capabilities in ensemble data assimilation techniques and artificial intelligence, the time has now come to address explicitly the importance of parameter assignment in primary production models, and in exploring the spatial and temporal variability in the parameters. We have theoretically justified why such parameter variability is to be expected both in the satellite-based models (where some models already employ variable parameters albeit in a simple fashion) and ecosystem models (where assignment of variable parameters is still quite rare), at least in models are of high complexity. In the case of primary production, the number of phytoplankton classes that are included in the model is a key differentiator of the model complexity. Relatively simpler models, such as the ecosystem models used as part of ESMs in climate projections, have limited capability to resolve phytoplankton communities. For such models, spatio-temporally varying parameters could provide a means to account for the unresolved phytoplankton variability and processes.

Spatio-temporally variable parameter calibration can shed light on the sources of differences between low or medium complexity ecosystem models typically used in ESMs and satellite-based primary-production models. Since variable parameters can capture, in a simple manner, processes or conditions that are not explicitly included in a model, analysing the drivers of parameter variability could help identify how best to overcome current model drawbacks. Furthermore, providing those models with spatio-temporally varying parameters could remove many apparent differences between models, both potentially reducing the spatial and temporal biases in model parameter calibration and enabling the simpler ecosystem models to better represent the effects of unresolved processes or phytoplankton classes. It would also create opportunities for improved intercomparison across models of different complexity, including the ability to understand more about unresolved variability in simpler models by comparing them with the higher-complexity models. One could argue that the spatio-temporally varying parametrisation could help reduce the existing high uncertainty both in historical estimates and future projections of marine PP, provided that independent information is used to avoid all models converging towards a systematically biased outcome. Due to the importance of primary production for climate research, improving its prediction can have a major impact on both climate mitigation and adaptation planning.

In the context of our climate, we need to understand how marine ecosystems in general, and phytoplankton in particular, respond to change. Three types of changes need investigation: changes in (i) phytoplankton biomass (whether they be measured as chlorophyll a, carbon or nitrogen concentration, or all of them); (ii) the rates of biological processes, with marine primary production being a key process in the global carbon cycle; and (iii) community structure. All these objectives are intimately linked to parameter variability, with the third one in particular calling for resolution of parameter variability at the level of major components of the phytoplankton community.

For many decades, we have relied on comparisons and analyses of (both satellite and ecosystem) model outputs with each other, and with in situ data, for insights into model performance, and for identifying the way forward. It is now time to shift the emphasis toward understanding the behaviour of model parameters, across models, across multiple phytoplankton types, and across multiple spatial and temporal scales. This focus has the potential to reduce uncertainties, unify divergent model results, and provide a stronger foundation for predicting marine primary production under changing climatic conditions.

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