Modeling the Vertical Flux of Organic Carbon in the Global Ocean

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Abstract

The oceans play a fundamental role in the global carbon cycle, providing a sink for atmospheric carbon. Key to this role is the vertical transport of organic carbon from the surface to the deep ocean. This transport is a product of a diverse range of physical and biogeochemical processes that determine the formation and fate of this material, and in particular how much carbon is sequestered in the deep ocean. Models can be used to both diagnose biogeochemical processes and predict how the various processes will change in the future. Global biogeochemical models use simplified representations of food webs and processes but are converging on values for the export of organic carbon from the surface ocean. Other models concentrate on understanding specific processes and can be used to develop parameterizations for global models. Model development is continuing by adding representations and parameterizations of higher trophic levels and mesopelagic processes, and these are expected to improve model performance.

Contents

1. INTRODUCTION

The oceans play an important role in the global carbon cycle by taking up carbon dioxide (CO_2) from the atmosphere and sequestering carbon in the deep ocean. The transfer of CO_2 from the atmosphere to the deep ocean involves a complex mix of physics, biology, and chemistry (Wanninkhof et al. 2009, DeVries 2022, Iversen 2023) and results in the ocean being a net sink of anthropogenic carbon such that in 2021 the oceans took up an estimated 2.9 ± 0.4 Pg C (Friedlingstein et al. 2022), approximately 25% of the total carbon emissions by humans. The vertical transport of organic carbon from the surface to the deep ocean is a key component of this process and is instrumental in driving the uptake of atmospheric CO_2 (Ito & Follows 2005, Kwon et al. 2009). This transport also provides food to support ecosystems in the deep ocean (Turner 2015), and helps maintain the observed vertical gradient of inorganic carbon in the oceans (Volk & Hoffert 1985). Many of the physical and biogeochemical processes driving the vertical transport of organic carbon can change with climate change, making the overall transport susceptible to change and consequently it is important to understand and quantify these changes.

Export Flux: The vertical flux of organic carbon transported across a given depth horizon, usually the euphotic zone, into the ocean interior.

Euphotic Zone: The surface layer of the ocean receiving sufficient light for net primary production (NPP)

Transfer Efficiency: The fraction of export flux that reaches a given depth horizon, often the base of the mesopelagic at 1000 m

The mechanisms that take organic carbon from the surface to the deep ocean make up the ocean's biological carbon pump (Boyd et al. 2019, DeVries 2022). Inorganic carbon in the well-lit ocean's surface waters gets taken up by photosynthetic organisms, converting it to organic carbon during primary production. Most of this organic material is recycled in the surface waters via consumption and respiration, but a small fraction of primary production is exported as export flux from the surface waters into the deep ocean. The flux of organic carbon is observed to attenuate with depth as it is decomposed and consumed as it moves downward through the water column allowing the organic carbon to be remineralized back into dissolved inorganic carbon (DIC) through respiration. The transfer efficiency characterizes the amount of flux attenuation that occurs in the mesopelagic and provides an important measure of the capacity of the ocean to sequester carbon (Buesseler et al. 2020, Dinauer et al. 2022). The biological pump contributes about 60% of the observed vertical gradient in DIC in the ocean, with the remainder coming from the solubility pump that depends on the temperature dependence of solubility of CO_2 and the large scale circulation of the ocean. However, the solubility pump transports DIC, and will not be considered in detail here.

Models require observations for validation and parameterization, but quantifying the vertical flux of organic carbon is difficult because observations currently tend be quite sparse spatially and temporally. Observations of the vertical flux of particulate organic carbon (POC) have traditionally been made using sediment traps (McDonnell et al. 2015, Estapa et al. 2020, Buesseler et al. 2007) and recent developments (e.g. the addition of gel layers within traps) allow the trapped particles to be characterized (Durkin et al. 2015, 2021) and their settling speeds measured (Peterson et al. 2005, Lampitt et al. 1993, Giering et al. 2016). However, sediment trap data can be confounded because the collected particles can originate from areas of 10s to 100s km^2 depending on the depth of the trap and the current velocities (Siegel & Deuser 1997, Siegel et al. 2008, Liu et al. 2018). Estimates of POC export from the surface ocean can also be obtained by making use of thorium disequilibrium which provides a measure of thorium scavenging by sinking particles if the ratio of organic carbon to thorium for the sinking particles is known (Buesseler et al. 1992, Burd et al. 2000, Buesseler et al. 2006). This allows for more spatially resolved measurements of POC flux but, on its own, cannot easily provide information on particle characteristics.

Th disequilibrium: The departure from equilibrium of activities of uranium and its decay product thorium.

Improvements in imaging technology and image analysis techniques have led to the development of an array of new instruments for measuring particles in the ocean. These include the Underwater Vision Profiler (Picheral et al. 2022) and the Imaging FlowCytobot (Olson & Sosik 2007) and the Laser Optical Plankton Counter (LOPC) (Checkley Jr. et al. 2008). Machine learning algorithms are used to identify objects in the images (Stemmann & Boss 2012) resulting in particle identification, abundance, and particle size distributions. Combining this with allometric relationships for POC and settling speed leads to estimates of the POC flux (Guidi et al. 2008, 2015, Cram et al. 2018). Particulate material in the oceans can also be measured using scattering of laser light using a LISST (Laser In Situ Scattering Transmissometer) (Giering et al. 2020). These instruments provide spatially and temporally valuable information on the make up and characteristics of POC in the water column.

Net Primary Production: The net production of organic carbon by photosynthesizing organisms

Export Ratio: The ratio of POC flux leaving the euphotic zone to net primary production

Remote sensing platforms can provide a global coverage that the above methods cannot. Satellites provide spectral reflectance which, when combined with semi-empirical algorithms can be used to estimate net primary production (NPP). This in turn can be combined with semi-empirical relationships relating sea surface temperature and chlorophyll to the export ratio (Laws et al. 2000, Dunne et al. 2005, Henson et al. 2011) and so provide estimates of export production. Autonomous platforms such as BGC-Argo floats can also provide information on the sinking particles (Claustre et al. 2021). Similarly gliders can be used to look at spatial and temporal changes in POC and they have been used to look at export across small-scale physical features such as fronts and eddies (Omand et al. 2015).

Models provide useful tools to help synthesize these disparate types of measurements as well as to provide global estimates of vertical flux from measurements that are sparsely distributed in both space and time. Different modeling approaches can be used to address different questions. For example, diagnostic modeling can be used in combination with data to quantify different aspects of the biological pump (Siegel et al. 2023). Large-scale global biogeochemical models, such as those used to inform the reports of the IPCC, can be used to estimate the effects of different future scenarios (Wilson et al. 2022) or examine the interactions between hydrodynamics and the biological pump. Detailed mechanistic models can be used to examine the role of individual biogeochemical or physical processes (Stemmann et al. 2004a).

Current semi-empirical model estimates of the amount of organic carbon transported vertically out of the surface ocean vary from < 5 to > 12 Pg C y^{-1} (Laws et al. 2000, DeVries & Weber 2017, Dunne et al. 2007, Henson et al. 2011, Siegel et al. 2014, Henson et al. 2022, Wilson et al. 2022). This range encompasses the anthropogenic emissions of carbon into the atmosphere. Predictions of export flux vary by a greater amount (Henson et al. 2022, Wilson et al. 2022) showing there is a clear need for improving model estimates. This review examines the way that models use to determine the vertical flux of organic carbon in the oceans and concentrates on transport of POC; export of dissolved organic carbon (DOC) accounts for approximately 20% of the total export from the surface ocean (Hansell et al. 2009). According to the Science Citation Index, the number of published papers containing the topic keywords *carbon, flux, ocean, model* has risen from 62 in 1998 to 271 in 2021 with a total of 3956 publications over those 23 years. Consequently, this review can only be a small, perhaps idiosyncratic, glimpse at the developments in modeling organic carbon transport in the oceans.

2. A MENAGERIE OF CARBON FLUX MODELS

We can classify models in many ways, but one instructive classification examines the model's structure and parameterization. The structure of the model describes the number of variables in the model, their dependencies, and interactions. For example, a box model might represent the total amount of organic carbon in three ocean domains with different modes of carbon transport between them. A global biogeochemical model might divide the world's oceans into hundreds of thousands or millions of cells depending on the spatial resolution of the model and be embedded within a 3-dimensional circulation model. Within each cell the biogeochemical model may track the time evolution of dozens of variables and their transport between cells; intermediate complexity models will sit somewhere in the middle, often having a lower spatial resolution and tracking fewer variables. The model structure chosen for a specific application depends largely on its purpose and the questions it is being used to address. For example, a simple box model (Section 2.2) may be sufficient to show the role that the oceans play in controlling atmospheric CO_2 concentrations. A more complicated model, possibly combined with a physical circulation model, may be needed to show seasonal and regional effects in the ocean's carbon cycle.

The parameterization of the model describes the mathematical representation of the interactions between the variables in the model. For example, a model with two classes of sinking POC may represent their sinking speeds as constant, or changing with depth (Kriest & Oschlies 2008). Computationally the former scheme is cheaper, but the latter may do a better job at reproducing observed profiles of POC with depth. As model structures have become more complicated many models represent some variables implicitly rather than explicitly as this provides a means to incorporate the effect of some variable (e.g. bacteria) without the computational expense of tracking it explicitly.

Models can also be used in different ways. A model can be run as a diagnostic model to evaluate the effect that different variables and processes have on observed ocean biogeochemistry (Bisson et al. 2020, Nowicki et al. 2022, Siegel et al. 2023). Models can also be run prognostically to make predictions of how the ocean carbon cycle changes, for example with future climate change (Henson et al. 2022, Wilson et al. 2022), or even how it behaved in the past (Hülse et al. 2017). What follows is a brief, roughly historical tour of some of the different types of models used for examining organic carbon flux in the oceans.

2.1. Empirical models

Empirical models play an important role in biogeochemical modeling. Models should be able to reproduce the observed spatial and temporal patterns of the variables being modeled and empirical models provide a description of the major trends seen in the data. Empirical models also can be used to provide parameterizations for implicit variables within a model. For example, the Martin curve

$$F(z) = F(z_0)\left(\frac{z}{z_0}\right)^{-b} \qquad 1.$$

represents the POC flux F at a depth z given the flux at a depth z_0 (Martin et al. 1987). The parameter b measures how fast POC is attenuated in the water column, with larger absolute values of b indicating more rapid attenuation. Martin et al. (1987) fitted Equation 1 to data from the Pacific Ocean and obtained a mean value of $b = 0.858$, though values ranged from $b = 0.319$ for a station off the coast of Peru to $b = 0.973$ for a station north of Hawaii. Equation 1 has been used in large-scale biogeochemical models to redistribute sinking organic carbon and nutrients through the ocean interior. This is done by explicitly calculating the flux sinking through some depth horizon (e.g. the base of the euphotic zone) and then using Equation 1 to attenuate POC flux below that depth horizon with the organic matter lost at each depth being transformed to DIC and inorganic nutrients which are calculated stoichiometrically. This allows the model to represent the remineralization of organic matter without explicitly modeling microbial and zooplankton concentrations below the mixed layer. However, the value of b is known to vary (Schlitzer 2002, Henson et al. 2012, Guidi et al. 2014) and Equation 1 does not work in the surface ocean where it predicts unrealistically large fluxes. Other functional forms have been suggested, such as an exponential form (Banse 1990, Armstrong et al. 2002) which overcomes the problem the power-law faces at shallow depths, but still requires regional parameterization.

2.2. Box models

Early models of the ocean carbon cycle were developed to understand the uptake of atmospheric CO_2 by the oceans (Caldeira et al. 2000). These were coupled box models with differing numbers of boxes representing either depth regimes in the ocean or latitudinal regions or both (Figure 1). An early application of the box-model approach was a three-box model used to examine the effects of the solubility and biological pumps on atmospheric pCO_2 (Volk & Hoffert 1985). If neither the solubility pump nor biological pump are operating then atmospheric pCO_2 levels would be 720 ppm, the solubility pump alone reduces this to 460 ppm, and adding the biological pump reduces it further to 260 ppm.

Box models have the computational advantage that the dynamics of the model can be represented as a relatively small number of coupled ordinary differential equations where each variable is a function only of time and solving them numerically is computationally quite fast. However, this simplification produces problems (Archer et al. 2000, Toggweiler et al. 2003) with box models being sensitive to deepwater formation at high latitudes. In particular, comparison between a three box model and the results of general circulation

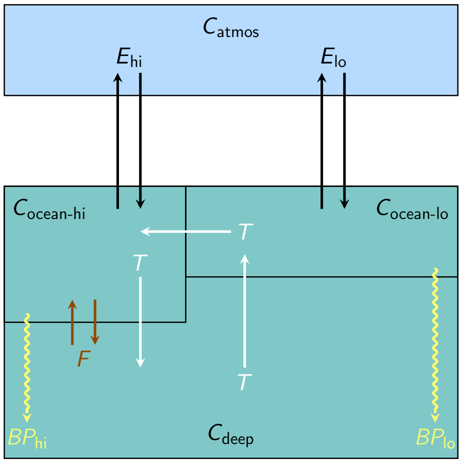

Figure 1

A box model with an atmospheric and a three-box ocean component; a high latitude surface ocean box, a low latitude surface ocean box, and a deep ocean box. The carbon within each box is represented by C_{atmos} for the atmosphere and $C_{\text{ocean-hi}}$, $C_{\text{ocean-lo}}$, and $C_{\text{ocean-deep}}$, for the high-latitude, low latitude and deep ocean boxes respectively. The physical transports of material between the boxes are depicted by arrows; T represents the thermohaline circulation, F the physical exchange between the deep ocean and high latitude box, and E_{hi} and E_{lo} represent atmosphere-ocean exchanges. Transport by the biological pump is shown by the wavy lines (after Sarmiento & Toggweiler (1984)).

models (GCMs) reveals that the organic carbon pump is weaker in the box models because in the box model the deep ocean tends to be equilibrated with $p\text{CO}_2$.

Box models still have a role to play in understanding the export of organic carbon in the oceans. Their relative simplicity makes their results easy to interpret and they can often be used to study oceanic carbon fluxes during paleoclimates where an understanding of large-scale patterns is needed (Hülse et al. 2017). However, the development of low spatial resolution (e.g. 2°×2°) ocean models and new computational technologies such as the transfer matrix method are making box-models less popular.

2.3. Coupled global models

Ocean biogeochemical models began to be coupled to large-scale ocean circulation models in the late 1980s and early 1990s (Maier-Reimer & Hasselmann 1987, Sarmiento et al. 1988, Toggweiler et al. 1989, Maier-Reimer 1993). These early models had very coarse spatial resolution compared with modern models. Like box-models, the performance of these early models was mainly assessed using the distribution of inorganic nutrients and oxygen. As distributions of other biogeochemical variables have become available (through remote sensing, time series stations, and field campaigns) these too have been used to assess the performance of these models. Early global models tended to use overly-simplified representations of the ocean biogeochemistry and carbon transport. For example, the HAMOCC-3 model converted primary production into POC which sinks and is remineralized instantaneously at a depth determined using an empirical power-law relationship (Maier-Reimer 1993). The early Princeton model diverted half of the calculated primary production into

POC which sinks and with a depth profile given by the Martin curve, the remaining half of primary production being converted to DOC which is remineralized as a first-order decay process (Murnane et al. 1999). Although these early global models gave broadly similar results (except in the Southern Ocean, which remains an area of active research), there were clear differences in the extent to which the biological pump affected the air-sea exchange of CO_2 (Sarmiento et al. 2000).

Differences between model formulations and the results that these early global models produced led to the formation of the Coupled Model Intercomparison Project (CMIP) and the Ocean Carbon Model Intercomparison Project (OCMIP) under the auspices of the Working Group on Coupled Modeling (WGCM) as part of the World Climate Research Program. The latest versions of CMIP, CMIP5 (endorsed by WGCM in 2008 and used in the IPCC's 5th Assessment Report in 2013) and CMIP6 (published in 2016 (Eyring et al. 2016) and contributed to the IPCC's 6th Assessment Report) contain models with much more sophisticated representations of the ocean biogeochemistry. In general, model representations of sinking particles have increased in complexity between CMIP5 and CMIP6 versions with several models now using attenuation parameterizations or including more classes of particles (such as refractory sinking POC) (Séférian et al. 2020). Generally there is better agreement on POC flux values in the CMIP6 suite of models than there was in the CMIP5 models with a global average POC flux at 100 m depth of 7.24 ± 2.28 Pg C yr^{-1} in the CMIP5 models (range 2.42–11.86 Pg C yr^{-1}) and 7.48 ± 1.87 Pg C yr^{-1} in the CMIP6 models (range 4.78–10.4 Pg C yr^{-1}. Almost all CMIP6 models predict that changes in the biological pump during the 21st century will lead to increases in ocean carbon storage. However they under-estimate changes in carbon storage that have taken place over the last half century as a result of changes in the biological pump, with a modeled change of -0.5–$+2$ Pg C per decade compared with observational estimates of 7 Pg C per decade (Wilson et al. 2022, Henson et al. 2022). Export from 100 m for 19 CMIP6 models (Figure 2) shows a significant range, similar to that seen in diagnostic models. The range of values increases over the period from 1850 to 2100, with the maximum model value being approximately 3.1 times the minimum in the current time. However, although the range of modeled values has increased, this is driven by only a handful of models. The standard deviation of all the model export predictions peaked in the late twentieth century and decreases between the years 2000 and 2100 indicating increasing levels of model agreement in the vertical transport of POC leaving the surface ocean.

2.4. Small-scale models

Global biogeochemical models are able to model the transport of POC by using simplifying parameterizations of complex biogeochemical processes. An alternative approach is to develop models that reflect the complexity of these biogeochemical processes but at the expense of spatial coverage. Such models can give insight into processes bot explicitly incorporated into global models and can be used to help develop parameterizations that can be used in large-scale models.

For example, global models use at most two classes of sinking POC and parameterize the processes attenuating that flux below the euphotic zone. Stemmann et al. (2004a) developed a model with 23 size classes covering a particle size range from 4.6 µm to 0.36 cm to examine UVP data from the DYFAMED site in the northwest Mediterranean Sea. A series of models progressively added processes of particle aggregation, microbial degradation, zooplankton-

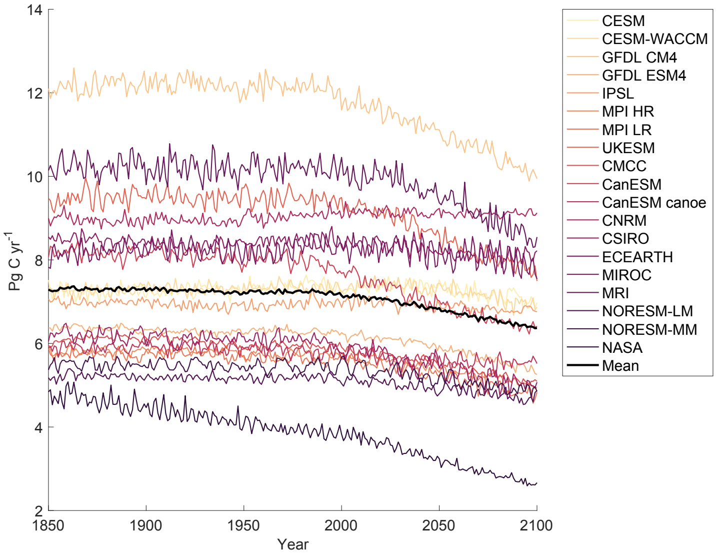

Figure 2

A comparison of the modeled export flux at 100 m depth from 19 CMIP6 models forced with the SSPS-8.5 scenario. Data were extracted from the WRCP CMIP6 archive at `https://esgf-data.dkrz.de/projects/cmip6-dkrz`.

Inverse Model: A modeling approach that uses observations to quantify variables such as unknown sinks and sources.

induced fragmentation and grazing of particles by filter feeders and flux feeders. This was done at the expense of the model being a 1-dimensional model from 100 to 1000 m depth. Comparing modeled and observed size distributions allowed estimates to be made of the importance of different processes in the mesopelagic. This analysis revealed that particle aggregation played a minimal role in particle dynamics in the mesopelagic because particle concentrations were sufficiently low that collisions between particles were infrequent. It also showed that attenuation due to mesozooplankton was more important in the upper mesopelagic with microbial degradation of sinking POC being more important deeper in the water column. Such changes are not resolved in global models and reveal the importance of deep-water ecosystem dynamics to the vertical transport of POC (Robinson et al. 2010, Cavan et al. 2019). A simple mesopelagic food web model suggested that microbial respiration was the main sink of POC whereas zooplankton mostly transformed the POC to detritus and DOC (Anderson & Tang 2010). Mesopelagic ecosystem dynamics may also alter the timing of POC sinking to the deep ocean and either decouple or dampen temporal variations in the deep water flux from those of the POC flux leaving the surface depending on the model parameterization (Jackson & Burd 2002).

More detailed models can also be used to examine the composition of POC flux. Jackson (2001) developed a model that couples a simple surface food web model to a size-resolved particle aggregation model tracking both fecal pellets and marine snow formed by aggregating phytoplankton and fecal pellets. This model highlighted the importance of characterizing the properties of the particles involved such as phytoplankton stickiness and size and fecal pellet size and density. Such approaches can be used to determine parameterizations for global models and models parameterizing aggregation processes have been incorporated into global biogeochemical models (Kriest & Evans 2000, Aumont et al. 2015).

Detailed models have also been used to examine how particle properties affect the flux of POC and its fate. Omand et al. (2020) developed a depth-dependent model of particle flux that included different parameterizations of remineralization over a range of particle sizes. A particle size distribution was required to reproduce flux profiles similar to the Martin curve (Equation 1) but neither a power-law nor an exponential function provided better fits to the modeled profiles. Multiple models predict a flattening of the particle size distribution with depth as smaller, slower sinking particles get preferentially remineralized over larger, faster settling ones (Kriest & Oschlies 2008, DeVries et al. 2014, Omand et al. 2020) but this is not seen in measured size distributions (Guidi et al. 2009). This discrepancy could be a result of the models not including particle disaggregation, a process that is poorly understood and rarely included in POC transport models (Burd & Jackson 2009).

Most models of POC transport, whether they be global biogeochemical models or detailed mechanistic models, do not consider the component particles making up the POC. Many models include different chemical components of POC, such as iron, and ballasting materials, but few consider the effects that different source particles (e.g. diatoms, coccolithophores, fecal pellets etc.) have on the POC flux. The coupled aggregation-food-web model by Jackson (2001) mentioned previously considered the effects of fecal pellets and phytoplankton on marine snow formation and flux. Another approach used Monte Carlo techniques within an agent-based framework to model the formation and fate of sinking POC in a 1-dimensional open ocean setting (Jokulsdottir & Archer 2016). The model incorporated a suite of processes that are usually neglected such as the formation of TEP. Comparison of modeled flux profiles with observations from different locations showed that the model performed well in some cases, such as the Equatorial Pacific and the North Central Pacific Gyre, but less so in others such as the Panama Basin.

Marine snow: Large (> 500 µm) heterogeneous aggregates or organic particles such as phytoplankton cells and fecal pellets.

Agent-Based Model: A model that uses autonomous, decision-making entities to represent populations instead of averaged variables.

TEP: Transparent Exopolymer Particles, gel-like particles resulting from exudations of phytoplankton and bacteria.

3. MODELING PROCESSES THAT AFFECT VERTICAL TRANSPORT

There are many processes that affect the vertical transport of organic carbon (Figure 3) and, for any model, choices need to be made about which ones to include and how to represent or parameterize them. These choices are constrained by the computational cost of the model, as is the case for global biogeochemical models. Sometimes, our understanding of a given processes is not sufficient to arrive at a single representation so that different models use different parameterizations of the same process. These differences can make it difficult to compare model results, but help explain the range of results produced by different models such as seen in Figure 2 (Laufkötter et al. 2015, Wilson et al. 2022, Henson et al. 2022).

In general, the time evolution of a biogeochemical variable X (e.g. POC), which varies over space and time, is represented by a series of coupled, partial differential equations that have the form

$$\frac{\partial X}{\partial t} + (\text{Advection of } X) + (\text{Diffusion of } X) = \text{Sources of } X - \text{Sinks of } X. \qquad 2.$$

The advection and diffusion terms represent the physical transport of X and are provided by the physical model. The sources and the sinks represent all the biological, chemical, and physical processes that lead to the addition of X (e.g. fecal pellet production by zooplankton, aggregation of small particles into larger ones) and the removal of X (e.g.

decomposition of the fecal pellets). Models can differ in the number of biogeochemical variables they contain and this in turn can affect the source and sink terms — e.g. a model with large and small phytoplankton and zooplankton allows for additional connections between these variables (Gruber & Doney 2019, Fennel et al. 2022). For example some models have a single class of sinking detrital POC whereas others have multiple classes characterized by particle size or sinking speed. The degree of complexity of the model structure also helps inform the complexity of the parameterizations used. For example, modeling the flux F of gravitationally sinking POC simply requires knowing the concentration (C) of POC and its sinking speed w_s: $F = Cw_s$. However, sinking POC is composed of many different types and sizes of particles, all having their own concentrations and sinking velocities. Choosing a single sinking velocity for sinking POC implicitly makes assumptions about the properties (e.g. density, size etc.) of those particles. But, expanding the structure of the model to incorporate such variability dramatically increases its computational cost. Consequently, there is a need to develop parameterizations that capture the natural variability in these process while simultaneously keeping the model computationally practical.

3.1. Particle Formation Processes

POC that is transported vertically in the oceans is composed of a wide variety of different particles such as phytoplankton cells, fecal pellets, marine snow, and other biological detritus such as carcasses and discarded zooplankton feeding structures (Turner 2002). The rates at which each of these are formed depend on the ecosystem structure and will vary spatially and temporally, and not all the processes are independent. The number of model variables representing sinking POC and the interactions between them are important components of a POC flux model. One of the simplest ways to represent sinking POC is to consider just a single POC variable that contains detritus from phytoplankton and zooplankton combined (e.g., Fasham et al. 1990). This combined pool is assigned a single sinking speed and there is no differentiation between different particle types and their fate. The formation rate of the detritus is then determined by the rates of different biological processes such as zooplankton egestion and phytoplankton cell mortality. The most important types of particles for vertical transport of organic carbon are marine snow and fecal pellets. On a global basis, modeling studies suggest that fecal pellets are the dominant form of sinking POC (Nowicki et al. 2022) though this can vary spatially and temporally (Laurenceau-Cornec et al. 2015a) and the model result may depend on the structure of the food-web model that was used.

Large marine snow particles are formed by the aggregation of smaller particles , a process that depends on the concentration of particles and their properties and has been modeled in many ways (Jackson 1990, Jackson & Lochmann 1992, Kriest & Evans 1999, 2000, Burd & Jackson 2009, Ruiz et al. 2002). The more complicated of these models use 20–30 contiguous particle size classes making them computationally expensive. Global models that explicitly include aggregation include the BEG model (Moore et al. 2002) and PISCES2 (Aumont et al. 2015), but their parameterizations differ. The BEG model uses coagulation theory to model aggregation rates from small to large particles using a constant specific rate constant multiplied by the square of the phytoplankton concentration (Moore et al. 2002, 2013). PISCES2 includes a more detailed size-dependent coagulation model that incorporates different collisional processes (Kriest & Evans 1999, 2000). This latter model assumes the particle size distribution follows a power-law which allows the coagulation equations to be greatly simplified (Kriest & Evans 1999, 2000). Including this

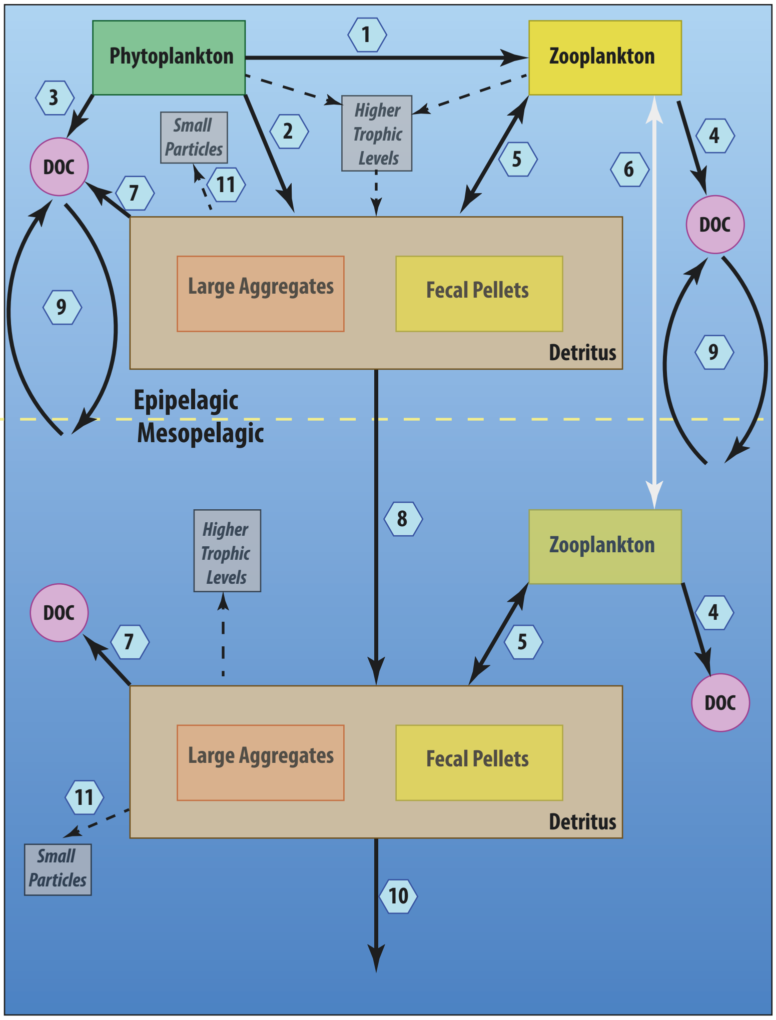

Figure 3

A schematic of the pathways affecting the vertical transport of organic carbon in the oceans. Opaque boxes and dashed arrows indicate variables and connections that are rarely represented in current models. Processes are labelled by number — 1, grazing of phytoplankton by zooplankton; 2, aggregation of phytoplankton into marine snow; 3, production of DOC by phytoplankton via exudation and viral lysis; 4, production of DOC by zooplankton by excretion; 5, production of particles by zooplankton via egestion and sloppy feeding and consumption of particles by zooplankton; 6, active flux resulting from the vertical migration of zooplankton; 7, solubilization of particles by microbial activity ; 8, transport of particles by passive sinking and subduction; 9, vertical mixing of DOC; 10, passive sinking of POC; 11, fragmentation of large particles.

simplified size distribution representation in models is essential for reproducing the ratio of export to primary production and generally improves agreement between modeled and observed deep water fluxes (Gehlen et al. 2006). However, including a detailed aggregation model introduces parameters whose values are largely uncertain. For example, an important

Stickiness: A parameter representing the probability that two particles will adhere once they have collided.

parameter is the stickiness which is thought to depend on TEP concentrations (Passow 2002, Mari et al. 2017) and there are few models that incorporate TEP explicitly (Jackson 1995, Mari & Burd 1998, Jokulsdottir & Archer 2016) (Table 1).

Few models explicitly include fecal pellets as a component of the sinking POC flux. Zooplankton fecal pellets can contribute between 0–100% of the total sinking POC flux depending on location and time (Turner 2002, Durkin et al. 2021). Changes in fecal pellet characteristics with depth may also provide indications of zooplankton consuming and repackaging sinking POC within the mesopelagic (Wilson et al. 2008). Explicitly modeling fecal pellet flux is challenging, in part because fecal pellets can also be aggregated and be a component of marine snow particles (Jackson 2001).

Table 1 The representation of aggregation and sinking POC in a selection of CMIP6 models.

Model	Sinking POC classes	Agg.	Disagg	TEP	Reference
MARBL-BEC	1	No	No	No	(Lima et al. 2014)
PISCES v2	small, large	Yes	No	No	(Aumont et al. 2015)
COBALT v2	3[a]	Yes	No	No	(Stock et al. 2020)
BLING v2	1	No	No	No	(Dunne et al. 2020)
NOBM	4	No	No	No	(Lerner et al. 2021)
MEDUSA	1 explicit, 1 implicit	No	No	No	(Yool et al. 2013)
OECO2	1	No	No	No	(Hajima et al. 2020)
HAMOCC v6	1	No	No	No	(Paulsen et al. 2017)

[a] Labile, semilabile, semirefractory

3.2. Community Composition

The composition of surface plankton communities can affect the export of organic carbon from the surface waters. The phytoplankton community is often simplified in models to only diatoms and picophytoplankton, with only the larger diatoms causing export (Michaels & Silver 1988, Boyd & Newton 1995, 1999). Similarly, different zooplankton species produce different size fecal pellets with larger fecal pellets tending to sink faster (Turner 2002, Iversen et al. 2017). In general one expects faster sinking particles to sink deeper into the water column before being remineralized. Explicitly representing each type of phytoplankton and zooplankton fecal pellet in a model is impractical, and so some degree of simplification and parameterization is required. Most models use the idea of a functional group to represent species of plankton that perform the same biogeochemical function (e.g. diatoms taking up silica) (Moore et al. 2002, Anderson 2005, hood et al. 2006). This allows models to use a small number of functional groups to represent the gamut of different phytoplankton and zooplankton species (Table 2). Increasing the number of functional groups comes at the price of increasing the complexity of the model making it more computationally expensive to run

The parameterization of the processes associated with these functional groups varies from model to model. For example, PISCES2 models diatom nutrient limitation as the minimum of nutrient uptake factors for phosphate, nitrate, iron and silica (Aumont et al. 2015) whereas MEDUSA-2.0 uses a product of Michaelis-Menton factors (Yool et al. 2013).

These differences will affect the population dynamics and phytoplankton community composition in the models which in turn will affect the formation of sinking POC. Zooplankton community composition will not only affect the sizes of sinking fecal pellets, but also the consumption and repackaging of sinking POC. Many models include two zooplankton functional groups in the surface ocean ecosystem, mesozooplankton and microzooplankton, in a size-dependent food web. The PISCES2 model explicitly allows microzooplankton to graze on small POC whereas mesozooplankton can graze on large and small POC (Aumont et al. 2015). MEDUSA-2.0 on the other hand only allows them to feed on small, slow sinking detritus while remineralization of large, fast sinking particles is handled implicitly (Yool et al. 2013). Microbial communities are very diverse and they are not often modeled explicitly in global models, but instead their impact on sinking POC is modeled implicitly (Table 2); this means that there is no variable representing the microbial population and its dynamics in the model, instead their effect on sinking POC is represented by a mathematical function (such as Equation 1) representing the change in POC flux with depth.

Functional models have difficulty in capturing the range of organism behaviors that are seen in the oceans and many models do not explicitly represent community structure and ecosystem dynamics in the mesopelagic or incorporate higher trophic levels. These are difficult to incorporate, especially for large-scale models, and our understanding of pelagic fish and mesopelagic ecosystems does not allow for good parameterizations to be developed (Anderson & Tang 2010, Burd et al. 2010, Robinson et al. 2010, Cavan et al. 2019, Saba et al. 2021).

Another important component of community structure that is missing in models is mixotrophy. A model of the marine pelagic planktonic food web showed that including mixotrophy increased the carbon flux sinking out of the surface ocean by approximately 35% by increasing the transfer of biomass to larger organisms (Ward & Follows 2016). Mixotrophs can directly contribute to the carbon flux by creating feeding structures that trap phytoplankton and sink, adding to the flux of material (Cohen 2022).

Mixotroph: An organism that can obtain energy via autotrophic and heterotrophic processes.

Table 2 The treatment of community structure in different CMIP-6 models.

Model	Phytoplankton	Zooplankton	Bacteria	Reference
MARBL-BEC	small, diatom, diazo, *cocco.*	1	implicit	(Lima et al. 2014)
PISCES v2	diatom, nano	micro., meso.	implicit	(Aumont et al. 2015)
COBALT v2	small, diatom, diazo., *cocco.*	micro, 2 meso	explicit	(Stock et al. 2020)
BLING v2	2 *implicit*	implicit	implicit	(Dunne et al. 2020)
NOBM	chlorophyte, diatom, cocco., cyano	1		(Lerner et al. 2021)
MEDUSA	diatom and 1 other	micro, meso	implicit	(Yool et al. 2013)
OECO2	diazotroph, non-diazotroph	1	implicit	(Hajima et al. 2020)
HAMOCC v6	cyano and 1 other	1	implicit	(Paulsen et al. 2017)

3.3. Particle Sinking Speeds

Developing a simple and accurate parameterization of particle sinking speed in the oceans has been an elusive goal for a long time. Investigations have been made of sinking speeds of individual diatom cells (Smayda 1970, Miklasz & Denny 2010), fecal pellets (Madin 1982, Saba & Steinberg 2012, Turner 2002), marine snow (Alldredge & Gotschalk 1988, Diercks

& Asper 1997), and bulk POC (Peterson et al. 2005) and no clear parameterizations of sinking with size have been developed. Small-scale models can afford to to vary particle sinking speed with particle type and particle size, but large-scale biogeochemical models tend to use either constant sinking speeds or specify a depth-dependent function for sinking speed (Table 3).

Table 3 The treatment of particle sinking speed in different CMIP-6 models.

Model	Sinking particle classes	Sinking speeds (m d^{-1})	Reference
MARBL-BEC	Implicit		(Lima et al. 2014)
PISCES v2	small, large	2, 30–200 depth dependent[e]	(Aumont et al. 2015)
COBALT v2	1[a]	100 m d^{-1}	(Stock et al. 2020)
BLING v2	1[b]	50–180 m d^{-1} depth dependent[f]	(Dunne et al. 2020)
NOBM	2[c]	depth dependent[g]	(Lerner et al. 2021)
MEDUSA	2[d]	2.5 m d^{-1}	(Yool et al. 2013)
OECO2	1	5 m d^{-1}	(Hajima et al. 2020)
HAMOCC v6	1	3.5–80, depth dependent[h]	(Paulsen et al. 2017)

[a] COBALT models three classes of sinking particle, all with the same sinking speed but with different labilities — labile, semilabile, and semirefractory; [b] based on lability; [c] diatoms and detritus, but detritus is subdivided into detrital carbon, detrital silica, and detrital iron, all with different depth-dependent sinking speeds; [d] MEDUSA models a slow sinking population of particles explicitly, and a fast sinking population of particles implicitly; [e] the simpler, two size class PISCES model uses a constant sinking speed for small particles and a parameterized, increasing depth-dependent sinking speed for large particles representing the effects of ballast; [f] BLINGv2 uses a parameterized sinking speed that represents the effects of ballast and produces an increasing sinking speed with depth; [g] dependent on viscosity, detrital class, and concentration; [h] the sinking speed increases linearly with depth.

Basic theory shows that the sinking speed for a spherical particle sinking through a fluid under conditions of laminar flow depends on the viscosity of the fluid, the excess density of the particle, and the particle size through Stokes' Law

$$w_s = \frac{2}{9}\frac{g}{\nu}\frac{\Delta\rho}{\rho_f}r^2. \tag{3.}$$

Equation 3 suggests a simple increasing size-dependence for particle sinking speed, but this is generally not observed for marine particles (Diercks & Asper 1997, Stemmann et al. 2004b, Laurenceau-Cornec et al. 2015b, 2020) with some observations suggesting that sinking speeds may even decrease with particle size (McDonnell & Buesseler 2010). A Bayesian regression analysis of sinking speed data emphasizes that particle size, composition, and density all play important roles in determining sinking speeds (Cael et al. 2021b), but the variety of these relationships are still complicated with different parameters for aggregates and fecal pellets, diatoms and non-diatoms, ballasted and non-ballasted particles. Analysis of sinking speed data indicates that diatom morphology, (i.e. whether the diatoms have spines or are chain forming) plays a significant role in determining marine snow sinking speed (Laurenceau-Cornec et al. 2015b). However, most POC flux models consider only a single, generic diatom and distinguishing between different morphological types is computationally infeasible. Mineral ballasting can play a significant role in determining the settling speed function (Armstrong et al. 2002, Klaas & Archer 2002, Laurenceau-Cornec et al. 2020) and many models incorporate this implicitly by providing a fitting function parameterized

Mineral Ballast: Biogenic and lithogenic minerals that affect the density of particles.

by surface and deep sinking velocities (i.e. the models do not include explicit calculations of the change in particle density). The sinking speed of marine snow has also been modeled using a modified Stokes' Law with particle porosity obeying a fractal relationship (Burd & Jackson 1997, Stemmann et al. 2004b, Laurenceau-Cornec et al. 2020).

Using the same sinking speed for all sinking POC (Table 3) is not necessarily borne out by observations, where particles of similar size have sinking speeds that encompass a range of 3 to 4 orders of magnitude (Stemmann et al. 2004b, Laurenceau-Cornec et al. 2015b, 2020). In some cases, bimodal distributions of sinking speed have been observed, though the fast sinking particles alone were sufficient to explain abyssal POC fluxes (Alonso-González et al. 2010, Riley et al. 2012).

Some models use a sinking speed that changes with depth (Table 3). This is to be expected as particles get remineralized as they journey through the water column, but the changing physical properties of the water can also lead to a change in sinking speed. For example, the NASA Ocean Biogeochemical Model (NOBM) uses a sinking speed (w) that changes as a function of depth with the changing viscosity of seawater (Ito et al. 2020),

$$w(z) = \nu(z) a e^{bC_d} \qquad 4.$$

where z is depth, $\nu(z)$ is a function that represents the effect of viscosity on sinking speed (colder waters have a greater viscosity which increases drag and so reduces sinking speed)(Taucher et al. 2014), C_d is the concentration of a specific detrital pool, and a and b are constant parameters whose values differ for each detrital pool.

Diel Vertical Migration: Daily vertical migrations undertaken by zooplankton and fish.

Ontogenetic Vertical Migration: Vertical migrations associated with organism life-history.

3.4. Active Flux

Organic carbon can be transported from the surface to depth by organisms that undergo diel vertical migration (DVM) and ontogenetic vertical migration (OVM). During DVM, carbon consumed by zooplankton and fish in surface waters is transported into the mesopelagic as respired CO_2, excreted DOC, or egested POC (Steinberg & Landry 2017). The resulting flux of organic carbon can be quantitatively similar to the sinking flux of POC (Steinberg et al. 2000, 2008), though this varies spatially and temporally and depends on the migrator community composition (Takahashi et al. 2009, Putzeys et al. 2011).. Ontogenetic vertical migration is part of the life-cycle of some copepod species, particularly in subarctic regions. These animals migrate to depth at the end of the spring phytoplankton bloom and before doing so increase their lipid composition thereby transporting this carbon to depth where some of it is respired during the winter months (Darnis & Fortier 2012, Jónasdóttir et al. 2015).

Currently, none of the global biogeochemical models that are part of CMIP-6 include active flux. Bianchi et al. (2013) parameterized DVM in a one-dimensional, size-structured NPZD model reproducing the broad scale patterns of migrating biomass at two locations in the Pacific Ocean (K2 and ALOHA) but overestimated migrating biomass in the EQPAC region. The model suggested that active fluxes were 15%–40% of the passive particle flux. A different model of zooplankton DVM was incorporated into a global ecosystem model which was driven diagnostically using satellite measurements (Archibald et al. 2019) and showed that DVM accounted for approximately 14% of average global export, a value similar to that found in other diagnostic modeling results (Nowicki et al. 2022).

Diagnositic modeling: Combining a model with observations to determine the relative importance of different processes.

The composition of the community that vertically migrates is difficult to put into the models. Bianchi et al. (2013) used a diffusion term to represent variations in zooplankton vertical migration swimming speeds. An alternative approach is to use an agent-based framework that can resolve different species and their behaviors (Wallace et al. 2013, Countryman et al. 2022). These models show that zooplankton behavior and community structure, in particular the feeding preference (herbivore, carnivore, omnivore), can significantly affect the fecal pellet flux in the mesopelagic.

3.5. Physical Processes

Vertical motions of water that carry particulate and dissolved matter and transport them from the surface to the deep ocean can be hard to represent in global biogeochemical models (Boyd et al. 2019). Three such processes have been identified. The mixed-layer pump transports surface POC and DOC into the mesopelagic as the mixed layer deepens in the winter. Models that include a representation of mixed-layer dynamics will include this transport mechanism, which is more important in regions where the winter mixed layer is deepest, such as in mid to high latitudes where is can contribute to approximately 20% of the flux supplied by sinking particles (Dall'Olmo et al. 2016).

Subduction of POC and DOC is driven by Ekman pumping which can produce transport velocities between 1–100 m d^{-1} over large regions of the ocean. Eddy subduction is associated with ocean fronts and occurs on scales of 1–10 km and so is not resolved in current global biogeochemical models. However, high-resolution models show it can be important on small scales where it can transport material into the upper mesopelagic and can contribute as much as half the total POC export (Omand et al. 2015, Resplandy et al. 2019) and enhance export 2–3 times above that of surrounding regions Stukel et al. (2017). Modeling studies indicate that, in general, these physical subduction processes account for approximately 20% of the total organic carbon export from the surface ocean (Levy et al. 2013, Nowicki et al. 2022).

3.6. Attenutation

As organic carbon is transported deeper into the ocean interior it is consumed and transformed leading to an overall decrease in flux with depth. This decrease is often described functionally using either a power-law (Martin et al. 1987) or exponential function (Banse 1990, Lutz et al. 2002, Armstrong et al. 2002). These models imply a fixed length scale over which sinking organic matter is remineralized. Such fits to data provide useful parameterizations for global ocean models because they provide a means of attenuating flux and redistributing organic carbon below the surface ocean without having to explicitly model the microbial and zooplankton populations in the mesopelagic and below. However, this approach does not include any of the biogeochemical mechanism leading to attenuation and this can cause disagreement between modeled and observed ocean biogeochemistry (Moore et al. 2013) indicating that important mechanisms are missing from such simple parameterizations. Such formulations also cannot predict future changes to those processes. Kriest & Oschlies (2008) examined the effects of different treatments of organic carbon flux and suggested that using a depth-dependent remineralization length scale provided a closer match to observed nutrient profiles in the oceans, but this is based on a size-dependent sinking model.

Accurate modeling of the consumption of sinking POC likely requires modeling mesopelagic ecosystems to a similar level of detail as those in the epipelagic. However, this would be computationally expensive, and our understanding of these ecosystems is far from sufficient. Consequently, a suitable parameterization needs to be used. For example, temperature has been found to be and important predictor of remineralization rates (Iversen & Plough 2013, Marsay et al. 2015), especially in conjunction with dissolved oxygen concentration (Devol & Hartnett 2001). These effects of temperature and oxygen concentration have been combined into a parameterization of remineralization (Laufkötter et al. 2017) and they are now included in many models. This results in an increase in POC flux at higher latitudes, because the POC is remineralized deeper in the water column there, and reduces the size of modeled O_2-minimum zones.

Such parameterizations improve the comparison between model results and data, but they still do not represent the suite of biological and physical processes that attenuate POC flux below the euphotic zone. For example, observations (Briggs et al. 2020) and modeling studies (Stemmann et al. 2004b,a, Collins et al. 2015) suggest that particle fragmentation may play an important role in controlling flux attenuation and particle size distributions in the deep ocean. This processes is poorly understood (Burd & Jackson 2009, Mayor et al. 2020) and, for particles below the mixed layer where turbulence levels are low, presumably depends on zooplankton-particle interactions and hence on zooplankton community structure. For example, flux feeders trap particles in their feeding structures and their interaction rate with sinking particles is a function of the relative downward speed between the particle and the organism (Jackson 1993). On the other hand, interaction rates of filter feeders with sinking particles will depend on the concentrations of animals and particles.

Such parameterizations improve the comparison between model results and data, but they still do not represent the suite of biological and physical processes that attenuate POC flux below the euphotic zone such as particle fragmentation. Observations suggest that particle fragmentation may play an important role in flux attenuation in the deep ocean (Briggs et al. 2020). Results from modeling studies also suggest that fragmentation of sinking particles by zooplankton is important for determining deep-ocean particle size distributions and attenuation (Stemmann et al. 2004b,a, Collins et al. 2015). Particle fragmentation is one of the key areas of POC flux dynamics that is poorly understood (Burd & Jackson 2009, Mayor et al. 2020) Interestingly, fragmentation rates presumably depend on the zooplankton community structure in the mesopelagic. For example, flux feeders trap particles in their feeding structures and their interaction with sinking particles is a function of the relative downward velocity between the particle and the organism (Jackson 1993).

Particle fragmentation is difficult to study and involves many unknowns such as the size distributions of particles produced from disaggregation events and the strength of particles. For example, models of particle fragmentation resulting from fluid turbulence typically assume particles are eroded (i.e breaking off small particles from the edges of a larger one) and splitting (breaking a large aggregate into roughly equal sized pieces) (Hill 1996). Size distributions of marine snow produced from zooplankton-particles interactions tend to be more complicated. Just over half of the particles produced from interactions of marine snow with euphausiids remained in the marine snow size class, i.e. > 5 mm (Goldthwait et al. 2004). If there is a strong dependence of sinking speed on particle size, then one would expect disaggregation to affect the vertical transport of POC (Burd & Jackson 2002). The model developed by Stemmann et al. (2004a,a) contains a simplified model of disaggregation and showed that fragmentation of particles by mesozooplankton below the mixed layer was important for model agreement with data.

4. SIMPLE OR COMPLEX?

How complicated do model representations of ecosystems have to be to accurately predict the production and fate of organic carbon? Vertically transported organic carbon is formed and transformed by ecosystems from the surface ocean to the seafloor. Different models represent these ecosystems with different structures having different levels of complexity. For example, some models represent all zooplankton as one functional group whereas others seaparate microzooplankton from mesozooplankton. Some do not represent particle aggregation at all while others do (Table 2). Given this diversity in complexity one might wonder what happens to model results if we increase the complexity further and how much of the difference in model results comes about from differences in model structure. In other words, how complex should we make the models? This is an important question because more complex models are computationally more expensive and require longer times to run.

Increasing the number of phytoplankton and zooplankton functional groups gives the model greater flexibility in how carbon flows through the model. Twelve, one-dimensional biogeochemical models with varying complexity have been assessed for their predictive skill in two regions of the ocean, the Equatorial Pacific and Arabian Sea (Friedrichs et al. 2007). Comparison of the different models showed that at a specific location simpler models performed as well as the more complex ones (Friedrichs et al. 2007). However, models with multiple phytoplankton functional groups performed better (i.e. had better agreement with observations) when the models were used at multiple sites.

The way a model parameterizes particles affects the vertical transport of organic carbon. Gehlen et al. (2006) examined different ways to parameterize particles in a global model, from a simple two size-class model with prescribed settling speeds to a size-spectrum model with prognostic sinking speeds. Although the size-spectrum model improved model-observation agreement, to a first order, reproducing the mean POC fluxes at 2000 m did not depend on the size resolution of the size spectrum. Kriest et al. (2010) examined models with different levels of complexity in regards to export and remineralization and found little difference between models, though their models were neither optimized nor tuned.

Another way to increase model complexity is to use increasingly complicated parameterizations with the same model structure. Bisson et al. (2020) used a simple food-web model driven by satellite data to examine the effect that increasing model parameterizations had on export flux. The different parameterizations they examined included a model that had a simplified but explicit particle aggregation model, and explicitly incorporating size and temperature dependence for zooplankton fecal pellet production rates. They found relatively little change in global export flux between the different models, but significant changes regionally depending on the parameterizations that were used.

Biogeochemical models require some degree of simplification to be computationally practical. Using a single functional group to represent a diverse group of organisms (e.g. diatoms) requires choosing representative values for parameters such as nutrient uptake half saturation constants. However, such parameters vary between species and within a species under different environmental conditions (e.g. Timmermans et al. 2004). However, many of the relationships between variables and parameters (e.g. nutrient uptake rate as a function of the half-saturation constant) are non-linear and Jensen's Inequality implies that choosing the average parameter value can result in under- or over-estimates of calculated values (Denny 2017, Wilson & Gerber 2021).

There is no clear answer to the question of how complex we should make our models. Practically, the level of detail is constrained by the computational expense — if a model is so complex that it takes a year of real time to run a 1 year simulation, then the practical value of the model may be limited. Adding new variables, such as an additional particle size class, will add to the computational expense because this variable has to be advected with the other variables and interact with them. Adding missing processes, such as aggregation, can done in such a way to minimize adding new variables (e.g. Kriest & Evans 1999, Aumont et al. 2015) and can improve the agreement between model results and observations. But doing so requires simplifying assumptions about the processes, such as assuming a power-law particle size distribution in the case of adding aggregation.

5. Looking to the future

Considerable progress has been made in modeling and understanding the vertical transport of organic matter over the last few decades. Advances in instrumentation such as the UVP and gel traps has provided insights into processes affecting POC flux in the mesopelagic, and new programs such as EXPORTS (Siegel et al. 2016) provide highly detailed and rich data sets to inform and test ideas and provide testbeds for diagnostic models to identify dominant processes (Bisson et al. 2020, Siegel et al. 2023) and for testing prognostic models. Global biogeochemical models are converging on a narrower range of values for export production although models still give a significant range of values (Wilson et al. 2022, Henson et al. 2022). There is also a growing understanding of what process are either missing from these models or in need of improvement (Henson et al. 2022). In addition, alternative modeling frameworks such as trait-based modeling (e.g. Serra-Pompei et al. 2022) and agent-based modeling (Countryman et al. 2022), provide ways to explore the ecological and biogeochemical processes driving POC transport and can provide insight into better parameterizations for global models. Although significant progress has been made, there remain important aspects that are either not incorporated into models or are only just starting to be explored.

Trait-based model: An approach that models functional traits of organisms rather than the organisms themselves, often using a master trait (e.g.) size and allometric relationships. ‘

Processes in the mesopelagic are generally modeled in a manner that ignores the ecosystem dynamics there; for example, by representing flux attenuation in the mesopelagic with a simple, functional relationships such as Equation 1. These simple parameterizations are well-known to have problems Kriest & Oschlies (2008), Cael & Bisson (2018), Omand et al. (2020) and there is an increasing understanding of the importance of mesopelagic food webs in determining the fate of sinking POC (Jackson & Burd 2002, Gehlen et al. 2006, Anderson & Tang 2010, Archibald et al. 2019). Particle fragmentation and its ramifications for POC flux attenuation is emerging as another important piece of the puzzle (Briggs et al. 2020) and a recent inverse model analysis of particle cycling at Station P in the North Pacific revealed that disaggregation contributes to the loss of large particles more than remineralization does (Amaral et al. 2022). Modeling particle processes in the North Atlantic indicated particle fragmentation and subsequent remineralization of the resulting suspended particles was a significant contribution to flux attenuation between 50 and 300 m depth (Collins et al. 2015).

Models are being developed with increasingly complex structures by adding important classes of organisms. For example, a data-driven 3-dimensional carbon cycle model indicates that gelatinous zooplankton may contribute 32%–40% of global export flux, but equally importantly this material has a high transfer efficiency (38%–62% to 1000 m) indicating a greater propensity for this material to be sequestered in the deep ocean (Luo et al. 2020). Higher trophic levels are also generally absent from biogeochemical models, but fish can be important contributors to both passive and active organic carbon flux and may contribute 16% ± 13% to the total flux leaving the euphotic zone (Saba et al. 2021). A simple food web model indicated that vertically migrating mesopelagic fish could have a significant impact on the vertical flux of organic carbon but emphasized the lack of knowledge about mesopelagic food webs and the physiological ecology of these organisms (Anderson et al. 2019). Some global biogeochemical models are starting to incorporate some of these different components of the food web. For example, the COBALT model implicitly models the effect of higher trophic levels on zooplankton and the effect of viruses on bacteria and small phytoplankton thereby incorporating a viral shunt Stock et al. (2020). However, there remain some potentially important ecosystem components, such as small particles (e.g. individual phytoplankton cells and small fecal pellets), that are not generally incorporated into models. Small particles may contribute up to approximately half of the POC flux (Dall'Olmo & Mork 2014, Durkin et al. 2015, 2016, Richardson 2019) though it is unclear if they sink as aggregates or fecal pellets that get fragmented at depth, or sink as individual particles.

Spatial and temporal variability on scales that are currently unresolved in global models may be important for improving predictions of organic carbon transport. For example, an analysis of a global database of observed POC fluxes reaching the seafloor shows that this flux follows a log-normal probability distribution, mimicking that of net primary production (Cael et al. 2021a). Consequently, high flux events have a disproportionately large contribution to POC flux, with 29% of the flux measurements accounting for 71% of the measured flux near the seafloor. Such episodic, high flux events have been noted before in time-series data and can be due to a combination of high flux from a sinking phytoplankton bloom combined with inefficient remineralization (e.g. Conte et al. 1998).

The use of detailed biogeochemical models targeted to addressing some of these issues can help in developing parameterizations for large-scale global models. The use of technologies such as the transport matrix method (Khatiwala 2007) can help with this by allowing different models to be run with the same physical context. In addition, focused field programs such as EXPORTS (EXport Processes in the Ocean from Remote Sensing) (Siegel et al. 2016) and COMICS (Controls of Oceanic Mesopelagic Interior Carbon Storage) (Sanders et al. 2016) and the deployment of new generations of autonomous platforms such as BGC-Argo floats (e.g. Arteaga et al. 2019) will improve our understanding of processes affecting POC transport . With a combination of traditional and new modeling approaches and field programs, our understanding of organic carbon transport will improve, improving the predictive skill of global biogeochemical models.

Transport Matrix Method: A computationally efficient numerical method for transporting biological and chemical tracers in an ocean model that uses output from a full hydrodynamic model.

SUMMARY POINTS

1. Global biogeochemical models still predict a wide range of values for organic carbon transport, but their results for current and predictions for future global export are converging.
2. New models and modeling approaches are helping identify areas of further research need and develop new parameterizations.
3. Our understanding of mesopelagic processes affecting organic carbon transport, such as ecosystem dynamics and particle fragmentation, are important areas where progress needs to be made.

FUTURE ISSUES

1. Better understanding and parameterizations of biotic and abiotic processes in the mesopelagic are needed to better model the attenuation of organic carbon transport.
2. Better parameterizations of the effects of gelatinous zooplankton, viruses, and fish on food webs and organic matter transport are needed.
3. New comprehensive spatial and temporal data sets from intense field programs and global coverage by autonomous observation platforms will help improve model accuracy.

DISCLOSURE STATEMENT

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