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Key Points:

- Plankton structure drives export efficiency, while zooplankton fecal pellets enhance transfer efficiency in high export efficiency regimes
- Global transfer efficiency is sensitive to processes related to sinking speed and remineralization, while export efficiency is insensitive
- The global pattern of transfer efficiency can be explained by assumptions about ballasting and background sinking speed

Supporting Information:

Supporting Information may be found in the online version of this article.

Correspondence to:

O. Karakuş, onur.karakus@uit.no

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The Role of Ballasting, Seawater Viscosity and Oxygen-Dependent Remineralization for Export and Transfer Efficiencies in the Global Ocean

Onur Karakuş^{1,2,3}, Cara Nissen^{1,4,5}, Christoph Völker¹, Wilhelm Hagen^{6,7}, Morten Iversen^{1,6}, Laurent Oziel¹, Özgür Gürses¹, and Judith Hauck^{1,8}

¹Alfred-Wegener-Insititut Helmholtz-Zentrum für Polar- und Meeresforschung, Bremerhaven, Germany, ²Physical Oceanography Department, Woods Hole Oceanographic Institution, Woods Hole, MA, USA, ³Department for Geosciences, iC3: Centre for ice, Cryosphere, Carbon and Climate, UiT the Arctic University of Norway, Tromsø, Norway, ⁴Department of Atmospheric and Oceanic Sciences and Institute of Arctic and Alpine Research, University of Colorado Boulder, Boulder, CO, USA, ⁵Department of Freshwater and Marine Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, The Netherlands, ⁶MARUM and University of Bremen, Bremen, Germany, ⁷BreMarE, Marine Zoology, University of Bremen, Bremen, Germany, ⁸University of Bremen, Bremen, Germany

Abstract The particulate organic carbon (POC) flux from the euphotic zone to the deep ocean is central to the biological carbon pump. It is typically evaluated using "export efficiency" and "transfer efficiency," which reflect POC formation and sinking and carbon sequestration efficiency in the ocean's interior, respectively. Since observations of these metrics are limited, biogeochemical models can elucidate the controls of large-scale patterns. This study uses the global ocean-biogeochemical model FESOM-REcoM, with a new sinking routine that accounts for ballast minerals, seawater viscosity, and oxygen-dependent remineralization in POC sinking and remineralization, to identify the drivers of global export and transfer efficiency. We find that export efficiency is highest at high latitudes, where diatoms, mesozooplankton, and macrozooplankton dominate the plankton community, but that high export efficiency does not always imply high transfer efficiency. Omitting ballast minerals decreases export efficiency by 20% in the Southern Ocean, yet the globally integrated POC flux out of the euphotic zone $(5.4-5.6 \text{ Pg C yr}^{-1})$ and the global average export efficiency (14.7%-15.4%) are relatively insensitive to seawater viscosity, mineral ballasting, or oxygen-dependent remineralization. In contrast, global transfer efficiency is more sensitive to these processes and varies between 21% and 25% in the simulations, with the largest reduction by 23% observed when omitting ballasting in subtropical, lowproductivity regions. Our findings suggest that assumptions about ballasting and background sinking speed could explain previous discrepancies in the literature regarding the highest transfer efficiencies in low or high latitudes. Notably, while plankton community structure determines export efficiency regimes, zooplankton fecal pellets drive high transfer efficiencies in regions with high export efficiency, like the Southern Ocean.

Plain Language Summary This study looks at how carbon moves from the ocean's surface to its deeper layers, which is important for the global carbon cycle. We used a model to study how different factors, such as minerals that help particles sink, the thickness of seawater, and the amount of oxygen, affect this movement. Our results show that while the amount of carbon leaving the surface stays about the same when these processes are considered, the amount of carbon reaching deep ocean layers varies. We found that minerals in carbon particles are more important than other factors, like seawater thickness or oxygen levels, in carrying carbon to deeper parts of the ocean. Importantly, our results highlight that faster-sinking fecal pellets from small floating animals play a key role in efficiently moving carbon to deeper layers.

1. Introduction

The ocean's biological carbon pump (BCP) consists of various processes that produce and transport particulate organic carbon (POC) from the euphotic zone to the mesopelagic zone, and from there to the deep ocean, including the bathypelagic zone (Volk & Hoffert, 1985). It plays a significant role in the global carbon cycle, as without it, the atmospheric CO_2 concentration would be about 200 ppm higher in preindustrial conditions (Maier-Reimer et al., 1996; Parekh et al., 2006). POC is first produced by marine phytoplankton in net primary production (NPP). A part of this organic material is transferred to secondary producers such as zooplankton that graze on phytoplankton



and is assimilated into their biomass (Steinberg & Landry, 2017). Another portion of carbon, that is, marine snow, fecal pellets, rains out from the euphotic zone (Boyd et al., 2019). Only a fraction of biogenic carbon reaches the deep ocean below 1,000 m (typically less than 20%; Omand et al., 2020; Passow & Carlson, 2012). The amount of carbon reaching the deep ocean depends on multiple factors, such as the remineralization of particles by bacteria (Belcher et al., 2016; Buchan et al., 2014; Iversen & Ploug, 2010), plankton composition (Cavan et al., 2015; Turner, 2015), fragmentation of particles by zooplankton (Giering et al., 2020) and the density of the particles (Iversen & Robert, 2015; Klaas & Archer, 2002). The density of particles increases when they contain minerals such as calcium carbonate, opal, and lithogenic material, which consequently enhances the sinking speed of particles and reduces the time available for remineralization (Armstrong et al., 2001; Klaas & Archer, 2002). While the efficiency of the BCP is ultimately set by the balance between biologically mediated downward POC transfer and physically driven upward transport of remineralized carbon and nutrients (Frenger et al., 2024), the strength of the BCP is often quantified by two metrics assessing the fraction of photosynthetically fixed carbon that reaches the mesopelagic and deep ocean: Export efficiency and transfer efficiency (Buesseler et al., 2020).

Export efficiency (e-ratio), is defined as the fraction of NPP that is exported as POC from a certain depth horizon, for example, the euphotic zone. Observational studies using thorium-based export flux estimates and sediment trap measurements of particle export generally suggest that export efficiency is higher in the high latitudes and lower in the low latitudes of the global ocean (Henson et al., 2012). Many studies tried to explain patterns of export efficiency based on physical and biological conditions at the time of observing, with partially contradictory results between global and regional studies. On a global scale, previous studies suggested a negative relationship between the e-ratio and sea surface temperature (SST) (Laws et al., 2000, 2011) or a positive relationship between the e-ratio and NPP (Dunne et al., 2005; Henson et al., 2011). Other studies explained the global pattern by empirical equations that depend on SST and chlorophyll concentrations (e.g., Dunne et al., 2005) or on SST and NPP (e.g., Henson et al., 2011; Laws et al., 2011). Further, Siegel et al. (2014) illustrated that global monthly anomalies of large phytoplankton biovolume can explain the patterns of the e-ratio in the global ocean, with a high fraction of large phytoplankton being associated with high e-ratios. Regionally, exceptions to the globally established relationships between NPP, SST, and e-ratio were reported. For example, Maiti et al. (2013) found that the e-ratio is negatively correlated with NPP in the high southern latitudes, and the relation with SST is weak. Furthermore, opal ballasting was shown to be a key process for carbon export and e-ratio in the Southern Ocean (Arteaga et al., 2018; Britten et al., 2017; Klaas & Archer, 2002). Henson et al. (2019) showed that the high export efficiency is related to the low abundance of macrozooplankton and bacteria or high mesozooplankton biomass rather than to phytoplankton community composition. Biogeochemical models can complement observational studies in analyzing global patterns and drivers of the e-ratio. Models generally predict the same large-scale gradient as observation-based estimates (Henson et al., 2012), that is, a high (15%-25%) e-ratio in the high latitudes and a low e-ratio toward the equator (Henson et al., 2015; Laufkötter et al., 2016). However, Laufkötter et al. (2016) showed that the e-ratio at a fixed depth horizon of 100 m differs strongly regionally between four three-dimensional ocean biogeochemical models due to the different parametrizations of plankton functional types and process representation among the models.

Transfer efficiency (T_{eff}) is the ratio between the POC flux to the deep ocean (e.g., across 1,000 or 2,000 m) and the flux exported from the upper ocean (e.g., from the euphotic zone or across 100 m). As such, it provides information about the ocean carbon sequestration efficiency (Buesseler et al., 2020). Here, the "sequestration flux" defines the sinking of biogenic carbon to the deep ocean below 1,000 m (Lampitt et al., 2008; Passow & Carlson, 2012). In contrast to the general agreement on the latitudinal pattern of the e-ratio, there is no consensus on the pattern of transfer efficiencies. The T_{eff} varies spatially, and different patterns were proposed. Henson et al. (2012) found high T_{eff} in low latitudes (>20%) and low T_{eff} (<5%) in the Southern Ocean, based on Thorium-based export observations of transfer efficiency. In contrast, Weber et al. (2016) showed low T_{eff} in the subtropics (5%) and high T_{eff} (25%) in the high latitudes from deep ocean nutrient concentrations in an ocean inverse model. Possible explanations for this difference are data collection biases of sediment traps or analytical errors associated with the Th-based export observations (de Melo Viríssimo et al., 2024; Weber et al., 2016). Similar to the export efficiency, T_{eff} also depends on ballast minerals (Weber et al., 2016), temperature (due to its enhancing effect on remineralization; Iversen & Ploug, 2013) and oxygen (Devol & Hartnett, 2001). The relative importance of all these factors is an area of intense research. For example, Marsay et al. (2015) illustrated that a warmer mesopelagic zone could cause a decrease in the transfer efficiency and consequently reduce carbon storage in the ocean. Henson et al. (2012) emphasized that ecosystem structure is a key factor that controls T_{eff} . As

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one of the few examples where a biogeochemical model was used to analyze the transfer efficiency, Maerz et al. (2020) showed a high transfer efficiency of POC in high latitudes, the equatorial Pacific, and the Indian Ocean after parametrization of composition, microstructure, porosity and density of marine aggregates in a global ocean biogeochemical model. Cram et al. (2018) found a strong influence of temperature and particle size on T_{eff} by using a one-dimensional particle model, and Laufkötter et al. (2017) illustrated the strong effect of the influence of oxygen-dependent remineralization on the T_{eff} in the tropical Pacific.

Mirroring the current state of research on carbon export fluxes, export efficiency, and transfer efficiency from field studies, simulations of these properties in biogeochemical models are associated with high uncertainty. Currently, Earth System Models do not agree on the magnitude and direction of the change in export flux by the year 2100 (Henson et al., 2022). Furthermore, they are still missing sufficient mechanistic process formulation to produce robust projections for the future. For example, the effects of seawater viscosity, mineral ballasting, and oxygen-dependent remineralization on particle dynamics in the models were identified as important but missing processes in the gap analysis of Henson et al. (2022). Previous studies have shown that omitting the seawater viscosity effect on particle sinking likely causes a positive bias in present-day export estimates (Taucher et al., 2014), while omitting mineral ballasting is expected to lead to a negative bias (Le Moigne et al., 2014; Wilson et al., 2012). Furthermore, not considering oxygen-dependent remineralization would also lead to a positive bias in present-day estimates of export flux (Devol & Hartnett, 2001; Laufkötter et al., 2017).

Here, we quantify the impacts of these potentially important but often overlooked processes on the spatial patterns of export and transfer efficiencies in an ocean biogeochemical model. To achieve this goal, we implemented, for the first time in a global biogeochemical model, a modified version of the one-dimensional particle model proposed by Cram et al. (2018) to address (a) to what extent the e-ratio and T_{eff} are affected by the parametrization of mineral ballasting, seawater viscosity, and oxygen-dependent remineralization and (b) whether high export efficiency is an indicator of high transfer efficiency.

2. Methods

2.1. Model Description: FESOM2.1-REcoM3

In this study, we use the global ocean general circulation model FESOM2.1 (Danilov et al., 2017) coupled to the biogeochemical model REcoM3 (Gürses et al., 2023). FESOM2.1 is based on a finite-volume discretization on an unstructured mesh which allows for high resolution in areas that are more dynamic than others (Danilov et al., 2017; Gürses et al., 2023). The version of REcoM3 used here consists of two phytoplankton classes (small phytoplankton and diatoms) and three zooplankton functional types (micro-, meso- and macrozooplankton; Karakuş et al., 2022). It is an intermediate-complexity ocean biogeochemical model (Fennel et al., 2022) resolving carbonate chemistry and the cycling of the nutrients dissolved inorganic nitrogen, silicic acid, and iron. REcoM3 applies varying cellular stoichiometry for diatoms (N:C:Chl:Si) and small phytoplankton (N:C: Chl:CaCO₃) after Geider et al. (1998) and Hohn (2008). A fraction of the small phytoplankton group (2%) represents calcifying phytoplankton in the model (Gürses et al., 2023).

Figure 1 summarizes the POC fluxes in REcoM3, where POC from phytoplankton organic matter is redistributed among zooplankton and sinking POC compartments. In the version used in this study, the three zooplankton functional types graze on the two phytoplankton groups, representing the food web fluxes. Sinking POC is divided into two pools: One slow-sinking and one fast-sinking detritus group (for a more detailed description, see Gürses et al., 2023; Karakuş et al., 2022). The slow-sinking detritus class is fueled by phytoplankton aggregation, microzooplankton mortality, and microzooplankton mini-pellet production. Fecal pellets, sloppy feeding, and mortality of the meso- and macrozooplankton are the sources of fast-sinking detritus particles. Before implementing the new parametrization for this study (see Section 2.2), the slow-sinking particles had an initial sinking speed of 20 m d⁻¹ at the surface, which increases linearly with depth, and the fast-sinking particles had a constant sinking speed of 200 m d⁻¹ (Gürses et al., 2023). In the existing version of REcoM3 (Gürses et al., 2023), the sinking POC is remineralized as a function of temperature, and remineralization products are transferred to the dissolved organic carbon pool (DOC).



Particulate Organic Carbon Fluxes in REcoM

Figure 1. Particulate organic carbon (POC) fluxes and related processes in the updated ocean biogeochemical model REcoM3 with three zooplankton groups (Karakuş et al., 2022). Two phytoplankton groups (small phytoplankton and diatoms) are responsible for net primary production (NPP), and three zooplankton groups (micro-, meso- and macrozooplankton) graze on the phytoplankton groups. Microzooplankton is also grazed on by the other two zooplankton groups. Phytoplankton aggregation, microzooplankton mini pellet production, and the mortality from microzooplankton compose the slow-sinking POC pool. Fecal pellets, mortality, and sloppy feeding from the meso- and macrozooplankton groups form the fast-sinking POC pool. Remineralization of both slow- and fast-sinking POC transforms POC to dissolved organic carbon (DOC).

2.2. New Parameterization of Particle Sinking Speed and Remineralization

For this study, we modified the model parametrization of particle sinking speed as well as particle remineralization to include dependencies on particle density, seawater viscosity, temperature and oxygen. These processes are implemented into REcoM3 using a modified version of the particle sinking model by Cram et al. (2018). In particular, in the new version of REcoM's particle sinking routine, we use a parametrization that allows for spatio-temporal variability in sinking speeds due to the effect of ballast minerals (Iversen & Ploug, 2010) and seawater viscosity (Taucher et al., 2014). Further, we add a dependency of the remineralization of sinking POC on oxygen concentration (Devol & Hartnett, 2001) to the already existing temperature dependence in REcoM3. In the modified version, we compute the particle sinking speed as a function of seawater viscosity and the density difference between the particle and the seawater. However, we do not apply the effect of particle size on sinking speed as described in Cram et al. (2018). Instead, our model accounts for particle size in two different ways. First, we differentiate between two particle classes: slow-sinking and fast-sinking, which serve as simplified representations of small and large particles, respectively. Second, we apply a depth scaling that accelerates particle sinking speed with depth, assuming that larger particles with higher sinking velocities reach deeper into the ocean interior (Kriest & Oschlies, 2008).

The new parametrization for calculating particle sinking speeds (m d^{-1}) can be written as:

$$w_{sink}(Z, \Delta \rho_{particle}, \mu_{SW}) = w_{ref} \cdot \underbrace{\frac{\Delta \rho_{particle}}{\Delta \rho_{ref}}}_{\text{Density Scaling}} \cdot \underbrace{\frac{\mu_{ref}}{\mu_{SW}}}_{\text{Viscosity Scaling}} + \underbrace{ds \cdot Z}_{\text{Depth Scaling}}.$$
 (1)

Table 1

The Relevant Parameters for the New Sinking Routine in REcoM-3

Parameter (Unit)	Symbol	Value	Reference
POC density (kg m ⁻³)	ρ_C	1,033	Oliver et al. (1981)
			Klaas and Archer (2002)
			Cram et al. (2018)
PON density (kg m ⁻³)	$ ho_N$	1,033	Oliver et al. (1981)
			Klaas and Archer (2002)
			Cram et al. (2018)
CaCO ₃ density (kg m ⁻³)	ρ_{CaCO_3}	2,830	Cram et al. (2018)
			Klaas and Archer (2002)
Opal density (kg m ⁻³)	$ ho_{opal}$	2,090	Mursky and Thompson (1958)
			Cram et al. (2018)
Reference particle density (kg m ⁻³)	$ ho_{ref}$	1,230	Alldredge and Gotschalk (1988)
			Cram et al. (2018)
Reference seawater density (kg m ⁻³)	$ ho_{swref}$	1,027	Cram et al. (2018)
Reference seawater viscosity (kg $m^{-1} s^{-1}$)	μ_{ref}	0.00156	Cram et al. (2018)
Half-saturation coefficient for oxygen	k_{O_2}	15	DeVries and Weber (2017)
dependent remineralization (mmol m ⁻³)			Cram et al. (2018)
Reference sinking speed of slow-sinking particles (m d ⁻¹)	W_{ref_1}	10	_
Reference sinking speed of fast-sinking particles (m d ⁻¹)	W_{ref_2}	200	_
Depth scaling factor (d^{-1})	d_s	0.01	_
Maximum sinking velocity (d ⁻¹)	W _{max}	250	_
Reference remineralization rate (d^{-1})	r _{ref}	0.15	_

In Equation 1, the particle sinking speed (w_{sink}) is a function of depth (Z), the density difference between the particle and the seawater density $(\Delta \rho_{particle})$ and sea water viscosity (μ_{SW}) . The reference particle sinking speeds are 10 m d⁻¹ $(w_{ref_1}, \text{Table 1})$ and 200 m d⁻¹ $(w_{ref_2}, \text{Table 1})$ for slow and fast sinking particles, respectively. The density scaling is defined as the ratio of the density difference between the particle $(\rho_{particle})$ and the seawater (ρ) at depth $Z(\Delta \rho_{particle})$ to a reference density difference $(\Delta \rho_{ref})$. Here, $\Delta \rho_{ref}$ is calculated from a reference particle density $(\rho_{ref}, 1,230 \text{ kg m}^{-3}, \text{Table 1})$ and the reference seawater density $(\rho_{swref}, 1,027 \text{ kg m}^{-3}, \text{Table 1})$.

Sinking particles (slow- or fast-sinking) are represented by four state variables: carbon (D_{POC} , mmol m⁻³), nitrogen (D_{PON} , mmol m⁻³), calcium carbonate (D_{CaCO_3} , mmol m⁻³), and silicate (Dopal, mmol m⁻³). First, we calculated the proportion of mass within a control volume (V_i , where i = POC, PON, CaCO₃, opal) by dividing each state variable by the total sum of all components (Equation 2). We then used these proportions to calculate the particle density (Equation 3). The density of the particle ($\rho_{particle}$) is determined based on the densities (ρ_{POC} , ρ_{PON} , ρ_{CaCO_3} , ρ_{opal} ; see Table 1) and the proportion of mass within a control volume of organic matter (V_{POC} , V_{PON}), carbonate (V_{CaCO_3}), and silicate (V_{opal}) that constitute the particles, as follows:

$$V_i = \frac{\mathbf{D}_i}{\mathbf{D}_{POC} + \mathbf{D}_{PON} + \mathbf{D}_{CaCO_3} + \mathbf{D}_{opal}}$$
(2)

$$\rho_{particle} = V_{POC} \cdot \rho_{POC} + V_{PON} \cdot \rho_{PON} + V_{CaCO_3} \cdot \rho_{CaCO_3} + V_{opal} \cdot \rho_{opal}$$
(3)

For the computation of $\rho_{particle}$, its mineral content is accounted for (see Equation 1 in Supporting Information S1). If the sinking particles are composed mainly of particulate organic carbon and nitrogen, the ratio is <1, and the density scaling factor acts to reduce the sinking speed. In contrast, if the fraction of ballasting agents (opal and calcite) in the particle is high, the ratio exceeds 1, and the density scaling factor acts to enhance the sinking speed

Table 2

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Overview of Model Simulations						
	Particle s	Particle remineralization				
Simulation	Ballast minerals	Seawater viscosity	Oxygen			
REF	Yes	Yes	Yes			
NO_DENSITY	No	Yes	Yes			
NO_VISCOSITY	Yes	No	Yes			
NO_OXYGEN	Yes	Yes	No			

Note. Simulations differ in the parameterization of particle sinking speed and organic matter remineralization. The active processes in each experiment are indicated. In all simulations, the effect of the particle sizes is implemented by the depth scaling factor, and temperature-dependent remineralization was used. See text for details.

(ballasting). The viscosity scaling is defined as the ratio of a reference seawater viscosity (μ_{ref} , 0.00156 kg m⁻¹ s^{-1} , Table 1) to the in-situ seawater viscosity (μ_{sw} , see Equation 2 in Supporting Information S1). Seawater viscosity affects the sinking speed such that when the seawater viscosity is lower than the reference viscosity, the sinking speed increases. Conversely, when the seawater viscosity is higher than the reference viscosity, the sinking speed decreases. Lastly, the depth scaling represents the increase of the sinking speed of a particle with depth. Here, this term is only applied to the slow sinking particles. A maximum sinking velocity of 250 m d⁻¹ was used for both sinking POC classes to ensure numerical stability. The 5-year mean of sinking speeds and the profiles of sinking speeds in four subregions are shown in Figures S9 and S10 of Supporting Information S1, respectively.

To mimic the bacterial metabolism, the remineralization rate of particles r_{remin} is dependent on both temperature (Lopez-Urrutia & Moran, 2007) and oxygen concentrations (Devol & Hartnett, 2001) in the new version of **REcoM3** following:

$$r_{remin} = r_{ref} \cdot \exp\left(-4500 \cdot \left(\frac{1}{T} - \frac{1}{T_{ref}}\right)\right) \cdot \frac{[O_2]}{k_{O_2} + [O_2]}.$$
(4)

In the above equation, the remineralization rate of the particles (r_{remin}) is a product of a reference remineralization rate $(r_{ref}, 0.15 \text{ d}^{-1})$, the Arrhenius temperature function, and an oxygen dependence. The remineralization rate increases exponentially with increasing temperature. The oxygen sensitivity of the remineralization rate follows Michaelis-Menten kinetics and is described by prevailing oxygen concentrations $([O_2])$ and a half-saturation constant ($k_{0,}$, 15 mmol m⁻³), so that the remineralization rate is lower when oxygen concentrations are low (Cram et al., 2018).

The relevant parameters (Table 1) were taken from empirical and modeling studies (Alldredge & Gotschalk, 1988; Cram et al., 2018; Klaas & Archer, 2002; Mursky & Thompson, 1958; Oliver et al., 1981), except for a few less well constrained parameters, namely the reference sinking speeds (w_{ref1} , w_{ref2}), depth scaling factor (ds), maximum sinking velocity (w_{max}), and reference remineralization rate (r_{ref}). The impact of these parameter choices on our model results is discussed in the results Sections 3.1 and 3.2. In addition, an evaluation of the particle flux through point-wise comparison with the observational data set of Mouw et al. (2016a, 2016b) are provided in the Text S1 and Figure S1 in Supporting Information S1. While most observations are from the Northern Hemisphere, there are few data points for comparison in the Southern Hemisphere. The root mean square errors for particle flux in the Northern and Southern Hemispheres are 4.41 and 7.08 mmol C m⁻² d⁻¹, respectively.

2.3. Model Simulations

We conducted four simulations to analyze the effects of different processes on carbon export and transfer efficiencies with the newly implemented sinking routine (Table 2). First, the reference simulation (REF) accounts for all processes impacting particle dynamics described in Section 2.2, namely ballast minerals, seawater viscosity, and temperature- and oxygen-dependent remineralization. In addition, we performed three sensitivity simulations

to quantify the impact of each of these processes separately. In each one, the impact of one process on particle dynamics is switched off. In particular, these simulations exclude (a) the density scaling of sinking speeds, that is, the ballast effect, in Equation 1 (NO_DENSITY), (b) the viscosity scaling of sinking speeds in Equation 1 (NO_VISCOSITY), and (c) the oxygen-dependent particle remineralization in Equation 4 (NO_OXYGEN; note that remineralization is still temperature-dependent). In the NO_OXYGEN simulation, the depth scaling term ("ds.Z") in Equation 1 maintains the same assumptions about remineralization rates (i.e., smaller particles will be remineralized further up in the water column than large particles) as in REF, since depth scaling remains unchanged when oxygen-dependent remineralization is switched off. However, we tested the effect of including or excluding depth scaling in Equation 1 and found that it has only a marginal impact on the results (i.e., 0.1% points difference in terms of e-ratio, Table S3 and Figure S13 in Supporting Information S1). Similarly, the effect of oxygen-dependent remineralization on T_{eff} is 2.7% points (24.3% in REF, 21.6% in NO_OXYGEN) with depth scaling and 2.4% points without depth scaling (22.4% in REF, 20.0% in NO_OXYGEN, Table S3 in Supporting Information S1). In addition, we performed eight parameter sensitivity simulations to assess the impacts of less well constrained parameter (w_{ref_1} , w_{ref_2} , ds, r_{ref} , w_{max}) choices on global NPP, EP, EP₁₀₀₀, e-ratio, and T_{eff} values and their spatial patterns. These parameter sensitivity simulations tested different values for w_{ref_1} , w_{ref_2} , ds, r_{ref} , and w_{max} (Table S1 in Supporting Information S1).

In all simulations, the global model was forced with the JRA-55-do atmospheric data set version 1.3.1 (Tsujino et al., 2018). Repeated year 3-hourly forcing fields from the year 1961 of surface downwelling short and longwave radiation, surface rainfall and snowfall fluxes, near-surface (2 m) air temperature, specific humidity, eastward and northward wind components, and sea level pressure were used. Freshwater runoff and the surface salinity field for a weak surface salinity restoring (Sidorenko et al., 2011) are taken from the CORE-II climatology (Griffies et al., 2009). Dissolved inorganic nitrogen and dissolved silicic acid were initialized with World Ocean Atlas 2013 data sets (Garcia et al., 2013), and dissolved inorganic carbon and alkalinity from Global Ocean Data Analysis Project version 2 (Lauvset et al., 2016). While dissolved iron was initialized with PISCES model output (Aumont et al., 2003) which was corrected using observed profiles for the Southern Ocean (Boye et al., 2001; de Baar et al., 1999), oxygen was initialized with World Ocean Atlas 2018 data set (H. E. Garcia et al., 2019). All other tracers were initialized with a small number.

We performed 60 years-long simulations and analyzed the last 5 years of the model runs. As demonstrated in an earlier study (Karakuş et al., 2021), this simulation time is long enough for the upper ocean ecosystem to be in quasi-steady state. In addition, we employed two 300-year simulations—one with the new parameterization of particle sinking (Section 2.2) and one without (Section 2.1)—to investigate the effect of this new parameterization on nutrient profiles in different ocean basins. The differences in nutrient profiles between simulations with and without the new parametrization for particle dynamics are small (Figure S2 in Supporting Information S1).

2.4. Analysis of Particle Export and Transfer Efficiencies

The export efficiency or "e-ratio" defines the ratio between the POC export flux at the depth horizon (EP_{DH}) and integrated NPP between the surface and the depth horizon (DH):

e-ratio =
$$\frac{EP_{DH}}{\int_0^{DH} NPP}$$
. (5)

Since the integrated global POC flux, NPP and e-ratio vary depending on the choice of the depth horizon (Palevsky & Doney, 2018), we here use different depth horizons to assess the sensitivity of our calculations to this choice: seasonally varying euphotic depth, annual mean euphotic depth, seasonally varying MLD, annual maximum MLD, 100 m, and 190 m (see Table 3). In addition, we use the monthly calculated euphotic depth (first row in Table 3) in this study because the base of the euphotic depth separates the photosynthetic processes that produce POC from the deeper layers where respiratory processes, such as remineralization, dominate the factors affecting sinking POC.

The transfer efficiency (T_{eff}) is defined as the ratio between the POC flux at 1,000 m (EP₁₀₀₀) and the POC flux at a given depth horizon (EP_{DH}):

Table 3

Global Net Primary Production (NPP), Particulate Organic Carbon (POC) Export, and Export Efficiency (e-Ratio) for Different Depth Horizons in the REF Simulation

Depth horizon	Definition	Integrated NPP from surface to depth horizon (Pg Cyr ⁻¹)	Global POC flux across depth horizon (Pg Cyr ⁻¹)	Global e- ratio (%)
Euphotic Zone	Monthly calculated euphotic depth where PAR $<= 0.01 \cdot PAR_{surf}$	35.5	5.4	15.3
Annual mean euphotic zone	Annual mean of euphotic depth, determined for each grid point	35.3	5.4	15.3
Mixed Layer Depth (MLD)	MLD from the model, monthly output for each grid point	21.1	5.8	27.9
Annual mean MLD	Annual mean of MLD from the model, determined for each grid point	30.4	4.6	15.1
Annual maximum MLD	MLD from the model, maximum value in a year for each grid point	33.7	4.3	12.8
100 m	Constant for each grid point	35.4	4.9	13.7
190 m	Constant for each grid point	35.4	3.7	10.5

Note. MLD: mixed layer depth, PAR: photosynthetically active radiation. The spatial distributions of the annual mean euphotic depth, the annual mean MLD, and the maximum annual MLD in the REF simulation are shown in supplementary Figure S11 in Supporting Information S1.

$$T_{eff} = \frac{EP_{1000}}{EP_{DH}}.$$
 (6)

While the e-ratio comprises both POC formation and its sinking across the depth horizon, the T_{eff} describes the efficiency of POC transfer to the deep ocean.

We use the simulation REF to assess the averaged global values and spatial distribution of the e-ratio and T_{eff} . This simulation is also used to assess how spatial variability in temperature and plankton composition impact the variability in the e-ratio and the T_{eff} . The additional three simulations (NO_DENSITY, NO_VISCOSITY, NO_OXYGEN) are used to separate the effects of seawater viscosity, ballast minerals, and oxygen-dependent remineralization on the e-ratio and the T_{eff} .

Following Henson et al. (2019), we divide the global ocean into different regimes according to the magnitude of primary production and export efficiency averaged over the last 5 years of the simulation. All regions above the median of primary production are defined as regions of *high productivity* and vice versa (Figures 2a and 2b). Similarly, regions with an e-ratio above the median of the e-ratio are classified as regions of *high export efficiency* and vice versa. After applying this criterion, the four subregions are low productivity, high export efficiency (LPHE), low productivity and low export efficiency (LPLE), high productivity and high export efficiency (HPHE), and high productivity and high export efficiency (HPHE). Furthermore, we applied similar criteria for defining regions according to the spatial distribution of export and transfer efficiencies. All regions above (below) the median of export efficiency are regions of *high (low) export efficiency*. Similarly, regions with a transfer efficiency above (below) the median of the transfer efficiency are classified as regions of *high (low) transfer efficiency*. After applying this criterion, the four subregions are low export efficiency and low transfer efficiency (LELT), low export efficiency and high transfer efficiency (LEHT), high export efficiency and low transfer efficiency (HELT), and high export efficiency high transfer efficiency (HEHT) as seen in Figures 2c and 2d. The median of NPP, export efficiency and transfer efficiency over all grid points are 86 g C m⁻² d⁻¹, 16.7% and 20.3% respectively.

3. Results

3.1. Globally Integrated NPP and POC Fluxes

Globally integrated NPP and POC export fluxes vary substantially for different depth horizons (Table 3). The modeled global NPP varies from 21.1 to 35.5 Pg C yr⁻¹ across depth horizons and amounts to 35.5 Pg C yr⁻¹ across the euphotic zone. This is on the low side of observational estimates of depth integrated NPP (35-70 Pg C)





Figure 2. (a) 5-year mean net primary productivity (NPP) plotted against export efficiency (e-ratio) in the REF simulation. The horizontal solid red line indicates the median export efficiency which is used as the threshold for high and low export efficiency regimes; the vertical solid red line indicates the median NPP, which is used as the threshold for high and low NPP regimes (see Methods). (b) Map showing the spatial distribution of the four regimes in the reference simulation (REF). Low NPP/low e-ratio (LPLE) is shown in orange, low NPP/high e-ratio (LPHE) is shown in dark red, high NPP/low e-ratio (HPLE) is shown in light green, and high NPP/high e-ratio (HPHE) is shown in dark green. (c) 5-year mean export efficiency (e-ratio) plotted against transfer efficiency (T_{eff}) in the REF simulation. The horizontal solid red line indicates the median transfer efficiency which is used as the threshold for high and low transfer efficiency regimes (see Methods). (d) Map showing the spatial distribution of the four regimes in the reference regimes (see Methods). (d) Map showing the spatial distribution of the four regimes in the reference regimes (see Methods). (d) Map showing the spatial distribution of the four regimes in the reference simulation (REF). Low e-ratio/low T_{eff} (LELT) is shown in white, low e-ratio/high T_{eff} (LEHT) is shown in light purple, high e-ratio/low T_{eff} (HELT) is shown in purple, and high e-ratio/high T_{eff} (HEHT) is shown in dark purple.

 yr^{-1} ; Carr et al., 2006; Kulk et al., 2020). Similarly, the modeled global POC flux across different depth horizons ranges from 3.7 to 5.8 Pg C yr⁻¹, which is near the lower end of the range suggested by observations (4–13 Pg C yr⁻¹; Dunne et al., 2007; Henson et al., 2011). While the global e-ratio is 15.3% when using the euphotic zone as the depth horizon, it varies between 10.5% and 27.9% for other definitions of the depth horizon (Table 3). These results align with Palevsky and Doney (2018), who showed that global POC flux rates vary by 30% and global e-ratios by 21% across different choices for the depth horizon within a single biogeochemical model. Across parameter sensitivity simulations (Table S1 in Supporting Information S1), global NPP ranges from 34.8 to 39.1 Pg C yr⁻¹, while EP at the base of the euphotic zone varies between 5.6 and 6.2 Pg C yr⁻¹ (Table S2 in Supporting Information S1). Consistent with the small changes in NPP and EP, the global average e-ratio remains relatively stable, ranging from 15.2% to 17%. However, EP₁₀₀₀ and T_{eff} are more sensitive to parameter choices. EP₁₀₀₀ varies from 0.9 to 1.9 Pg C yr⁻¹, while transfer efficiency ranges from 15.9% to 33.9% (Table S2 in Supporting Information S1).

In FESOM-REcoM3, small phytoplankton and diatoms contribute 71.6% and 28.2%, respectively, to the total NPP in the euphotic zone (Figure 3). In the model, the microzooplankton group is the main consumer of phytoplankton, and it grazes 22.3% of the annual primary production. This is lower than the estimated 60% of consumption by Calbet and Landry (2004). The slow-sinking POC pool constitutes 72.9% of the total sinking particles and is dominated by phytoplankton aggregates (61.2% of the slow-sinking particles). The fast-sinking particles are formed by mesozooplankton and macrozooplankton processes, for example, fecal pellet production, and make up 27.1% of the total sinking particles. The slow-sinking and fast-sinking particles contribute 3.7





Figure 3. Routing of particulate organic carbon (POC) fluxes (Pg C yr⁻¹) between the model compartments in the REF simulation. Fluxes are reported as annual averages of the last 5 years of the simulation. The percentage values are reported as a proportion of total NPP, except for slow- and fast-sinking POC where percentage values refer to the sum of both sinking POC groups.

and 1.7 Pg C yr⁻¹, respectively, to the POC flux out of the euphotic zone. However, the main difference between slow- and fast-sinking particles is the amount of carbon that reaches the depth of 1,000 m. While 47.1% of the fast-sinking particles that sink out of the euphotic zone reach 1,000 m, only 13.5% of the slow-sinking particles reach that level. This is consistent with the previously reported important role of zooplankton fecal pellets for carbon export (Henson et al., 2019; Turner, 2015).

3.2. Global Spatial Patterns of NPP, EP, e-Ratio and T_{eff}

The spatial distribution of the modeled NPP is similar to the satellite-based distributions presented by Behrenfeld and Falkowski (1997), with higher NPP in the high latitudes and the Equatorial Pacific and lower NPP in sub-tropical gyres (Figure 4a). In the model, POC export across the euphotic depth is high in the high latitudes and equatorial upwelling regions (Figure 4b), which is in agreement with the spatial distribution of carbon export estimates from satellite-derived products or other models (Henson et al., 2011; Lauf-kötter et al., 2016).

Mirroring the distribution of NPP and POC export, the simulated e-ratios are higher in the high latitudes and the equatorial Pacific (Figures 4a and 4c). While the spatial mean of the e-ratio is 18% north of 40°N, it is 8% in the low latitudes ($40^{\circ}N-40^{\circ}S$), which is lower than those at both the northern and southern high latitudes. The southern high latitudes show a particularly high average e-ratio (36%) compared to the rest of the ocean. Our results show a similar latitudinal gradient for the e-ratio as in the observational data compiled by Henson et al. (2019), that is, a low export efficiency in the low latitudes and a high export ratio in the high latitudes.



Figure 4. Maps of (a) net primary production (NPP) integrated over the euphotic zone, (b) the export flux of particulate organic carbon (POC) at the base of the euphotic zone, (c) export efficiency and (d) transfer efficiency averaged over the last 5 years of the REF simulation. Panel c denotes the ratio of the fields in panels b and a, while panel d shows the ratio of the POC flux at 1,000 m and panel (b) The zonal averages of each field are shown on the right side of the maps. The shaded areas represent the minimum and maximum as derived from monthly output. The figure showing the zonal average of the export efficiency in panel c includes observational data (blue dots from Maiti et al. (2013) and purple dots from Henson et al. (2019)).

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Figure 5. The modeled 5-year average export efficiency (e-ratio) versus integrated net primary production (NPP, g C m⁻² yr⁻¹) in the euphotic zone, with points colored by sea surface temperature (SST, °C) in the REF simulation. Lines denote empirical relationships between NPP and the e-ratio, as calculated using the equations from Laws et al. (2011), which depend on temperature and NPP, at 5.3° C (solid black), 18° C (dash-dotted black), and 30° C (dashed black). Additional lines represent relationships from Arteaga et al. (2018, solid red) and Britten et al. (2017, dashed red), both of which also depend on temperature and NPP, with the equation from Britten et al. (2017) also incorporating silicic acid concentration. For the latter two equations, SST was set to 5.3° C, and for the equation from Britten et al. (2017), silicic acid concentration was set to 10 mmol Si m⁻³.

In contrast, the simulated transfer efficiency shows a different pattern than export efficiency (Figure 4d). While the spatial mean of T_{eff} is 13% north of 40°N, it is 26% in the low latitudes (40°N–40°S), which is higher than those at both the northern and southern high latitudes. The latitudinal gradient of the transfer efficiency is similar to the satellite-based estimates and in-situ observations of Henson et al. (2012), which show a higher transfer efficiency in the low latitudes (up to 20%). Similar to NPP, EP, and the e-ratio, the transfer efficiency exhibits strong seasonality (as shown in the zonal mean plot in Figure 4), particularly in the high latitudes, where it ranges from less than 1%–190%.

Our parameter sensitivity simulations (Table S1 in Supporting Information S1) shows that the spatial pattern of the e-ratio remains largely unaffected (Figure S12 in Supporting Information S1), with patterns such as high values in high latitudes and the equatorial Pacific consistent across simulations. In contrast, transfer efficiency exhibits greater sensitivity. While the overall pattern remains similar, with locally high values in the Southern Ocean, equatorial Pacific, and coastal upwelling regions, its magnitude varies (Figure S12 in Supporting Information S1). Notably, changing the reference sinking speed or reference remineralization rate has a greater impact on the magnitude of transfer efficiency (Figure S12 in Supporting Information S1).

3.3. Drivers of e-Ratio and T_{eff}

Spatial variability of the e-ratio and T_{eff} suggests differences in the factors controlling their distributions. For the e-ratio, the influence of several factors—such as NPP, temperature, ballast minerals, silicic acid concentrations, and the abundance of macrozooplankton and bacteria—has been discussed in the literature (e.g., Arteaga et al., 2018; Britten et al., 2017; Henson et al., 2019; Laws et al., 2011). The large variability in the model cannot be explained by the empirical equation of Laws et al. (2011, see Figure 5), which accounts for SST, especially in the high latitudes' low primary production and high export efficiency regions (see Figure S3 in Supporting Information S1). In fact, the suggested empirical equations for the Southern Ocean by Britten et al. (2017) and Arteaga et al. (2018), which account for temperature and silicic acid concentration, explain the inverse relation between NPP and e-ratio better (Figure 5). Especially the equation including silicic acid concentration (Britten et al., 2017) agrees well with the model in the southern high latitudes (see Figure S3 in Supporting



Figure 6. Relationship in the low productivity low export regime (LPLE, (a, c)) and in the low productivity high export regime (LPHE, (b, d)) between (a, b) the export flux at the euphotic depth (EP, g C m⁻² yr⁻¹) and integrated net primary production (NPP, g C m⁻² yr⁻¹) and between (c, d) the export flux at 1,000 m (EP₁₀₀₀, g C m⁻² yr⁻¹) and the export flux at the euphotic depth in the REF simulation. The panels are colored by (a) sea surface temperature (SST, °C), (b) the relative contribution of diatoms to total NPP (%), (c) the relative contribution of small phytoplankton to total NPP (%), (d) mean surface large zooplankton (meso- and macrozooplankton) concentration (mmol C m⁻³). We used a combination of factors in the subregions when selecting coloring variables, including the dominant PFT type, zooplankton importance, average SST (Table S4 in Supporting Information S1), and *R*² values (Figure S4 in Supporting Information S1).

Information S1). However, these empirical equations still do not explicitly account for the plankton composition, even though this has been proposed to be a key factor in in-situ observations (Henson et al., 2019).

In our model, the magnitude of carbon export and transfer efficiencies is affected by several factors, resulting in various productivity and export regimes. Figures 6 and 7 illustrate the effects of plankton composition and SST on export and transfer efficiencies for the low productivity and high productivity regimes, respectively (see Figure 2).

In our model, the LPLE regions are located in some parts of the Arctic Ocean and predominantly in the subtropical gyres (Figure 2b) and are characterized by the dominance of small phytoplankton (94% of the total NPP). As a result, the export efficiency is lower than 16.7% (red line in Figure 6a), with values as low as 1% in areas with high SSTs (Figure 6a). This indicates that remineralization plays a role in controlling export efficiency in warm ocean regions. Additionally, the transfer efficiency of carbon in this region is mostly higher than the median of 20.3% (red line in Figure 6c). In our simulation, carbon transfer efficiency in the LPLE regime exceeds 20.3% in areas where small phytoplankton significantly contribute to total NPP (yellow colors in Figure 6c). In this region, the average density of slow-sinking particles, which dominate sinking particulate carbon, is 1,814 kg m⁻³, with an average density scaling factor of 3.9 (Table S2 in Supporting Information S1). This suggests that ballasting plays a key role in determining the transfer efficiency in this regime, as the small phytoplankton group includes calcifiers in FESOM-REcoM3. In addition, the average viscosity scaling factor is 1.5 (Table S2 in Supporting Information S1), suggesting that seawater viscosity enhances the sinking speed of particles and thus the transfer efficiency in this region.





Figure 7. Relationship in the high productivity low export regime (HPLE, (a, c)) and in the high productivity high export regime (HPHE, (b, d)) between (a, b) the export flux at the euphotic depth (EP, g C m⁻² yr⁻¹) and integrated net primary production (NPP, g C m⁻² yr⁻¹) and between (c, d) the export flux at 1,000 m (EP₁₀₀₀, g C m⁻² yr⁻¹) and the export flux at the euphotic depth in the REF simulation. The panels are colored by (a) sea surface temperature (SST, °C), (b) the relative contribution of diatoms to total NPP (%), (c) the relative contribution of small phytoplankton to total NPP (%), (d) mean surface large zooplankton (meso- and macrozooplankton) concentration (mmol C m⁻³). We used a combination of factors in the subregions when selecting coloring variables, including the dominant PFT type, zooplankton importance, average SST (Table S4 in Supporting Information S1), and R^2 values (Figure S4 in Supporting Information S1).

The LPHE regions are located in the high latitudes in our model (Figure 2b), where diatoms are an important contributor to total NPP (41.7%). Our analysis shows that the export ratio typically exceeds 33.4% in locations where the diatoms' contribution to total NPP is more than 60% (Figure 6b). In the LPHE region, the transfer efficiency of carbon can exceed 40.6% (Figure 6d), and the co-occurrence of large zooplankton biomass (shown in yellow in Figure 6d) with high transfer efficiency suggests that fecal pellet production by meso- and macro-zooplankton drives the system to a maximum (~50%) transfer efficiency (Figure 6d). While the average viscosity scaling factor is 0.93 in this subregion, due to the cold SST (average 3.3° C, Table S2 in Supporting Information S1), the density scaling factor enhances the sinking speed of both slow- and fast-sinking particles, as the average particle densities (1,379 and 1,258 kg m⁻³ for slow- and fast-sinking particles, respectively, Table S2 in Supporting Information S1) are greater than the reference particle density of 1,230 kg m⁻³.

The HPLE regions are located in the tropical areas and mid-latitudes in our model (Figure 2b), where small phytoplankton are the main contributor to total NPP (77.8%). In this region, annual mean SST is generally high (30° C (shown in yellow in Figure 7a), and export efficiency mostly ranges between 8.4% and 16.7%. Similarly, we do not observe a large spread of transfer efficiency values in this region (mostly between 20.3% and 40.6%). In contrast to the other three regions, there is not a clear relationship between plankton composition and transfer efficiency of carbon for the HPLE regime (Figure 7c and Figure S4 in Supporting Information S1). In this region, slow-sinking particles dominate the sinking POC, with an average density of 1,567 kg m⁻³ and a density scaling factor of 2.7 (Table S2 in Supporting Information S1). This suggests that ballasting plays an important role here. Additionally, the average viscosity scaling factor of 1.6 (Table S2 in Supporting Information S1) indicates that seawater viscosity enhances the sinking speed of particles.





Figure 8. Sensitivity of export and transfer efficiency to process representation in POC cycling. The maps show (a–d) export efficiency at the base of euphotic zone and (e–h) transfer efficiency (a, e) in the baseline simulation REF and in REF compared to (b, f) the simulation NO_DENSITY, (c, g) NO_VISCOSITY, and (d, h) NO_OXYGEN. All data are 5 year means. Note that the scales for the export and transfer efficiencies are different.

The HPHE regions are located in the equatorial Pacific, subantarctic zone, north Pacific and Atlantic in our model (Figure 2b), where small phytoplankton and diatoms share similar portions in total NPP (52.7% and 47.3%, respectively). Similar to the LPHE region, large zooplankton is simulated to be an important component of plankton biomass in the HPHE region, contributing 8% of total plankton biomass. Our analysis shows that the export ratio often exceeds 33.4% in the locations where the contribution of diatoms to total NPP exceeds 60% (Figure 7b). In the HPHE region, the transfer efficiency of carbon is generally higher than 20.3%, and large zooplankton-related processes enhance the transfer efficiency of carbon (>40.6%, Figure 7d). While the average viscosity scaling factor in this subregion is 1.28 (with an average SST of 14.1°C, Table S2 in Supporting Information S1), the density scaling factor enhances the sinking speed of slow-sinking particles, as the average particle density (1,359 kg m⁻³, Table S2 in Supporting Information S1) exceeds the reference particle density of 1,230 kg m⁻³.

Overall, our model results indicate that high carbon export efficiency regimes (>16.7%, LPHE and HPHE) generally also display a high transfer efficiency (>20.6%). Diatoms reach the highest contribution to total NPP in these regions, and large zooplankton are a major factor in driving the high transfer efficiency. In contrast, low carbon export efficiency regimes (<16.7%, LPLE and HPLE) do not automatically imply a low transfer efficiency.

3.4. Sensitivities of e-Ratio, T_{eff} and POC Fluxes to Different Processes

To quantify the relative role of particle density, temperature and oxygen in affecting sinking and remineralization and subsequently the export and transfer efficiencies in the model, we ran sensitivity experiments where one factor was held constant at a time (see Section 2.3). Our results suggest that the export and transfer efficiencies are most sensitive to the ballast minerals (Figures 8b and 8f), which are produced by diatoms and small phytoplankton and increase particle density. The effect of particle density enhances the export efficiency by up to 45% in the Southern Ocean, which hosts a high share of diatom biomass and where sinking particles consequently contain opal. While seawater viscosity slightly decreases the export efficiency at high latitudes, its overall effect on the eratio is minor (Figure 8c). Similarly, oxygen-dependent remineralization has only a small impact on the export efficiency compared to that of particle density (Figures 8b and 8d). Overall, the absolute effect of these processes is larger for the transfer than for the export efficiency (note the different scales in the panels of Figure 8). Similar to the export efficiency, the strongest impact on the transfer efficiency (increases by up to 50%) comes from the effect of particle density displays the strongest control on the sinking speed of particles (see Figure S5 in Supporting Information S1). While the effect of seawater viscosity is relatively small throughout the global ocean, oxygen-dependent remineralization notably affects the transfer efficiency in oxygen minimum zones

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Figure 9. Panel (a) shows profiles of the particulate organic carbon (POC) flux in the four productivity and export efficiency, regimes LPLE (yellow; low productivity, low export efficiency), LPHE (dark red; low productivity, high export efficiency), HPLE (light green; high productivity, low export efficiency), and high production and high export (dark green; high productivity, high export efficiency) in the simulation REF. See Figure 2 for the locations of each regime. Panels (b–e) show the relative change in % of the POC flux in the simulations NO_DENSITY, NO_VISCOSITY, and NO_OXYGEN relative to the baseline simulation REF. Note that the relative change is calculated as REF minus the simulations NO_DENSITY (red), NO_VISCOSITY (purple), and NO_OXYGEN (gold; see Methods), respectively.

(OMZs) (up to 30% in the Equatorial Pacific and Indian Oceans), which coincides with previous findings of Laufkötter et al. (2017).

Unsurprisingly, the dominant role of ballast materials is also evident when assessing average profiles of POC fluxes across the four regimes. In the REF simulation, the general shape of the particle flux profile is similar for the LPLE, LPHE, HPLE and HPHE regimes (Figure 9a), but the magnitude of the fluxes are different. For all regions, the POC flux reaches a maximum at or above the euphotic depth and decreases with depth (Figure 9a). While the POC flux is the highest in HPHE, it is lowest in the LPLE region. In the LPLE region, ballast minerals enhance the particle flux below 200 m (by up to 60%), and reduce the flux by up to 25% above 100 m (Figure 9b). This indicates that ballast minerals play an important role in carrying the particles from the surface layer to the mesopelagic. Ballast minerals affect the particle flux in the LPHE region in the same way, although the effect is smaller (up to 30%; Figure 9c). In the two LPLE and LPHE regions, high concentrations of small phytoplankton or diatoms lead to greater content of CaCO₃ or opal in particles respectively, enhancing their sinking speed. In comparison, the effect of seawater viscosity and oxygen-dependent remineralization on the profile of sinking POC is smaller than the effect of ballast minerals in these two regions. In the HPLE region, the effect of seawater viscosity, ballast minerals or oxygen dependent remineralization on particle organic carbon flux is smaller than in both low-productivity regimes (Figure 9d). For instance, the effect of ballast minerals (seawater viscosity) only increases (decreases) the POC flux up to 13% (10% in the upper 100 m). In the HPHE region, ballast minerals have the strongest impact on POC fluxes, increasing the flux by up to 34% above 400 m (Figure 9e). In addition, the effect of seawater viscosity increases the POC flux by up to 11% throughout the water column.

Our results indicate that low and high export efficiency regimes are closely linked to plankton community structure in the euphotic zone (Figure 10). In low export efficiency regimes, the small phytoplankton group dominates the total plankton biomass in the euphotic zone, accounting for 89% in LPLE and 65% in HPLE. These regions have relatively low biomass of large zooplankton (meso- and macrozooplankton), with less than 1% in LPLE and 1% in HPLE. Conversely, high export efficiency regimes (LPHE and HPHE) are characterized by a higher proportion of diatoms (33% in LPHE and 35% in HPHE) and larger zooplankton (12% in LPHE and 7% in HPHE). While plankton community structure determines export efficiency, it also influences transfer efficiency through ballast minerals, as seen in the average transfer efficiency values in the subregions (Figure 10). In the LPLE region, the contributions of small phytoplankton, diatoms, microzooplankton, and large zooplankton to total plankton biomass are 89%, 6%, 4%, and 1%, respectively (Figure 10). The mean export ratio remains unchanged at 4% in NO_DENSITY, NO_VISCOSITY, and NO_OXYGEN simulations compared to the reference (REF). However, unlike export efficiency, the simulated mean transfer efficiency is sensitive to the representation of ballast minerals (+23%), seawater viscosity (+1%), and oxygen-dependent remineralization (+3%). When particle density is neglected (NO_DENSITY) in the LPLE region, the transfer efficiency drops to 3%, which is





Figure 10. Summary of the spatial mean of export and transfer efficiencies in four subregions and in all simulations: The 5year average shares of diatoms (dark green), small phytoplankton (light green), microzooplankton (yellow), mesozooplankton (orange), and macrozooplankton (dark orange) for total plankton biomass in the euphotic zone are illustrated in the pie charts for the four subregions in the reference (REF) simulation. The black and yellow arrows represent export and transfer efficiencies, respectively. The numbers next to the arrows indicate the mean export and transfer efficiencies in the simulations REF (black), NO_DENSITY (red), NO_VISCOSITY (purple), and NO_OXYGEN (orange). The signs in the parenthesis show the direction of changes relative to the REF simulation. The plus, minus, and equal signs indicate an increase, decrease, and no change.

almost nine times lower than in all other simulations. In the LPHE region, the contributions of small phytoplankton, diatoms, microzooplankton, and large zooplankton to total plankton biomass are 41%, 33%, 14%, and 12%, respectively. Here, the mean export ratio decreases slightly in NO_DENSITY and NO_OXYGEN (by 2% and 1%) but remains unchanged in NO_VISCOSITY compared to REF. The transfer efficiency is lowest (13%) in NO_DENSITY and highest (21%) in NO_VISCOSITY, highlighting the critical role of ballast minerals in the transfer of carbon to the deep ocean. In the HPLE region, the contributions of small phytoplankton, diatoms, microzooplankton, and large zooplankton to total plankton biomass are 65%, 18%, 15%, and 1%, respectively. The transfer efficiency in HPLE is sensitive to mineral ballasting and oxygen-dependent remineralization. It decreases from 20% in REF to 15% in NO_DENSITY and to 18% in NO_OXYGEN. In the HPHE region, the contributions of small phytoplankton, diatoms, microzooplankton, and large zooplankton to total plankton biomass are 34%, 35%, 24%, and 7%, respectively. Similarly, in this region, carbon transfer efficiency decreases from 25% in REF to 21% in NO_OXYGEN. Although the effect of seawater viscosity is visible in the flux profiles (Figure 9, panels



Figure 11. Classification of the ocean according to their annual mean export and transfer efficiencies. To define the different regimes, we applied the threshold method described in section 2.4 to 5-year mean export (the median 16.7%) and transfer efficiency (the median 20.3%) fields. The regimes are marked as low export efficiency and low transfer efficiency (LELT), low export efficiency and high transfer efficiency (LEHT), high export efficiency and low transfer efficiency (HELT), and high export efficiency and high transfer efficiency (HEHT). One map is shown per simulation: (a) NO_DENSITY, (b) NO_VISCOSITY, and (c) NO_OXYGEN.

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b–e), its impact on transfer efficiency is relatively minor, with a maximum decrease of 1% in LPLE and a maximum increase of 1% in LPHE, compared to the effects of other processes (Figure 10).

Taken together, our results suggest that ballast minerals, seawater viscosity, and oxygen-dependent remineralization are more critical for the transfer efficiency than for the export efficiency of carbon (Figure 10). The results indicate that export out of the euphotic depth is more closely related to food web processes (net primary production, grazing) in the euphotic layer and hardly affected by ballast minerals, seawater viscosity, and oxygen-dependent remineralization. Therefore, the global distribution of LPHE, LPLE, HPLE, and HPHE regions do not show significant differences among the different simulations (see Figure S6 in Supporting Information S1). However, the classification of regions by export and transfer efficiency varies among simulations. Accounting for particle density leads to an expansion of the regions defined as low export efficiency and high transfer efficiency and low transfer efficiency (LEHT) in the subtropical gyres (light purple color; compare Figures 2d and 11a). The low export efficiency and low transfer efficiency regimes (high latitudes and Equatorial Pacific; darker purple colors in Figure 2d), many regions also display high transfer efficiencies, which we relate to large zooplankton abundance (Figures 6d and 7d). Large zooplankton fecal pellets drive the high transfer efficiency of carbon (dark purple areas, Figure 11), which is in agreement with the spatial distribution of the high contribution of fast-sinking particles to the total particles (see Figure S7b in Supporting Information S1).

4. Discussion

4.1. Export Efficiency

In FESOM-REcoM3, an inverse relationship between NPP and export efficiency is found in the global ocean (Figure 5). However, this inverse relationship varies spatially and is more prominent in high latitudes (see Figure S3 in Supporting Information S1). Our model specifically characterizes high latitudes and coastal areas with high export efficiency, which is consistent with previous studies (Henson et al., 2012, 2019; Nowicki et al., 2022). Similarly, low export efficiency regimes are mainly located in the oligotrophic gyres and equatorial Atlantic, Pacific and also in the Arabian Sea which is also in agreement with previous estimates (Henson et al., 2019). This consistency with observational and modeling studies demonstrates REcoM3's capability to capture particle sinking and remineralization dynamics in the global ocean. Considering the sparsity of measurements both spatially and temporally, our analysis using a medium-complexity ocean biogeochemical model can help identify larger-scale patterns.

One of the exciting questions in ocean biogeochemistry is identifying the mechanisms that determine low or high export efficiency regimes. After decades of research, it has become clear that abiotic environmental conditions alone do not fully explain the decisive mechanisms behind these regimes (Henson et al., 2019; Serra-Pompei et al., 2022; Wassmann, 1997). Factors such as plankton composition (Boyd & Newton, 1999; Buesseler, 1998), seasonality (Laurenceau-Cornec et al., 2023; Wassmann, 1997), and bacterial abundance (Buchan et al., 2014; Iversen & Ploug, 2010) play significant roles. In the REcoM3 model, we observed similar results, demonstrating a direct link between export efficiency and plankton community structure. High export efficiency regimes are associated with high diatom and macro- and mesozooplankton biomass, whereas low export efficiency regimes are dominated by small phytoplankton cells (Figure 10). In other words, low production and low export efficiency (LPLE) and high production and low export efficiency (HPLE) regimes behave more like retention ecosystems which recycle organic matter and minimize sinking losses (Wassmann, 1997), while HPHE and LPHE regimes are typical of export ecosystems. Furthermore, our study revealed that the large-scale spatial patterns and magnitude of export efficiency are determined by plankton community composition, rather than changes in particle sinking speed (Figure 10). Sensitivity experiments showed that neither the distribution of export efficiency regimes nor large-scale mean values are affected by ballasting, seawater viscosity, or oxygendependent remineralization (Figure 10). However, this does not imply that these processes are unimportant. For instance, we can see a large effect of ballasting, particularly in the Southern Ocean (see Figure 8b). Additionally, our analysis was primarily conducted using annual mean metrics. Considering the importance of seasonality (Laurenceau-Cornec et al., 2023; Wassmann, 1997), these processes might have more significant effects on seasonal scales.

4.2. Transfer Efficiency

In contrast to the export efficiency, there are comparatively fewer data to quantify the carbon transfer efficiency in the ocean, which makes it difficult to characterize large-scale spatial variability (Weber et al., 2016). In FESOM-REcoM3, transfer efficiency of carbon shows strong temporal and spatial variability, and while the zonal mean of transfer efficiency is higher in the low latitudes, high latitudes shows a strong seasonality (Figure 4d). Previous studies produced spatial patterns of transfer efficiency by using an ocean inverse model (Weber et al., 2016) or an ocean biogeochemical model (Maerz et al., 2020). Both studies illustrated high transfer efficiency in the high latitudes and lower transfer efficiency in the low latitudes (except for the Equatorial Pacific). Their results partly contradict previous findings based on thorium-based and sediment trap particle export measurements, which show high transfer efficiency (>20%) at low latitudes and low transfer efficiency (<5%) at high latitudes (Henson et al., 2012). It was discussed that this could be a result of the collection biases of bottom-moored sediment traps and/or analytical errors associated with the Th-based export observations used (Weber et al., 2016). Our results indicate a similar latitudinal gradient (Figure 4d) as described in Henson et al. (2012). However, there are two exceptions for the high latitudes: (a) The effect of seasonality and (b) large zooplankton abundance. First, the transfer efficiency reaches a maximum of 1 depending on the season in the high southern latitudes (Figure 4d, zonal mean), which aligns with recent findings suggesting that the different patterns of T_{eff} can be explained by seasonality (de Melo Viríssimo et al., 2024). We do not see a similar seasonal effect in the low latitudes. Second, high transfer efficiency is rather related to fast sinking particles (i.e., large zooplankton abundance) in high latitudes (Figure 6d). In addition, our sensitivity simulations provide insights into why we observe a different pattern compared to previous studies that show low transfer efficiency in the subtropical gyres (DeVries & Weber, 2017; Marsay et al., 2015; Weber et al., 2016). Our sensitivity simulations (Table 2) suggest that this pattern may be related to the ballasting effect, as we observe higher transfer efficiency in the subtropical regions when we include the ballasting effect on sinking speed (Figure 11). Similarly, we find that transfer efficiency is highly sensitive to changes in the background sinking speed of slow-sinking particles, which dominate in the subtropical gyres in our model (Figure S12 in Supporting Information S1). Based on our results, we hypothesize that, in addition to the effect of seasonality, both the ballasting effect on sinking speed and the background sinking speed could explain the observed pattern in Henson et al. (2012), even though they did not find a direct relationship between CaCO₃ and POC flux in their data. Therefore, further research on particle sinking speed and the ballasting effect in subtropical gyres could become a key area of future study.

In FESOM-REcoM3, the transfer efficiency of carbon in the LPLE regions (in subtropical gyres, Figure 2) is highly sensitive to the inclusion of mineral ballasting (Figure 8f). In all three simulations that include mineral ballasting (REF, NO_VISCOSITY, and NO_OXYGEN), the subtropical gyres are characterized as having low export efficiency (<16.7%) and high transfer efficiency (>20.3%). When the ballasting minerals are excluded from the model, these regions have low export efficiency (<16.7%) and low transfer efficiency (<20.3%). A previous study showed that the transfer efficiency of carbon is greatest in the subtropical gyres because of little remineralization due to ballasting by calcium carbonate (Francois et al., 2002). This spatial feature is captured when ballast minerals are included in the model (Figures 10 and 11).

As noted before, the magnitude of the transfer efficiency is more sensitive to the presence of ballast minerals, seawater viscosity, and oxygen-dependent remineralization than the export efficiency (Figure 8). Similar results were provided by Maerz et al. (2020) after the implementation of microaggregates, which impact sinking velocity and led to a threefold increase in the mean transfer efficiency in the Antarctic zone. This region falls into the LPHE region in our study, and we show that omitting ballast minerals results in a 44% lower transfer efficiency in this region (Figure 10). Maerz et al. (2020) do not report a significant impact of ballast minerals on the mean transfer efficiency in the low latitudes. In contrast, we find that the presence or absence of ballast minerals affects the transfer efficiency in the low latitudes (e.g., LPLE, HPLE), where calcifying small phytoplankton produce notable amounts of ballasting calcite in our model. However, we need to note here that the calcifying phytoplankton is represented in the small phytoplankton group in our modeling studies and this yields to have a large spatial extent of calcifiers. Previously, Seifert et al. (2023) explicitly represented only coccolithophores as calcifiers in the another version of REcoM and its extent is more limited with occurrences in the equatorial Pacific, North and South Atlantic.

Two key mechanisms influence POC transfer efficiency in OMZs. The first mechanism is related to remineralization rates, where higher oxygen concentrations lead to increased remineralization (Devol & Hartnett, 2001). The second mechanism involves the impact on zooplankton populations in OMZs; the lack of oxygen inhibits zooplankton interactions with particles, such as the fragmentation and repackaging of sinking POC (Cavan et al., 2017). While biogeochemical models incorporate the relationship between oxygen concentrations and remineralization rates (Aumont et al., 2015; Dunne et al., 2013), they often do not account for the direct effects of OMZs on zooplankton biomass. Similarly, in FESOM-REcoM3, we focus only on the impact of oxygen on remineralization. Future studies could address the effects of OMZs on zooplankton biomass and their indirect impact on POC export in ocean biogeochemical models. Our analyses in this study demonstrate the role of oxygen-dependent remineralization in determining the magnitude of transfer efficiency in the HPLE and HPHE regions, where OMZs are located, consistent with the findings of Laufkötter et al. (2017). Neglecting oxygen-dependent remineralization reduces carbon transfer efficiency in these regions, as low oxygen levels decrease remineralization rates. The sensitivity of transfer efficiency to oxygen-dependent remineralization in OMZs observed in our model underscores the importance of addressing the overestimation of OMZs in CMIP-type models (Bopp et al., 2013; Maerz et al., 2020).

Observations from deep-ocean sediment traps have shown strong correlations between organic carbon fluxes and ballast minerals, and this was associated with the effect of ballast minerals on the particle sinking speed and/or protection of the organic matter from remineralization (Armstrong et al., 2001; Francois et al., 2002; Klaas & Archer, 2002). Iversen and Robert (2015) showed that ballast minerals enhance the sinking speed of particles, but the hypothesis of "protection from remineralization" was not confirmed. While we use globally uniform parametrizations to quantify large-scale patterns, field studies demonstrated that the impact of ballast minerals is not uniform in the global ocean (Wilson et al., 2012). For instance, ballast composition had little or no effect on particle settling velocity in the Mediterranean Sea (Lee et al., 2009). Therefore, our parameterizations could mirror current understanding, but should be revisited after major new data syntheses or mechanistic understanding has been obtained.

4.3. Limitations and Caveats

Our results are associated with limitations due to the use of a single biogeochemical model. Therefore, the results are affected by the structure and the parametrization of the model REcoM3. For instance, the version of REcoM3 used in this study explicitly divides the spectrum of sinking particles into two pools: Slow-sinking and fastsinking particles (see Methods). This separation gives a strong geographical separation between two sinking particle pools. For example, the model results suggest that slow-sinking particles can, in some locations, make up 100% of total sinking particles (see Figure S7 in Supporting Information S1). Although a single type of sinking particle can drive the entire export flux in some regions and seasons (Markussen et al., 2020), the bulk of sinking particles usually consists of many different sources such as fecal pellets and marine snow (Laurenceau-Cornec et al., 2015; Turner, 2015). Similarly, the fast-sinking particles dominate the euphotic zone only in the regions with high meso- and macrozooplankton biomass, which inevitably causes a high carbon transfer efficiency. The transfer efficiency of carbon is relatively high in our model compared to Henson et al. (2012) and Weber et al. (2016). This is probably at least partly related to the high sinking velocity of fast-sinking particles in the model. In this regard, our parameter sensitivity simulations show that while global export at the base of the euphotic zone (5.4-5.9 PgC yr⁻¹) and the e-ratio (15.2%-17%) exhibit small variability in response to changes in parameters related to particle sinking and remineralization, EP_{1000} (0.9–1.8 PgC yr⁻¹) and T_{eff} (15.9%–33.9%) are much more affected. These results highlight the importance of new and sustained observations to constrain sinking speeds in biogeochemical models.

Given the complexity of particle sinking and remineralization dynamics, there are some aspects not considered in this study. First, despite the high complexity of the biogeochemistry in our model, the ecological complexity is relatively simple. The roles of diel vertical migration of zooplankton (Archibald et al., 2019) and fish (Pinti et al., 2023) in the BCP are not represented. Our model focuses on simple relationships within the lower trophic levels. For instance, our results may be affected by not representing important groups like gelatinous zooplankton (Luo et al., 2020). Second, the aggregation and disaggregation of particles play a key role in determining POC flux and attenuation (Briggs et al., 2020; Iversen, 2023). In our parameterization, aggregation directs particles to the slow-sinking POC pool, while disaggregation is partially represented by zooplankton grazing on sinking particles (Gürses et al., 2023). However, we did not analyze these two processes and their impact on transfer efficiencies in depth. Third, in our parameterization of particle sinking speed, we assumed that the sinking speed

is higher in warm water than in cold water. However, the effect of temperature on particle sinking speed is not clear. Previously, Bach et al. (2012) reported that a warming of 9°C leads to an increase in sinking speeds by 40%. While intuitively, higher water viscosity at colder temperatures should decrease the sinking speeds, Iversen and Ploug (2013) could not confirm such a relationship in laboratory experiments.

Our description of POC sinking and remineralization dynamics aligns well with previous studies by incorporating state-of-the-art relationships between sinking speed and ballast minerals, seawater viscosity and oxygendependent remineralization. However, we acknowledge that different parametrizations of ballast minerals, temperature, and oxygen dependencies in biogeochemical models (DeVries & Weber, 2017; Dinauer et al., 2022; Laufkötter et al., 2017; Maerz et al., 2020) could lead to results that differ from ours. These uncertainties may be related to differences in model structure (e.g., number of PFTs) or process parametrizations (Laufkötter et al., 2016) in addition to the physical state of the modeled ocean. A number of studies shows that the effect of ballast minerals is primarily due to the density effect on sinking speed rather than to mineral protection of particulate organic matter degradation (Iversen & Ploug, 2010; Iversen & Robert, 2015; Ploug et al., 2008). Our ballasting parameterization therefore accounts for the effect on sinking speed of POC, but not on the remineralization rate due to the sometimes discussed mineral protection effect (Armstrong et al., 2001; Engel et al., 2009; Moriceau et al., 2009). The unresolved understanding adds uncertainty to the description of ballasting in models, although evidence is not sufficient currently to include mineral protection into models. Similar to the ballast effect, the potential effect of seawater viscosity on sinking speed and POC flux has been less investigated by modelers (Cram et al., 2018; Taucher et al., 2014) and is based on only a few studies of the temperature dependency of viscosity (Cram et al., 2018). In previous parametrizations (Taucher et al., 2014), as well as in ours, both the effect of seawater viscosity and the difference between particle density and seawater density are explicitly parametrized. However, since seawater viscosity and density are closely related to temperature, there is a potential issue of double-counting the temperature effect. Therefore, revisiting and further investigating the effect of seawater viscosity would be beneficial to avoid this issue. Additionally, we have been parametrizing bacteria implicitly, considering the influence of temperature and oxygen on their rate of POC remineralization. This is based on laboratory measurements showing an increase in remineralization in response to temperature (Iversen & Ploug, 2013) and the fact that oxic remineralization requires oxygen (Laufkötter et al., 2017). However, the diversity and metabolic activity of heterotrophic bacteria and archaea in the ocean (Azam & Malfatti, 2007), and their role in shaping and being shaped by particles (Kiørboe et al., 2002), could also be considered. For example, bacteria establish populations by settling on sinking particles, but may also detach from them (Nguyen et al., 2022). Further research and model developments in this direction could lead to a more comprehensive representation of POC export and attenuation in ocean biogeochemical models.

4.4. Implications

Developing a simple parametrization of POC sinking speed has been a long-standing goal by the scientific community, but observational data often disagree on the factors dominating POC sinking speed (Burd, 2024). This is because the sinking speed of particles depends in complex ways on factors such as size, density, shape, composition (including mineral ballasting), and their association with transparent exopolymer particles (TEPs) (Iversen & Ploug, 2010; Mari et al., 2017; McDonnell & Buesseler, 2010). While these factors are recognized as important in the scientific literature, they are often difficult to incorporate into biogeochemical models in the absence of observation-based quantitative relationships between these factors and POC sinking speed. A good example is the representation of the "ballast effect" in biogeochemical models. Over the past two decades, the scientific community has debated the impact of the ballast effect, particularly whether it influences remineralization (Armstrong et al., 2001; Engel et al., 2009; Moriceau et al., 2009) or sinking speed (Berelson, 2001; Iversen & Robert, 2015; Klaas & Archer, 2002). Most parametrizations of sinking speed in models have focused on the latter (Gehlen et al., 2006; Long et al., 2021), partly because the "mineral protection effect" could not be reproduced in laboratory experiments (Iversen & Robert, 2015). Some models have even abandoned the representation of ballasting due to a lack of clear observational relationships between sinking speeds and the mineral composition of particles in the global ocean (Aumont et al., 2015; Lee et al., 2009). Given the numerous unknowns related to particle sinking speed, most models either use constant sinking speeds or specify a depthdependent function for sinking speed (Burd, 2024; Henson et al., 2022). Therefore, the uncertainty in magnitudes and patterns of carbon transfer to depth arising from the sinking speed parametrization remains an active research topic for large-scale ocean biogeochemical models. Recent studies by (Dinauer et al., 2022; Maerz

et al., 2020) suggest that using a variable sinking speed based on Stokes' law (Rubey, 1933; Stokes, 1851), where the sinking speed of a spherical particle depends on the viscosity of the fluid and the particle's excess density, and which parametrizes the impact of mineral ballasting, diatom frustules, and particle composition, can provide more accurate estimates of carbon transfer efficiency due to a more realistic representation of the processes. By following current evidence from the literature (e.g., Maerz et al., 2020), our approach contributes to the ongoing work related to the effect of different factors on large-scale spatial patterns of transfer efficiency, using a normalized version of Stokes' law that combines theoretical predictions and empirical findings, as proposed by Cram et al. (2018). Based on our results, ballasting has a strong influence on T_{eff} , highlighting the importance of parametrizing the various factors affecting sinking speed. We therefore recommend continuing the ongoing developments in large-scale ocean biogeochemical models (this study, Maerz et al., 2020) regarding variable sinking speed parametrization.

This study contributes to estimate the possible effect of previously neglected processes on carbon export in biogeochemical models. In our model, the effect of ballasting, seawater viscosity, and oxygen-dependent remineralization hardly affect the total integrated POC flux across the euphotic depth (5.4–5.6 Pg C yr⁻¹ in all four simulations). The impacts of all three processes could increase or decrease the POC flux regionally (see Figure S8 in Supporting Information S1). According to the summary of Henson et al. (2022), not considering mineral ballasting in models likely causes a negative bias, but the size of the effect is unknown on the global scale. We find that the globally integrated export flux across the euphotic depth decreases by 3.7% from 5.6 in NO_DENSITY to 5.4 Pg C yr⁻¹ in REF accounting for mineral ballasting. It shows that more particles are transferred to below the euphotic zone due to the enhancing effect of ballasting on sinking speed. Consequently, the POC flux across the euphotic depth decreases. Henson et al. (2022) also mention that omitting seawater viscosity could cause a positive bias in present-day estimates. However, our results show that omitting seawater viscosity causes a negative bias and the globally integrated POC flux decreases by 1.3% (5.35 Pg C yr⁻¹ in NO VISCOSITY and 5.42 Pg C vr^{-1} in REF). Our results differ from the findings of Taucher et al. (2014), which show that incorporating seawater viscosity decreases export flux at 130 m by 2.8%. When selecting a comparable depth horizon of 135 m in our model, the export flux increases by 3.9% when incorporating the effect of seawater viscosity on particle sinking speed. This discrepancy might result from differences in the parametrization of particle sinking and remineralization dynamics between the two models. However, both studies confirm that the effects of seawater viscosity on particle sinking speed are unlikely to affect modern-day export estimates significantly (Henson et al., 2022). Finally, we considered oxygen-dependent remineralization, and when this process is omitted, the globally integrated export flux increases by 1.8% (from 5.4 Pg C yr⁻¹ in REF to 5.5 Pg C vr^{-1} NO OXYGEN). This finding is consistent with the synthesis by Henson et al. (2022), which shows that omitting oxygen-dependent remineralization likely causes a positive bias in export flux estimates. Overall, our results emphasize the critical need to represent the missing processes related to carbon export fluxes in global ocean biogeochemical models. First, this could help to assess the regional effects of these missing processes on export efficiency, as observed in the Southern Ocean (Figure 8b). Second, it would improve estimates of modernday export flux, particularly transfer efficiency, and enable Earth System Models to more accurately capture climate feedbacks in future projections.

5. Conclusion

This modeling study contributes to ongoing investigations into the representation of processes related to carbon export in ocean biogeochemical models. The modified particle sinking routine, as described in Cram et al. (2018), provides an approach to incorporate mineral ballasting, seawater viscosity, and oxygen-dependent remineralization in REcoM3. The updated model version was thus used as a testbed to analyze the potential impacts of these processes on particulate organic carbon flux. Our results show that parameterizing mineral ballasting, seawater viscosity, and oxygen-dependent remineralization has minimal effect on global export efficiency in REcoM3, except for a regional effect of ballasting in the Southern Ocean. These three processes hardly change the estimates of export fluxes across the euphotic depth.

However, ballasting, viscosity and oxygen-dependent remineralization play a critical role in determining carbon transfer efficiency in our model. In FESOM-REcoM3, the global mean carbon transfer efficiency varies between 21% and 25% across different sensitivity simulations. Our results particularly highlight the importance of ballast minerals in influencing particle sinking speed and, consequently, transfer efficiency. Incorporating the effect of

ballast minerals on particulate organic carbon sinking speed results in high transfer efficiency in large areas, such as subtropical gyres. More importantly, it differentiates regions of high transfer efficiency within high export efficiency areas in the high latitudes. This underscores the need to represent processes like mineral ballasting, seawater viscosity, and oxygen-dependent remineralization to capture the spatial variability in particulate organic carbon export dynamics. Notably, these processes can be implemented without significantly increasing computational costs. Additionally, the representation of meso- and macrozooplankton, along with their fast-sinking fecal pellets, is crucial in determining high transfer efficiency in these high export efficiency regions. These findings clearly demonstrate that ecosystem structure and particulate organic carbon export flux dynamics interact and play a decisive role in shaping large-scale spatial patterns. Therefore, we suggest increasing the ecosystem complexity of global ocean biogeochemical models used for particulate organic carbon export-related questions, alongside the processes that affect sinking speed and particulate organic carbon remineralization.

Data Availability Statement

Curated and post-processed data from FESOM2.1-REcoM3 model outputs used in this study are available at Zenodo (https://doi.org/10.5281/zenodo.13955957; Karakuş, 2025). The particulate organic carbon data set from Mouw et al. (2016a, 2016b) is available at https://doi.org/10.1594/PANGAEA.855600. The FESOM2.1–REcoM3 source code is available at https://github.com/FESOM/fesom2/tree/fesom2.1_recom (FESOM-REcoM source code in github [model], 2017), and a manual can be found at https://recom.readthedocs.io/en/latest/.

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