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RESEARCH ARTICLE

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Key Points:

- A new estimate of sinking particulate carbon fluxes from the surface ocean is developed from reconstructions of particle size distribution
- Smaller particles contribute more to the total sinking carbon flux than large particles
- Carbon flux estimates from two depth horizons suggest net heterotrophy in the deeper euphotic zone, rather than autotrophy

Supporting Information:

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

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New Estimate of Organic Carbon Export From Optical Measurements Reveals the Role of Particle Size Distribution and Export Horizon

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Abstract Export of sinking particles from the surface ocean is critical for carbon sequestration and to provide energy to the deep biosphere. The magnitude and spatial patterns of this export have been estimated in the past by in situ particle flux observations, satellite-based algorithms, and ocean biogeochemical models; however, these estimates remain uncertain. Here, we use a recent machine learning reconstruction of global ocean particle size distributions (PSDs) from Underwater Vision Profiler 5 measurements to estimate carbon fluxes by sinking particles (35 μm –5 mm equivalent spherical diameter) from the surface ocean. We combine global maps of PSD properties with empirical relationships constrained against in situ flux observations to calculate particulate carbon export from the euphotic zone ($5.8 \pm 0.1 \text{ Pg C y}^{-1}$) and annual maximum mixed layer depths ($6.1 \pm 0.1 \text{ Pg C y}^{-1}$). The new flux reconstructions suggest a less variable seasonal cycle in the tropical ocean and a more persistent export in the Southern Ocean than previously recognized. Smaller particles (less than 418 μm) contribute most of the flux globally, while larger particles become more important at high latitudes and in tropical upwelling regions. Export from the annual maximum mixed layer exceeds that from the euphotic zone over most of the low-latitude ocean, suggesting shallow particle recycling and net heterotrophy in the deep euphotic zone. These estimates open the way to fully three-dimensional global reconstructions of particle fluxes in the ocean, supported by the growing database of in situ optical observations.

1. Introduction

At the ocean surface, primary production and other biogeochemical processes interact to form organic particles that drive the ocean's biological pump (Honjo et al., 2008; Siegel et al., 2022; Turner, 2015; Volk & Hoffert, 1985). Aggregation and sinking of particulate organic matter store inorganic carbon and nutrients in the deep ocean for timescales ranging from decades to centuries (Boyd et al., 2019; DeVries et al., 2012), reducing surface carbon concentrations and leading to a decrease in atmospheric CO_2 (Kwon et al., 2009). Sinking particles provide organic matter sustaining the deep ocean biosphere (Robinson et al., 2010) and shape the ocean's microbiome (Bianchi et al., 2018; Fontanez et al., 2015; Karl et al., 1984).

Export of particulate organic matter results from the interaction of complex physical and biological processes (Boyd et al., 2019; Siegel et al., 2022; Turner, 2015). Gravitational settling of particles denser than seawater, including fecal pellets, phytodetritus, and heterogeneous aggregates, is thought to be the primary export mechanism, contributing to about 60% of the total carbon export and more than half of the carbon storage in the deep ocean (Boyd et al., 2019). Other export processes, such as organic matter transport and repackaging by vertically migrating organisms (Bianchi et al., 2013; Longhurst et al., 1990; Steinberg et al., 2000) and physical injection (Carlson et al., 1994; Omand et al., 2015; Stukel et al., 2017; Dall'Olmo et al., 2016), make up the remainder (Boyd et al., 2019). The importance of large sinking particles in driving the export flux has been well described (A. L. Allredge & Gotschalk, 1988; Honjo et al., 2008; Turner, 2015), although several studies have also highlighted the importance of smaller aggregates (Alonso-González et al., 2010; Durkin et al., 2015; Kiko et al., 2017; Richardson, 2019).

Export fluxes are commonly quantified as organic matter crossing globally variable reference “surfaces,” here referred to as “depth horizons.” Among these horizons, the euphotic zone depth and mixed layer depths are common choices, underlying complementary interpretations: export from the euphotic zone provides an ecosystem-level viewpoint, while export from the mixed layer provides an estimate of carbon storage for timescales longer than a year. Observational and model-based estimates generally evaluate export at the base of the euphotic zone, as defined by the 1% or 0.1% light levels (Buesseler & Boyd, 2009; Buesseler et al., 2020; Siegel et al., 2014). On annual timescales or longer, organic carbon export balances net community production (Emerson, 2013), and, since synthesis of new particles is greatly reduced below the euphotic zone, it also provides an upper limit to the energy that can fuel subsurface ecosystems. Meanwhile, carbon exported below the maximum mixed layer depth is removed from contact with the atmosphere for timescales longer than a year and thus is relevant for oceanic carbon sequestration. Recent work with a global biogeochemical model indicates that the magnitude and patterns of carbon export are sensitive to the choice of depth horizon (Palevsky & Doney, 2018). However, tests of this sensitivity based on global observations are missing.

Because of its central role in ocean biogeochemistry, the global particle export has received significant attention, resulting in a wide range of estimates—from less than 3 to more than 10 Pg C y⁻¹ (DeVries & Weber, 2017; Dunne et al., 2007; Henson et al., 2011; Siegel et al., 2014), with some of the discrepancies depending on the methods used (Quay et al., 2020). Biogeochemical models yield a global export of 4–6 Pg C y⁻¹ when tuned to match particle flux observations (Siegel et al., 2014) but can reach up to 10 Pg C y⁻¹ when tuned to match in situ profiles of nutrients and other biogeochemical tracers (DeVries & Weber, 2017). A similar range is suggested by recent global IPCC-class Earth System Models, which produce global carbon exports from 2.4 to 12 Pg C y⁻¹, with an average of 7.4 Pg C y⁻¹ (Séférian et al., 2020). Data-driven estimates that combine satellite-based primary production with empirical measures of particle export ratios often result in fluxes near the upper range (Dunne et al., 2007; Guidi et al., 2015; Laws et al., 2011), with some exceptions (Henson et al., 2011).

A global export of around 10 Pg C y⁻¹ is comparable to biogeochemical estimates of annual net community production in the mixed layer (Emerson, 2013; Quay et al., 2020). However, on long timescales, community production must be balanced by multiple export processes (Boyd et al., 2019; Siegel et al., 2022) that also include subduction of nonsinking organic carbon (Carlson et al., 1994; Dall’Olmo et al., 2016) and export via vertical migration of zooplankton and fish (Bianchi et al., 2013; Longhurst et al., 1990; Steinberg et al., 2000). Using the euphotic zone as export horizon, and considering only gravitational settling, particle flux estimates have begun to converge on a value of 6 Pg C y⁻¹, although with significant uncertainty (Boyd et al., 2019).

In the field, both sediment traps and thorium-234 measurements have been used to quantify sinking particle fluxes. However, both types of observations lack detailed particle size information, have poor vertical resolution, and are characterized by known biases, making extrapolations to global scales difficult (Buesseler et al., 2007; Le Gland et al., 2019). Recently, optical methods have gained traction as a way to estimate particle export. These methods are based on in situ observations of particle size distribution (PSD), that is, the number of particles, or abundance, as a function of size (Bourne et al., 2019; Guidi et al., 2008). Among optical instruments, the Underwater Vision Profiler 5 (UVP5) measures the abundance of particles in the 80 μm–2.6 cm range (Picheral et al., 2010) and is routinely deployed on oceanographic expeditions (Kiko et al., 2022). The high vertical resolution of UVP5 observations, combined with empirical, size-dependent relationships for carbon content and sinking speed (Guidi et al., 2008; Kriest, 2002; Stemmann et al., 2004), enables a uniquely detailed view into the three-dimensional ocean particle flux (Guidi et al., 2016). Observations from UVP5 have been used to quantify particulate fluxes from the surface ocean on a regional basis (Cram et al., 2018; Forest et al., 2012; Kiko et al., 2017) and to reconstruct carbon export across large-scale biomes based on limited sets of measurements (Guidi et al., 2015).

The growing number of UVP5 observations, their global distribution, high vertical resolution, and ability to resolve multiple particle size classes offer an unprecedented opportunity to reevaluate global carbon fluxes from the ocean’s surface, testing the importance of the choice of depth horizon, the role of small versus large particles, and the degree of autotrophy (i.e., net particle production) versus heterotrophy (i.e., net particle consumption) across the euphotic zone. In this study, we use a global reconstruction of PSDs from UVP5 observations (Clements et al., 2022) to provide a new estimate of the magnitude and patterns of particulate carbon export from the ocean’s surface. The approach relies on empirical relationships that relate particle size and abundance to sinking fluxes (Guidi et al., 2008; Kiko et al., 2017; Kriest, 2002), which we tune against a global compilation

of in situ sediment trap and thorium-derived particle flux observations (Bisson et al., 2018). We exploit the high vertical resolution of UVP5 measurements to estimate particle export at two depth horizons—the base of the climatological euphotic zone and the maximum mixed layer depth, which we expect to occur during the winter-time (de Boyer Montégut et al., 2004; Kara et al., 2003)—elucidating the importance of the export horizon for net carbon export and sequestration.

The rest of the paper is organized as follows. Section 2 describes the methods used to estimate particle fluxes from global PSD reconstructions and in situ observations. Section 3 presents the results of the new export estimates, comparing them to prior work, and discussing the implications, uncertainties, and caveats inherent to our approach. Section 4 summarizes the main findings and future directions.

2. Methods

2.1. Calculating Particle Flux From PSD

The flux of particulate organic carbon (ϕ , $\frac{mg\ C}{m^2\ day}$) at any given depth can be expressed as a function of three size-dependent quantities: the number (#) of particles of a given size, that is, the PSD ($n(s)$, $\frac{\#}{m^3\ cm}$), the sinking speed ($w(s)$, $\frac{m}{s}$), and the organic carbon content of each particle ($c(s)$, $\frac{mg}{\#}$), according to the following equation (Guidi et al., 2008; Stemann & Boss, 2012):

$$\phi = \int_{s_{\min}}^{s_{\max}} n(s) \cdot w(s) \cdot c(s) ds, \quad (1)$$

Here, s (cm) indicates the particle equivalent spherical diameter (ESD), or size, and s_{\min} and s_{\max} indicate the minimum and maximum size of particles considered for export. Following previous work, we assume that the quantities in Equation 1 can be approximated by power laws that depend on particle size, each characterized by an intercept (the size-independent coefficient) and a slope (the exponent for size-dependence) (Stemann & Boss, 2012):

$$n(s) = n_0 \cdot s^{-\beta} \quad (2)$$

$$w(s) = w_0 \cdot s^{\eta} \quad (3)$$

$$c(s) = c_0 \cdot s^{\zeta}, \quad (4)$$

By combining Equations 2–4, the total particle flux can be expressed as follows:

$$\phi = \int_{s_{\min}}^{s_{\max}} n_0 \cdot w_0 \cdot c_0 \cdot s^{-\beta+\eta+\zeta} ds = \int_{s_{\min}}^{s_{\max}} n_0 \cdot m_0 \cdot s^{-\beta+\mu} ds, \quad (5)$$

where we combined the intercepts and exponents of the sinking speed and carbon content relationships by setting $m_0 = w_0 \cdot c_0$ and $\mu = \eta + \zeta$, following the approach of Guidi et al. (2008). In practice, we use a numerical approximation of Equation 5 by discretizing the size range between s_{\min} and s_{\max} into 20 log-spaced bins, following the typical approach adopted for UVP5 data (Clements et al., 2022; Kiko et al., 2022; Picheral et al., 2010) and summing the argument of the integral across size classes.

We use PSD properties (i.e., the intercept n_0 and the slope β in Equation 2) from the global climatological reconstructions by Clements et al. (2022), discussed in Section 2.2. We combine these PSD reconstructions with empirical relationships for the sinking velocity and carbon content parameters m_0 and μ , which we set as globally constant values, to estimate particle fluxes by solving Equation 5. Since m_0 and μ are poorly constrained (Kiko et al., 2017; Kriest, 2002; Stemann & Boss, 2012), we optimize them by minimizing the mismatch between predicted particle fluxes and in situ observations from sediment traps and thorium-uranium disequilibrium at the base of the euphotic zone (Bisson et al., 2018; see Section 2.3).

We further exploit the three-dimensional nature of UVP5 observations to calculate particle fluxes at two different export horizons: the base of the euphotic zone (here defined by the 1% light level following Morel et al. (2007)) and the annual maximum mixed layer depth (Johnson et al., 2012).

2.2. Reconstructions of PSD

We reconstruct monthly climatologies of PSD biovolume (BV) and slope at the euphotic zone and mixed layer depth horizons based on the approach discussed in Clements et al. (2022). Briefly, these reconstructions are based on a machine learning algorithm (a bagged Random Forest [RF] ensemble) applied to a global data set of UVP5 observations (Kiko et al., 2022), binned on a regular 1° resolution global grid. From these observations, we obtain the slope of the PSD β by fitting a linear least squares regression through the log-transformed particle abundance $n(s)$ as a function of the log-transformed particle ESD. Similarly, we calculate the PSD BV from observed particle abundance, by applying the BV definition:

$$BV = \int_{s_{\min}}^{s_{\max}} n(s) \cdot \frac{\pi}{6} \cdot s^3 ds. \quad (6)$$

We then use a bagged RF algorithm (the “fitensemble” function in MATLAB) to extrapolate the gridded PSD BV and slope at both the euphotic zone and mixed layer depth horizons, based on monthly climatological predictors that include temperature, salinity, oxygen, nutrients, satellite chlorophyll, mixed layer depth, and other biogeochemical variables, following the approach of Clements et al. (2022). These reconstructions are based on the ensemble average of 100 RF realizations with variable hyperparameters (the number of trees and their complexity) and a random selection of predictors, with the intermodel spread representing the error (Clements et al., 2022). The resulting reconstructions are shown in Figure 1 (Figures S1 and S2 in Supporting Information S1). Note that the PSD slope and BV reconstructions at the euphotic zone depth are identical to those in Clements et al. (2022), while those at the mixed layer depth, while similar, are novel to this study.

From the BV and slope reconstructions, we determine the PSD intercept n_0 by substituting Equation 2 into Equation 6 and inverting it to obtain the following equation:

$$n_0 = \frac{6 \cdot BV}{\pi} \cdot \left(\frac{s_{\max}^{4-\beta}}{4-\beta} - \frac{s_{\min}^{4-\beta}}{4-\beta} \right)^{-1}. \quad (7)$$

We then use the resulting global maps of intercept and slope to calculate sinking particle fluxes, based on Equation 5.

2.3. Optimization of Particle Sinking Speed and Carbon Content

Equation 5 requires knowledge of the combined sinking speed and carbon content of particles as a function of size. These quantities have been empirically evaluated using power law relationships analogous to Equations 3 and 4, for example, as compiled in Kriest (2002) and Stemann et al. (2004). Individually, most observational studies measure a range of particles that does not wholly encompass the sizes detected by the UVP5. Furthermore, these relationships are defined for specific particle types, which are not distinguished in the PSD reconstruction used here (Clements et al., 2022).

Since estimates of total flux are sensitive to the sinking speed and carbon content relationships encapsulated by the parameters m_0 and μ , we apply an optimization procedure to keep our results consistent with in situ particle flux measurements. Specifically, we find the values of m_0 and μ that minimize the sum of the square errors between the log of the particle flux reconstructions (Equation 5) and colocated, monthly gridded in situ carbon flux measurements (Bisson et al., 2018). We use a compilation of both trap and thorium flux data corrected to be representative of the flux at the base of the euphotic zone, as described in Bisson et al. (2018). For this study, we do not perform any additional quality control than the processing described by Bisson et al. (2018).

We average together all in situ data onto the same grid of the PSD reconstructions (Clements et al., 2022), that is, into 1°-resolution grids, by month, so that the optimizations are performed on a climatological basis. Because in situ carbon flux measurements are uncertain (Bisson et al., 2018), we adopt a Monte Carlo approach for this optimization, repeating it 1,000 times after perturbing each flux observation after applying a random error to the observations, assuming a log-normal distribution and an uncertainty of 1 standard deviation on the measurements. The introduction of this random error provides a first-order estimate of potential sampling bias and uncertainty introduced by the thorium and sediment trap flux observations. The Monte Carlo ensemble also allows us to estimate the error associated with the optimization of the sinking speed and carbon content parameters.

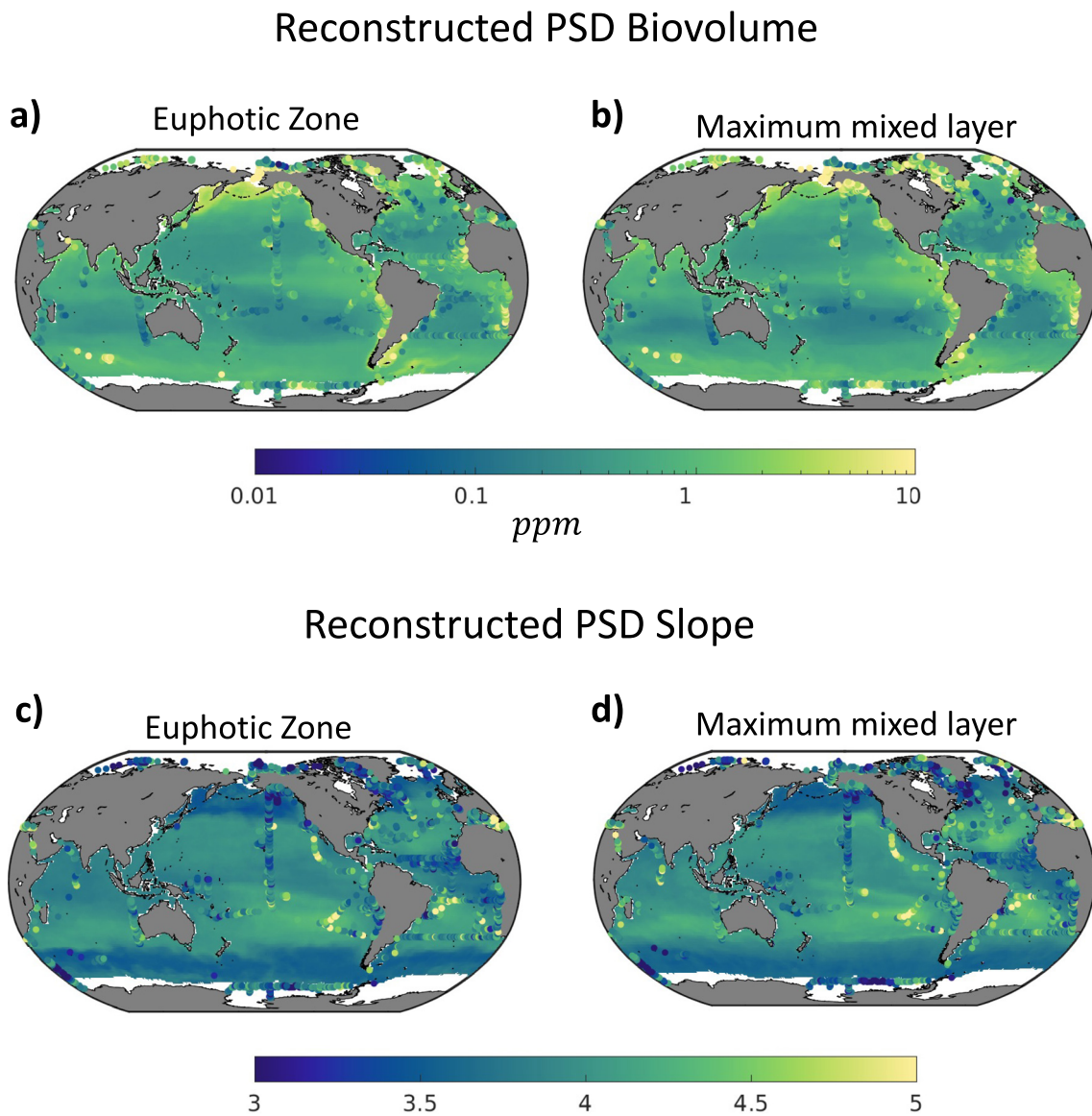


Figure 1. Annual mean global reconstructions of (a and b) PSD biovolume (ppm) and (c and d) particle size distribution (PSD) slope (nondimensional) at the base of the euphotic zone (a and c), and the base of the maximum mixed layer (b and d), based on a machine-learning extrapolation of in situ UVP5 observations (Clements et al., 2022). Color contours show reconstructed variables as annual means. Dots show in situ quantities from UVP5 observations. Note that observations reflect specific months of the year, explaining some of the mismatches with annual mean quantities shown by the background colors.

Because the size distribution of particles that contribute to the flux is poorly constrained, we perform this optimization for a range of plausible minimum and maximum sizes for Equation 5, selecting a physically reasonable combination for the final estimate. Ultimately, when optimizing the sinking carbon parameters, the total global export flux is not sensitive to the size range selected; however, the resulting empirical relationships are. The insensitivity of the carbon flux to the size range indicates a compensatory effect between the sinking carbon parameters and the size range selected for the optimizations. Thus, choosing different size combinations would result in a similar total flux, although it may slightly alter spatial or temporal patterns in a compensatory way (Figure S1 in Supporting Information S1).

Our final choice of size range is informed by average sinking speeds and carbon content previously reported (Kriest, 2002). Based on this optimization analysis, we set the minimum size class to be 35 μm , where the average sinking speed is near 1 m d^{-1} (Kriest, 2002; Smayda, 1970). Although this value is lower than the detection limit of the UVP5, the power law slope can likely be extended to this size range, as demonstrated for example, by

observations in the Pacific Ocean (Stemmann, Eloire, et al., 2008). Most organic particles smaller than this size are likely rapidly remineralized, making their contribution to the sinking flux negligible (Riley et al., 2012). Even if some smaller particles could sink more rapidly (e.g., because of higher concentrations of mineral “ballast” and higher density) and could contribute more substantially to the total flux, neglecting them would not significantly affect our final export because the optimized flux is nearly insensitive to the size range selected (Figure S3 in Supporting Information S1). We choose 5 mm as the maximum size, that is, the same maximum size used for the PSD reconstructions (Clements et al., 2022), roughly corresponding to the size where zooplankton become important contributors to the particle BV detected by UVP5 in a variety of regions (Forest et al., 2012; Stemmann & Boss, 2012; Stemmann, Youngbluth, et al., 2008).

Overall, this optimization approach results in a median value of 2.63 ± 0.06 for the exponent μ and $18.0 \pm 2.8 \text{ mg C m s}^{-1} \text{ cm}^{-2.63}$ for the intercept m_0 , both in the range suggested by in situ observations (Kriest, 2002) and comparable to values adopted by previous studies (Bianchi et al., 2018; Guidi et al., 2008; Kiko et al., 2017; Kriest, 2002; Stemmann et al., 2004). Given the covariation between μ and m_0 , and the dependence of the optimization on the selected particle size range, interpretation of these values and comparison with prior estimates should be done with care. The values found here are overall compatible with the range reported by prior work (e.g., Kriest, 2002). However, attributing a range of uncertainties to previous observational estimates is not straightforward because these studies often focus on different types of particles and size ranges, resulting in large uncertainties. This is particularly true for the values of the intercept m_0 , which can span orders of magnitude, depending on particle types, sizes, and the value of the slope parameter μ . Syntheses of multiple observational data sets of carbon content, together with similar efforts for particle sinking speed (e.g., Cael et al., 2021), could help shed light on this variability. Our optimized parameters are also entirely consistent with the fractal nature of marine aggregates, whereby both carbon content and sinking speed increase with size slower than they would for spheres of constant density, which would obey Stokes' Law (Kriest, 2002). However, the relative role of sinking speed and carbon content cannot be disentangled by our optimization, which targets them in combination.

2.4. Flux Reconstruction, Error and Evaluation

We first present results for fluxes estimated at the climatological euphotic zone depth and then repeat the calculation at the maximum mixed layer depth. We keep the same sinking speed and carbon content parameters, assuming that they do not change substantially between the two depths, which are often not too far apart from each other. Thus, the only methodological difference between the two estimates is the depth of the PSD reconstruction used to calculate the flux.

We take the ensemble mean of the Monte Carlo optimizations (Section 2.3) as the final carbon flux estimate. Error in this estimate could arise not only from the uncertainty in the particle sinking speed and carbon content parameters but also from the uncertainty in the PSD reconstructions (Clements et al., 2022). We combine these two sources of error by summing the variances of two ensembles of carbon flux reconstructions. The first consists of the Monte Carlo optimization ensemble, based on the mean PSD. The second uses 100 different realizations of PSD from the machine learning reconstructions but sets m_0 and μ to the median values from the optimization. The final uncertainty is taken as the square root of the combined variances.

We evaluate reconstructed particle export fluxes by comparing them to in situ flux observations and previous global reconstructions (see Section 2.5). Specifically, we compare total fluxes, zonal averages, and seasonal cycles. For these comparisons, we divide the ocean into 14 biogeochemically consistent regions based on the boundaries identified by Weber et al. (2016), with an additional boundary along the equator to separate Northern and Southern Hemispheres.

2.5. Comparison to Other Estimates of Particle Carbon Export

A variety of approaches have been used to estimate carbon export from the surface ocean (generally referenced to the base of the euphotic zone), based on empirical relationships, mechanistic models, or a combination of the two. Both Dunne et al. (2007) and Henson et al. (2011) provide estimates of particle export that rely on empirical estimates of the “ef-ratio,” that is, the ratio between carbon fluxes at the base of the euphotic zone, and net primary production, which is in turn estimated from satellite-based algorithms. Henson et al. (2011) specifically use particle fluxes from thorium disequilibrium measurements at around 100 m depth, rather than exactly at the

euphotic zone depth, while Dunne et al. (2007) combine estimates of both the ef-ratio and the pe-ratio (an explicit measure of particle-driven export). Use of ef-ratio or pe-ratio to obtain particle export is thus dependent on the NPP product used, which may lead to variability in the final estimates. Additionally, ef-ratios may include export pathways other than sinking particles, adding to the uncertainty. Despite these caveats, both estimates provide valuable empirical representations of particulate carbon export from the euphotic zone and have been widely adopted.

In contrast, Siegel et al. (2014) provide an estimate of the particle export from the base of the euphotic zone, defined as the 1% light level, based on a mechanistic ecosystem model that takes as input satellite-based net primary production, and partitions it into simplified food-web pathways that lead to the production of sinking particles. A similar modeling approach is adopted by DeVries and Weber (2017) who additionally assimilate subsurface oxygen observations with an ocean circulation inverse model, estimating annual mean carbon export resulting from a combination of both sinking particles and other mechanisms.

3. Results and Discussion

3.1. Euphotic Zone Export Fluxes

Our resulting global carbon flux reconstruction at the base of the euphotic zone compares well with monthly averaged, gridded in situ sediment trap and thorium-based observations (Figure 2), performing in a similar way as previous estimates (Dunne et al., 2007; Henson et al., 2011; Siegel et al., 2014). Compared to previous work, we improve performance relative to thorium and sediment trap observations, as expressed by the lower root mean square error and bias. However, our method also reduces the range of reconstructed fluxes, that is, it overestimates the flux at low values and underestimates it at high values compared to observations. This bias could be related to a similar underestimate of the range of PSD BV and slope (Clements et al., 2022) that likely depends on the specific machine learning method used to extrapolate UVP5 observations. It is also likely that the optimization approach against a sparse global data set of in situ fluxes fails to capture extremes in monthly averaged observations of particle export at both the high and low range of observations. Our reconstructions target monthly climatological fluxes and thus cannot capture episodic variations in flux on shorter timescales or interannual variability.

Comparing gridded sediment trap and thorium-based observations to the various estimates of Figure 2 highlights the relative strengths and weaknesses of each approach. The results from Dunne et al. (2007), based on combining satellite primary production with empirical estimates of particle export ratios, match the observed values well but tend to overestimate the largest fluxes (not shown on these figure axes). The estimate by Henson et al. (2011), based on a similar approach as Dunne et al. (2007), follows a similar pattern as observations, as indicated by the high r^2 but systematically underestimates the flux magnitude, as shown by the negative bias. The satellite-driven, model-based estimate from Siegel et al. (2014) captures the overall magnitude of export but misses some of the variability of observations, as indicated by the relatively low r^2 . Overall, all estimates in Figure 2 show combinations of strengths and weaknesses, and it would be difficult to highlight a specific model as unconditionally superior. This suggests that a combination of estimates should be used to assess export of carbon from the surface ocean and that future efforts should strive to reduce the biases discussed above, potentially combining strengths from different approaches.

Extrapolated to the whole ocean, our method reveals spatial patterns of export fluxes in broad agreement with previous studies, with some notable differences (Figure 3). Similar to other estimates, particle fluxes tend to decrease from high to low latitudes and from coastal regions to the open ocean. A local maximum of export is reproduced along the equator and is particularly evident in the Pacific Ocean. Compared to previous work, our method produces somewhat weaker gradients between coastal and offshore waters, with slightly higher fluxes near the centers of subtropical gyres and suggests an asymmetry between the subpolar Atlantic and Pacific Oceans, with more intense particle export along the Gulf of Alaska than in the North Atlantic (see also Section 3.1.2). We also reconstruct substantially stronger export than previously found in the Southern Ocean, in particular south of 50S (see discussion in Section 3.2).

Globally integrated, we estimate a particle export flux from the euphotic zone depth horizon of 5.8 ± 0.1 Pg C y^{-1} , in good agreement with the range of observational and model-based estimates of the biological gravitational pump (4–9 Pg C y^{-1} , Boyd et al., 2019). Compared to other spatially resolved reconstructions, our global flux sits between the low-value of Henson et al. (2011) (3.0 ± 0.3 Pg C y^{-1}) and the high-value of Dunne

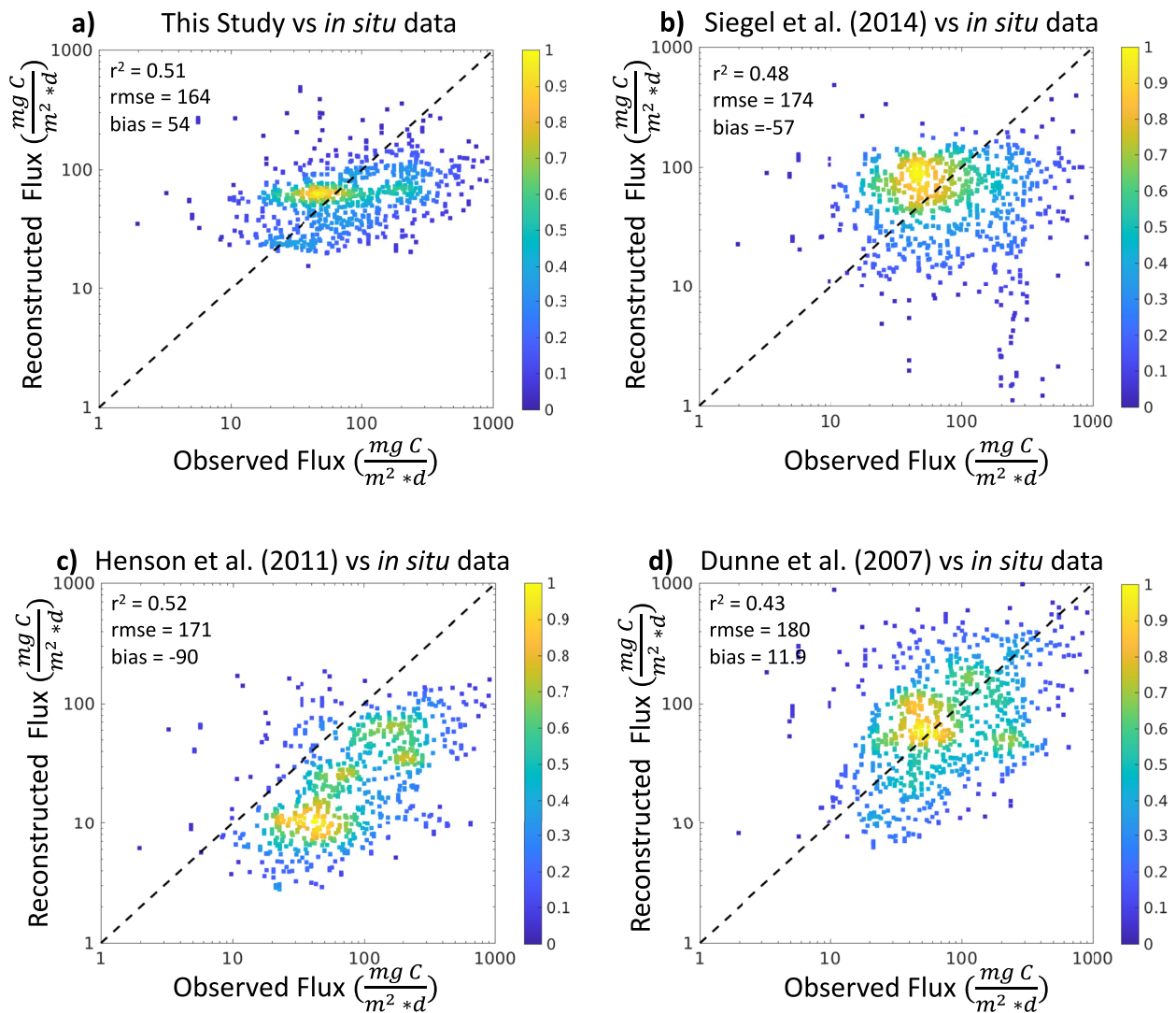


Figure 2. Density scatter plots showing the relationships between in situ flux observations and global flux reconstructions ($\text{mg C m}^{-2} \text{d}^{-1}$) at the base of the euphotic zone from (a) this study, (b) Siegel et al. (2014), (c) Henson et al. (2011), and (d) (Dunne et al., 2007). Colored dots represent the relative density of grid points surrounding the data point, and the dashed line indicates a 1:1 ratio. Annotations show the coefficient of determination (r^2), root mean square error, and average bias. Note that to keep similar x-axes and allow better comparison between the different estimates, a limited number of points with flux larger than $1,000 \text{ mg C m}^{-2} \text{d}^{-1}$ have been omitted from the figures.

et al. (2007) ($9.8 \pm 0.8 \text{ Pg C y}^{-1}$). Seasonal maps of the export and standard deviation are shown in Figures S4 and S5 in Supporting Information S1.

3.1.1. Role of Particle Size in Export

Variations in export patterns derived with our approach reflect a combination of spatially varying PSD BV and slope (Clements et al., 2022). We can quantitatively describe the effect of the PSD as the relative contribution of small ($35\text{--}418 \mu\text{m}$) versus large particles ($418 \mu\text{m}\text{--}5 \text{ mm}$) to the total flux (Figure 4), where $418 \mu\text{m}$ is the geometric mean of the size range considered here.

BV and PSD slope generally correlate in such a way that both factors contribute to increasing export fluxes in particle-rich productive waters, where large, rapidly sinking particles tend to be relatively more abundant than small particles and to decreasing export fluxes in particle-poor oligotrophic waters where small particles dominate (Clements et al., 2022) (Figure 4).

High export in the eastern equatorial and tropical Pacific can be attributed to high BV rather than a dominance of large particles, that is, “flatter” slopes and is reflected in the near equal contribution of small and large particles in the total

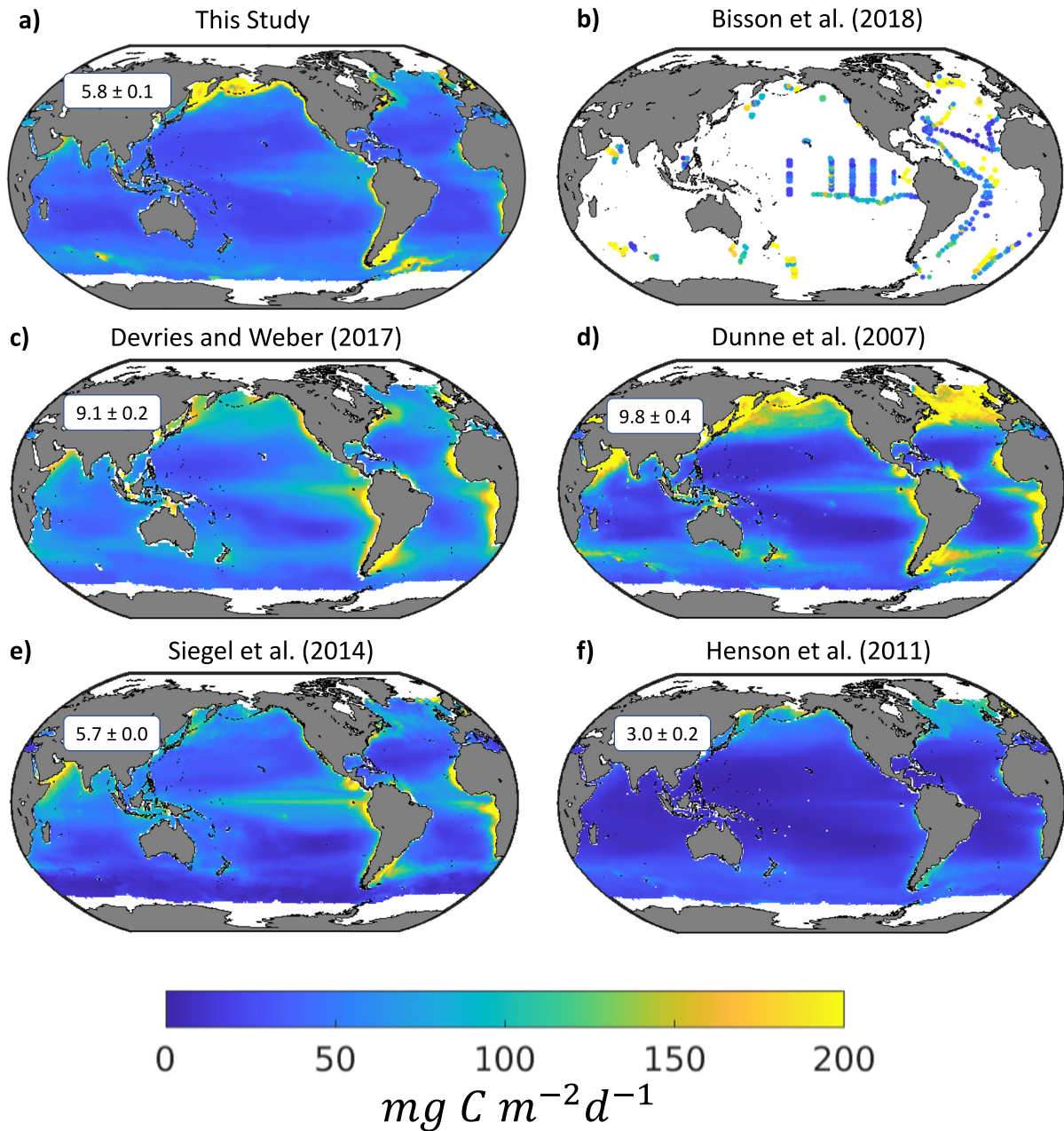


Figure 3. Annual average particle export flux ($mg\ C\ m^{-2}\ d^{-1}$) from the euphotic zone for (a) the global particle size distribution-derived flux from this study compared to (b) the in situ data of Bisson et al. (2018), (c) the steady state satellite-driven model of DeVries et al. (2017), (d) the empirical model of Dunne et al. (2007), (e) the satellite-driven euphotic zone food web model Siegel et al. (2014), and (f) the empirical model of Henson et al. (2011). Annotations in each figure show the globally integrated export in $Pg\ C\ y^{-1}$ and the uncertainty reported by each study.

flux (Figures 1 and 4). In the equatorial Atlantic Ocean, a more substantial flattening of the PSD supports a greater contribution from large particles. A similar interaction of particle abundance and size-structure dramatically intensify fluxes at high latitudes, such as in the subpolar North Pacific and Southern Ocean and to a lesser extent the subpolar Atlantic, where an increase in particle abundance is accompanied by a shift of the PSD toward large particles.

In general, we find that particle BV and fluxes are robustly and positively correlated, indicating that regions with larger standing stocks of particles support stronger sinking fluxes. In contrast, the slope of the PSD and sinking fluxes are generally negatively correlated, although the relationship appears to be weaker than for BV (Figures S6 and S7 in Supporting Information S1). An increase in fluxes when larger particles are relatively more abundant suggests that variations in community structure, for example, in the average size of phytoplankton and their

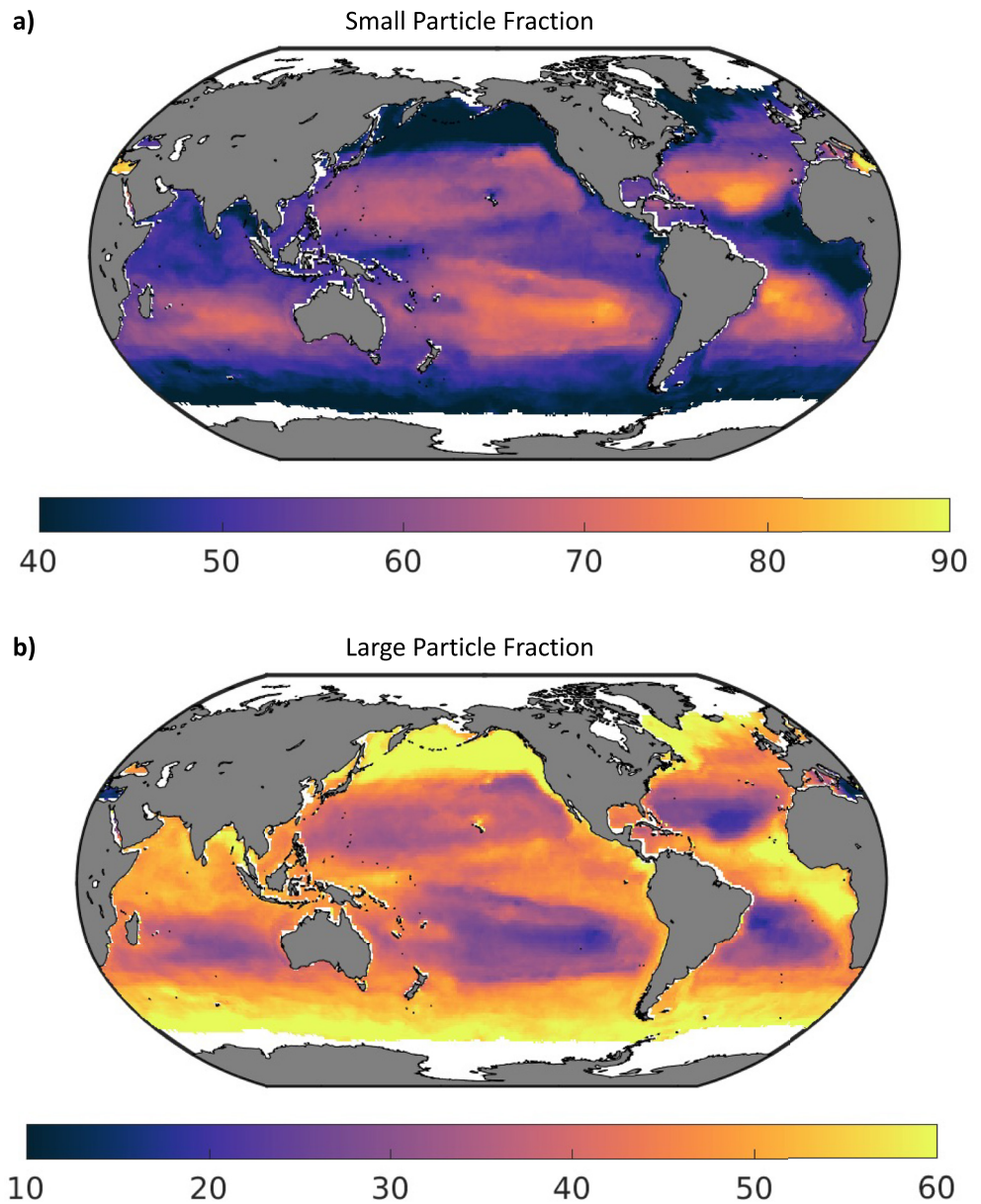


Figure 4. Role of small versus large particles. The two panels show the fraction of carbon flux at the base of the annual mean euphotic zone from (a) small particles (35 to 418 μm equivalent spherical diameter [ESD]) and (b) large particles (418 μm to 5 mm ESD).

grazers, explain part of the shift in export fluxes from less productive to more productive regions that cannot uniquely be attributed to particle BV changes.

3.1.2. Spatial Variability

We illustrate the main spatial differences between our and other reconstructions by considering zonally averaged export fluxes (Figure 5). The largest export rates are observed around the equator, in the subpolar Pacific Ocean, and in the midlatitudes to high latitudes of the South Atlantic Ocean, while more uniform export is observed in the Indian Ocean. In all basins, the minimum export rates are generally located at the latitude of the subtropical gyres. While export is nearly symmetrical around the equator in the Pacific Ocean (Figure 5a), in the Atlantic Ocean, it dramatically increases moving from the Northern to the Southern Hemisphere (Figure 5b). These patterns reflect a combination of open ocean and shelf enhanced particle fluxes. Specifically, high export in the

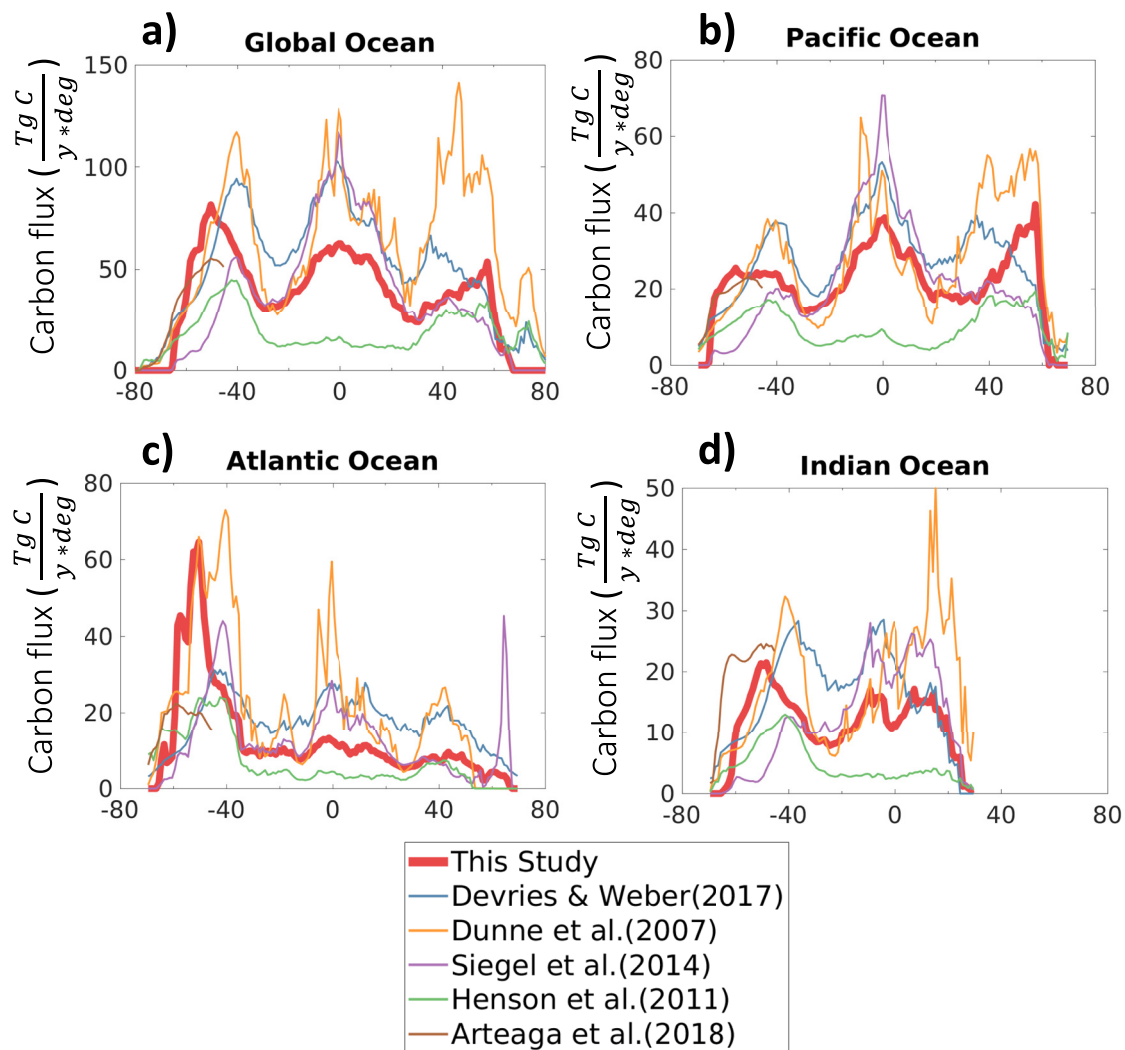


Figure 5. Zonally integrated annual mean export ($\text{Tg C y}^{-1} \text{ degree}^{-1}$) from the base of the euphotic zone for (a) the Global Ocean, (b) the Pacific Ocean, (c) the Atlantic Ocean, and (d) the Indian Ocean. Each color represents a different study, as shown by the legend (bottom).

Northern Pacific and Southern Atlantic Oceans are partly driven by large fluxes in the Bering Sea, the Sea of Okhotsk, and the Patagonian shelf. At lower latitudes, coastal upwelling systems sustain particularly high export in the northern Indian Ocean and the tropical to subtropical Atlantic.

Our reconstruction shows broad meridional patterns similar to previous estimates (Figure 5); however, significant regional-level discrepancies remain. For example, in the low latitudes, we predict somewhat less intense equatorial export peaks and subtropical lows, compared to the estimates of Dunne et al. (2007) and Siegel et al. (2014). In this respect, our reconstruction is more in line with that of DeVries and Weber (2017). In the northern Pacific, we broadly underestimate the transition zone as a persistent feature; however, seasonally, it is present (Figure S2 in Supporting Information S1). Overall, in the subpolar North Pacific, our estimate shows a northward shift of maximum export toward the continental margins that is comparable to the results of Dunne et al. (2007). This is likely caused by intensification of particle fluxes in coastal waters and marginal seas, which may be related to regional processes such as more efficient nutrient recycling in shallow regions or iron leakage from continental shelves (Nishioka et al., 2020) supporting large phytoplankton sizes. In the Atlantic Ocean, the gradual increase of export from northern to southern latitudes (mostly driven by high export near the coast) and the rapid increase in the Southern Ocean (caused by high export near the Patagonian shelf) are similar to the reconstruction of Henson et al. (2011), although the magnitude is larger. In the Indian Ocean, our reconstruction matches other studies at low latitudes; however, it shows a more dramatic increase in export toward the Southern Ocean sector (Section 3.2).

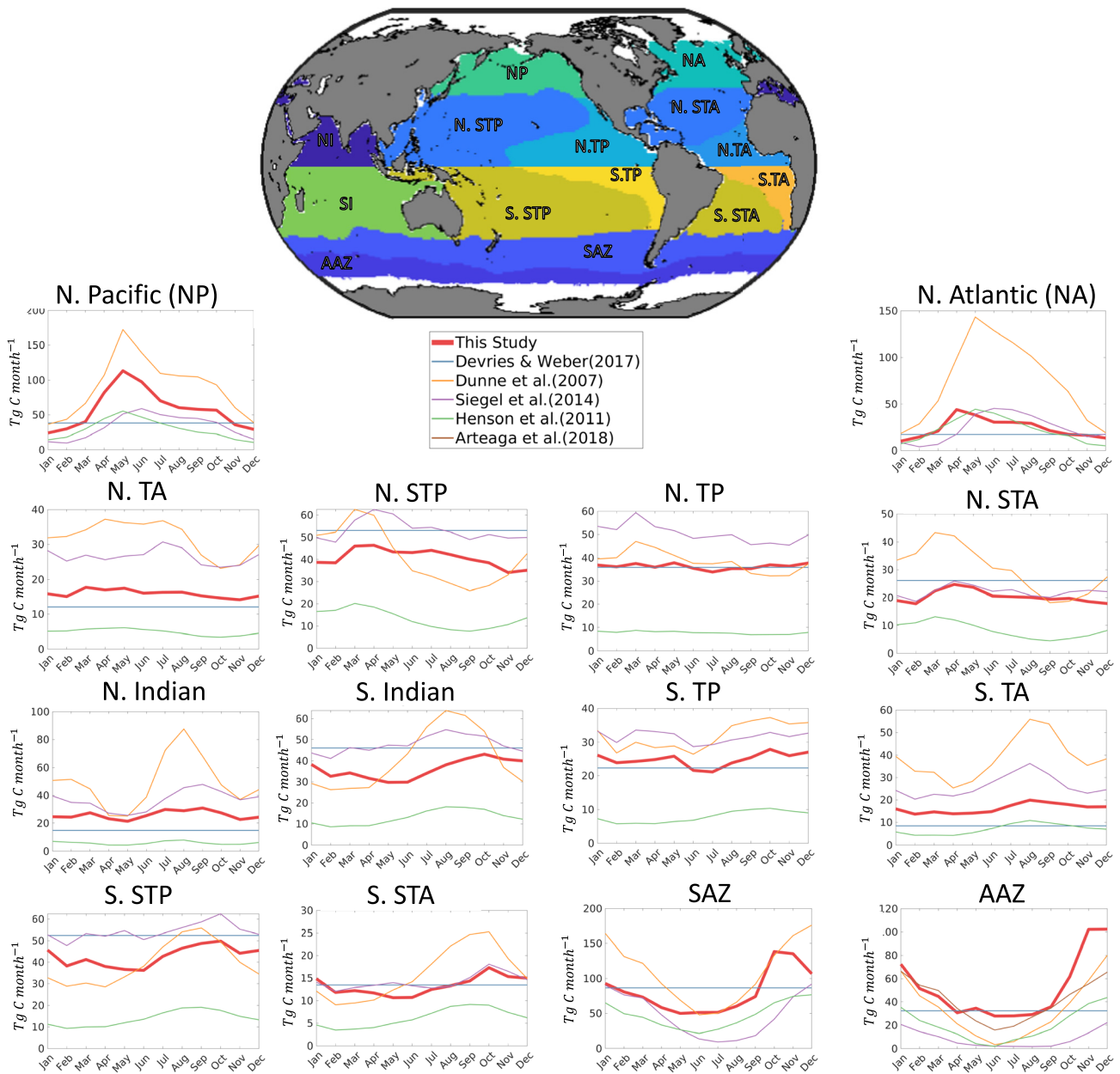


Figure 6. Annual seasonal cycle of particle flux from the euphotic zone ($Tg C y^{-1}$) for the regions specified in the map (top). Each line corresponds to a different estimate, as listed by the legend below the map. The same seasonal spatial mask was applied to each study. Note that the study by DeVries and Weber (2017) provides annual mean export fluxes, which are shown here as horizontal lines.

3.1.3. Seasonal Cycle

The seasonal cycle of particle export is comparable to previous studies, when averaged over large-scale coherent biomes (Figure 6). However, significant discrepancies are also revealed. In general, our seasonal cycle is more muted than previous work, suggesting weaker month-to-month variability in some regions, while other regions match previous reconstructions more closely. The most significant discrepancy is observed in the Southern Ocean, in particular in the Antarctic zone, where our reconstruction is substantially higher than previous estimates, with sustained export throughout winter months (Section 3.2).

The lower seasonality in our estimate is consistent with the reduced spatial gradients and suggests overall weaker variations in net community production and export than previously assumed. The machine learning approach used here relies on nonlinear relationships with multiple ocean variables to reconstruct global PSD, which may

accentuate compensatory relationships between different predictors. Surface chlorophyll, temperature, and net primary production have all been used in previous global reconstructions (Dunne et al., 2007; Henson et al., 2011; Siegel et al., 2014) but rarely together with additional variables that may be important in modulating spatial and seasonal patterns of export. It is also possible that our method somewhat underestimates variability compared to previous work. As previously noted, our PSD reconstructions reduce extremes in both BV and PSD slope (Clements et al., 2022), which may lead to underestimating variability in particle export fluxes derived from these quantities.

3.2. Southern Ocean Export

Export flux in the Antarctic zone of the Southern Ocean are larger in our estimate than other global reconstructions, especially during austral summer (Figure 6). We also find a southward shift in export, with a peak around 50S, rather than around 40S as in other estimates. A regional study based on 10 years of biogeochemical Argo measurements from 2006 to 2014, combined with satellite-based net primary production and export algorithms, similarly suggests higher than previously reported particle fluxes throughout the region (Arteaga et al., 2018), in better agreement with our results (Figure 7). This similarity is mostly evident in the open ocean and varies depending on the primary production algorithm chosen for the comparison. However, our estimate also suggests substantially higher export near landmasses, for example, South Georgia and the South Sandwich Islands and the Kerguelen Plateau. Although estimates from Arteaga et al. (2018) do not show the same high flux in austral winter through the end of the year as our reconstruction, they do demonstrate that export fluxes from the Antarctic zone of the Southern Ocean likely never decrease to the nearly negligible levels shown by other global estimates (Figure 6).

The discrepancy in export from the Antarctic zone relative to prior global estimates could arise from a combination of factors. Observations in the Southern Ocean, particularly in austral winter, are scarce. This is true for both the UVP5 measurements and the climatological predictors used to reconstruct PSD (Clements et al., 2022). The UVP5 data compilation (Kiko et al., 2022) includes two major cruises in the Southern Ocean, which only cover the months of March to May. Satellite-based reconstructions of chlorophyll and primary production from ocean color are on the other hand poorly resolved in austral wintertime. Other climatological variables, such as nutrients and oxygen, are also the results of interpolation of fewer in situ observations relative to the rest of the ocean. The scarcity of observations to train the machine learning model used for the PSD reconstructions results in significant uncertainty in predicted PSD and export fluxes in this region (Clements et al., 2022).

Our reconstruction reveals significant export primarily next to island masses. Proximity to Southern Ocean islands have been shown to increase productivity and carbon flux (Jouandet et al., 2014; Stemann, Eloire, et al., 2008), presumably via enhanced vertical mixing and iron fertilization from sedimentary sources in otherwise high-nutrient low-chlorophyll waters (Gaiero et al., 2003). It is possible that other methods of flux reconstructions (DeVries & Weber, 2017; Henson et al., 2011; Siegel et al., 2014) underestimate this increased export, in particular during winter, when observations are scarce. Expanding the number of in situ particle flux and UVP5 observations from the Antarctic zone, downstream of major land masses and over the entire seasonal cycle, could help shed light on the patterns of export and their variability in this undersampled region.

3.3. Mixed Layer Export

Globally integrated, export from the maximum annual mixed layer depth is $6.1 \pm 0.1 \text{ Pg C y}^{-1}$, that is, marginally larger than the global export from the euphotic zone. This estimate is lower than observational estimates of organic carbon export and annual net community production from the same depth horizon (Emerson, 2013), which would include additional export mechanisms.

Overall, export from the maximum annual mixed layer follows broad spatial patterns similar to the export from the euphotic zone (Figure 8a). The tropics and subtropics show larger mixed layer export fluxes (locally, up to a few times), while high latitudes show overall weaker values (Figure 8b). The low-latitude intensification of mixed layer fluxes is similar in all ocean basins and more than compensates for the reduction at high latitudes (Figure S8 in Supporting Information S1) thus producing an overall larger export from this horizon. Because of this low-latitude intensification, export from the mixed layer shows stronger gradients between the tropics and high latitudes. Gradients between the equatorial export peak and the subtropical export low are also intensified. Finally, export from the mixed layer in the Southern Ocean is substantially depressed compared to export from the euphotic zone. Similar to export from the euphotic zone, export from the mixed layer tends to be dominated by smaller particles (Figure S9 in Supporting Information S1).

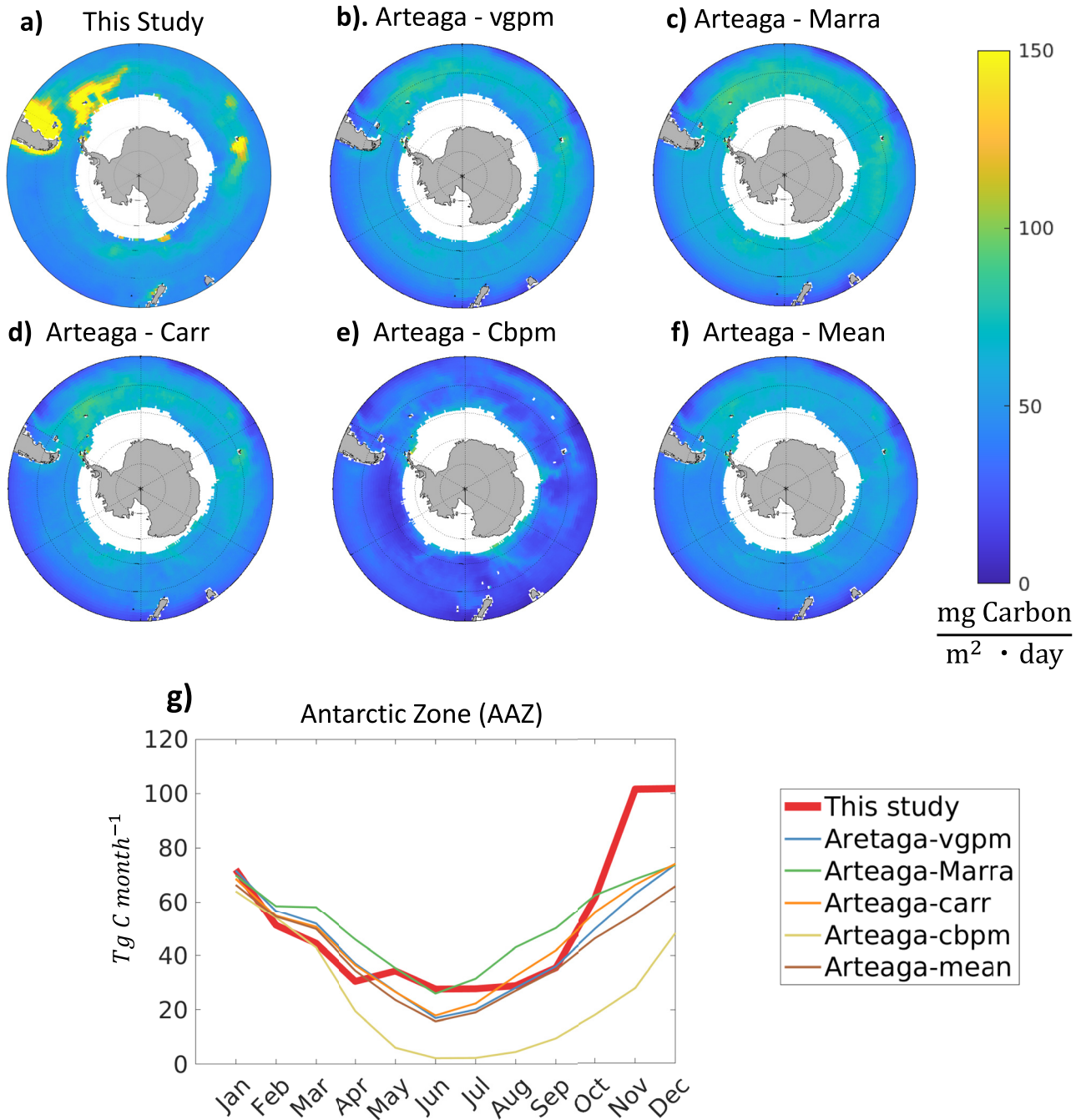


Figure 7. Southern Ocean particle export ($\text{mg C m}^{-2} \text{d}^{-1}$) for (a) this study, (b–e) different data-based estimates from Arteaga et al. (2018), and (f) the mean from that study. Each data-based estimate from Arteaga et al. (2018) uses a different net primary production algorithm to derive export. (g) Seasonal cycle of export for each estimate in the Antarctic zone (shown in Figure 6).

3.4. Drivers and Patterns of Differences in Export

We attribute differences between the export at the base of the mixed layer and euphotic zone (Figures 8a and 8b) to differences in depth between these horizons (Palevsky & Doney, 2018) (Figure 8c). The maximum mixed layer is on average shallower than the euphotic zone in the tropics and sub-tropics, and is deeper in the high latitudes (Figure 8c)—a pattern that is reflected by the differences in export shown in Figure 8b. These ratios suggest that shallower export horizons are characterized by higher fluxes than deeper export horizons, which we attribute to remineralization of particles in surface layers. Specifically, we identify three main latitudinal bands with different

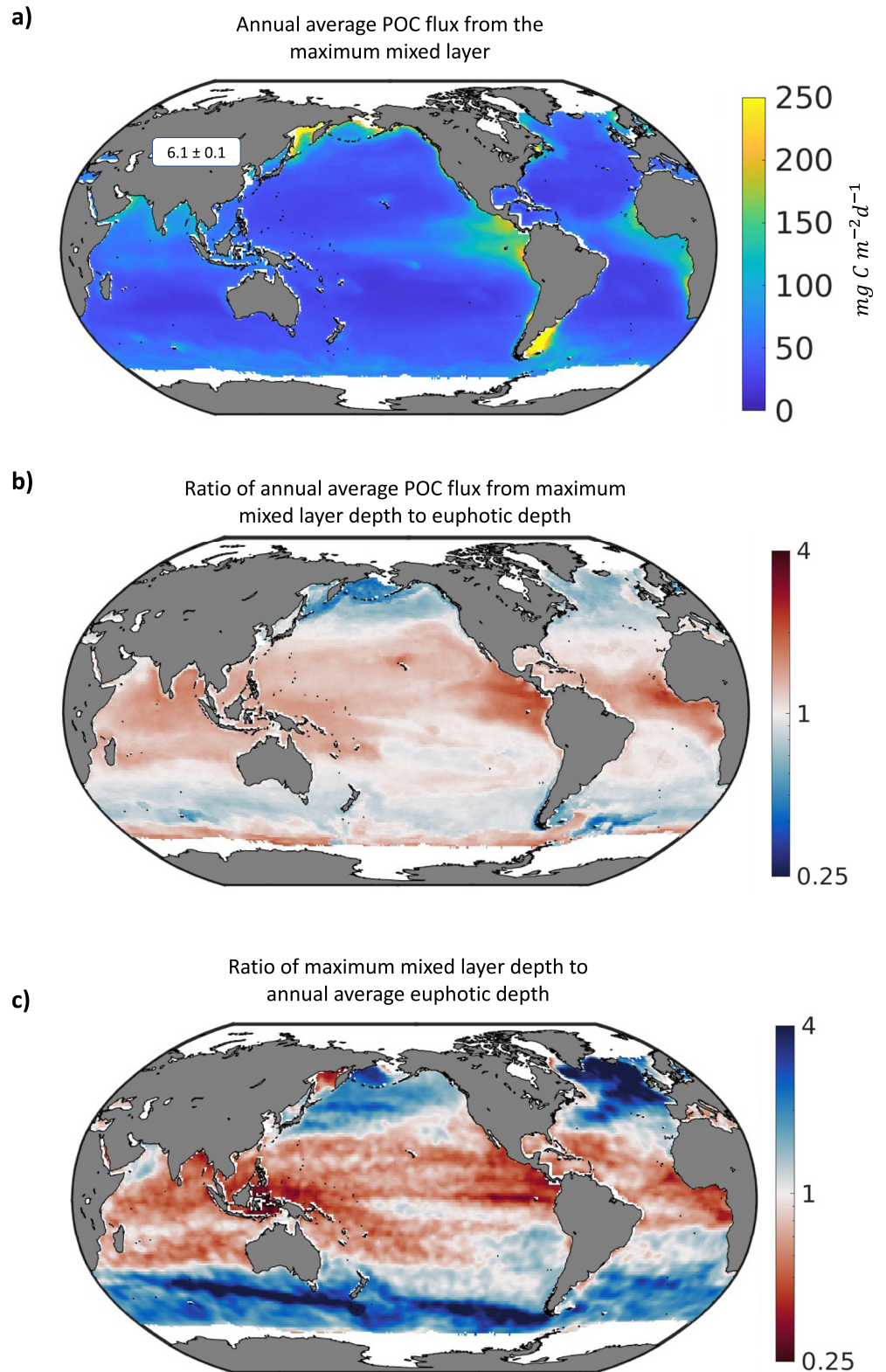


Figure 8. (a) Annual mean particle export ($\text{mg C m}^{-2} \text{d}^{-1}$) from the maximum mixed layer depth. Total export is 6.1 Pg C y^{-1} . (b) Ratio of the export from the maximum mixed layer depth to the export from the base of the euphotic zone. Red indicates regions with higher export from the mixed layer, relative to the euphotic zone. (c) Ratio of the annual mean euphotic zone depth to the maximum annual mixed layer depth. Red indicates regions where the euphotic zone is deeper than the maximum mixed layer.

horizon depth ratios and resulting export patterns, roughly corresponding to tropics and subtropics, midlatitudes, and subpolar regions.

Over most of the tropics and subtropics, the maximum annual mixed layer is shallower on average than the climatological euphotic zone (blue colors in Figure 8c). Here, particle remineralization between the maximum mixed layer and the euphotic zone depth likely reduces export from the latter horizon, suggesting net heterotrophy in the deeper layers of the euphotic zone, consistent with observations of shallow particle regeneration in the tropics (Pavia et al., 2019).

Over subpolar regions, the annual maximum mixed layer is deeper on average than the climatological euphotic zone. Thus, export fluxes reach maximum values within the euphotic zone, and decrease below it following typical flux attenuation profiles (Guidi et al., 2009; Martin et al., 1987). Finally, over most of the midlatitudes, the annual maximum mixed layer is deeper on average than the climatological euphotic zone. However, export fluxes from the mixed layer and euphotic zone are very similar in magnitude, suggesting a close seasonal compensation between enhanced euphotic zone fluxes when this horizon is found above the annual maximum mixed layer and reduced euphotic zone fluxes when it is found below it.

Ultimately, differences in export between the euphotic zone and the maximum mixed layer horizons are relevant when considering the role of the biological pump for carbon sequestration (Palevsky & Doney, 2018). Export below the maximum mixed layer removes carbon from contact with the atmosphere for timescales longer than 1 year. Our results suggest that, over most of the ocean, more carbon is sequestered below the maximum mixed layer than leaves the euphotic zone. We speculate that this reflects particle consumption by heterotrophs (microbes and zooplankton), which would reduce the abundance of organic particles in the lower euphotic zone, making it net heterotrophic rather than primarily autotrophic. The inferred strong heterotrophy at the base of the mixed layer is consistent with earlier studies proposing flux feeding and particle fragmentation by zooplankton followed by bacterial remineralization in the upper layers as important processes (Jackson & Checkley, 2011; Stemann et al., 2004). This hypothesis could be further investigated with the expected massive profiling of the water column provided by future observation with the new UVP6 (Picheral et al., 2022). While deep chlorophyll maxima may be important at these depths, recent analysis suggests that the deepest maxima are the result of photo adaptation and high chlorophyll to carbon ratios of phytoplankton, rather than increased biomass and primary production (Cornec et al., 2021). More work is needed to better understand the variability of particle production and remineralization throughout the euphotic zone and better constrain models (Palevsky & Doney, 2018).

4. Caveats to Our Approach

Our method relies on global PSD reconstructions from UVP5 observations, as well as in situ particle flux measurements, both of which are spatially and temporally limited. This in turn reduces the ability of our approach to obtain an accurate climatological picture of PSD and fluxes and extrapolate local observations to larger regions and other times of the year. In particular, about 43% of monthly particle flux observations contain only one data point, and entire ocean basins are represented by a handful of measurements (Figure 2b). While more widely distributed than flux measurements, UVP5 observations are also characterized by large gaps in space and time (Kiko et al., 2022). Additionally, current optical methods used to determine particle sizes and abundances still suffer from limitations (Giering et al., 2020).

As previously discussed (Clements et al., 2022), regional correlations between environmental properties and PSD observations from UVP5 may not be well captured by extrapolation with a machine learning algorithm trained on data from different regions, especially when nonlinear relationships between variables become important. Similarly, our reconstructions rely on the assumption that PSD can be well approximated by power law distributions. Analysis of UVP5 data suggests that this assumption is generally valid in the open ocean (Clements et al., 2022), although locally it may be flawed and other distributions may be more accurate (Reynolds & Stramski, 2021). For example, Bisson et al. (2022) suggest that UVP5 observations may be better approximated by a truncated power law across a broader size range than considered here. The conversion of PSD to export flux encapsulated by Equations 1 and 5 also suffers from limitations. Converting standing stocks of particles from UVP5 observations to sinking carbon flux using size-dependent relationships assumes that (a) all particles of a given size have the same carbon content and (b) they all sink at a similar speed proportional to their size. Known biases exist with both assumptions. For example, densely packed fecal pellets often contain more carbon and sink faster than

heterogeneous aggregates and marine snow of the same size (A. Allredge, 1998). Biogenic and lithogenic minerals could alter these relationships on a regional basis, for example, near continental margins, where lithogenic particles are generally more abundant (Reynolds et al., 2010; Trudnowska et al., 2020). Furthermore, we assume globally uniform relationships between particle size, sinking speed, and carbon content. However, these relationships remain highly uncertain (A. Allredge, 1998; Cael et al., 2021; Stemmann & Boss, 2012; Stemmann, Eloire, et al., 2008) and are likely to depend on region and time of the year, reflecting variable particle characteristics and underlying oceanographic and ecological processes.

Our approach, which optimizes carbon content and sinking velocity parameters against in situ particle fluxes, reduces to some extent the effect of these uncertainties. More work combining in situ and optical measurements should focus on constraining these quantities and their regional and temporal variability. Future studies could also improve our approach by distinguishing living and nonliving particles, as well as particle type and composition, for example, by analysis of UVP5 images or other optical methods in conjunction with in situ particle samples (Trudnowska et al., 2021).

Errors in observed and gridded particle fluxes, which are notoriously difficult to measure, are likely to introduce additional uncertainty in our estimates. These observations are still sparse, which may cause biases on our optimization against data. We attempt to alleviate some of these errors by using a Monte Carlo approach in the flux optimization, while adding a random perturbation to observed fluxes. Use of climatological averages may further smooth the real variability of observations. Additionally, these flux observations are corrected to the euphotic zone depth, which can lead to biases upward of 60% (Bisson et al., 2018). In fact, extrapolating carbon fluxes by distances greater than 30 m in the vertical direction using a Martin curve (Martin et al., 1987) can lead to significant errors (Cael & Bisson, 2018; Cael et al., 2021).

5. Conclusions and Future Work

We provide a new, data-constrained estimate of particle export fluxes by combining global reconstructions of PSD from UVP5 observations and in situ export flux measurements. Our estimate of particle export captures regional and seasonal variability in fluxes and allows reconstruction of export fluxes from spatially variable euphotic zone and mixed layer depths, highlighting the importance of the choice of export horizon (Palevsky & Doney, 2018).

We obtain a global particle export flux of $5.8 \pm 0.1 \text{ Pg C y}^{-1}$ from the euphotic zone, in line with previous work, although with regional and temporal differences. Our results suggest weaker spatial and seasonal variability compared to previous studies, in particular in the open ocean, and highlight the importance of coastal waters and marginal seas for export at high latitudes. Results from the Southern Ocean suggest that processes that sustain elevated fluxes, in particular in wintertime and early austral summer, may not be completely captured by other global reconstructions and that waters downstream of coasts and islands may harbor a significant source of carbon export to the deep ocean, which is only partially captured in one other reconstruction (Dunne et al., 2007).

We illustrate the ability of our method to obtain particulate organic carbon fluxes at multiple depth by reconstructing and comparing carbon export from the euphotic zone and the annual maximum mixed layer depth. Export from the mixed layer is overall stronger than export from the euphotic zone in low and midlatitudes, and weaker in high latitudes, driving a marginally larger flux of $6.1 \pm 0.1 \text{ Pg C y}^{-1}$. Differences between euphotic zone and mixed layer export are only partially consistent with results from large scale models (Palevsky & Doney, 2018) and suggest important organic matter remineralization in the deeper parts of the euphotic zone. Three-dimensional reconstructions of particle fluxes would allow a closer investigation of the processes controlling export changes with depth and their implications for particle transfer efficiency and carbon sequestration.

Our results highlight the relative importance of particle abundance and size structure in driving export. Total particle BV and the PSD slope are correlated in such a way to act synergistically on particle fluxes (Clements et al., 2022). Consistently, higher fluxes are reconstructed in regions with larger particle BV and “flatter” slopes. We also suggest distinct deviations from these patterns, for example, in the tropical and northern subtropical Pacific Ocean, where high abundance of all particles, rather than dominance of large relative to small particles, appears to drive elevated export. We further highlight the importance of the PSD by comparing export for small and large particles (here separated at a cutoff size of $418 \mu\text{m}$), showing that while small particles ($35\text{--}418 \mu\text{m}$

range) overall dominate export, large particles (418 μm –5 mm range) become proportionally more important in high latitudes and tropical regions, where they can account to up to 60% of export fluxes.

We identify sources of uncertainty and limitations that should be addressed in future work. There remain areas of the ocean and times of the year with limited UVP5 observations and, critically, in situ flux measurements, driving uncertainty in both the PSD and flux reconstructions. As UVP5 observations increase in number, our analysis can be refined, for example, by expanding comparison with in situ sediment trap and thorium-based particle flux observations (Mouw et al., 2016). New machine learning approaches should aim at better capturing fluxes at the high and low end of their range, reducing current biases (Clements et al., 2022). Furthermore, better constraints should be placed on particle carbon content and sinking speed parameters, reflecting regional variability and particle types.

The three-dimensional nature of UVP5 observations paves the way for fully three-dimensional reconstructions of particle export fluxes in the ocean interior. This will greatly benefit from particle flux compilations that span the full depth of the ocean (Mouw et al., 2016) and that harmonize discrepancies between different flux measurement methods (Bisson et al., 2018). Ongoing deployments of UVP instruments, including on Argo floats, will rapidly increase the number of PSD observations with high vertical resolution (Picheral et al., 2022). In turn, three-dimensional reconstructions of export will enable a better characterization of the ocean's ability to sequester carbon (Boyd et al., 2019) and, in combination with models (DeVries & Weber, 2017; Siegel et al., 2014), a better understanding of the processes behind the ocean's biological pump (Siegel et al., 2022), including disaggregation (Briggs et al., 2020), diel vertical migrations (Bianchi et al., 2013), and transport by ocean currents.

Data Availability Statement

Data generated by this work can be found on the Biological and Chemical Oceanography Data Management Office (BCO-DMO), <https://doi.org/10.26008/1912/bco-dmo.856942.2>.

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