



The role of biologically-mediated fragmentation in carbon flux attenuation in a 1-D mechanistic particle model

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Abstract. The efficiency of particulate organic carbon (POC) transport through the water column is the foundation of the biological carbon pump's capability to sequester atmospheric CO₂ into the ocean interior over prolonged timescales. However, constraining the magnitude and composition of POC flux reaching ~ 1 km depth remains challenging, due to diverse biotic and abiotic processes that alter particle morphology, composition and sinking speed. Recent studies have highlighted biologically-mediated fragmentation, which breaks up particles into smaller, slower-sinking POC, as a potential primary driver for POC flux attenuation in the mesopelagic zone. Here, we use a vertical mechanistic particle model, based on the SISSOMA mixed-layer model, to assess the role of biologically-mediated fragmentation on diverse aggregates and POC flux attenuation. Our model resolves a spectrum of particles across size and density, incorporating a representation for particle associated copepods as key agents of fragmentation below the mixed layer. Sensitivity experiments show fragmentation is critical to reproducing the observed initial decrease in particle size with depth. Fragmentation is shown to have a greater contribution to POC flux loss when export is increased and is composed of relatively larger particles, suggesting it is likely to be a more significant process for flux attenuation in more productive regions. We also demonstrate that the initial slope of particle size distribution at the export depth significantly influences the extent to which transformation processes affect particle size profiles and flux attenuation. While our results highlight the necessity of including fragmentation in biological pump models, fragmentation alone cannot fully account for observed profiles in particle size structure and transfer efficiency. We propose that additional sources of POC (e.g., fecal pellets) and transformation processes (e.g., differential remineralisation, ballasting) likely contribute to the discrepancies between our model and observations. Our results highlight the importance of explicitly representing fragmentation and particle diversity in biological pump models to improve mechanistic understanding and predictions of ocean carbon sequestration.

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1 Introduction

The biological carbon pump (BCP) encapsulates crucial mechanisms within the ocean by which particulate (and dissolved) organic carbon (POC), produced from net primary production (NPP) in surface waters, is transported into the ocean interior. This process effectively sequesters carbon away from the atmosphere, acting as a major sink of atmospheric CO₂; without the BCP, atmospheric CO₂ concentrations would be 160 – 200 ppm greater than pre-industrial concentrations (Parekh et al., 2006; Tjiputra et al., 2025; Wilson et al., 2022). The magnitude

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of export flux (POC leaving the mixed layer) and sequestration flux (POC reaching the base of the mesopelagic zone) is regulated by a complex interplay of spatially and temporally variable abiotic and biotic processes, ultimately shaping the efficiency of carbon sequestration (Iversen, 2023). As a result of the diverse pathways and timescales that POC can follow as it travels through the water column (Boyd et al., 2019), quantifying the BCP remains challenging. Considerable uncertainty remains in its magnitude and efficiency, for example global export flux estimates range from $\sim 4\text{--}12 \text{ Pg C yr}^{-1}$ (Devries and Weber, 2017; Henson et al., 2011; Dunne et al., 2005), while transfer efficiency (T_{eff} ; ratio of export flux to flux at 1000 m) spatially and temporally ranges between 5–35% (De Melo Virissimo et al., 2024; Lima et al., 2014). Among BCP pathways, the “gravitational” pump, where POC sinks according to its size and density, is often considered dominant, accounting for $\sim 70\%$ of global carbon export based on in situ and satellite observations (Le Moigne, 2019).

The individual particles that contribute to sinking POC flux are subject to various transformations that can either accelerate or decelerate their sinking velocities by altering their mass and morphology. Processes that accelerate sinking velocities include aggregation (Jackson and Burd, 2015) and ballasting (Iversen and Robert, 2015), while processes that decelerate sinking include disaggregation (Lam and Marchal, 2015), fragmentation and ingestion (Briggs et al., 2020; Mayor et al., 2020) and microbial degradation, which can remove POC mass entirely (Turner, 2015). The relative dominance of these transformations, both spatially and temporally, ultimately determines the magnitude and efficiency of POC flux.

Fragmentation breaks up marine snow into smaller, slower-sinking particles and in the mesopelagic it is typically driven by zooplankton activity (Mayor et al., 2014; Mayor et al., 2020) and “sloppy” zooplankton feeding and repackaging (Burd and Jackson, 2009; Goldthwait et al., 2004). Using optical backscattering data, Briggs et al. (2020) found that $\sim 50\%$ of large-particle loss in the mesopelagic could be attributed to fragmentation, with this effect diminishing at greater depths, consistent with a major role of zooplankton grazing on particles. *In situ* measurements suggest microbial degradation accounts for only 7–29% of POC flux attenuation (Bressac et al., 2024), with the remainder likely linked again to zooplankton activity. Additionally, modelling by Mayor et al. (2020), which identified particle-associated copepods (PAC) as the “principle agents” of fragmentation, predicted that these copepods are responsible for $\sim 81\%$ of fast-sinking detritus attenuation at the Porcupine Abyssal Plain (North Atlantic Ocean). Despite these recent findings, fragmentation is largely neglected in global biogeochemical models used for climate predictions, with only one CMIP6 model currently explicitly including this process (Henson et al., 2022).

Recent advances in observational techniques have significantly enhanced our ability to quantify the composition and magnitude of POC flux globally, particularly with respect to particle size distributions (PSD). Sensors such as the lab-based high-resolution FlowCam (Bach et al., 2016) and the *in situ* Underwater Vision Profiler (UVP) have allowed detailed investigations into the size structure of POC flux and its temporal and spatial variability (Picheral et al., 2022). For example, Clements et al. (2022) applied machine learning to a UVP dataset from Kiko et al. (2022) and revealed large regional and seasonal variations in PSD slopes, with a global average of ~ 4 (ranging from ~ 2 to 5). Higher absolute slope values correspond to a greater relative abundance of small versus large particles. Optical backscattering, routinely measured by BGC-Argo floats, can also provide proxy estimates of flux and particle size (Briggs, 2026). Whilst the spatial and temporal coverage of such datasets continues to expand, driven in part by the deployment of BGC-Argo floats equipped with optical sensors like



the UVP (Bittig et al., 2019), they remain globally sparse. Additionally, these observational techniques do not directly quantify the underlying particle transformation processes (e.g. fragmentation). This limitation leaves open important questions on what impact flux composition (both in terms of size structure and magnitude) has on its fate in the mesopelagic, and ultimately on the efficiency of the BCP.

In this study, we develop a novel mechanistic particle model to examine the impact of individual particle transformation processes on the attenuation of POC flux within the mesopelagic zone. Our 1-D vertical model builds on the SISSOMA mixed layer model (Kandylas and Visser, 2026), and resolves aggregate particle dynamics (fragmentation, remineralisation and sinking) across 30 size and 10 excess density (the difference between aggregate and seawater density) classes, by extending it into the mesopelagic. In addition, to simulate biological fragmentation, we incorporate a modified version of the particle-associated copepod (PAC) model developed by Mayor et al. (2020). In this approach, PAC intercept sinking POC and redistribute mass into smaller size classes via fragmentation. We present a series of sensitivity experiments to explore the effects of fragmentation and remineralisation, as well as the magnitude of initial POC flux and its associated particle size distribution at the export depth.

2 Methodology

2.1 Model description

We used the mechanistic marine aggregate particle model SISSOMA (v1), developed for the mixed layer as per Kandylas and Visser (2026), and extended it into a vertical 1-D framework for tracking the composition and transformations of sinking material through the mesopelagic zone. Our model builds upon SISSOMA's representation of aggregate properties and dynamics, which characterises a 10 x 30 state space of excess density and size, respectively (Kandylas and Visser, 2026). This structure allows for mechanistic estimates of aggregate sinking speeds and other characteristics that govern particle transformation processes, such as fragmentation and remineralisation. It also enables a flexible framework for representing diverse sinking material types with contrasting physical properties, spanning densely packed to loosely bound “fluffy” aggregates.

Whilst the original SISSOMA model describes particle transformations within the mixed layer, the dominant drivers of particle fate shift at greater depths due to changes in physical conditions and biological interactions. For instance, in SISSOMA.v1, aggregation and fragmentation are primarily driven by turbulence, a factor that generally becomes negligible below the mixed layer (Takeuchi et al., 2019). To account for these changes, our model reformulates the diagnostic equation for particulate organic carbon (POC) for a given particle of size class i and density class j as:

$$\frac{dPOC_{i,j}}{dt} = -\lambda \cdot POC_{i,j} - w_{i,j} \cdot \frac{dPOC_{i,j}}{dz} \pm Frag_{Net,i,j} \quad (1)$$

where λ is the remineralisation rate, set as constant across all particle size and density classes (0.01 day^{-1}), $w_{i,j}$ is the sinking speed of the particle size class i and density class j (m day^{-1}) and z is depth below the mixed layer (m). Sinking speed is determined by excess density and size according to a modified Stoke's law (Kandylas and Visser, 2026). $Frag_{net,i,j}$ refers to the net mass change of the particle class, accounting for both mass gain from



the fragmentation of larger particles and mass loss into smaller size classes and from zooplankton ingestion (Eqn. 4).

115 In our model, fragmentation is mediated by particle-associated copepods (PAC), identified as the primary agents of detrital breakdown in the mesopelagic (Mayor et al., 2020). The model configuration and parameter values are adapted from Mayor et al. (2020), where PAC preferentially ingest and fragment detritus (POC in our model) based on particle sinking speed, increasing with slower-sinking particles. Accordingly, we determine the mass loss from size class i due to PAC fragmentation ($Frag_{i,j}$) as:

$$120 \quad Frag_{i,j} = (1 - \psi) \cdot g_{PAC} \cdot PAC_z \quad (2)$$

where ψ is the fraction of ingested POC (i.e. the ingested mass for a size class is identical to Equation 2, except ψ replaces $1 - \psi$), g_{PAC} is the PAC feeding rate (0.35 day^{-1}) and PAC_z is the PAC biomass at a given depth (mmol C m^{-3}). In our model, ψ_i is prescribed as a single average value (0.3), while PAC_z is dynamically linked to the available POC concentration (see supplementary material for more details; Fig. S9-11). Specifically, PAC_z is set as a fixed ratio of the local POC concentration, set to a ratio $\sigma = 0.1$, akin to outputs from Mayor et al. (2020). Implementing a fully dynamic PAC model, including growth, mortality and trophic interactions, would require introducing a zooplankton functional type, substantially increasing model complexity and computational cost. The feeding rate g_{PAC} depends on the maximum feeding rate g_{max} (day^{-1}), the total POC biomass across all size classes (POC_T) and the total feeding intake (γ^{POC}), which follows a Holling III functional response (Eq. 3) with a half-saturation feeding constant of $0.1325 \text{ mmol C m}^{-3}$ (Mayor et al., 2020).

$$130 \quad g_{PAC} = g_{max} \cdot \frac{POC_{Lj}}{POC_T} \cdot \gamma^{POC} \quad (3)$$

$$Frag_{Net,i} = \left(\sum_{i+1}^{i_{end}} Frag_i \right) - Frag_i \quad (4)$$

The redistribution of fragmented POC from size class i into smaller size classes ($Frag_i$) follows the logarithmic approach described by Kandylas and Visser (2026). In this approach, the $(i - 1)$ size class receives the largest proportion of $Frag_i$, with progressively smaller proportions allocated to successively smaller size classes. The smallest size class ($i = 1$) does not experience fragmentation and loses mass only through PAC ingestion and remineralisation. Sensitivity tests demonstrate that adopting a logarithmic redistribution has minimal impact on model outcomes compared to a random redistribution of $Frag_i$ (see Supplementary Material; Fig. S11). This finding is consistent with laboratory observations, which suggest no systematic copepod behavior during aggregate breakup (Toullec et al., 2019).

We configured the model to represent particle sizes ranging from 1 to 1000 μm in radius, corresponding to sinking speeds of $\sim 0.1 - 200 \text{ m day}^{-1}$. The maximum density (1300 kg m^{-3} ; minimum is 1000 kg m^{-3}) is higher than that used in the SISSOMA.v1 model, which primarily considers production material that predominantly remains in the mixed layer, but is still within observational range (Lombard et al., 2013a). Model runs are forced with an initial particle flux that ranges from $10^0 - 10^8 \text{ particles m}^{-3} \text{ day}^{-1}$, akin to Estapa et al. (2021), for a given size class that is determined by the initial particle size distribution (PSD; Table 1). For example, a PSD slope of 4 implies that particles within the 1–10 μm range are 10^4 times more abundant than those within the 10–100 μm range.



We performed ten simulations, 8 with constant initial export fluxes, and 2 with seasonal initial export fluxes (Table 1). Runs are named according to the transformations included (remineralisation and/or fragmentation, or neither), with runs featuring a non-zero PSD slope prefixed with "s". Seasonal runs (sSEAS and fSEAS) prescribe PSD slope and initial total particle flux as cosine oscillations, consistent with machine-learning driven observations by Clements et al. (2022). Output from the sSEAS experiment is included in the supplementary material (Fig. S15). All runs are run to steady state (10 years), with results presented from the final year.

Table 1: Summary of model simulations presented in this study. Simulations differ in initial export flux configuration (initial particle flux, particle size distribution (PSD) slope, and seasonality) and in the inclusion (tick) or exclusion (cross) of particle transformation processes (remineralisation and fragmentation).

Run	Cycle	PSD slope of initial flux	Initial particle flux (particles m ⁻² day ⁻¹)	Remineralisation	Fragmentation
NONE	Uniform	0	10 ⁹	×	×
REMIN	Uniform	0	10 ⁹	✓	×
FRAG	Uniform	0	10 ⁹	×	✓
FRAG+REMIN	Uniform	0	10 ⁹	✓	✓
s2,3,4NONE	Uniform	2,3,4	10 ⁹	×	×
s2,3,4REMIN	Uniform	2,3,4	10 ⁹	✓	×
s2,3,4FRAG	Uniform	2,3,4	10 ⁹	×	✓
s2,3,4FRAG+REMIN	Uniform	2,3,4	10 ⁹	✓	✓
fSEAS	Seasonal	2	[10 ⁸ -10 ¹⁰]	✓	✓
sSEAS	Seasonal	[2 – 4]	10 ⁹	✓	✓

2.2 Observations

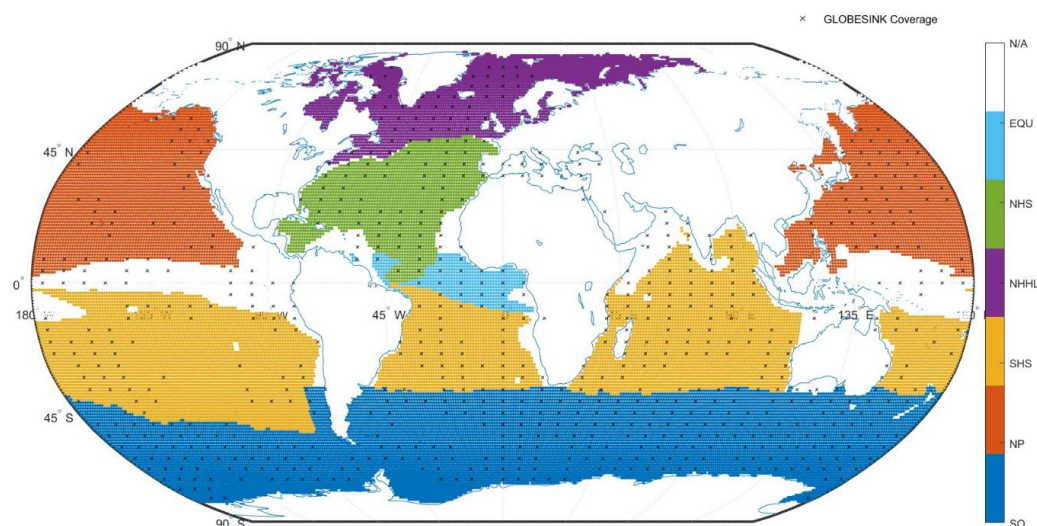
We compared our model results with mean particle diameter estimated from optical backscattering (GLOBESINK dataset; Fig. 1) measured by BGC-Argo floats (Briggs, 2026). The dataset is gridded at 4° latitude x 8° longitude resolution and aggregated monthly. Depth intervals increase from 10–975 m to minimise instrument noise, which increases at greater depths due to platform effects. To further reduce noise, only mean diameter estimates made from > 100 observations are included in the data assimilation. Mean particle size estimates (Fig. 2 and 3) are weighted by cross-sectional area and expressed as equivalent spherical diameter (ESD) as per Briggs et al. (2013). Only estimates within the 1–800 µm size range for GLOBESINK are plotted, with modelled averages matching this range, to avoid potentially skewed spikes in the data due to zooplankton interference as they may be attracted to the backscattering sensor's lights. Another consideration is the likely refractory background of small particles, which may skew average size calculations, especially at low POC concentrations (Briggs et al., 2020). Further description of the quality control and data within the GLOBESINK product are outlined in Briggs (2026).



For large-scale comparison, GLOBESINK output was first separated into Fay and McKinley (2014)'s 17 core biomes and subsequently combined into six superbiomes based on similarity of ESD depth profiles and regional-
 175 regional-ity (see Fig. 1 and Fig. S1-7), akin to Carroll et al. (2022). The North Pacific Ice biome (NP ICE) is not covered by the GLOBESINK dataset, therefore excluded. Data from the East and West Pacific Equatorial biomes (Pac EQU E and W) did not meet the observation threshold (> 1000 profiles) and were also excluded.

Further comparisons are made using the UVP5 dataset from Kiko et al. (2022) in Fig. S8 which presents depth profiles of the large-to-small particle ratio (Λ_{LS}). The Kiko et al. (2022) dataset provides a comprehensive
 180 overview of particle distributions regionally, spatially and temporally, enabling extraction of key size-related trends. We classed particle concentration fractions of size classes > 0.512 mm as large particles, with an upper bound of 2.58 mm to align with our model's size class range. The large-to-small particle ratio was then averaged across the superbiomes.

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**Figure 1: Global coverage of the GLOBESINK optical backscattering dataset, with pixels containing vertical profiles indicated by 'x'. These observations are overlain onto superbiomes derived from the Fay and McKinley (2014) biomes, with some excluded due to lack of coverage or insufficient observational
 190 points. The superbiomes are categorised as the North and Southern Hemisphere Subtropics (NHS - green and SHS - yellow), North Pacific (NP - orange), Northern Hemisphere High Latitudes (NHHL - purple), Equatorial (EQU - light blue) and Southern Ocean (SO - dark blue).**



195 3 Results

3.1 Regional and seasonal variations in particle size in observations

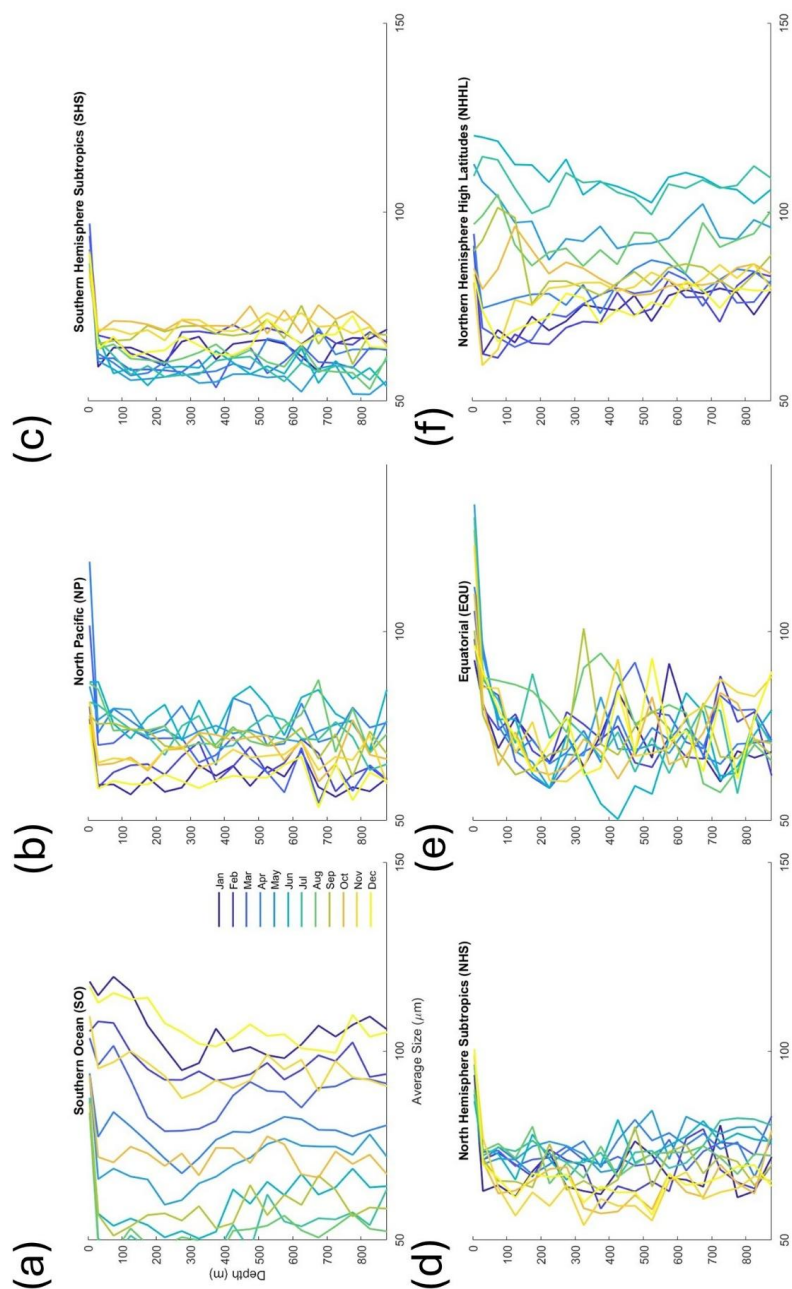




Figure 2: Monthly cross-sectional area-weighted equivalent spherical diameter (ESD, μm) from the GLOBESINK optical backscattering dataset for particles in the $\sim 1\text{-}800\ \mu\text{m}$ size range. Size profiles are shown for each superbiome (described in Fig. 1).

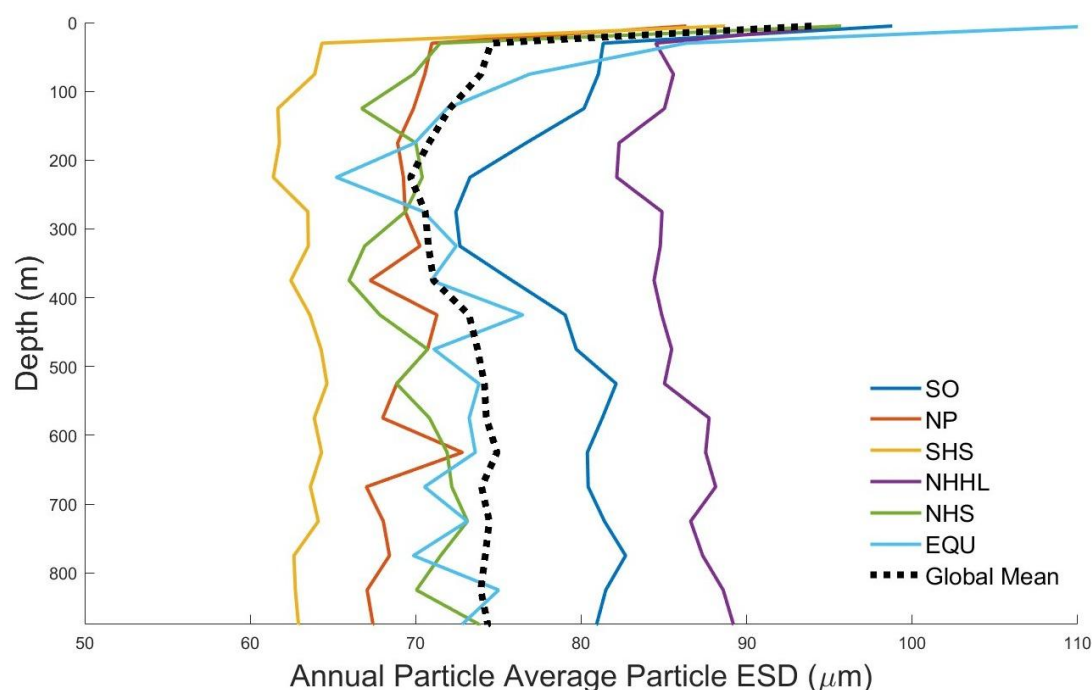


Figure 3: Annual average cross-sectional area-weighted equivalent spherical diameter (ESD; μm) of particles from the GLOBESINK optical backscattering dataset for a size range of $\sim 1\text{-}800\ \mu\text{m}$. Size profiles are given for the different superbiomes (see Fig. 1) and the global mean (black dashed line). North and Southern Hemisphere Subtropics (NHS - green and SHS - yellow), North Pacific (NP - orange), Northern Hemisphere High Latitudes (NHHL - purple), Equatorial (EQU - light blue) and Southern Ocean (SO - dark blue).

We compare our particle model outputs with particle size profiles derived from the GLOBESINK dataset, which utilises BGC-Argo optical backscattering to characterise average particle size globally (Briggs et al., 2013). This dataset shows clear spatial and seasonal variability (Fig. 2 and 3) across six observationally-defined superbiomes (Fig. 1). Across all superbiomes, the average equivalent spherical diameter (ESD) of particles peaks within the surface of the ocean, likely within the mixed layer. Average ESD in the surface ranges from ~ 80 to $140\ \mu\text{m}$ and decreases with depth to $\sim 900\ \text{m}$ to $\sim 55\text{--}110\ \mu\text{m}$ (Fig. 2). In most cases, particle ESD declines within the upper $\sim 400\ \text{m}$ before stabilising in deeper waters. Superbiomes such as North and Southern Hemisphere Subtropics (NHS and SHS), North Pacific (NP) and the Equatorial (EQU) exhibit relatively minimal absolute seasonal variations, with maximum monthly variations in average ESD at any given depth of $\sim \pm 20\ \mu\text{m}$ ($\sim \pm 30\%$; Fig. 2). Conversely, superbiomes like the Northern Hemisphere High Latitudes (NHHL) and Southern Ocean (EQU) present significantly greater absolute seasonality, with monthly absolute ESD changes of $30\text{-}50\ \mu\text{m}$ ($\sim \pm 50\%$). Whilst most superbiomes exhibit ESD at $100\ \text{m}$ of $\sim 60\text{-}80\ \mu\text{m}$, the NHHL and



SO stand out with higher ESD averaging $\sim 80 \mu\text{m}$ at the MLD. Below 400 m, all superbioomes show annual average particle ESD staying fairly constant with depth and with a global mean particle ESD maximum of $\sim 90 \mu\text{m}$ near the surface, which decreases to a deep water baseline of $\sim 75 \mu\text{m}$ (17% decrease; Fig. 3). However, many superbioomes present seasonal ESD fluctuations between $\sim 400 - 900 \text{ m}$ depth, ranging $\sim 10 \mu\text{m}$ around the baseline. The SO biome exhibits the most prominent deep water (500 m) increase from subsurface minima (~ 75 to $81 \mu\text{m}$). Overall, these observations highlight a consistent pattern of decreasing average particle size in the upper half of the ocean on the global scale, with a stabilisation or marginal increase in deeper waters.

3.2 Disentangling the effects of remineralisation and fragmentation on vertical particle size distribution and flux attenuation

The particle size distribution (PSD) of POC provides key information on particle dynamics, as size strongly influences ecological and biogeochemical interactions (Stemmann and Boss, 2012). The PSD is typically quantified by its slope, which refers to the relative abundance of smaller versus larger particles on a logarithmic scale. Greater absolute slope values correspond to a higher relative abundance of small versus large particles.

We applied our vertical particle model to investigate the potential impact of various transformations on particle size and associated POC flux with depth through a series of sensitivity experiments (Table 1). We first examine the coupled dynamics of PAC-driven fragmentation, sinking and microbial remineralisation under a uniform initial particle size distribution of exported POC (i.e., a PSD slope of 0, where all size classes start with equal particle flux). This prescribed initial condition allows us to disentangle the effects of fragmentation and remineralisation on the average particle size and vertical flux profiles. Expectedly, an initial slope of 0 produces larger average particles sizes throughout the water column (Fig. 4b) than those observed in the GLOBESINK dataset (Fig. 3), where smaller particles typically dominate (characterised by a PSD initial slope of 2-4 akin to Clements et al. (2022)). When neither remineralisation nor fragmentation are enabled (NONE experiment; Fig. 4b), unlike in the observations, the model predicts a gradual, yet modest increase in particle size with depth from $\sim 200 \mu\text{m}$ at the base of the mixed layer to $\sim 220 \mu\text{m}$ at 1000 m (a 10% increase). This increase arises from differential sinking speeds, where larger particles sink faster, leading to a higher average ESD at depths (Fig. 4b). Interestingly, introducing remineralisation alone (REMIN experiment) amplified this depth-dependent increase, with ESD rising from $\sim 200 \mu\text{m}$ at the MLD to $\sim 270 \mu\text{m}$ at 1000 m, (a 35% increase). This trend results from the uniform remineralisation mass removal rate (0.01 day^{-1}) applied across all size classes. Faster (and larger) sinking particles experience less remineralisation per meter than their slower (and smaller) counterparts at a given constant rate. These size trends in the NONE and REMIN experiments contrast sharply with both GLOBESINK and UVP observations, which show initial decreasing particle size with depth. This discrepancy highlights the need for incorporating additional transformations to reproduce observed vertical particle size patterns.



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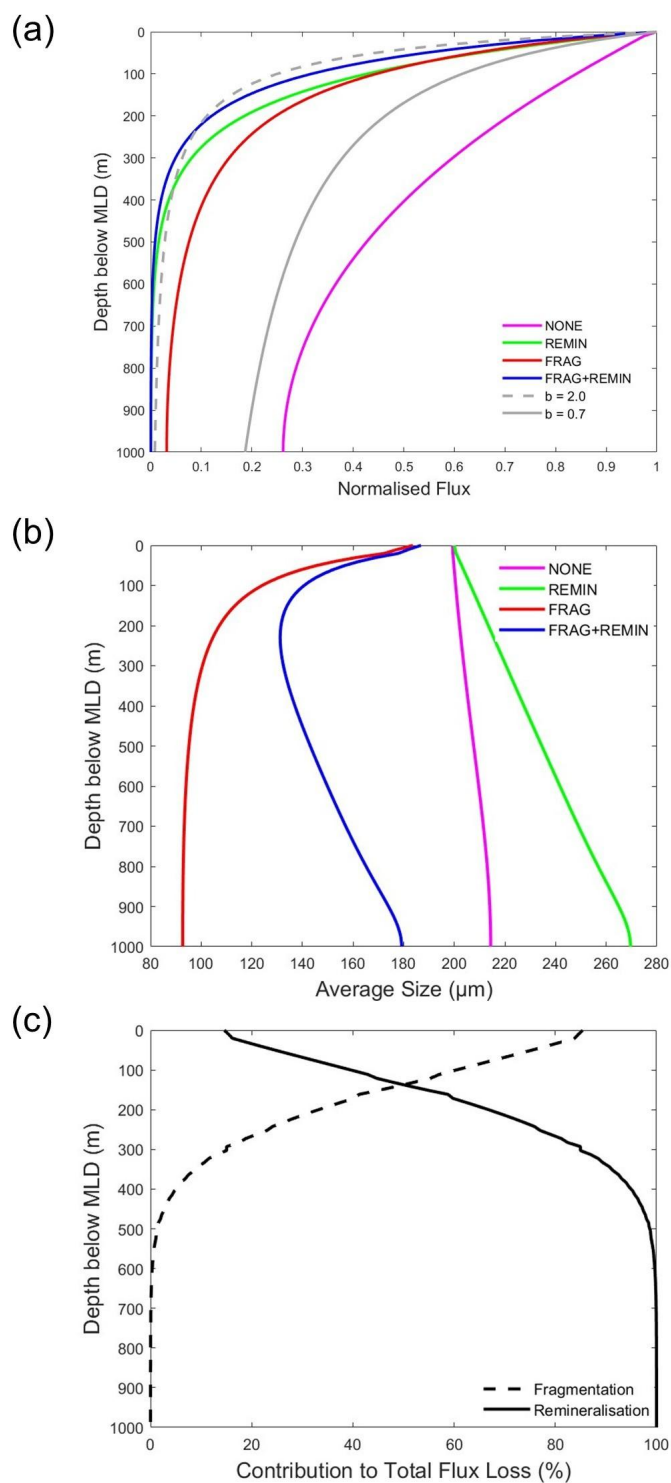




Figure 4: Depth profiles for runs with an initial particle size distribution slope of 0 (equal initial abundance across all size classes) showing (a) normalised (relative to initial flux) POC flux (no unit) and (b) average equivalent spherical diameter (ESD; μm) weighted by cross-sectional area. Colours indicate different model experiments: NONE (pink) with no fragmentation or remineralisation, REMIN (green) with remineralisation only, FRAG (red) with fragmentation only, and FRAG+REMIN (blue) with both processes enabled. In panel (a), dashed and solid grey lines represent upper (2.0) and lower (0.7) bound value of the Martin's curve attenuation coefficient b at an assumed MLD of 100m. The relative contributions of fragmentation and remineralisation to flux loss (%) for the FRAG+REMIN run are plotted in (c).

Indeed, when fragmentation is introduced in isolation (FRAG experiment), average ESD decreases with depth. Particle size decreases rapidly within the first ~ 300 m below the MLD, from $\sim 200 \mu\text{m}$ to $\sim 90 \mu\text{m}$ (a 55% decrease). This pattern reflects the activity of particle-associated copepods (PAC), as ESD stabilises once POC flux attenuation slows (Fig. 4a), consistent with PAC biomass being prescribed as a fixed fraction of POC in the model (0.1; see Methodology). The decrease of ESD between the MLD and the base of the mesopelagic aligns with GLOBESINK observations (Fig. 3).

When both fragmentation and remineralisation are included (FRAG+REMIN experiment), depth profiles largely reflect a combination of the two processes. In the upper 150 m, fragmentation dominates over remineralisation for total POC flux loss (Fig. 4c), reducing ESD below $150 \mu\text{m}$ (25% decrease). At greater depths, remineralisation becomes dominant, increasing ESD toward values closer to the NONE experiment and producing a “C”-shaped profile (Fig 4b). The rapid decrease in ESD in the upper mesopelagic is present in the observations, and in some cases (e.g. SO biome) deeper ESD values increase (Fig. 3), although not to the extent shown in our results.

Only simulations incorporating fragmentation (FRAG and FRAG+REMIN experiments) result in an initial decrease in particle size with depth, like observed in GLOBESINK and UVP datasets. The sensitivity tests also produce differing flux attenuation profiles (Fig. 4a). Additionally, all simulations fall within the observed range of the Martin curve attenuation coefficient for the first 200 m, except for the NONE experiment where no processes are enabled (Fig. 4a). Besides, enabling more processes causes the attenuation curve to more closely resemble higher b values, demonstrating that a simple Martin curve approach cannot distinguish between the impacts of individual particle transformations. It must be noted that the constant remineralisation rate applied in the model expectedly exceeds the Martin curve as you get deeper, as attenuation decreases with depth in a Martin curve. Comparing the normalised flux curves also enables inference of the rate and depth at which attenuation takes place for the differing scenarios. In the upper mesopelagic (~ 200 m), remineralisation (REMIN) and fragmentation (FRAG) follow similar normalised flux profiles (Fig 4a.), suggesting they both attenuate flux at a similar rate. Whilst remineralisation (and ingestion) directly removes mass from the system, fragmentation can also dampen flux by moving mass into smaller, slower sinking size classes. Despite these processes attenuating flux at similar rates in the upper water column, their normalised flux profiles diverge (reducing POC flux to 10% of its initial value at ~ 275 m below MLD in REMIN and ~ 415 m in FRAG; Fig. 5). This subsequently results in differing transfer efficiencies (T_{eff}), with more flux reaching the base of the mesopelagic for FRAG compared to REMIN. While fragmentation strongly impacts the upper mesopelagic



average size POC and thus its flux attenuation, remineralisation continually drives POC flux loss with depth, leading to minimal flux at 1 km depth.

Total integrated POC flux loss across the entire water column further highlights these differences. Total loss is substantially larger for the REMIN experiment (~ 76% relative to the NONE experiment; Fig. 5) than for FRAG (~ 56%), highlighting that remineralisation directly removes mass, whereas fragmentation only redistributes it.

However, in the top 100 m FRAG and REMIN produce equal attenuation, with fragmentation-driven attenuation declining with depth due to decreasing PAC concentration, whereas remineralisation is sustained at a constant rate. The combined FRAG+REMIN experiment increases integrated POC flux loss by ~ 5% compared to REMIN, with fragmentation accounting for ~ 75% of the total water column POC flux loss, with the majority of this occurring in shallow waters (Fig. 4c). Additional sensitivity experiments varying remineralisation rate ($0.01 - 0.05 \text{ day}^{-1}$) and fragmentation strength (PAC biomass:POC concentration ratio of $0.01 - 1$) confirm that remineralisation consistently dominates deep flux attenuation whilst fragmentation is more prominent in shallower waters under a range of transformation scenarios (see supplementary material; Fig. S9 and S12).

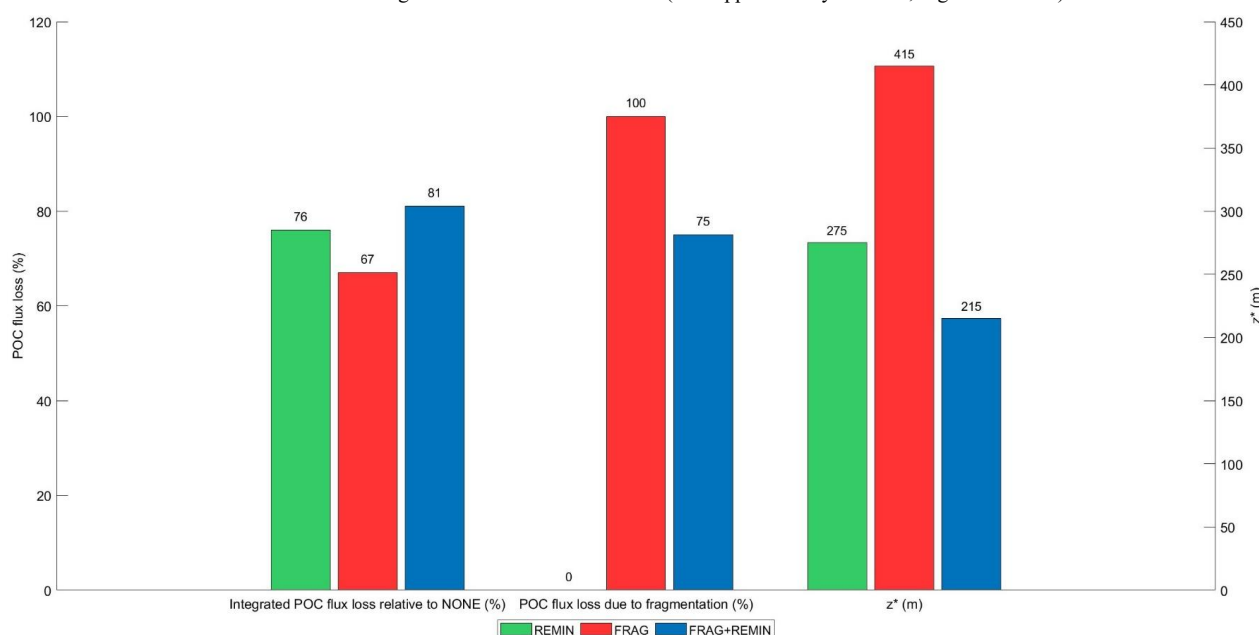


Figure 5: POC flux characteristics for sensitivity tests using a uniform initial particle size distribution (slope = 0). POC flux loss is shown relative to the NONE experiment, where neither fragmentation nor remineralisation are enabled. The contribution of POC flux loss due solely to fragmentation is also indicated. Integrated flux is calculated from the total loss across the entire water column. z^* represents the depth at which flux is at 10% of its respective surface value.



Thus, when initialised with a uniform particle size distribution, the model reproduces the observed vertical decrease in particle size only when fragmentation is included as a particle transformation process.

Fragmentation is the dominant attenuator of flux in the upper mesopelagic, where particle-associated copepod (PAC) and other zooplankton biomass is greatest. In deeper depths, however, the attenuation of the remaining flux is solely driven by remineralisation, which is also reflected in the size profile which moves from decreasing (due to fragmentation dominating) to increasing (where remineralisation dominates as the constant rate removes relatively more smaller particles).

3.3 Impact of varying initial particle size distribution

We previously investigated the impact of transformation processes on particle dynamics using a uniform initial PSD (slope = 0) to disentangle individual contributions. However, observations indicate that PSDs at the MLD typically exhibit slopes of ~ 2-4 (Clements et al., 2022). To explore the effect of a non-zero slope, we varied the initial slope between 2-4 while keeping remineralisation rate, PAC biomass to POC concentration and the initial total particle abundance the same as before (Table 1; see Method Section). This approach allows us to isolate the impact of initial PSD slope in shaping exported POC.

As with the uniform PSD sensitivity experiments (Section 3.2), the processes of fragmentation and remineralisation were successively enabled. Here, we discuss the output of the s_FRAG+REMIN experiments (Fig. 6), while outputs of the individual runs (s_NONE, s_REMIN and s_FRAG) are provided in the supplementary material (Fig. S14).

Varying the initial slope alters the extent to which fragmentation impacts vertical particle size profiles. In the s2FRAG+REMIN experiment, the decrease in particle size (due to PAC-induced fragmentation) is less pronounced than that of the FRAG+REMIN experiment (~4% decrease in size vs 25% decrease). However, the deep water remineralisation-driven trend where average ESD increases with depth persists. Increasing slope value (s3FRAG+REMIN and s4FRAG+REMIN; Fig. 6b) further diminishes the impact of PAC-induced fragmentation on the vertical size profile. This is because steeper slopes imply fewer large particles, leaving less mass available (relative to a slope = 0) to be redistributed into smaller particles and reducing the capacity of fragmentation to alter particle sinking flux and size profile. Further, with PAC biomass reliant on POC, the further sinking (s2FRAG+REMIN) runs allow fragmentation to contribute 41% of water column flux loss, most prominently in surface waters, whereas this drops to ~ 1% in s3FRAG+REMIN and s4FRAG+REMIN (Fig. 7). Thus, fragmentation's role in flux attenuation and the reduction of average particle size with depth is amplified with lower initial PSD (where more larger, faster-sinking particles are present).

Another significant impact of changing the initial PSD slope is its influence on remineralisation's ability to terminate flux at depth. Steeper slopes lead to ESD profiles that decline to 0 μm within the mesopelagic (<1000 m; Fig. 5b), indicating complete remineralisation and hence removal of flux from the system, whilst also potentially revealing the impacts of absences within our model, e.g. fecal pellets (see Discussion). Increasing the initial PSD slope pushes this termination of flux (and thus size) to shallower values with (~ 850 m and 200 m for s3FRAG+REMIN and s4FRAG+REMIN respectively; Fig. 6b). This occurs because the majority of mass resides in slower sinking size bins relative to FRAG+REMIN, so there will be more attenuation in shallow waters (flux is 10% of its initial value at 300 m for FRAG+REMIN, and < 50 m for s4FRAG+REMIN, Fig. 6a).



355 Even with the average global initial slope of ~ 4 (Clements et al., 2022; Kiko et al., 2022), flux is attenuated at
very shallow depths, suggesting model absences related to particle robustness (composition, type etc.) may
facilitate deeper flux at higher slope values (see Discussion). Integrated flux further highlights these dynamics:
while remineralisation has a relatively constant impact on attenuation regardless of the initial PSD slope,
fragmentation's role diminishes as slope steepens, that is as the particle flux becomes increasingly dominated by
small particles (Fig. 5c, Fig. 7).



360

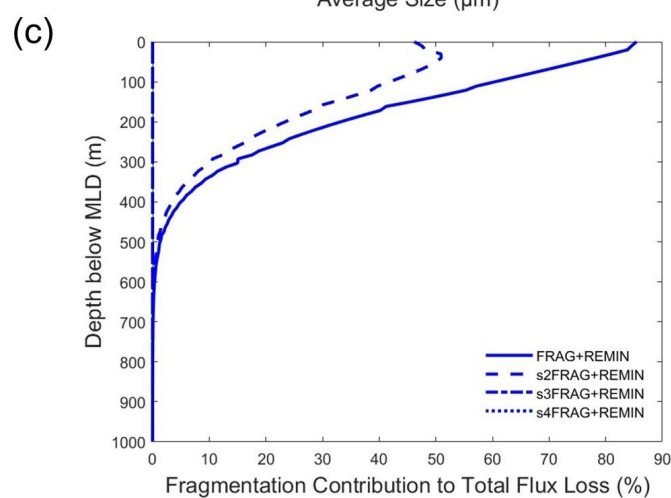
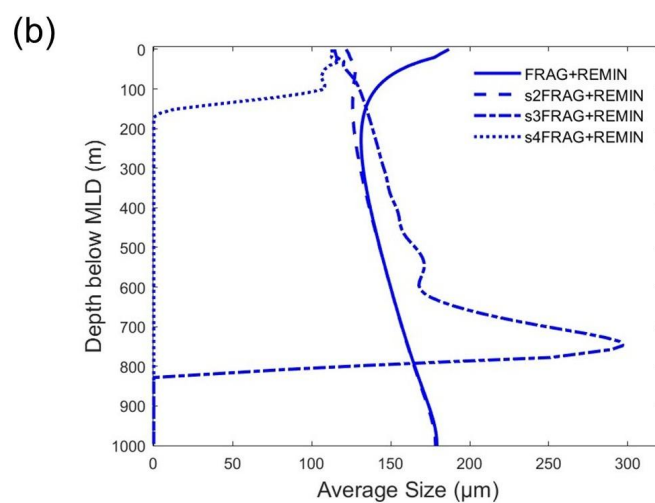
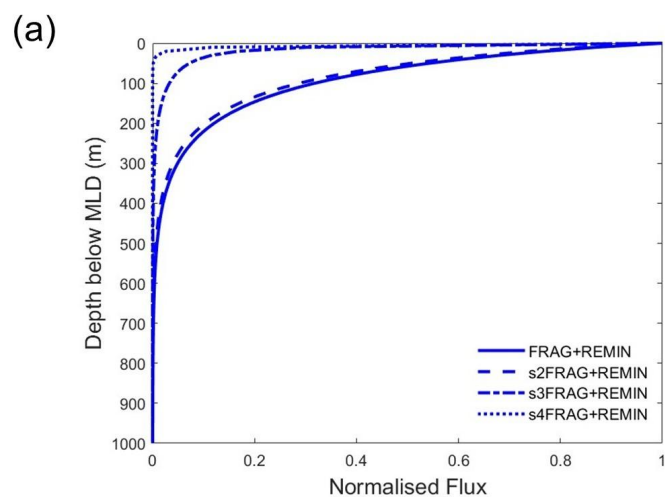




Figure 6: Normalised flux depth profiles (a) and (b) average particle equivalent spherical diameter (ESD; μm) for varying initial particle size distribution slope values where fragmentation and remineralisation are enabled. Initial slope values are 2 (s2FRAG+REMIN – dashed line), 3 (s3FRAG+REMIN – dot-dashed line) and 4 (s4FRAG+REMIN – dotted line), within the observational range (Clements et al., 2022). These are plotted against the previous initial slope = 0 experiment (FRAG+REMIN – solid line). The contribution of solely fragmentation (c) to flux loss (%) is also plotted with depth.

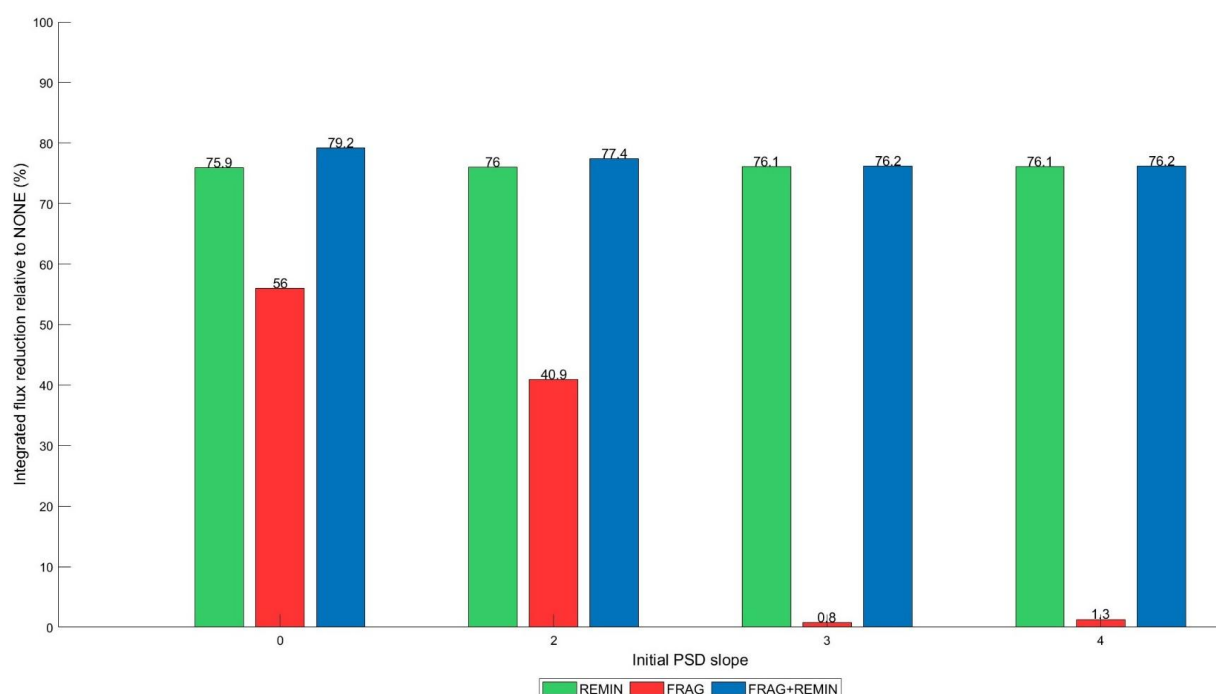


Figure 7: Impact of varying particle initial slope on integrated POC flux. We report the percentage of flux reduction relative to corresponding NONE experiment. For example, the s2FRAG+REMIN experiment (FRAG+REMIN with an initial slope of 2) has a 79.2% reduction in integrated flux compared to s2NONE.

To summarise, the initial particle size distribution slope is a critical regulator of the rate at which POC flux is attenuated, as it dictates the relative abundance of large, fast-sinking particles capable of transporting carbon deeper into the water column. The proportion of these larger particles additionally determines the impact on vertical particle size profiles due to fragmentation acting as an additional input to the smaller particle pools. A constant remineralisation rate enables its relative contribution (vs fragmentation) to flux loss to increase as the role of fragmentation recedes, with this especially prevalent in deeper waters.



3.4 Effect of seasonality

380 Seasonality of primary production can be an important driver for particle size distribution, through phenomena
such as phytoplankton succession during bloom periods (Wentzky et al., 2020). Such changes can further
influence the attenuation of POC flux, e.g. via changes in exported particle types (Bach et al., 2016). In the
previous sensitivity tests, we consider a constant initial export flux configuration (fixed PSD slope and total
particle flux), representing a non-seasonal regime. To simulate a seasonal export scenario (akin to mid-to-high
385 latitude biomes), we first varied the magnitude of the initial particle flux following a sinusoidal cycle (Fig. 8a)
while keeping the initial PSD slope at 2 (to isolate the impact of changing magnitude of exported material). An
additional run, where total particle abundance was kept constant and the PSD slope value varied seasonally, is
presented in the supplementary material (Fig. S15).

In the seasonal experiments (fSEAS, Table 1), total initial particle flux was varied to simulate simple seasonality
390 of exported material at the MLD (Fig. 8a). Generally, the resulting ESD depth profiles follow the
FRAG+REMIN trend, with an initial decrease due to PAC fragmentation followed by gradual increase below ~
400 m due to remineralisation (Fig. 8c and 8d). The strength of the PAC-induced size decrease varies seasonally,
with increasing particle fluxes producing decreases in ESD deeper in the water column (e.g. ~ 15% decrease in
size relative to the surface value at 200 m for Month 8 vs 100 m for Month 5). This variation in ESD is likely
395 due to higher POC encouraging more PAC biomass to feed and fragment mass into small particle classes, e.g.
fragmentation makes the greatest and deepest contribution to flux attenuation in Month 12 (Fig. 8d). During
months of increasing particle flux (Months 6 to 12), fragmentation accounts for > 80% of total water column
flux loss (Fig. 8b), while in periods of decreasing particle flux its contribution declines to < 30% (Month 2).
Below 400 m, however, remineralisation dominates, accounting for >90% of flux loss regardless of season (Fig.
400 8d), and there is less annual variation in ESD. This suggests that variations in particle size depth profiles
shallower than 500 m observed in the GLOBESINK dataset (Fig. 2) could be attributed to changes in POC flux
magnitude, potentially through export pulses where there is more fragmentation into smaller particles (Briggs et
al., 2020). Thus, the relative contribution of fragmentation in attenuating flux depends on the magnitude of
exported material, with it acting more significantly in periods of higher export.

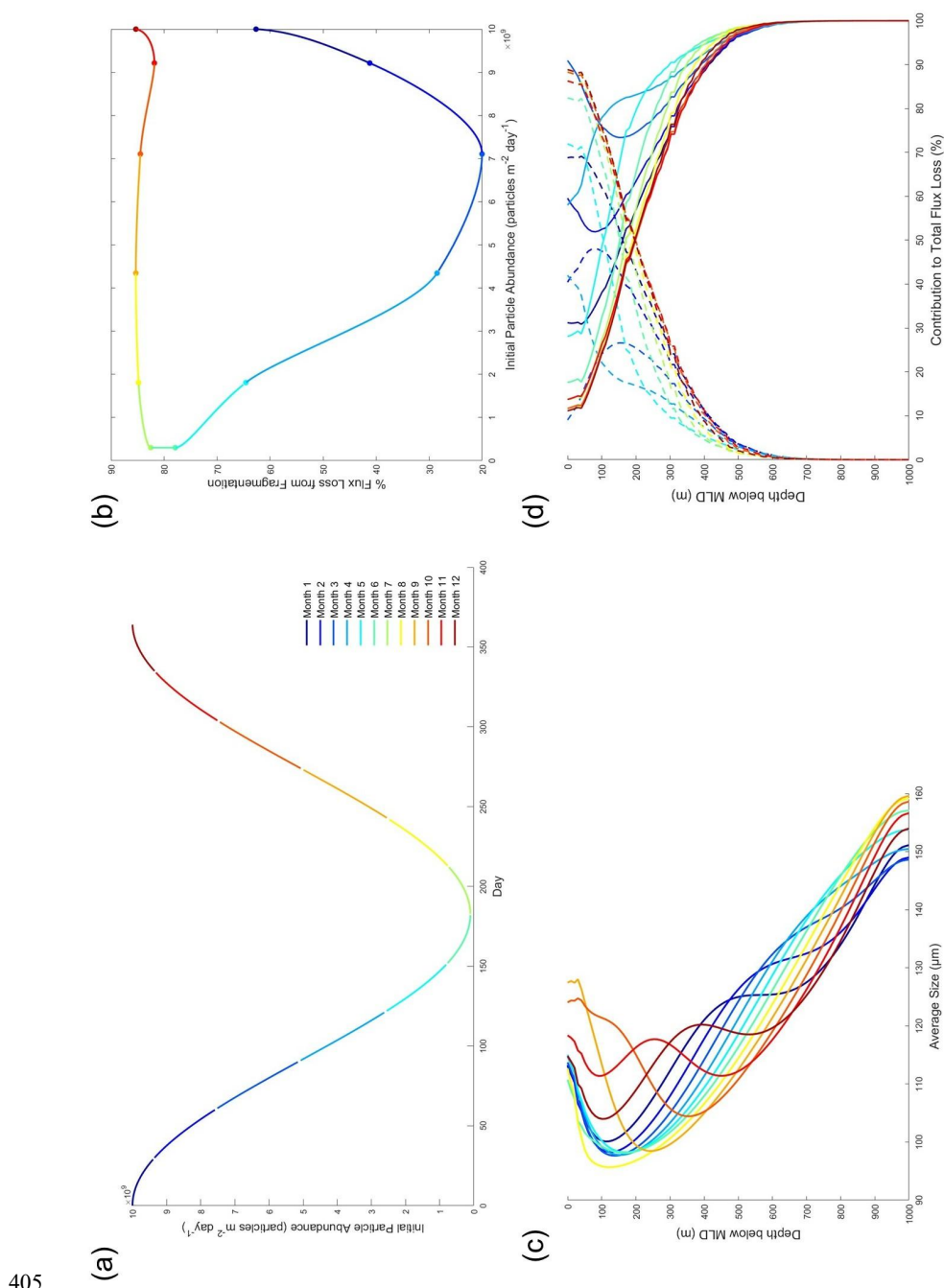


Figure 8: Results from the seasonal export experiment (fSEAS). In this experiment, we fixed the initial particle size distribution slope at 2 while varying the initial total particle flux sinusoidally over an annual cycle. (a) Prescribed seasonal variation in initial total particle flux (particles $\text{m}^{-2} \text{d}^{-1}$). (b) Monthly depth-integrated flux loss (%) attributed to fragmentation. (c) Depth profiles of particle equivalent spherical



410 **diameter (ESD, μm) weighted by cross sectional area. (d) Depth profiles of flux attenuation due to fragmentation (dashed lines) and remineralisation (solid lines), expressed as % contribution.**

4 Discussion

Among the processes included in this model, PAC-driven fragmentation is the main driver of particle size profiles in the upper mesopelagic zone. This result is consistent with optical backscattering observations of large
415 vs small particle concentrations by Briggs et al. (2020), who reported decreasing fragmentation rates with depth, although found fragmentation explained a high fraction of flux attenuation throughout the entire mesopelagic, whereas in this study it is constrained in the upper mesopelagic. The strong influence of PAC-induced fragmentation on size profiles and flux attenuation in our sensitivity tests points to the need to incorporate fragmentation into biological carbon pump (BCP) models to better represent POC flux attenuation with depth.

420 Our sensitivity experiments show that higher POC flux enhances the relative impact of fragmentation on flux loss compared with remineralisation, particularly in the upper water column. We also find fragmentation is more influential when export flux is composed of more large particles (small PSD slope), conditions analogous to the high-flux/productivity regions and events studied by Briggs et al. (2020) and Bressac et al. (2024). These results suggest that the importance of biologically-mediated fragmentation in attenuating POC flux is regionally
425 variable, with fragmentation contributing less to attenuation relative to sustained remineralisation in low production/export areas. Varying fragmentation contribution to attenuation also affects the resulting particle size profiles. Our modelling shows these profiles can provide a fingerprint of the dominating particle transformation processes throughout the water column. The changes in average particle size as flux sinks may enable inference of the types of particles (e.g. slow vs fast and large vs small) we can expect to observe at a given depth, and
430 their likelihood to contribute to carbon sequestration (e.g. what transformation processes are likely to be dominant as they sink). Further, these size characteristics can point to dynamics in flux-associated biological activity (copepod feeding and microbial degradation) and at what depth it occurs (Mayor et al., 2014; Briggs et al., 2020).

To represent the effect of PAC-driven fragmentation, we implemented a fixed PAC biomass to POC
435 concentration ratio in the model, assuming PAC biomass responds instantaneously and proportionally to the available POC. This formulation does not capture potential lags in PAC response that may arise from behavioural characteristics related to swimming, encounter rates, and particle detection (Lombard et al., 2013b; Buskey, 1984). This study also assumes PAC have a sustained presence and no seasonality in reproduction, nor ontogenetic migration (Neill, 1992). In addition, our model only considers PAC as the principal agents of
440 fragmentation in the mesopelagic, whereas other modes of copepod and other mesozooplankton feeding are also observed, such as filter feeders preferentially selecting smaller particles (Humphries, 2009). Their absence in the model may lead to bias towards smaller particles when calculating average ESD, thus community composition and which feeding strategy dominates may influence particle size profiles and the magnitude of flux reaching deeper waters. In addition, lab experiments by Toullec et al. (2019) show that aggregate abundance can vary in
445 the presence of copepods with varying functional traits (cruise, filter and mix feeders), although no consistent net effect on fragmentation was found, presumably due to the complex interplay of these behaviours. Finally, our model does not consider the full impact of organic matter quality. Despite considering the available flux as a



key characteristic of the extent of PAC feeding, copepods have also been observed to undertake “microbial gardening” (Mayor et al., 2014) and can reject particles due to their organic content (Meunier et al., 2016), which would create a particle pool that is not subject to fragmentation, allowing larger particles to sink further and bolster POC flux at depth. Further exploration into the complex feeding behaviour of copepods that could further modulate fragmentation would benefit BCP flux attenuation studies, although these are yet to be investigated in a modelling context.

Within our model, each size class has the same remineralisation rate, a key assumption potentially ignoring the impact of porosity (hence surface area) and other effects that may also be enhanced by particle break up via fragmentation (Burd and Jackson, 2009; Anderson et al., 2023; Cavan et al., 2017b). Observations of microbial degradation of organic matter can vary by, aggregate origin and type, depth and temperature (Bach et al., 2019; Iversen and Ploug, 2010; Cavan et al., 2017a), thus methodological effects create high uncertainty in constraining remineralisation rate, which is kept constant across size classes in this study. The remineralisation rate also does not change with depth within the model, although temperature and oxygen (Laufkötter et al., 2017), lability of organic matter such as robust faecal pellets (Zakem and Levine, 2019; Turner, 2015), pressure (Amano et al., 2022) and other depth effects (Bressac et al., 2024) may play a role. Further to this, with both fragmentation and remineralisation included in the model, the increase in ESD with depth as remineralisation becomes the dominant particle degradation process is observed in the GLOBESINK dataset, although not as significantly as our modelling shows, potentially suggesting that microbial degradation in reality may become less significant with depth, or indeed vary across size classes, which may lead to more flux leaving the mesopelagic layer.

In the observations, many of the superbiomes display deeper water (below 500 m, e.g. NP in Fig. 2) average ESD peaks that are not captured in the model, suggesting additional large particle sources or mechanisms that allow particles to survive degradation processes. Our modelling experiments currently only test for differing size distribution and flux magnitude, but not for particle nature (e.g. density of faecal pellet vs aggregates, and the quality of this organic matter). Lithogenically-sourced, e.g. via river input (Bach et al., 2016), or biogenic minerals, e.g. diatom silicate frustules (De La Rocha et al., 2008), within a particle can act as ballast (Armstrong et al., 2001), which can buffer organic degradation (Iversen and Robert, 2015) and increase the particle’s specific gravity (Klaas and Archer, 2002), potentially enabling it to sink further through the water column and facilitate elevated T_{eff} . This study also only considers particles exported from surface waters, with deeper flux sources not included. Pellet production (i.e. dense, fast-sinking particles) via diel vertical migration (DVM) can reach as deep as ~ 400 m (depths at which PAC fragmentation is diminished in our model) as part of the “migrant pump” (Steinberg and Landry, 2017). The magnitude of this pump is difficult to constrain, with DVM absent in all CMIP6 models (Henson et al., 2022), although it is likely a notable contributor to instances of deeper mesopelagic flux and higher average ESD at depth. More specialised models that have explored DVM (Putzeys and Hernández-León, 2005; Nowicki et al., 2022) consistently conclude it has a notable impact on the biological pump, with Bianchi et al. (2013) suggesting delayed egestion can bolster deep flux. The absence of particle diversity, POC flux sources, and other particle transformation processes with the current models’ configuration may lead to the low modelled T_{eff} discussed in Section 3.2. It is expected that the expansion of the model’s current framework to include diversified particle type, feeding strategies and further sophistication of



transformation processes will enhance deep water flux and result in T_{eff} values within observational range (De Melo Virissimo et al., 2024; Lima et al., 2014).

5 Concluding remarks

490 We developed a new 1-D vertical mechanistic particle model that resolves the particle size and density spectra
of POC flux and investigated the relative influence of initial POC flux properties, and subsequent particle
transformations within the mesopelagic, including sinking speed, fragmentation and remineralisation. We found
that fragmentation is a critical transformation to capture the observed initial decline in particle size with depth,
as recorded in optical backscattering. Whilst playing a key role, we find that fragmentation's contribution as a
495 driver of particle size and flux attenuation is dependent on the magnitude of exported flux and its particle size
distribution, suggesting that its importance may vary regionally and temporally. Additional particle
characteristics (POC composition, lability etc.), and biological activity (DVM, feeding modes etc.) may also
play roles in the sustained deep water fluxes that drive high transfer efficiency, whilst also influencing the
particle size profile at depth. Finally, we suggest that future POC flux modelling studies explicitly incorporate
500 fragmentation as a degradation driver.

Code and data availability

Code required to run an example experiment within this study (s2FRAG+REMIN) and instructions to alter code
to reproduce other experiments can be accessed at the following doi: 10.5281/zenodo.19708026. For further
information please contact AANB. The GLOBESINK dataset can be accessed at the following doi:
505 10.5281/zenodo.19558504.

Author contributions

ANB and FMM designed the experiments. NB produced the observational dataset. ANB wrote the manuscript
draft which was reviewed and edited by FMM, NB and SH.

Competing interests

510 The authors declare that they have no conflict of interest.

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