

IDEAS & SPECULATIONS

Thoughts & Opinion

Ocean carbon sequestration: Particle fragmentation by copepods as a significant unrecognised factor?

Explicitly representing the role of copepods in biogeochemical models may fundamentally improve understanding of future ocean carbon storage

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Abstract

Ocean biology helps regulate global climate by fixing atmospheric CO₂ and exporting it to deep waters as sinking detrital particles. New observations demonstrate that particle fragmentation is the principal factor controlling the depth to which these particles penetrate the ocean's interior, and hence how long the constituent carbon is sequestered from the atmosphere. The underlying cause is, however, poorly understood. We speculate that small, particle-associated copepods, which intercept and inadvertently break up sinking particles as they search for attached protistan prey, are the principle agents of fragmentation in the ocean. We explore this idea using a new marine ecosystem model. Results indicate that explicitly representing particle fragmentation by copepods in biogeochemical models offers a step change in our ability to understand the future evolution of biologically-mediated ocean carbon storage. Our findings highlight the need for improved understanding of the distribution, abundance, ecology and physiology of particle-associated copepods.

KEYWORDS

biological carbon pump, climate regulation, detritus, fragmentation, ocean carbon cycle, zooplankton

INTRODUCTION**Carbon storage in the ocean**

Photosynthetic unicellular organisms in the sun-lit, euphotic zone of the open ocean produce ~48 gigatonnes (Gt) of organic carbon each year, almost half of total global primary production.^[1] Between 5 and 12 gigatonnes of this organic matter sinks down into the mesopelagic zone,^[2] nominally defined as the region of water between 100 and 1000 m deep, as a mixture of dead or dying cells, animal carcasses

and feces. Most of this sinking flux is remineralised via ocean biology before it reaches 1000 m.^[3-5] The depth at which organic matter is remineralised determines the residence time of the constituent carbon in the ocean, with important consequences for global climate.^[6] It is estimated that the suite of biological processes that result in the storage of carbon in the deep ocean, collectively known as the "biological carbon pump" (BCP), reduce the concentration of atmospheric CO₂ by up to 50% of what it would otherwise be.^[7] Understanding the mechanisms that control the strength and efficiency of the BCP is integral to developing our capacity to reliably predict future climate.

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The BCP is typically quantified by measuring the sinking carbon flux at a range of water depths throughout the mesopelagic via a variety of techniques, including the use of neutrally-buoyant sediment traps. The resulting relationship between sinking carbon flux and depth is frequently characterised empirically by fitting particle flux data using a power-law known as the “Martin curve,” with a fixed shallow reference depth:^[3]

$$F_z = F_{100} \left(\frac{z}{100} \right)^{-b} \quad (1)$$

where F_z is flux at depth z , F_{100} is (in this case) flux at a reference depth of 100 m, and the exponent b quantifies the rate at which the sinking flux is attenuated with depth. As such, b is often used as a metric when examining the proximate controls on the efficiency of the BCP, i.e., the fraction of organic carbon leaving the euphotic zone that penetrates the mesopelagic to a given depth. Geographical variation in b correlates with various factors including ocean temperature, seawater oxygen concentrations and surface biological properties;^[8–10] consensus on the relative importance of these factors has yet to be reached. The marine ecosystem components of contemporary Earth System models, including those used to inform IPCC climate assessments, typically represent the BCP via a range of semi-empirical formulations that generate Martin-type curves. These include the use of particle turnover rates that are fixed or depend on temperature or oxygen, increasing sinking speed of detritus with depth, and mineral ballasting [e.g., 11–15]. The underlying biological processes (e.g., respiration, ingestion) and ecological interactions (e.g., predation, fragmentation) that ultimately control the fate of sinking detritus (particulate organic carbon, POC) are usually implicit within such parameterisations. The uncertainties associated with empirical approaches are large and may amplify when making projections of the future strength of ocean carbon storage. One way of reducing these uncertainties, and hence increasing confidence in future climate predictions, is to explicitly account for the biological processes that attenuate the sinking flux of organic particles.^[16]

Particle fragmentation in the mesopelagic zone controls the biological carbon pump

The first budget to balance the sources and sinks of organic carbon in the mesopelagic zone to within observational errors was published in 2014.^[4] Analysis of this budget using a simple, steady-state flow-analysis model suggested that zooplankton may intercept half of all fast-sinking organic matter and fragment approximately 30% of this fraction while feeding upon it. The identity of the animals responsible for particle fragmentation, was, however, not resolved in that study and there was no analysis of the consequences of particle fragmentation for flux attenuation, i.e., Martin’s b , in the water column. New observational data from multiple ocean regions, generated using autonomous profiling biogeochemical “Argo” floats [<https://argo.ucsd.edu/>], reinforce this apparently counterintuitive finding: on average, 49% (± 22) of the observed decrease in particle flux with depth in the mesopelagic zone during high-flux events can be solely attributed to the

transformation of large, fast-sinking particles into small, slow-sinking fragments.^[17] Accordingly, particle fragmentation is suggested to be “the single most important process in determining the depth at which fast-sinking organic carbon is remineralised”.^[17] Here, we speculate that the primary agents of particle fragmentation in the mesopelagic zone of the ocean are small particle-associated copepods (PAC). We use a new ecosystem model, embedded within a simple 1-dimensional representation of water column physics, to explore the role of particle fragmentation by PAC in controlling the magnitude and depth-scale of particle flux attenuation in the ocean, and thereby the efficiency of the BCP.

Particle-associated copepods lessen the flux of sinking organic matter

The suggestion that zooplankton play a quantitatively important role in attenuating the vertical flux of carbon is not new.^[18] Numerous small copepods are reported to associate with detrital particles, including the cyclopid genera *Oithona*, *Oncaea* and *Corycaeus*, and harpacticoids of the genus *Microsetella*^[19–21] (Figure 1). These animals are typically <1 mm long and, despite frequently being under sampled using “standard” 200 μm zooplankton nets, are believed to be amongst the most abundant animals on Earth.^[20,22] Several studies have identified PAC as the “gate-keepers” of particle flux at the base of the euphotic zone,^[21,23–26] but exactly how they attenuate the flux of sinking particles remains poorly understood. PAC are reported to consume a diversity of living and non-living food items including ciliates, dinoflagellates and diatoms, along with detrital particles and the fecal pellets of larger animals.^[23,27–29] Numerous studies note the capacity of PAC to fragment, rather than ingest, detrital particles.^[27,30] Such activities may be associated with searching for attached or embedded ciliates or other microbes.^[31,32]

Here, we develop the hypothesis that mesopelagic PAC fragment, rather than consume, the majority of the detrital particles that they encounter. This counter intuitive trophic strategy is consistent with findings from previous work^[4] and provides a mechanistic explanation for why almost half of all large fast-sinking particles are converted into smaller ones within the upper mesopelagic zone.^[17] We propose that when mesopelagic PAC encounter fast-sinking detritus, their primary action is to mine these particles for attached microbes^[31,32] and, in doing so, inadvertently fragment them. This “search and destroy” feeding mode exploits the widely reported phenomenon that particles of detritus amplify the abundance of bacteria and protists by several orders of magnitude relative to the surrounding seawater^[33,34] and provide a diet that is nutritionally superior to consuming non-living detritus alone.^[35] The associated fragmentation also reduces or arrests sinking particulate fluxes and simultaneously increases the total surface area available for microbial colonisation. Particle fragmentation has previously been suggested as a means by which mesopelagic zooplankton exploit the enzymatic machinery of microorganisms to stimulate the local production of nutritious, harvestable biomass.^[36]

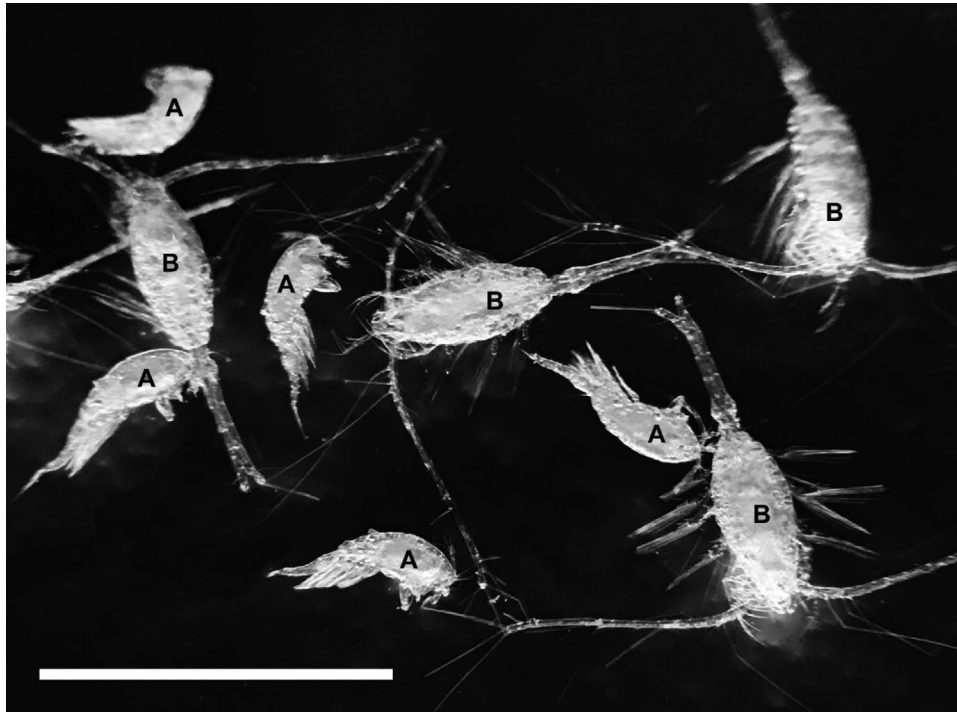


FIGURE 1 Various marine copepods, including the cyclopoid families Oncaeidae (A) and Oithonidae (B), are frequently associated with sinking particles of detritus in the ocean. Scale bar $\approx 1000 \mu\text{m}$. Image copyright Daniel Mayor.

Explicitly representing PAC in a plankton ecosystem model

We develop a mathematical characterisation of PAC population dynamics that is suitable for implementation in marine ecosystem models. We chose to incorporate it within the intermediate-complexity model MEDUSA (Model of Ecosystem Dynamics, nutrient Utilisation, Sequestration and Acidification) that is used to simulate global ocean biogeochemical cycles and which includes non-diatoms, diatoms, microzooplankton and mesozooplankton, slow-sinking detritus, nitrate, silicate and iron as state variables.^[12] MEDUSA has an implicit representation of fast-sinking detritus via instantaneous remineralisation in the water column. We replace this formulation with an explicit representation where large detritus is divided into two classes. The first represents relatively slower-sinking aggregates of particles from a range of sources, including dead phytoplankton and zooplankton, and is assigned a sinking rate of 35 m day^{-1} based on typical values for this class of “marine snow” of between 20 and 50 m day^{-1} .^[37,38] The second class represents zooplankton fecal pellets that are fast-sinking owing to their increased density and more streamlined shape. A value of 115 m day^{-1} is specified for the fastest sinking fraction based on the upper limit of fast-sinking particles,^[17] and which is consistent with field estimates.^[34] Small detritus, in contrast, sinks at 0.5 m day^{-1} in the model. The ecosystem is embedded within 1-dimensional physics model in which the water column is divided into 5 m layers (0 to 1000 m) where the surface layers are completely mixed with an imposed seasonal cycle. Nutrients are dynamic within the modelled mixed layer but present in a fixed profile below, whereas the rest of the ecosystem,

including PAC and both fast-sinking detritus variables, is modelled throughout the entire vertical domain. The model is set up to simulate the seasonal cycle at the Porcupine Abyssal Plain (PAP) site in the North Atlantic Ocean ($49^\circ\text{N } 16.5^\circ\text{W}$). A complete description of the model is provided in the Supporting Information Sections S1-S6.

Our representation of PAC is necessarily speculative because the physiology and ecology of these animals is poorly understood, particularly in the mesopelagic. Key parameterisations in the model are a functional response with low maximum feeding rate that is compensated by the ability to feed effectively at low food concentrations, low respiration and low mortality. PAC are adapted to efficiently locate sinking aggregates via their chemical plumes^[39,40] and spend much of their time motionless, interspersed with vigorous hops when particles pass within their field of perception.^[41] This ambush mode of feeding has several consequences. Feeding rates tend to be relatively low because of slow gut throughput that increases absorption of energy and matter in their variable food environment. In compensation, feeding thresholds are also low meaning that PAC are able to feed at low prey concentrations.^[42,43] Ambush feeding is energetically efficient compared to the filter-feeding activities of larger copepods such that metabolic rates of PAC may be as much as 2-8 times lower than in calanoids.^[43-45] Low respiration imparts starvation tolerance, which allows animals to exploit environments with low food concentrations,^[41] such as the mesopelagic zone. Intercepting and feeding upon microbes attached to fast-sinking particles further reduces the amount of energy required to find otherwise diffuse prey and minimizes their chance of detection by predators.^[46] Another key feature of the model is that, consistent with their search and destroy

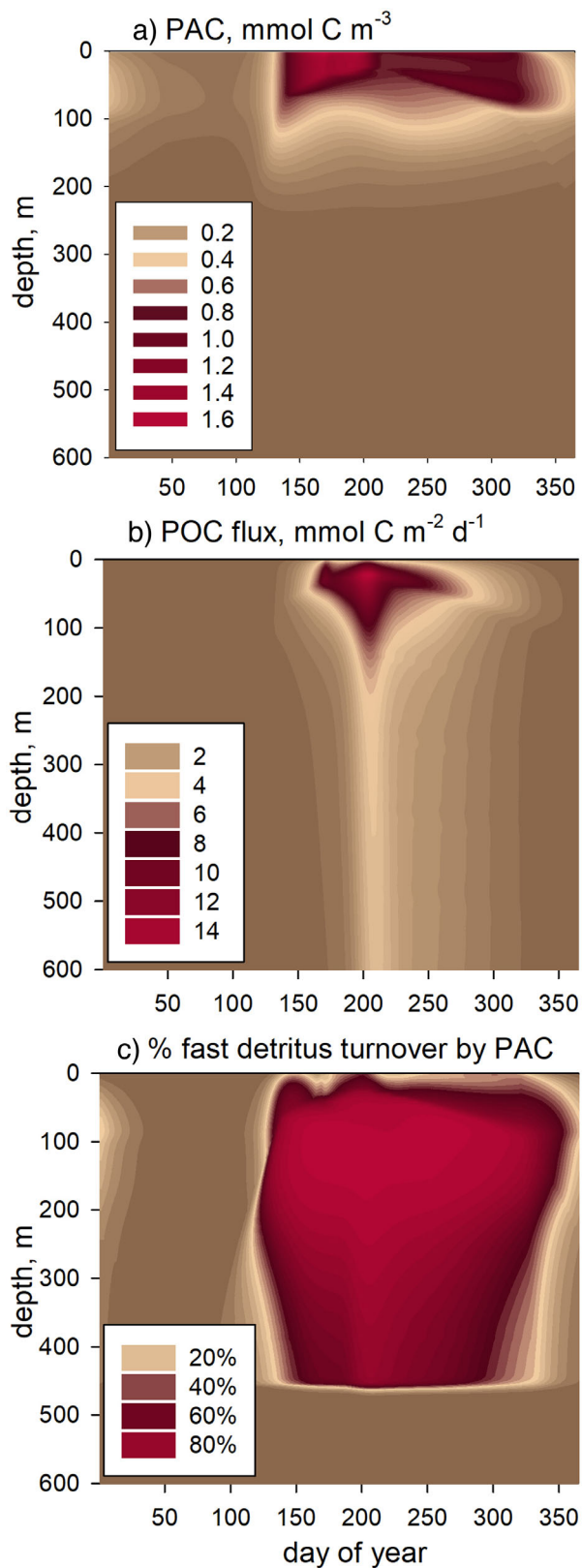


FIGURE 2 Model predictions for the Porcupine Abyssal Plain site in the eastern North Atlantic ($49^{\circ}\text{N } 16.5^{\circ}\text{W}$), 0–600 m, illustrating the seasonal evolution of: (a) Particle-associated copepod (PAC) biomass, (b) sinking detritus (particulate organic carbon, POC) flux, and (c) the proportional contribution of PAC to the attenuation of the flux of fast sinking detritus (remainder to bacterial respiration)

feeding mode, PAC are assumed to ingest only 20% of all intercepted particles of fast detritus (this fraction represents the biomass of attached protists), the remainder being fragmented into small detritus. The density of protists on detritus increases as particle size decreases owing to the increased surface area:volume ratio that favors microbial colonisation;^[47] PAC are, therefore, assumed to consume 40% of the captured small detritus and fragment the remainder. The flux of fast-sinking detritus is attenuated with depth either by interception and processing by PAC, or by microbial respiration, which is represented as a temperature-dependent rate in the model. Parameter values for PAC were carefully selected to best represent current understanding of how these animals feed, in terms of their food preferences and functional response, and also their likely response to predation (Supporting Information Section S6).

Particle fragmentation by PAC dominates the attenuation of detrital flux

The model recreates expected ecosystem dynamics in the surface mixed layer (Supporting Information Figure S1) and predicts vertical profiles of PAC biomass (Figures 2a and 3a) that are consistent with field-observed values.^[48,49] Following the phytoplankton bloom in surface waters, the simulated vertical flux of sinking detritus and its attenuation is highly variable through time (Figure 2b; Supporting Information Figure S3). This result has important implications for the timing of field programs, the operational deployment of equipment for measuring flux attenuation and interpretation of the resulting data. The model achieves a good fit to flux data derived from neutrally-buoyant sediment traps at the study location during the key period of export (Figure 3b, green line), thereby showing good correspondence with the empirically-fitted “Martin curve” for this period (Figure 3b, dashed grey line). Predicted particle fragmentation by PAC accounts for 81% of the annual flux attenuation of fast-sinking detritus in the mesopelagic (Figure 2c), dominating over microbial respiration in the upper mesopelagic (Figure 3c). A large mismatch with data occurs when the modelled particle flux is attenuated by microbial respiration alone, i.e., when PAC are removed from the model (Figure 3b, red line). Removal of PAC alleviates competition with mesozooplankton in the mixed layer and results in a higher flux of large (fecal pellet) detritus throughout the mesopelagic.

CONCLUSIONS AND PROSPECTS

Particle-associated copepods are an integral component of oceanic food webs. The proposed PAC model, which is based on our best understanding of the physiology and ecology of these tiny zooplankton, provides the first quantitative demonstration that PAC may be largely responsible for attenuating particle flux in the upper mesopelagic zone of the ocean. Our results thus indicate that PAC potentially play a pivotal role in modulating carbon sequestration in the ocean and hence climate regulation. Explicit representation

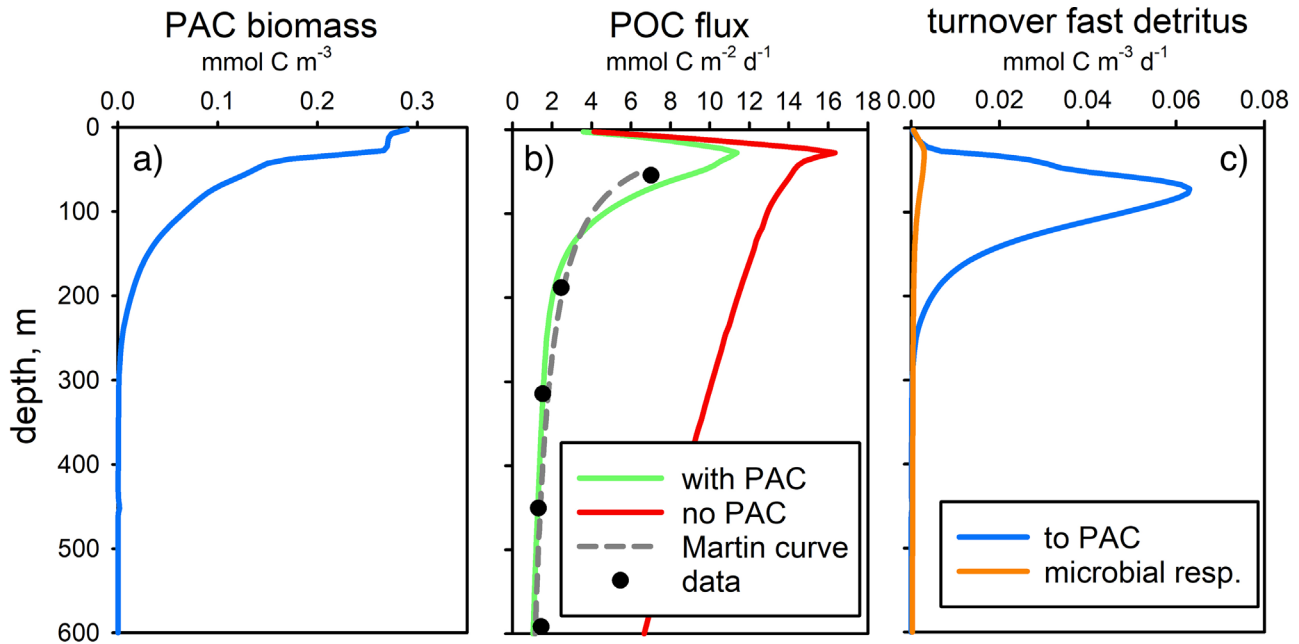


FIGURE 3 Predicted vertical profiles on Julian day 190 of the simulation: (a) Particle-associated copepod (PAC) biomass (mmol C m^{-3}); (b) particulate organic carbon (POC) flux ($\text{mmol C m}^{-2} \text{d}^{-1}$), comparing the standard simulation (PAC included; green line) with an equivalent no-PAC simulation (PAC removed such that remineralisation is solely by bacteria respiration; red line) and the power-law equation: $F_z = F_{50}(z/50)^b$ with the associated data;^[41] (c) contributions of PAC and microbial respiration to turnover of fast detritus ($\text{mmol C m}^{-3} \text{d}^{-1}$)

of particle fragmentation by PAC in ecosystem and biogeochemical models, and how these “tiny but mighty” animals will respond to environmental change, could therefore fundamentally improve our ability to explain observed spatiotemporal variation in the BCP and how it will evolve in response to continued anthropogenic perturbations.

Representing PAC in biogeochemical models is currently compromised by a lack of quantitative information on their physiology and understanding of their ecological niche, as well as a relative paucity of data on their abundance and distribution in the mesopelagic ocean. Despite the ubiquity of PAC such as *Oithona*, we are currently unable to fully explain how they simultaneously maintain viable populations in the epipelagic and mesopelagic zones of the ocean, where the physiological (e.g., temperature and hydrostatic pressure) and ecological (e.g., quantity and quality of available food and presence of predators) constraints are very different. Further observations and experiments are urgently required to provide new, detailed understanding of basic terms such as ingestion rates and food preferences of epipelagic- and mesopelagic PAC, their capacity to tolerate food deprivation, and life history parameters such as longevity and mortality.

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DATA AVAILABILITY STATEMENT

The model code is available upon request from Tom Anderson (tra@noc.ac.uk).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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