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## Abstract

Pelagic tunicates (salps, pyrosomes) and fishes generate jelly-falls and/or fecal pellets that sink roughly 10 times faster than bulk oceanic detritus, but their impacts on biogeochemical cycles in the ocean interior are poorly understood. Using a coupled physical-biogeochemical model, we find that fast-sinking detritus decreased global net primary production and surface export, but increased deep sequestration and transfer efficiency in much of the extratropics and upwelling zones. Fast-sinking detritus generally decreased total suboxic and hypoxic volumes, reducing a "large oxygen minimum zone (OMZ)" bias common in global biogeochemical models. Newly aerobic regions at OMZ edges exhibited reduced transfer efficiencies in contrast with global tendencies. Reductions in water column denitrification resulting from improved OMZs improved simulated nitrate deficits relative to phosphate. The carbon flux to the benthos increased by 11% with fast-sinking detritus from fishes and pelagic tunicates, yet simulated benthic fluxes remained on the lower end of observation-based estimates.

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**Main points:**

- We incorporated fast-sinking detritus from pelagic tunicates and fishes into a modified version of the ocean biogeochemical model COBALT.
- The fast-sinking detritus increased carbon sequestration and transfer efficiency to depth, but decreased surface productivity and export.
- Fast-sinking detritus decreased the size of oxygen minimum zones (OMZs) and water column denitrification, a common model bias.

**Abstract**

Pelagic tunicates (salps, pyrosomes) and fishes generate jelly-falls and/or fecal pellets that sink roughly 10 times faster than bulk oceanic detritus, but their impacts on biogeochemical cycles in the ocean interior are poorly understood. Using a coupled physical-biogeochemical model, we find that fast-sinking detritus decreased global net primary production and surface export, but increased deep sequestration and transfer efficiency in much of the extratropics and upwelling zones. Fast-sinking detritus generally decreased total suboxic and hypoxic volumes, reducing a "large oxygen minimum zone (OMZ)" bias common in global biogeochemical models. Newly aerobic regions at OMZ edges exhibited reduced transfer efficiencies in contrast with global tendencies. Reductions in water column denitrification resulting from improved OMZs improved simulated nitrate deficits relative to phosphate. The carbon flux to the benthos increased by 11% with fast-sinking detritus from fishes and pelagic tunicates, yet simulated benthic fluxes remained on the lower end of observation-based estimates.

**Plain Language Summary**

Marine ecosystems play a critical role in the global carbon cycle through the food web regulation of air-sea carbon fluxes and the transfer of particulate matter from the upper oceans to depth. Recent evidence has suggested that the detritus from fishes and gelatinous zooplankton (GZ), specifically the pelagic tunicates such as salps and pyrosomes, may have a disproportionate impact on the ocean's biological pump due to them sinking approximately 10x faster than bulk detritus. These fluxes result in increased sequestration of particulate carbon and nutrients into the deep oceans, but their impact on biogeochemical cycles at depth is poorly understood. Here, we investigated the sensitivity of deep ocean carbon, oxygen, and nutrient cycles to fast-sinking detritus from tunicates and fishes. We found that the fast-sinking detritus decreased surface productivity and export, as well as the size of ocean oxygen minimum zones (OMZs). Also, we examined whether observational evidence of seafloor oxygen consumption could support the increased detrital fluxes (and respiration) at depth, and found that even with the increased oxygen consumption, the modeled values were still below the observations. This suggests that these processes could be realistically incorporated into future generations of Earth System Models.

## 1. Introduction

In the ocean's biological carbon pump, carbon dioxide ($CO_2$) is fixed in the surface oceans by algal photosynthesis, and particulate carbon sinks from the surface to depth and regulates the vertical gradient of carbon and nutrients in the ocean (Sarmiento & Gruber, 2006). The strength of this pump is measured by not only how much particulate organic carbon (POC) it exports from the surface oceans (between 4-10 Pg C $y^{-1}$; DeVries & Weber, 2017; Dunne et al., 2007; Henson et al., 2011), but also how efficiently that exported material sinks to the deep sea (i.e., transfer efficiency or $T_{eff}$; Francois et al., 2002; Wilson et al., 2022). A range of factors influence $T_{eff}$: the presence of ballast materials (Armstrong et al., 2002), temperature and oxygen-dependent remineralization (Cram et al., 2018; Marsay et al., 2015), and phytoplankton size structure (Weber et al., 2016). While this understanding is largely based on sediment trap observations (e.g., Armstrong et al., 2002; Martin et al., 1987), a less commonly considered factor is the presence of fast-sinking carcasses (jelly-falls) and/or fecal pellets from gelatinous zooplankton and fishes, which are not well captured in the sediment record.

Gelatinous zooplankton (GZ), and in particular, pelagic tunicates (salps, pyrosomes), are notable for their extremely fast-sinking fecal pellets and carcasses, which can exceed 1500 m $d^{-1}$ (Bruland & Silver, 1981; Caron et al., 1989; Lebrato, Mendes, et al., 2013) and result in mass depositions on the seafloor (Henschke et al., 2013; Lebrato, Molinero, et al., 2013; Lebrato & Jones, 2009). Similarly, the fecal pellets of marine fishes can also sink quickly, as the few studies that have measured them show average sinking speeds of 750-1100 m $d^{-1}$ (Robison & Bailey, 1981; Saba & Steinberg, 2012; Staresinic et al., 1983). This is in contrast to marine snow, phytoplankton aggregates, and small crustacean zooplankton (e.g., copepod) fecal pellets that sink at *ca.* 30-300 m $d^{-1}$ (Turner, 2015). Accordingly, several modeling studies have investigated the impact of fast-sinking GZ-mediated POC on $T_{eff}$ (Clerc et al., 2023; Lebrato et al., 2019; Luo et al., 2020), yet none have investigated the combined effect of GZ and fishes, nor more importantly, the impact of these fast-sinking detritus on biogeochemical cycles in the deep ocean.

In addition to direct estimates of detrital flux (sediment traps, Thorium-234 isotopes; Buesseler et al., 2020), the oxygen and macronutrient (e.g., nitrate) concentrations deep in the water column and at the seafloor can also constrain estimates of the biological pump (Andersson et al., 2004; Sulpis et al., 2023). Organic matter remineralization consumes oxygen, but slows significantly in oxygen minimum zones (OMZs) as oxygen is depleted and anaerobic processes, such as denitrification, dominate (Devol & Hartnett, 2001; Van Mooy et al., 2002; Weber & Bianchi, 2020). Unfortunately, the representation of OMZs in coarse-resolution global models has historically been a challenge, with models generally overestimating the extent and misrepresenting the change in OMZs relative to observations (Cabré et al., 2015; Oschlies et al., 2018; Stramma et al., 2012). While these discrepancies have been attributed in part to weak ventilation and poorly resolved equatorial currents (e.g., Busecke et al., 2019; Duteil et al., 2014), other factors such as the stoichiometry of exported organic matter (Devries & Deutsch, 2014; Moreno et al., 2018), and the representation of zooplankton vertical migration (Bianchi et al., 2013) and associated zooplankton-particle interactions (Cavan et al., 2017; Cram et al., 2022) may also influence models' ability to represent observed ocean oxygen patterns. It is unknown, however, whether the inclusion of fast-sinking detritus will exacerbate or alleviate model biases in the OMZs.

In this study, we investigate the effects of fast-sinking detritus from tunicates, fishes, and both on biogeochemical cycling using perturbation experiments with a coupled ice-ocean-biogeochemistry model. We assess their impacts on the horizontal and vertical distribution of POC and oxygen in the mesopelagic and deep sea, and quantitatively attribute the fraction of oxygen consumption in the deep sea arising from fast-sinking detritus.

## 2. Methods

### 2.1 Fast-sinking detritus flux

We introduced a new, fast-sinking detritus (1000 m $d^{-1}$) to the GZ-COBALT model. GZ-COBALT (Luo et al., 2022) incorporated two new (gelatinous) zooplankton groups into the COBALTv2 model (Stock et al., 2020): small and large pelagic tunicates, representing appendicularians and thaliaceans (salps, doliolids, pyrosomes), respectively, with all detritus sinking at the bulk detritus rate (100 m $d^{-1}$). The other marine ecosystem components (heterotrophic bacteria, small and large phytoplankton, diazotrophs, small, medium, and large zooplankton) remain unchanged. Both pelagic tunicate groups are microphageous generalists, able to consume phytoplankton, bacteria, and heterotrophic nanoflagellates, but preferring smaller sized prey. They are predated upon by mesozooplankton and the unresolved higher trophic-level predators. The higher trophic-level predators, which also predate upon the two mesozooplankton classes, serves as a density-dependent loss for zooplankton (Steele & Henderson, 1992). This provides an estimate of the carbon flux from plankton to epipelagic fishes shown to be consistent with observed cross-ecosystem patterns in fisheries catch (Stock et al., 2017). However, this class excludes mesopelagic fishes, which are not represented in our model, despite potentially comprising significant biomass (Irigoien et al., 2014; Proud et al., 2019). Thus, we will henceforth refer to this group as ‘fish’ and utilize the flux to provide a first-order assessment of epipelagic fish.

Detritus in GZ-COBALT is produced from a range of phytoplankton, zooplankton, and fish sources, including phytoplankton aggregation and zooplankton/fish egestion. The fraction of zooplankton egestion going to sinking detritus ranges from 16.7% for microzooplankton to 100% for large mesozooplankton; the rest is partitioned to various dissolved organic matter pools (Stock et al., 2020). Fish and tunicates also generate detritus from 100% of their egestion (fecal pellets), but for fish their egestion fraction is a fixed 35% of ingestion, whereas for tunicates it varies from 20-75% as a function of prey concentration, due to their unique feeding ecology (Harbison et al., 1986; Lombard et al., 2011; Luo et al., 2022). An additional source of tunicate detritus are jelly-falls, which is a mortality that is triggered when ingestion drops below 10% of maximum ingestion rate. Here, only the detritus from large tunicates (thaliaceans) were configured for fast-sinking: 100% of jelly-falls and 75% of egestion. The other 25% of large tunicate egestion is assumed to always sink more slowly (100 m $d^{-1}$) and represents a combination of pyrosome fecal pellets (Drits et al., 1992) and slow sinking salp and doliolid fecal pellets (Deibel, 1990; Iversen et al., 2017; Patonai et al., 2011; Yoon et al., 2001). For fish, all detritus were fast-sinking (Saba et al., 2021; Saba & Steinberg, 2012; Staresinic et al., 1983).

COBALTv2 utilizes seven prognostic tracers to track the various components of detritus: nitrogen (N), phosphorus (P), silica (Si), iron (Fe), lithogenic dust, calcite, and aragonite (Stock et al., 2020). Carbon is associated with detrital N following the Redfield ratio (106:16). COBALTv2 detritus is assumed to sink at 100 m $d^{-1}$ and undergoes temperature- and oxygen-

dependent remineralization (Laufkötter et al., 2017). Remineralization is inhibited by the presence of ballast materials such as Si, dust, and calcium carbonate (Armstrong et al., 2002; Klaas & Archer, 2002), as well as above 150 m to account for euphotic zone bacterial colonization (Laufkötter et al., 2017; Mislan et al., 2014). Sinking detritus that reaches the seafloor is subject to remineralization or burial following the parameterization of Dunne et al. (2007), with a ramp down function to reduce burial in nearshore areas. Further dynamics from the simple sediment layer are described in the COBALTv2 documentation (Stock et al., 2020).

For fast-sinking detritus, we implemented three new prognostic tracers (for a total of 38) to track fast-sinking N, P, and Fe, which are assumed to sink at 1000 m $d^{-1}$. This sinking rate represents an approximate median characteristic velocity of salp, pyrosome, and fish fast-sinking detritus (Bruland & Silver, 1981; Caron et al., 1989; Lebrato, Mendes, et al., 2013; Phillips et al., 2009; Saba & Steinberg, 2012; Staresinic et al., 1983; Steinberg et al., 2022). The fast-sinking detritus is also subject to the same temperature- and oxygen-dependent remineralization as the slow sinkers, but not the remineralization inhibiting effects of ballasting nor colonization.

## 2.2 Experiments

GZ-COBALT with fast POC was run in a global ocean-ice configuration using the Modular Ocean Model 6 (MOM6) and Sea Ice Simulator 2 (SIS2) at a nominal 0.5° horizontal resolution (Adcroft et al., 2019). The model was forced using the 60-year Common Ocean-Ice Reference Experiment II (CORE-II) dataset (Large & Yeager, 2009) and other forcings and initializations as described in Luo et al. (2022). A control and three perturbation experiments were run for five 60-year cycles, or 300 years:

1) No fast-sinking detritus. All detritus sank at 100 m $d^{-1}$. (Control simulation)
2) Only tunicate detritus was fast-sinking.
3) Only fish detritus was fast-sinking.
4) Both tunicate and fish detritus were fast-sinking.

In the experiments, no other changes to the model were made. Outputs from the last 20 years of the $5^{th}$ cycle were computed into a climatological mean for analyses.

## 2.3 Evaluation

For model evaluation, we used particle flux data from 21 observational sites where either free-floating sediment trap or Marine Snow Catcher data were available, compiled by Dinauer et al. (2022), and oxygen and macronutrient concentrations ($NO_3$, $PO_4$) from World Ocean Atlas 18 (Garcia et al., 2019a, 2019b). Modeled sediment oxygen utilization rates (OUR) was computed based on POC flux to the bottom, minus burial flux based on Dunne et al. (2007) and sediment denitrification following Middelburg et al. (1996). This was compared with a new global data product of sediment OUR from Jørgensen et al. (2022; hereafter J22), which was constructed using a regression fit to 798 in-situ benthic measurements.

## 3. Results

The integration of fast-sinking detritus into GZ-COBALT resulted in an overall decline in net primary production (NPP) and particulate organic carbon (POC) export flux past 100 m relative to the control. NPP decreased 7.8%, 9.5%, and 15%, while export decreased 5.6%, 6.8%, and 11% in the tunicate-only, fish-only, and combined cases, respectively, relative to the GZ-COBALT control (NPP: 52.4 Pg C $y^{-1}$; export: 6.17 Pg C $y^{-1}$). Declines in the subtropical gyres were most pronounced as the already limiting surface nutrients redistributed further down in the water column due to the fast-sinking detritus (Fig. 1A). Overall, there was a vertical redistribution of nutrients and detritus, with the tunicate-only and fish-only cases exhibiting similar spatial patterns and magnitudes and the combined case giving values slightly less than the sum of the two others. In the top 100 m, fast-sinking detritus production comprised 6.4%, 8.1%, and 13.9% of the total detritus production in the tunicate-only, fish-only, and combined cases, respectively, but the relative proportion of detritus that was fast-sinking increased with depth.

At the sequestration depth, the fast-sinking detritus increased POC flux past 1000 m by 19%, 21%, and 37% (to 1.01, 1.02, and 1.15 Pg C $y^{-1}$ for tunicate-only, fish-only, and combined, respectively; control: 0.84 Pg C $y^{-1}$), with large increases in much of the extratropics and in upwelling zones (Fig. 1B). A few areas exhibited large declines in POC flux past 1000 m, such as at the northern equatorial Pacific, the northern Indian ocean, the northern Benguela current, and the Canary current. These are all areas where OMZs reduced in size with fast-sinking detritus (Fig. 1B, Fig. 3A) leading to enhanced remineralization rates under newly aerobic conditions. Both transfer efficiency ($T_{eff}$) and remineralization length scales between 100 m to 1000 m exhibited similar patterns as the POC flux past 1000m, albeit significantly muted (Fig. S1A, Fig. 1D). In the subtropical gyres, the POC flux at 1000 m with fast-sinking detritus was slightly lower than the control, but transfer efficiency increased, indicating this pattern was primarily driven by differences in surface production. Overall, remineralization length scales increased globally, except for the aforementioned areas near OMZs.

POC flux reaching the seafloor showed broad spatial patterns coherent with those at 100 and 1000m. Globally, there were relatively modest enhancements due to the fast-sinking detritus of 5.6%, 6.3%, and 11% (to 1.33, 1.34, and 1.4 Pg C $y^{-1}$ for tunicate-only, fish-only, and combined, respectively) relative to the control (1.26 Pg C $y^{-1}$; Fig. 1C). Though, at seafloor depths of 2000 m or deeper, the impact of the fast-sinking detritus was much greater (increases of 36.7%, 39.9%, and 67.2%, respectively, relative to 0.28 Pg C $y^{-1}$ in the control). Due to faster detritus sinking speeds, the relative contribution of coastal zones (200 m or shallower) to global seafloor fluxes decreased, from 59% in the control case to 52% for both tunicate-only and fish-only, and 47% for tunicates and fish combined. This comes as transfer efficiency to the seafloor ($T_{eff\_btm}$) was globally enhanced, with the largest increases in the eastern equatorial Pacific (Fig. S1B).

A comparison of the POC export flux profiles at 21 sites (Dinauer et al., 2022; Fig. S2) shows that overall, the model simulations with fast-sinking detritus fell within range of the observations (Fig. 2). Given that the COBALT flux attenuation dynamics were tuned to many of the same observations (Laufkötter et al., 2017), it is unsurprising that the observational match, in terms of bias, RMSE, and correlation coefficient, was best in the control simulation at most sites, though in many cases the differences were quite small (Fig. S3; 14/17, or 82%, and 11/21, or 52%, of sites had correlation and bias within 5% and 25% of the control, respectively). However, notable exceptions were the MX, VERTEX II, III, and GUAT sites off the western Mexico and

Central American coasts, where more fast-sinking detritus significantly improved the model-observational fit. These sites were generally in areas where anaerobic conditions limited export in the control simulation, but not after adding fast-sinking detritus (Fig. 2, S3).

An assessment of the biogeochemical impacts of fast-sinking detritus showed the OMZs shrunk and deepened relative to the control, particularly in the combined case (Fig. 3A, Fig. S4-7). An evaluation of the total hypoxic ($O_2 \leq 60$ mmol $m^{-3}$) and suboxic ($O_2 \leq 5$ mmol $m^{-3}$) volume showed that fast-sinking detritus slowed down the expansion of low oxygen zones following model initialization to WOA, and thus reduced the overexpression of hypoxia and suboxia common in global models (Fig. 3D-E). Hypoxia expansion was reduced in all fast-sinking detritus cases through *ca.* 200 years, though the tunicate-only case accelerated to the control simulation afterwards. This was not the case for the fish-only or combined simulations, which remained at a lower hypoxic volume than the control. All fast-sinking detritus experiments decreased the total suboxic volume, with the tunicates and fish combined simulation decreasing suboxia by approximately 40% globally (Fig. 3E). Accordingly, other biogeochemical processes that occur under low oxygen conditions (e.g., denitrification) were also reduced. In the eastern equatorial Pacific, the nitrate deficit in the mesopelagic was much reduced relative to the control (Fig. 3B) and more consistent with observations, as can be seen through the N* field, which is a metric of the excess nitrate over phosphate (Gruber & Sarmiento, 1997). In the abyssal zone (>3km deep), the high transfer efficiency of fast-sinking detritus increased nitrate and decreased oxygen, resulting in modest biases in each. Nonetheless, in a zonal slice of the eastern Pacific following the P18 line, model skill metrics for $NO_3$, N*, and to a lesser degree, $O_2$, improved with the addition of fast-sinking detritus (Fig. S4-7).

The increased supply of POC to the seafloor resulted in increases in benthic oxygen consumption of 6.5%, 7.1%, and 12% (to 110, 111, and 116 Tmol $O_2$ $y^{-1}$ for tunicate-only, fish-only, and combined) relative to the control (103 Tmol $O_2$ $y^{-1}$). Even still, values are far lower than the J22 data product, which predicts benthic oxygen utilization rates (OUR) from a linear relationship between NPP and seafloor depth (Fig. 4). This relationship, which was derived from sparse observations, suggests a mean OUR of 1.74 mmol $O_2$ $m^{-2}$ $d^{-1}$, which totals approximately 225 Tmol $O_2$ $y^{-1}$ globally (given a seafloor area of 3.54E14 $m^2$). While J22 did not publish a total range, an estimated range (roughly derived from their 95% CIs) is ~120-430 Tmol $O_2$ $y^{-1}$ globally. In the combined case, the modeled OUR in the extratropics and upwelling zones approaches the J22 mean, but values in the subtropics from all models were still significantly lower. However, the simulated global OUR in the fast-sinking detritus cases does approach the J22 lower range.

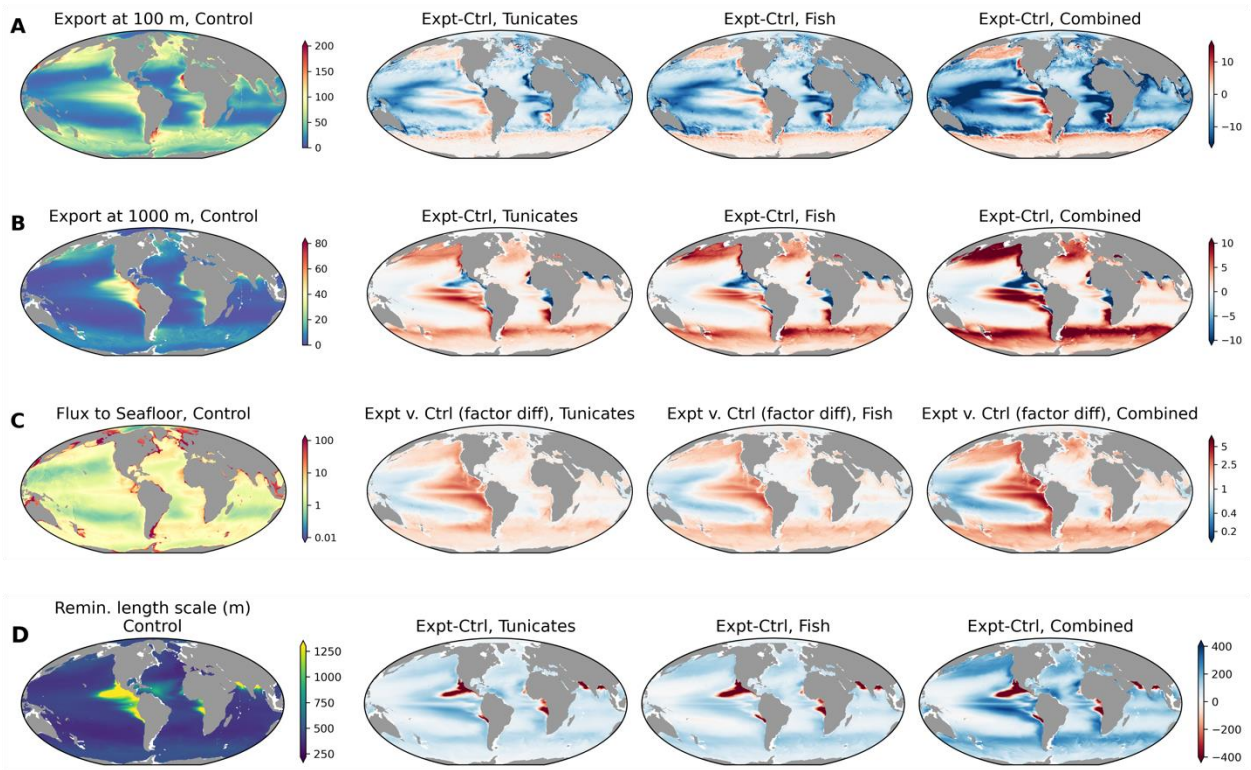


**Figure 1. Detrital carbon fluxes and remineralization.** (A) Particulate organic carbon (POC) export at 100 m (mg C $m^{-2}$ $d^{-1}$), showing (left) raw values from the GZ-COBALT control (center to right) the differences between the control and experiments. (B) Same as (A) but at 1000 m. (C) Same as (A) but at the seafloor; note the non-linear colorbars and the use of factor differences. (D) Average remineralization length scale between 100-1000 m, calculated as r = (1000-100) / ln($export_{100}$/$export_{1000}$), where $export_n$ refers to the POC export flux at *n* depth. Colorbars are restricted for display purposes. In the Eastern Tropical North Pacific (ETNP) between 12-18° N and 92-112° W, the remineralization length scales were 2240 m, 1748 m, 1611 m, and 1416 m for the control, tunicates only, fish only, and combined experiments, respectively. These are associated with transfer efficiencies of 65%, 59%, 57%, and 52%, respectively.

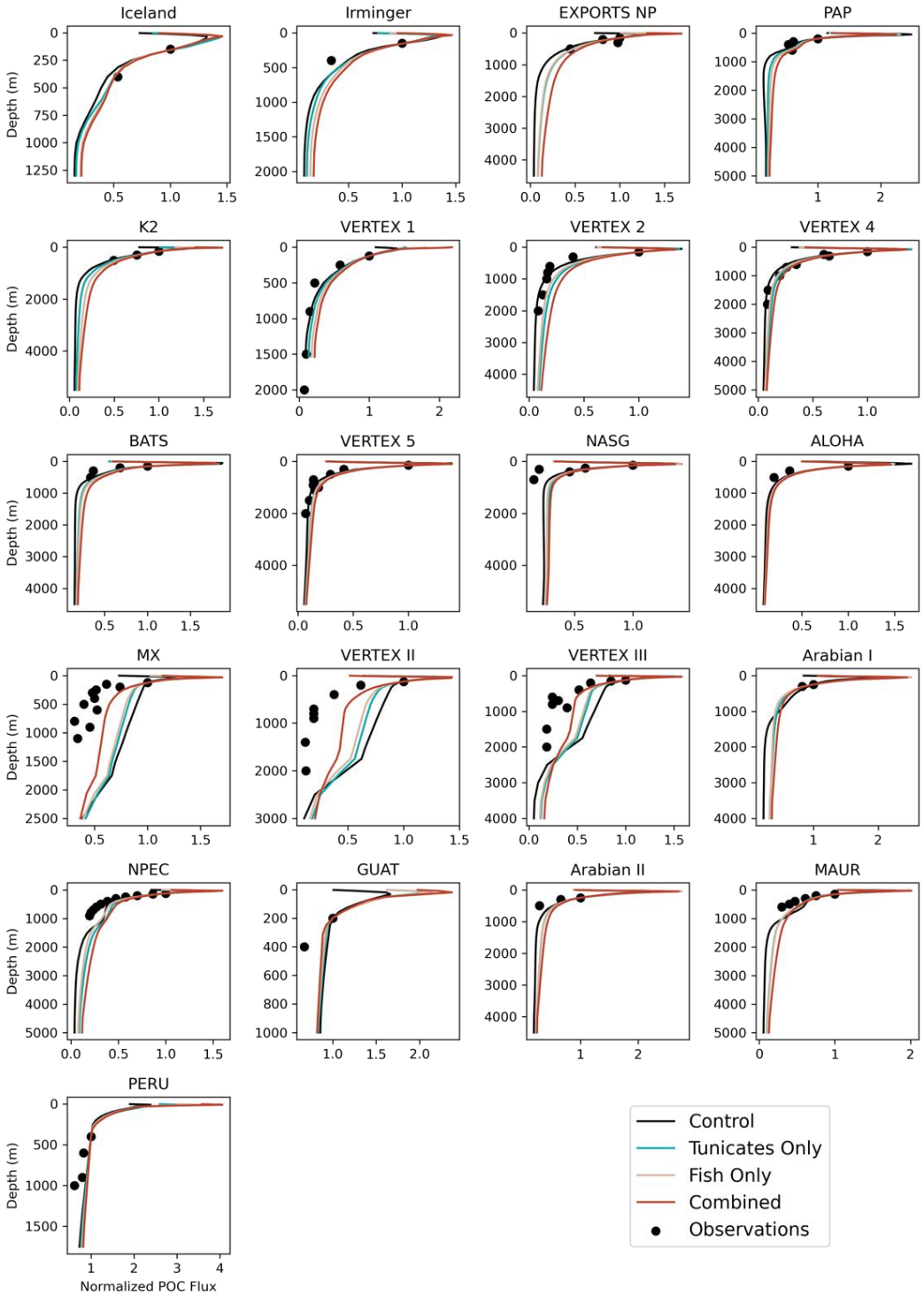


**Figure 2. Normalized POC export flux** at 22 sites (see Fig. S2), comparing the GZ-COBALT control and the three fast-sinking POC simulations with a set of compiled observations of POC flux profiles from either free-drifting sediment traps or with Marine Snow Catchers (Dinauer et al., 2022). Given the seasonal difference in POC flux profiles, model results from only the season, or a 3-month period, in which the observations were obtained were plotted. Comparison statistics are given in Fig. S3.

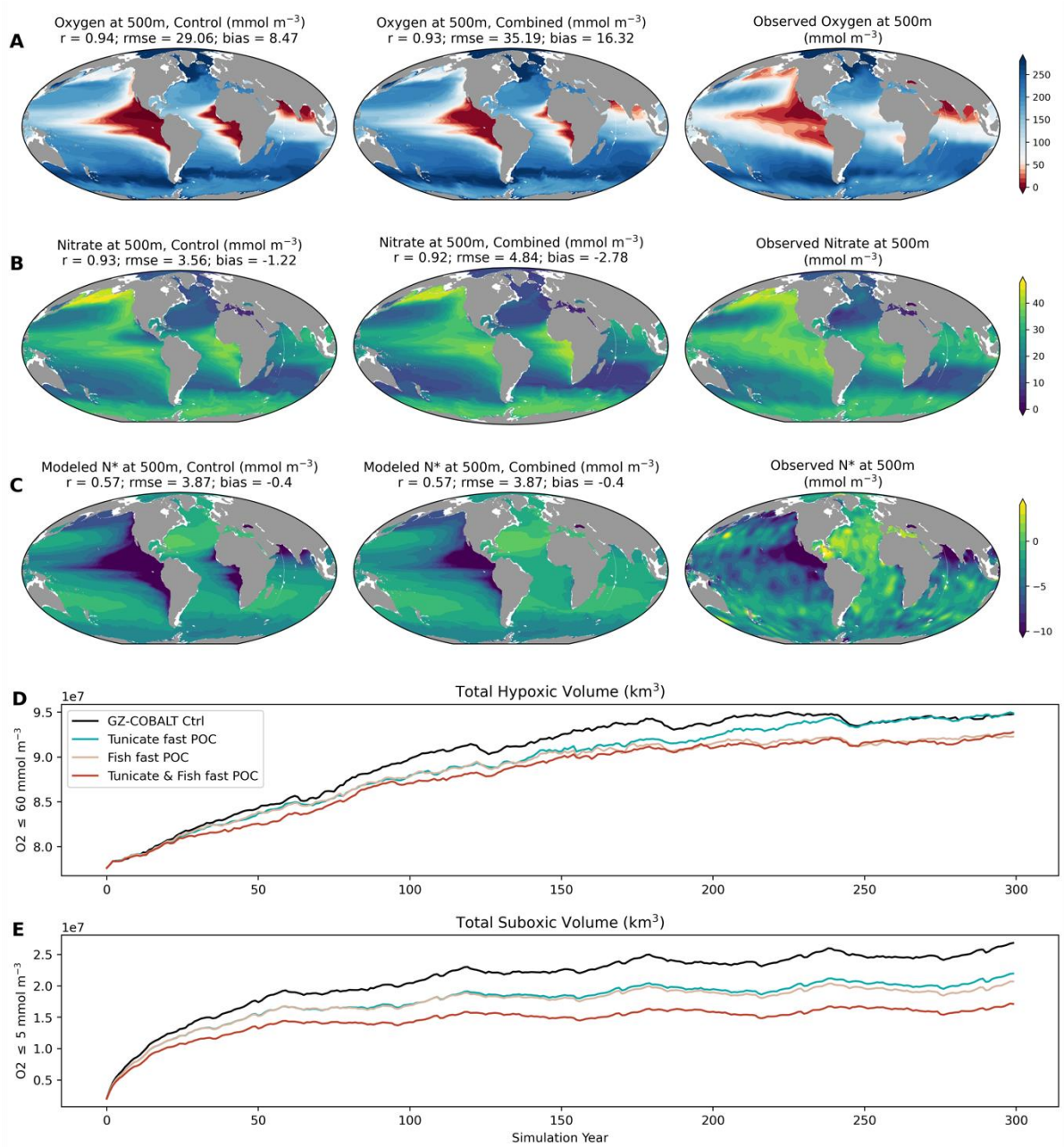


**Figure 3. Ocean biogeochemical impacts of fast-sinking detritus.** Comparisons of (A) oxygen concentrations (mmol $O_2$ $m^{-3}$), (B) nitrate concentrations (mmol $NO_3$ $m^{-3}$), and (C) N* ($NO_3$ – 16*$PO_4$; mmol $m^{-3}$) at 500 m depth between the GZ-COBALT control, the tunicates and fish combined case, and observations from the World Ocean Atlas (WOA). Total (D) hypoxic ($O_2 \leq$ 60 mmol $m^{-3}$) and (E) suboxic ($O_2 \leq 5$ mmol $m^{-3}$) ocean volume (in $km^3$) by simulation year, shown for the GZ-COBALT control and all three fast-sinking detritus cases. Note that simulations were initialized from WOA, so the size of the departure from the initial condition in panels (D) and (E) is proportional to the model bias.

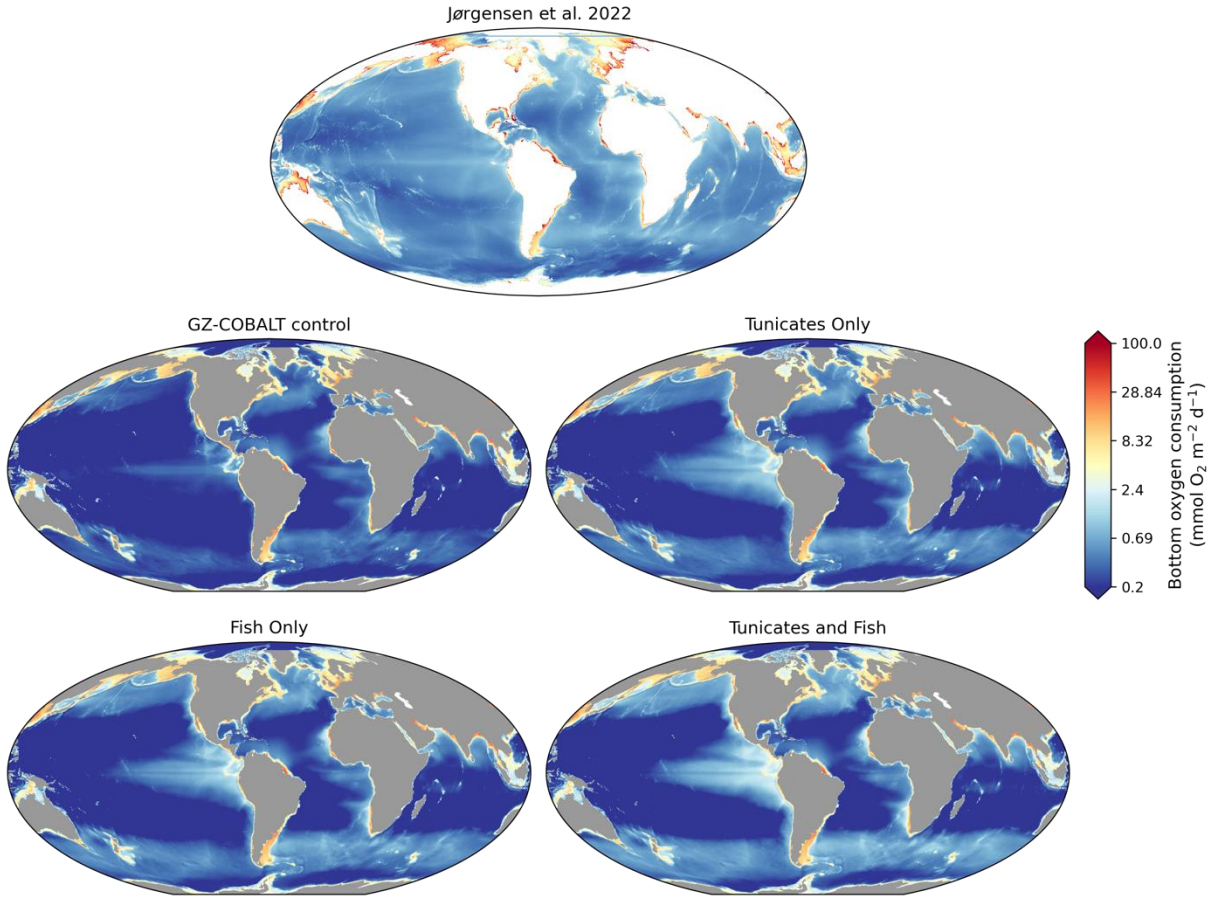


**Figure 4. Benthic oxygen utilization.** Comparisons between the Jørgensen et al. (2022) observational product (top) and simulated oxygen consumption at the ocean bottom in the GZ-COBALT control and three experimental cases (tunicate-only, fish only, and tunicates and fish combined).

## 4. Discussion

We used a coupled ocean physical-biogeochemical model to assess the biogeochemical fingerprints of fast-sinking detritus from both pelagic tunicates (e.g., salps, pyrosomes) and fishes in a series of perturbation experiments. The different fast-sinking detritus cases showed that the tunicates-only and fish-only cases were roughly similar in magnitude and spatial extent, with the latter slightly higher along the coasts and in the high productivity regions than the former, consistent with the large scale contrast between tunicates and mesozooplankton in Luo et al. (2022).

Overall, addition of fast-sinking detritus decreased global NPP from 52 to 44-48 Pg C $y^{-1}$, due to the redistribution of ocean nutrients (N, P) from the upper ocean to depth. Accordingly, POC export at 100 m also declined (from 6.2 to 5.5-5.8 Pg C $y^{-1}$; Fig. 1A), despite increases in the export ratio. While these declines yielded values still within their range of uncertainty (Carr et al., 2006; Dunne et al., 2007; Field et al., 1998), our results highlight that the processes of generating additional and/or fast-sinking ocean detritus reduces euphotic zone productivity, at least on multi-centennial timescales. Compared to a model that adjusted for the surface impacts of some fast-sinking detritus (e.g., Clerc et al., 2023), our results show a much greater decline in surface export flux. This suggests that recalibration of the bulk POC remineralization scheme (Laufkötter et al., 2017) may be necessary to integrate the full spectrum of sinking detritus into an Earth System Model (ESM).

Accordingly, model skill in representing normalized export fluxes from observations (Dinauer et al., 2022) were slightly degraded, consistent with modifying a component of a tuned model (Laufkötter et al., 2017). Still, there were notable areas in which normalized export fluxes with fast-sinking detritus were a better match for observations than the control, primarily within eastern boundary currents and in OMZs (Fig. 2, S3). This arises due to the interactive effect of fast-sinking detritus on oxygen and remineralization rates. The total remineralization occurring within a given water volume within the mesopelagic decreases due to fast-sinking detritus, and oxygen increases accordingly (Fig. 3). This results in less anaerobic and more aerobic remineralization. Since aerobic remineralization rates are faster, the remineralization length scales are decreased (Fig. 1D). In COBALT, temperature- and oxygen-dependent aerobic remineralization occurs until oxygen reaches a minimum, 0.8 μmol $kg^{-1}$, below which anaerobic remineralization occurs at 1/10 the aerobic rate (Laufkötter et al., 2017; Stock et al., 2020). This results in a threshold effect and remineralization length scales within OMZs to be up to 10 times longer than in oxygenated waters (Fig. 1D). In the control simulation, the average mesopelagic remineralization length scale in the Eastern Tropical North Pacific (ETNP) was 2240 m, compared to 1416 m in the fish and tunicates combined case. While there is evidence of long remineralization length scales and high transfer efficiencies in the ETNP, the observations instead support remineralization length scales between 800-1650 m (Devol & Hartnett, 2001; Van Mooy et al., 2002), favoring the simulations with fast-sinking detritus (Fig. 2).

Biases in the modeled OMZs have often been attributed to sluggish ventilation and under-resolved equatorial currents in coarse-resolution models (Busecke et al., 2019; Duteil et al., 2014; Getzlaff & Dietze, 2013). So far, the evidence regarding zooplankton-mediated effects on OMZs have indicated that they increase OMZ volume, both through diel vertical migration to the upper margins of the OMZs (Bianchi et al., 2013) and via zooplankton-mediated particle disaggregation (Cram et al., 2022). We acknowledge that there are still significant uncertainties in representing the contribution of fast-sinking detritus from tunicates and fish, such as

proportion of detritus that is fast-sinking in both groups (c.f., Iversen et al., 2017) and mineral ballasting in fecal pellets, which is included for the slow-sinking but not fast-sinking detritus in this current formulation. Additionally, we omitted representation of fish carcasses, which may be non-negligible in high productivity areas (Drazen et al., 2012; Higgs et al., 2014), as well as mesopelagic fishes, where there is still substantial uncertainty regarding both overall biomass and metabolic rates governing their contribution to the biological pump (Davison et al., 2013; Irigoien et al., 2014; McMonagle et al., 2023; Proud et al., 2019). Still, the reduction of OMZ volume and associated biases implies an additional, biological mechanism via fast-sinking tunicate and fish detritus for improving OMZ simulation in ocean biogeochemical models.

The reduced expansion of OMZs in the fast-sinking detritus cases was most pronounced in the suboxic (<5 mmol $O_2$ $m^{-3}$) rather than hypoxic (<60 mmol $O_2$ $m^{-3}$) waters (Fig. 3). This is likely due to the shifting of the OMZs deeper due to abyssal respiration (Fig. S4-7). Accordingly, water column denitrification, the reduction of oxidized nitrogen (here, $NO_3$) to $N_2$ under low oxygen conditions, also declined, resulting in improvements in negative $NO_3$ biases between 500-2000 m (Fig. S4-7). The modeled oxygen patterns are qualitatively consistent with a recent study by Bianchi et al. (2021), which suggests that fish POC comprise an substantive fraction of oxygen utilization below 1000 m. However, in our simulations, fish POC production comprises 0.56-0.73 Pg C $y^{-1}$, significantly less than the 1.5 and 3.0 Pg C $y^{-1}$ as suggested by Saba et al., (2021) and Bianchi et al. (2021), respectively. Further, contrary to the suggestion that present day ocean deoxygenation (Schmidtko et al., 2017) may be partially masked by declines in fish populations relative to the preindustrial ocean (Bianchi et al., 2021), our results indicate that in a world with significant declines in fish populations, fish detritus would instead be redistributed to be mediated by mesozooplankton instead, which would sink at the slower, “bulk” rate and redistribute nutrients higher in the water column. This would result in an expansion of OMZs, as remineralization would be shifted towards the surface rather than the mesopelagic to abyssal ocean. It is unclear how tunicate populations are likely to respond in the case of significant fish population declines, but as they primarily compete with microzooplankton rather than mesozooplankton (Luo et al., 2022; Stukel et al., 2021), it is unlikely that fast-sinking tunicate detritus could compensate for decreases in fish detritus.

A key difficulty in constraining deep-sea biogeochemical fluxes is the lack of observational data; however, sedimentary oxygen utilization may be used as an independent, large-scale biogeochemical constraint, as the seafloor serves as the terminal sediment trap (Andersson et al., 2004; Dunne et al., 2007; Middelburg, 2019). Past estimates have suggested a large-scale concurrence between organic matter respiration as estimated from water column sediment traps vs. sedimentary oxygen utilization rates (OUR), particularly in the open ocean (Dunne et al., 2007; Jahnke, 1996), but it was not clear *a priori* whether such observations would support increased fluxes to the bottom from fast-sinking detritus. Our results show that recent seafloor OUR observations (Jørgensen et al., 2022; J22) support increased organic matter fluxes from fast-sinking detritus relative to our control simulation. Indeed, even with the highest $T_{eff\_btm}$, modeled seafloor OUR was a factor of 2 lower than J22, though likely within uncertainty bounds. Reasons for this discrepancy (see also Andersson et al., 2004; Sulpis et al., 2023) could include biases in both the observations (uneven sampling and bias towards coasts and high productivity areas) and the models (coastal productivity in a coarse-scale model is biased low despite broad skill in simulating NPP; Stock et al., 2014). The large-scale benthic flux patterns between oligotrophic gyres and high latitudes as seen in J22 are better reproduced in the fast-sinking detritus case, but fluxes in subtropical regions remain low. These differences highlight a

broader need to reconcile pelagic POC export fluxes with benthic sedimentary demands in ESMs, particularly with increasing focus on coastal zones, blue carbon, and other climate mitigation strategies, where sedimentary dynamics may be increasingly important to resolve.

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**Open Research**

All model outputs necessary to reproduce the results in this manuscript are available at Zenodo at https://doi.org/10.5281/zenodo.8431830. Fortran code for the model code modifications are at https://github.com/jessluo/ocean_BGC/tree/gz_COBALT, and the analysis codes are available at https://github.com/jessluo/gz_COBALT_fastPOC_analysis.

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