Deep sea carbon export is measurably enhanced by daily vertical migrations of midwater animals

The manuscript by Benoit-Bird et al., uses a novel optical particle trap coupled with upward facing acoustics to investigate the influence of diel vertical migrants to the export of carbon to the seafloor (~900 m). I found this topic very relevant and the approach both interesting and compelling. The manuscript is generally well-written. My overarching comments are:

1. **Contextualising carbon export, flux and sequestration within established literature**. As this topic is increasingly relevant considering future perturbation as mentioned by the authors (i.e. mesopelagic fisheries), and future management strategies (i.e. NCS), care needs to be given here, especially considering the broad audience of this journal.

    a. Carbon export, both via the gravitational pump (termed background export in this study) and the migrator contribution measured in this study is at the seafloor (~900 m). The authors found that the background export was enhanced by migrators (through of assumptions I address in comment 2), and while they do not explicitly state this enhancement by migrators is primary export production (i.e. migrators are transporting fresh carbon from the surface), my fear is that it is implied. This implication is reflected in the authors comparison of their results to studies measuring active carbon export across a shallower depth horizon (i.e. 100 – 200 m in many of the cited studies, like McMonagle et al., 2023) – see specific comment below: L. 146 – 149. Furthermore, because "export" typically refers to carbon transfer from the surface ocean to the subsurface (Collins et al., 2025; doi: 10.1029/2024GB008393), the current phrasing implies that the observed seabed export pulses are driven namely by migrator transport from the sea surface. Without further clarification, readers may assume this is the authors' conclusion, a claim that is neither supported by the data nor likely intended.

    It appears from the acoustics that a proportion of the migratory mesopelagic community migrates to the surface, while other portions may make shorter migrations within the mesopelagic. It is possible, the DVM associated pulses in carbon export seen at the seafloor could reflect carbon transferred through multiple trophic interactions within the mesopelagic, supporting Vinogradovs ladders of migration (Vinogradov 1960). Therefore, migrations within the mesopelagic may facilitate the transport of carbon already exported out of the surface layer deeper in the water column. **This warrants future studies linking mesopelagic food web dynamics and carbon cycling which is highly**

relevant, and I'd argue, is perhaps the most significant outcome this work. I would have liked to see more discussion around this.

b. Also, the authors found mean biomass is not an important predictor of DVM mediated carbon export, finding parameters reflecting behaviour to be more important. I do suggest the multiple linear regression methods to be reviewed by a statistician as the decisions made could greatly influence the explanatory power of predictors. However, assuming these conclusions are justified, these predictors are important to export on the seafloor, which may not be the case when considering export across a 200 m depth horizon. Therefore, I think it's important to be more explicit when comparing export results from this study with previous work. The strength of this study is in the support of migrating animals greater contribution of export at depth. Therefore, these animals may not appear as important to export out of the epipelagic zone, but have an outsized role in transporting carbon to deeper in the water column (whether that's primary export or through trophodynamics within the mesopelagic zone). Importantly, carbon transported deeper in the water column increases the time it's sequestered. (see specific comment below - L. 202 – 210)

Overall, I think a paragraph in the discussion addressing these would be very beneficial to the community and would greatly enhance the importance of this work.

2. **The transparency of using proxies for animals.** While the authors do state acoustic volume backscatter at 38 kHz is used as a proxy for the density and biomass of midwater animals in Figure 1 and provide a description in the methods, there are several times (lines highlighted below) where perhaps conclusions are overstated (i.e. L. 153 – carbon export was affected little by how many animals were present). Acoustics are certainly a powerful tool, but, without biological ground truthing, it is important to be clear, conclusions made are interpretations. I would have liked to see more phrasing along the lines of, "taken together, the evidence most strongly points to…" I think a few lines/paragraph outlining the assumptions, biases and recommendations for future work is necessary and would make a richer discussion.

Specific comments:

Introduction:

L. 37. – The reference cited, Friedlingstein et al., 2006 does not appear to support this statement. Please verify this and provide a more appropriate estimate, or revise the

statement. I suggest looking up this more recent study by Tjiputra et al., 2025 (https://doi.org/10.1038/s41467-025-57371-y) which models historic and future projections including abiotic simulations which also include land-ocean feedback for a reframed statement.

L. 51. – I like the "biological conveyor belt" analogy. However, it's important to describe not only how animals transport, i.e. feed at surface and migrate, but how they inject carbon into the water column. The first mention of fecal pellets is in the discussion. Studies quantifying c export driven by migrators include POC, DIC and DOC, or some combination. I suggest adding a sentence introducing all injection pathways – egestion, excretion, respiration and mortality and state this study will explicitly consider fecal pellets at the end of intro – and why.

L. 52. – Steinberg et al., 2000 – may not be the best reference here as they explicitly look at the transport of DOC and DIC. Why not use a study that includes POC transport as well since this is the focus of this paper?

L. 53 – add 'on climate relevant timescales (i.e. > 100 years)' after 'atmosphere'.

L. 55 – 58. I am unable to reconcile the claim that DVM is three times as important to the health of our planet as the Amazon rainforest before its widespread disturbance. "important to the health of our planet" is similarly vague. Also, 5- 50% of total carbon flux and 10-90% of particulate organic carbon flux as referenced in the previous sentence does not equate to carbon dioxide removal (from atmosphere) or, storage. The cited study here, Heinrich et al. (2021) report on the standing carbon stocks and carbon sequestration rates of secondary forests in the Brazilian Amazon, so it is unclear what value was used to compare a DVM metric to the rainforest capacity "before its widespread disturbance". The cited global modelling studies do provide compelling evidence for the substantial contribution of DVM to carbon export and sequestration. For example, Nowicki et al. (2022) estimate migrant-mediated carbon export of approximately 1.0 Pg C yr^{-1} and a sequestration inventory of approximately 150 Pg C. However, it is unclear which quantities were compared to derive the threefold estimate. I suggest the authors provide the calculation and clarify the metrics and timescales involved, or remove the comparison. In particular, differences in carbon flux or storage should not be interpreted as equivalent differences in overall planetary importance.

Additional intro comment:

- It would be helpful to include a line describing micronekton – e.g. size and broad taxonomic groups.

Results:

L. 69 – 70. Is abundance appropriate here? Authors describe using NASC as a proxy for total biomass, but do not describe how they derive abundance (perhaps sv within layers?). Can authors provide this description if abundance is indeed appropriate? Otherwise, I suggest change this to match both the methods and description in figure 1. (i.e. acoustic volume backscatter, a proxy for the biomass of midwater animals).

L. 71. It would be helpful to include a line describing light attenuance in this study for readers unfamiliar with optical methods. i.e. "briefly, the more particles caught on the trap reduced the light penetrating through the disk; therefore, increased light attenuance (hereby attenuance) = increased export". Attenuance, although an established optical metric, could be confusing for readers used to thinking about particle attenuation through the water column due to microbial remineralisation or flux feeders.

L. 87 – it should either be carbon flux or attenuance – carbon flux attenuance reads POC remineralised in water column

L. 105. Should this be daily mean, not daily total?

L. 116 – add 'weighted mean' before noon depth

Discussion:

L. 126 – It's unclear to me how the authors found fishes to be the dominant scatterer based on the results presented. As much of the discussion is centred on the contribution of fish fecal pellets, it would be helpful to make this clearer in the results section along with the associated assumptions and biases in the discussion.

L. 128 – I suggest adding a line connecting carbon flux to sequestration. This is the most important finding in this study, so it needs to be very clear. This study shows show DVM enhances C export to deep sea (seafloor). Perhaps, "The deeper carbon is transported in the water column, the longer it remains our of circulation (Siegel et al., 2023; https://doi.org/10.1146/annurev-marine-040722-115226)". Therefore, "these findings highlight an underappreciated ecosystem service ….".

L. 139 – 141 – new results presented here – i.e. particle composition – I suggest removing from discussion and replace in results (paragraph starting on line 75). This would help 'ground truth' the optical trap data when they're presented which gives the conclusions more strength – e.g. intact pellets suggest egestion by migrators.

L. 142 – 145. It's important to note here, these studies used empirical modelling to estimate active export, which of course is very different from the methodology used here. While this may add some context, I don't think it's appropriate to make this comparison without making this methodological distinction, as well as being explicit about the region and time of year from each study.

L. 146 – 149 – My interpretation of this line is that the authors assume export measured in this study consists of new export from the surface, is this correct? If that's the case, I don't think there's evidence to support this as I described in my first overarching comment. While export production estimates measured at the base of the euphotic zone or mixed layer provide a coarse jumping off point to predict sequestration, we can not assume based on the methods applied here that the increases in POC observed at the seafloor were shunted directly by migrators feeding at the surface (i.e. the export production measured at the base of the euphotic zone). Perhaps a proportion that originated in the mesopelagic is also shunted to the seafloor (refer to overarching comment 1a).

L. 153 – I suggest removing "carbon export was affected little by how many animals were present". The results of this paper do not reflect this as the abundance of animals were not enumerated. The following line appropriately describes the results.

L. 155 – add "to the seafloor" after flux

L. 159 – add "Our results suggest…"

L. 162 – McMonagle et al. 2023 presents a bioenergetic model, not geophysical. Also, it is important to make a distinction between models that quantify export across a shallower depth horizon (i.e. McMonagle sensitivity analysis used 100 – 200 m depth as export horizons) from this study quantifying export at the seafloor. I suggest adding *to the seafloor* after "… regulating carbon export" and *measuring export across shallower depth horizons (i.e. 100 -200 m)* after "…models".

L. 165 – POC export peaks?

L. 181 – 183 – This sentence seems to contradict the previous paragraph. The previous paragraph notes that to drive an 8 hr delay, pellets would have to travel up to 900 m, necessitating an upper limit of a 2700 m d-1 sinking speed, which the authors note is in range of previous studies. Since the MARS observatory is 900 m deep, this suggests that fecal pellets produced at the surface should, in theory sink through the whole water column. Therefore, why assume that the carbon produced through the night high in the water column would not make it to the seafloor?

L. 185 – "…consistent with the hypothesis that particulate carbon reaching the seafloor in two pulses each day.." – in this study? If so, add, otherwise reword for clarity.

L. 202 – 210 – The authors advocate for better parameterisation of carbon flux models with important metrics found in this study. However, considering most carbon flux models including those cited here use the base of the euphotic zone - i.e. 100 – 200 m as their export depth horizon, the two most important variables in this study may not be relevant. 'Weighted mean depth at noon' – export in the modelling studies is shallower than this, so would it make a difference if they reside at 400 m or 500 m? 'midnight-noon change in depth layer', again, I wonder if this makes a difference for carbon crossing 200 m. This study

adds critical information that is left out of these modelling studies – e.g. how much of this exported material (primary and secondary) reaches the seafloor – which is a very important conclusion in itself. I'd just caution against overstating the importance of the conclusions when it comes to current carbon export models. Instead, these conclusions support the importance of incorporating these parameters into future models – advocating to push the field further – away from just looking at export, but ultimately how the mesopelagic food web may contribute to sequestration. More discussion around this is welcome.

Additional discussion questions:

- could authors discuss non-significant linear relationship between % of C from migrators to total flux per day? What could be driving the large variations in both fluxes?

- There appears to be a reduction in backscatter intensity mid June – July in Figure 1. Could the authors comment on potential affects of seasonality in the study region?

Methods:

L. 250 – I thought macrozooplankton are generally masked at 38Khz, sensitive more to gas-bladdered organisms. Krill are sensitive at 120Khz according to the study cited. Can the authors clarify?

L. 254 – 258 – If scattering layers are based on values at constant depth, how is this method used to detect migration. Could the authors rephrase this for more clarity?