Title: Including different mesozooplankton feeding strategies in a biogeochemical ocean model impacts global ocean biomass and carbon cycle
Authors: Di Matteo et al.
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Reply to reviewers' comments

The authors would like to thank the three reviewers for their feedback and constructive comments. All suggestions were considered and the issues raised were addressed, which in our opinion led to increasing the clarity of the revised manuscript. Below are the authors' point-by-point responses to the comments.

Reviewer comments are in bold blue and responses are in normal font. Changes to the manuscript are in italics. Line numbers mentioned below refer to the revised manuscript.

Reviewer #1

General comments:

The manuscript concerns the implementation of 3 functional groups into the mesozooplankton of the NEMO-PISCES modelling framework. The manuscript describes the model setup, does a validation exercise by comparing with available data, describes the emerging biogeography of mesozooplankton, and examines different setups of the model to understand the importance of the model assumptions, and finally explores the impact of the increased diversity on carbon flux estimations.

Overall, the work present a very timely and relevant extension of the PISCES model system, the model is well executed, and the results well presented. In general I find this a great piece of work. I do have a few technical concerns and some places where I think the presentation could be improved.

The authors would like to thank the first reviewer, Ken Andersen, for his valuable and useful comments.

Major comments:

1. I find the presentation of the dynamic foraging effort on page 6 very difficult to understand - and I was even the one who formulated the theoretical model in the Kiørboe (2017) paper. I suggest to rewrite this section completely. First, focus less on the equations, but rather on the concepts. The idea is that a zooplankton optimizes its fitness, which is either growth/mortality or growth - mortality (when growth/mortality < 1). Growth emerges from a functional response minus respiration; mortality is a background + predation risk. The

equations 2-3 could even be put in an appendix, and the result could be presented with reference to figure 2.

Thank you for this comment. Following your suggestions, Equations 2 to 6 are now in the Appendix A2 and the foraging effort is now presented as follows:

Page 7 (L. 157-171): *"In addition to the explicit representation of these three PFTs (Figure 1), the FOREFF configuration implements a non-dimensional foraging effort p for active feeding organisms (i.e. cruisers). The foraging effort p varies between 0 and 1 and represents an optimization of the fitness via the fraction of time spent foraging. The parameter is adapted from Kiørboe et al. (2018a) and implemented in Equation 1 (see Appendix A2 for more details). It is based on the assumption that ambushers have an invariant foraging effort due to their passive behaviour, while cruisers may modify their foraging effort in response to prey abundance to optimize their fitness (Tiselius et al., 1997; Kiørboe et al., 2018a). The foraging effort of cruisers varies in response to prey density (see Figure 2 for the theoretical curve) to maximize their fitness, balancing food intake, predation risk, and the metabolic cost of searching for food (Kiørboe et al., 2018a; Werner and Anholt, 1993; van Someren Gréve et al., 2019). At high prey densities, cruisers reduce their foraging effort to lower both predation risk and metabolic expenditure. Meanwhile, at intermediate prey densities, foraging effort reaches its maximum value of 1. At low prey densities, foraging effort decreases, implying that cruisers no longer swim or swim very little but do not have access to food, so they eventually die. Moreover, the foraging effort is set to zero when prey concentration falls below a minimum threshold concentration* R_{min} *(see equation A7), as in Kiørboe et al. (2018). In our case, this threshold is 1.56* $mmol/m^3$*, which corresponds to the minimum prey concentration at which the energetic gain from foraging offsets the maintenance costs of cruisers."*

2. There is actually an inconsistency in the formulation of the dynamic foraging as it is implemented here. The actual mortality that the cruisers experience is a quadratic mortality, which is not the same as the one that is used in the underlying optimization argument. Neither is the respiration the same, because in (2) respiration has a "functional response" type of formulation. Therefore the cruisers will actually not be performing optimal in the model. For them to do that it requires that the respiration and mortality in eqs. 4 and 5 are the ones used in the formulation of the optimal foraging effort (2). However, (2) is probably a good qualitative approximation. I think it is important to make this mis-match between model (2) and the dynamic foraging argument clear (or reformulate (1) or (2), but that requires a re-run of the entire set of simulations).

Thank you for the very insightful comment. In fact, in the formulation of the foraging effort, only the ratio between mortality due to an active behaviour and baseline mortality is used, i.e. the parameter m in our study equivalent to parameter μ in Kiørboe et al. (2018). As a result, the linear dependence of mortality to the total mesozooplankton concentration cancels out in the ratio:

$$m = \frac{m^{M_{CF}} \sum M_X - m^{M_{AF}} \sum M_X}{m^{M_{AF}} \sum M_X} = \frac{m^{M_{CF}} - m^{M_{AF}}}{m^{M_{AF}}} \tag{1}$$

In contrast, the formulation of the ratio between active and basal respiration, parameter r (equivalent to parameter m in Kiørboe et al. (2018)), is different from that of Kiørboe et al. (2018) to account for the dependence of basal respiration on the biomass of the considered functional group. r, which represents the ratio of active to basal respiration is therefore (see Equation 3 of the manuscript):

$$r = \frac{r^{M_{CF}} - r^{M_{AF}}}{r^{M_{AF}} \frac{M_{CF}}{K_m + M_{CF}}} \tag{2}$$

In our formulation, the denominator includes a dependency on M_{CF} which is absent in the formulation of m in Kiørboe et al. (2018).

Equation 3 (now in Appendix A.2, L.741-744) has been rewritten with these details.

3. I find the inclusion of the activity metabolism into the growth efficiency to be slightly incorrect. It would be more correct to make active metabolims a term that is subtracted in the growth equation to reflect the actual activity respiration (see point 2 above). However, there may also be a further issue, because the respiration is turned in the CO2, while I imagine the efficiency loss of the mesozooplankton is partitioned between CO2 and POM in the PISCES system. In this way as term that should be respiration (CO2) becomes POM.

In our model formulation, we differentiate two metabolic costs: an active metabolic loss related to prey handling and assimilation which is a fixed fraction of ingestion (represented by parameter e^{M_X} in equation (1)) and a cost which corresponds to basal respiration and swimming activity which is independent of ingestion, that is parameter r^{M_X}. Both metabolic losses are routed to DOM and CO2, but not to POM. In addition to these losses, part of the ingested food is not assimilated and is instead lost as fecal pellets (POM). This non-assimilated fraction of ingested food was indeed not included in Equation 1 of the manuscript. We corrected Equation 1 to explicitly account for this non assimilated fraction:

$$\begin{aligned}\frac{\partial M_X}{\partial t} = (1 - \sigma_{unass}) \times e^{M_X} \times G^{M_X} \times f_{M_X}(T)(1 - \Delta(O_2))M_X \\ -r^{M_X} f_{M_X}(T) \left(\frac{M_X}{K_m + M_X} + 3\Delta(O_2) \right) M_X \\ -m^{M_X} f_{M_X}(T)(1 - \Delta(O_2))M_X \sum_X M_X\end{aligned} \tag{3}$$

The following text has been added in the revised version of the manuscript:

L. 143: "*where σ_{unass} is the non-assimilated fraction of ingested food*" and L. 145-146: "*The second term represents mesozooplankton metabolic losses due to basal respiration and* *swimming activity, at a rate* r^{M_X} *and where* K_m *is a half-saturation constant."*

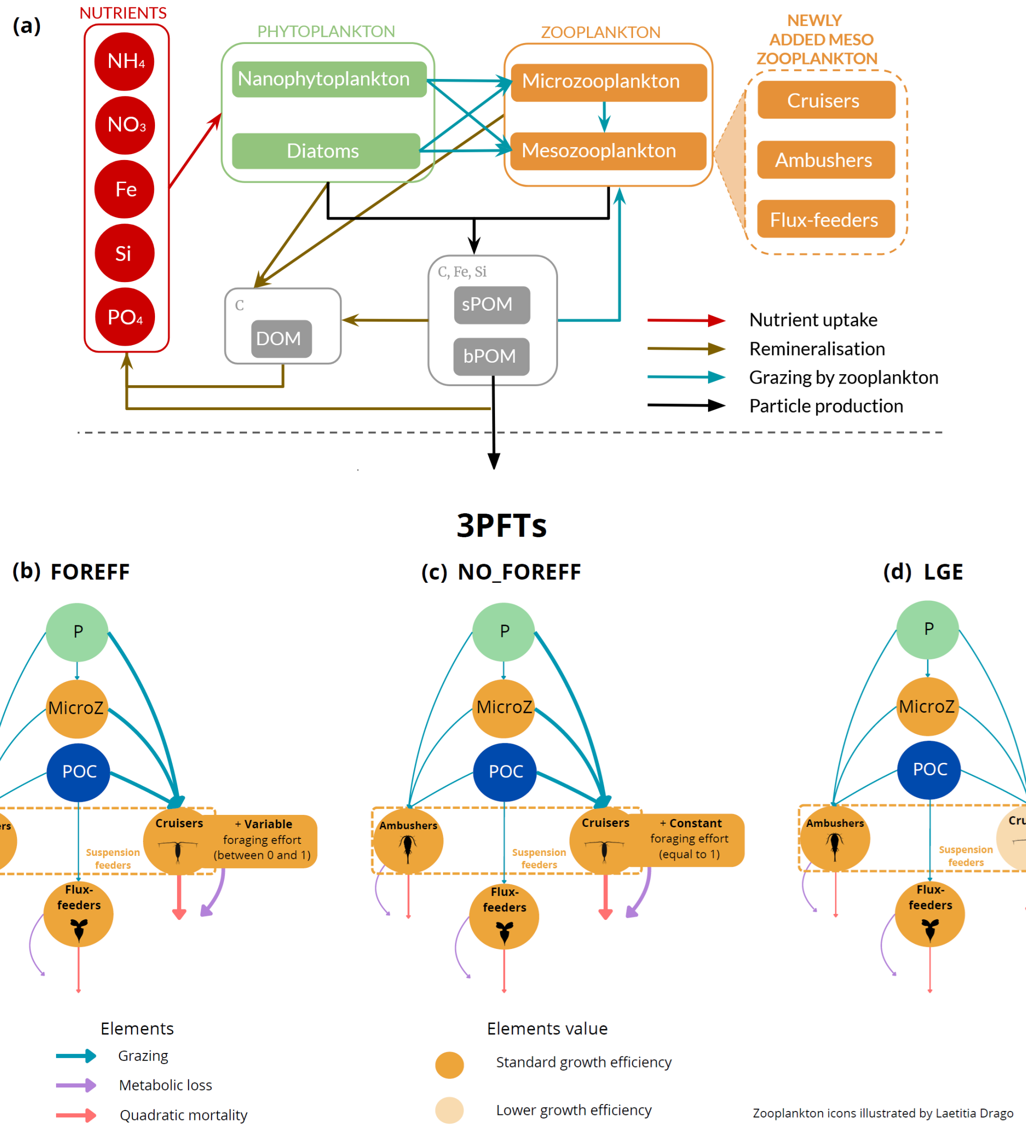
4. I find the $M_X/(M_X+K_m)$ term in the basal metabolism odd. Why is there a "functional response" type formulation in here? Is it to maintain correspondence with the PISCES formulation of respiration? Please justify this term.

This is indeed to maintain correspondence with the PISCES formulation of respiration. A Michaelis Menten formulation is used to avoid extinction of mesozooplankton at very low food concentration. Mortality is also enhanced in low O_2 waters.

We will modify the text of the manuscript as follows: L. 141-143: *"In this equation,* M_X *represents the mesozooplankton biomass of one of the three newly modelled feeding groups X (AF, CF and FF) based on a Michaelis–Menten parameterization with no switching and a threshold, to avoid extinction of mesozooplankton at very low food concentration (Aumont et al., 2015)."*

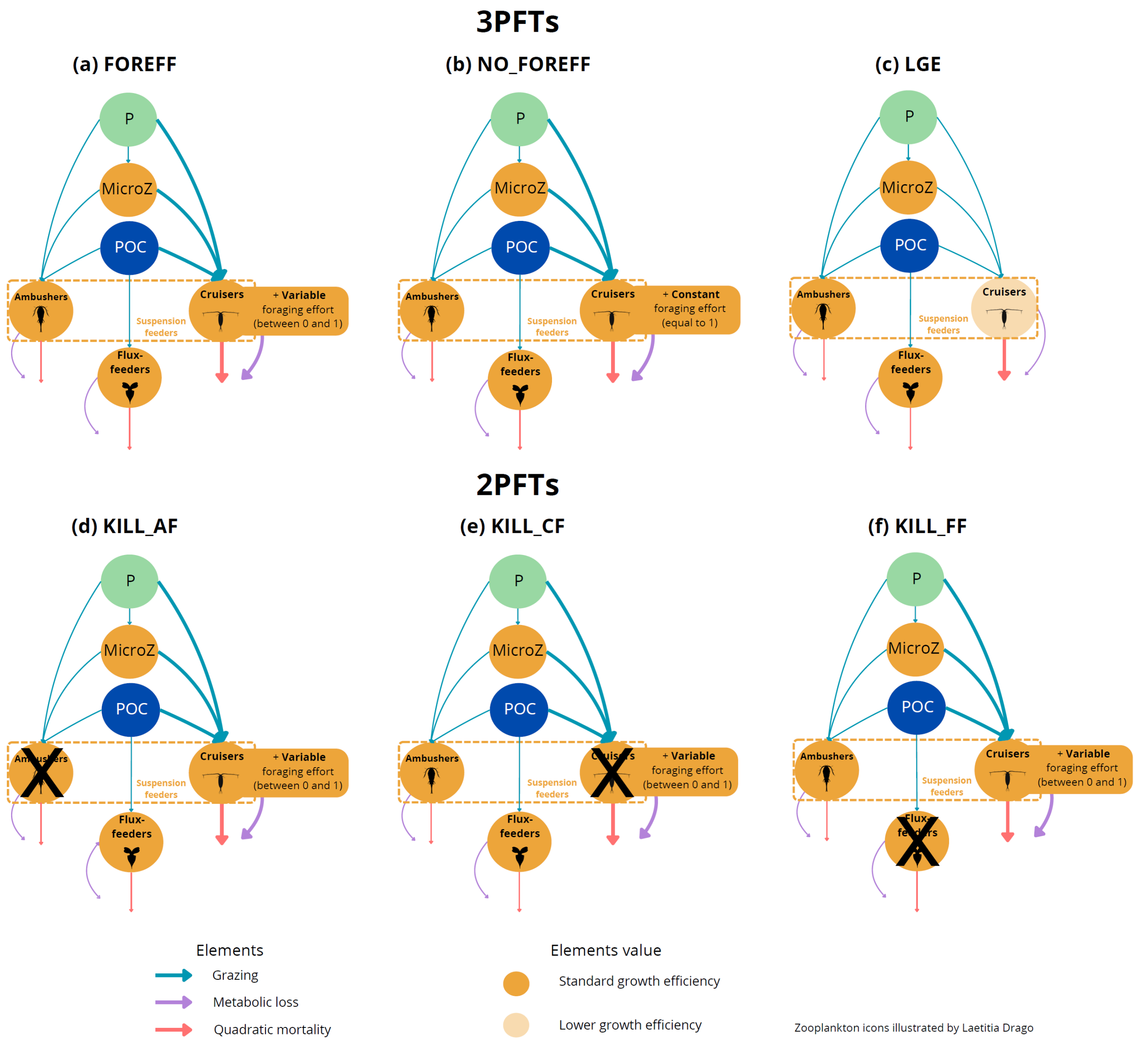
5. I struggled to keep track of the three mesozooplankton groups and in particular on the assumptions in the different experiments throughout. The text does a good job in explaining, it is just that there are many concepts to keep track of. It would be great to have a visual presentation of the three functional groups. Further, the visual presentation could also show the three different model "experiments". Such a presentation would be a big help for the reader.

Thank you for suggesting to add a summary figure, we agree that it would make these experiments easier to follow for the readers. Figure 1 has been changed to present the PISCES model structure for the FOREFF configuration, as well as the experiments with 3PFTs and figure 2 has been added in the Appendix A1:



Zooplankton icons illustrated by Laetitia Drago

Figure 1: (a) Architecture of the PISCES biogeochemical model, omitting oxygen and the carbonate system for the sake of clarity. In the FOREFF (FORaging EFFort) configuration presented in this study, three mesozooplankton functional groups are considered. They are represented in the right corner of the figure. POM is for particulate organic matter and DOM is for dissolved organic matter. Figure adapted from Aumont et al. (2015), (b) FOREFF reference configuration, (c) NO_FOREFF experiment and (d) LGE experiment. The thickness of the lines account for the intensity of the grazing rate $g^{M_{SF}}$ or flux-feeding rate $g^{M_{FF}}$ (blue), metabolic loss parameter r^{M_X} (purple) and quadratic mortality parameter m^{M_X} (red). The transparent orange shading for cruisers in LGE (d) accounts for the lower growth efficiency e^{M_X} . NO_FOREFF (c) is the same as FOREFF (b) but with a constant foraging effort equals to 1. P stands for phytoplankton and MicroZ for microzooplankton.



Zooplankton icons illustrated by Laetitia Drago

Figure 2: (a) FOREFF reference configuration, (b) NO_FOREFF experiment, (c) LGE experiment and (d, e, f) KILL_XX experiments (where XX accounts for CF (cruisers), AF (ambushers) and FF (flux-feeders)). The thickness of the lines account for the intensity of the grazing rate $g^{M_{SF}}$ or flux-feeding rate $g^{M_{FF}}$ (blue), metabolic loss parameter r^{M_X} (purple) and quadratic mortality parameter m^{M_X} (red). The transparent orange shading for cruisers in LGE (c) accounts for the lower growth efficiency e^{M_X} . NO_FOREFF (b) is the same as FOREFF (a) but with a constant foraging effort equals to 1. The KILL_XX experiments are the same as FOREFF (a) but one group is removed. P stands for phytoplankton and MicroZ for microzooplankton.

L. 183-184: *"A visual representation of the various configurations and sensitivity experiments (FOREFF, NO_FOREFF, LGE and KILL_XX experiments) can be found in Appendix A1."*

6. Conclusion. I think this could be omitted. What I would love to see would be a reflection about when this enhanced model should be use, how much it would overall matter, and whether the increased realism is worth the extra computational costs of additional state variables.

Thank you for this comment. Accordingly, we rewrote the final paragraph reflecting on the computational costs and when this configuration could be used. The section now reads as follows:

L. 706-719:"*While the lack of representation of mesozooplankton functional diversity (in grazing for instance) is considered as the greatest uncertainty in climate projections of carbon cycle (Rohr et al., 2023), this study showed the importance of various predation strategies at global scale and the necessity to enhance the representation of mesozooplankton functional diversity in biogeochemical models. It also underlined the need for more in situ and experimental quantitative data, to better quantify the trade-offs between functional traits and thus better constrain our modelling framework. Data obtained in controlled laboratory experiments would allow us to better represent and parametrize predation strategies in biogeochemical models, hence contributing to better evaluating the impact of feeding strategies on global biomass and biogeochemical fluxes. Such representation does not drastically modify the marine biogeochemistry at global scale. Hence, if computing cost is a concern and details in the mesozooplankton description are not a priority, this more detailed representation could likely be omitted. However, if mesozooplankton dynamics are central, for instance when investigating higher trophic levels (Mitra et al., 2014), this configuration is worth considering. Furthermore, an interesting perspective would be to use this configuration in the context of climate projections to investigate how the biogeography of the various mesozooplankton groups would evolve under climate change, as well as evaluate the projected changes in ecosystem-driven carbon fluxes.* "

Minor comments:

1. I struggled to understand the "suspension feeders", and it was only late I discovered that it was the sum of two groups. It is probably made clear in the text, but other readers might have the same struggle. I suggest to write "suspension feeders (cruisers + ambushers)" a few times in the text to remind the reader of the definition.

Thank you for this comment. We mention it clearly on lines 12, 203, 237, 279, 329, 559, 577 and 699 and in the legend of table 1 and in the titles of sections 3.2.2 and 3.3.

2. Throughout: units should not be in italics. Also "." as a multiplication sign is not generally used outside of France.

Yes you are right, sorry for the inconvenience. We have modified this throughout the manuscript accordingly.

3. Eq. (1). I find it difficult to interpret that there is a superscript that indicates all groups (Mx), but then subscripts for individual groups. I suppose the SF subscripts means terms only for suspension feeders. Perhaps it would be clearer to formulate an equation with the g term separately for the three groups?. Second: what is the functional form of each g-term?

Thank you for this comment. Equation (1) was rewritten in the manuscript with a better description of the different terms and more details on the grazing formulation of mesozooplankton are provided in the Appendix A2.

$$
\begin{aligned}
\frac{\partial M_X}{\partial t} = (1-\sigma_{unass}) \times e^{M_X} \times G^{M_X} \times f_{M_X}(T)(1-\Delta(O_2))M_X \\
-r^{M_X} f_{M_X}(T)\left(\frac{M_X}{K_m+M_X} + 3\Delta(O_2)\right)M_X \\
-m^{M_X} f_{M_X}(T)(1-\Delta(O_2))M_X \sum_X M_X
\end{aligned}
\tag{4}
$$

"Where G^{M_X} is the total ingested matter by mesozooplankton. A full description of the equations for G^{M_X} is provided in Appendix A2."

In the Appendix A2, the following details were added:

"Mesozooplankton grazing terms for suspension feeders in PISCES are concentration-dependant and based on a Michaelis–Menten parameterization with no switching and a threshold (Aumont et al., 2015; Gentleman et al., 2003)."

$$
G^{M_{SF}} = g^{M_{SF}}(P) + g^{M_{SF}}(D) + g^{M_{SF}}(sPOC) + g^{M_{SF}}(Z) \tag{5}
$$

"Where the different preys are nanophytoplankton (P), diatoms (D), microzooplankton (Z) and small organic particles (sPOC). $g^{M_{SF}}(I)$ represent the grazing rate of suspension feeders (cruisers and ambushers) on the different preys I: "

$$
\begin{aligned}
g^{M_{SF}}(I) &= g_m^{M_{SF}} \frac{F_{lim}}{F} \frac{p \times P_I^{M_{SF}} I}{K_g + p \times F} \\
F &= \sum_I P_I^{M_{SF}} I \\
F_{lim} &= \max(0,\ F - \min(0.5F,\ F_{thresh}^{M_{SF}})
\end{aligned}
\tag{6}
$$

"Where F is the food availability of each prey I, F_{lim} is a food limitation term, K_g is the half-saturation constant for grazing, P_I is the preference on prey I (set to 0.3 for nanophytoplankton and sPOC and 1 for diatoms and microzooplankton, Aumont et al. (2015)) and $F_{thresh}^{M_{SF}}$ is a food threshold. p is the foraging effort for cruisers. It is thus only implemented in the grazing formulation of cruisers."

"Flux-feeding is accounted such that it depends on the product of the concentration of particles by the sinking speed.

$$
\begin{aligned}
G^{M_{FF}} &= g^{M_{FF}}(bPOC) + g^{M_{FF}}(sPOC) \\
g^{M_{FF}}(I) &= g_m^{FF} w_I I
\end{aligned}
\tag{7}
$$

"Where $g^{M_{FF}}(I)$ is the flux-feeding on small and big particles I (sPOC and bPOC) and $g_m^{M_{FF}}$ is the flux-feeding rate."

4. Eq (1): The oxygen term is not mentioned.

Thank you for this comment. The equation (1) for mesozooplankton dynamics had been oversimplified. In line with the reviewer's comment, we rewrote it to account for the oxygen dependency in all terms.

L. 154-156: *"and, as we assume that mesozooplankton are unable to cope with anoxic waters, the growth rate and quadratic mortality are reduced and the metabolic losses are enhanced in oxygen depleted regions ($\Delta(O_2)$, Aumont et al., 2015)"*.

5. Eq (1): the density-dependence term is important. Why is it a sum over the three groups and not each group individually? If it represents disease, then it would be more relevant having it individually on each term. Please justify the choice made here.

The formulation of quadratic mortality has been chosen to model predation by a generalist predator that is not explicitly modelled in PISCES. This suggests strong selective pressure resulting in distinct habitat distributions: the more advantageous a strategy is in a given region, the more it tends to outcompete and exclude alternative strategies.

Another possible choice, that was not made here, would have been to consider a specialist predator. In that case, the quadratic mortality of one mesozooplankton PFT would then only depend on its own concentration.

L. 148-150: *"Here we choose a formulation of quadratic mortality corresponding to predation by a generalist predator: the predation pressure on one group depends on the total mesozooplankton biomass. Consequently, the more advantageous a strategy is in a given region, the more it tends to outcompete and exclude alternative strategies."*

6. Eq (1): What is GOC - is is not on figure 1.

In PISCES, particulate organic matter is modelled using two tracers corresponding to the two size classes: POC for the smaller class (1–100 μm) and GOC for the larger class (100–5000 μm) (Aumont et al., 2015).

Equation A.1: POC was changed in *"sPOC"* and GOC in *"bPOC"* and details on the representation of particulate organic matter are provided in the revised manuscript.

L. 109-110: "*with two size classes: sPOC for the carbon content of small organic particle (1–100 μm) and bPOC for the carbon content of big organic particles (100–5000 μm), total alkalinity and dissolved oxygen (Aumont et al., 2015))*"

7. Line 119. Please mention also the acronym for ambushers here.

Done.

8. Line 138: I do not see a temperature term on g in eq. (1).

Equation (1) was rewritten to provide more details. The sentence at line 153-154 now reads: *"All three terms have the same temperature dependence $f_X(T)$, with a Q_{10} set to 2.14."*

9. Line 141: Define “p”. It is a non-dimensional number btw 0 and 1, which could represents the fraction of time spent foraging.

Thank you for this suggestion. The description of the foraging effort has been changed in the manuscript (P. 7) and now includes a definition of "p".

10. Line 150: Shouldn’t the ref be Kiørboe et al (2017)?

Yes, you are right. The reference was changed.

Kiørboe, T., Saiz, E., Tiselius, P., and Andersen, K. H.: Adaptive feeding behavior and functional responses in zooplankton, Limnology and Oceanography, 63, 308–321, https://doi.org/10.1002/lno.10632, 2018a.

11. Line 153: Respiration is a loss term, but it is not a mortality (even though one cannot mathematically distinguish them).

Yes, indeed, but we have called the respiration "linear mortality" to remain consistent with Aumont et al. (2015). It is now changed to "metabolic loss" for more clarity in the description of equation (1) and in table 1.

12. Figure 2: Drop “theoretical curve of the “.

Done.

13. Table 1. “K_M” is for respiration, not mortality.

Done.

14. Table 1: g_{FF}: shouldn’t the units be in 1/d? And drop “*” as multiplication sign.

As shown now in Appendix A2, the formulation of the flux feeding differs from that of suspension feeding. The flux feeding rate is multiplied by the particulate organic carbon vertical flux, which is in mol/dm2/d. To obtain a growth rate in 1/d, then the unit of g_m^{FF} should be 1/(mol/d m2).

The unit for flux-feeding rate was wrong and was changed in Table 1 as follows: $(molC\ d^{-1}\ m^{-2})^{-1}$

15. Line 296: Strictly speaking the foraging effort declines in areas of high prey concentration (which often correlates to high production).

Yes. We modified the text accordingly as follows: L. 311: *"The foraging effort declines in areas of high prey concentration"*

16. Line 296: Why 11.4? On figure 7.4 it seems to be around 7.4.

Thank you for spotting this error. Yet, as this value relates to the theoretical curves and not model outputs, it was removed for the sake of clarity.

17. Line 297-298. Why does it suggest that ?

The foraging effort is implemented in all three terms of equation 1. At low prey concentrations (lower than R_{min}, now defined in Appendix A2), the foraging effort rapidly decreases to 0, thus the grazing decreases to 0.

18. Line 477: "cruisers have access to a larger range of prey". Isn't that by definition in the model (and therefore not a finding)?

Yes, you are right. We rephrased this sentence as follows:
L. 490-492: *"We also explicitly considered the cost of the foraging of cruisers, where they have access to a larger range of prey despite a higher predation risk due to their active behaviour and higher metabolic costs when actively foraging."*

19. Section 4.2: Here there was some repetition of information that belong in the methods sections, like Line 527-530.

Yes, we agree with the reviewer's comment. The sentence at Lines 527-530 was removed and the description was rewritten to better fit in the methods section.

L. 128-130: "*Despite having a lower feeding efficiency and lower probabilities of finding mates, this strategy has the advantage of a much lower mortality rate (up to an order of magnitude (Van Someren Gréve et al., 2017)) as well as lower metabolic expenses (Kiørboe et al., 2015).*"

20. Line 640: " notably inducing more co-dominance since there would be a very rapid switch of feeding mode". I think it would be the other way around. The fast switching would mean that one state variable actually represent two function groups (in a crude way). The fast switching group would be more optimal than the non-switching groups, and there would therefore be less, not more, co-existence.

Thank you for this comment. You are right, when considering a fast switching organism, less co-dominance would be observed as it will always switch to be optimum in its environment. However, we were referring to the frequency of occurrence of the feeding groups where in that case, the switching between feeding modes would lead to more co-dominance of the modes. We modified our text as follows:

L. 652-654: *"[...] notably inducing more co-dominance of the predation modes since there would be a very rapid switch of occurrence of the feeding mode whereas, in our approach, a change in the dominance by a feeding mode is only achieved through a change in the relative abundances of the corresponding functional groups."*

Reviewer #2

General comments

The manuscript by Di Matteo explores global simulations of a coupled ocean biogeochemical model distinguishing three feeding strategies for mesozooplankton. In a series of sensitivity experiments, the authors then test different assumptions of their model formulations regarding trade-offs between growth, mortality and metabolic losses. They discuss their results in relation to other hypothesised biogeographies based on modelling and observational data. In the light of most OBGCMs using only one mesozooplankton compartment, the present study presents a valuable step forward. The study requires, however, a more careful introduction of the model, in particular for those readers not familiar with standard PISCES, and would benefit from a description of the results focused more on explaining underlying processes than on comparing numbers (i.e., more like the discussion which I liked a lot better). In particular, the structure of the food web (who eats whom) needs to be presented in the model description, and their effects on the results need to be discussed.

The authors would like to thank Reviewer #2 for their useful comments.

Specific comments

Figure 1: please explain acronyms (sPOM, bPOM). Otherwise, the existance of the two size classes suddenly pops up in the results sections.

Thank you for this comment. The sPOM and bPOM (as well as DOM) abbreviations are now explicitly defined in the caption of Figure 1. From L. 109, they are restricted to sPOC and sPOC to refer to the carbon content of organic particles. You can find a more detailed answer in our response to minor comment 6 of Reviewer #1.

lines 119 ff: Definition of ambushers: please introduce the abbreviation AF, in case it has not been done (I may have overlooked it). You state that you do not distinguish between ambushers with active and passive prey capture, naming pteropods as example for the latter. However, pteropods also seem to be represented in the flux feeders. Can you explain the distinction between the two PFTs?

Thank you for noticing this duplicate. In our study, we do not make the distinction between active and passive ambushers and we present this feeding group as passive suspension feeders, adopting a "sit-and-wait" strategy. Pteropods may indeed be considered as passive ambush feeders (Kiørboe, 2011) but the organisms that best represent ambushers here (according to the hypotheses we made on the choice of parameters) are Oithonid copepods (Kiørboe, 2011; Almeda et al., 2018). We thus removed "pteropod" in our description of ambushers to avoid confusion, since flux-feeders are the functional group that should be closest to pteropods based on our assumptions (i.e., mainly passive organisms with mucus-feeding webs feeding on sinking particles).

lines 130 ff: the equation names g_{SF}^{Mx} as grazing term of suspension feeders. What does the functional responses look like for the different sensitivity experiments? I take it this includes ambushers. Do ambushers really prey on diatoms and POC? What are the prey preferences of the different zooplankton groups?

Thank you for this comment. The functional response is of Holling type II, similar to that used by Aumont et al. (2015) and this formulation is used for all feeding groups and in all experiments.

Here, we also assume that suspension feeders feed indiscriminately on small living organisms and particulate marine snow, similar to the standard representation of mesozooplankton in Aumont et al. (2015). Only flux-feeders feed exclusively on particles, due to their feeding mode. Detailed information on mesozooplankton grazing can be found in our response to minor comment 3 of Reviewer #1.

L. 116: "*and has a Holling type II functional response.*" and L. 151-153: "*Both suspension feeders feed indiscriminately on small living organisms and particulate marine snow, similar to the standard representation of mesozooplankton in Aumont et al. (2015). Only flux-feeders feed exclusively on particles, due to their feeding mode.*"

lines 137: why does predation, parameterised by the quadratic mortality, depend on the sum of all three mesozoo groups? Is predation not dependent on feeding strategy, i.e. whether you swim / produce a feeding current or just sit and wait?

Thank you for your comment. You can find a detailed answer to this comment in our response to minor comment #5 of Reviewer #1.

lines 140 ff: from the equation for foraging effort alone it is difficult to understand what it does, I guess it ranges between 0 and 1, and looks like Fig. 2? Do equations 4 and 5 replace the 2nd and 3rd row of equation 1 for cruisers? Where and how does R_{min} enter the equation? Does it affect ingestion? Where is this shown? And what is gm in Eq. 3 and 6?

Thank you for your comment. The description of the foraging effort was modified and the equations placed in the supplementary materials for more details. Please find a more detailed answer in our response to Reviewer #1.

lines 217 ff: was it possible at all to validate estimates of flux feeders?

Thank you for your comment. To our knowledge, although data on flux-feeder distribution would be highly valuable for better quantifying their abundance and role in the carbon cycle, such a dataset does not exist currently. This makes an extensive empirical evaluation of our results challenging on a global scale, if not impossible. However, we were able to compare our study with other studies (section 4.3) that focus on the role of flux-feeders, giving us confidence in our results regarding the important role they play in carbon export at depth.

line 238: rather use indicated instead of confirmed. What causes the overestimated phytoplankton and mesozooplankton biomass?

Thank you for the suggestion, we modified L. 238. The model is far from being perfect but still represents the patterns of high/low productivity which could be due to the way it is tuned or the forcing used. Moreover, if we had used another product for chlorophyll for instance, we may have found an underestimation.

lines 296 ff: this interpretation suggests that foraging effort affects ingestion in the model, but this is not clearly shown in the equations. To me, the present equations seem to show that mortality and metabolic losses for cruisers reduce to those of ambushers for near-zero foraging effort. Cruisers would then have the same losses as ambushers in case of low prey concentration, no? Or is it related to Rmin? I probably misunderstood, but the model description may need improving, maybe with a few graphs comparing equations for cruisers and ambushers, and a table with all the symbols used in the manuscript.

The model description was oversimplified in the first version of the manuscript and it was not clear where the foraging effort was implemented in the ingestion. We will revise the model description to provide a more detailed description of our model formulations which we detailed in our response to similar concerns raised by Reviewer #1.

lines 320 ff: no alternation between suspension feeders: no difference in prey preferences and seasonality of different prey communities?

Thank you for your comment. Here, we observe that the model is not able to predict seasonal alternation between the two modelled suspension feeder groups. Since both groups have the same prey preferences, variations in the relative abundance of different prey types cannot induce such alternation in our modelling framework. This is a strong model limitation that certainly contributes to the simulated stability. However, our model suggests that seasonal variations in the total prey abundance alone do not generate alternation in feeding modes when only specialists are represented (i.e., each feeding mode is represented by a distinct functional group). This is, in our opinion, an interesting result.

L. 654-657: "*Representing this ability to switch and having more co-dominance would also lead to predicting seasonal alternations among suspension feeders, which is not the case here, as both groups have the same prey preferences. Thus in our modelling framework, variations in the relative abundance of different prey types cannot induce such alternations.*"

lines 352 ff, 365: by keeping foraging effort to the maximum you strongly reduce cruisers in pretty much all of the ocean. Maybe the resulting loss rates are simply too high? How do results look like for an intermediate, constant value of the foraging effort? What is the effect of the value being constant, and what results from it being higher than in FOREFF?

Indeed, keeping the foraging effort for cruisers to its maximum value everywhere leads to a maximum swimming activity and thus more loss in regions where prey concentration is not high enough to compensate for these metabolic losses. However, an experiment where the foraging effort is intermediate and constant, so around 0.5 would lead to a strong decrease in cruisers abundance as there are only very few regions where the foraging effort is actually 0.5 (most areas where the annual mean foraging effort is close to 0.5 as shown in Figure 6a, correspond to situation where the foraging effort seasonally alternates between 0 when food is low and 1 when food is more abundant).

line 366: increase in microzoo and phyto: who is preying on what (see comment above)?

In the model, both zooplankton groups feed on phytoplankton and organic particles and mesozooplankton also feed on microzooplankton. It is mentioned in the model description, L. 112-113. For mesozooplankton, we kept the prey preferences from Aumont et al. (2015), with a preference of 0.3 for nanophytoplankton and sPOC and of 1. For diatoms and microzooplankton. The latter is added in the appendix, see the detailed description of mesozooplankton grazing in our response to minor comment 3 of Reviewer #1.

line 376: again, what is the functional response? Please add a graph.

In the standard version of PISCES, the chosen parametrization is a Michaelis–Menten one, with no switching and a threshold (Aumont et al., 2015). We kept this parametrization and the Holling type II functional response in our configuration and added this precision in the new version of the manuscript. With this information now clearly mentionned in the manuscript, we prefered not to add an extra graph.

L. 142-143 *"based on a Michaelis–Menten parameterization with no switching and a threshold (Aumont et al., 2015)"*

line 387: How does the higher ambusher biomass lead to a stronger mortality for cruisers? The explanation only comes in line 408.

In our configuration, the quadratic mortality depends on the concentration of total mesozooplankton. Thus, the more competitive a strategy is, the more it excludes other strategies. In this case, the biomass of ambushers increases, reinforcing the quadratic mortality of cruisers.

L. 399-401: *"Additionally, because mesozooplankton experience quadratic mortality based on their total concentration, the significantly higher biomass of ambushers increases overall mortality rates, disproportionately affecting cruisers and further reinforcing ambusher dominance."*.

line 392: I thought suspension feeders were cruisers and ambushers - why

then "the other two groups"?

Thank you for noticing this error. We removed it in the manuscript as the LGE experiment consists in keeping the same grazing rate for both suspension feeders.

L. 406: *"in the experiment where suspension feeders are assigned the same grazing rate (i.e., LGE)"*

line 477: what do you mean with cruisers having access to a larger range of prey - prey concentration, different prey types, ...?

We actually referred to the fact that cruisers have a higher grazing rate and a foraging effort that modulate their swimming activity, allowing this group to feed more efficiently. We modified the revised manuscript to be more precise as follows:

L. 489-492: "*Yet, cruisers may outcompete ambushers in the most productive regions thanks to their higher grazing rates. We also explicitly considered the cost of the foraging of cruisers, where it optimizes their swimming activity and leads a more efficient feeding despite a higher predation risk due to their active behaviour and higher metabolic costs when actively foraging.*"

Technical corrections

entire document, e.g., line 116, 120, 163: prey items instead of "preys"

Thank you for this suggestion. "Preys" has been replaced by "prey items" throughout the manuscript when it refers to a countable quantity.

line 23 one of the most studied size classes encompasses the mesozooplankton ...

Thank you for this suggestion. Done.

line 57 with in situ cameras

Done.

line 82 feeding strategies affect

Done.

line 109 the ratio of flux-feeding to total mesozooplankton grazing

Done.

line 124 ctenophores or foraminifera

Done.

line 135 please spell out the symbols used in the equation (e.g., g, f, P, D, GOC, ...).

The equation was simplified and put in the supplementary materials with a description of the symbols.

Figure 1: please explain acronyms (sPOM, bPOM).

Done.

line 625: loss instead of lost

Done.

Figure and Table layout

Figure 1: represented in the right corner of the figure.

Done.

Figure 1: why is phosphate not included in the figure?

Thank you for spotting this mistake. Figure 1 was changed and now includes phosphate in the nutrient compartment.

Reviewer #3

This paper introduces three distinct mesozooplankton functional types – ambush feeders (AF), cruise feeders (CF) and flux feeders (FF), to the PISCES biogeochemical model to study the factors determining the global distribution of these groups and their biogeochemical impacts. Tradeoffs included CFs expending more energy and being exposed to more predation to increase encounter and consumption rates relative to AFs. Types were also differentiated by prey availability, and CFs were allowed to optimize their foraging behavior in accordance with the foraging model of Kiorboe et al. (2018).

The authors present an initial model parameterization suggesting that AFs are most abundant globally, CFs prevail at higher latitudes, and FFs dominate biomass below the euphotic zone. The parameterization also suggests that FFs strongly attenuate particle fluxes in high productivity regions. A series of sensitivity experiments suggests that dominance patterns can be altered significantly by changes in parameter values within the range of observed constraints. This substantial parameter uncertainty helps explain the differences between this study and prior ones (e.g., Visser, 2007; Prowe et al., 2019) suggesting that, contrary to this study's results, AFs may dominate at high latitude/high productivity conditions and CFs in low productivity regions. The author's cite recent observation-based niche modeling work based on presence/absence data to support the prevalence of CFs at high latitude/high productivity areas that their study shows (i.e., Fig. 10, Bennedetti et al., 2023), but temper this by acknowledging that this approach does not predict biomass.

I found the paper results interesting and feel that they will be of interest to the Biogeosciences community. I also, however, had a number of concerns and suggestions that I hope the authors can consider.

We would like to thank Reviewer #3 for their positive and valuable comments.

First and foremost, one of the primary results of the paper seems to be that the simulated zooplankton biogeography could be changed substantially – even reversed - by altering parameters within their broad uncertainty bounds. The authors discuss this at length. The abstract, however, focuses on the results of the initial formulation. Lines 11-13, for example, makes definitive and quantitative statement about what the "configuration shows". The configuration also shows, however, that the latitudinal patterns of dominance can be changed substantially by parameter shifts within uncertainty bounds. This is an abstract-level result and should be stated soon after you provide your base model values.

Yes, we agree with the reviewer. It has been added in the abstract that our sensitivity experiments show varying biogeographies of suspension feeders. The abstract now reads as follows:

Abstract: "*The change of parameters, thus trade-offs, in our sensitivity experiments also* *shows how we can modulate and even reverse the latitudinal pattern of suspension feeders"*

Second, I found myself wondering whether the sensitivities would have been better posed as systematic variations of the tradeoffs within the base model. The Low Growth Efficiency (LGE) sensitivity considers a fundamentally different approach, making it hard to understand its motivation and interpret its outcomes. I found myself wondering why the authors did not simply modulate the tradeoffs within their base model (e.g., increase/decrease the consumption, metabolic, and predation risk tradeoffs for CFs versus AFs) and see how those could alter the biogeography? Wouldn't this offer a more mechanistic and interpretable sensitivity analysis?

Thank you for your comment. This kind of experiment, where parameter values were increased or decreased (such as the quadratic mortality rate or growth efficiency of cruisers, the maximum grazing rate or the half saturation constant for grazing of both suspension feeders), was actually performed but not presented in this study. This is because we observed no significant changes in biogeography, and the results showed no unexpected sensitivities warranting further discussion. For instance, decreasing the quadratic mortality of cruisers increased their concentration in regions where the group was already present. In particular, none of these sensitivity experiments enabled us to drastically alter or even generate a completely different biogeography as in LGE, where a different set of hypotheses was tested.

We also performed an experiment using the same configuration as FOREFF but with the parameters for suspension feeders set as in LGE (not presented in the study), and obtained a distribution similar to that in LGE. The main difference was that the foraging effort became one almost everywhere due to the parameter changes (and thus cruisers concentration decreased slightly).

Third, I was excited to see the Benedetti niche modeling results in Fig. 10. The authors admirably discuss all the limitations and caveats associated with relating this model – which is based on presence-absence data – to the biomass data in the model, but I couldn't help but wonder if it could offer an emergent constraint on the tradeoff space. I would consider bringing this result into the paper framing earlier. The contrast between this result and the Visser and Prowe results strongly motivates this work. While the latitudinal dominance patterns can be shifted considerably by modulating tradeoffs within reasonable bounds, perhaps Niche modeling provides a starting point for an emergent constraint on these tradeoffs? The discussion could then more directly assess possible ways to strengthen this constraint?

Thank you for the supportive comment here. We modified the introduction in the revised version of the manuscript to better account for the differences between these modelling frameworks:

L. 78-83: *"These variations in the mesozooplankton community thus have impacts on the global, regional and vertical distribution of the feeding traits (Brun et al., 2016). These biogeographies may even contradict one another depending on the modeling framework. For* *example, the niche modeling study by Benedetti et al. (2023) shows an opposite distribution of ambushers and cruisers compared to the dynamic model of Prowe et al. (2019). Such discrepancies can lead to variations in the trophic web and in carbon export to the deep ocean, as highlighted by Stukel et al. (2019)."*

However, we do not consider that niche modelling, as presented in Benedetti et al. (2023), would be an appropriate way to constrain trade-offs in our mechanistic model. While such models are highly effective for predicting the global spatial distribution of plankton species, they are based on the probability of presence or absence of a taxon rather than its biomass. This would make quantitative estimates of parameters, as required in models such as PISCES, very challenging.

We thus believe that keeping figure 10 in the discussion rather than in the results section is more appropriate as it allows us to discuss more on the comparison between studies but also because it is only a visual comparison (since we compare the dominance index and not biomasses).

Lastly, the flux feeders had a big impact on export with the base settings, but I was wondering how sensitive this result is to parameter uncertainty and whether the big changes in remineralization profiles that would arise from this case are supported by data? Also, some of those regions have very low oxygen. How does your FF group respond to low oxygen.

All mesozooplankton groups respond the same way to low oxygen concentrations: their growth rate and quadratic mortality are reduced and their metabolic losses are enhanced. We provided more information on the dependence of our feeding groups on oxygen L. 148-150 and you can also see our response to minor comment 4 of Reviewer #1 as well as the rewritten Equation 1.

In our study, no experiment was performed to modulate the parameters of flux-feeders. We thus kept the same parameters for flux-feeders as in PISCES-STD, where they where implicitly represented (Aumont et al., 2015). Indeed, only a few studies focus on flux-feeders and provide quantitative estimates, making it hard to constrain parameter values. Moreover, our aim here was to study the biogeographies of the different groups and as flux-feeders occupy a specific niche and do not share most of the water column with the suspension feeders, a change in parameter would not lead to drastic variations. We also mention in the discussion of the manuscript the recent study by Bressac et al. (2024) that found a strong influence of zooplankton on flux attenuation. It supports our findings and thus, indirectly and to some extent, our parameter choice for flux feeding. However, observations remain too scarce to meaningfully constrain the parameter values.

Detailed comments:

Introduction: See my general comments about framing with Beneddeti 2023 and earlier results from Visser and Prowe.

L. 78-83 were modified to emphasize on the difference between the modelling frameworks of Benedetti et al. (2023) and Prowe et al. (2019).

Fig. 1: Do you need an arrow from POM to flux feeders?

Yes, an arrow was added to account for the grazing of zooplankton on POM in figure 1, thank you for noticing this mistake.

Equation 1: I found this notation a bit difficult to digest (pun intended). Perhaps it would be clearer to separate the SF and FF equation? Also, the growth efficiency that you have defined seems like it is the maximum growth efficiency before accounting for the respiration losses in the second term of the equation. Wouldn't you need to account for the respiration in this second term to get to the actual growth efficiency?

Thank you for your comment. Equation 1 was rewritten to simplify it in the manuscript and to provide more details in the supplementary materials, including by clearly providing the equation for each PFT (but please see our response to Reviewer #1).

Section 2.2: See my general comments concerning the sensitivity and the LGE experiment.

Our sensitivity experiments aim not only to investigate variations in parameter values, but also how the system would behave under a different approach based on other studies.

Moreover, the LGE experiment does not hold when considering the foraging effort, as we calculate a "background metabolism" based on the difference between the metabolic loss parameter of cruisers and ambushers. In the LGE experiment, this parameter is the same for both groups, raising issues when calculating the foraging effort which is thus not representative and comparable to other studies.

Section 3.2.1: I would consider putting a figure with the top 3 panels of Figure A.3 in the main text. This is the figure that I was really hoping to see after getting through the methods. It would provide a concise visual of the primary result. I would also consider comparing the SF dominance patterns and comparing with Beneddeti in this Section (with appropriate caveats), or at least earlier in the paper. This comparison seems too important to wait for Fig. 10.

The first three panels of Figure A.3 have been moved to the result section and we rewrite the paragraph on biomass, adding elements on spatial distribution as follows:

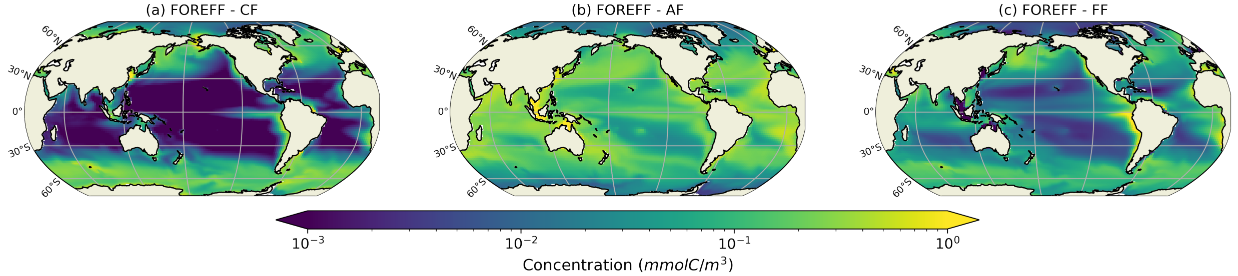


Figure 3: Log scale annual mean concentrations of the mesozooplankton feeding strategies (cruisers: CF, ambushers: AF and flux-feeders: FF) for the different experiments averaged over the top 150 m.

L. 263-268: "*Ambushers are the dominant mesozooplankton group at global scale (Figure 4b), representing 54.8 % of total mesozooplankton, with a simulated integrated biomass of 0.11 GtC and a mean global concentration of 0.154 mmolC/m*^{3} *over the top 150 m. Flux-feeders are especially abundant in coastal regions (Figure 4c, with an integrated biomass of 0.06 GtC and a mean global concentration of 0.077 mmolC/m*^{3}*), and cruisers are only present in productive regions and at high latitudes (Figure 4a). Their integrated biomass over the top 150 m is significantly lower (0.03 GtC, with a mean concentration of 0.093 mmolC/m*^{3}*) and remains consistently below the average biomass of ambushers, no matter the depth layer.* "

We also agree that the comparison with Benedetti et al. (2023) is relevant in our study. However, as mentioned earlier, we believe that keeping figure 10 and the comparison with other studies in the discussion makes more sense.

Section 3.4.3, line 409-410: Presumably this is also because there is more food left over for the remaining zooplankton groups?

Thank you for this comment. This precision was added in the revised manuscript.

L. 422-424: "*In the absence of competition from ambushers, the grazing of cruisers increases as there is more food available for the remaining groups (Figure A.5d) and the biomass concentration of cruisers increases significantly (+42%, Figure 8d), with this increase primarily occurring at low to mid-latitudes.* "

Fig. 9: See general comments on export constraints that support or rebut the strong impact of FF on the export flux, and constraints on FF activity in low oxygen water.

As mentioned earlier, all mesozooplankton groups have the same response in low oxygen waters (a reduced growth rate and quadratic mortality and higher metabolic losses).

While no experiment linked to flux-feeders parameters was done in this study, we were able to study the impact of flux-feeders on carbon export at depth and compare this impact with other studies.

Section 4.1: I found myself wondering whether the Prowe and Visser studies,

and the Benedetti results in Fig. 10 may offer a powerful way to frame the contributions of this paper relative to past work from the outset. That is, should the apparent disagreement between Visser/Prowe and Benedetti be raised in the Introduction and should a comparison with Benedetti occur in the Results?

Thank you for this comment. We added a sentence in the introduction (L. 78-82) that presents the different biogeographies in Prowe et al. (2019) and Benedetti et al. (2023). However as mentioned earlier, we chose to keep the comparison with Benedetti et al. in the discussion as we believe that it makes more sense in this part, where we are also able to compare with the study of Prowe et al.

Section 4.3: Do global datasets support a large role for flux feeders in the areas where you simulate them?

To our knowledge, there is no observational dataset for flux-feeders, so we are not able to make a comparison similar to the one we did with suspension feeders. Moreover despite the few studies on flux-feeders, they all seem to agree on the fact that this feeding group play a major role on carbon cycle and export at depth.

Line 610: Parameter constraints, no increased complexity, seems to be the most critical model limitation.

Thank you for this comment. We agree that parameter constraints are critical for a model, but so does an increased complexity as we do in our configuration. At this point, we preferred to keep it this way, but we could rephrase this sentence if needed.