We would like to thank the reviewer for the strongly supportive comments towards our study as well as the thoughtful and constructive points. The latter helped us to improve the description of our model in the method section and Appendix of our manuscript. Please find below our reply to each reviewer's comments (highlighted in blue).

Referee 1

The authors present an impressive effort in developing and analysing the first trait-based model of planktonic foraminifera based on an existing size-based plankton model. As observations on foraminifera traits and trade-offs related to calcification are scarce, they use their model results to estimate costs and benefits by selecting plausible simulations from a large range of sensitivity simulations. They employ two different model trophic structures and reveal distinct effects of temperature and resource competition on prolocular and adult stages. While the results are relevant, interesting and stimulate further research, the presentation of the model and the methods needs to be clarified to allow the reader to better assess the predictive capability of the model and the generality of the model results. In particular, I would appreciate more details and clarification about the implications and effects of the grazing parameterisation described in Appendix B (see the following questions):

1. Could you please supply a plot of the different functional responses (with and without prey refuge) employed?

We have added in the Appendix A a plot showing the different grazing rate with and without a prey refuge (Figure A1, also shown below as Figure 1) as well as including a better description of the prey refuge term (l945-979). The prey refuge in our model accounts for the fact that a prey at a low biomass is hard to find, and thus less prone to predation. Therefore, when the prey refuge is included in the grazing term, the grazing rate decreases with low densities (Figure A1).

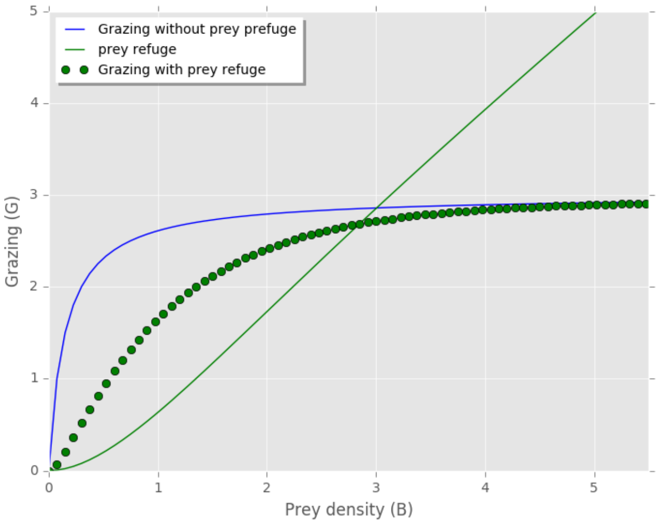

Figure A1: Zooplankton grazing on one prey with and without the prey refuge term included. Prey refuge $= (1 - e^{-\Lambda F}) * F$. Grazing without prey refuge: $G = G_{max} * \gamma_T * \frac{F}{F + K_{zoo}}$. Grazing with prey refuge included : $G = G_{max} * \gamma_T * \frac{F}{F + K_{zoo}} *$ Prey refuge. Temperature limitation (γ_T), prey palatability (φ) and prey refuge constant (Λ) equals to 1, and $F = \varphi * B$.

2. You parameterised foraminifera as the only group *with no prey refuge to account for the cost of their inability to escape predation* (lines 899-900). Does the prey refuge operate only at low prey concentration or does it reduce predation rates at all prey concentrations? I guess an advantage due to escape ability should apply to any predator-prey encounter independent of prey concentration.

Thank you for this valid point. As explained above, the prey refuge term in our model relies on prey's density and palatability and decreases the predation rate when the prey's biomass is low. As a result, the prey refuge term in our model does not represent directly a motility effect as might be suggested here. In the real ocean, prey can use defence mechanisms to escape predation (including motility but not exclusively, e.g. toxins, shell, spines, colony formation), which are independent of their density. Our model does not include these mechanisms because of still too limited mechanistic understanding (e.g. Pančić and Kiørboe, 2018).

Pančić M., and Kiørboe, T.: Phytoplankton defence mechanisms: traits and trade-offs, *Biological reviews,* 93 pp. 1269 – 1303, https://doi.org/10.1111/brv.12395, 2018.

3. I would think that a prey refuge is a property of the predator and depends on the dominant foraging strategy in a given prey environment (Kiørboe et al. 2018) but does not differ for different prey types in a mixed environment. If the non-motile foraminifera were the only food available, would predators not likely choose an active feeding strategy exhibiting a feeding threshold (i.e. a prey refuge for the forams) to encounter their prey? In a mixed prey environment, I think it is not understood yet whether active or passive feeding strategy would be picked; but I find it hard to imagine that predators would switch to passive feeding without threshold/prey refuge when it perceives a foram (which it could not perceive well when ambushing anyways since the foram is non-motile (Kiørboe et al. 2010, Greve et al. 2017). In the absence of conclusive experimental evidence, I would find it reasonable to assume a prey refuge depending on total available food, but not differencing for different types of prey and chose a different way to resolve potential escape reactions.

The predator prey interactions depend mostly on predator-prey length ratio (Kiørboe, 2008), prey's availability (Kiørboe, 2008) and ability to escape predation (van Someren Gréve et al., 2017; Pančić and Kiørboe, 2018) and predator's feeding behaviour (Kiørboe et al., 2018). The prey refuge term in our model only includes prey's density and palatability terms as it has been described in our reply for comments 1 and 2. We chose to exclude the prey refuge term for predation on planktonic foraminifera in order to study better the role of planktonic foraminifera's shell as a protection against predation, assuming that the excluded prey refuge balances their immotility. We chose to increase the complexity of the model and the uncertainty of the results, by adding motility. Therefore, in the discussion we emphasize that including motility in the model is the next important step for better understanding the predation on planktonic foraminifera (l455-456). For more regarding planktonic foraminifera motility please read our reply to reviewer's comment 6.

Kiørboe, T.: A mechanistic approach to plankton ecology. Princeton University Press, p.107-114,2008.
Kiørboe, T., Saiz, E., Tiselius, P., and Andersen, K.H.: Adaptive feeding behaviour and functional responses in zooplankton. Limnology and Oceanography 63: 308–321. https://doi:10.1002/lno.10632, 2018.
van Someren Gréve, H., Almeda, R. and Kiørboe, T.: Motile behavior and predation risk in planktonic copepods, Limnology and Oceanography, https://doi.org/10.1002/lno.10535, 2017.

Pančić, M., and Kiørboe, T.: Phytoplankton defence mechanisms: traits and trade-offs, *Biological reviews,* 93 pp. 1269 – 1303, https://doi.org/10.1111/brv.12395, 2018.

4. Does the applied formulation imply that at low food concentration foraminifera become the only zooplankton prey source for zooplankton? Could you describe if and how your results may change if the prey refuge is also applied to foraminifera?

Planktonic foraminifera in our "low biomass" and "plausible" scenarios exist with very low biomass and coexist with another zooplankton group of the same size. The latter has a higher biomass than the foraminifera so that foraminifera is never the dominant source of food. With our model, we tested the effect of prey refuge on foraminifera ecology and found that for both versions of the model, the mortality rate should be decrease in order to keep planktonic foraminifera's biomass within the observation range with and without the prey refuge being included. We added this information on the Appendix A l974-980.

5. You reduce the background mortality to allow foraminifera to achieve a high enough biomass to meet the 'low biomass' criterion, if I understood correctly (l238-240). Would it still need to be decreased if you allowed a prey refuge also for foraminifera?

In both versions of our model (food chain and food web), we need to decrease the background mortality in order to sustain planktonic foraminifera biomass within the observed range with or without the prey refuge term. This is thus a robust result as well which we refer too now as well in the manuscript (l974-980).

6. As non-spinose foraminifera are immotile, I would expect them to be perceived and encountered at a similar rate as (immotile) phytoplankton of the same size (Visser 2007, Gonçalves and Kiørboe 2015). Motile zooplankton of similar size might be perceived easier and thus be encountered at higher frequency (Kiørboe et al. 2010, Almeda et al. 2017, Greve et al. 2017). Does your model resolve such a difference? If not, might this combined with the missing prey refuge add to the need of a reduced background mortality to allow foraminifera to coexist?

This is a very good observation. The model does not represent difference in motility within the plankton community. Despite being important, as pointed out here by the reviewer, no published study exists regarding planktonic foraminifera's motility. Based on our general understanding of motility on animal and plankton ecology (e.g. Broglio et al., 2001; Almeda et al., 2017), we suggest that the main traits of planktonic foraminiferal immotility are to save energy and protect from predation. The associated trade-offs of immotility are lower prey efficiency and inability of escape from predation when they encounter their predator. As the focus of the present study is to understand the costs and benefits of calcification, we did not add motility as this would increase the complexity of the model and the uncertainty of the results in light of the lack of experimental evidence on planktonic foraminifera. We chose to exclude the prey refuge to study better the function of the shell as an armour against predation by making the assumption that the lack of prey refuge could balance the cost of their immotility. We agree with the reviewer that by removing the prey refuge term is a very simple way to represent that and not the correct one. We believe that exploring the traits and trade-offs of planktonic foraminifera motile is an important next step for studying further the predation of planktonic foraminifera; as we stated in the discussion (l454-462).

Almeda, R., van Someren Gréve, H., and Kiørboe, T.:. Behavior is a major determinant of predation risk in zooplankton. Ecosphere 8(2). https://doi:10.1002/ecs2.1668, 2017.

Broglio, E., Johansson, M. and Jonsson, P. R.: Trophic interaction between copepods and ciliates: effects of prey swimming behavior on predation risk. Marine Ecology Progress Series 179: 179– 186, https://doi.org/10.3354/meps220179, 2001.

7. in line 904 you state that zooplankton are allowed to switch feeding behaviour from filter herbivorous to ambush carnivorous. Can you clarify in words under which conditions the zooplankton switch in your model? Do prolocular foraminifera as pure herbivores (cf. l.97) also switch? Do zooplankton in both model configurations (food chain and food web) switch?

Thank you for pointing this out. We improved the description of zooplankton feeding in the manuscript (l973-977) as it was misleading. In the food web version of the model, zooplankton are defined as omnivorous predators, able to consume in parallel more than one phytoplankton and zooplankton preys but we do not distinguish them between herbivorous or carnivorous. The predator can actively choose to feed mostly on phytoplankton (Φ_P) or zooplankton (Φ_Z) prey, depending on prey's palatability ($\varphi_{j_{pred},j_{prey}}$) and density ($B_{j_{prey}}$) weighted in total prey density (B_{prey}) (Gentleman et al., 2003; Ward et al., 2012). For the food chain version of our model, zooplankton are defined as specialist herbivorous predators. As we wanted to test the benefit of shell protection from a specialist predator on planktonic foraminifera biomass, we made an exception by defining one zooplankton group to be omnivorous, feeding with one phytoplankton prey and planktonic foraminifera only. For both versions of our model, both life stages of planktonic foraminifera are defined as herbivorous feeders only.

Gentleman, W. C., Leising, A., Frost, B., Strom, S., Murray, J.: Functional responses for zooplankton feeding on multiple resources: A review of assumptions and biological dynamics, Deep-Sea Research II, 50: 2847–2875, https://doi.org/10.1016/j.dsr2.2003.07.001, 2003.

Ward, B. A., Dutkiewicz, S., Jahn, O., Follows, M.J.: A size-structured food-web model for the global ocean. Limnology Oceanography, 57(6), p.1877–1891, http://dx.doi.org/10.4319/lo.2012.57.6.1877, 2012.

2 Specific comments

1. l51, l217: I could not find the reference for Buitenhuis et al. 2014.

It is a mistake. We have now corrected this.

2. l57-59: unclear, could you reword?

We rephrased the sentence to: *"The development and application of numerical ecological models can help fill in this knowledge gap. Particularly promising to address ecological questions, **trait-based models examine individual's** physiological traits and their associated trade-offs." (l58-59)*

3. l69: can you specify if the compilation of foraminifera traits was done as part of this study or otherwise add a reference ?

This is the first time that an overview of the traits and trade- offs of planktonic foraminifera has been presented. We are in the process of writing a more in-depth review study of planktonic foraminifera's traits and trade-offs to be submitted in the coming year (Edgar, Monteiro, Grigoratou and Schmidt, in prep).

4. l71: what are "growth optimal environmental conditions" - environmental conditions that are optimal for growth?
That is correct. We modified as suggested in the manuscript (l71).

5. l186: how do you mean more realistic: in terms of the setup or in terms of the results, or both? Productive/eutrophic regions are thought to have shorter food chain length than oligotrophic regions (??).
We meant that the food web is more realistic in terms of the setup. This is because it better represents the predator: prey interactions between phytoplankton and zooplankton communities than the food chain model. These trophic interactions are commonly found in both oligotrophic and eutrophic regions (e.g. Calbet and Saiz, 2005). We clarify this point now in the manuscript (l192-193).

Calbet, A. and Saiz, E: The ciliate-copepod link in marine ecosystems, Aquat Microb Ecol, 38: 157–167, 2005.

6. section 2.3: I find this section somewhat difficult to understand, partly because of typos and unclear wording. Would you make it clearer?

- l216-217: is the Buitenhuis et al. 2014 data MAREDAT data for all micro and mesozooplankton (there is only Buitenhuis et al. 2013 in the list of references) and the Schiebel and Movellan 2012 data for foraminifera?

That is correct. We improved the section “planktonic foraminifera biomass” in order to reduce confusion (l230-251).

- l227: is the observed relative biomass range starting at 0.07%, 0.01% (l223) or 0.007% (l966)?

The observed relative biomass range should be 0.007 % to 0.09 % (and not 0.07% as we wrote in l227). We corrected this error in l223 to l227.

- l227: are referred to here as ’low biomass’ simulations.

Done.

- l238: you need to decrease m to prevent foraminifera from going extinct, right? change to: "to keep planktonic foraminifera biomass within the ’low biomass’ range defined above"

Changed accordingly in l264.

- l240: this interpretation is difficult to follow at this point of the ms without having seen the results.

We rephrased the sentence to *“following suggestions that planktonic foraminifera can use their shell* ***as a protection against other factors than predation (e.g. pathogens) (Armstrong and Brasier, 2005).”*** (l264-265)

- l248: do you mean: "... to compare our ... results with, from the ’low biomass’ simulations we selected model simulations with 0% to 30% reduction in maximum growth and background mortality ..."?

Until now there are no direct quantifying estimates of the energetic cost and benefits of calcification in planktonic foraminifera to compare our model results with. Therefore, we selected a maximum 40% range between the minimum and maximum value of maximum growth $(\mathrm{G}_{\max})$ and mortality (m) reduction of as most likely (e.g., 10-50 % or 20-60 % reduction). This is a way to account for the non-unlimited plasticity of an organism. We added this information in l272-276.

- l248: 0% to 30% reduction in [...] background mortality: in Figs. 4-7 and in the supplement xls file it looks like plausible simulations have 0% to 30% reduction in max growth rate but 0% to 50% reduction in background mortality. Also, the red font colour in the xls file is not clear: it seems to mark some, but not all simulations named LB.

The range between the minimum and maximum value of each growth and background mortality is indeed less than 40%. The red mark in the xls file represent the biomass within the observation range, which applies for all the 'plausible' and 'low biomass (LB)' simulations and some scenarios testing different predation rates. As this clarification wasn't included in the excel file, we agree that the red mark was confusing and have changed it accordingly. The following information has now been added in every excel sheet: *"In red: biomass within the observation range. "*

7. section 2.4: can you describe more clearly which experiments were done in the text? Improving the layout of Table 3 (including legends for O, M and E) would also help.
We improved the layout of Table 3 as suggested.

8. l259-266: this section is very helpful information. Can you bring it earlier on in the methods section?
This paragraph has been now transferred in the beginning of the 2.3 section (l221-227).

9. l290: you refer to steady state changes in Fig. B3 but "dynamics" sounds more like changes in time. How about "community structure" or "size structure"?
This is a very good suggestion. We rephrased the sentence ass suggested (l315)

10. l314: "showed a decrease" instead of "resulted"?
Done.

11. l327-328: no 'plausible' simulations for the eutrophic ecosystem at 20 °C: but the bottom centre panel of Fig. 7 has a green star?

That is correct. We do have a plausible scenario for the eutrophic ecosystem at 20°C. We have corrected this mistake in the manuscript (l355).

12. l476: does this refer to adults in the food chain model and prolocular stages in the food web model (cf. Fig. 5, 6), but not to adults in the food web model and prolocular stages in the food chain model?

We can see there could be a confusion and rephrased the sentence to clarify this point:
*"Moreover, the inability of our **food web** model to sustain **adult** stages of non-spinose foraminifera in warm oligotrophic regions agrees with observations as planktonic foraminifera are dominated by symbiont bearing species in these regions (Bé and Tolderlund, 1971). "* (l500-503).

13. Fig. 2: for which stage are the two schemes? As adults and prolocular stages have different size, I guess they would be positioned at different locations on the vertical/size "axis"?
We agree that it might not be very clear from the plot in Figure 2. As suggested, the prolocular life stage should be at a lower position on plankton size "axis" than the adult one. To prevent this type of confusion, we added the following sentence to the figure legend:

"Note that the figure does not present the accurate position of the *planktonic foraminifera size group ran in the model but a generic position for illustrate how they interact with the rest of the plankton community.*"

14. Figs. 4-7: "total" in the legend is confusing. use "other"?; can you explain why the food chain simulations are all confined within an ellipse (Figs. 4, 5) while the food web shows this pattern only for some environmental conditions?

We changed the "total" to "other" after the reviewer's useful suggestion. We tested fewer simulations in the food web model than in the food chain model, hence a different spread of model results in Figures 4 and 5. We tested fewer simulations based on our food chain model results that showed that in many tested scenarios, planktonic foraminifera were extinct. On the contrary, for the food web, in a range of a 0 to 40% reduction on the mortality rate, the relative biomass of planktonic foraminifera was high and outside the observation range. As a further reduction of the mortality rate would result in an additional increase of relative biomass, the sensitivity analysis was not required. We added the above explanation in Figures 6 and 7 (l835-839, l846-851).

15. Eq. A1: what is R?
R is temperature sensitivity of plankton growth rate. We defined R in the text (l894-895) and Table 1.

16. l890: the reference is missing in the list of references
The reference has now been included.

3 Technical corrections

- l31: protection other than predation instead of "among". Done
- l54: either "to grow" or "to be grown". Done
- l61: can address (missing space) . Done
- l86: responses instead of "responds". Done
- l96: feeders (missing s) . Done
- l100: larger than themselves. Done
- l121: Fraile et al. 2009? (missing e). Done
- l125: limitation is that they are based. Done
- l126: from laboratory studies. Done
- tense: please check uniform tense (past or present) particularly in sections 2.2, 2.3 (e.g. l200: assume instead of assumed, l203: is instead of was, ...). Done
- l216-222, l269: add spaces to units, e.g. Pg C instead of PgC. Done
- l224: Schiebel and Movellan's (2012). Done
- l249: denoted as. Done
- l280: the supplement has only figures B1-B3?
The figure B1-B3 are part of the appendix B. The supplement materials include the code scripts and the excel file with all the ran simulations.
- l305: remove "the" before "all environments". Done
- l316: for the mesotrophic environment. Done
- l317: due to a high decrease; compared with. Done
- l394: ellipse? Done
- l416, 418: pellets. Done
- l428: shells. Done

- l431: it is difficult. Done
- l438: of grazing protection. Done
- l445: controls. Done
- l451: generalist herbivory and omnivory? We change the sentence to "*generalist herbivory **and** omnivory **diet***" (l476)
- l460-461: are very successful ... predators. Done
- l476: oligotrophic. Done
- l487: suggests. Done
- l490: environment. Done
- uniform referencing style for figures, equations: currently Fig., fig., figures, Eq, Eqs. eq() are all used. Done
- References list: please check carefully for typos (and citation format)

– taxon names in italics (ll 570, 574, 576, 585) . Done

– l548: Foraminifera. Done

– l612: non-italic (d'Orbigny) . Done

– l620: Verlag. Done

– l643: trade-offs in. Done

– l659: Menden-Deuer. Done

– l660: . or , before journal name? Done

– l667: Müren. Done

- Figs. 8, 9: Temperature Done
- Fig. 9: this is for the adult, not for the prolocular stage, right? please explain the different colour shading for the prey palatability. Done
- l827: sizes. Done
- l848: Eq. S2, S3 are A2, A3? Thank you for the valid point. Indeed Eq. S2, S3 are A2, A3, and this this mistake is now corrected (l906, l925)
- l852: via the Monod. Done
- l857: half-saturation. Done
- l861: reflects instead of is represented. Done
- l862: Prochlorococcus in italics. Done
- l863: for the remaining (not rest) . Done
- l876, 902: is PV Z the same as PorZ? We have corrected this mistake in the manuscript (l926)
- l889: on the Redfield; which ratio do you use? We used the 106:16 Carbon: Nitrogen Redfield ratio. This clarification now has been included (l941).
- l892: K in italics We changed the format of the parameters in the manuscript and now all the parameters are consistently not written in italics.
- l893: using Mayzaud. Done
- l899: account for the. Done
- l900: Kiørboe. Done
- l905:) as a; size (Gentleman. Done
- l965: Within the coloured. Done

Figure and Table layout:

- Tables 1-2: enhance clarity with the first column left justified and text on one line if possible. Done

- Figs. 4-7: maybe use shading to identify the 'plausible' range of simulations? We changed the colour scale and added black edges for the 'plausible' and 'low biomass' symbols to make the figures easier to read.

- Figs. 8, 9: please mention the size ranges for pico, nano, micro here again

The following sentence has been included in figures’ 8 and 9 legend (l856-857, l866-867): *“**Six pico- (0.6-2.0 µm), ten nano- (2.6- 20 µm) and nine micro- groups (25-160 µm) are included in the model set up**.”*