

Interactive comment on “A trait-based modelling approach to planktonic foraminifera ecology” by Maria Grigoratou et al.

Anonymous Referee #1

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1 General comments

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

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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?
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.
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 (Kjørboe 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 (Kjørboe 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.
4. Does the applied formulation imply that at low food concentration foraminifera become the only zooplankton prey source for zooplankton? Could you de-

- scribe if and how your results may change if the prey refuge is also applied to foraminifera?
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 (I238-240). Would it still need to be decreased if you allowed a prey refuge also for foraminifera?
 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?
 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. I.97) also switch? Do zooplankton in both model configurations (food chain and food web) switch?

References:

- Almeda, R., H. v. S. Greve, and T. Kiørboe. 2017. Behavior is a major determinant of predation risk in zooplankton. *Ecosphere* 8. doi:10.1002/ecs2.1668.
- Gonçalves, R. J., and T. Kiørboe. 2015. Perceiving the algae: How feeding-current feeding copepods detect their nonmotile prey. *Limnol. Oceanogr.* 60: 1286–1297. doi:10.1002/lno.10102.

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Greve, H. v. S., R. Almeda, and T. Kiørboe. 2017. Motile behavior and predation risk in planktonic copepods. *Limnol. Oceanogr.* 62: 1810–1824. doi:10.1002/lno.10535.

Kiørboe, T., H. Jiang, and S. P. Colin. 2010. Danger of zooplankton feeding: the fluid signal generated by ambush-feeding copepods. *Proc. R. Soc. Lond. B* 277: 3229–3237. doi:10.1098/rspb.2010.0629.

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

Visser, A. W. 2007. Motility of zooplankton: fitness, foraging and predation. *J. Plankton Res.* 29: 447–461.

1. Does the paper address relevant scientific questions within the scope of BG?
yes.
2. Does the paper present novel concepts, ideas, tools, or data?
yes.
3. Are substantial conclusions reached?
yes.
4. Are the scientific methods and assumptions valid and clearly outlined?
in general yes, but the methods should be described more clearly.
5. Are the results sufficient to support the interpretations and conclusions?
yes, but the above effects of the grazing parameterisation should be described/discussed.
6. Is the description of experiments and calculations sufficiently complete and precise to allow their reproduction by fellow scientists (traceability of results)?

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- partly. Some typos and missing values in equations/tables and some unclear wording might hinder reproduction.
7. Do the authors give proper credit to related work and clearly indicate their own new/original contribution?
yes.
 8. Does the title clearly reflect the contents of the paper?
yes.
 9. Does the abstract provide a concise and complete summary?
yes.
 10. Is the overall presentation well structured and clear?
partly. The methods section should be improved and the wording in places.
 11. Is the language fluent and precise?
partly. Some wording is misleading/confusing.
 12. Are mathematical formulae, symbols, abbreviations, and units correctly defined and used?
mostly (few exceptions).
 13. Should any parts of the paper (text, formulae, figures, tables) be clarified, reduced, combined, or eliminated?
the methods section and some figure legends (detailed below).
 14. Are the number and quality of references appropriate?
yes.
 15. Is the amount and quality of supplementary material appropriate?
yes.

2 Specific comments

1. I51, I217: I could not find the reference for Buitenhuis et al. 2014.
2. I57-59: unclear, could you reword?
3. I69: can you specify if the compilation of foraminifera traits was done as part of this study or otherwise add a reference ?
4. I71: what are "growth optimal environmental conditions" - environmental conditions that are optimal for growth?
5. I186: 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 (??).
6. section 2.3: I find this section somewhat difficult to understand, partly because of typos and unclear wording. Would you make it clearer?
 - I216-217: 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?
 - I227: is the observed relative biomass range starting at 0.07%, 0.01% (I223) or 0.007% (I966)?
 - I227: are referred to here as 'low biomass' simulations.
 - I238: 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"
 - I240: this interpretation is difficult to follow at this point of the ms without having seen the results.

- I248: 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 ..."?
 - I248: 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 marks some, but not all simulations named LB.
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.
 8. I259-266: this section is very helpful information. Can you bring it earlier on in the methods section?
 9. I290: you refer to steady state changes in Fig. B3 but "dynamics" sounds more like changes in time. How about "community structure" or "size structure"?
 10. I314: "showed a decrease" instead of "resulted"?
 11. I327-328: no 'plausible' simulations for the eutrophic ecosystem at 20 degC: but the bottom centre panel of Fig. 7 has a green star?
 12. I476: 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?
 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"?

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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?
15. Eq. A1: what is R?
16. l890: the reference is missing in the list of references

3 Technical corrections

- l31: protection other than predation instead of "among"
- l54: either "to grow" or "to be grown"
- l61: can address (missing space)
- l86: responses instead of "responds"
- l96: feeders (missing s)
- l100: larger than themselves
- l121: Fraile et al. 2009? (missing e)
- l125: limitation is that they are based
- l126: from laboratory studies
- 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, ...)
- l216-222, l269: add spaces to units, e.g. Pg C instead of PgC

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- l224: Schiebel and Movellan's (2012)
- l249: denoted as
- l280: the supplement has only figures B1-B3?
- l305: remove "the" before "all environments"
- l316: for the mesotrophic environment
- l317: due to a high decrease; compared with
- l394: ellipse?
- l416, 418: pellets
- l428: shells
- l431: it is difficult
- l438: of grazing protection
- l445: controls
- l451: generalist herbivory and omnivory?
- l460-461: are very successful ... predators
- l476: oligotrophic
- l487: suggests
- l490: environment
- uniform referencing style for figures, equations: currently Fig., fig., figures, Eq, Eqs. eq() are all used.

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- References list: please check carefully for typos (and citation format)
 - taxon names in italics (ll 570, 574, 576, 585)
 - l548: Foraminifera
 - l612: non-italic (d'Orbigny)
 - l620: Verlag
 - l643: trade-offs in
 - l659: Menden-Deuer
 - l660: . or , before journal name?
- l667: *M uren*
- Figs. 8, 9: Temperature
- Fig. 9: this is for the adult, not for the prolocular stage, right? please explain the different colour shading for the prey palatability
- l827: sizes
- l848: Eq. S2, S3 are A2, A3?
- l852: via the Monod
- l857: half-saturation
- l861: reflects instead of is represented
- l862: Prochlorococcus in italics
- l863: for the remaining (not rest)
- l876, 902: is Φ_{PVZ} the same as Φ_{PorZ} ?

- 1889: on the Redfield; which ratio do you use?
- 1892: K in italics
- 1893: using Mayzaud
- 1899: account for the
- 1900: Kiørboe
- 1905:) as a; size (Gentleman
- 1965: Within the coloured

Figure and Table layout:

- Tables 1-2: enhance clarity with the first column left justified and text on one line if possible
- Figs. 4-7: maybe use shading to identify the 'plausible' range of simulations?
- Figs. 8, 9: please mention the size ranges for pico, nano, micro here again

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