

We would like to thank the reviewer for her strongly supportive comments towards our study as well as her 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 reviewer's comments (highlighted in blue).

5

Referee 2

This article presents a new trait-based model for planktonic non-spinose foraminifera in order to test several trade-offs among foraminifera feeding, growth and survival, and more specifically among size, trophic regime, feeding behaviour, predation avoidance, and shell calcification.

The introduction is easy to follow and presents clearly all the needed information on planktonic foraminifera. However, the sentences on trait-based approaches could be rewritten to avoid some fuzziness in the presentation of the concept of trait. For instance, traits are defined at the individual level (see the recent review by Kiorboe, Visser Andersen, 2018, A trait-based approach to ocean ecology. ICES Journal of Marine Science (2018), doi:10.1093/icesjms/fsy090). The context of the study is clearly stated (model for foraminifera growth) and the study is well justified (need of a traitbased generic model, using body size, calcification, and feeding behaviour).

We change the presentation of traits to: "*Trait-based approaches provide mechanistic understanding of individuals, populations or ecosystems functioning as they describe these systems from first principles by defining individuals' key traits (e.g. feeding, competition, predation, reproduction) and associated trade-offs like energetic needs and predation risks (e.g. Litchman and Klausmeier, 2008; Litchman et al., 2013; Barton et al., 2016; Hébert et al., 2016; Kiørboe, 2018).*" (I63-65)

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In the method section, the authors present the trait-based model of planktonic nonspinose foraminifera growth (including two life stages: prolocular and adult) they have developed in order to investigate the cost and benefits (trade-offs) of calcification and feeding behaviours under different environmental conditions (temperature and nutrient concentration). The model set up adopted in the study is original and provides very interesting results.

The discussion is clear and relatively short, but the authors suggest several hypotheses to explain their results (observed trade-offs among calcification and growth) and the adequate literature is cited. Out of curiosity, I am wondering what type of trade-offs could exist in spinose foraminifera species.

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We would like to thank the reviewer for finding out discussion clear and useful. A more detailed review study on planktonic foraminifera (non-spinose and spinose) traits and trade- offs is in preparation from Edgar, Monteiro, Grigoratou and Schmidt.

40 The conclusion is clear and concise. Therefore, I recommend minor revisions before publication. Indeed, the presentation of the manuscript should be improved in order to present the model more clearly (see comments below).

2) Specific comments

2.1) Remarks on the Model:

I have several comments on the way the equations are indicated. Indeed, this section was difficult to follow, as many precious information was available in the annex and not in the main text of the manuscript.

50 I recommend to follow, when possible, writing standards for model equations (e.g., keep capital letters for variables and lower case letters for parameters, use mu for growth rates, etc. See comments bellow). The authors should make the equations much more clear, even for modellers, as this sections is difficult to follow.

55 Note that I appreciate that the code is freely available. I thank the authors for this effort of sharing their work to the scientific community.

Miscellaneous comments on the model:

I 116: what is a species model?

60 We apologise for the confusion, we meant models which are built for specific species of planktonic foraminifera. We rephrased our sentence to "However, until now, **only species-specific ecological models have been developed to study the ecology of modern planktonic foraminifera species: Žarić et al. (2006) (from now on Žarić06), PLAFOM (Fraile et al., 2008; Fraile et al., 2009) and FORAMCLIM (Lombard et al., 2011; Roy et al., 2015).**" (I115)

65 I 145: 2.1. Model environment => is "environment" the good term?

We changed model environment to model description (I145).

I 150: why is the duplication rate called kappa? Usually, it is called d or D in chemostat models.

70 As we built our model from Ward et al. (2012) and Ward et al. (2014) modelling studies, we followed their symbols and definitions for consistency.

I 146-147: Looking at your equations, it rather seems that nutrient availability is named N on your equations. Accordingly, replace the notation NO3- by N.

75 Done.

I153: each term of Equation 1 needs to be defined: what are j_{prey} , $B_{N,j}$, $P_{growth,j}$? Why j_{prey} and not j_{phyto} (indeed, zooplankton can be a prey, but would not do photosynthesis and impact the nutrient concentration)? Why do you use [and] in your equation? It seems not useful and hence confusing. Besides, it is usually written "parameter. Variable" in such differential equations: please reverse the writing and indicate: $P_{growth,j}B_{N,j}$. More generally, please distinguish more clearly among parameters (lower case), functions (with brackets indicating their variables), and variables (capital letters). Clearly indicate in the text that P and G are in fact functions and refer to the annex section.

85 We present the equations in a similar format to Ward et al., 2012, for consistency. We added the following sentences to the manuscript (I166-169) "**Phytoplankton growth ($P_{growth,j}$) depends on limitation from light, temperature and nutrient availability, following a Monod response (Appendix, eq. A2). Zooplankton grazing is controlled by the biomass and size of the prey and is described through a Holling type II response (Eq. (A3)).**"

90 I 156 to 159: move these sentences after having presented the equations with mortality terms and sloppy feeding terms.

95 Done.

I 163: shouldn't it be BN;j of Bj rather than B in the left side of equation 2? Note that the subscripts N are not useful here, unless you will later use an other currency than N for the biomass? Please rather

100 indicate 3 equations: one for the autotrophic plankton, one for the heterotrophic plankton, and one for the mixotrophic plankton. What is b in $\lambda_{ib,j}$?

We have removed the "N" from the biomass and the b in λ , which was a typographic mistake. In our model we include only autotrophs and heterotrophs but no mixotrophs. For consistency with Ward et al., 2012, we decide to keep one generic equation for plankton biomass (Eq.2).

105 Impact of linear growth (instead of a Michaelis-Menten functional response) on your results? Considering only linear growth is a strong assumption and the reasons to do so (and potential consequences) should be clearly indicated.

As specified above, the growth of phytoplankton depends on the limitations from light, temperature and nutrient availability, which follow a Monod-type response (Appendix, eq. (A2))

110 I181: from a biological and ecological point of view, what would be a "specialist predator on planktonic foraminifera", as included in your simple food chain model? What would be its characteristics?

115 The prey-predator interactions between planktonic foraminifera and other zooplankters are still not well understood. Parts of planktonic foraminifera's shells have been found on salps faecal pellets, which are filter feeders and hence non-specialised. Current evidence suggests that planktonic foraminifera do not have a specific zooplankton predator and they are indiscriminately grazed by filter feeding organisms (Hemleben et al., 1989). As one aim of our study is to understand the role of 120 shell as protection from predation, we chose to test two scenarios, one where predators are specialised on planktonic foraminifera (i.e. planktonic foraminifera are the only zooplankton group which prey on, food chain), and one where opportunist predators can use planktonic foraminifera as part of their diet (food web). From a biological and theoretical point of view having a specialist predator on plankton foraminifera seems to be unrealistic but as predation on planktonic 125 foraminifera is not well understood we chose to test both hypotheses.

Hemleben, C., Spindler, M. and Anderson, O.R.: Modern Planktonic Foraminifera. Springer Verlag, New York, 1989, p135.

130 I 222: is it realistic to consider that the "protocalar biomass is similar to the adult biomass"? I would have expected to have much more protocalar biomass than adult biomass, especially given their slow growth (but I am not a specialist of foraminifera...)

135 This is a fair point. It has been suggested that the biomass of early stages can be up to three times higher than adults (Schiebel and Movellan, 2012) but data regarding the abundance and biomass of planktonic foraminifera's early stages are scarce due to sample limitations specifically a combination of their planktonic foraminifera's low abundance and the focus on nets with mesh size >100 μm . For the present study, we decided to extend our estimations for the size fraction 150-200 μm and 140 converted the biomass range by a factor of three to include a global representation of planktonic foraminifera, sampling errors, and early stages. As planktonic foraminifera's cytoplasm (organic biomass) is growing parallel with the shell, we argue that our estimated biomass range for the adult with size 160 μm can also represent the early stages, even though prolocular's abundance is higher than the adults, adult's biomass per individual is higher due to their bigger cytoplasm. Based on that 145 we believe that the prolocular biomass cannot be less than define range. More biomass data are needed in order to improve our biomass estimations, but we believe that as the aim of our study is

to explore the costs and benefits of calcification in different life stages, our biomass range can be used for both life stages.

- 150 Buitenhuis, E. M., Vogt, R., Moriarty, N., Bednarsek, S.C., Doney, S. C., Leblanc, K., Le Quéré, C., Luo, Y. W., O'Brien, C., O'Brien T., Peloquin J., Schiebel, R., C. Swan, C.: MAREDAT: towards a world atlas of MARine Ecosystem DATa. Earth System Science Data, Copernicus Publications, 5, 227-239 <https://doi.org/10.5194/essd-5-227-2013>, 2013.
- 155 Schiebel, R. and Movellan, A.: First-order estimate of the planktic foraminifer biomass in the modern ocean, Earth Syst. Sci. Data, 4, 75-89, <https://doi.org/10.5194/essd-4-75-2012>, 2012.

I 260: Table 3 is difficult to follow as the horizontal and vertical lines are not indicated. Please make it easier to read. For instance, why is there 3 identical rows for Nutrient region? I would assume that you used the 3 different regimes (O, M, E) for each of the Temperature conditions (10, 20, 30), but it is not what I read in Table 3. Similarly, in the part entitled "Study traits", the rows of "Prolocular (20 m)" and "Adult (160 m)" are identical. If this is correct, then please merge them.

Thank you for these useful suggestions. We applied all changes to our Table.

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2.2) Remarks on the Results:

- I find it strange to start this section with Figures that are all in Annex and not in the main text (Figures B1 and B2).

170 We added Figure B1 into the main text (now referred as Fig.3) and left Figure B2 in the Appendix A.

2.3) Remarks on the Figures:

Fig. 1: useful, but indicated in the legend that this figure is inspired from the topology of zooplankton traits proposed by Litchman et al 2013 in JPR.

175 We added the following sentence into the legend: "*The presentation of planktonic foraminifera's traits was inspired from the topology of zooplankton traits proposed by Litchman et al. (2013).*" (I789-790).

Legend of Figure 3: indicate the name of the parameter σ .

180 We now included the figure of prey palatability in Fig.2 and indicated the name of parameter (σ) (I800).

Figures 4 to 7: the symbols for 'plausible' and 'low biomass' are very difficult to distinguish, especially because the stars and triangles are light green on a light grey background. Please modify (an provide figures with a better resolution).

We changed the colour scale and added black edges for the 'plausible' and 'low biomass' symbols to make the figures easier to read.

Figure 4 to 7: why not use the same setting as in Figures 8 to 9, with an horizontal arrow indicating the increase in Temperature (please correct the typo: Tempertature), and a vertical arrow indicated the increase in Nutrient concentration (O-M-E) ?

Done.

195 **3) Technical corrections:**

Please find below additional minor comments: [Done](#)

- Check and remove double spaces throughout the ms [Done](#)

- Please revise the manuscript to remove all typos, for instance (in the beginning of the manuscript, I have not indicated all of them here):

200 | 23: extra space (on trait theory). [Done](#)

| 56: change in police size. [Done](#)

| 61: no space (canadress). [Done](#)

| 90-91 : change in police size. [Done](#)

| 103: " It has been speculated that the higher abundance...": higher than what?. We changed that to
205 "higher abundance of spinose species compared to the non-spinose is the result of their carnivory"
(|104).

| 125: the subject ("they"?) is missing in "is that are based". [Done](#)

| 139: no comma in "interactions of planktonic foraminifera, with...". [Done](#)