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).

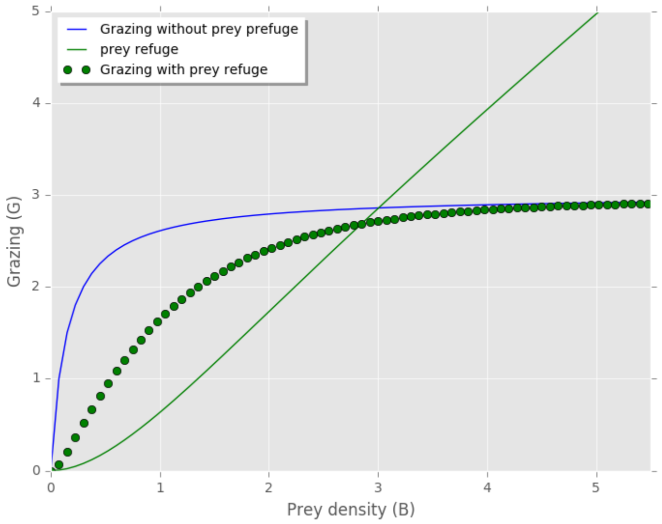

Figure A1: Zooplankton grazing on one prey with and without the prey refuge term included. Prey refuge $= (1 - e^{-\Lambda F}) * F$. Grazing without prey refuge: $G = G_{max} * \gamma_T * \frac{F}{F+K_{zoo}}$. Grazing with prey refuge included : $G = G_{max} * \gamma_T * \frac{F}{F+K_{zoo}} *$ Prey refuge. 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**.”*

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).

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)****.*" (l63-65)

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.

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.

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.
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.
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:

l 116: what is a species model?
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)."* (l115)

l 145: 2.1. Model environment => is "environment" the good term?
We changed model environment to model description (l145).

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

l 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.
Done.

l153: 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.

We present the equations in a similar format to Ward et al., 2012, for consistency. We added the following sentences to the manuscript (l166-169) ***"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))."***

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

l 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 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 a., 2012, we decide to keep one generic equation for plankton biomass (Eq.2).

Impact of linear growth (instead of a Michaelis-Menten functional response) on your results? Considering only linear growth is a string 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))

l181: 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?

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 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 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.

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

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 scare 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 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 160µm 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 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.

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.

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.

l 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.

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).

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.

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)."*** (l789-790).

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

We now included the figure of prey palatability in Fig.2 and indicated the name of parameter (σ) (l800).

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.

3) Technical corrections:

Please find bellow 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):

l 23: extra space (on trait theory). Done

l 56: change in police size. Done

l 61: no space (canadress). Done

l 90-91 : change in police size. Done

l 103: " It has been speculated that the higher abundance...": higher than what?. We changed that to ***"higher abundance of spinose species compared to the non-spinose is the result of their carnivory"*** (l104).

l 125: the subject ("they"?) is missing in "is that are based". Done

l 139: no comma in "interactions of planktonic foraminifera, with...". Done

A trait-based modelling approach to planktonic foraminifera ecology

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Abstract:

Despite the important role of planktonic foraminifera in regulating the ocean carbonate production and their unrivalled value in reconstructing paleoenvironments, our knowledge on their ecology is limited. A variety of observational techniques such as plankton tows, sediment traps and experiments, have contributed to our understanding of foraminifera ecology. But, fundamental questions around costs and benefits of calcification, and the effect of nutrients, temperature and ecosystem structure on these organisms remain unanswered. To tackle these questions, we take a novel mechanistic approach to study planktonic foraminifera ecology based on trait theory. We develop a 0-D trait-based model to account for the biomass of prolocular (20 µm) and adult (160 µm) stages of non-spinose foraminifera species and investigate their potential interactions with phytoplankton and other zooplankton under different temperature and nutrient regimes. Building on the costs and benefits of calcification, we model two ecosystem structures to explore the effect of resource competition and temperature on planktonic foraminifera biomass. By constraining the model results with ocean biomass estimations of planktonic foraminifera, we estimate that the energetic cost of calcification could be about 10-50% and 10-40% for prolocular and adult stages respectively. Our result suggest that the shell provides protection against processes other than predation (e.g. pathogen invasion). We propose that the low standing biomass of planktonic foraminifera plays a key role in their survival from predation, along with their shell protection. Our model suggests a shift from temperature as a main regulator of foraminifera biomass in the early developmental stage to resource competition for adult biomass.

1. Introduction

Planktonic foraminifera as a group comprise fifty holoplanktonic heterotrophic protozoans (Kucera, 2007). They are the most widely-used zooplankton group to reconstruct past marine environments, with proxies devised that are based on their abundance, assemblage composition, and/or physio-geochemical characteristic of their shell (e.g. Schmidt et al., 2003; Schiebel and Hemleben, 2005). They are also the most important calcifying zooplankton group, supplying between 23-55 % of the total marine planktonic carbonate production (Schiebel, 2002), and hence are a key contributor to the composition of marine sediments (Schiebel and Hemleben, 2005).

In contrast to their high abundances in sediments, they tend to grow at very low abundance in the ocean and never dominate the zooplankton community, representing less than 5% of total microprotozooplankton abundance (Beers and Stewart, 1971). Based on plankton tow observations, abundances range from 1 ind. m^{-3} in blue waters, 20-50 ind. m^{-3} in oligo- and mesotrophic waters (Schiebel and Hemleben, 2005) to >1000 ind. m^{-3} in polar regions (Volkmann, 2000). Their global biomass in the water column has been estimated to be between 0.002 and 0.0009 Pg C and their contribution to global plankton biomass to be ~ 0.04 % (Buitenhuis et al., 2013).

Despite their importance in palaeo- and modern biochemical oceanography, our knowledge of planktonic foraminifera's physiology, development and ecology is limited to a few observations. Planktonic foraminifera are difficult to grow in culture and it has been impossible to grow a next generation (Hemleben et al., 1989). Consequently, information regarding the intraspecies and interspecies competition, as well as a mechanistic understanding of their physiology through their whole life cycle is missing.

Trait-based approaches can be useful for improving our knowledge of planktonic foraminifera ecology as they can address fundamental questions around the cost of growth across developmental stages, their position in the global food webs and calcification. Trait-based approaches provide mechanistic understanding of individuals, populations or ecosystems, as they describe these systems from first principles by defining individuals' key traits (e.g. size, feeding, 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). For example, body size is considered as a master trait for plankton, impacting many physiological and ecological aspects such as metabolic rates (e.g. growth), diet, abundance, biomass and reproduction (e.g. Litchman et al., 2013).

Several traits and trade-offs have been identified for planktonic foraminifera, summarised in Figure 1. The size of planktonic foraminifera can be regarded as a 'master' trait and can be used as an indicator for environmental conditions that are optimal for growth (e.g. Caron et al., 1983; Schmidt et al., 2004a). Planktonic foraminifera development is divided into five stages, defined based on shell size and wall structure: prolocular, juvenile, neanic, adult and terminal (gametogenesis) (Brummer et al., 1986, 1987). Their shell diameter ranges from about 10 µm for the prolocular life stage to more than 1250 µm for the adult under optimal conditions (Schmidt et al., 2004a). Planktonic foraminifera are considered to reach the adult stage and subsequently be sexually mature when their shell size reaches around 100 µm (Brummer et al., 1986, Caromel et al., 2016). Shell size increases from low to high latitudes (Schmidt et al., 2003, 2004b) and is related to reproductive success (gametogenesis), as bigger individuals release more gametes (e.g. Caron and Bé, 1984; Hemleben et al., 1987). Temperature and food availability are suggested to be the main environmental factors which regulate their size (e.g. Anderson et al., 1979; Spero et al., 1991; Caron et al., 1983; Schmidt et al., 2004a), but a mechanistic understanding of the response of shell size to temperature and food is missing.

Calcification is another important trait of planktonic foraminifera, relative to shell size, but the costs and benefits of possessing a shell and the nature of the associated trade-off are not well understood. Paleo records indicate changes in size (Schmidt, 2004a), thickness (Barker and Elderfield, 2002), and morphology of planktonic foraminifera shell, as responses to changing climates (Malmgren and Kennet, 1981; Norris, 1991). Determining the cost and benefit of producing a shell is fundamental to quantifying the influence of climate change on planktonic foraminifera ecology, distribution, and carbonate production in the past, present and future.

The feeding strategies of planktonic foraminifera are also an important trait as they are crucial for survival and influence plankton community ecology. Planktonic foraminifera are inactive organisms and passive feeders. They do not detect their prey but encounter them while drifting, using a rhizopodial network which extends from their body (e.g. Anderson and Bé, 1976). As planktonic foraminifera are typically collected for experimental work at sizes >60 µm and subsequently grown as individuals, information regarding the feeding behaviour of the early (prolocular and juvenile) life stages, the cost and benefits of being inactive passive feeders, and interactions with other plankton are missing. It has been suggested that at the prolocular stage all species are herbivorous (Hemleben et al., 1989) and subsequently widen their food sources. Field and laboratory observations suggest that spinose species use their spines, which start growing during the neanic stage, to capture and control active zooplankton prey, that are often larger than themselves (e.g. Anderson, 1983; Spindler et al., 1984). Spinose species tend to be either omnivorous or carnivorous (Schiebel and Hemleben, 2017) and many have developed a symbiotic relationship with photosynthesizing algae (Schiebel and Hemleben, 2017) which allows them to be successful in oligotrophic areas. It has been speculated that the higher abundance of spinose species compared to the non-spinose is the result of their carnivory as oligotrophic areas are characterized by relative low phytoplankton concentration but relative high abundance of copepods (Schiebel et al., 2004; Moriarty and O'Brien 2013). Non-spinose species are often omnivorous/herbivorous (Anderson et al., 1979; Hemleben and Auras, 1984), with the ability to catch and feed on small zooplankton or dead organic matter resulting in their maximum abundance in high-productivity regions (Schiebel and Hemleben, 2017).

Trait-based models can supplement the physiological and ecological understanding of foraminifera gained in the field and cultures (Fig. 1) to improve our understanding of planktonic foraminifera ecology. Trait-based models have been successfully applied to phytoplankton (e.g. Follows et al., 2007; Litchman and Klausmeier, 2008; Monteiro et al., 2016) with little development and application on zooplankton (e.g. Banas, 2011; Maps et al., 2011; Ward et al., 2012; 2014; Banas et al., 2016). 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). Žarić06 developed an empirical model which relates the global fluxes of eighteen species of planktonic foraminifera to environmental conditions based on observations. PLAFOM models field observations to predict the influence of temperature (Fraile et al., 2008) and food availability (Fraile et al., 2009) on the global biogeography of five species. FORAMCLIM represents eight species of planktonic foraminifera and studies the influence of temperature, food availability, light and climate change on growth rates and global distribution. These models provide important insights into the interaction between planktonic foraminifera and their habitat. Their main limitation is that they are based on empirical (Žarić et al., 2006; Fraile 2008; 2009) or laboratory data (Lombard et al., 2011; Roy et al., 2015) and their application is thus species-specific and limited to specific environmental ranges (Roy et al., 2015).

Here, we describe the first trait-based generic model of planktonic foraminifera using body size, calcification and feeding behaviour as key traits to investigate the mechanisms behind planktonic foraminifera ecology. We focus on modelling non-symbiotic non-spinose species because these species are predominantly herbivorous throughout their whole life and do not develop spines and algal symbionts, all of which increase complexity and are not sufficiently constrained by basic physiological data. Our trait-based planktonic foraminifera model was derived from the size-structured plankton models of Ward et al. (2012; 2014) which use cell and body size as the eco-physiological trait to study the phyto-zooplankton food web. We investigate the energetic costs and benefits of calcification, their feeding behaviour and resource competition with other zooplankters, as well as the environmental controls on two different developmental stages. Model results assess and quantify the biotic and abiotic factors influencing their physiology and ecology, and the interactions of planktonic foraminifera with phytoplankton and other zooplankton, as well as their environment.

2. Methods

2.1. Model structure

Our model represents a chemostat experiment in a zero-dimensional (0-D) setting. It accounts for one source of nutrients (here defined as nitrates, NO_3^-) and fifty-one generic phytoplankton (autotrophs) and zooplankton (heterotrophs) size classes from pico- to mesoplankton (Schiebel 1978).

The nutrient availability (N) depends on the input nutrient concentration (N_o) interpreted as either a nutrient-rich vertical source of nutrient (typical of high-productivity regions) or a less-rich horizontally advective nutrient source (typical of oligotrophic gyres), dilution rate κ and phytoplankton uptake (Eq. (1)).

$$\frac{dN}{dt} = \kappa * (N_o - N) - \sum_{j_{phyto}=1}^{J} P_{growth,j} B_j \qquad (1)$$

We investigated a range of N_o values (0-5 mmol N m^{-3}) to account for a range of different nutrient regimes, from oligotrophic to eutrophic (Ward et al., 2014).

Plankton populations are modelled in terms of nitrogen biomass (B) with the rate of change of biomass described by:

$$\frac{dB_j}{dt} = P_{growth,j} B_j + B_j \lambda \sum_{jprey=1}^{J} G_{jprey} - \sum_{jpred=1}^{J} B_{jpred} G_{jpred,j} - B_j m_j \qquad (2)$$

where $P_{growth,j}$ represents the phytoplankton growth (Eq.A2), $B_j \lambda \sum_{jprey=1}^{J} G_{jprey}$ the zooplankton grazing (Eq. (A3)), $\sum_{jpred=1}^{J} B_{jpred} G_{jpred,j}$ the plankton losses due to zooplankton grazing and m_j the plankton background mortality (Table 1). 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)).

We assumed that the terms of plankton mortality and zooplankton sloppy feeding (prey which is lost from the predator during feeding (Lampert, 1978)) are exported out of the chemostat. There is no nutrient recycling in the model. The model parameters and symbols are defined in Tables 1 and 2 and a more detailed description of the model and plankton growth is available in Appendix A.

2.2. Complexity of the ecosystem structure

We modelled two simplified ecosystems: a simple food chain and a more complex food web (Fig. 2). In the simple food chain model, zooplankton were herbivorous size-specialist predators feeding on one prey size group. In order to examine the grazing pressure of a specialist predator on planktonic foraminifera, we made an exception by defining one zooplankton group to be omnivorous, capable of consuming only planktonic foraminifera and one phytoplankton group with the same size as planktonic foraminifera. Resource competition occurred mostly at the phytoplankton level. In zooplankton, the only competition was between individual planktonic foraminifera and with zooplankton of the same size group (Fig. 2a). This simple representation of the marine ecosystem allowed us to better understand the model behaviour and the top-down and bottom-up controls on foraminifera while testing the grazing pressure of a specialist predator on planktonic foraminifera.

In the food web model, resource competition occurred at both phytoplankton and zooplankton levels. Zooplankton predators were size-generalist omnivorous predators able to consume more than one prey (Fig. 2b). This more complex version helped us to better understand how the herbivorous non-spinose planktonic foraminifera can compete with other omnivorous zooplankters and handle multi predation pressure. The food web model has a more realistic representation of the plankton community 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, but these dynamic interactions within the groups are more challenging to disentangle (Banas 2011; Ward et al., 2014). With the two versions of the model we were able to examine how the resource competition within plankton community as well as predation, influences different life stages of planktonic foraminifera.

The switch from the food chain to food web version was implemented through predators' grazing kernel, which dictates the relative palatability of potential prey (Fig. 2c, Eq. (3)). In this parameterization, the prey palatability ($\varphi_{\mathrm{jpred,jprey}}$) expresses the likelihood of a predator to eat a prey (Eq. (3)) and it depends on the optimum predator:prey length ratio $\left(\theta_{\mathrm{opt}}\right)$, the log size ratio of each predator with each prey ($\theta_{\mathrm{jpred,jprey}}$), and the standard deviation (σ) which shows the width of size prey preference and defines how specialist or generalist the predator can be (Fig. 3).

$$\varphi_{\mathrm{jpred,jprey}} = \exp\left[-\left(\ln\left(\frac{\theta_{\mathrm{jpred,jprey}}}{\theta_{\mathrm{opt}}}\right)\right)^2\left(2\sigma_{\mathrm{jpred}}^2\right)^{-1}\right] \tag{3}$$

We assumed a 10:1 predator - prey length ratio as the optimum size for zooplankton to feed upon, as is often observed for zooplankton (Kiørboe, 2008). Prey with a size ratio equal to this optimum therefore had the highest prey palatability of this particular predator. For the food chain model, predators could only consume one prey group that was exactly ten times smaller than themselves ($\sigma = 0.0001$). In the food web model, we allowed zooplankton to be more generalist predators and feed on prey of size around this optimum ratio but with a smaller palatability to acknowledge that zooplankton can feed on prey of a wider size range (Kiørboe, 2008) ($\sigma = 0.5$). When considering generalist planktonic foraminifera (foob web model), we tested a range of different grazing kernels ($\sigma = 0.5 - 1.0$). This is because the model results showed that being more generalist than other zooplankton groups is a condition for planktonic foraminifera to survive.

2.3. Adding planktonic foraminifera in the model

We explored the potential ecological controls on planktonic foraminifera ecology by means of a series of ensembles of model experiments (Table 3). Each individual ensemble was designed to explore a wide range of potential parameter value combinations of growth, predation and background mortality rates and hence different trade-off assumptions and growth conditions. The ensembles were repeated for different potential assumed ecological structures and life stages (prolocular and adult) of planktonic foraminifera. We applied a series of 'plausibility' filters on the model results to derive a series of sub-sets of experiments that we analyse in detail and discuss the implications of.

Planktonic foraminifera biomass

We estimated that the contribution of the prolocular and adult stage of non- spinose planktonic foraminifera to zooplankton biomass ranges from 0.007 % to 0.09 % based on Schiebel and Movellan's (2012) and Buitenhuis et al. (2013) studies. According to Schiebel and Movellan (2012), adults with a shell size fraction of 150 -200 µm contribute 12.4% in total planktonic foraminifera biomass on the North Hemisphere. Buitenhuis et al. (2013) estimated that the contribution of planktonic foraminifera to micro- and mesozooplankton biomass (Pg C) ranges from 0.05 to 0.08 %, based on Schiebel and Movellan's (2012) data. To compare our modelled biomass to observations from Schiebel and Movellan (2012) and Buitenhuis et al. (2013), we converted Pg C and µg C to mmol N m^{-3}, using the carbon molecular weight (12 g C mol^{-1}) and a C:N Redfield stoichiometry of 6.625. We assumed that non-spinose species represent 50 % of the Schiebel and Movellan's (2012) samples and there is no correlation between the species and the size fractions, to estimate that the relative biomass of the non-spinose planktonic foraminifera 150- 200 µm size fraction to micro- and mesozooplankton biomass ranges from 0.02 % (5x10^{3} mmol N m^{-3}) to 0.03 % (1x10^{4} mmol N m^{-3}).

Due to the lack of data, we presumed that the prolocular biomass is similar to the adult biomass. To include sampling errors, methods' bias for estimating the contribution of planktonic foraminifera to global zooplankton biomass due to their low biomass (Buitenhuis et al., 2013) and a global biomass representation of early stages, we extended the biomass range to be from 0.007 % to 0.09 % based on Schiebel and Movellan's (2012) suggestion that biomass of early stages can be up to three times higher than adults with size <125 µm. Model simulations for which planktonic foraminifera relative biomass was within the observed range of 0.007 % to 0.09 % are referred here as 'low biomass' simulations.

Calcification

With the model we tested basic hypotheses to investigate the trade-offs of shell size and calcification and the effect of resource competition on planktonic foraminifera biomass for two life stages, prolocular (20 µm) and the adult (160 µm). Each life stage was modelled independently. As the costs and benefits of foraminifera's calcification are not experimentally known, we added a calcifying zooplankton type in the model with an associated trade-off for calcification, following the Monteiro et al. (2016) representation of a calcifying phytoplankton type (coccolithophore). To model non-spinose planktonic foraminifera, we used the same parameterization and equations as for zooplankton, hypothesizing that the main cost for shell development is energy loss, and the main benefit of calcification is protection. Preliminary experiments showed that the background mortality (m) had to be decreased to keep planktonic foraminifera biomass within the ’low biomass’ range defined, following suggestions that planktonic foraminifera can use their shell as a protection against more than just predation (Armstrong and Brasier, 2005).

To estimate the cost and benefit of calcification we ran a sensitivity analysis by decreasing planktonic foraminifera maximum grazing $(\mathrm{G_{max}})$ and background mortality (m) rate from 5% to 95% and 0 to 95% (in 5% steps) respectively, to represent calcification’s energy loss and benefit. Studies have shown that zooplankton metabolic rate and biomass can vary with temperature (Ikeda, 1985), but the reasons behind the correlation between habitat and mortality rate are still very not well understood (Aksnes and Ohman, 1996). There are currently no quantitative estimates of the energetic cost and benefits of calcification in planktonic foraminifera. Hence, we selected as most likely (herein denoted as ‘plausible’ simulations) the simulations that had a range of reductions of $\mathrm{G_{max}}$ and m smaller than 40% throughout all tested environments (e.g. 10-50 % or 20-60 % reduction). This is a way to account for the non-unlimited plasticity of an organism.

In the end, to quantify the benefit of predation protection, we chose a number of simulations to examine different predation pressures on planktonic foraminifera by decreasing the grazing term $\left(\mathrm{G_{jpred,prey}}\right)$ (Eq. (A3)) by 100% (no grazing pressure on planktonic foraminifera), 75 %, 50 %, 25 % and 0 % (no protection from grazing pressure) of its initial value.

2.4. Model set up and numerical simulations

We set-up a series of experiment ensembles to systematically test traits and trade-offs for nine different environmental combinations; with three input nutrient concentrations (No= 1, 2.5 and 5 mmol N m^{-3}) to represent oligo-, meso- and eutrophic environments respectively and three water temperatures (10°C, 20°C, 30°C) (Table 3). Each ensemble comprises a series of model experiments that explore a wide range of potential parameter value combinations of growth, predation and background mortality rates in different environmental conditions (temperature and nutrient concentrations). The ensemble set-up is then repeated for two life stages of planktonic foraminifera (prolocular and adult) using both the food-chain and the food-web model.

Every individual experiment was initialised with the concentration of all plankton groups set to 0.0001 mmol N m^{-3} and run for 10,000 days (~27 years). For the food chain, the experiments reached steady state (biomass ± 0.01 mmol N m^{-3}). In the food web version, the majority of the experiments reached an oscillatory steady state close to an equilibrium which was still present after running the model for more than 270 years (results not shown). This oscillatory behaviour is a common feature in ecosystem models (e.g. Baird et al., 2010) especially of planktonic communities (e.g. Petrovskii and Malchow 2001a; Petrovskii et al., 2001; Banas et al., 2011).

We present the absolute and relative biomass of planktonic foraminifera from all tested scenarios of calcification costs and benefits in supplementary materials (SM) based on the last 1000 days of the simulations. From 921 (500 for the food chain and 421 for the food web) tested simulations 9.5 % (88 simulations) were within the ‘low biomass’ criterion. From the ‘low biomass’ simulations, 75 % (64 simulations) cover the conditions of the ‘plausible’ criterion. Due to the low number of ‘plausible’ simulations (<4) per environment (Figs. 4-7, SM), we were not able to perform statistical analysis and instead we provided ranges of values for costs and benefits of calcification in non-spinose planktonic foraminifera for each life stage. We ran 100 simulations for both stages and model versions to examine different predation on planktonic foraminifera.

3. Results

3.1. General plankton distribution at different environments

Both versions of the model showed an increasing diversity and biomass from oligo- to eutrophic environments and from cold to warmer environments (Fig. 3) capturing the main patterns of marine plankton community structure (e.g. Irigoien et al., 2004; Müren et al., 2005; O'Connor et al., 2009). In the food chain version, biomass of phytoplankton and zooplankton increased continuously with the number of coexisting size groups (Fig. B1a). In contrast, the food web version had a patchy distribution of biomass with fewer coexisting groups, equivalent to "winners" of resource competition, and an overall lower biomass than the food chain model (Fig. B1b) in agreement with previous studies (e.g. Armstrong et al., 1994; Banas et al., 2011).

Pico-, nanophytoplankton and nano- microzooplankton dominated the plankton biomass at 10°C in both versions (Fig. 3b) as they outcompete the larger cell sizes through resource competition. As the concentration of the incoming nutrients ($\mathrm{N_o}$) was increased from oligo- to eutrophic the growth rate and coexistence of phytoplankton groups also increased, leading to a higher grazing pressure of zooplankton, biomass and zooplankton co-existence. In the food chain model, microphytoplankton survived in the eutrophic environment at low temperatures (10°C) and all the nutrient environments at 20°C and 30°C model. In the food web, microphytoplankton were present in meso- and eutrophic environments at 20°C and 30°C. Mesozooplankton were sustained in meso- and eutrophic environments at 20°C for the food chain model, in eutrophic environments at 20°C for the food web model, and in all environments at 30°C at both versions of the model (Fig. 3b). Since our model captured the general trends of plankton community through different environments, we used it interrogate the importance of individual traits and trade-offs.

3.2. Planktonic foraminifera ecology

3.2.1. Cost of calcification

We estimated the potential energetic cost of calcification in non-spinose planktonic foraminifera by decreasing their growth rate. In the food chain model, of the 500 simulations, 10.6 % (54 simulations) were within the 'low biomass' and 8 % (39 simulations) with the 'plausible' criteria. The 'plausible' simulations showed a decrease of foraminifera growth rate by 10 to 30% for the prolocular stage and 10 to 20 % for the adult stage (Figs. 4, 5). For the adult stage, we found no 'plausible' simulations for the mesotrophic environment at 20°C due to a high decrease of the background mortality (>60 %) compared with the low reduction (10%) of their growth rate.

Of the 421 food web simulations, 8 % (34 simulations) were 'low biomass' and 6 % (25 simulations) 'plausible'. The biomass of the prolocular stage increased with temperature and nutrients. The model could not produce any 'low biomass' simulation of early life stages of foraminifera at 30°C as values were significantly too high (1-7.3 % of the total zooplankton biomass, Fig. 6). In all environments at

10°C and for oligotrophic environment at 20°C the 'plausible' simulations showed a 10-35 % decrease of growth rate. To maintain the prolocular biomass within the defined low biomass range in meso- and eutrophic environments at 20°C, the calcification cost was equal to a 50 % reduction of the growth rate (Fig. 6). The model did not generate results for adults in oligotrophic waters at 10°C as only small zooplankton groups (<63 µm) could survive for that environment. There were no 'plausible' simulations for the eutrophic environment at 30°C, as planktonic foraminifera relative biomass was higher than the defined range (Fig. 7). For all the other environment the cost of calcification for the adult stage ranged from 10-40 % (Fig. 7).

3.2.2. Potential benefits of calcification in planktonic foraminifera

Both versions of the model showed that to maintain planktonic foraminifera within the defined biomass range, the background mortality rate of both prolocular and adult stages had to be reduced by 10- 50 % (Figs. 4-7). Our results suggest that planktonic foraminifera use their shell not only for predation protection but for other reasons e.g. against pathogens, like bacteria or viruses and parasites.

Regarding the use of the shell as protection from predation, both model versions showed different results. This is due to different feeding behaviour of zooplankton (specialist vs generalist) as in both models, predation depends on the feeding behaviour of the predator, prey size and biomass.

In the food chain model, the foraminifera biomass could be maintained inside the observed range when grazing pressure was reduced by 25 % for the prolocular and 50 % for the adult stage compared to full predation (Fig. B2). Therefore, both low biomass and possession of hard parts are important mechanisms against specialist predators.

Shell protection against predation had no effect on the relative low biomass of foraminifera in the food web model as their biomass remained the same with or without predation at both life stages (Fig. B2). The food web version suggests that low biomass is a more efficient protective mechanism than the shell against a generalist predator. We found that with a combination of higher than observed biomass of planktonic foraminifera and a predation pressure lower than 50 %, planktonic foraminifera became a dominant group with up to 22 % of the total zooplankton biomass suggesting that the shell has a protective function (results not shown).

3.2.3. Temperature and feeding control amongst different life stages of planktonic foraminifera

We focus on the results of the food web as it considers resource competition between planktonic foraminifera and the rest of zooplankton and simulates the plankton food web better than the food chain. Our model suggested that being herbivorous is a successful strategy for the prolocular stage as their optimum size prey group (≈2-3µm, as determined by the 10:1 predator-prey size ratio) was present in high abundance in all environments (Fig. 8). Resource competition is therefore not a determinant factor for the prolocular stage. The model results suggest that temperature had a stronger control on this stage, resulting in higher biomass (1-7 %) at 30°C (Fig. 6, Supplementary Material).

Adult foraminifera in the model achieved realistic relative biomass only when they became more generalist feeders by increasing their prey palatability by 20 % (σ= 0.6) for meso- and eutrophic conditions and by 80 % (σ= 0.8) to 100 % (σ =1.0) in oligotrophic environments (relatively to σ= 0.5 for other zooplankton) (Fig. 9). Without this change, adult herbivorous foraminifera in the model were out-competed by omnivorous predators. To understand if feeding behaviour or the lower growth rate and mortality associated with calcification led them to become more generalists, we switched the feeding behaviour in the model from herbivorous to omnivorous. The results showed that omnivorous planktonic foraminifera did not need to be more generalist than the other zooplankters (results not shown). Resource limitation had therefore an important role in controlling for the non-spinose planktonic foraminifera adult stages.

4. Discussion

We developed the first size-based 0-D model of two life stages (one prolocular, 20 µm and one adult, 160 µm) of planktonic non-spinose foraminifera to investigate the cost and benefits of calcification and feeding behaviours under different environmental conditions (temperature and nutrient). It is important to note that the present model, like other size structured models, cannot capture the complexity of the plankton community (Banas, 2011) but represents general patterns and encapsulates basic physiological relationships. The model shows that diversity increases from oligo- to eutrophic environments and from cold to warmer environments. The model therefore captures the increase in complexity in planktic ecosystems toward the tropics and eutrophic systems (Irigoien et al., 2004).

In the ocean, phytoplankton biomass and productivity are controlled by nutrient availability, light, temperature and grazing pressure (Irigoien et al., 2004). In oligotrophic areas, nutrient limitation leads to the dominance of small size phytoplankton cells as there is not enough energy to sustain larger cells (Menden – Duer and Kiørboe, 2016). As nutrient availability increases, phytoplankton size diversifies. Zooplankton shows similar pattern; oligotrophic environments are dominated by small heterotrophs, while the size of the species increases in eutrophic environments (Razouls et al., 2018). Our model captured this general pattern, but it struggled to sustain a high biomass of the largest size groups of microphytoplankton and metazooplankton especially in non-eutrophic environments. We suggest that the oversimplification of physiological and behavioural traits, especially for zooplankton, leads to this limitation, as species are represented as spheres with fixed half-saturation (K_{zoo}) and assimilation efficiency (λ) (more details in supplementary methods). Changing the shape of the body from a sphere towards an ellipse for representing metazoans, combined with variable half-saturation, may circumvent this problem. Including motility, an important trait for organisms' survival (e.g. feeding, predation protection) with strong influence on metabolic rates (e.g. Ikeda, 1985), could also improve model results.

In the present study we tried to quantify the cost and benefit associated with calcification in planktonic foraminifera. Our model suggests a cost of calcification in non-spinose planktonic foraminifera of 10-50 % for the early life stages and 10-40 % for the adults. This cost is similar to estimates for coccolithophores (~30 %; Monteiro et al., 2016) and for shell production of marine benthic molluscs (22-50 %; Palmer, 1992). While biocalcification evolved in the Precambrian and across many clades, metabolic costs may be comparable as pathways and constraints are similar for a range of organisms (Knoll, 2003). Our model results suggest that planktonic foraminifera calcify for a combination of reasons (e.g. protection from pathogen, parasites and grazers), as suggested by other studies on planktonic foraminifera (Armstrong and Brasier, 2005) and phytoplankton (Hamm et al., 2003; Hamm and Smetacek 2007; Monteiro et al., 2016). Observations show that bacteria can attack the cytoplasm of unhealthy or dead planktonic foraminifera (Schiebel and Hemleben, 2017). More field and laboratory studies are needed to gain a deeper knowledge on the interaction between planktonic foraminifera and pathogens.

Predation on planktonic foraminifera is still not well understood (Schiebel and Hemleben, 2017). While benthic foraminifera are selectively preyed upon by scaphopods (Murray, 1991), evidence for predation on planktonic foraminifera is limited. It is difficult to detect remains of early developmental states in faecal pellets due to their small size, thin walls and low biomass resulting in the lack of data (Schiebel and Hemleben, 2017). Shell and spines of adults have been detected in faecal pallets of metazooplankton groups (like salps, copepods, pteropods, and euphausiids) and nekton shrimps (Be et al., 1977; Bradbury et al., 1970; Berger, 1971b). Our results highlight that low biomass is a main mechanism for protection against predation in planktonic foraminifera. The food web model results showed that reducing grazing pressure could be a potential benefit of calcification for planktonic foraminifera if they were to become more abundant. The earliest planktonic foraminifera are thin shelled and very small (Gradstein et al., 2017), while modern species have more complex morphologies with larger and thicker shells (Schmidt et al., 2004). While the planktonic ecosystem became more complex over the last 150 Ma, we speculate that their low abundance and thick shells may have prevented the evolution of a specific predator in contrast to other dominant phytoplankton groups with shells like diatoms (Hamm et al., 2003; Hamm and Smetacek 2007). As planktonic foraminifera are immotile organisms, it is difficult for predators to sense them (Kiørboe, 2008; Van Someren Gréve et al., 2017). Their thick shell can then act as an armour when a grazer reaches them to counter-balance their non-motility. Based on the results of our model and our current knowledge on foraminiferal physiology, we propose that the combination of low abundance and a carbonate shell protect planktonic foraminifera against predation. Planktonic foraminifera are thus high-energy-demand prey: they are hard to find and digest, corroborating earlier suggestions that foraminifera do not have specific predators (Hemleben et al., 1989). We suggest that planktonic foraminifera non-motility is an important behavioural trait to be further tested in order to improve our understanding of grazing protection.

Temperature and food appear to be the main controlling factors of planktonic foraminifera ecology and distribution in the ocean (e.g. Ortiz et al.,1995; Bé and Tolderlund, 1971) corroborated by modelling studies (Žarić et al., 2006; Frail et al., 2008, 2009; Lombard et al., 2009; Roy et al., 2015). Studies have shown that sea surface temperature (SST) is one of the most important environmental factors of planktonic foraminifera's diversity (Rutherford et al., 1999) and size (Schmidt et al., 2006;2004a). Field observations (e.g. Bé and Tolderlund, 1971), geochemical analysis (Elderfield and Ganssen, 2000) and culture experiments (Caron et al., 1987a, b) show that adult species have a specific optimum temperature range which controls their size development and abundance (Schmidt et al., 2004a; Žarić et al., 2005; Lombard et al., 2009). In the present study, we use our trait-based model to study planktonic foraminifera as a group of species to investigate the general patterns of the influence of temperature and resource on planktonic foraminifera biomass on both juvenile and adult stages.

We find that temperature is the main limiting factor for the prolocular life stage, since there is no food limitation. Our model provides insights on the importance of resource availability and competition during development, resulting in a switch to generalist herbivory and omnivory diet at adult stages. Food availability impacts planktonic foraminifera ecology (e.g. Ortiz et al., 1995; Schmidt et al., 2004a). Culture experiments highlight that the amount and type of food have a strong influence on growth rate (e.g. Spindler et al., 1984; Anderson et al., 1979), shell size (Bé et al., 1981) and gametogenesis (Caron et al., 1981; Caron and Bé, 1984; Hemleben et al., 1987). The model results support the hypothesis that during early stages planktonic foraminifera have a herbivorous diet. It also indicates that food availability is a key controlling factor of the biomass of non-spinose adult stages and defines their type of feeding strategy for different nutrient concentration environments.

We propose that non-spinose adult planktonic foraminifera are very successful herbivorous predators, capable to prey on different phytoplankton size groups or that they can be omnivorous and use other food sources like bacteria, detritus and zooplankton. Observations suggest an opportunistic feeding behaviour for non-spinose species. Diatoms are usually considered to be their primary prey (e.g. Spindler et al., 1984; Hemleben et al., 1985) though some can also consume dinoflagellates (e.g. Anderson et al., 1979), and cryophytes which are either slowly digested or used as symbionts (Hemleben et., 1989). Animal tissues have been found in several non-spinose species (Anderson et al., 1979; Hemleben and Spindler, 1983a). *Globorotalia menardii*, an abundant and the biggest non-spinose species, is suggested to actively control microzooplankton (ciliates) prey (e.g. Hemleben et al., 1977). Culture experiments suggest cannibalism between non-spinose but never between spinose species (Hemleben et al, 1989). These observations support our results that non-spinose adult species can feed on different types and size of phytoplankton or switch to omnivory when phytoplankton concentrations are rare.

Our model provides important information on how resource competition among planktonic foraminifera and other zooplankters influences the feeding behavior of different life stages and their distribution. 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). Our model results can provide new perspectives regarding the development of symbiosis as an additional energy source in planktonic foraminifera and hence adding symbiosis in the model can be a next important step for improving our understanding of planktonic foraminifera ecology.

5. Conclusions

This study takes a first step towards including planktonic foraminifera ecology as part of the plankton community in a trait-based framework and estimates the energetic cost of calcification and the associated benefits. We find that the energetic cost of calcification for varies between 10-30 % in the food chain model for both prolocular and adult stages and 10-50 % in the food web model for the prolocular and 10-40 % for the adult. We consider that both low biomass and the carbonate shell are key elements for protection of planktonic foraminifera from predation. A reduction in mortality by 10-50 % suggests that the shell may be more important for pathogens and parasites than against grazing pressure.

Similar to coccolithophores (Monteiro et al., 2016), the costs and benefits of calcification in planktonic foraminifera vary with the environment. In the model, temperature is the dominant factor for the prolocular stage, whereas both temperature and resources are important for the adult. Consequently, the adults are more impacted by resource competition driven by less available food in the optimal size of their prey resulting in feeding on a wider range of prey size, particularly in oligotrophic environments where food is scarce. We therefore suggest that the adults are generalist herbivorous or omnivorous or use other resources in oligotrophic environments such as symbiosis.

To develop the model further, data on energy allocated to growth, calcification and motility are needed to better understand the physiology and ecology of this important paleoclimate proxy carrier and producer of marine carbonates. Other traits and trade-offs such as feeding mechanism (rhizopodial network, spines), mobility, symbiosis with algae need to be tested in the future and supported by culture experiments.

Code access

The code can be found online at the supplement materials, https://doi.org/10.5281/zenodo.1487877.

Author contributions

MG, FMM and DNS designed the study. MG, JDW and BAW developed the model. MG prepared the manuscript. All authors contributed to writing and editing the final version of the manuscript.

Competing interests

The authors declare that they have no conflict of interest.

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Table 1. Model parameters (Ward et al., 2014 and references with in).

Parameter	Symbol	Value or formula	Units
Temperature sensitivity	R	0.05	-
Deep N concentration	N_0	Variable (0-5)	$\mathrm{mmol\ N\ m^{-3}}$
Chemostat mixing rate	κ	0.01	$\mathrm{day^{-1}}$
Light limitation	li	0.1	-
Optimal predator: prey length ratio	θ_{opt}	10.0	-
Standard deviation of $\log_{10}(\theta)$	σ	0.001[*], 0.5[a], 0.6[b], 0.8[c], 1[d]	-
Total prey half- saturation	K_{zoo}	0.1501	$\mathrm{mmol\ N\ m^{-3}}$
Assimilation efficiency	λ	0.7	-
Prey refuge parameter	Λ	1	$\mathrm{mmol\ N\ m^{3}}$
Phytoplankton mortality	m_P	0.02	$\mathrm{day^{-1}}$
Zooplankton mortality (food web)	m_z	0.02	$\mathrm{day^{-1}}$
Zooplankton mortality (food chain)	m_z	$0.05V^{-0.16}$	$\mathrm{day^{-1}}$
Maximum phytoplankton growth rate at 20°C	μ_{max}	$\dfrac{P_C^{max}\, V_N^{max}\, \Delta Q}{V_N^{max}\, Q_N^{max} + P_c^{max} Q_N^{min}\, \Delta Q}$	$\mathrm{day^{-1}}$
Half- saturation for phytoplankton growth	K_N	$\dfrac{P_C^{max}\, K_{NO_3}\, Q_N^{min}\, \Delta Q}{V_{NO_3}^{max}\, Q_N^{max} + P_C^{max}\, \Delta Q}$	$\mathrm{mmol\ N\ m^{-3}}$

[*]: value for the simple food chain, [a]: zooplankton and prolocular stage of planktonic foraminifera, [b]: adult stage of planktonic foraminifera for meso- and eutrophic ecosystems, [c, d]: adult stage of planktonic foraminifera for oligotrophic ecosystem of 20°C and 30°C respectively.

Table 2. Size- dependent parameters (adapted from Ward et al., 2012, see references within). Coefficients a and b are used in the power-law function that assigns parameters as a function of plankton cell volume $\mathrm{p} = \mathrm{aV}^{\mathrm{b}}$.

Parameter	Symbol	a	b	Units
Maximum photosynthetic rate	$\mathrm{P}_{\mathrm{C,prochlorococcus}}^{\mathrm{max}}$	1.0	-0.15	day^{-1}
	$\mathrm{P}_{\mathrm{C,synechococcus}}^{\mathrm{max}}$	1.4	-0.15	day^{-1}
	$\mathrm{P}_{\mathrm{C,other}}^{\mathrm{max}}$	2.1	-0.15	day^{-1}
	$\mathrm{P}_{\mathrm{C,diatoms}}^{\mathrm{max}}$	3.8	-0.15	day^{-1}
Maximum nitrogen uptake rate	$\mathrm{V}_{\mathrm{NO_3}}^{\mathrm{max}}$	0.51	-.027	day^{-1}
Phytoplankton minimum N quota	$\mathrm{Q}_{\mathrm{N}}^{\mathrm{mim}}$	0.07	-0.17	$\mathrm{mmol\ N\ (mmol\ C)}^{-1}$
Phytoplankton minimum N quota	$\mathrm{Q}_{\mathrm{N}}^{\mathrm{max}}$	0.25	-0.13	$\mathrm{mmol\ N\ (mmol\ C)}^{-1}$
Maximum grazing rate	$\mathrm{G}_{\mathrm{max}}$	21.9	-0.16	day^{-1}

Table 3: Summary of studied traits and environmental conditions for the non-spinose planktonic foraminifera. O: Oligotrophic, M: Mesotrophic, E: Eutrophic regions.

Plankton interactions

Model version	Structure	Plankton size groups
food chain	One prey per predator Zooplankton: passive, herbivorous Planktonic foraminifera: passive, herbivorous	25 phytoplankton 25 zooplankton 1 planktonic foraminifera
food web	Multi prey per predator Zooplankton: passive, omnivorous Planktonic foraminifera: passive, herbivorous	

Environmental Conditions

Model version	Temperature (°C)	10	20	30
food chain & food web	Nutrient region	O M E	O M E	O M E

Study traits

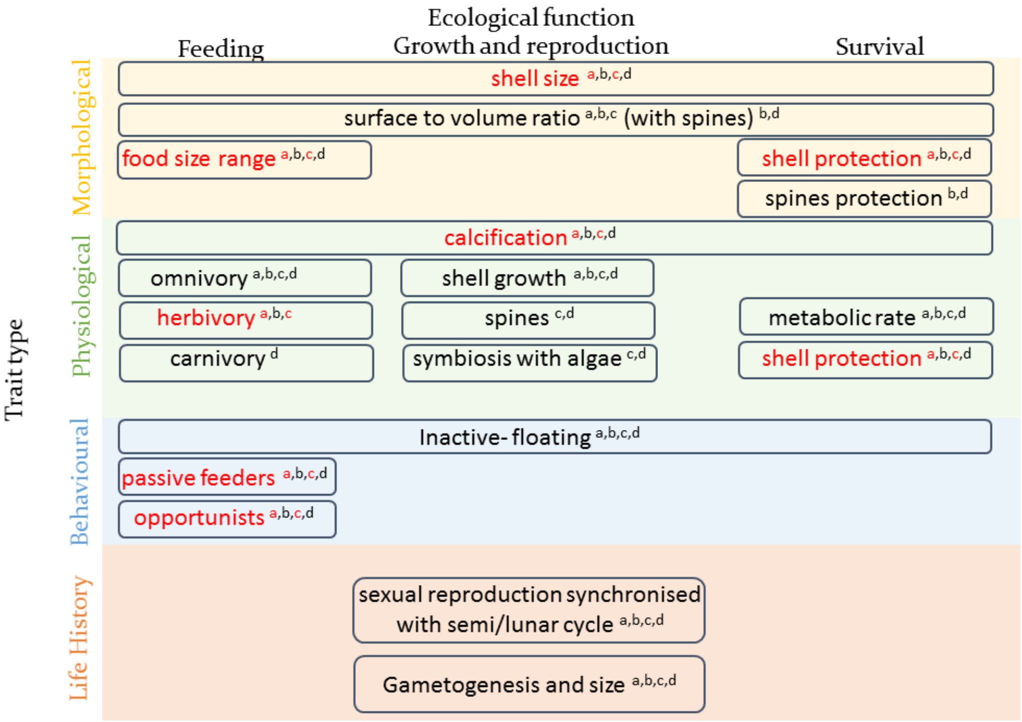
Shell size: prolocular (shell size: 30 µm)
adult (shell size: 160 µm)
Calcification: energy loss (cost)
protection from predation and other reasons than can cause mortality like pathogens and parasites (defined as background mortality in the model) (benefit)
Feeding behaviour: passive herbivory

Main outcomes

Model version	Shell size	Calcification			temperature & resource control (results based on the food web)
		Energy loss (%)	Protection		
			predation	morality reduce (%)	
food chain	Prolocular (20 µm)	10-30	Shell & low biomass *	10-40	Temperature
food web		10-50	low biomass **		
food chain	Adult (160 µm)	10-20	Shell & low biomass *	10-40	Resource
food web		10-45	low biomass **		

*The model showed that both shell and low biomass are important for protection from predation.

**The results showed that low biomass is more important than shell for protection from predation.



^{a}: prolocular ^{b}: juveline ^{c}: non – spinose adult ^{d}: spinose adult

Figure 1. Schematic presentation of planktonic foraminifera traits and tradeoffs. The examined traits of the present study are shown in red. The presentation of planktonic foraminifera's traits was inspired from the topology of zooplankton traits proposed by Litchman et al. (2013).

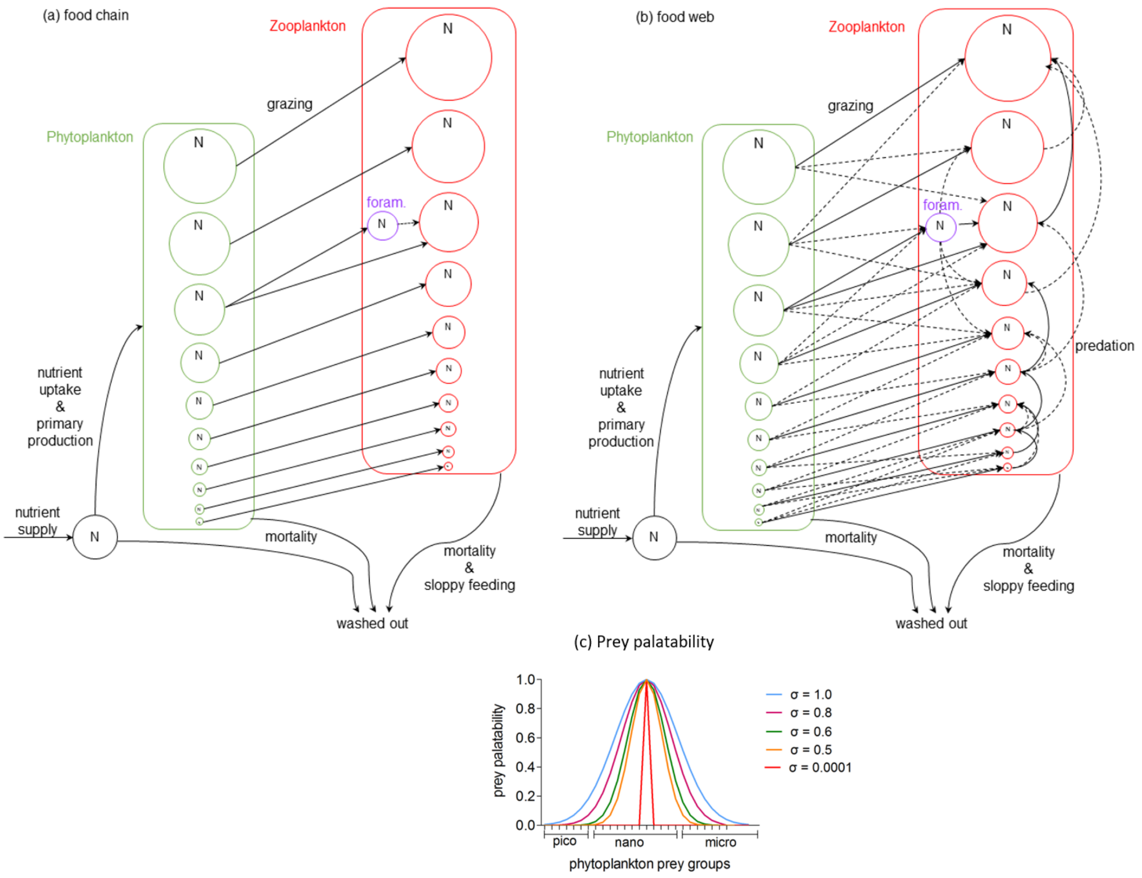


Figure 2.: Schematic description of the two model versions of the size-trait-based model of planktonic foraminifera: **(a)** food chain; and **(b)** food web (adopted with permission from Ward et al., 2012). Note that the figure does not present the accurate position of the planktonic foraminifera size group ran in the model but a generic position for illustrate how they interact with the rest of the plankton community. (**c**) Illustration of the prey palatability of one herbivorous predator (160 μm size) with phytoplankton prey groups. Size specialist predator (present in the food chain version) is characterised by standard deviation (σ) equal to 0.0001. Size generalist predator (present in the food web version) is characterised by σ ≥ 0.5.

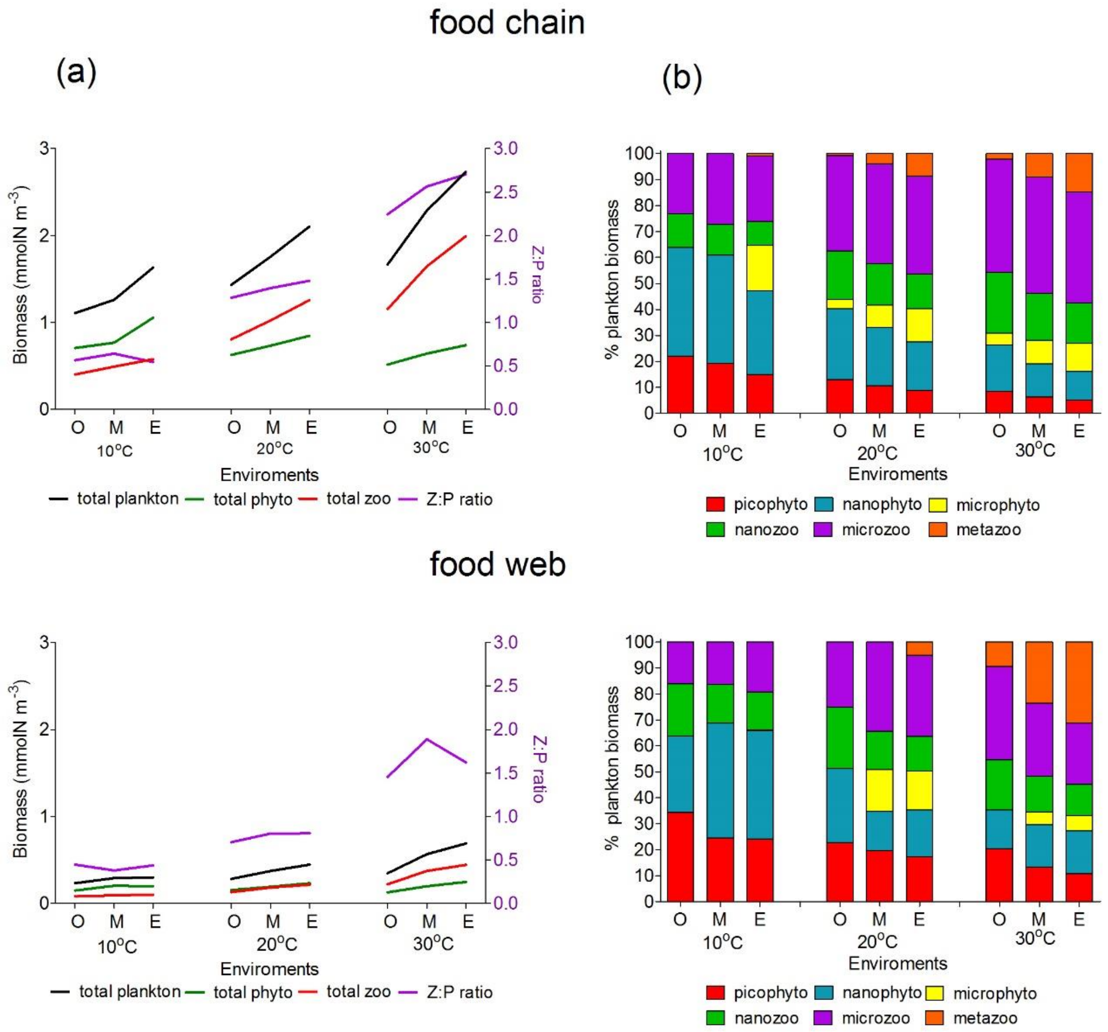


Figure 3. Plankton total biomass and group diversity for all environments (O: Oligotrophic, M: Mesotrophic and E: eutrophic environments). **(a)**: Right axis: biomass of phyto- (green line), zoo (red line) and total plankton (black line) (mmolNm^{-3}). Left axis: zooplankton: phytoplankton biomass ratio (purple line). **(b)**: relative (%) biomass of phytoplankton and zooplankton size groups.

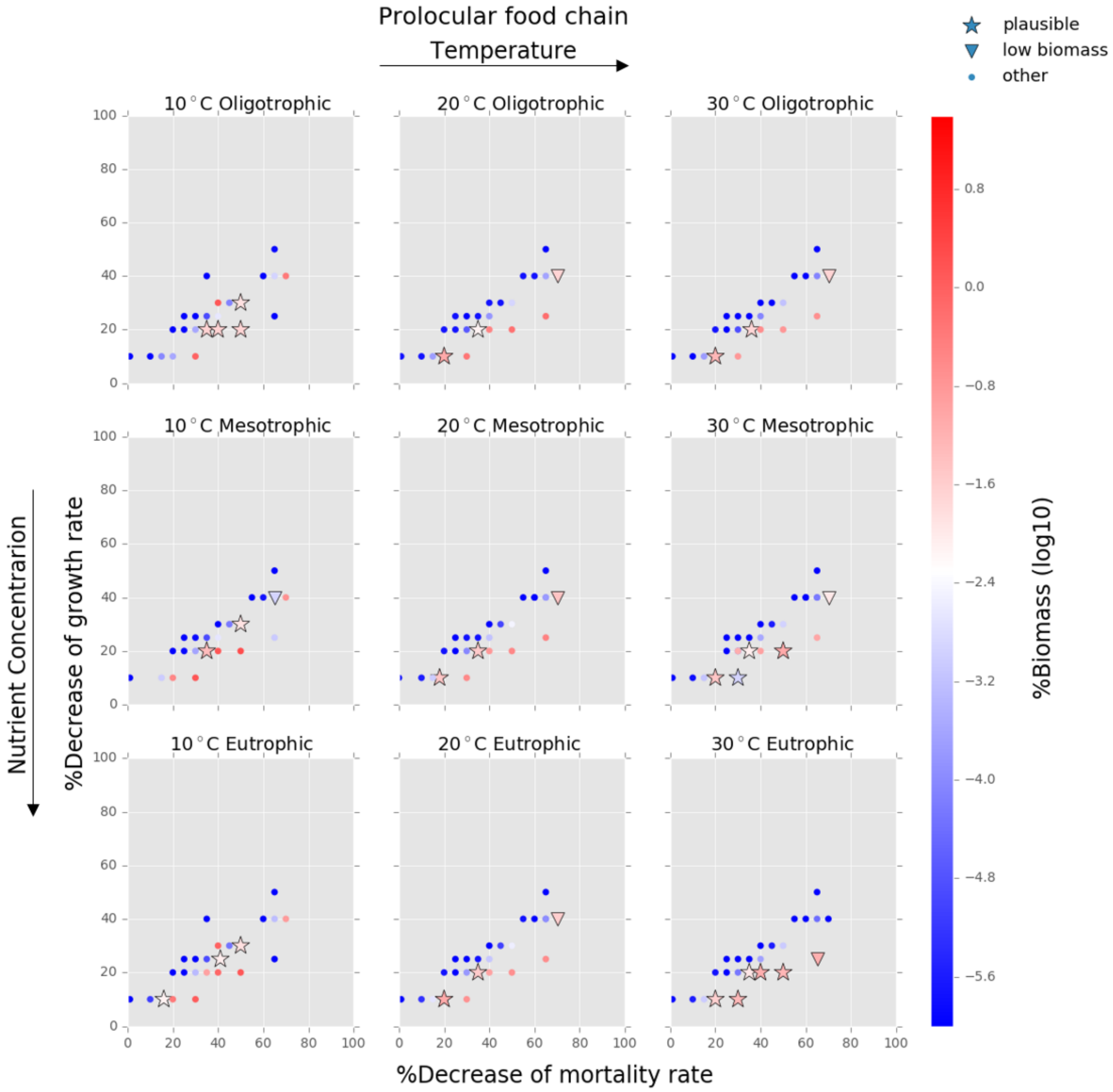


Figure 4. Results from the food chain model for the calcification cost (reduction of growth) and benefit (reduction of mortality rate) for the prolocular life stage of planktonic foraminifera. Legend shows 'total' for total tested simulations, 'low biomass' for simulations for which their biomass is within the defined range, and 'plausible' for the simulations we consider to be as most likely. More details for 'low biomass' and 'plausible' simulations in the Methods, section 2.3: adding planktonic foraminifera into the model.

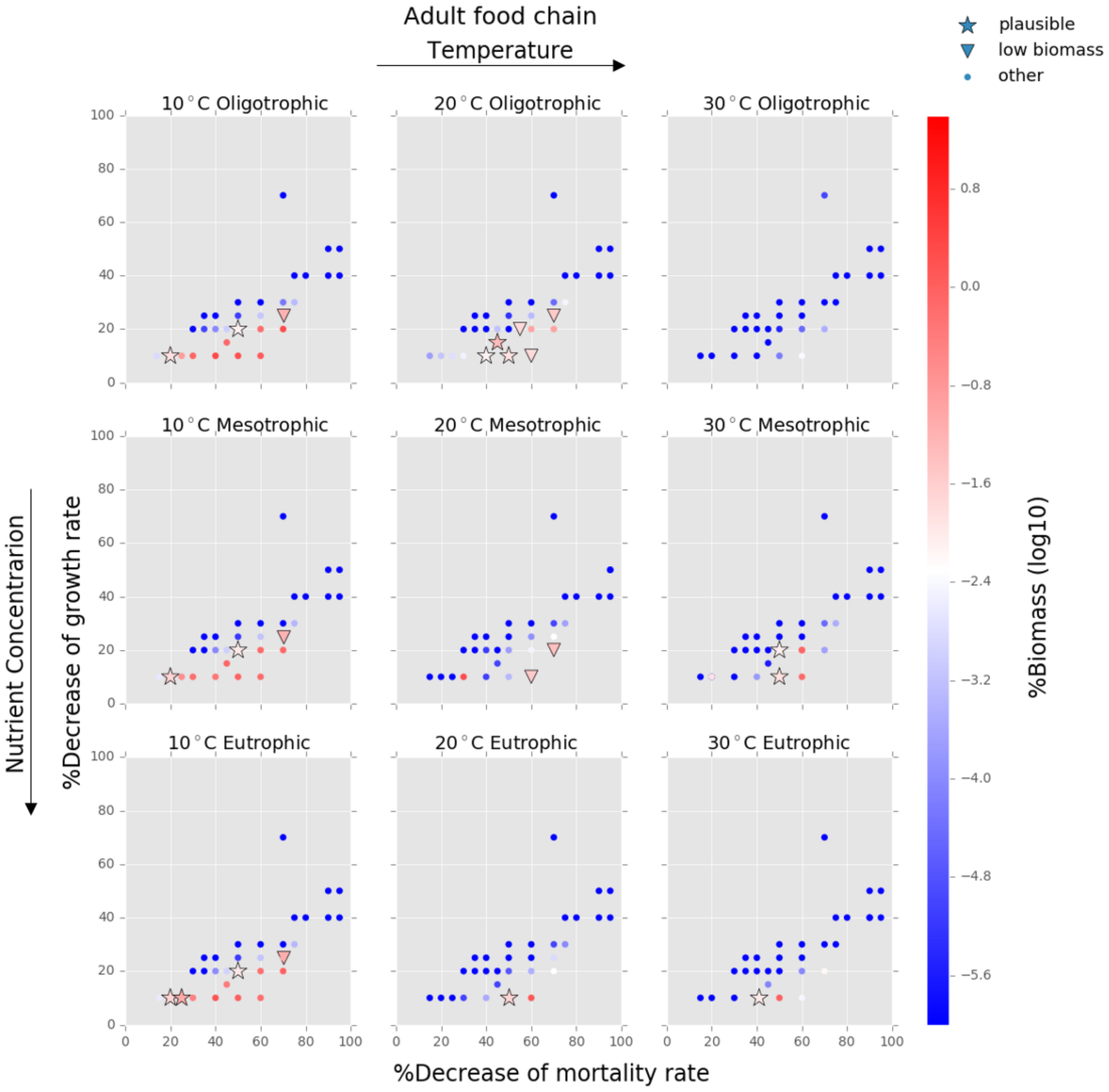


Figure 5. Results from the food chain model for the calcification cost (reduction of growth) and benefit (reduction of mortality rate) for the adult life stage of planktonic foraminifera. Legend shows 'total' for total tested simulations, 'low biomass' for simulations for which their biomass is within the defined range, and 'plausible' for the simulations we consider to be as most likely. More details for 'low biomass' and 'plausible' simulations in the Methods, section 2.3: adding planktonic foraminifera into the model.

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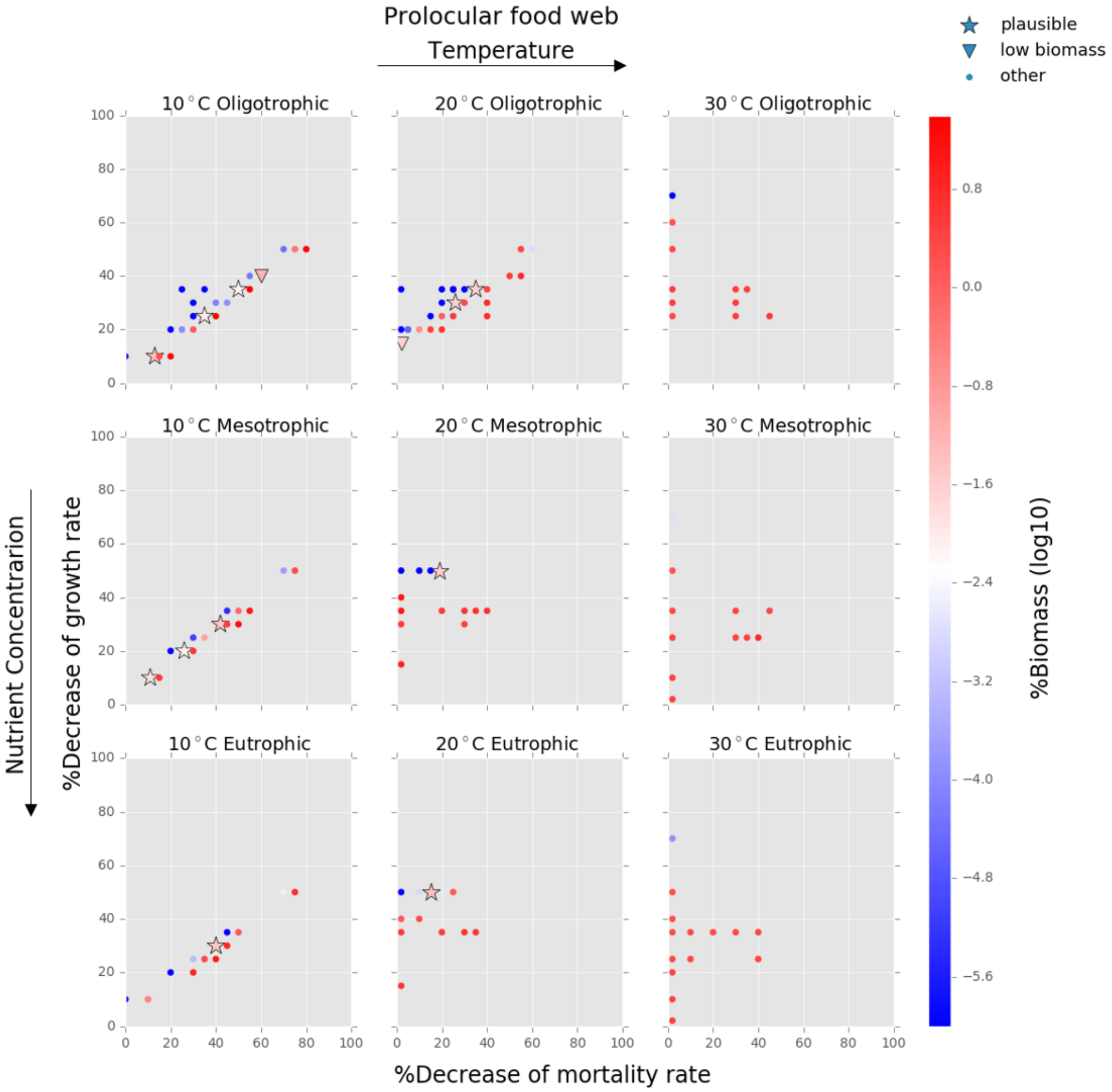


Figure 6. Results from the food web model for the calcification cost (reduction of growth) and benefit (reduction of mortality rate) for the prolocular life stage of planktonic foraminifera. Legend shows 'total' for total tested simulations, 'low biomass' for simulations for which their biomass is within the defined range, and 'plausible' for the simulations we consider to be as most likely. More details for 'low biomass' and 'plausible' simulations in the Methods, section 2.3: adding planktonic foraminifera into the model. For the meso- and eutrophic of 20^{o}C and all environments of 30^{o}C, the pattern of the simulations is more scattered than for the rest environments. This is because in a range of a 0 to 50 % 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.

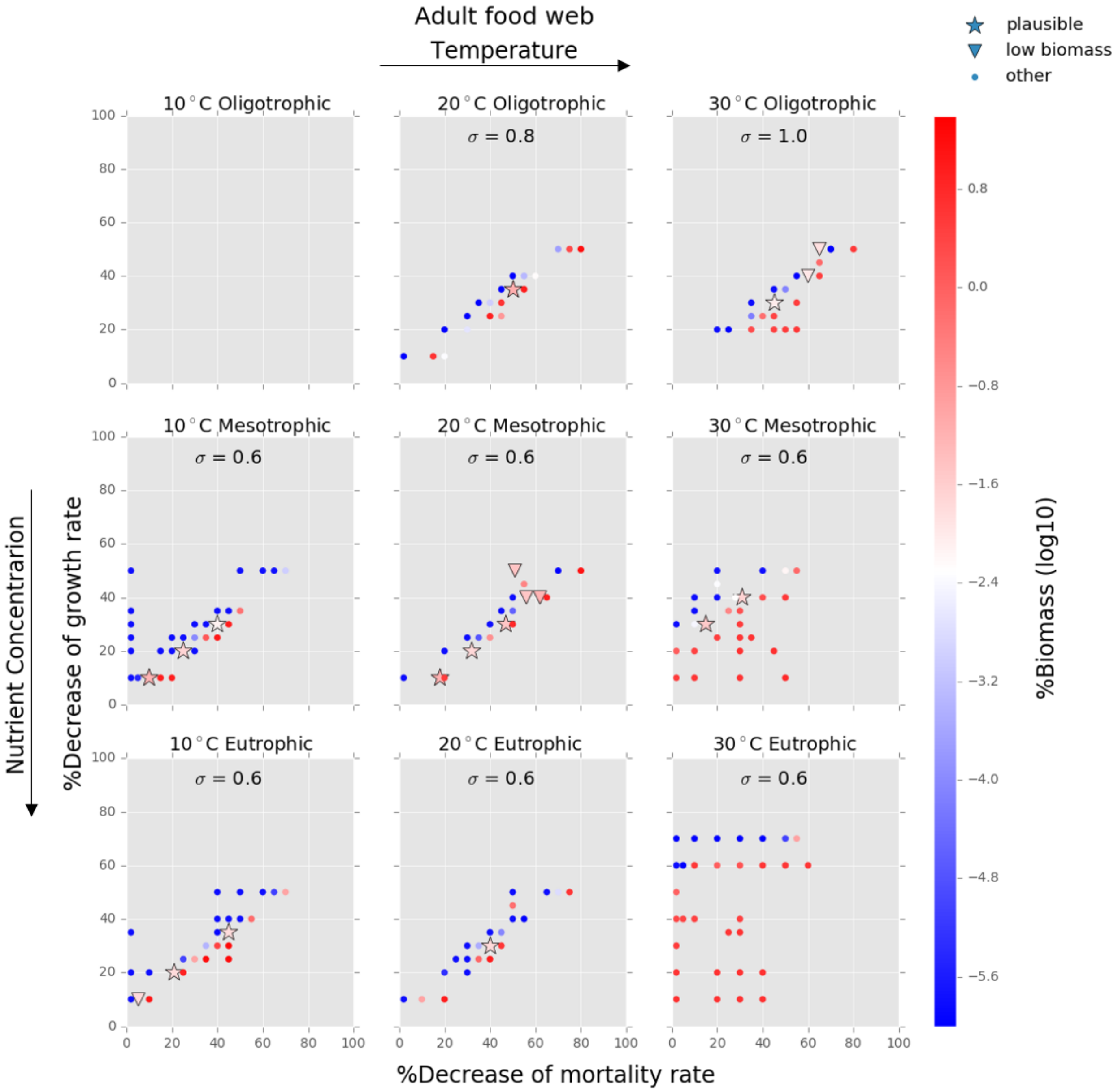
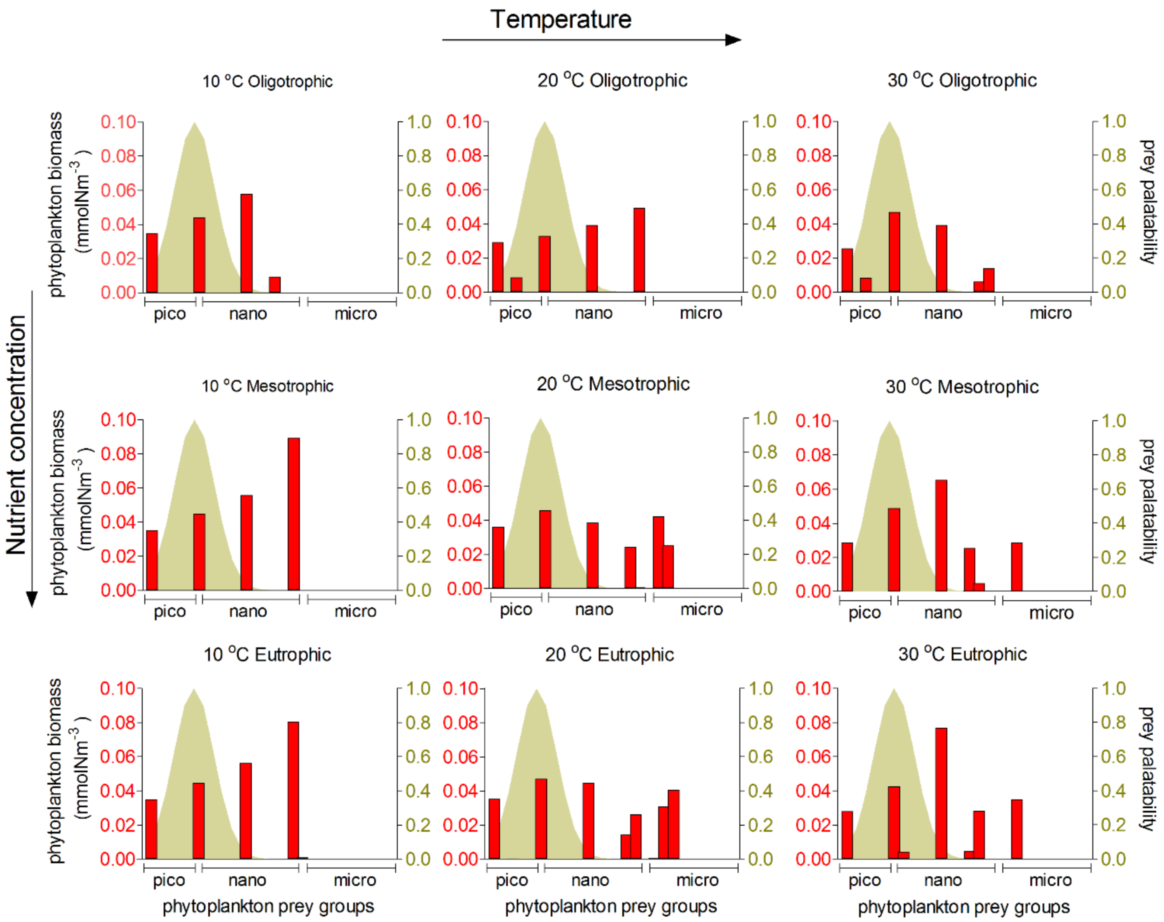


Figure 7. Results from the food web model for the calcification cost (reduction of growth) and benefit (reduction of mortality rate) for the adult life stage of planktonic foraminifera. Legend shows 'total' for total tested simulations, 'low biomass' for simulations for which their biomass is within the defined range, and 'plausible' for the simulations we consider to be as most likely. More details for 'low biomass' and 'plausible' simulations in the Methods, section 2.3: adding planktonic foraminifera into the model. For all environments of 30^{o}C, the pattern of the simulations is more scattered than for the rest environments. This is because in a range of a 0 to 50 % reduction on the mortality rate, the relative biomass of planktonic foraminifera in some scenarios 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.



1435 **Figure 8**. Model results of resource competition for the prolocular stage (20 µm) of planktonic foraminifera in the food web version. Left axis (red columns): biomass (mmolN m^{-3}) of phytoplankton size groups. Right axis (colored shadow): prey palatability of planktonic foraminifera using a σ = 0.5. 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.

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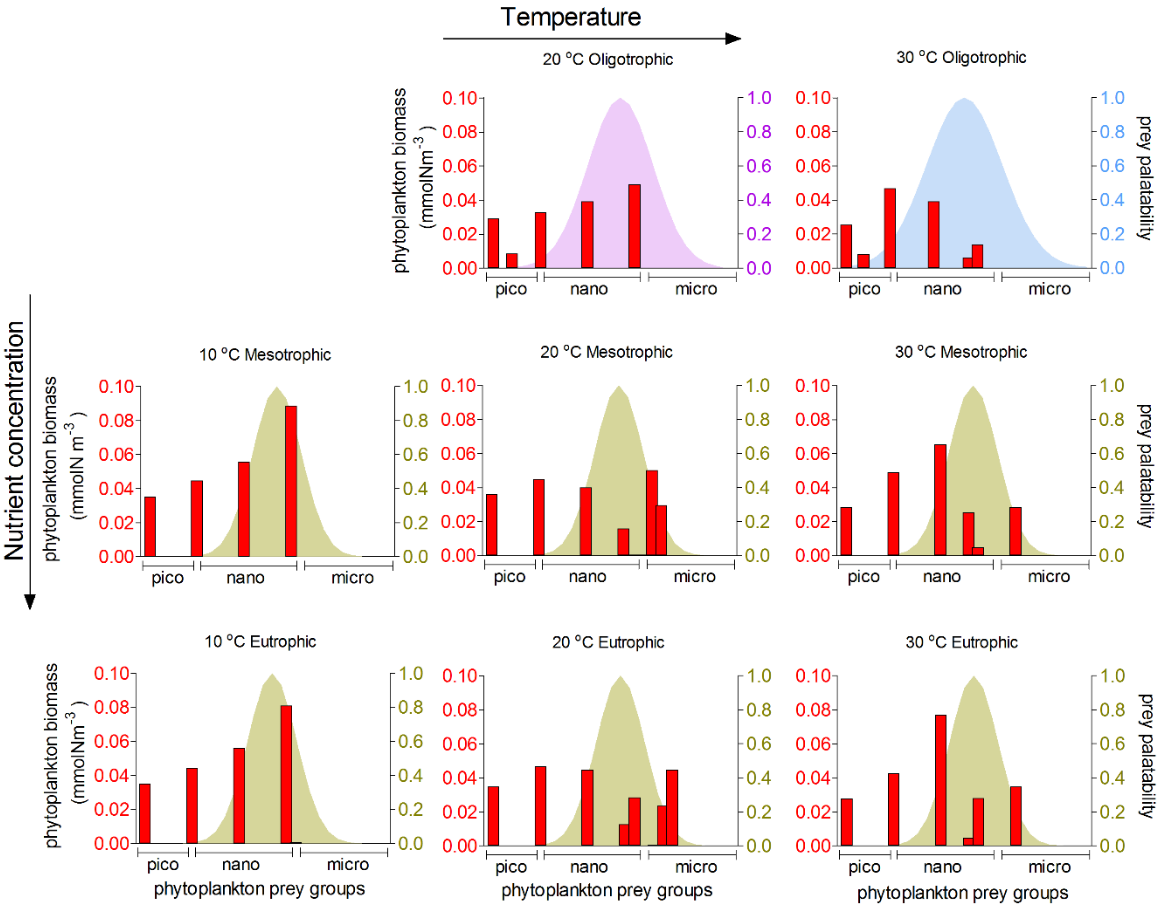

Figure 9. Model results of resource competition for the adult stage (20 µm) of planktonic foraminifera in the food web version. Left axis (red columns): biomass (mmolN m^{-3}) of phytoplankton size groups. Right axis (colored shadow): prey palatability of planktonic foraminifera. For oligotrophic enviroments, σ = 0.8 (violet) and 1 (light blue) for 20°C and 30°Crespectively. For all meso- and eutrophic ecosystems σ = 0.6. No zooplankton larger than 100 µm and adult stage of planktonic foraminifera survived in the oligotrophic ecosystem at 10°C for the model set up. 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.

Appendix A

Model description

Our model represents a chemostat experiment in a zero-dimensional (0D) setting, with one source of nutrients and fifty-one generic plankton (autotrophs and heterotrophs) size classes from pico- to mesoplankton (Schiebel 1978).

Plankton size groups

We selected plankton cell sizes in the model so that the volume of each plankton doubles from one class to another similar to Ward et al. (2014). We set up the model to have six pico- (0.6-2.0 µm), ten nano- (2.6- 20 µm) and nine micro- groups (25-160 µm) for the phytoplankton; and six nano- (6-20 µm), ten micro- (26- 200 µm) and nine (250- 1600 µm) meso- groups for the zooplankton. The diagnostic equation for plankton biomass (phytoplankton and zooplankton) is given in Eq. (1) and shows the generic dependence of biomass with nutrient uptake, zooplankton grazing and mortality. The symbols are explained in Tables 1 and 2.

Environmental variables

The model accounts for two environmental variables influencing plankton growth: light and temperature. Light limitation (li) is represented as a fixed parameter set to 0.1 (equivalent to 90% of light limitation; Ward et al., 2014). The influence of temperature on plankton metabolic rates (γ_{T}) is represented by an Arrhenius-like equation (Eq. (A1)) with $(\mathrm{T}_{\mathrm{ref}})$ the reference temperature at which $\gamma_{\mathrm{T}} = 1$ is 293.15 K (20°C), (T) the ambient temperature of the water (K) and (R) the temperature sensitivity of plankton growth rate.

$$\gamma_{\mathrm{T}} = e^{\mathrm{R}(\mathrm{T}-\mathrm{T}_{\mathrm{ref}})} \qquad \text{(A1)}$$

We tested three ambient water temperatures (T) : 10, 20 and 30°C characteristic of subpolar, subtropical and tropical regions respectively. Temperature limitation (γ_{T}) has a proportionate impact on both phytoplankton and zooplankton growth (Eq. (A2), (A3)).

Phytoplankton growth

Phytoplankton growth $(\mathrm{P}_{\mathrm{growth,j}})$ is size-dependent and described via the Monod equation assuming there is a balance between the nutrient uptake and growth of phytoplankton (Monod, 1950) (Eq. A2).

$$\mathrm{P}_{\mathrm{growth,j}} = \frac{\mu_{\mathrm{max}} * \mathrm{N}}{\mathrm{N}+\mathrm{K}_{\mathrm{N}}} * \mathrm{li} * \gamma_{\mathrm{T}} \qquad \text{(A2)}$$

Phytoplankton half-saturation $(\mathrm{K}_{\mathrm{N}})$ and maximum specific growth rate (μ_{max}) are cell-size dependent (Table 1). The maximum uptake rate (μ_{max}) has been normalised to 20°C and is a function of the maximum photosynthetic rate ($\mathrm{P}^{\mathrm{max}}$), the cell volume ($\mathrm{V}_{\mathrm{N}}^{\mathrm{max}}$) and the phytoplankton quota (Tables 1 and 2) (Ward et al., 2014). The maximum photosynthetic rate ($\mathrm{P}^{\mathrm{max}}$) for each size class of phytoplankton reflects observations of *Prochlorococcus* for the two first pico- groups (0.6 and 0.8 µm) and of *Synechococcus* for the remaining four pico- groups, other eukaryotes for nano- and diatoms for microphytoplankton (Irwin et al., 2006) (Table 2).

Zooplankton growth

We used the zooplankton grazing term as has been described in Ward et al. (2012) applied for two different feeding behaviours of zooplankton: specialist (i.e. consume one prey) herbivorous for the food chain and generalist (i.e consume more than one prey) omnivorous predators for the food web. Zooplankton grazing ($\mathrm{G}_{\mathrm{jpred,jprey}}$) is represented using the Holling type II function (Eq. (A3)). Although most of zooplankton have different feeding behaviours in different life stages, Holling type II better illustrates predator-prey relationships of many ambush zooplankton groups in the lab over a long-term period (Kiørboe et al., 2018).

$$\mathrm{G}_{\mathrm{jpred,jprey}} = \mathrm{G}_{\mathrm{max}} * \gamma_{\mathrm{T}} * \frac{\varphi_{\mathrm{jpred,jprey}} * \mathrm{B}_{\mathrm{jprey}}}{\mathrm{F}_{\mathrm{jpred}} + \mathrm{K}_{\mathrm{zoo}}} * \text{Prey refuge}_{\mathrm{jprey}} * \Phi_{\mathrm{P,Z}} \tag{A3}$$

where $\mathrm{G}_{\mathrm{max}}$ is the maximum grazing rate, γ_{T} is temperature limitation, $\varphi_{\mathrm{jpred,jprey}}$ is prey palatability, $\mathrm{B}_{\mathrm{jprey}}$ prey's biomass, $\mathrm{F}_{\mathrm{jpred}}$ is the total available biomass for each predator, $\mathrm{K}_{\mathrm{jpred}}$ is predator's half-saturation constant, $\text{Prey refuge}_{\mathrm{jprey}}$ is the prey refuge, and $\Phi_{\mathrm{P,Z}}$ is predator's "switching" between phytoplankton and zooplankton prey.

The maximum prey ingestion rate ($\mathrm{G}_{\mathrm{max}}$) is size dependent (Table 2). The prey palatability ($\varphi_{\mathrm{jpred,jprey}}$) express the likelihood of a predator to consume the prey (Eq. (3)). It depends on the log size ratio of predator:prey length ratio with the optimum predator:prey length ratio (θ_{opt}).

The total prey biomass available to each predator ($\mathrm{F}_{\mathrm{jpred}}$) is calculated as a sum of prey biomass weighted by their prey palatability (Eq. (A4)).

$$\mathrm{F}_{\mathrm{jpred}} = \sum_{\mathrm{jprey}=1}^{\mathrm{J}} \varphi_{\mathrm{jpred,jprey}}\, \mathrm{B}_{\mathrm{prey}} \tag{A4}$$

We set the zooplankton half-saturation constant ($\mathrm{K}_{\mathrm{zoo}}$) to 0.1051 mmol N m^{-3}. This value is a conversion of Ward et al. (2012) value (1 mmol C m^{-3}) from carbon to nitrogen based on Redfield ratio (106:16). While observations show evidence of a variable half-saturation constant for zooplankton (e.g. Hansel et al., 1997), there is not enough information to tease apart its value for the different species, so we assumed a constant $\mathrm{K}_{\mathrm{zoo}}$ among our zooplankton groups.

Prey refuge

The predator prey interactions depend mostly on predator-prey length ratio (Kiørboe 2008), prey's availability and ability to escape predation (e.g. van Someren Gréve et al., 2017; Pančić and Kiørboe, 2018) and predator's feeding behaviour (Kiorobe et al., 2018). As immotile phytoplankton species cannot physically escape predation, they use other defence mechanisms, like shell, spines, toxins and colony formation (Pančić and Kiørboe, 2018). We believe that planktonic foraminifera, as immotile organisms, use their shell as a defence mechanism against predators, to balance their inability to escape predation through movement.

In our study we include a prey refuge term which is based on prey's size and density using Mayzaud and Poulet's function (1978) (Eq. (A5)). The prey-refuge term describes how predators' grazing rate change with prey density and never satiate (Gentleman and Neuheimer, 2008). At high prey density the grazing rate is similar to Holling type I, where it becomes linearly related to the prey availability ($F_{N,j_{pred}}$) (Fig. A1, Eq. (A5)). When the prey density is low, the decay constant parameter (Λ) decreases the grazing pressure such as the grazing rate is similar to Holling type III without any saturation (Figure A1) (Gentleman et al., 2003).

$$\text{Prey refuge}_{j_{prey}} = \left(1 - e^{-\Lambda F_{j_{pred}}}\right) \tag{A5}$$

The present version of the model does not include prey's movement and other defence mechanisms because of limited understanding (van Someren Gréve et al., 2017; Almeda et al., 2017). As the main aim of our study is to better understand calcification and the function of shell as a defence mechanism, we removed planktonic foraminifera's prey refuge term, by making the assumption that the lack of prey refuge could balance the cost of their immotility. We are aware that this is a very simply way to represent the trade-offs of immotility, but we chose not to add motility and increase the complexity of the model and the uncertainty of the results, as the costs and benefits of planktonic foraminifera's motility are not studied yet. Our model can be used as a first step for building a mechanistic understanding and more studies can follow focusing on planktonic foraminifera's defence mechanisms.

We ran simulations with and without planktonic foraminifera's prey refuge included (results not showed). For the food chain the prey refuge had a stronger influence than the food web. This is an expected result, as specialist predators (food chain) feed only on specific preys, while generalist ones (food web) can consume multi preys and find other sources when one's prey density is low. We found that the general trend of our model output doesn't change and a reduction on mortality rate is still needed with or without the prey refuge term. In the present study we present the results with the prey refuge excluded (Figs 4-7, Fig B2).

Zooplankton feeding

Omnivorous zooplankton can consume in parallel more than one phytoplankton and zooplankton prey. 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; Kiørboe, 2008; Ward et al., 2012), so as $\Phi_P + \Phi_Z = 1$ (Eq. (A6), (A7)).

$$\Phi_P = \frac{\sum_{j_{phyto}=1}^{J} \varphi_{j_{pred},j_{phyto}} B_{j_{phyto}}{}^{2}}{\sum_{j_{prey}=1}^{J} \varphi_{j_{pred},j_{prey}} B_{prey}{}^{2}} \tag{A6}$$

$$\Phi_Z = \frac{\sum_{j_{zoo}=1}^{J} \varphi_{j_{pred},j_{zoo}} B_{j_{zoo}}{}^{2}}{\sum_{j_{prey}=1}^{J} \varphi_{j_{pred},j_{prey}} B_{prey}{}^{2}} \tag{A7}$$

Plankton mortality

Phytoplankton has a linear mortality term for both versions of the model. We assumed a size-dependent mortality term for zooplankton in the food chain model due to the absence of predation on zooplankton (Table 1) (Ward et al., 2014). As in the food web model predation on zooplankton exists, we assumed a linear mortality term equals to phytoplankton (Table 1) (Ward et al., 2012).

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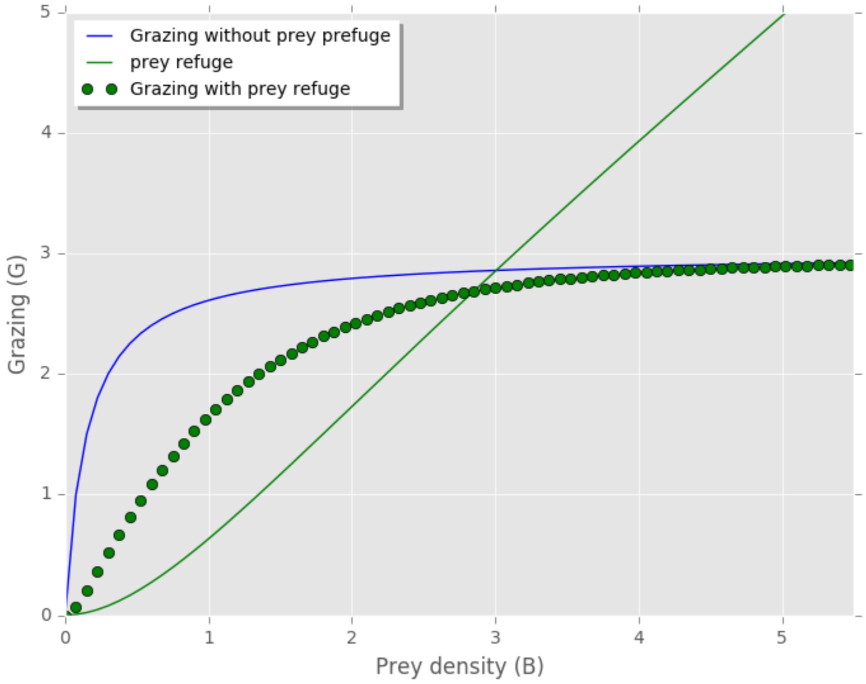

1630 Figure A1: Zooplankton grazing on one prey with and without the prey refuge term included. Prey refuge $= (1 - e^{-\Lambda F}) * F$. Grazing without prey refuge: $G = G_{max} * \gamma_T * \frac{F}{F+ K_{zoo}}$. Grazing with prey refuge included: $G = G_{max} * \gamma_T * \frac{F}{F+ K_{zoo}} *$ Prey refuge. Temperature limitation (γ_T), prey palatability (φ) and prey refuge constant (Λ) equals to 1, and $F = \varphi * B$.

Appendix B

In the Appendix B, we the coexistence of plankton size groups in different nutrient environments (Fig. B1) and the examples of planktonic foraminifera’s shell protection against different predation pressures in the food chain and food web (Fig. B2).

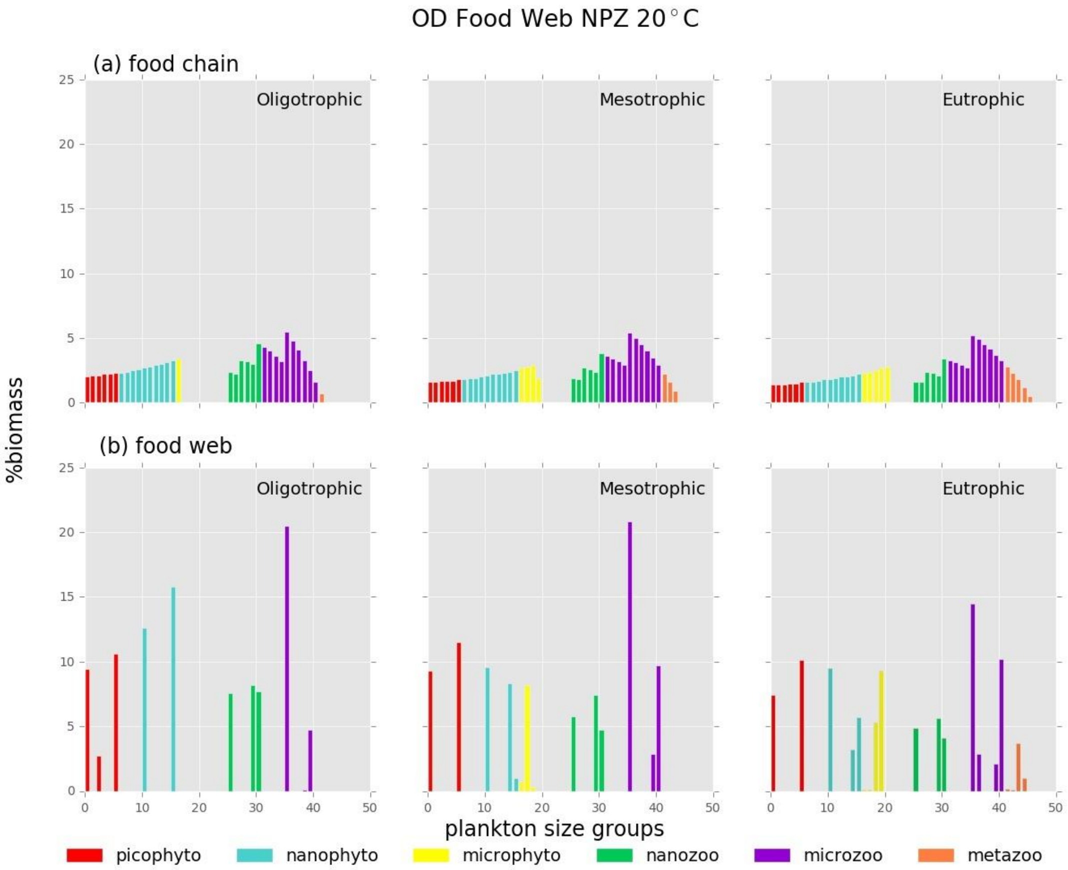

Figure B1. Relative biomass (%) of each phyto- and zooplankton group in (a) food chain and (b) food web for oligo-, meso- and eutrophic environments at 20°C.

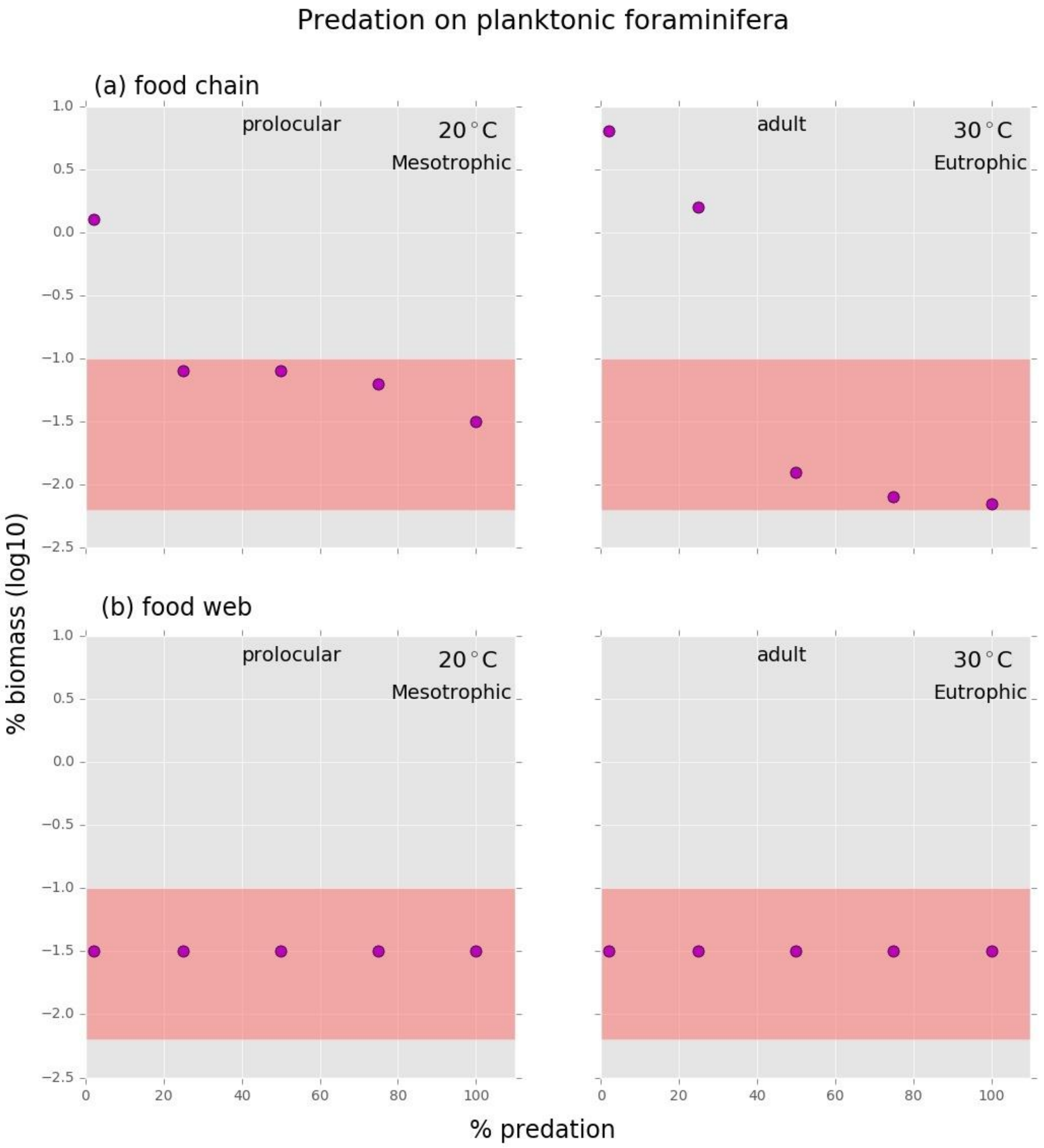

Figure B2: Results from the (a) food chain and (b) food web for different predation on planktonic foraminifera. Within the coloured frame are the different grazing pressures on planktonic foraminifera for which their relative biomass is within the defined range (0.007% to 0.09%).