



## ***Interactive comment on “Simulating the growth and distribution of planktic foraminifer using an ecophysiological multi-species model” by F. Lombard et al.***

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1) The empirical calibration of individual growth versus population density that is used to “scale” the modeled individual growth to changes in population size ignores the effect of changes in body-size distribution across different populations of a given species. The scaling from individual growth to population growth by itself is already a leap of faith, as it explicitly ignores ecological interactions, but I agree with the authors that it is a legitimate first approximation. However, it only works as long as population density is proportionate to the total biomass of the population in the same way throughout the range of the modeled species. This is, unfortunately, not true in the case of planktonic

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foraminifera. Here, the distribution of body sizes varies strongly as a function of temperature (and other less well constrained factors). Because volume (and thus mass) is proportional to the cube of size, even small shifts in shell size have a large effect on the change in biomass. Thus, if the size (measured as shell diameter) of a planktonic foraminifera increases by 25%, its biomass will double. This phenomenon is in my opinion responsible for much of the scatter in figure 3. I believe the authors need to take this issue into consideration both when they are calibrating their model but also when they validate it by observations. In both cases, population densities are directly equated by the authors to population biomass, which is not correct. I am aware that Fraile et al. (2008) have not discussed this effect either, but because that model provided explicitly population biomass, the potential error due to changing body size distribution occurred only once, when comparing model results with observations. In this paper, the error is made twice, when the population biomass is estimated and when it is compared with observations. This is why I feel the authors absolutely need to respond to this issue.

Response: You are right on this, our model do not include any population dynamic that may solve all the issues about links between individuals growth and body size and other population dynamic related processes (see point 2 and 3). However those points cannot be solved currently until model assimilation of population development observation (which are rare). We want to precise that we do not use at any moment any population biomass estimates. The model core just estimate individual growth rate in function to selected environmental forcing. This growth rate is then directly scaled to the population abundance. Of course some variations can occurs regarding individuals size, however we believe that larger individuals (which results from individuals that have larger growth rate if the assumption that they reproduce at fixed intervals, such as lunar cycles, is true), then have larger reproduction potential which means may produce more offspring. Of course our model does not include any population dynamic (including size of the individuals) and thus cannot take into account the action of external factors on the mean size of individuals or in a larger extend cannot distinguish between populations composed of numerous small individuals (that may correspond to

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young populations) and lower densities-large individuals (corresponding to older population after a certain mortality). This concept is mainly explained in Fig 2 and in the manuscript, but will be corrected by taking in consideration the reviewer comment.

2) The simulated growth rate is limited by nutrition saturation (line 124). This is a reasonable assumption for individuals, but I wonder what exactly the implications of this are for the scaling of individual growth with population growth. Population growth cannot be limited by nutrition saturation in the same way as it is for individuals. Instead, it is limited by the amount of nutrition and ecological interactions.

Response: In population dynamics, population growth rate corresponds grossly to individual growth rate pondered by reproduction capacity and success and by mortality (and by export and import of population when considering spatially explicit models). We should also take in consideration that “saturation” here only means that the individual cannot process more food giving their enzymatic capacities (and thus at the population level cannot reproduce even faster without ingesting more food). Then “saturated” growth corresponds to a maximal value for which the population increases exponentially. Individual growth rate have a saturation after a certain food density (which do not mean that population size attain a maximum at this point, on the contrary it corresponds to its maximum increase see Fig 2), but population growth rate may even increase if reproduction capacity and success continue to increase (for instance because gametes fusion is easier due to large density of individuals) and/or mortality decrease. As stated in the manuscript, we cannot in the current step include population dynamics, but taking it into account would certainly decrease some of the model uncertainties.

3) Having seen the entire discussion on the plankton data and the ways in which the comparison is biased by the peculiarities of the validation dataset (as discussed on page 19), I am not sure the data by Bé and Tolderlund (1971) are really useful. I know this is the largest and most consistent survey, but the data itself are no longer available and the “synoptic” representation is fraught with so many assumptions that I almost

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tend to believe the authors should forget about this comparison and focus on fewer but better constrained surveys.

Response: we chosen this dataset because it offer (with all the bias linked to it) a synoptic view of foraminifers abundance and dominance with the great advantage that it is a homogeneous dataset (same depth: sea surface; same net; same expert in foraminifer identification) and because Bé & Tolderlund used surface tows, we can use with confidence satellite images. Additionally, on a large scale, few data only exist together with environmental measurements. Those other surveys were used, but because they were better constrained we used those to calibrate the model. Then because calibrated on those surveys the model of course reproduce those correctly (see Figure 3 and the R2 associated). We had chosen to not validate the model on the same type of data that were used for calibration, and validate both on plankton assemblages (Bé & Tolderlund) knowing that the model already reproduce multinet data and core top data (MARGO database).

4) There seems to be several distinct areas where the model underperforms. One such area, as the authors note, represents the marginal seas (Red Sea and the Mediterranean). This is interesting, because these are also the regions where factors other than those considered in the model may be affecting the species distribution. The second area where the model failed is the Western Pacific Warm Pool. Do the authors have any explanation for the low diversity and wrong species dominance in that region as implied by the model?

Response: yes we have several explanations to this that were briefly mentioned in the manuscript. Firstly, data in pacific (and Indian) ocean are less secure because could be subject to selective dissolution (the seabed is deeper and the deep water CO<sub>3</sub><sup>2-</sup> is higher), then species with thicker shells could be over-represented. Secondly it can also be explained because we used in those figures satellite images to simulate the model and then potentially ignore deep chl a maximums (or deep but still illuminated layers due to oligotrophy), using PISCES model instead partly solve those problems.

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Finally, and this is the more promising such discrepancy between model and data may also reveal the action of external factors not considered in the model (such as salinity in Mediterranean and Red Sea) that may control the foraminifer assemblage in these special location.

5) The growth model implies that *G. ruber* is better adapted to oligotrophic conditions than *G. sacculifer*. This is interesting, as it directly contradicts what we have observed in the Red Sea (Siccha et al., 2009). Could the authors comment on this discrepancy?

Response: The fact is that our modeling attempt indicates that in most cases *G. ruber* better deal with oligotrophy than *G. sacculifer*. This seems be the case in most part of the oceans (Fig 4 & 7). However our calibrating data set does not include data originating from closed basins where other factors (such as salinity, oxygen concentration, etc..) can potentially have a great impact on those species. We largely discussed about potential biases of our approach, and in the case of the red sea, it appear that salinity (and oxygen), which is not taken in account in the present model, seems to affect considerably the foraminifer assemblage (Siccha et al., 2009). We thus believe that this local discrepancy between model and observations is caused by those factors that are not included in the model. This discrepancy will be discussed in the manuscript.

6) I note that the implied depth of maximum growth for the species used in the model is inconsistent with the observed calcification depths for these species as known from the literature, which are in all cases much deeper. Could the authors comment on this discrepancy?

Response: The model only simulates where the environment is more favorable for each species and then where they can achieve their higher potential growth rate. All the species of Fig 9 usually occurs in the epipelagic stratified layer, which corresponds to model results. However we have to keep in mind that important processes where not taken into account such as the vertical mixing within the stratified layer (relocating individual uniformly in the mixed layer), possible sedimentation of animals through the

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thermocline or enhanced potential predation near the surface which can all results in translocation of the population to deeper depth than expected by theoretical considerations. This will be discussed in the manuscript.

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