

## ***Interactive comment on “A dynamic global model for planktonic foraminifera” by I. Fraile et al.***

**I. Fraile et al.**

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Our manuscript has received constructive interactive comments by J. Bijma. We are most grateful for the very helpful comments. Herewith, we would like to respond to the main points brought forward in the review.

### **Answers to the comments of referee J. Bijma:**

Comment: *'My major concern is twofold: 1) Do we know all the biotic and abiotic parameters that control the distribution and population dynamics of planktonic foraminifera? 2) Does the model capture all of these? As my answer to the first question is "No" it automatically implies a negative answer to the second one (and I am sure the authors would agree). Therefore, the model does not provide a prognostic tool (and was not meant to be) but, as the authors state, a*

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**"...tool to explore the response of planktonic foraminifera to different boundary conditions,...".**

We would like to remark that we are interested in the spatial distribution and temporal variability of planktonic foraminifera (PF) from a paleoceanographic perspective. Our aim is to develop a tool to improve foraminifera-based paleotemperature reconstructions. Eykhoff (1974) defined a mathematical model as a "representation of essential aspects of an existing system". Accordingly, the objective of our work is to simulate the first order parameters that control the distribution of PF. "Including all the biotic and abiotic factors that control the population dynamics of PF" is a difficult task, for which the current knowledge of PF ecology is inadequate. Our work does not focus on simulating the absolute biomass of foraminifera. We chose units of carbon biomass to make the link to the ecosystem model easier, but our discussion is restricted to the relative abundances between species and temporal variation of the maximum production peaks. Therefore, the minimum foraminiferal biomass of  $0.01\text{mmolC/m}^3$  has no biological meaning and is purely empirical value, which is needed to preserve a viable PF population throughout the year.

**Comment: '(...) As such, and because our knowledge of planktonic foraminiferal ecology and population dynamics is limited, I suggest that the authors should first carry out a sensitivity analysis of the parameter space itself (Table 1).'**

Following the suggestion of several reviewers, we carried out a sensitivity analysis of the parameters and included it into the new version of the manuscript (sections 2.6, 4.3 and Table 3). To test which parameters influence the most the model result we used the variation of RMSE index.

**Comment: '(...) From culture experiments it seems that heterotrophic ciliates may be the main predators of foraminifera (unpublished data) but data on ciliate densities are not generated by the ecological model (see below). It is also**

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**difficult to see how "competition" can play an important role when the concentration of preferred foraminiferal food (copepods and/or phytoplankton) is much higher than realistic densities of the consumers (...) Respiration (starvation) may be an important factor for juvenile mortality but seems to play a minor role for adult foraminifera (...).**' The main model structure is widely used to describe the pelagic system of marine environments, and is the same as used by Moore et al. (2002) in their ecosystem model. We split mortality between "natural mortality", "predation" and "interspecific competition". It is difficult to estimate what determines mortality, to determine if competition plays an important role or to quantify predation. Difficulties in keeping PF in laboratory cultures further hamper the quantification of these processes. We would like to emphasize again that our foraminifera model is based on fundamental ecological principles and our aim is to characterize and synthesize the major components of the system. We tried to summarize the available information from the literature about PF ecology and capture them in the model. Competition: as long as the foraminifera live in the same spot, at the same time, and feed on the same prey, they compete with each other. One must not see competition as two individuals fighting for the same shrimp but as the fact that the presence and activity of one individual influences negatively the resource availability for the other one. Foraminifera species compete for the fraction of the phyto- and zooplankton that is in a given ecosystem allocated to them. The strongest competition for resources in total would of course be with other groups of zooplankton, but the competition for the type of resources available to foraminifera would be strongest between species, as these follow the same basic strategy.

Comment: **'At this stage, the authors should address a different set of questions: 1) Are the parameterisations and parameters values of PLAFOM sufficient and realistic? (...) The model parameters of PLAFOM have been chosen according to the principle of the "best educated guess" but it remains unclear how the authors arrived to the values in Table 1. For instance, food preferences are set**

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**according the "general rule" that spinose species are carnivorous and non-spinose species are herbivorous but how was the fine tuning done (partitioning between small phytoplankton, diatoms, zooplankton and detritus)? (...) With regard to the parameterisations used in the model, several basic questions arise. For instance, the change in the concentrations of foraminifera is calculated via (estimated) carbon biomass, "growth efficiency" and "mortality". However, the applied relationship (Michaelis-Menton kinetics) including factors such as  $\alpha$ , although intellectually clever and understandable, remain purely empirical. Maximum growth rates depend on the food source and, although this probably makes sense (zooplankton having a higher nutritional value than phytoplankton), are the values freely chosen. What determines the mortality?'** The parametrization of food preferences for each species is based on several publications, all of which report qualitative data for foraminiferal diet. Consequently, the absolute values selected for the model are rough estimates from experimental data. But various parameters (maximum growth rates [ $G_{\max}$ ], half-saturation constant [ $g$ ], respiration loss [ $r$ ] and gross growth efficiency [ $GGE$ ]) are kept constant for all species. The consistency within all species and within the global domain gives certain solidity to the parameters. The value of the parameter  $k$  is purely empirical, based on the theoretical assumption that under favorable food conditions foraminifera can accept wider temperature ranges.

Comment: **'In my opinion they should test the values of the parameter space on a local scale, using sediment trap data as stated above. Globigerinoides sacculifer is the only one of the 5 species investigated that seems to have only one genotype. In addition to that, a detailed data set on its population dynamics (in the Red Sea) has been published (Bijma et al., 1990, 1994). Hence, this seems to offer an opportunity to test ("tune") the behaviour of this species.'**

Our goal was to reproduce the global patterns of the species; thus, "tuning" the parameters to some local scale will not help to better represent the global distribution.

In the mean time, we are looking forward to future laboratory or observational works, which could considerably improve the parametrization in the future versions of the model.

Comment: ***'(...) Is the output generated by the ecological model enough to drive PLAFOM?'***

Considering that food availability is one of the most important parameters controlling the distribution of foraminifera we decided to couple the foraminifera model to an existing and well established ecosystem model (Moore et al., 2005a,b). Despite that the ecosystem model has some differences with observational data (ex. Arabian Sea) we believe it can drive our PF model. Using an ecosystem model instead of direct observations ensures that both models can be forced with past climatic conditions. With this approach, we could potentially study variations in the distribution and seasonality of PF through time.

Comment: ***'Another issue that remains unexplained is the distribution of the population in and below the mixed layer in dependence of the mixed layer thickness. (...)'***

As in the underlying ecosystem model (Moore et al., 2002), we present a two dimensional model for the surface mixed-layer. We made the basic assumption that the mixed-layer can be considered biologically homogeneous. Thus, we neglected the vertical structure in the mixed layer focusing in the mean values for the mixed-layer (Page 4333, line 25 in the original manuscript) This is a simplification and including depth habitats of the species will be one of the next steps of our work, but falls outside the scope of the current study.

### **Terminology:**

The typos and references have been corrected and updated.

## References

Eykhoff, P.: System Identification. Parameter and State Estimation, John Wiley Sons, London, 1974.

Moore, J.K., Doney, S.C., Kleypas, J.A., Glover, D.M., and Fung, I.Y.: An intermediate complexity marine ecosystem model for the global domain, Deep-Sea Res. II, 49, 403-462, 2002.

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