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

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The authors have developed a numerical model (PLAFOM) that generates a geographical distribution of the abundance of 5 species of planktonic foraminifera. PLAFOM is forced by a global hydrographic dataset and by "food availability" as provided by an ecosystem model. The manuscript builds on an earlier paper by Zaric, Schulz and Mulitza (Biogeosciences, 3, 187-207, 2006; see <http://www.biogeosciences.net/3/187/2006/bg-3-187-2006.pdf>) and is certainly relevant for BG. However, the authors are overambitious and running a bit too fast in my opinion. Indeed, temperature and food are probably the two most important drivers of planktonic foraminiferal distributions and if these parameters are dominant controls in a model it shouldn't come as a surprise that the model shows a temperature and food dependent response mimicking real data on a large scale. However, mismatches with real data are difficult to interpret in terms of the PLAFOM parameter space as a

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whole. Which (combination of) parameters ("food preference", "predation", "competition", factors α , k , etc.) are responsible for the mismatch? As a consequence, the discussion is reduced to possible explanations without any "hard" evidence.

Before going into more detail, I like to mention that this is an original and potentially important contribution that can serve as a basis for future improvements of a model on the flux of calcareous plankton. Its value becomes especially important in an acidifying ocean! Whether it should be published in its current state or not I leave up to the editor. If yes, the authors should at least state more clearly where improvements are made with regard to the Zaric; et al. paper. 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 "...tool to explore the response of planktonic foraminifera to different boundary conditions,...". 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).

At this stage, the authors should address a different set of questions: 1) Are the parameterisations and parameters values of PLAFOM sufficient and realistic? 2) Is the output generated by the ecological model enough to drive PLAFOM?

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 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)? In their defence I should add that, even after almost 25 years of grow-

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ing foraminifera in the laboratory and studying them in the field, I would be unable to provide absolute numbers. However, wouldn't it be possible to narrow down values for at least some of the parameters by testing the model on a local scale? Thereby reducing the variability in some of the variables? For instance, foraminifera collected in a sediment trap have all "seen" the same abiotic factors and shared the same biotic interactions. Such "per sediment trap" data, collected at different sites (i.e. under different conditions) might be used to constrain the parameter values, such as "food preference", "predation", "competition", "mortality", etc.

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? Again, some (smart) parameterisation is developed but how close is it to reality? Mortality is assumed to be the sum of predation, respiration and competition. Again, although the choice of these parameters is intellectually understandable, data to back it up are completely lacking and it is difficult to assess how well it mimics real mortality. 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 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 (ca. 1 to 100 (?) adult foraminifera per m³) and estimated feeding rates for spinose species of 1 prey item every 1 to 3 days (Spindler et al., 1984). Respiration (starvation) may be an important factor for juvenile mortality but seems to play a minor role for adult foraminifera. From a study on the population dynamics of *G. sacculifer* in the Red Sea (e.g. Bijma, Hemleben and Wellnitz, 1994), it became clear

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that juvenile mortality is huge (lack of symbionts (see below)?; starvation?) but once a certain size was attained mortality was replaced by "death" through gametogenesis (the parent cytoplasm divides into hundred thousands of gametes). This brings me to another issue of the foraminiferal lifecycle, which, however, may not be critical for the model as it is based on "carbon units". Most of the foraminifera under consideration have a life cycle that is tuned to the lunar cycle. Upon full moon not all adult specimens in a population have reached a similar size. Assuming that the total biomass of an individual determines the number of gametes it produces, this means that the population structure (absolute numbers per size fraction) around full moon determines the success of this species. However, as stated above, using "carbon units" may be a clever way to circumvent this.

The model uses a minimum foraminiferal biomass of 0.01 mmolC/m³ as a limit for sustaining a population. Where does this number come from? Is that the carbon content of one foraminifer?

The parameter k (to control temperature tolerance depending on the food availability) seems to be introduced to correct for the mismatch of a species distribution pattern (notably *N. pachyderma* (dex.) and *G. bulloides*) where temperature preferences of some genotypes are lacking. Except for creating a better global fit, what is the (biological) basis?

Another issue that remains unexplained is the distribution of the population in and below the mixed layer in dependence of the mixed layer thickness. Peeters and Brummer have done an excellent job in describing depth distributions of certain species of planktonic foraminifera and should be consulted (Peeters, F., 2000, The distribution and stable isotope composition of living planktic foraminifera in relation to seasonal changes in the Arabian Sea, PhD thesis, Amsterdam).

It is clear that in the current set-up, the input parameters for PLAFOM are limited to the output parameters of the ecological model. The question is whether this is sufficient to

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drive the foram model? I would argue not. For instance, symbiont bearing foraminifera have to acquire a specific dinoflagellate (*Gymnodinium béii*) when they are juvenile. Hence, it seems reasonable to assume that their success critically depends on abundance and seasonality of these symbionts. This information is not provided by the ecological model. In addition (as stated above), information on heterotrophic ciliates (possible predators of foraminifera) is also not an output parameter of the ecological model. Finally, although *G. ruber* and *G. sacculifer* are both carnivorous, it seems that the former cannot handle larger prey items. Hence, the ecological model should ideally provide information on more than just one class of zooplankton.

Below, I provide other general or more specific comments.

The references used in the introduction seem random. In many cases it might be better to refer to review papers or books such as Hemleben et al. (1989), "Modern Planktonic Foraminifera" and/or Sen Gupta (1999), "Modern Foraminifera" and references therein. On the other hand, some specific references that seem relevant were not used (see below).

- 1) P. 4329; lines 23-25: Rephrase: When zooplankton is the food source, G_{max} is set higher than when diatoms, small phytoplankton or detritus are the food source. This is done because zooplankton carbon concentration is most of the time much lower than phytoplankton carbon concentration.
- 2) P. 4329; lines 28: take out "marked".
- 3) P. 4330; lines 25: Table 2 should be Table 1.
- 4) P. 4342; lines 21: "grown" should be "grows"
- 5) P. 4343; lines 19: "than the" should be "than that".
- 6) P. 4343; lines 25: "It use to be" should be "It used to be".
- 7) P. 4348; lines 3: "sedimment-trap" should be "sediment-trap"

8) P. 4348; lines 11: ".....monsoon seasons Gupta et al. (1997)." should be ".....monsoon seasons (Gupta et al., 1997)."

After all I want to restate that I consider this kind of work of very high priority and the group in Bremen seems to be the only one working on this issue. 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.

With regard to the temperature preference and distribution of left and right coiling *N. pachyderma* the paper by Bauch et al.(2003) should be consulted. Regarding the discussion on the impact of the monsoon in the Indian Ocean, Peeters et al (see below) should be consulted.

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