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Biogeosciences
Discussions

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

I. Fraile et al.

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Answers to interactive comments by referee 1:

Comment: ***'(...) Simulated flux and repartitions are unfortunately poorly compared to real data and the author claims that the results "match well" without clear use of statistics to quantify this fitting: for worldwide distribution a little indication is given in the form of a 'root mean squared error' without indication of how it is calculated and no statistic is used for sediment trap comparison.(...)'*** We use Root mean Square Error (RMSE) to asses the deviation between model and data. On Page 4334, line 22-28 in the original manuscript it is explained how it is calculated. To compare time-series records we used all the sediment-trap data we found in literature. The sampling period is variable, often with a duration of one year; and most of the data have some gaps during this period. Furthermore, the distribution of the sampling locations is not uniform: most of the sediment-trap data are located

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in coastal areas, whereas open ocean lacks data. All of this makes a statistical comparison difficult.

Comment: *’(...) **How do you integrate the model results in time (method?) and what is the time step used (and the time step of data?)? Do you interpolate the monthly results from platform or directly integrate from one month to an other? If this is the latter method that you use what is the effect of this? Please give precisions on that.(...)’*** The foraminifera model is implemented within the ecosystem model and uses the same Runge-Kutta algorithm for integration. More details about model settings, resolution and boundary conditions is available in the original paper (Moore et al., 2002a,b) and at http://usjgofs.whoi.edu/mzweb/jkmoore/areadme.html.

Comment: ***’(...) Page 4326, line 17-18: The author put in contrast his study to the model of Žarić et al. (2006) which use a totally empirical approach. However the present model is based also on an empirical approach at least on the estimation of the temperature dependence (which comes from the same statistical analysis from Zaric et al 2006 see page 4330). Then the present study is more an extension of Žarić et al. (2006) model (...)’***

The temperature tolerance range (σ) is parametrized based on observational data (Žarić et al., 2005). The empirical model of Žarić et al. (2006) is a static model, which characterizes the state of the system by describing the information known about it at any point in time. In contrast, our model is a dynamic model which considers the processes that produces the observations to describe the behavior of the system through the time. In the corrected version we explain this point better to make it more clear for the reader. (Page 3, line 27 - Page 4, line 3).

Comment: ***’Page 4327 line 1-16: How the ecosystem model was used? Were only output data from Moore et al model used to force the foraminifer model (that***

would explain the non inclusion of horizontal advection and the fact that only one simulation per month is simulated versus sediment trap) or did foraminifers have been included in this model? Please add this precision'
The foraminifera module is include within the ecosystem model. See answer above.

Comment: ***'Why ignoring the vertical structure and only considering a mean value for the surface mixed layer? Knowing that different species are located at different depth in the water column, some near surface (G ruber, G. sacculifer) other near maximum chlorophyll (G. bulloides, N. pachyderma) and other deeper in the water column (N. dutertrei) this assumption seems to be very strange for me and limit the meaning of the results. I understand that Moore model is a 2D model without horizontal advection, but how do you justify choosing this model rather that a 3D model simulating the whole water column and taking in consideration horizontal advection (that are needed in order to simulate upwelling for example).'***
The species modeled in out study used to live in shallow or intermediate waters (Bé, 1982), and they are often used as upper water mass indicators in paleoceanographic reconstructions. The extension of the present model to include water depth would require major changes to the underlying ecosystem model. This would constitute a major project and falls beyond scope of this study.

Comment: ***'General comment on platform model: How do you calibrate the different parameters? It appears nowhere in the manuscript and it is an important information to know if this model is calibrated with a statistical method or "manually". Looking the table 1, my first impression is that this model has been manually tuned rather than searching the parameter set that minimize the errors between model and observations.'***
Ecological data available in literature is all qualitative information. For a model this

information has to be quantified. Taking into account the number of free parameters and species, a statistical approach to calibrate the parameter values is computationally unrealizable. The calibration is done "manually", but the differences of the parameters between species are chosen according to what is known about foraminifer ecology.

Comment: ***’Page 4328 line 1-10: I agree fully about the fact that different species could have different diet. However I have some questions: it seems that spinose species are mostly carnivorous without exclusion to use phytoplankton, in your parametrization you assume that they can use diatoms but not small phytoplankton (which are the most common phytoplankton in warm oceans where spinose species are found).’***
The ecosystem model simulates high concentrations of small phytoplankton in upwelling areas whereas diatom concentration is relatively higher in open ocean. The two spinose species modeled here (*G. ruber* and *G. sacculifer*) are species adapted to oligotrophic waters, thus, to open ocean conditions.

Comment: ***’In a same manner, despite the fact that some muscle tissues in digestion are found in non spinose species, why did theses species do not use zooplankton as a prey in your model (parameter p(Z) in table 1).’***
We tried to simplify the ecological information in order to maintain the model as simple as possible. Phytoplankton concentration is in general much higher than zooplankton. Including a herbivorous part to the diet of spinose species (mainly carnivorous) does affect to the results; whereas including a small part of carnivorous diet to non-spinose species (mainly herbivorous) does not change the results fundamentally.

Comment: ***’[...] And finally whereas no indications exist on feeding on detritus, spinose species (which have the more predator behavior) have detritivorous behavior in your model. How do you support these hypotheses?’***

Spinose species feed mainly on zooplankton (e.g. Hemleben et al., 1989). Detritus includes the bodies of dead organism or fragments of organisms.

Comment: ***'Page 4328 line 13-16: Value(s) for GGE are missing and appear nowhere (also it do not appear in table 1 whereas it signification is given as a footnote).'***
Included in the updated version (Table 1).

Comment: ***'If I clearly understand, this gross growth efficiency does not depend on prey type. However we can expect that an animal prey should be more efficiently digested and assimilated than detritus (that include already digested matter) and then should have a higher GGE. Here I suspect confusion between the parameter GGE (gross growth efficiency) and Gmax (maximum growth rate) expressed in the grazing equation (equ 2). Firstly in the way of the parameterization,*** $G_{\max}$ ***should be a Maximum grazing rate and GGE****$G_{\max}$ ***represent in this way Maximum gross growth rate (as respiration is not included).'***
In principal the reviewer is right. But we did not want to change the framework of the ecosystem model, and mathematically the results does not change. Therefore, we keep the value of GGE the same value as in the ecosystem model, that is 0.3. $G_{\max}$ (named now as maximum grazing rate), varies with the food source: the value is higher when feeding on zooplankton, and lower if phytoplankton or detritus are the food source. This is done because in the output of the ecosystem model phytoplankton concentration is always much higher than zooplankton concentration. Thus, under optimal growth conditions, carnivore species can grow as fast as herbivore species.

Comment: ***'Secondly, knowing that foraminifer does not graze actively (and do not move actively) we can mostly talk about Maximum encountering rate between predator and prey. In this way we can expect that the encountering***

rate of the different prey should be mostly the same for the same foraminifer species (with however difference between motile and non motile prey) and different between foraminifer species (depending on their spinose surface for example). In this way Gmax is effectively modeled as different between motile (zooplankton) and non motile prey but remain the same for all the foraminifer species. However the justification for that (Page 4329 line 23-27) concern the parameter GGE (gross growth efficiently) and is not accurate for the parameter Gmax (max grazing rate).'
We disagree with the referee that this level of distinction is important at the level of description we are aiming at.

Comment: ***'In a same manner, the parameter alpha (relative abundance in relation to temperature) calibrated empirically from relative abundance should be a "relative efficiency for grazing" in this equation (calibrated from relative abundance). If it is a "relative abundance" it has nothing to do in this equation.'***
It has been corrected.

Comment: ***'Page 4329 line 5: the author claims that "the food requirement varies for the different foraminifera species" but the parameter g (half saturation constant for grazing) does not varies between species. In this way only the adaptation for different food types is modeled, not the adaptation of the species to different productivity regimes.'***
We cannot rule out that food preference (p) varies as function of productivity. However, adding such a relationship without additional data-based constrains would only increase the degrees-of-freedom in the model and would not necessarily give a better representation of the first-order distribution of PF, which is our main interest.

Comment: ***'Page 4329 line19-22. I do not understand what mean this sentence in***

modeling terms. Do it means that you use different input data (maximum chl a and nutrient) rather than classic input (mean monthly chl a and nutrient data)? In this case did the seasonal cycles obtained for sediment trap depends only on temperature?'
Chlorophyll and nutrient concentrations are not directly used to calculate foraminiferal growth rate. The parameters used are phytoplankton or zooplankton concentration, which at the same time depend on nutrients. In case of *G. ruber* (white) and *G. sacculifer* we used the classic input data in the same way as the other species; but we add two extra variables: maximum chlorophyll and nutrient concentration. We applied a negative relation to the foraminiferal growth rate, thus, these species grow where maximum chlorophyll and nutrient are relatively low. We clarified this point in the updated manuscript (Page 7, line 15-19). See also answer to the "comment 6" from F. Peeters.

Comment: ***'Page 4330: you use a Gaussian distribution for relative distribution. However relative distributions (Zaric et al 2005) and foraminifer growth rates (Bijma et al 1990) seems mostly to have a non symmetrical distribution and growth rates. Why do you not used asymmetrical relationships (skewness kurtosis) for a better fitting?'***
The approximation of temperature dependence to a 'normal distribution' is based on the extensive data summarized by Žarić et al. (2005). Most of the species seem to be distributed normally. *N. pachyderma* (sin.), *G. ruber* and *G. sacculifer* appear an asymmetrical distribution, but we think it could be due to the fact that they live at extreme sea-water temperatures (*N. pachyderma* (sin.) at lower limit and *G. ruber* and *G. sacculifer* at upper limit), and the asymmetrical distribution is more due to lack of data outside this range.

Comment: ***'Page 4332: Here you choose to represent the "mortality" as the sum***

of predation, respiration and competition. Did the term "mass loss" is not more accurate if respiration is included inside? '
We substituted the term "Mortality" by "Mass loss".

Comment: ***'Concerning predation: did this biological process have a real importance for foraminifer in the field?? Except some few indications concerning euphausids or some non selective filter feeders (salps) there is to my knowledge few to no indication that predation limit foraminifers populations.'***
Although there is not known organism specialized feeding on foraminifera, we assume that predation pressure exist from non selective predators.

Comment: ***'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). (...)'***
Since the ecological niches are often dominated by few species we assume interspecific competition occurs. (see also answer to the comment 3 by Bijma). We performed a sensitivity analysis of the parameters (included in the updated version, new Table 3), and shows the variation of RMSE when we reduce competition pressure.

Comment: ***'You said line 15 that food consumption typically increases with increasing temperature. Did this 8216;8216;typical8221; behavior does not miss in your grazing equation (equ2)?'***
From a bioenergetic perspective food consumption rates typically increase with increasing temperature. Different predators may not have the same impact, but grouping all the predators together this assumption seems to be justified. Our model is represents the species level and the temperature relationship is incorporated via the param-

eter alpha (α).

Comment: ***'In a same manner the temperature dependence of respiration is totally absent and a fixed fraction (6%) of the foraminifer carbon biomass is respired whatever the temperature. Did this parameterization is coherent with previous studies concerning the respiration rate of foraminifers (Spero Parker 1985, Rink et al. 1998, Koehler-Rink Kuehl 2005, Jaergensen et al. 1985)?'***
We choose a respiration loss of 6%, the same as in the underlying ecosystem model (Moore et al., 2002).

Comment: ***'Concerning competition: knowing the low abundance of foraminifers compared to the high abundance of their prey (copepods, algae etc) it seems to me unrealistic that competition would limit foraminifer abundance. The more surprising is that competition exist only between species (parameters C/N species in table 1) but not between individuals of the same species. But if these different species compete for the same resources, taking in consideration that they have different feeding regimes, the higher competition would take place between individuals of the same species and not between species.'***
Intraspecific competition is assumed to be part of "natural mortality". Accordingly, if population size is larger, natural mortality rate is also higher.

Comment: ***'In a same manner, competition would act in a similar manner for the two species in competition and not in an asymmetrical way for example N. pachyderma (sin) does not reduce the abundance of any species but N. pachyderma (sin) abundance is reduced by the presence of N. pachyderma (dex) (cf table 1). For me this competition term is mostly here to limit some species when other species are present: for example when G bulloides is present G ruber and G. sacculifer can growth and are half limited (Clij=0.5) but when G ruber or G. sacculifer are present G. bulloides is strongly limited and***

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would certainly disappear (Clij=1). Then I wonder in what extend the seasonal successions of sediment traps are controlled by this competition term.’
The competition pressure is asymmetrical due to the differences in the absolute biomass values of the species. Some species show higher absolute values than others in the model. In order to balance competition pressure, these parameters have to be different.

Comment: ***’Moreover I wonder from where this competition term comes from, there is no reference that justifies this use of the competition. For me competition is when one species exhaust the resource (food) in regard to it grazing potential and food requirement then species with higher grazing ability (or lower food requirement) would continue to growth whereas the other species collapses. Then for me competition had to be expressed in function to food availability and grazing potential and not in function to species presence. Finally if competition play a so important role for foraminifers I wonder how this model can really fit the data knowing that other important and abundant species of foraminifer are absent (N. duterterei, T. quiqueloba, G. glutinata and G. siphonifera for example).’***
See answer above (comment 19).

Comment: ***’Page 4333 line 17-19: how are the data smoothed and modified to take into account upwelling? Line 24-end: does it means that foraminifers simulated for mixed layer are "extended" to depth using this relationship? Why do not simulate concentration of foraminifers assuming the same model.’***
The foraminifera module is indeed included within the ecosystem model. We used the same forcing fields as Moore et al. (2002). The authors describe the routine for simulating the velocity field near the equator. The statement in the manuscript could indeed lead to a misinterpretation. Accordingly, we removed this sentence and refer to

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the paper by Moore et al. (2002).

Comment: ***'Page 4334: are the top core data modified in order to give proportion of each species within only the five targeted or the figures present a percentage on the whole community?'***
Yes, as it is mentioned in the original manuscript (Page 4334, line 13-14). We modified the text in order explain it more clearly in the revised manuscript (Page 11, line 28 8211; Page 12 line 1).

Comment: ***'Page 4335: why are the results from sediment traps (in individuals m-2 d-1) not transformed in carbon biomass in the same way that you did for top cores? This would facilitate the comparison.'***
The units have not been transformed because our aim is not to compare the biomass of foraminifera. Our comparison focuses on the timing of the maximum the foraminiferal production; which is relevant to interpret paleoceanographic reconstructions.

Comment: ***'Page 4338 line 8-10: What is the sieve size used for top core assemblages?'***
150μm; as described in the original papers (Prell et al., 1999; Pflaumann et al., 1996; Martinez et al., 1998).

Comment: ***'Page 4341. For me this is not a sensitivity analysis. A sensitivity analysis test if the model is robust to small deviation of parameters and then give an indication on the parameter that mostly control the model and then need a confident calibration. Here you test the model behavior to input data (food availability) which is not a parameter (as stated on line 25).'***
Following the suggestion of various reviewers we include a sensitivity analysis of the

parameters. We rename this experiment (Model experiment with constant mixed-layer temperature) to avoid confusion.

Comment: ***'Fig 4: G. bulloides. The fact that the model represents a very high abundance only in the Arabian sea and not in other upwelling (that are represented by Moore et al (2002b) model see figure 4) such as Namibian, Peru or Mauritanian upwelling needs to be discussed.'***
G. bulloides shows higher abundances in the Arabian Sea than in other upwelling areas due to the lack of *N. pachyderma* (dex.) in the Arabian Sea. In the upwelling off Peru, western Africa or Benguela the abundance of *N. pachyderma* (dex.) is overestimated and therefore the competition exerting upon *G. bulloides* species is too large (Page 4344, line 13-15 in the original manuscript).

Comment: ***'Table 1: what are the parameters Zingest, p2SP, p2D, p2Z and p2DR They appear nowhere in the text and have no signification in the footnotes. What means the SP and LP exponent for parameter k for N. pachyderma (dex) and G. bulloides. Parameters d and b are not presented as footnotes. Parameter GGE is missing.'***
We corrected and included the information in Table1.

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