

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

Anonymous Referee #1

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General comments:

The manuscript by Fraile et al presents an attempt to model (with the PLATFORM model) the concentration and biogeography of different planktonic foraminifer's species. This model uses a global ecosystem model (Moore et al 2002 a,b) to force the hydrology and biology that in turn control the foraminifer growth and mortality. The model results simulate the worldwide proportion of five species (cumulating the overall water column and seasons) that are compared with top core observations and the model is afterward used to simulate seasonal flux that are compared to sediment trap data. 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. This model for me point in the right direction: using

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biology to try to understand foraminifer's species distribution in time and space a topic that is generally studied only in a geologic or paleoclimatologic point of view without considering the biological constraints that applies on foraminifers. This study is to my knowledge the first to try to do that without using a totally statistical approach. The model itself is relatively complex and takes in consideration different type of biological processes such as grazing on different prey types, predation, respiration, competition and temperature dependence. However my principal doubts concern methodological and theoretical aspects that need strong justification or modification. 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. In general, different aspect of this model seems to me very confusing and the authors should take attention on several points: can the parameter used in the model be compared to what is currently known about foraminifer biology? Did the biological processes included in the model have a sense for foraminifera? And are these processes modelled in the right form? For each of theses questions my personal impression is that the response is not necessarily "Yes" depending on the processes used. All these points need to be justified in the publication for each biological process. For these reasons, I recommend major revisions before publication.

Detailed comments:

Page 4326, line 17-18: The author put in contrast his study to the model of "aric" 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 "aric" et al 2006 see page 4330). Then the present study is more an extension of "aric" et al 2006 model.

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

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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

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 than a 3D model simulating the whole water column and taking in consideration horizontal advection (that are needed in order to simulate upwelling for example).

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 minimise the errors between model and observations.

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 parameterisation 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). In a same manner, despite the fact that some muscle tissues in digestion are found in non spinose species, why did these species do not use zooplankton as a prey in your model (parameter $p(Z)$ in table 1). And finally whereas no indications exist on feeding on detritus, spinose species (which have the more predator behaviour) have detritivorous behaviour in your model. How do you support these hypotheses?

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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). 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 G_{max} (maximum growth rate) expressed in the grazing equation (equ 2). Firstly in the way of the parameterisation, 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). 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 G_{max} is effectively modelled 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 G_{max} (max grazing rate). In a same manner, the parameter ? (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.

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 modelled, not the adaptation of the species to different productivity regimes.

Page 4329 line 19-22. I do not understand what mean this sentence in modelling terms. Do it means that you use different input data (maximum chl a and nutrient) rather than

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classic input (mean monthly chl a and nutrient data)? In this case did the seasonal cycles obtained for sediment trap depends only on temperature?

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? Line 25: Table 1 I mean rather that table 2

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? Concerning predation: did this biological process have a real importance for foraminifer in the field?? Except some few indications concerning euphausiids or some non selective filter feeders (salps) there is to my knowledge few to no indication that predation limit foraminifers populations. Is really necessary to model this process?? This predations seems to me to be more a term of “autolimitation” than a real predation: effectively predation on species of foraminifer depends only on it own abundance (and not on predator abundance) and more a species is abundant, more it have predation. You said line 15 that food consumption typically increases with increasing temperature. Did this “typical” behaviour does not miss in your grazing equation (equ2)? 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 parameterisation is coherent with previous studies concerning the respiration rate of foraminifers (Spero & Parker 1985, Rink et al. 1998, Köhler-Rink & Kühl 2005, Jørgensen et al. 1985)? Concerning competition: knowing the low abundance of foraminifers compared to the high abundance of their prey (copepods, algae ect) 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

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they have different feeding regimes, the higher competition would take place between individuals of the same species and not between species. 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 grow and are half limited ($C_{lij}=0.5$) but when *G. ruber* or *G. sacculifer* are present *G. bulloides* is strongly limited and would certainly disappear ($C_{lij}=1$). Then I wonder in what extend the seasonal successions of sediment traps are controlled by this competition term. 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 its grazing potential and food requirement then species with higher grazing ability (or lower food requirement) would continue to grow 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).

Page 4333 line 17-19: how are the data smoothed and modified to take into account upwelling? Line 24-end: does it mean that foraminifers simulated for mixed layer are “extended” to depth using this relationship? Why do not simulate concentration of foraminifers assuming the same model. (line 28 shallow means thin I guess?)

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?

Page 4335: why are the results from sediment traps (in individuals $m^{-2} d^{-1}$) not trans-

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formed in carbon biomass in the same way that you did for top cores? This would facilitate the comparison.

Page 4338 line 8-10: What is the sieve size used for top core assemblages?

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 behaviour to input data (food availability) which is not a parameter (as stated on line 25).

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 upwellings needs to be discussed.

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.

Jørgensen, B. B., J. Erez, N. P. Revsbech, and Y. Cohen. 1985. Symbiotic photosynthesis in a planktonic foraminiferan, *Globigerinoides sacculifer* (Brady), studied with microelectrodes. *Limnol Oceanogr* 30: 1253-1267. Köhler-Rink, S., and M. Kühl. 2005. The chemical microenvironment of the symbiotic planktonic foraminifer *Orbulina universa*. *Marine Biology Research* 1: 68-78. Rink, S., M. Kühl, J. Bijma, and H. J. Spero. 1998. Microsensor studies of photosynthesis and respiration in the symbiotic foraminifer *Orbulina universa*. *Mar Biol* 131: 583-595. Spero, H. J., and S. L. Parker. 1985. Photosynthesis in the symbiotic planktonic foraminifer *Orbulina universa* and its potential contribution to oceanic productivity. *J Foraminifer Res* 15: 273-281.

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