

Response to Anonymous Referee #1

NOTA: The initial reviewer comments are in italic, our answers are in bold, action taken in the revised version of the manuscript are underlined.

The manuscript by D. Roche et al, proposes a new module to simulate the effect of foram species-specific habitat (namely depth and season) on their isotopic content. This short and well-structured manuscript builds on the FORAMCLIM model to draw conclusions on the specific living depth of foraminifera. I greatly appreciated the fact that the code is open source, which will be of help not only for modellers but also for the paleo and modern foram community.

The manuscript posits that the growth and habitat of planktonic foraminifera can be simply described using a set of parameters, derived from culture experiments, which are mostly dependent of the temperature. This is based on the Lombard et al, 2009 FORAMCLIM model. This model is compared to the Late Holocene MARGO data-set, in order to have a first order idea of the distribution of planktonic foraminifera, and through the coupling with the $d_{18}O$ module computation from salinity-regressions, the range of $d_{18}O$ one could expect for a significant cooling ($\Delta T=4^{\circ}C$).

This is a stimulating contribution which from a micropaleontologist point of view raises a few questions, and two main ones.

We thank the reviewer for this positive view on our approach and on the manuscript. Responses to individual comments are dealt with below.

My first concern in the manuscript is the model-data comparison: there are some visual comparisons by overlying the percentage of foraminifera species to the presence at some time of the year, with an ad-hoc threshold at 10%. As the focus is based on the oxygen isotopes, I wonder why the authors use the species distribution for testing this model which has been already validated by Lombard on plankton nets and surface sediments (just using the surface temperature).

FORAMCLIM, the model validated by Lombard on plankton nets and surface sediments, computes foraminifer abundances based on food availability, light and temperature (Lombard et al., 2011). In contrast, FAME does not compute species abundances, but only growth rates as a function of temperature. Consequently, the validation steps we present for FAME have not been previously published. We would also like to stress that unlike Lombard's validation, we do not compare simulated against observed abundances, but simulated absence/presence against observed absence/presence. For these two reasons, the test we performed is different from the validation of the FORAMCLIM model published in Lombard et al. (2011).

We used a threshold at 10% to account for the census counts uncertainty is thus used as an indication of the absence / presence only. The reviewer is

perfectly right that this 10% threshold is ad hoc. We have thus removed it from the revised version of the manuscript, where we present the MARGO data with colored abundances from 0 to 100%.

Action taken:

We have modified the previous figure 3 and A2 to comply with the reviewer's suggestion of not using an ad hoc threshold of 10%. The accompanying text as been modified accordingly.

The issue here is to find an independent data-set to validate their isotopic model. I wonder if some stable isotope sediment trap data could not be a better benchmark to validate the model, rather than the comparison with surface sediments. There are some time series in the South China Sea (Lin et al, 2011); in the Gulf of Mexico (Thiraulamai et al, 2015), and the works lead by R. Thunell among others.

The FAME module was developed in order to be coupled to the iLOVECLIM climate model and other climate models to simulate the isotopic signal of foraminifera in marine sediment cores. In doing so, our purpose is to enable model-data comparison via the simulation of planktonic foraminifer isotopic signals that can be directly compared to data derived from sediment cores. It is thus more relevant to validate the model against data from the sediment than from sediment traps or plankton tows. For the latter, the short cup window (~7-8 days), which is shorter than the duration of the foraminiferal life cycle in many cases, can add further sources of error when integrating the climate signal"

An additional problem is the availability of multiple species from sediment trap data: it is a real issue to find all needed species on a common sediment-trap data. On the other hand, the MARGO database yields directly a product which is very much comparable since it was compiled with inter-species comparison in mind.

A second concern is the propagation of errors throughout the model which is not properly dealt. As the model picks a best fit for the response of the growth of foraminifera to temperature, and that in the code (and in the original paper), the uncertainties are given, it would be useful to propagate the errors of the response (growth) of foraminifera to temperature. It would be extremely useful for the community, as it would give the reader a sense of the sensitivity of the models. This point is also detailed below.

In the original manuscript of Lombard et al., 2009 (LO09), the errors are given on the individual parameters, and it is not possible (we tried) to reconstruct directly the exact equations used for plotting the 95% confidence intervals, since the parameters are not independent from each other. In order to nonetheless propose an analysis of the effect of the uncertainty on our results, we modified the coefficients of the growth functions used initially as per the figure and table below and analyzed its effect on the depth calibration and the

associated error on the comparison to the MARGO dataset. The chosen range of values is close to the 95% range of LO09 for most species and larger than the 95% confidence interval for the others. The values obtained are thus a maximum range in all values given.

Regarding depth calibration, we find our results to be largely insensitive to the use of these upper-bound and lower-bound values for the growth functions. Specifically, the uncertainty in the maximum growth depth is largest on *N. pachyderma* (range of 475 to 600 meters) and *G. bulloides* (400 to 450 meters). It is somewhat smaller for *G./T. sacculifer* (100 to 125 meters) and *N. incompta* (60 to 65 meters). There is no impact for *G. ruber*. If keeping depths constant and computing the impact of the growth function on the mean difference between simulated and MARGO d18O values shown in Figure (2), the resulting change is lower than 0.1 per mil for each individual species. This additional analysis shows that our results are very robust.

Action taken: We have added an additional supplementary figure in the manuscript showing the ranges used for the error analysis and added corresponding text to highlight further the impact of using these other, within error curves, on the computation of the d18Ocalcite.

Technical comments :

[l. 18 page 1]: Expand the connection between the stratified nets and the isotopic derived values of Emiliani more in details. In Jones, there is no reference whatsoever to any isotopic analyses. You are making the connexion, but this was not put forward by Jones.

The line the reviewer is referring to does not say that Jones used isotopic analysis: "Through in situ water column sampling via opening-closing plankton nets, (Jones, 1967) corroborated the depth habitats of Emiliani (1954)." We hence interpret this as a need for clarification in this section of the text.

Action taken: To clarify this point, the statement is altered in the revised version of the manuscript and now reads: "Through in situ water column sampling via opening-closing plankton nets, Jones (1967) through faunal abundance counts corroborated the depth habitats that Emiliani (1954) inferred through isotopic analysis."

[page 2]: "It is this tempting to make one additional step": I do not understand this statement : It is a fact that oxygen isotopes have been implemented in models, but yet, this is not the topic of the paper as the d18O values of seawater are computed from empirical basin correlations between d18Osw and salinity, not from water isotopes enabled models. I would recommend to move this sentence in the perspectives, as it is misleading here and one quick reader might think that isotope models were used.

Action taken: we have followed the recommendation of the reviewer and removed this sentence.

[equation 1, page 3]: I would add here a reference to the original work (Kooijman 2000) which formalized this equation as referred in Lombard et al (2009).

Action taken: We have added the reference to Kooijman, 2000

[line 5, page 4]: The authors do use a TL of 280 for *G. bulloides* instead of 281.1. This shows that the model is extremely sensitive to a minor change in TL : could you please elaborate a bit on the reason on this 1.1°K shift ? Did you perform some sensitivity analyses to reach this temperature ? This is appealing because the overall inferred isotopic equilibrium depth calculated for this species is off the charts (see point below).

As explained in l. 5-9, p. 4, comparing FAME's output with the subpolar North Atlantic sediment trap data published in Jonkers et al. (2013), we found that the nominal value of *G. bulloides* lower boundary of the growth tolerance range, TL = 281.1 K, was too high and was responsible for the absence of growth outside of the 3 summer months. In contrast, sediment trap data indicate that, on average over the four years of observations, significant *G. bulloides* fluxes prevailed from the end of June to the middle of November. We tested a few other values for TL and chose the value closest to the nominal value that allowed the extension of the growing season into the fall, in agreement with the data pattern.

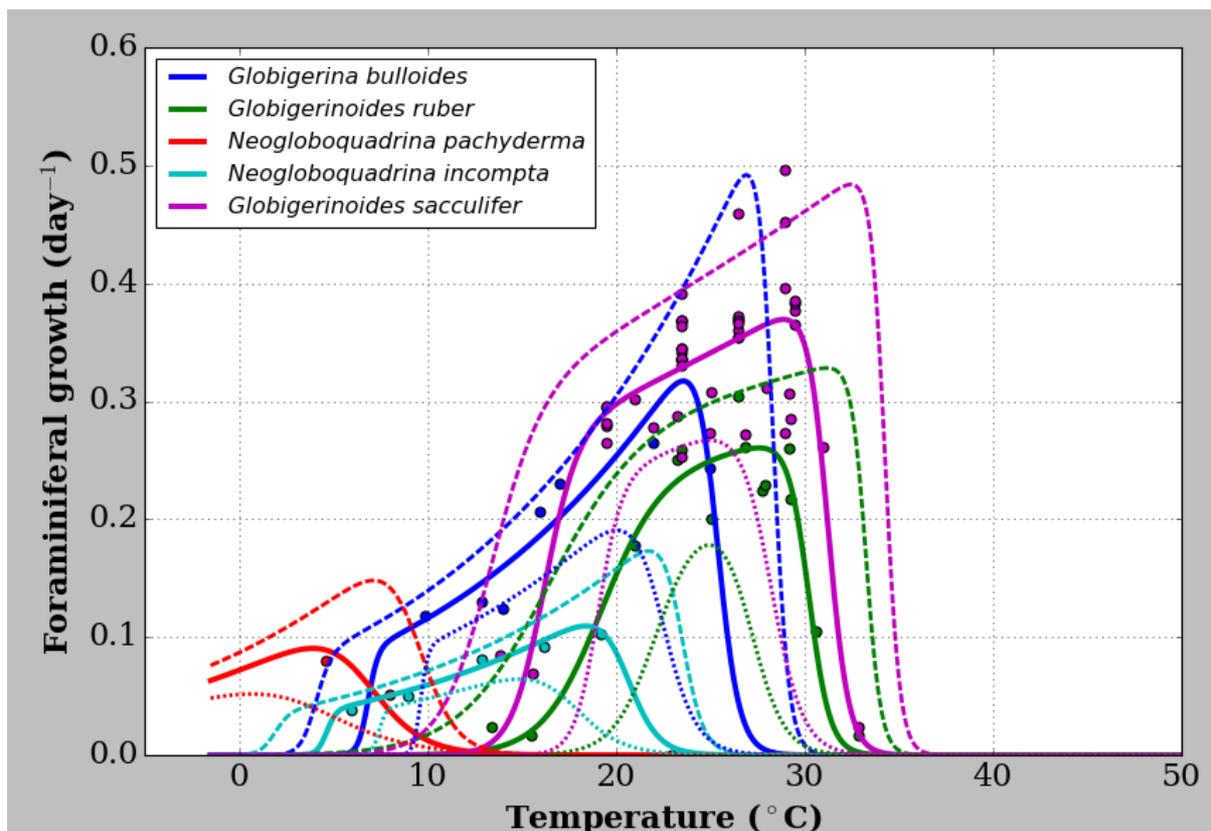
Action taken: we have revised the text in the area of former lines 5-9, page 4 to hopefully arrive at a better formulation. The revised text now reads:

"In the present study, we use the nominal values of equation (1) parameters given in Lombard et al. (2009) with the exception of TL for *G. bulloides*. Indeed, comparing the output of FAME with sediment trap data from the subpolar North Atlantic (Jonkers et al., 2013) showed that the nominal value of TL = 281.1K was likely too high, causing an absence of growth outside of the 3 summer months. In contrast, subpolar North Atlantic sediment trap data indicate that, on average over the four years of observations, significant *G. bulloides* fluxes prevailed from the end of June to the middle of November. We hence chose a value of TL closest to the nominal value of Lombard et al. (2009) that would allow the extension of the growing season into the fall in agreement with the data pattern. Hence a value of TL = 280 K was used for *G. bulloides* within FAME."

[Figure 1 page 4]: Fig 1 - I would add the original data as in this figure we lose the range of amplitude observed in cultures

Adding all the data into Figure 1 results in a rather messy figure as can be seen from the new Appendix figure A1, added nonetheless. Rather than reproducing separated panels as in the figure of Lombard et al. (2009) in the main text, we prefer to show how the different growth curves differ between species.

Action taken: We have added a figure to the Appendix that takes into account the comment of the reviewer for both the error analysis and the original data of Lombard, 2009, see new figure A1 as below.



[Figure 1 page 4]: Add reference to Lombard et al., 2009 in the figure caption
 Action taken: We thank reviewer #1 for pointing out this omission. We have corrected it.

[page 7] Calculation of the best-fitting maximum depth:

- What is the rationale for assuming that the Late Holocene equilibrium isotopic value would be the maximum depth in the model? Do you imply that the isotopic signature of foraminifera is biased toward the maximum calcification depth?

We do not imply that the isotopic signature of foraminifera is biased toward the maximum calcification depth. In the formulation of FAME, planktonic foraminifera have the possibility to grow anywhere between the sea surface and a so-called “maximum depth” (see equations (7) and (8)). This maximum depth of growth is an additional model parameter for each species. As explained in section 2.3, we have determined the values of these maximum depths of growth parameters, such that the agreement between computed and measured MARGO core top $\delta^{18}O$ is optimal. In doing so, we define the version of FAME that provides the best fit to core top isotopic data under present-day conditions. This approach is consistent with our goal of developing a module enabling model-data comparison with isotopic records from marine sediment cores (see our answer to reviewer #1’s first concern).

Action taken: We have added the following sentence to section 2.3 to clarify this: “The rationale behind this choice is to specifically design FAME to enable model-data comparison with isotopic records from marine sediment cores.”...

- *The range of the depths calculated by the model are very deep compared to observed living depth. The most extreme case is *G. bulloides*: if one uses the last textbook written by R. Schiebel & Hemleben (Modern planktonic foraminifera, 2017) “Ecology: *Globigerina bulloides* mainly dwells above the thermocline within the upper 60 m of the water column, and is a non-symbiotic species”. The ecology of this species is extremely problematic, and likely due to a combination of multiple cryptic species (eg Morard et al), I would tend to think that the cultures did not catch the overall variability in the dataset.*

We agree with reviewer #1 that the ecology of *G. bulloides* is problematic and that this difficulty is likely related to the existence of multiple cryptic species. There is indeed a wide variety of living depths reported in the literature. Note that our results are in good agreement with the observations of Rebotim et al. (2017) who provide very interesting data from vertically resolved plankton hauls in the subtropical eastern North Atlantic showing that living *G. bulloides* are found down to 300 m, with a median living depth of ~90 m.

Action taken: We have added 2 columns to Table 1 in order to document the observed living depths of the different species: column 6 gives the range of observed living depths for each species and column 7 lists the corresponding references. In addition, we have added a third column (column 5) giving the range of depths of maximum growth computed by FAME and shown in Fig. 4.

- *I do not understand how does *G. ruber* has a living range reaching $+\infty$. $+\infty$ is the mathematical result, which corresponds to a maximum living depth of 0 m in the present case. Re-reading the manuscript, we agree with the reviewer that the notation was confusing.*

Action taken: We have modified this in Table 1 to simplify.

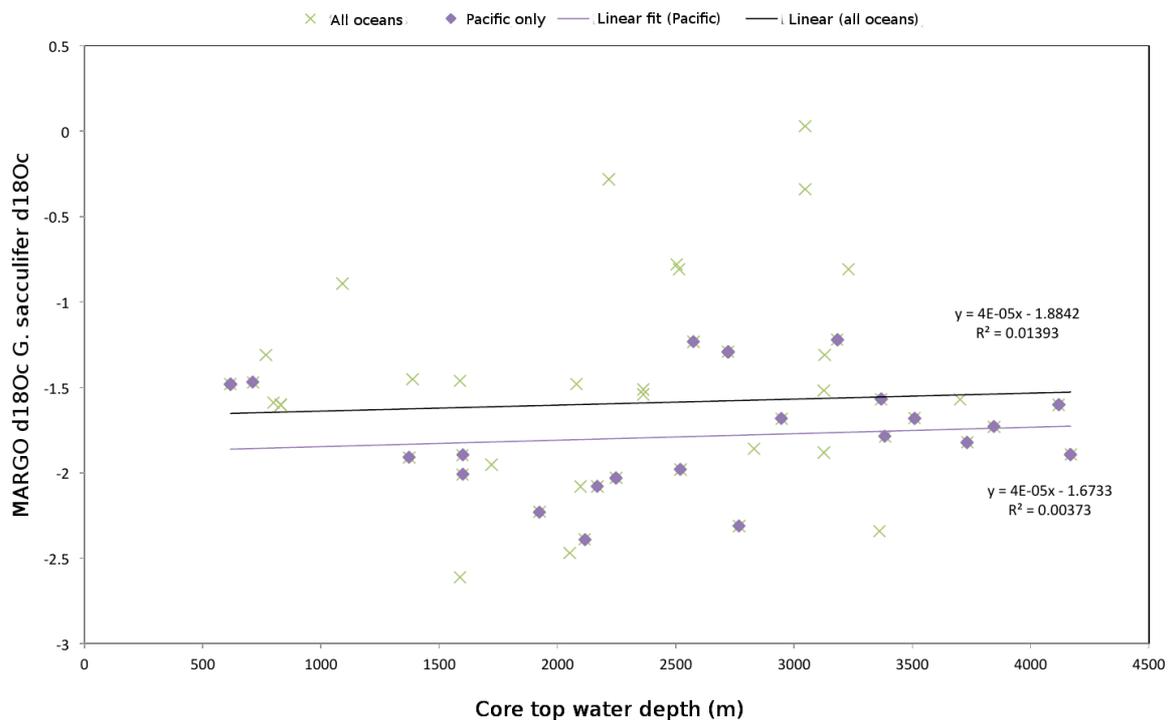
It would be extremely useful to have a figure putting into context the ranges (by comparing with Rebotim et al, for example even though this is a single figure).

We hope that the information added to Table 1 fulfills this role and will suffice to respond to the reviewers' concern.

*[lines 18-24 - page 7]: I do agree that those two effects (gametogenic calcite and dissolution) can somehow impact the signature of $d18O_c$ in *G. sacculifer*. Yet, as *G. sacculifer* is bearing symbionts, it does have to live in the euphotic zone, which is not the case in the model. I suggest that the authors make a more solid case by removing the deep Pacific sites that they supposed*

to be influenced by the dissolution to check whether the origin of this deep signature is indeed mostly gametogenic

To check this suggestion, we have verified that there is no dependence of *G. sacculifer* $\delta^{18}O_c$ on depth in MARGO data set, whether only the Pacific or the whole dataset was used (see figure below). Hence, it is unlikely that there is a dissolution signal in the $\delta^{18}O_c$ from *G. sacculifer* from MARGO. Also, the updated data added to Table 1 in response to previous comments shows that the calculated maximum depth of growth for *G. sacculifer* is in agreement with observations. Most notably, Rebotim et al, 2017 reports *G. sacculifer* being found alive down to 100 or 200 meters.



Action taken: we have removed the suggestion that the signal could be due to dissolution in the text of the revised version of the manuscript, previously on p. 7 (l. 20-24)

[lines 28-30 - page 7]: As the error scheme does not include the error linked to the calibration of the FORAMCLIM model. It would be extremely interesting to have an idea of the sensitivity of the FAME model to the max/min range observed in the data set

We do not use any calibrated relationship from the FORAMCLIM model, but simply the growth rate functions derived from culture measurements of Lombard et al., 2009. Here, we suppose that this is what the reviewer refers to by "the calibration of the FORAMCLIM model".

Action taken: As described in the response to the reviewer's second concern, we have derived alternative temperature curves from the Lombard et al., 2009 equations that cover a large range of growth rates and are close to the error curves given in Lombard et al. 2009's original contribution, now presented in the new figure A1. The impact of using such curves is very limited on the computed maximum depth range, and hence on the $\delta^{18}O_c$ computed. We have modified the text in the manuscript to account for the new figure and included a discussion of this error propagation.

*[line 31 - page 7]: I disagree with the statement that *G. sacculifer* and *G. bulloides* can be called "deeper dwellers". The output of the model does rank them as deeper dwellers, but out at sea, they do live mostly in surface to subsurface layers of the ocean (see for example Schiebel and Hemleben, 2017)*

We agree with the reviewer that the term "deeper dwellers" is probably inadequate in this context, even though *G. sacculifer* is reported to be found alive up to 100-200 meters (Rebotim et al, 2017).

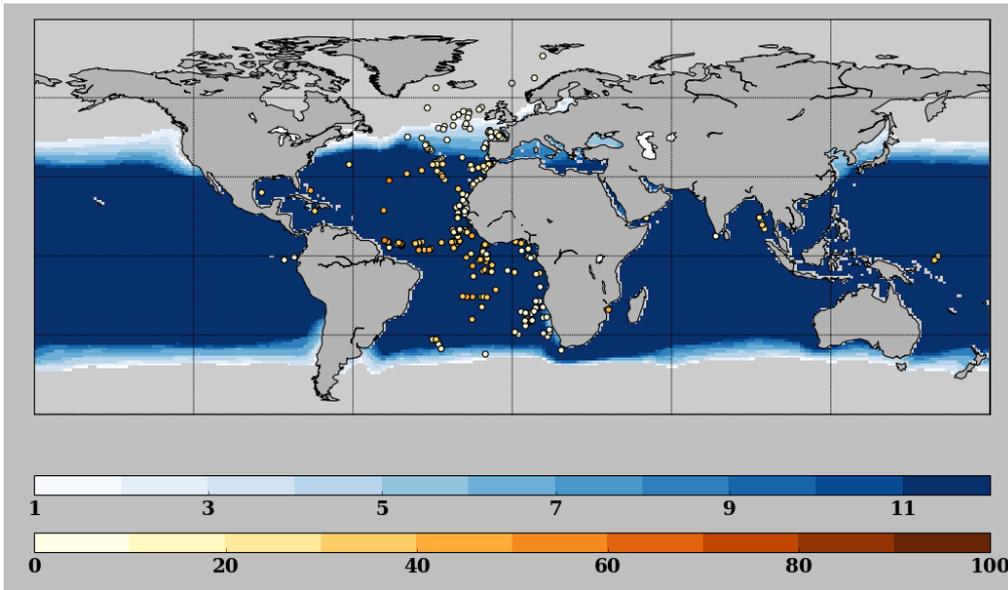
Action taken: the term "deeper dwellers" has been removed from the revised version of the manuscript. Ranges found in the literature have been added to the Table 1 to clarify where FAME stands with respect to what is found in the present-day oceans.

*[Table1 - page 8]: The range is definitely too deep for *G. bulloides* (ibid.)*

See our answer above.

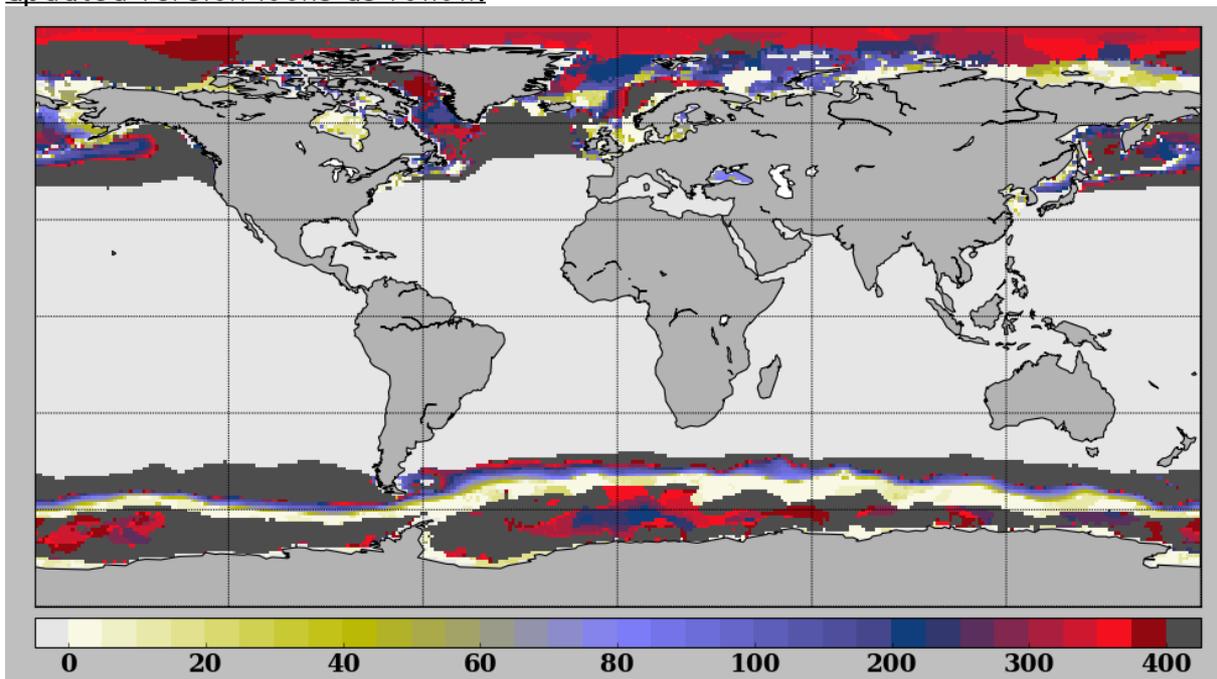
[Figure 3 - page 10]: I do not really understand what the figure does show : a percentage is highly depending of other species percentages - see my main comment #2. What is the rationale for the cutoff at 10% ? I do not see a physical nor biological rationale for this cutoff. I am wondering if the spatial coverage in the Indo Pacific Ocean is good enough to be included in the analysis as most core tops come the Atlantic Ocean.

We thank the reviewer for putting forward this point. As mentioned above, the revised version has been modified to improve the comparison between our presence/absence results and the abundances from the MARGO core top database. An example of such updated figure can be found below. The text of the manuscript has been modified accordingly.



[Figure 4 - page 11]: Consider changing the color scheme- rainbow does not give the best rendition.

Action taken: we have followed the advice of the reviewer and modified the color scheme. We hope it provides a better rendition of the results. The updated version looks as follow.



[page 12]: Add a latitudinal/depth plot, it would be more easy to read.

We do not quite understand what the reviewer means here. A latitudinal/depth plot of the depth referred to would merely give a white rectangle with a single line in it, giving the depth of maximum growth. Since a latitudinal/depth plot will require some form of averaging over longitudes, it will be equivalent to figure 5 albeit loosing the longitudinal contrasts. Since this does not seem very helpful, we assume that the reviewer had something else in mind?

Responses to Anonymous Referee #2

NOTA: The initial reviewer comments are in italic, our answers are in bold, action taken in the revised version of the manuscript are underlined.

The manuscript by Roche et al. summarises a noble and interesting attempt to improve our understanding of foram-based oxygen isotope data. The authors present a module ('FAME' – Foraminifers As Modeled Entities) they developed in order to predict changes in the oxygen isotope composition of the tests of different foraminifera species in response to changing climatic conditions. The model is forced by hydrographic data alone and incorporates a limited number of species-specific parameters, based on culture experiments, for each of five foraminifera species to describe their growth and habitat. Essentially, the model attempts to account for the effect of foraminifera depth habitat on their oxygen isotope composition, and to predict their oxygen isotope composition accordingly, as well as their presence/absence. To test their model they apply its methodology to reference datasets, namely the MARGO Late Holocene dataset. It is an interesting and concise presentation of their work and well-structured. I believe it will greatly contribute to research within the foraminifera and palaeoclimate community.

We are thankful for these positive and nice words on our work.

When such models are developed it's important to have some measure of their sensitivity. For that reason, I believe that error propagation in the model should be addressed given that several of the input parameters have errors associated with them.

We thank the reviewer for this remark. In response to this concern and to a similar concern expressed by the other reviewer, we have now included a discussion of the propagation of the errors in the Lombard growth equations into the maximum depth calculations and further in the distribution error of the previous figure 2, giving computed error arising from the propagation of the initial input parameter errors.

Action taken: In response to the reviewer and the other reviewer who had a similar request, we have tested a large range for the Lombard et al., 2009 growth rate curves and propagated the error in our results. The range tested are now presented in the new figure A1. Additions were made in the text where appropriate to describe these tests. The main message is that our results are very robust to such changes with an impact on the mean difference between computed and MARGO $\delta^{18}O$ below 0.1 per mil for all species.

*Secondly, and this may sound pedantic but the authors may consider changing *Globigineroides sacculifer* to *Trilobatus sacculifer* as per its genus reassignment by Spezzaferri et al. (2015). I will leave this to the authors' discretion as there are arguments for retaining *G. sacculifer* given that this is still the most commonly used name for this species. However, over time this will obviously*

change and the authors may want to introduce the new (and more taxonomically up-to-date) name.

We thank the reviewer for this comment that we have taken into account as suggested.

Action taken: The revised version makes reference to *Globigerinoides sacculifer* as the forma name (including *Globigerinoides trilobus*) in the first instance and uses *Trilobatus sacculifer* throughout.

In terms of convention, there are several instances where the author refers to oxygen isotopes incorrectly. For example, p1, line 16, the authors describe the 'oxygen-18 value', or in line 21, 'calcite oxygen-18', or elsewhere as 'species' oxygen-18' (e.g. p3, line 1). This is very pernicky but there are quite strict guidelines for isotopic notation. I suggest the authors double check their usage and perhaps refer to ratios rather than oxygen-18 content/signal as it's more in line with the literature.

Action taken : we have checked thoroughly the revised manuscript for mis-use of oxygen isotopes and have corrected them following the suggestion of the reviewer.

On page 7, line 16-17, you describe how you used a 0.1 per mil 'encrustation term'. Could you possibly elaborate as to where that value came from? It would make it easier for the reader as it seems a little arbitrary at present.

We have chosen a 0.1 ‰ value for the encrustation term in order to simulate maximum depths in agreement with the literature. The simulated depth of maximum growth shown in Fig. 4 and now summarized in the revised Table 1 do indeed match very well the available observations. For instance, Fig. 4e shows a deepening of *N. pachyderma* depth of maximum growth from 0-30 m in the Greenland Sea to 100-350 m in the Norwegian Sea, in agreement with the apparent calcification depths reconstructed by Simstich et al. (2003).

Action taken : we have added a few lines to summarize this to the text accompanying Table 1.

*Also, the authors should mention wherever necessary that species with symbionts e.g. *G. sacculifer* (*T. sacculifer*) cannot live at depths greater than the photic zone, as is hinted at on page 7, line 20.*

We agree with the reviewer that it is important to explicitly mention that *T. sacculifer* bears symbionts, like *G. ruber*. We would like nonetheless to emphasize a few aspects. Experimental determination by Spero suggests that the removal of symbionts drastically reduces the life-span of the host, therefore the reviewer is correct that symbiont bearing foraminifera should ideally inhabit the photic zone. However, the irradiance required for these

symbionts is not known and hence we cannot infer maximum depth from that perspective. And finally the host is known, prior to gamete release, to be symbiont barren therefore there is a portion of growth that can be below the photic zone.

Action taken : we have modified the text p. 7 to explicitly mention that T. sacculifer bears symbionts.

Some more specific comments:

Action taken : specific comments have been corrected following the suggestions of the reviewer but for one instance.

Page 1, line 17. Perhaps use 'reflected' rather than 'favoured'.

Line 20. Use 'throughout the year' rather than 'along the year' as this makes more grammatical sense.

OK

Page 2, line 7. I would consider adding a few more references here as several other studies have been done looking at carbonate ion and symbiotic effects. Pearson et al. (2012) gives a good summary of work up to that point.

OK

Line 26. Change 'being' to 'to be'

OK

*Page 3, line 19. Italicise *N. pachyderma*.*

OK

Page 5, line 21. Change 'weighs' to 'weight'?

No, weighs is what we mean here.

Page 8, line 2. Use a different word to 'ascertain' as this doesn't make sense in the context.

We replaced it by « check »

FAME (v1.0): a simple module to simulate the effect of planktonic foraminifer species-specific habitat on their oxygen isotopic content

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Abstract. The oxygen-18 ~~signal~~ to oxygen-16 ratio recorded in fossil planktonic foraminifer shells has been used for over 50 years in many geoscience applications. However, different planktonic foraminifer species generally yield distinct ~~oxygen-18~~ signals, as a consequence of their specific living habitats in the water column and along the year. This complexity is usually not taken into account in data – model integration studies. To overcome this shortcoming, we developed the FAME (Foraminifers
5 As Modeled Entities) module. The module predicts the presence or absence of commonly used planktonic foraminifers, and their oxygen-18 values. It is only forced by hydrographic data and uses a very limited number of parameters, almost all derived from culture experiments. FAME performance is evaluated using MARGO Late Holocene planktonic foraminifer calcite oxygen-18 and abundances data sets. The application of FAME to a simple cooling scenario demonstrates its utility to predict changes in planktonic foraminifer oxygen-18 to oxygen-16 ratio in response to changing climatic conditions.

10 1 Introduction

Since the early work of Emiliani (1955), oxygen-18 isotopic abundance in calcite fossil foraminifer tests recovered from oceanic sediments has been widely used to reconstruct the past variations in oxygen-18 content of seawater as well as its temperature, the two main variables that affect the ~~content-ratios~~ of oxygen-18 in calcite to oxygen-16 in calcite (hereafter $R^{18}O_c$). The recognition that different species of foraminifers from the same sediment-core yielded different ~~oxygen-18~~ $R^{18}O_c$
15 was made early on (e.g. Duplessy et al., 1970; Lidz et al., 1968; Berger, 1969; Fairbanks and Wiebe, 1980; Deuser, 1987), though it was ~~(Emiliani, 1954, 's)~~ Emiliani (1954) attempt to relate depth habitat of foraminifers to the density of seawater that led to the revelation that the ~~oxygen-18 value~~ $R^{18}O_c$ recorded by fossil foraminifers likely ~~favoured-reflected~~ the average depth habitat of individual species. Through in situ water column sampling via opening-closing plankton nets ~~(Jones, 1967)~~,
20 Jones (1967) through faunal abundance counts corroborated the depth habitats ~~of Emiliani (1954) that Emiliani (1954) inferred through isotopic analysis~~. However, increased plankton sampling (Bé and Tolderlund, 1971) and the advent of the sediment trap have shown that different species have different living habitats in the water column and ~~along-throughout~~ the year and that in some cases the foraminiferal ~~oxygen-18 content~~ $R^{18}O_c$ presents an offset with respect to equilibrium calcite oxygen-18 to

oxygen-18 ratio (Mix, 1987; Bijma and Hemleben, 1994; Ortiz et al., 1995; Kohfeld et al., 1996; Bauch et al., 1997; Schiebel et al., 2002; Simstich et al., 2003; Mortyn and Charles, 2003; Rebotim et al., 2017; Jonkers and Kucera, 2015). This complexity is usually not accounted for in paleoceanographic studies. Instead, the approximation is often made that each planktonic foraminifer species has an apparent living depth – defined as the water depth where equilibrium calcite formation would approximate their measured calcite ~~oxygen-18~~ $R^{18}O_c$ value in the water column – that can vary by hundreds of meters from one region to another. To correctly interpret the wealth of information coming from the calcite oxygen-18 to oxygen-16 ratio record, especially when multiple species are measured at the same geographical location, there is a need to take into account the impact of depth habitat and growth season on each species calcite oxygen-18. Minor contributors to the resultant calcite ~~oxygen-18 signal~~ $R^{18}O_c$, such as carbonate ion concentration (~~Spero et al., 1997~~) (Spero et al., 1997; Pearson, 2012) and symbionts (e.g. Ezard et al., 2015; Spero, 1998) may modulate the absolute values making species specific comparisons problematic, however their overall contribution may also covary and/or auto-correlate with temperature and latitudinal gradients, therefore this paper focuses on the major components only.

In recent years, the development of water isotope enabled ocean models has allowed the simulation of the two variables at the root of the calcite ~~oxygen-18~~ $R^{18}O_c$ record: seawater temperature and oxygen-18. ~~It is thus tempting to make one additional step and attempt to compute a calcite oxygen-18 content that can readily be compared with the foraminiferal record abundance.~~ So far, ~~oxygen-18 water isotope based~~ model-data studies have generally compared planktonic oxygen-18 ratios to equilibrium calcite ~~oxygen-18~~ $R^{18}O_c$ values. The equilibrium calcite ~~oxygen-18 ratio~~ in that case is computed from annual averaged seawater temperatures and oxygen-18 abundance taken either at surface or averaged over the upper 50 to 100 meters of the water column (e.g. Caley et al., 2014; Werner et al., 2016). To go one step further, it is necessary to account for species-specific habitat when computing calcite ~~oxygen-18~~ $R^{18}O_c$. The FAME (Foraminifers As Modeled Entities) approach is underpinned by two arguably simple principles: 1) that the weighting due to species-habitat is reflected in the calcite oxygen-18 ratio record and 2) that the model derived should be kept simple to allow its offline application to the output of climatic models without the need of re-running the entire climate model simulations.

After having developed the FAME methodology, we found out that the idea was already present in a theoretical framework in Mix (1987) and in one following study (Mulitza et al., 1997), in the latter referred to as *Mix's model*. The most notable difference between the early study of Mix (1987) and the present one is the actual definition of the weighting functions. Mix (1987) assumed them ~~being to be~~ simple Gaussians whereas we build ours on the laboratory culture-based equations of planktonic foraminifer growth rates as a function of temperature given in Lombard et al. (2009).

Since the early work of Mix (1987), other methods were developed to approach the species-specific complexity of planktonic foraminifers. Schmidt (1999) developed a simple module to compute planktonic foraminifer ~~oxygen-18 in an oxygen-18~~ $R^{18}O_c$ in an water isotope enabled global ocean model. However, in his approach, water depths at which planktonic foraminifers calcify and their seasonal growth patterns are fixed for each species. Therefore, such a module can not properly account for the

impact of climatic changes on foraminifer living conditions. Fraile et al. (2008) and Lombard et al. (2011) developed models predicting the abundance of common planktonic foraminifer species in response to hydrographic data and food concentration. Both these models predict the relative abundances of the different simulated foraminifer species, an information which is not needed to assess individual species oxygen-18 but entails a large number of empirical parameters, i.e. 21 and 15 parameters per planktonic foraminifer species in Fraile et al. (2008) and Lombard et al. (2011) respectively. Moreover, Fraile et al. (2008) derive the sensitivity of each species with respect to temperature from sediment-trap data, so that their model can only account for changes in seasonality, and not in depth habitat. In contrast, the FORAMCLIM model (Lombard et al., 2011) predicts both season and water depth of each species potential maximum abundance. In fact, FAME can be viewed as a simplified version of FORAMCLIM (only retaining FORAMCLIM's computation of growth rates as a function of temperature), expanded by a mechanistic calculation of species-dependent calcite oxygen-18. FAME is only forced by hydrographic data, and only uses 6 parameters per planktonic foraminifer species that are all derived from culture experiments, plus one parameter accounting for the effect of the accretion of a calcite crust by *N. pachyderma*. Taken together, these characteristics make FAME a uniquely simple and robust model designed to predict changes in the oxygen-18 to oxygen-16 ratio of commonly used planktonic foraminifers in response to changing climatic conditions.

15

2 Methodology

The calcite oxygen-18/oxygen-16 ratio (reported in $\delta^{18}\text{O}_c$, in per mil versus V-PDB in what follows) of planktonic foraminifers is intrinsically a 4-dimensional signal, acquired at a specific season (time dimension), over a specific depth range and area in the ocean (space dimensions). The mean $\delta^{18}\text{O}_c$ signal measured on a sample composed of a number of individual foraminifer shells of one species is thus the integration of many different single $\delta^{18}\text{O}_c$ paths in this 4-dimensional space. If we suppose that the sampled population is representative of the living conditions of the species, it is thus likely that there is an over-sampling of the areas and time representing favourable growth conditions and an under-sampling of area and time with unfavourable growth conditions. Hence, a reasonable way to predict the mean $\delta^{18}\text{O}_c$ of a foraminifer sample constituted of a number of individuals is to weight the oceanic conditions by the growth rate of each individual. The predicted $\delta^{18}\text{O}_c$ is then a weighted sum of these conditions in space and time.

25

2.1 Basic equations

To define the effect of the habitats of the different foraminifer species, we first consider a subset of the growth functions derived by Lombard et al. (2009) from culture experiments (Figure 1) following the original formulation of Kooijman (2000). For each

foraminifer species k considered, the growth function is written as:

$$\mu(T, k) = \frac{\mu(T_1, k) \cdot \exp\left(\frac{T_A}{T_1} - \frac{T_A}{T}\right)}{1 + \exp\left(\frac{T_{AL}(k)}{T} - \frac{T_{AL}(k)}{T_L(k)}\right) + \exp\left(\frac{T_{AH}(k)}{T_H(k)} - \frac{T_{AH}(k)}{T}\right)} \quad (1)$$

where $\mu(T, k)$ is the growth rate at temperature T for the species k , $\mu(T_1, k)$ is the growth rate for a chosen reference temperature T_1 (20°C or 293K), T_A is the Arrhenius temperature, $T_H(k)$ and $T_L(k)$ define the upper and lower boundaries of the growth tolerance range for the species k , $T_{AH}(k)$ and $T_{AL}(k)$ the Arrhenius temperatures for the decrease in growth rate respectively above and below these boundaries for species k (Lombard et al., 2009). In the present study, we use the nominal values of equation (1) parameters given in Lombard et al. (2009) with ~~one exception: we use TL = 280K instead of 281.1K for *G. bulloides* in order to improve the representation of the seasonal cycle. When compared the exception of TL for *G. bulloides*.~~ Indeed, comparing the output of FAME with sediment trap data from the subpolar North Atlantic (Jonkers et al., 2013), the use of nominal values does indeed lead to no showed that the nominal value of TL = 281.1K was likely too high, causing an absence of growth outside of ~~July, August and September, whereas the data show fluxes larger than 5 specimens per m² per day~~ the 3 summer months. In contrast, subpolar North Atlantic sediment trap data indicate that, on average over the four years of observations, significant *G. bulloides* fluxes prevailed from the end of June to the middle of November, ~~on average over the~~ four years of observations. We hence chose a value of TL closest to the nominal value of Lombard et al. (2009) that would allow the extension of the growing season into the fall in agreement with the data pattern. Hence a value of TL = 280 K was used for *G. bulloides* within FAME.

We compute the $\mu(T, k)$ coefficient for all values of $T(x, y, z, t)$ in the world ocean, T being a 4-D variable of space and time. This, in turn gives us the growth rate of the different foraminifer species considered in a 4-dimensional space as:

$$\mu(T, k) = \mu(T(x, y, z, t), k) \quad (2)$$

To avoid numerical issues in the code, we limit the value of $\mu(T, k)$ on the low end as follow:

$$\begin{aligned} \mu'(T(x, y, z, t), k) &= \mu(T, k) && \text{if } \mu(T, k) \geq 0.1 \cdot \max_T \mu(T, k) \\ &= 0 && \text{otherwise} \end{aligned} \quad (3)$$

25

Given a 4-dimensional input field for oceanic temperatures and $\delta^{18}\text{O}$ of seawater, the equilibrium inorganic calcite $\delta^{18}\text{O}$ value can be computed from the temperature equation of Kim and O'Neil (1997). Here we use the quadratic approximation of that equation given in (Bemis et al., 1998):

$$T = T_0 - b \cdot (\delta^{18}\text{O}_c - \delta^{18}\text{O}_{sw}) + a \cdot (\delta^{18}\text{O}_c - \delta^{18}\text{O}_{sw})^2 \quad (4)$$

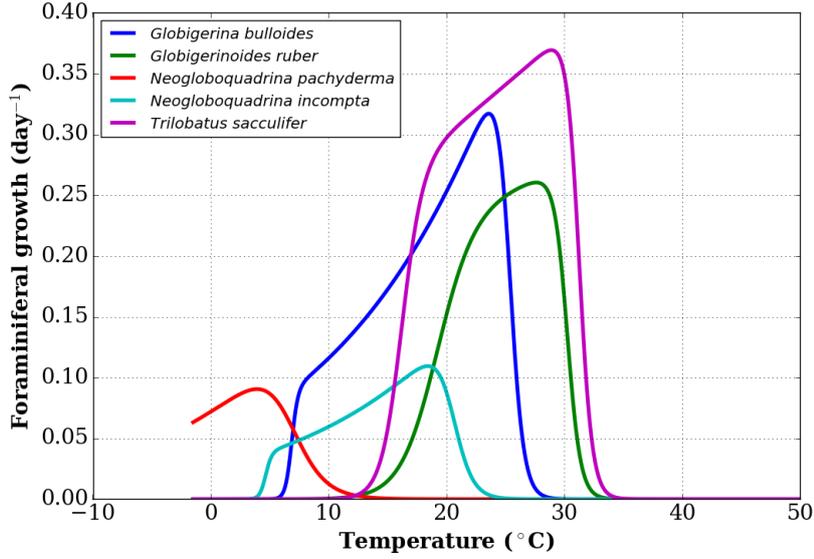


Figure 1. Growth functions corresponding to equation (1) over the full temperature range [considered, replotted from Lombard et al. \(2009\)](#).

where $T_0 = 16.1^\circ\text{C}$, $b = -4.64$ and $a = 0.09$, $\delta^{18}\text{O}_{sw}$ is the seawater $\delta^{18}\text{O}$. Since the seawater temperature ($^\circ\text{C}$) and $\delta^{18}\text{O}_{sw}$ (per mil) are inputs, we can solve this equation to determine the value of $\delta^{18}\text{O}_c$.

With the discriminant of the second degree equation being:

$$\Delta = b^2 - 4a \cdot (T_0 - T_{sw}) \quad (5)$$

5 it becomes:

$$\delta^{18}\text{O}_{c,eq} = \frac{-b - \sqrt{\Delta}}{2a} + \delta^{18}\text{O}_{sw} - 0.27 \quad (6)$$

where the constant, 0.27, correction (Hut, 1987) accounts for the difference in the reference scales of seawater (permil versus V-SMOW) and calcite (permil versus V-PDB).

10 In previous studies, we and others (Caley et al., 2014; Werner et al., 2016) computed the above $\delta^{18}\text{O}$ equilibrium value, averaged over time and the surface layer (typically the first 50 meters) to compare model results and measured $\delta^{18}\text{O}_c$ from planktonic foraminifers. In the following, we will refer to this method as the "old method", written formally as:

$$\delta^{18}\text{O}_{c,om}(x, y) = \frac{1}{n_t} \sum_{t=1}^{n_t} \frac{1}{n_z} \sum_{z=0}^{z_b} \delta^{18}\text{O}_{c,eq}(\delta^{18}\text{O}_{sw}(x, y, z, t), T_{sw}(x, y, z, t)) \quad (7)$$

where n_t is the number of time steps, n_z the number of vertical levels and z_b the maximum depth.

15 The formalism used clearly expresses the fact that the old method is not species-specific nor season-specific since all time steps

and vertical levels are averaged with the same weight. In contrast, the FAME method weighs the $\delta^{18}\text{O}_c$ both in time and in the horizontal and vertical space according to the population abundances using the foraminifer growth formula (1). We thus write:

$$\delta^{18}\text{O}_{c, fm}(x, y, k) = \frac{1}{n_t} \sum_{t=1}^{n_t} \frac{1}{n_z} \sum_{z=0}^{z_b(k)} \delta^{18}\text{O}_{c, eq}(\delta^{18}\text{O}_{sw}(x, y, z, t), T_{sw}(x, y, z, t)) \mu'(T(x, y, z, t), k) \quad (8)$$

5 where $z_b(k)$ is dependent on the species and constrained by core-top data (see below).

Using this set of equations, for any given seawater temperature and $\delta^{18}\text{O}$ provided as a 4-dimensional field and a given species k , we compute this species $\delta^{18}\text{O}_c$ over x, y (latitude, longitude) coordinates.

10 It should be clearly understood that this approach is not able and does not attempt to determine the relative abundances of the different species. Instead FAME provides a simplified approach to compute the $\delta^{18}\text{O}_c$ of a generic population of foraminifers if environmental conditions permit its growth. From a model – data perspective, this approach enables one to compute the calcite $\delta^{18}\text{O}$ for a given species, were it to exist in the sedimentary record. Due to the limitations set by equation 3, no calcite isotopic content is computed if μ' is zero and hence these areas will be masked out in the following.

15

2.2 Growth function uncertainties

In the original work of Lombard et al. (2009), 95% confidence intervals were shown for the per species growth functions, but no equation was given for them. In order to nonetheless estimate the bias introduced in FAME by using the given functions, we combined the different possible values for the parameters of the growth functions to obtain functions that are close to the 95% confidence intervals mentioned for most species and larger than the 95% confidence intervals for others. This result in an upper and lower growth function for each species, as shown in Figure A1, where the original datapoints of Lombard et al. (2009) is also given.

20

2.3 Reference datasets

In an attempt to validate the FAME approach, we apply its methodology to reference datasets, close to present-day observations. The first necessary step is the computation of a reference $\delta^{18}\text{O}_c$ field as obtained when forced by climatological data. For seawater temperature, we use the World Ocean Atlas 2013 (Locarnini et al., 2013) data at a monthly resolution. Considering that there is no equivalent seawater oxygen-18 gridded dataset available in the World Ocean Atlas fields and that the existing GISS gridded dataset (LeGrande and Schmidt, 2006) presents large deviations with respect to the seawater oxygen-18 ($\delta^{18}\text{O}_{sw}$) raw data in numerous locations, we derived a $\delta^{18}\text{O}_{sw}$ dataset based on seawater salinity to $\delta^{18}\text{O}_{sw}$ relationships. This dataset is built in two steps: a) derivation of regional $\delta^{18}\text{O}_{sw}$ – salinity relationships from GISS $\delta^{18}\text{O}_{sw}$ and salinity (Schmidt

25

30

et al., 1999) clustered by oceanic regions and b) computation of a $\delta^{18}\text{O}_{sw}$ field based on the World Ocean Atlas 2013 (Zweng et al., 2013) salinity fields. The resulting field is at the World Ocean Atlas spatial resolution and is used as reference seawater oxygen-18 in the following. Details on the derivation of the $\delta^{18}\text{O}_{sw}$ dataset are given in Appendix A.

5 As an independent test of the FAME results, we use the planktonic $\delta^{18}\text{O}_c$ measurements from the MARGO Late Holocene dataset (Waelbroeck et al., 2005) restricted to high chronozone quality levels (i.e. levels 1 to 4). A few errors have been corrected in the published data set: these concern the suppression of 10 *Neogloboquadrina incompta* (or *N. pachyderma right*) data points from the Nordic Seas where only *Neogloboquadrina pachyderma* should have been listed, and one outlier *N. pachyderma* value with no age control that was erroneously listed as having a level 4 chronozone quality. The corrected version of MARGO Late
10 Holocene planktonic oxygen-18 data set is available as supplementary material.

As a result, the dataset used in the present study contains 248 values for *Neogloboquadrina pachyderma*, 128 values for *Globigerina bulloides*, 59 values for *Neogloboquadrina incompta*, 135 values for *Globigerinoides ruber* and 51 values for [Globigerinoides sacculifer](#). [In the remainder of the manuscript and following the genus reassignment of Spezzaferri et al. \(2015\), we will refer to the latter as *Trilobatus sacculifer*.](#)

15

2.4 Calculation of the best-fitting maximum depth per foraminifer species

In equation 8, the maximum depth of integration per foraminifer species, $z_b(k)$, is a free parameter and needs to be determined. We have chosen to calculate it as the depth where the $\delta^{18}\text{O}_c$ simulated by FAME driven by the World Ocean Atlas 2013 temperature and derived seawater $\delta^{18}\text{O}$ datasets is closest on average to MARGO Late Holocene $\delta^{18}\text{O}_c$ data. [The rationale behind
20 this choice is to specifically design FAME to enable model-data comparison with isotopic records from marine sediment cores.](#)

To determine the optimal value of $z_b(k)$, we repeated successive runs of FAME with values of z_b ranging from 1,500 meters till the surface along the standard World Ocean Atlas vertical grid. The only difference between the different species at this stage are the species-specific terms in the equations presented and the each species data from the MARGO Late Holocene set. The
25 results obtained through this optimization procedure are given in Table 1. The maximum depths of calcification derived this way are remarkably close to what is known from the ecology of *G. ruber*, *N. incompta*, *T. sacculifer* and *G. bulloides* (Berger, 1969; Bijma and Hemleben, 1994; Ortiz et al., 1995; Schiebel et al., 2002; Mortyn and Charles, 2003; Rebotim et al., 2017). Only in the case of *N. pachyderma*, the computed value of z_b was much too deep (900 meters) with respect to what studies based on opening-closing plankton nets show. Also, plankton hauls studies have revealed that whereas *N. pachyderma* seems
30 to grow at relatively shallow depth, i.e. where the chlorophyll maximum is found, a calcite crust is added between 50 and 250 m, which greatly increases its mass (Kohfeld et al., 1996; Simstich et al., 2003). As a consequence, the $\delta^{18}\text{O}$ of *N. pachyderma* collected in deep sediment traps and in surface sediment is systematically heavier than that of living non-encrusted *N. pachyderma*. To account for this effect we have added a 0.1 per mil "encrustation term" to our calculation of *N. pachyderma* calcite $\delta^{18}\text{O}$ weighted by that species culture-based growth rates. ~~The relatively deeper habitat depth derived for *T. sacculifer* versus~~

~~*G. ruber* (maximum calcification depth estimates range from -200 to -75, best estimate = -100) could result from the increase in $\delta^{18}\text{O}$ due to accretion of gametogenic calcite. The encrustation term value has been chosen in order to simulate maximum depths in agreement with the literature. *N. pachyderma* simulated depth of maximum growth (Fig. 4e and Table 1) does indeed match very well the available observations. For instance, Fig. 4e shows a deepening of *N. pachyderma* depth of maximum growth~~

5 ~~from 0-30 m in the Greenland Sea to 100-350 m in the Norwegian Sea, in agreement with the apparent calcification depths reconstructed by Simstich et al. (2003).~~

~~Concerning *T. sacculifer*, although this species bears symbionts, and thus lives in the photic zone like *G. ruber*, it is known to produce calcite with higher $\delta^{18}\text{O}$ values than *G. ruber*. These heavier $\delta^{18}\text{O}$ values are thought to result from the accretion of gametogenic calcite (for a certain unknown fraction of the shell mass) or from the precipitation of its final sac-like chamber deeper in the water column. In addition, some of the *T. sacculifer* $\delta^{18}\text{O}_c$ data were obtained from deep Pacific cores in which dissolution might have induced a 0.2 to 0.5 enrichment in $\delta^{18}\text{O}$. Dissolution biases or contribution of a large anomalous signal to individual shells $\delta^{18}\text{O}_c$, as a terminal feature from deeper in the water column, may reconcile the discrepancy between apparent living depths recorded by water column sampling and sediment fossil assemblages. Duplessy et al. (1981). This characteristic explains the deeper habitat depth computed for *T. sacculifer* versus *G. ruber* (maximum calcification depth estimates range from -200 to -75 m, best estimate = -100 m). Note that a deeper habitat for *T. sacculifer* than *G. ruber* is in agreement with observations (Table 1).~~

10

15

2.5 Evaluation of the model performance

2.5.1 Error distribution

Since the depth parameter was constrained using the MARGO Late Holocene dataset by error minimization, it is not surprising

20 that the errors obtained with FAME are very small in average for each species considered (Figure 2). The error distribution obtained with FAME is very similar to the one obtained with the simple surface equilibrium assumption for the two species closest to the surface (*G. ruber* and *N. incompta*). For deeper dwellers (*T. sacculifer*, *G. bulloides* & *N. pachyderma*) FAME results are better than those obtained with the old method, as expected since deeper layers in the ocean are accounted for.

2.5.2 Robustness of results

25 ~~To test the robustness of our calibration in depth or error distribution, we performed a full set of additional analyses using the lower and upper growth functions as presented in figure A1, introduced hereabove.~~

~~Regarding depth calibration, we find our results to be largely insensitive to the use of these upper-bound and lower-bound values for the growth functions. Specifically, the uncertainty in the maximum growth depth is largest on *N. pachyderma* (range of 475 to 600 meters) and *G. bulloides* (400 to 450 meters). It is somewhat smaller for *T. sacculifer* (100 to 125 meters) and~~

30 ~~*N. incompta* (60 to 65 meters). There is no impact for *G. ruber*.~~

~~Another method to check the impact of the uncertainty in the growth functions on our $\delta^{18}\text{O}_c$ results is by keeping maximum computed depths constant and looking at the impact of the growth function on the mean difference between simulated and~~

Table 1. Maximum depth per species as computed from the optimization procedure. z_b is the depth yielding the smallest difference to the Late Holocene MARGO data (Waelbroeck et al., 2005). We computed a confidence interval $[\sigma_{z_d}^\uparrow, \sigma_{z_d}^\downarrow]$ corresponding to a change of ± 0.1 per mil in the mean error. The ∞ sign indicates that no value of z_b within the range $[0, -1500]$ yields the desired ± 0.1 per mil change.

Species	z_b (m)	$[\sigma_{z_d}^\uparrow, \sigma_{z_d}^\downarrow]$ (m)	Nb points	obs. living range (m)	References
<i>G. ruber</i>	-10	$[\infty, -30]$ $[0, -30]$	130	$0-120$	Ganssen and Kroon (2000); Anand et al. (2003) Kuroyanagi and Kawahata (2004); Farmer et al. (2007)
<i>N. incompta</i>	-65	$[-35, -150]$	60	$0-200$	Pak and Kennett (2002); Pak et al. (2004) Kuroyanagi and Kawahata (2004); von Langen et al. (2005)
<i>T. sacculifer</i>	-100	$[-75, -200]$	46	$0-200$	Ganssen and Kroon (2000); Anand et al. (2003) Kuroyanagi and Kawahata (2004); Farmer et al. (2007)
<i>G. bulloides</i>	-400	$[-100, -\infty[$	123	$0-300$	Bauch et al. (2002); Ganssen and Kroon (2000) Pak and Kennett (2002); Pak et al. (2004) Kuroyanagi and Kawahata (2004)
<i>N. pachyderma</i>	-550 ¹	$[-275, -900]$	244	$0-500$	Kohfeld et al. (1996); Bauch et al. (1997) Bauch et al. (2002); Simstich et al. (2003) Kuroyanagi and Kawahata (2004)

¹ an encrustation term of +0.1 per mil is taken into account in the case of *N. pachyderma* (see text)

MARGO $\delta^{18}\text{O}_c$ values shown in figure 2. When doping so (not shown) the resulting change is lower than 0.1 per mil for all individual species. It therefore shows that our results are very robust and largely insensitive to the errors arising in the growth functions used (Lombard et al., 2009).

2.5.3 Geographical distribution

5 To further ascertain-check our methodology against the MARGO Late Holocene dataset we compare the zone of presence of each species predicted by FAME (grossly determined by μ') with the observed presence-reported abundances in the MARGO dataset (restricted to chronology quality values 1-4). As noted above, we cannot predict the relative abundance of each species. However, the method determines the species absence or presence.

The results presented in Figure 3 show that, despite the exceptional simplicity of our approach, FAME predicts relatively well
10 the spatial limits of the area occupied by each species. The two species whose presence distribution is best predicted are again

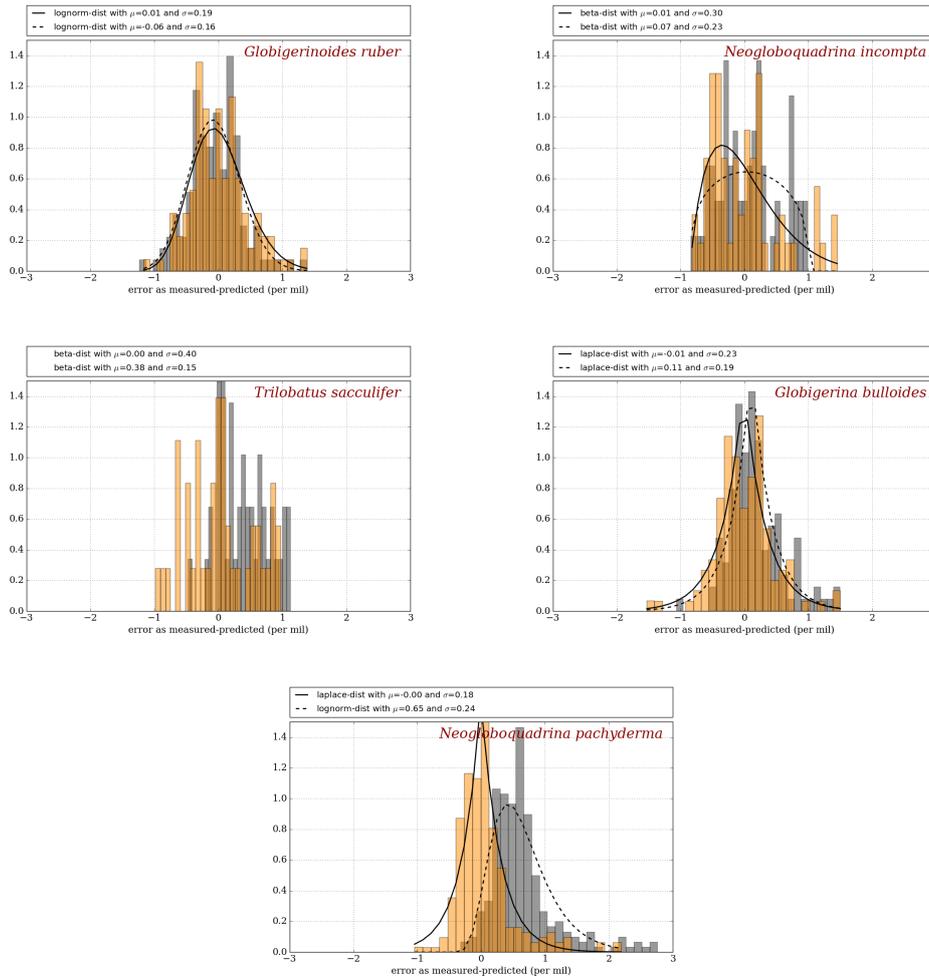


Figure 2. Error distribution for the "old method" (grey) and the "FAME method" (orange) using climatological datasets as compared to MARGO Late Holocene dataset (Waelbroeck et al., 2005). Best fitting distributions are calculated and plotted as a solid line for the "FAME method" and as a dashed line for the "old method", except for *T. sacculifer*, for which the small number of available data points yields a poor fit both for FAME and the old method. The mean and deviation are given for FAME and the old method at the top of each panels.

G. bulloides and *N. pachyderma*, both showing a quite remarkable model-data match of the transition zones from presence to absence. *N. incompta* and *G. ruber* also show quite satisfactory results, with only a few outliers in specific areas: FAME computes too extended coverages of *N. incompta* in the Gulf of Guinea and of *G. ruber* along the coast of Namibia.

- The computed spatial coverage of *T. sacculifer* is slightly too extended towards high northern and – possibly – southern latitudes. The very low number of high quality dated datapoints in the latter area prevents a definitive conclusion. Also, specific

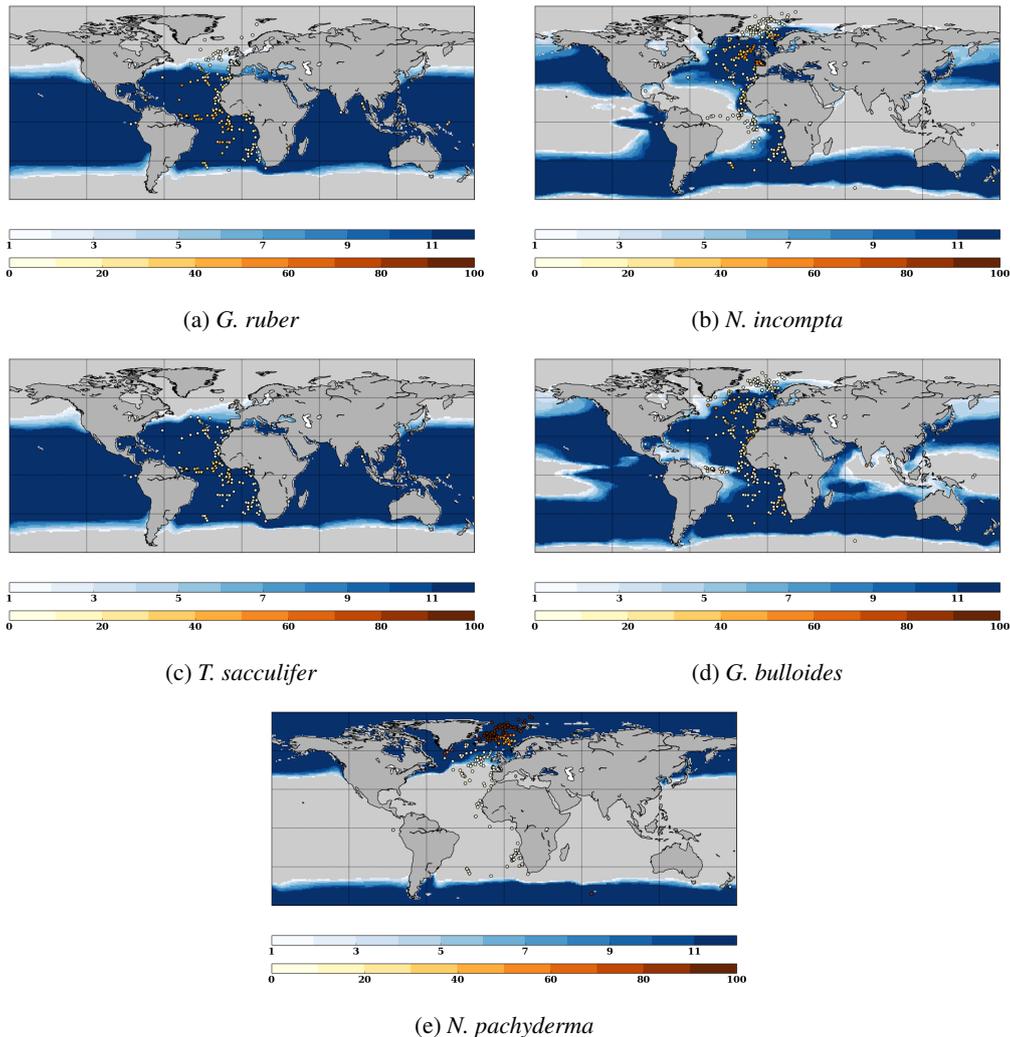


Figure 3. Model-data comparison of species abundances. Ocean regions where FAME predicts that the species is present at some time of the year ($\mu' > 0$) are plotted in blue, with shades of blue indicating the number of months of presence. Overlaid are the MARGO Late Holocene data -sites where the (quality levels 1-4) species' abundance is higher than or equal data, plotted using the yellow-white to dark-red colorbar and given in percent. A qualitative correspondance between simulated FAME presence/absence and the occurrence of 10% are shown by red dots while level in the other sites are marked by white dots difference species is noted.

zones, consistent for several species, may be noted such as the Benguela upwelling regions where FAME fails to predict the absence of *T. sacculifer* and *G. ruber*.

One possible explanation for this mismatch could be the impact of increased nutrient availability on observed abundances as a consequence of the upwelling systems, whereas nutrients are at present ignored in the FAME approach. Another possibility could be the quality of the vertical oceanic structure obtained from the World Ocean Atlas in those upwelling regions. Finally,

it should be noted that our comparison ignores the natural interannual variability since we are using climatologies. The inter-annual variability involves changes in the location of the fronts and currents and thus bears the potential of shifting the spatial boundaries between the different foraminifer species.

Further discussion of the abundance comparison including all datapoints from the MARGO Late Holocene dataset regardless of the dating quality is given in Appendix B.

To further investigate the functioning of the FAME model, it is useful to consider the spatial distribution of the depth at which each species' growth is maximum. An example is given for the month of July in Figure 4. It clearly shows that even though the maximum depth allowed for each species is fixed through the $z_b(k)$ parameter, the predicted/computed calcification depth varies according to the location in the world ocean. Except for *G. ruber* which always calcifies in the topmost ocean layers, the depth of maximum growth exhibits large spatial variations, notably at the edge of the species' domains; in July this is particularly marked in the case of *G. bulloides* and *N. pachyderma* (Figure 4d and 4e).

Likewise, it is useful to consider the seasonal variations in the depth of maximum growth for a given species. We propose to highlight this aspect for the two species that show the largest variations: *N. pachyderma* and *G. bulloides* at two extreme months (January and July) (Figure 5). For both species, the area of computed non-zero contribution varies along the year, with an expansion (reduction) of the area occupied by *N. pachyderma* in the northern hemisphere in January (July), while the regions occupied by *G. bulloides* shift towards higher (lower) latitudes in the northern hemisphere in July (January). These seasonal changes are a direct response of these species' preferred habitat to temperature. FAME thus mechanistically predicts the adaptation of planktonic foraminifer depth habitat to maintain optimal living conditions. For instance, Figure 5b and 5d clearly show that *G. bulloides* is predicted to dwell deeper at low latitudes when surface temperature rises above its preferred temperature range. Similarly, Figure 5b and 5d show that *G. bulloides* is present at higher northern latitudes in July than in January, so that the growing season actually tracks the species preferred living conditions, as observed (Jonkers and Kucera, 2015).

2.5.4 Effect of a large climatic change on the computed oxygen-18 content of the calcite

Though FAME gives realistic results when forced by atlas data, it is mostly designed to retrieve the species specific effect of climate change on the recorded $\delta^{18}\text{O}_c$. To highlight the effect of seasonal and vertical weighting of the $\delta^{18}\text{O}_c$ signal computed by FAME, we have performed a simplified experiment showing the effect of a change in the foraminifers living conditions on their $\delta^{18}\text{O}_c$ signal.

To simulate a change in climatic conditions, we apply a homogeneous 4°C decrease to the WOA13 sea temperature dataset and compute the anomaly in $\delta^{18}\text{O}_c$ between that new cold state and the original one for each species as well as for the surface equilibrium approach (Figure 6). This anomaly is noted $\Delta^{18}\text{O}_c$ in what follows.

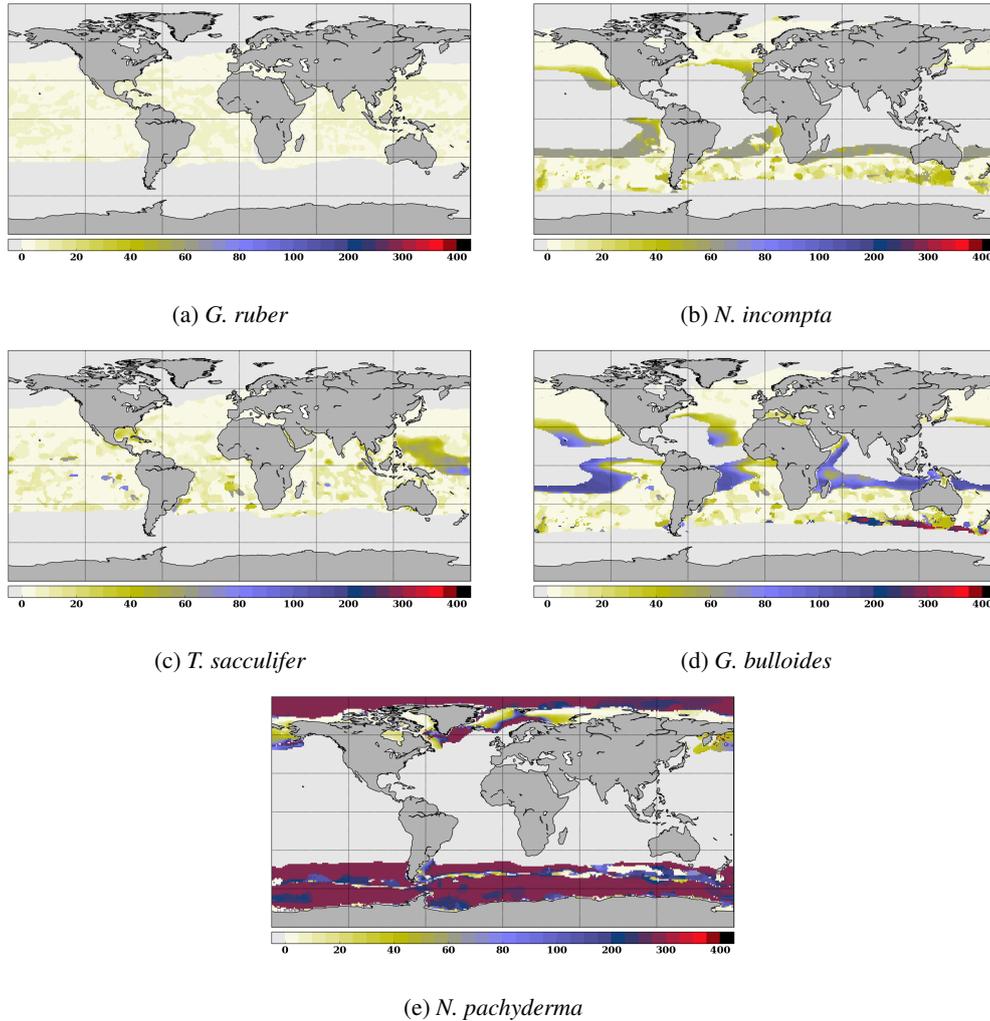


Figure 4. Depth of maximum growth for the species considered for the month of July. The color scale shows the depth in meters. Oceanic areas left in white correspond to areas where growth rates are below the threshold defined in equation (3).

Applying a spatially homogeneous temperature change should result in a quasi-homogeneous temperature change in the equilibrium calcite $\Delta^{18}\text{O}_c$, following equation 6. It is indeed what is obtained in panel (e) of figure 6, with $\Delta^{18}\text{O}_c$ values between 0.8 in the tropics to 1 per mil at high latitudes. When applying the FAME equations, we obtain large spatial variations in $\Delta^{18}\text{O}_c$ with values down to -0.75 and up to 1 per mil. All species share a common pattern of lower $\Delta^{18}\text{O}_c$ at the border of their living domain and close to equilibrium values at the center of their living domain. More specifically, the smallest differences to the equilibrium are recorded by *N. pachyderma* and the largest, negative, differences are computed for *G. bulloides*. The species with the smallest vertical living range, *G. ruber*, has the most homogeneous distribution. The range of values (minimum to maximum) is always close to one per mil with the exception of *G. bulloides* that presents a total range of 1.6 per mil. This large range of $\Delta^{18}\text{O}_c$ for *G. bulloides* is a consequence of its growth over a large range of temperatures (equation

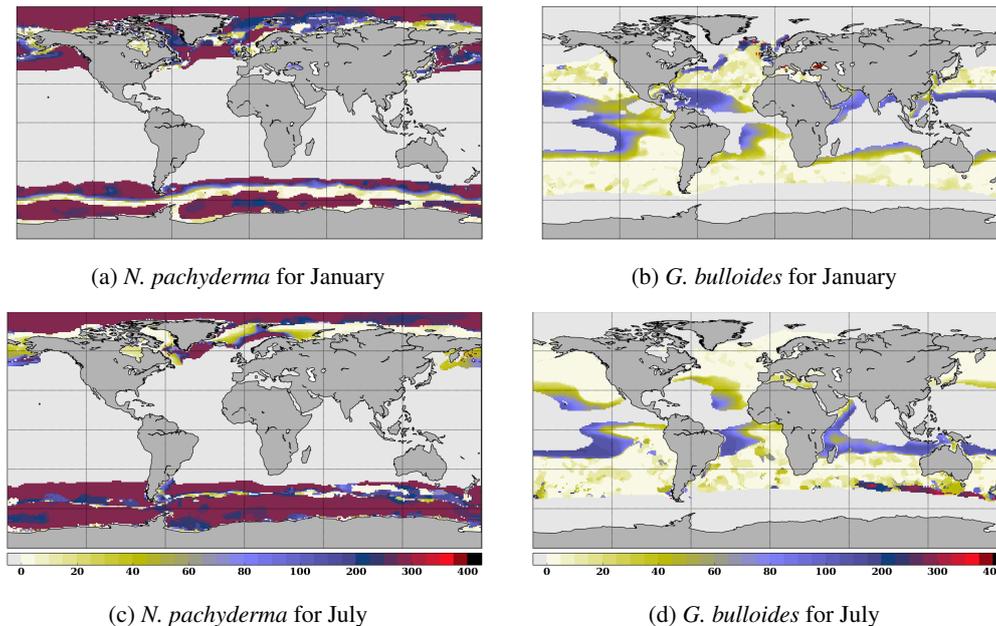


Figure 5. Comparison of the depth of maximum growth for *N. pachyderma* and *G. bulloides* for January and July. Color scale as in Figure 3.

1). In general, the maximum simulated $\Delta^{18}\text{O}_c$ are systematically 0.1 to 0.2 per mil lower than the equilibrium value.

This simple scenario, though unrealistic with respect to actual climatic applications, shows the potential of FAME to unravel the climatic signal embedded in multi-species isotopic records and thus opens the door to transient climate – data intercompar-
 5 ison where the species’ specific behaviour is taken into account.

3 Summary and conclusions

We developed the FAME (Foraminifers As Modeled Entities) module to account for planktonic foraminifer species-specific habitat when computing their calcite oxygen-18. In contrast to models predicting the abundance of planktonic foraminifers,
 10 FAME only aims at predicting the presence or absence of a given species and its oxygen-18 value. FAME is only forced by hydrographic data, and uses a very limited number of parameters, almost all derived from culture experiments. Taken together, these characteristics make FAME a uniquely simple and robust model predicting changes in the oxygen-18 of commonly used planktonic foraminifer species in response to changing climatic conditions. FAME performance is evaluated using MARGO Late Holocene planktonic foraminifer $\delta^{18}\text{O}_c$ and abundances data sets. We show that FAME predicts remarkably well the presence/absence of *G. ruber*, *N. incompta*, *N. pachyderma* and *G. bulloides* over most of the world ocean, while yielding
 15 a slightly less good prediction of *T. sacculifer* presence/absence. Investigating the simulated seasonal pattern, we show that

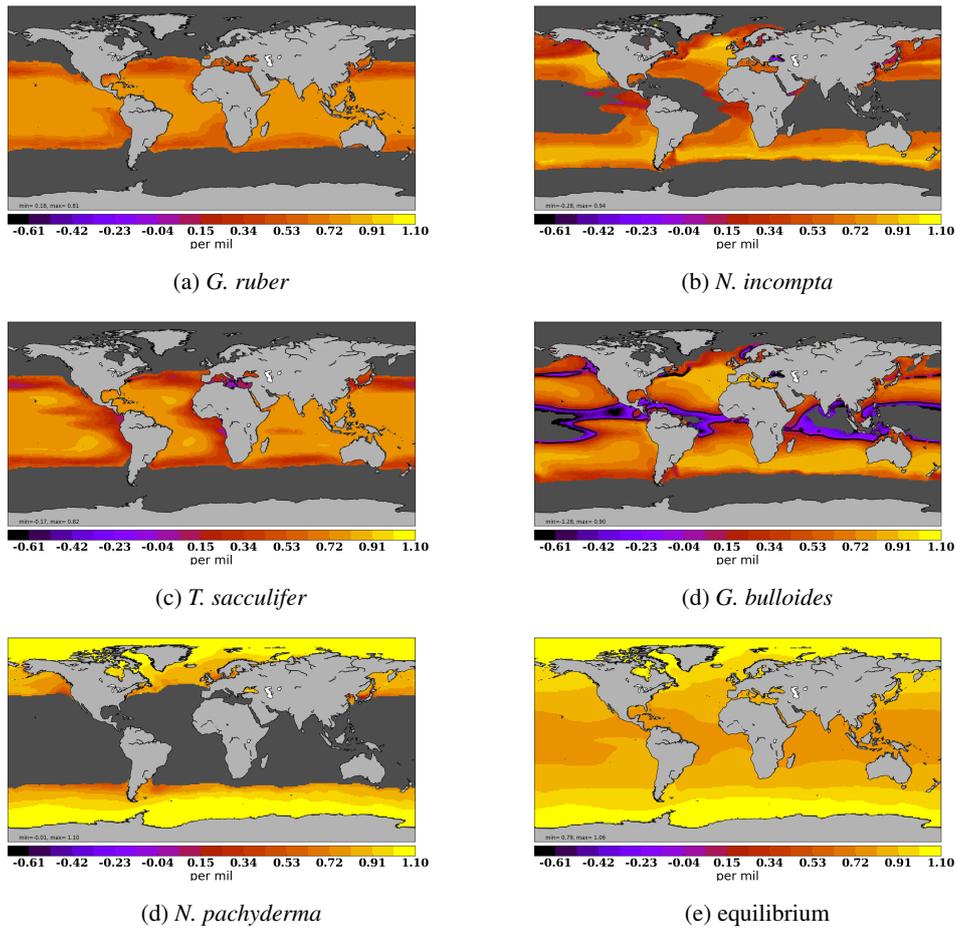


Figure 6. $\delta^{18}\text{O}_c$ response to a horizontally and vertically homogeneous 4°C cooling applied to the WOA13 dataset, $\Delta^{18}\text{O}_c$. Results are expressed in per mil for each species (panels (a-d)) and for the equilibrium surface calcite approach.

the predicted growing season and habitat depth track the species preferred living conditions, as observed in plankton hauls and sediment trap data. Finally, the application of FAME to a simple cooling scenario demonstrates that computed changes in species-specific $\delta^{18}\text{O}_c$ are much more spatially variable than the computed change in equilibrium surface calcite. Coupling the FAME module to isotope-enabled climate models makes it possible for the first time to extract the climatic information

5 contained in isotopic time series measured on different planktonic species at the same location. This opens the possibility to better reconstruct the evolution of the upper water column structure than ever before, notably over climate transitions.

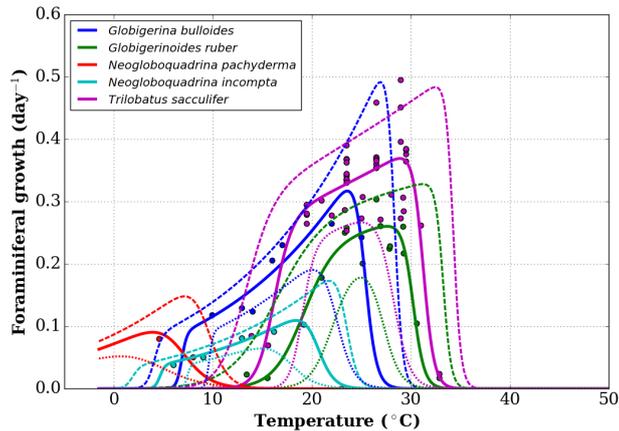


Figure A1. Growth functions corresponding to equation (1) over the full temperature range considered, with added lower-range and upper-range curves (resp. short and long dashed curves) chosen to mimick the 95% confidence interval of Lombard et al. (2009). Data points are the original data obtained by Lombard et al. (2009).

4 Code availability

The FAME module has been developed in python language version 3 and tested under version 3.5.1. The code is made available under the GNU General Public License <https://www.gnu.org/licenses/gpl.html> and is uploaded as a supplement of this manuscript.

5 5 Data availability

The World Ocean Atlas datasets used are available to all users directly from the provider. Derivation of the a reference $\delta^{18}\text{O}_{sw}$ dataset is detailed in the Appendix A. The masks file used in the latter procedure is provided as a supplement to the manuscript.

Appendix A: Derivation of the a reference $\delta^{18}\text{O}_{sw}$ dataset

We constructed our reference $\delta^{18}\text{O}_{sw}$ dataset at World Ocean Atlas standard resolution (1° grid) through a three steps methodology: a) construction of an appropriate basin mask to allow clustering the GISS global dataset regionally b) derivation of $\delta^{18}\text{O}_{sw}$ – salinity relationships for each of these basins and c) use of these relationships to obtain a $\delta^{18}\text{O}_{sw}$ field at WOA spatial resolution.

A1 Construction of the basin masks

Our native resolution being the 1° regular grid of the World Ocean Atlas, we first retrieved the available basin mask file on that grid from the NOAA website <https://www.nodc.noaa.gov/OC5/woa13/masks13.html> and converted it to a netCDF format file

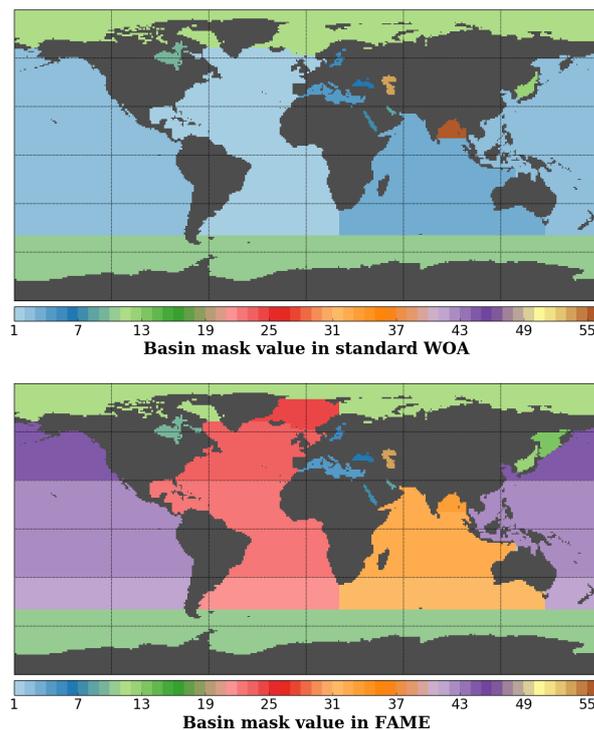


Figure A2. Basin masks as defined in the WOA standard mask file (above) and in FAME, on the same 1° resolution grid. Values corresponds to the basins defined in Table A1.

(<http://www.unidata.ucar.edu/software/netcdf>). The basins defined in the WOA base mask did not perfectly fit our purpose, we hence modified the masks to isolate some particular regions where the $\delta^{18}\text{O}_{sw}$ and salinities are specific (e.g. Sea of Okhotsk) or merge some regions of the WOA mask into larger ensembles (e.g. Hudson Bay). A summary of the basins in the original file and in ours is given in Table A1. The Pacific and Atlantic oceans were split into South, North and Tropical parts, based on boundaries at 30° North and South respectively. The Indian Ocean has been only split in two: North and South using the 30° South boundary. The Bay of Bengal has been kept a separated basin as in the original file. The GIN Seas were made a separated basin from the Arctic Ocean, using the boundaries at 80° North and at 20° East. We also extended the Hudson Bay mask area to include the Hudson Strait and Ungaya Bay, since these do not represent the same water mass properties as the North Atlantic Ocean. The limit used is -64.5° West, corresponding to the southern tip of Resolution Island on the grid given. Finally, the same procedure was applied to define the Okhostk Sea, using the official definition of the International Hydrographic Organization (IHO SP-23). The results of this whole procedure is shown in Figure A2. In Table A1, some values are annotated with a "*" to highlight basins having the same value in FAME as in the standard WOA but covering a different area: the Arctic Ocean from which the GIN seas have been taken out in FAME, Hudson Bay which covers a part of the former Atlantic basin of the WOA

Table A1. Comparative list of basin masks in WOA and FAME. The "value" field provides the integer value used in the netCDF file to specify the respective basin on the WOA grid.

Basin name	WOA value	FAME value
Atlantic Ocean	1	
South Atlantic O.		21
Tropical Atlantic O.		22
North Atlantic O.		23
GIN Seas		24
Pacific Ocean	2	
South Pacific O.		41
Tropical Pacific O.		42
North Pacific O.		44
Indian Ocean	3	
South Indian O.		31
North Indian O.		32
Mediterranean Sea	4	4
Baltic Sea	5	5
Black Sea	6	6
Red Sea	7	7
Persian Gulf	8	8
Hudson Bay	9	9*
Southern Ocean	10	10
Arctic Ocean	11	11*
Sea of Japan	12	12
Okhotsk Sea		13
Caspian Sea	53	53
Bay of Bengal	56	33

* highlights the regions where FAME and WOA regions do not cover the same area (see text))

given its afore mentioned expansion to the Hudson Strait and Ungaya Bay.

The netCDF data file resulting from this procedure is provided as a supplement to the manuscript.

A2 Computation of the $\delta^{18}\text{O}_{sw}$ – salinity relationships

The basins defined in the previous section are then used to cluster the raw data, $\delta^{18}\text{O}_{sw}$ and salinity, of the GISS database (Schmidt et al., 1999) in the respective basins. Furthermore, only data locations where both $\delta^{18}\text{O}_{sw}$ and salinity are given in

Table A2. Values obtained for the $\delta^{18}\text{O}_{sw}$ – salinity relationships

Basin name	slope	intercept	R ²	Nb. points
South Atlantic O.	0.52	-18.02	0.95	55
Tropical Atlantic O.	0.25	-8.19	0.60	241
North Atlantic O.	0.51	-17.65	0.67	738
GIN Seas	0.69	-23.72	0.73	1471
South Pacific O.	0.42	-14.45	0.92	19
Tropical Pacific O.	0.31	-10.36	0.76	417
North Pacific O.	0.43	-14.69	0.92	333
South Indian O.	0.53	-18.39	0.89	255
North Indian O.	0.10	-2.88	0.40	466
Mediterranean Sea	0.27	-8.98	0.61	196
Baltic Sea	0.34	-9.14	0.63	21
Black Sea	0.28	-6.77	0.06	18
Red Sea	0.28	-9.61	0.97	16
Hudson Bay	0.40	-15.33	0.47	286
Southern Ocean	0.42	-14.84	0.80	1005
Arctic Ocean	0.54	-18.82	0.72	2932
Sea of Japan	0.36	-12.83	0.94	45
Okhotsk Sea	0.42	-14.46	0.93	453
Bay of Bengal	0.24	-7.9	0.40	131

the original database for depths less than 200 meters are retained under the additional constraint that depth of the ocean should be more than 175 meters. The latter to ensure that the values are representative of high seas values and not to coastal areas, possibly under fluvial influence. Additionally, all values below 5 per mil in salinity are ignored for all basins. Lastly, for two basins (North Atlantic and Bay of Bengal), the existence of two different slopes where only one corresponds to open ocean conditions render necessary the addition of one additional condition to keep only the latter. We thus added a limit at 27 per mil in salinity for those two basins.

The resulting slopes, intercept and correlation coefficients are given in the Table A2. Using those relationships, we further compute the $\delta^{18}\text{O}_{sw}$ in the WOA geographical grid from the WOA salinity fields.

Appendix B: Further discussion of predicted and observed planktonic foraminifer abundances

In the main text, we have only compared the results of FAME to the datapoints in the MARGO Late Holocene database that were characterized by high chronological control quality. Since this drastically restricts the geographical extent covered by MARGO data and in the interest of completeness, we propose here a short discussion based on all points of the MARGO Late
5 Holocene database, regardless of their chronological control quality. The interest of figure A3 is to provide some information in the Southern, Pacific and Indian Ocean regions that are largely void of points in the previous figure. While the bulk of the conclusions given in the main text is unchanged by this new comparison, we may highlight the following.

The unsorted distribution for *G. ruber* is not very different from the one described above, albeit with a good definition of
10 the Southern Ocean abundance limit where FAME results are in good accordance with MARGO. Also, one may note a series of points without the presence of *G. ruber* in the equatorial Pacific in MARGO, an aspect which is not predicted by FAME. However, these points are mingled with points with *G. ruber* presence in the MARGO database, indicating they could be an artifact resulting from the presence of older sedimentary material in the unsorted MARGO database ; it is thus difficult to draw a firm conclusion.

15 Regarding *N. incompta*, the picture is pretty much the same as described in the main text to the exception of a number of mismatching sites in the tropical and mid latitudes in all southern ocean basins (Pacific, Indian and Atlantic).

The distribution for *T. sacculifer* shows a clear latitudinal mismatch of the limit of presence/absence when comparing the FAME results to the unsorted MARGO dataset. It seems obvious that the latitudinal spread of *G. ruber* in FAME should be considered as too extended in the mid to high latitudes in both hemispheres.

20 The joint comparison of unsorted *G. ruber* and *T. sacculifer* distributions points to the existence of consistent zones where FAME does not predict the absence of those two species. This was noted earlier for the Benguela upwelling region. It is also visible here for the Peru-Chili upwelling and the eastern Equatorial Pacific. All these zones correspond to upwelling regions (e.g. Mackas et al., 2006) and are characterized by strong contrasts in surface water properties with respect to the surrounding regions, large interannual and intra-seasonal variability, and high phytoplankton production. The existence of this consistent
25 pattern in upwelling regions in the unsorted database confirms that *G. ruber* and *T. sacculifer* distributions are not well simulated in upwelling regions, either because nutrients are presently not accounted for in FAME, or because the increased nutrient availability and/or the vertical structure of oceanic physical properties is not faithfully depicted in the 1° resolution WOA13 dataset we used in input.

The unsorted distribution for *G. bulloides* still presents an excellent match for the limits, but some discrepancies in the equato-
30 rial and tropical latitudes, albeit MARGO unsorted data do not present a large regional consistency outside the northern coast of Brazil (where FAME also predicts the absence of *G. bulloides*).

Outside some minor mismatches in the southern Indian Ocean, the conclusions for *N. pachyderma* are also largely unaffected by the use of all the points from the MARGO database.

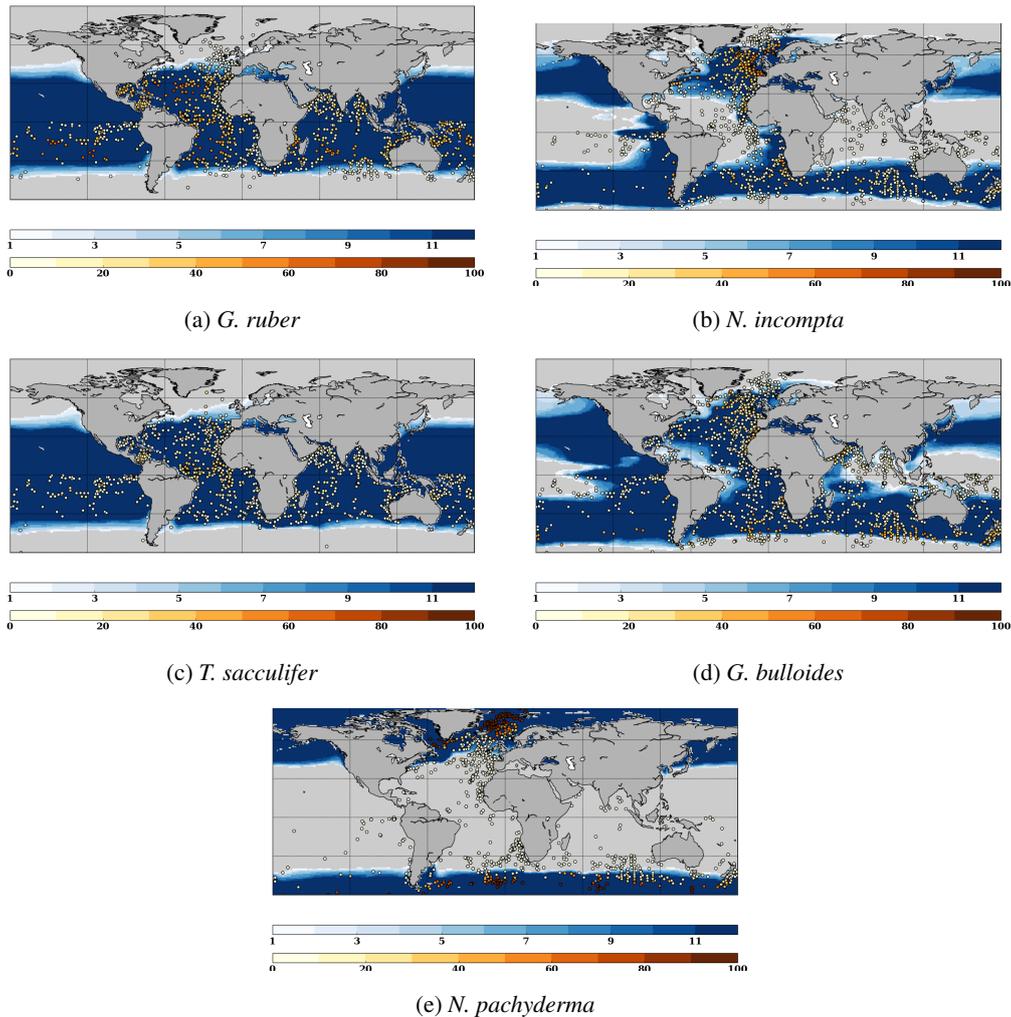


Figure A3. Model-data comparison of species abundances. Ocean regions where FAME predicts that the species is present at some time of the year ($\mu' > 0$) are plotted in blue, with shades of blue indicating the number of months of presence. Overlaid are the MARGO Late Holocene data :sites where the (all quality levels) species' abundance is higher than or equal data, plotted using the yellow-white to dark-red colorbar and given in percent. A qualitative correspondance between simulated FAME presence/absence and the occurrence of 10% are shown by red dots while level in the other sites are marked by white dots difference species is noted.

To conclude, the use of all the datapoints regardless of the quality of the chronological control in the MARGO Late Holocene database does not add much new information. Especially since the datapoints should be considered with caution as they could correspond to a different climate regime than the Late Holocene.

5 *Competing interests.* The authors declared no competing interests.

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