Ref.: Ms. No. bg-2017-429

Title: Modeling seasonal and vertical habitats of planktonic foraminifera on a global scale

Dear Lennart,

First of all we would like to thank the reviewers for their constructive comments and suggestions, which greatly helped to improve our manuscript “Modeling seasonal and vertical habitats of planktonic foraminifera on a global scale”.

In response to the reviewers' suggestions and due to an incorrect representation of the ocean circulation in the formerly used coarse resolution (i.e., ~3º) model configuration, we have made the following major changes to the manuscript:

- As we informed you earlier, we have noticed an inconsistency in the ocean state as represented in the originally used 3° physical model resolution setup. To resolve this inconsistency, we performed a new simulation of foraminifera distribution based on a physical model run with a 1° horizontal resolution, which yielded a more realistic ocean state. The spin-up was run for 300 model years, which we consider sufficient to ensure that at least the upper ocean, where the investigated foraminiferal species live, was in equilibrium. As expected, the evaluation of the thus obtained foraminifera distribution did not change the main findings of the paper. However, we note an improvement in the agreement between the model data and the observations regarding the horizontal, vertical and seasonal distribution of the analyzed planktonic foraminifera species, which we ascribe to the better representation of the upper ocean in the new physical model setup.
- In response to the comments of the referees, we carried out a more quantitative model-data-comparison by calculating the Bray-Curtis index of similarity between the model data and the core-top data and we extended the discussion regarding the model-data-mismatch by also considering limiting factors regarding the underlying complex model configuration.

We feel that thanks to the reviewers' suggestions and comments we were able to produce a more robust manuscript, which includes a broader critical analysis of the model-data-comparison and provides a thorough analysis of the overall model performance.

We append here the point-by-point responses to each review as well as the revised version of the manuscript (with the changes highlighted in red). All comments provided by the reviewers were taken into consideration and included in the revised version. We hope that our revised manuscript meets the criteria for publication in Biogeosciences.

Kind regards,

Kerstin Kretschmer (on behalf of all co-authors)

Response to Referee #1:

We would like to thank reviewer Inge van Dijk for her constructive comments and suggestions, which helped us to greatly improve our manuscript. Please find, in the following, the original comments in black and our responses in light blue; the indicated page and line numbers refer to the revised manuscript.

Referee #1 comments:

I have carefully read the manuscript 'Modeling seasonal and vertical habitats of planktonic foraminifera on a global scale' by Kretschmer and coauthors, which presents a model to predict global concentrations of five species of planktonic foraminifera and their depth habitat. This model could aid paleoclimatologists to correct for habitat depth when using shells of planktonic foraminifera to reconstruct ocean conditions. I need to remark that I have no experience using PLAFOM, or any practical experience with either the BEC model or CESM1.2(BGC) configuration. Therefore, my comments are rather general and an experienced user should review e.g. the use of model parameters and choice of configuration. I only have a couple of remarks that mainly focus on the usability and applicability of the model to reconstruct past depth habitats.

General comments

In general the authors should avoid certain 'model jargon', if they want to convince the broad foraminiferal society to use and apply this model. It is sometimes difficult to follow which steps are taken and assumptions were made to test or simulate certain scenarios (e.g. page 6, lines 23-25).

Thank you for pointing this out. We will change parts of the method section, also according to the higher resolution model configuration, and will include more or delete redundant information, when appropriate, for a better understanding. However, to ensure reproducibility of our study, we cannot avoid using a certain 'model jargon' to explain the applied modeling approach and the used model setup. We already tried to use as little model jargon as possible and provided in all conscience a comprehensible model description.

Even though habitat tracking is very important when using shells of planktonic foraminifera to reconstruct ocean conditions, it is still (more?) crucial to pinpoint the actual calcification depth within the depth habitat, since this is where the calcite is formed. Even though the model can reasonably well predict (globally) the vertical distribution, this does not mean that at this specific depth the environmental signal was 'logged' into the shell. Please include somewhere a couple of sentences on the reconstructed depth habitat compared to the actual calcification depth. Could this be the next step for PLAFOM3.0?

This is a valid point and in a next step, we would like to combine PLAFOM2.0 with a module, which specifically takes this into account and calculates species-specific isotope compositions of the modeled foraminiferal species, such that we could directly infer information about the calcification depth of each species. However, without any information about the species-specific habitats, it is difficult to provide a statement regarding the calcification depths of the individual foraminiferal species. Therefore, we at first intended to simulate realistic species-specific habitat depths and next we plan on obtaining realistic calcification depths. We included a paragraph in section 4.1.3 (p. 18, lines 18-27) regarding a comparison of the reconstructed depth habitat with the actual calcification depth of the individual species:

"We find that the modeled depth habitats of the five considered foraminiferal species are in agreement with the relative ranking of their apparent calcification depths, but the inferred absolute values of calcification depth are often deeper or show a broader range of depths (e.g., Carstens and Wefer, 1992; Kohfeld et al., 1996; Ortiz et al., 1996; Bauch et al., 1997; Schiebel et al., 1997; Ganssen and Kroon, 2000; Peeters and Brummer, 2002; Anand et al., 2003; Simstich et al., 2003; Nyland et al., 2006; Jonkers et al., 2010, 2013; van Raden et al., 2011). This is not surprising, because PLAFOM2.0 does not model species' ontogeny and cannot capture processes related to ontogenetic depth migration (e.g., Fairbanks et al., 1980;

Duplessy et al., 1981). The same limitation applies to estimates of living depth derived from plankton tow data, which often appears to deviate from apparent calcification depths (e.g., Duplessy et al., 1981; Rebotim et al., 2017). Nevertheless, as a first essential step in understanding the variability in calcification depths, PLAFOM2.0 provides a powerful tool that can aid the interpretation of proxy records."

Section 2.3.1. What about other ocean parameters that vary over geological timescales which might influence growth rates? Like [PO_4^{3-}] (Aldridge et al., 2012, BG) on SNW or the effect of carbonate chemistry on calcification rates? For instance Lombard et al., 2010 found lower growth rates of several species with lowered [CO_3^{2-}] conditions and Davis et al., 2017 (Sci. Rep.) observed lower calcification rates with decreasing pH. Why are these parameters not taken into account in the model? Are these effect minor compared to temperature and food availability?

This is a valid point again, but we are not attempting to model species-specific growth rates (as opposed to Lombard et al., 2011). Rather we aim to more directly estimate foraminifera abundance, which can be compared to the sediment record more directly. The relationship between growth rate and abundance is far from straightforward (cf. Lombard et al., 2011) and we are not aware of studies that have investigated the effect of those parameters on the abundance of planktonic foraminifera. We are aware that other ocean parameters might influence species-specific growth rates. The aim of this study, however, was to test if the existing planktonic foraminifera model is able to reproduce species-specific habitats when combined with a model configuration that resolves the vertical. One has to bear in mind that a model is only a simplification of reality and including more parameters would likely introduce more degrees of freedom and could lead to more model uncertainty and could additionally increase the computational costs. However, for a future model development it is worth considering those parameters. Here it is beyond the scope of this study to include more parameters to determine growth rates.

Section 2.5.2. and 2.5.3. The authors use the sediment trap/plankton tow samples to test the accuracy of the model in predicting seasonality & depth habitats. However, the amount of data used for this comparison is not covering the total range of oceanic settings, since big parts of the ocean are underrepresented. Is it possible to extend this database by adding other published sediment trap data? This way you can show your model can predict depth habitat in a wider range of ocean conditions, which will make it more robust for application in deep time. Just some quick suggestions: Mediterranean Sea: Mallo et al., 2017 BG; SW Atlantic: Venancio et al., 2016 Marine Micropaleontology; Mozambique channel: Steinhardt et al., 2014 Marine Micropaleontology; Panama basin: Thunell et al., 1983 EPSL; Indian Ocean: Guptha et al., 1997 JFR.

The reviewer rightly points out that our data compilation is not comprehensive. However, we pursued the strategy to acquire sediment trap and plankton tow data at more or less the same region to guarantee a consistent model-data-comparison throughout the manuscript when analyzing species-specific seasonal and vertical habitat patterns (see Figure 1b). We agree that this prerequisite limits the number of studies that can be used to evaluate the model, but the underlying data base covers all provinces and provides good estimates of the different species-specific habitats and their variability on a global scale that is sufficient to show the strength and weaknesses of our model.

Figure 2. Is it possible to add an ‘offset map’, in which you correlate e.g. the coretop data with the model data, to see where the model exactly over-/underestimates the data? This way you would be able to perform some (correlation) statistics, and this would clearly show the areas where the model did not predict the correct distribution. I understand you are trying to capture the global signal (as stated several times in the manuscript), but paleooceanographers are more interested in specific areas when correction for e.g. depth habitat, and these are often also in more complicated oceanic settings (for

example coastal/upwelling/river run off areas).

We included an additional map in Figure 2 that provides a more thorough comparison between modeled and observed assemblages. Therefore, we calculated the Bray-Curtis index of similarity between the model data and the core-top data, such that we provide a measure of confidence. Note for the calculation, we accounted for the different sizes of each species by using a relative size for each species based on the results of Schmidt et al. (2004) and recalculated the modeled relative abundances accordingly. We added this analysis to the manuscript (i.e., to section 3.1, p. 9, lines 11-15) to provide a thorough model-data-comparison. Nevertheless, the used model configuration consisting of three different models (i.e., POP2, BEC, PLAFOM2.0) could hamper a thorough statistical analysis as it is not unequivocally possible to differentiate which component might actually lead to a possible over-/underestimation of the data. Even the now used higher model resolution could likely lead to misrepresentations of small-scale processes, oceanic fronts, river runoff areas, and coastal upwelling regions, and could, thus, account for the model-data-mismatch. In addition, it is not possible to correlate the core-top data with the model data directly, because PLAFOM2.0 calculates foraminiferal concentrations via carbon biomass (i.e., in mmol C/m^3) and the core-top samples provide foraminiferal concentrations via number of specimens.

"For a direct comparison of the observed (i.e., the core-top data) and modeled foraminiferal community composition the Bray-Curtis index of similarity was used. The comparison reveals generally a good fit between the simulated and sedimentary assemblage composition with median Bray-Curtis similarity of ~ 68%. The fit is particularly good in the high latitudes and in the tropics (Bray-Curtis similarity > 80%) and only a few regions (off South America and southern Africa, in the equatorial and North Pacific, and in the eastern North Atlantic) reveal a poorer agreement with similarities of < 50% (Figure 2a)."

Page 11, line 27-31 and page 12, line 20-21. The authors state that part of the mismatch between the model and coretop data might stem from different genotypes having varying ecological preferences, and therefore their own unique model parameters. If so, does did not create a major bias for the whole model, especially when reconstructing depth habitats in deep time? For geological samples it is not possible to distinguish between genotypes, and therefore certain species might respond different in terms of depth habitat than the model will predict? Also, could it be that certain ecological preferences have changed over time? Can the authors predict how far in geological time you could still use this model to obtain reliable data on global distribution and depth habitat?

The reviewer points out two important considerations: i) cryptic species with different ecological preferences and ii) the question of stationarity. We would argue that both hold for all attempts to use planktonic foraminifera to reconstruct the past ocean. The assumption of stationarity of any proxy is fundamental to all paleoclimate reconstructions. The model can of course only be used for the time that the species have been present and for as long as we have indications that their ecology remained constant (cf. Huber et al., 2000 for *N. pachyderma*). The primary intended use of the model is to apply it to climate conditions covering the Last Glacial Maximum and/or the last couple of glacial-interglacial cycles, but not to deep time, when different species existed or extant species may have had different ecological preferences.

With respect to cryptic species the reviewer is right to point out that this forms an important caveat. However, as the reviewer also mentions, it is often impossible to distinguish between cryptic species in the fossil record, so this caveat applies to any reconstruction using planktonic foraminifera. This is exactly the reason why ecological preferences of cryptic species need to be resolved, so that reconstructions and modeling efforts can be improved. To clarify this point, we added this issue to the end of section 4.1.1 (p. 14, lines 16-23):

"[...] Likely an even larger part of the discrepancies between the model and core-top data stems from the underlying model parameterizations applied on a global scale, which do not distinguish between distinct genotypes of the different species with potentially varying ecological preferences. Theoretically, this problem could be solved by parameterizing all known

genotypes individually and approximating the total morphospecies abundance as the sum of its constituent genotypes. This would allow a comparison with sediment data, but not a diagnosis, since the sediment data provide no information on which genotypes are contained in the assemblages. Interestingly, the generally fair fit between the model and observations suggests that ecological differences between cryptic species are likely limited and that the model provides a useful first-order approximation of global species distribution."

Minor comments

Page 2, line 18, 32; Page 6, line 16; page 11, line 23: Some problem with bracketing, e.g. double bracketing etc.

We checked for the double bracketing and, where possible, we will delete the unnecessary brackets. However, for some cases (i.e., p. 6, line 19; p. 12, line 26) we will not change the bracketing as this would potentially cause a misunderstanding with the referencing.

Page 6, line 24: quasi-steady

Done.

Page 7, line 15: space missing between '(Figure 1a).' and 'We'

Done.

Page 8, line 5 and page 11, line 17: Arctic Circle

Done.

Page 12, line 10-14. Can you explain the underestimation of the model in scenarios were assemblages are dominated by two species?

Here, we actually meant that the model is not able to capture the full extent of the observed relative abundances in certain areas where a dominance of some species is actually expected.

Page 12, line 21: change or remove 'see'

Done.

References:

- Huber, R., H. Meggers, K.-H. Baumann, M. E. Raymo, and R. Henrich (2000), Shell size variation of the planktonic foraminifer *Neogloboquadrina pachyderma* sin. in the Norwegian-Greenland Sea during the last 1.3 Myrs: implications for paleoceanographic reconstructions, *Palaeogeography, Palaeoclimatology, Palaeoecology*, *160*, 193-212.
- Lombard, F., L. Labeyrie, E. Michel, L. Bopp, E. Cortijo, S. Retailleau, H. Howa, and F. Jorissen (2011), Modeling planktic foraminifer growth and distribution using an ecophysiological multi-species approach, *Biogeosciences*, *8*, 853-873.
- Schmidt, D. N., S. Renaud, J. Bollmann, R. Schiebel, and H. R. Thierstein (2004), Size distribution of Holocene planktic foraminifer assemblages: biogeography, ecology and adaptation, *Marine Micropaleontology*, *50*, 319-338.
- Thunell, R. C., W. B. Curry, and S. Honjo (1983), Seasonal variation in the flux of planktonic foraminifera: time series sediment trap results from the Panama Basin, *EPSL*, *64*, 44-55.

Response to Referee #2:

We would like to thank the reviewer for the constructive comments and suggestions, which helped us to greatly improve our manuscript. Please find, in the following, the original comments in black and our responses in light blue; the indicated page and line numbers refer to the revised manuscript.

Referee #2 comments:

The authors use existing sediment trap and plankton tow data to add seasonal and depth habitat information to the PLAFOM2.0 model. The authors then compare model results to modern data, concluding that they find a reasonable agreement between simulated and observed results for species-specific flux timing and depth habitat. The manuscript is well written, and the discussion of global trends in depth habitat is fantastic and alone an important contribution to the literature. Moreover, in light of an increasing understanding of the consequences of foraminifera habitat tracking for proxy data interpretation, the development of such a modeling tool is potentially quite useful.

The manuscript is successful in modeling modern depth preferences from unfortunately sparse observational data. While the model seems to reproduce broad trends (spinose species in near-surface waters) and earlier-when-warmer seasonality in some environments, figures 6-7 and the supplemental figures often show a strikingly poor fit between modeled and observed timing and depth preferences at specific sites. As the authors point out, the model tends to underestimate both amplitude of seasonal changes and potentially depth stratification. The authors should consider explicitly discussing why the model might be insensitive in replicating observed variability and how this would be likely to effect modeling of different climate inputs.

This is a good point and we extended the discussion in this regard especially by bearing in mind that the coarse 3º ocean model is not fully able to represent the ocean's physics properly. Apart from the uncertainty in the observational data (see section 4.2), it is due to the model complexity not trivial to determine which model component (i.e., POP2, BEC or PLAFOM2.0) contributes to what extent to the model-data-mismatch. Determining this would require a suite of sensitivity experiments with each model component. Whilst we agree that these would be useful – and will consider this for future work – we think that the model as it is already presents a useful contribution to improve the interpretation of foraminifera-based proxy records.

Nevertheless, we expanded the discussion on the model uncertainty in section 4.2 (p. 19-20, lines 23-5). We specifically addressed the dependence of the results on the individual model components. The inferred importance of temperature and food availability (provided by POP2 and BEC, respectively) on the distribution of foraminifera implies that each model component is important for an accurate representation of foraminifera distribution. Hence, as expected the higher resolution ocean model provides a more realistic representation of ocean physics, which cascades through the model hierarchy leading to an improved overall model skill. Nevertheless, sub-grid processes and known POP2 and BEC model issues (see, e.g., Danabasoglu et al., 2012, 2014; Moore et al., 2013) remain. These contributes to the model-data mismatch, but will not provide information/constraints on the planktonic foraminifera model per se.

“The underlying complex model configuration consists of three major model components (i.e., the POP2 ocean model, the BEC ecosystem model, and PLAFOM2.0), which follow a certain model hierarchy by interacting differently with each other. Both the BEC model and PLAFOM2.0 run within POP2 (see Moore et al., 2013; Lindsay et al., 2014; this study), which provides the temperature distribution used to determine, i.a., the phytoplankton, zooplankton, and/or foraminifera carbon concentrations. It was shown that POP2 exhibits several temperature biases (e.g., Danabasoglu et al., 2012, 2014). These include large warm SST biases originating in the coastal upwelling regions of North and South America and of South Africa, colder-than-observed subthermocline waters in the equatorial Pacific as well as cold temperature biases of up to 7◦C in the

North Atlantic emerging throughout the water column (see Figure S5 and Danabasoglu et al., 2012, 2014). These temperature biases influence the foraminiferal distributions directly and indirectly by affecting the distributions of their food sources in the BEC model. In addition, the BEC model also exhibits several biases, such as higher-than-observed (lower-than-observed) surface nutrient and chlorophyll concentrations at low (high) latitudes (Moore et al., 2013), implying potential misrepresentations of the modeled phytoplankton and zooplankton distributions, likely influencing the foraminiferal carbon concentrations. The inferred importance of temperature and food availability (estimated by POP2 and/or the BEC model) in PLAFOM (see Fraile et al., 2008; Kretschmer et al., 2016), on the distribution of planktonic foraminifera implies that each model component is important for an accurate representation of the foraminifera distribution. Therefore, it is difficult to unequivocally differentiate between the different model components of the CESM1.2(BGC+PLA) model configuration and their individual share likely leading to the model-data-mismatch."

When the authors discuss relative abundance of species, are they referring to relative abundance with respect to just modeled species or all foraminifera? Is this consistent throughout? It might be worth clarifying this point.

When we are discussing species relative abundances for the core-top data, we always refer to relative abundances with respect to only the five modeled species. We mention this in section 2.5.1 (page 7, line 25-26) and also in the caption of Figure 2.

Why have the authors chosen not to include sediment trap based habitat depth based assessments?

Since sediment traps provide export flux rates, which are not modeled here, and thus do not provide information about depth habitat, a sediment trap based depth habitat assessment is simply not possible. However, there exist calcification depth estimates based on chemical properties of foraminifera from sediment traps, but calcification depth is not identical to habitat depth. Therefore, we only use plankton tow data for a meaningful depth habitat assessment.

p8/l23 (and throughout) – Do the authors really mean differences in biomass as opposed to species abundances? If so, is the biomass different in different species and how is this accounted for? And how does this metric compare to species abundances, as presumably used in the modern data to which the model is compared?

PLAFOM2.0 calculates the foraminiferal abundance of each species via carbon biomass to be consistent with the ecosystem model (see section 2.3 in the manuscript and Fraile et al., 2008). In the manuscript we prefer to use this unit, rather than foraminifera abundance, since conversion to abundance requires, as the reviewer rightly points out, another step.

However, this conversion of biomass to abundance is only of importance for the comparison of the modeled and observed assemblages. For the global comparison with the core-top data, we are not interested in assessing absolute abundances and, therefore, calculate species' relative abundances. For this comparison, however, we now account for the different sizes of each species by using a relative size for each species based on the results of Schmidt et al. (2004) and recalculated the modeled relative abundances accordingly. This allowed for a sound comparison with the core-top data, which is evident in the newly introduced and considered Bray-Curtis similarity measure. We added this similarity analysis to the manuscript (i.e., to section 3.1, p. 9, lines 11-15) to provide a thorough model-data-comparison.

We would like to emphasize that the patterns of vertical and/or seasonal abundance are independent of the amount of carbon per shell (as long as there is no significant and systematic size variability). This allows us to directly compare modeled and observed data.

p9/l18 (and throughout this section) – I'm not sure it makes sense for "maximum production" to be "year-round." Could you clarify?

That is a very good point. Here, we actually wanted to say that uniform and/or constant species fluxes occur year-round, thus no seasonal peak is evident in the species production. We changed the wording throughout this section accordingly.

section 3.3 – might be helpful to define what you mean by “surface” and “subsurface” as these are pretty general terms but are being used as if the authors have a fairly specific depth range in mind.

Thank you for pointing this out. We now provide more precise depth ranges throughout section 3.3 and especially avoided the general term “subsurface”. The surface is in general defined from 0 to 10m water depth, which corresponds to the first vertical layer of the used model configuration.

p12/l30 –“prefer thriving” -> “thrive”

Done.

p12/l35 – delete "largely"

Done.

p14/l4 – delete "among each other"

Done.

p14/l11 – delete "preferably"

Done.

p14/l31 – “cold to transitional” compares a temperature to a zonation

We will changed “transitional” to “temperate” to be consistent in the wording.

p15/l22 – a -> the

Done.

p17/l2 – might be better to describe these as short time series as compared to plankton tows which really are “snapshots”

We agree and describe sediment trap time series now as short time series rather than snapshots (p.19, lines 2-4):

“[...] span at most a few years and hence represent short time series that are potentially aliased/biased by inter-annual, seasonal, and/or monthly variability. Similarly, plankton tow samples represent snapshots (of one particular day) [...].”

p17/l18 – or genotypes or phenotypes?

We agree that genotype is a more suitable term in this regard and changed the wording accordingly.

p17/l26 “a few”?

Done.

Figure 6 is extremely difficult to read given the mix of opacity and multiple symbols and colors. Is there a better way to present this data?

We agree, but could not find a better solution to present the data.

Figures 6 and 7 (a-c) suggest a quite poor fit of modeled data to sediment trap observations. i.e. 7c shows the model completing missing the flux timing of bulloides in JGOFS34. The authors include an overview or why there might be some data-model mismatch, but I think a wider discussion of why and how this could impact or limit interpretation of model results is warranted.

Please refer to our response to your first comment, where you address the same issues.

References:

- Danabasoglu, G., S. C. Bates, B. P. Briegleb, S. R. Jayne, M. Jochum, W. G. Large, S. Peakcock, S. G. Yeager (2012), The CCSM4 Ocean Component, *Journal of Climate*, *25*, 1361-1389.
- Danabasoglu, G., S. G. Yeager et al. (2014), North Atlantic simulations in Coordinated Ocean-ice Reference Experiments phase II (CORE-II). Part I: Mean states, *Ocean Modelling*, *73*, 76–107.
- Fraile, I., M. Schulz, S. Mulitza, and M. Kucera (2008), Predicting the global distribution of planktonic foraminifera using a dynamic ecosystem model, *Biogeosciences*, *5*, 891-911.
- Moore, J. K., K. Lindsay, S. C. Doney, M. C. Long, K. Misumi (2013), Marine Ecosystem Dynamics and Biogeochemical Cycling in the Community Earth System Model [CESM1(BGC)]: Comparison of the 1990s with the 2090s under the RCP4.5 and RCP8.5 Scenarios, *Journal of Climate*, *26*, 9291-9312.
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Response to Referee #3:

We would like to thank reviewer Jelle Bijma for his constructive comments and suggestions, which helped us to greatly improve our manuscript. Please find, in the following, the original comments in black and our responses in light blue; the indicated page and line numbers refer to the revised manuscript.

Referee #3 comments:

Scientific significance: Excellent

The manuscript by Kretschmer et al. represents a substantial contribution to scientific progress within the scope of Biogeosciences. It is the latest one in a series of “foram-flux modelling” papers from the Bremen group. In 2006, Zaric et al. Developed the first empirical model that described globally the fluxes of planktonic foraminifera at species level in dependence of sea-surface temperature, mixed-layer depth and export production. Over the years, the foram model itself, its parameterization, and its implementation and coupling to other models has evolved (e.g. Fraile et al., 2008; 2009; Kretschmer et al., 2016). The aim of all of these papers has always been to project the effect of changing environmental conditions on species distributional patterns in time and space. The current paper adds a vertical dimension to the existing foram model by applying the previously used spatial parameterization of biomass as a function of temperature, light, nutrition, and competition on depth-resolved parameter fields.

Scientific quality: good

The scientific approach and methods are valid. The results are discussed appropriately but the discussion lacks a critical analysis of the model-data comparison beyond the caveats mentioned in section 4.2 “Comparison with local observations”.

Please refer to our response to reviewer 2 for proposed additions to the discussion regarding this point.

Even though the model-data-comparison revealed several discrepancies and is subject to caveats, the model produces nonetheless seasonal and vertical abundance patterns that are consistent with our current understanding and which emerge without any explicit parameterization of abundance in time and space. These patterns emerge from the model itself.

In addition, each model component (i.e., POP2, BEC, PLAFOM2.0) of the used model configuration consists of a rather complex model structure itself and rendering sensitivity experiments will be very time-consuming, expensive and non-trivial. We find that for a first try we obtain very good results.

The authors write on p. 17 line 22-23: “This vertical migration of planktonic foraminifera during their ontogeny cannot be reproduced by PLAFOM2.0 as the model parameterizations do not include the individual species’ life cycles.”. It is quite understandable that implementing true reproduction cycles of cohorts of foraminifera, including “real” population dynamics and ontogenetic migration is beyond the present manuscript. Hence, the model does not calculate absolute or relative numbers of a certain species within a certain ontogenetic size class based on reproductive success and size specific growth- and mortality-rates, but rather calculates changes in species specific carbon concentration (in mmol C m^{-3}), which can be converted to numbers afterwards.

There is nothing wrong with this approach but it means that the parameterization of PLAFOM2.0 is based on practical “sum” or “composite” parameters. These are then used to tune the model outcome to the overall data. For instance, growth of all species is approximated using a modified form of Michaelis-Menton kinetics in dependence of species specific food availability and temperature sensitivity (Fraile et al., 2008). To account for the light dependence with depth, influencing the growth of only symbiont bearing foraminifera, the authors included a “photosynthetic growth rate”. They use “......a similar approach as Doney et al. (1996) and Geider et al. (1998), who determined phytoplankton growth rates by available light and nutrients..... (p.5 line 15-17)". Such a parameterization is normally used for phytoplankton, that has orders of magnitude higher densities and cell division rates that respond very fast (within a day) and directly to light and nutrients. The symbiont bearing forams in this manuscript obey a (semi) lunar reproduction cycle and occur in densities that are very much lower, such that a "phytoplankton" kind of response cannot be expected. The authors use it as an additional tuning parameter for symbiont bearing forams next to food preference and temperature to develop species specific depth (light/nutrient) habitat preferences. Although it is a valid approach, the authors should clearly state that it is artificial.

Here, we applied a similar approach as Doney et al. (1996) and Geider et al. (1998) as a first approximation to account for a photosynthetic growth rate for the symbiont-bearing species. We are aware that a phytoplankton kind of response to light is not transferable one to one to the response of planktonic foraminifera. We made this more clear in the manuscript (p.5, lines 15-18) and we state that this approach is a first approximation, and in that way it should be considered as rather artificial. Nevertheless, we also think that this is a valid approach, given that the photosynthetic growth rate accounts in numerical terms most likely only for the smallest proportion of the total growth.

Growth is balanced by mortality, which is not a formulation for "real" mortality but another tuning parameter: "we adjusted parts of the mortality rate equation to improve the model accuracy (p. 5 line 8-9).".

Overall, there are many factors that allow tuning, e.g. "p% represents the fraction of photosynthesis contributing to growth (p.5 line 31)". Interestingly, the authors have a higher p% for T. sacculifer (0.4) than for G. ruber (0.3), where I would have done it the other way around (see my comments on these species further below).

Here, we followed Lombard et al. (2011), who also used a somewhat higher $p_{\%}$ for *T. sacculifer* (0.40) than for *G. ruber* (0.37). We performed a few short preliminary test runs using different $p_{\%}$-values but obtained the best results on a first glance by using the given parameter values. We were not able to perform a suite of sensitivity experiments with changing the $p_{\%}$-values due to the long runtime of the used complex model configuration.

Another tuning factor is the temperature dependence of the predation term: "......we followed Moore et al. (2004) and adjusted the temperature dependence of the predation term (MLpred in mmolCm−3s−1) (p.6 line 3-4). Also "....we included a stronger competitive behavior of G. bulloides by adjusting the free parameters in the competition term. (p.6 line 10-11). Having collected planktonic foraminifera by SCUBA diving for many, many years and looking at average typical blue water densities of ca. 10 specimens per m3 per species, and 3 dominant species in an assemblage, it is hard to believe that they compete with each other for resources as each of them occupies a space of only a few mm3 and they are stationary in the water column.

A good point indeed. Whether or not planktonic foraminifera compete directly is a field of active research. However, we would like to point out that even though foraminifera occur at very low densities and may never directly meet, they are still likely to compete for scarce resources. It is therefore reasonable to include a competition term in the model.

Certain boundary conditions also correct model misfits, e.g. "...zero fluxes have been replaced by half of the observed minimum flux. (p.7 line 25-26)".

All of these parameters were introduced to allow a good fit between model output and data but maybe not for the right reason. As such, we do not know how realistic this parameterization represents real planktonic foraminiferal population dynamics which is more complex (including lunar based reproduction cycles, ontogenetic migration, etc.).

This is true, but nevertheless we are able to simulate the seasonal and vertical habitat of the five considered foraminiferal

species remotely realistic using our approach. However, for a more realistic representation of planktonic foraminiferal population dynamics, PLAFOM2.0 needs to be extended by, e.g., considering the ontogenetic migration, reproduction cycles as well as additional foraminiferal species. Thus, PLAFOM2.0 will become more complex and more parameters have to be introduced. In addition, using, e.g., reanalysis data as forcing instead of a climatological forcing could also lead to a more realistic representation of the modern foraminiferal population dynamics when considering a point-by-point comparison with present-day data.
However, even if our understanding of foraminiferal population dynamics will be largely improved in the future due to, e.g., more laboratory experiments, and if we are able to properly translate those complex processes into model code, we will still only be able to provide an approximation of the real dynamics.

Winter mixing, thermocline shoaling and annual irradiation changes are probably important parameters controlling foram population dynamics just as certain density layers may be important for gamete fusion in real foram life. I’m not sure how well these features are implemented in the models.
This is a very good point and all those processes you mentioned likely affect the dynamics of the foraminiferal population. Here we used an ocean-ice-only model configuration and applied a climatological forcing to obtain our results. Hence, there is no explicit interaction between the ocean and the atmosphere and additionally an inter-annual variability of the forcing variables can be excluded. In addition, the lower the resolution of the ocean model the less well represented are processes such as winter mixing, thermocline shoaling, and upwelling. Since we now present results of a 1° ocean model simulation, most of these processes are likely better represented than in the previously used 3° simulation, not only because of a more realistic representation of the ocean physics, but also due to the higher resolution, which likely improved our model results. However, some small-scale processes, oceanic fronts, river runoff areas, and coastal upwelling regions are still not well represented. In order to analyze inter-annual variability of the foraminiferal population and to investigate how annual radiation changes influence the population dynamics, the model system should be forced with reanalysis data rather than climatologies. Furthermore, using a fully coupled model configuration initialized from reanalysis data could also provide information on how annual changes in the atmosphere feed back on the foraminiferal population dynamics. This, however, was beyond the scope of this study. Here, we actually aimed for an approach that is as simple and general as possible, such that we specifically avoided an explicit parameterization of depth. This way our approach is also easier to follow and we can more easily ensure the reproducibility of our study.

The bottom line is that, even though I appreciate the model and the manuscript a lot, I would like to see a discussion on these issues and if possible a statistical verification of the model performance. The description of the results and the discussion on modeled geographical ranges, seasonal and vertical distribution, as well as on the modeled seasonal variability of depth habitat, lacks a statistical treatment of the data. How good is the model performance and how sensitive is it to each of the model parameters?
Here, we did not perform a sensitivity study in regard of the different model parameters, first, because the runtime of this new model configuration is too long (with a model throughput of ~11-20 simulated years/day for the 3° model configuration and/or a model throughput of ~9.5 simulated years/day for the 1° model configuration depending on the machine capacities) to yield scientifically reasonable results and, second, because Fraile et al. (2008), who introduced PLAFOM (which is the base of PLAFOM2.0), already performed a sensitivity study of the free parameters. Fraile et al. (2008) modified the values chosen for the foraminifera module and quantified the sensitivity by calculating the change in the root mean square error between each sensitivity experiment and the standard run. They found that none of the parameters led to a uniform change for all species and that not surprisingly the parameter controlling the temperature tolerance range (i.e., σ)

seems to be the most sensitive parameter (see Table 3 of Fraile et al., 2008). Since PLAFOM2.0 is in its base form identical to PLAFOM, we did not feel the need to perform another sensitivity analysis and also due to the high computational costs. We added the following statement (p. 6, lines 22-24):

"A parameter sensitivity assessment for PLAFOM was carried out by Fraile et al. (2008) and since PLAFOM2.0 is based on the same underlying formulation, we consider an extensive new sensitivity assessment not essential at this stage."

I would appreciate a more quantitative treatment of the model performance instead of statements like "The predicted global distribution patterns of the five considered planktonic foraminiferal species are in good agreement with the core-top data (Figure 2) (p. 11 line 14-15)?

To perform a more quantitative model-data-comparison and to provide some measure of confidence, we now calculated the Bray-Curtis index of similarity between the model and the core-top data. For this calculation, we account for the different sizes of each species by using a relative size for each species based on the results of Schmidt et al. (2004) and recalculated the modeled relative abundances accordingly. We added this analysis to section 3.1 (p. 9, lines 11-15) to provide a more thorough model-data-comparison.

The discussion on the global distribution patterns is mostly related to temperature. What about the other parameters: food, nutrients, productivity, light, etc.?

Our results indicate that the habitat variability and the foraminiferal distributions are primarily driven by temperature and for the colder water species (*N. pachyderma*, *N. incompta*, *G. bulloides*) also by food supply. This was also shown by Fraile et al. (2008) and Kretschmer et al. (2016). Fraile et al. (2008) demonstrated that the foraminiferal distribution patterns respond most sensitively to changes in the temperature tolerance ranges of the individual species, indicating the strong temperature dependence of the foraminiferal population dynamics. Therefore, we mainly relate our results to temperature, but also discuss the food dependency extensively (see sections 4.1.3 and 4.2); the other parameters, however, seem to be less effective.

How does it compare to the "Longhurst Biogeographical Provinces". He partitioned the world oceans into provinces ("Ecological Geography of the Sea") based on the prevailing physical factors as a regulator of phytoplankton distribution, including temperature, photic depth, mixed layer depth etc. (e.g. Longhurst 1995; 1998).

The underlying parameterizations used in PLAFOM itself are based on the parameterizations used in the ecosystem model of Moore et al. (2002a) and do not include a spatial parameterization. Since Longhurst's partitioning of the ocean is more or less only descriptive, a comparison with our model results is in our understanding not appropriate. In addition, to properly compare the simulated global distribution patterns with Longhurst (1995, 1998), we would have to take into account the characteristics of each biogeographical province in the model parameterizations, which would most likely result in an overfitting.

Having "fixed" model parameters simulates so called "habitat tracking" of the forams through the seasons (but also on timescales of climate change or on glacial/interglacial cycles). This is a very important aspect to verify and would call for a section/paragraph by itself (see also Rebotim et al., 2017). For instance, on p15 line 23-25 you write "Rebotim et al. (2017) identified an annual cycle in the habitat of T. sacculifer and N. incompta in the subtropical eastern North Atlantic. Both species appear to descend in the water column from winter to spring and reach their deepest habitat in spring to summer before ascending again to a shallower depth towards winter (Rebotim et al., 2017).". How does this fit the "habitat tracking" picture? The authors could probably use observations on G. ruber and T. sacculifer for that as well. I may be wrong but I always thought that G. ruber lives closer to the surface than T. sacculifer (see also table 3 in Rebotim et al., 2017)? From laboratory experiments I know that T. sacculifer can handle living prey such as copepods much better than G. ruber while the latter seems to rely more on symbiont carbon, i.e. shows a more "autotrophic" lifestyle. Is it possible to see this in the data based on a more rigorous model-data comparison?

Our results reveal that outside their preferred habitat, where they naturally have to face a changing environment, the seasonal occurrence of both *G. ruber* (white) and *T. sacculifer* is limited to the warm surface layer, whereas in the low latitudes both species exhibit a weak seasonal cycle in their depth habitat (see Figure 5 of the manuscript). This indicates that both species adapt to changing environmental conditions by adjusting their habitat to local circumstances, which is consistent with the concept of habitat tracking. We added this to section 4.1.3 (p. 18, lines 7-17).

In addition, we are not able to derive dietary preferences from the model, as those are prescribed for the underlying model parameterizations. In the model parameterizations, we do not distinguish between the heterotrophic and/or autotrophic lifestyle of the species, just the parameters determining the preference for a food source differ slightly among the species (see Table 1 in Fraile et al., 2008). Additionally, those parameters introduced to account for the light sensitivity of *G. ruber* (white) and *T. sacculifer* with depth differ also among them (see Table 1 of the manuscript). So by prescribing light sensitivity and food preferences a similar depth ranking compared to observations already emerges from the model. Nevertheless, for a more rigorous model-data-comparison a sensitivity study regarding the species-specific food preferences should be performed. We will bear this in mind for a future model development.

The results of the point-by-point comparative analysis for each site and species as provided in the Supplement (Figures S3 and S4) are very helpful but also show that the model is far from perfect and sometimes there is a complete mismatch. I would have appreciated a sensitivity study to determine the hierarchy of factors for the different species controlling the shell export fluxes regional and seasonal (including e.g. bimodal patterns) as well as the vertical distribution (including ALD). This would probably be a paper by itself but in my view a very important one.

This is a real good and true point and we also think that such a sensitivity study would improve PLAFOM2.0. Therefore, we agree that such a study would be very important and should be considered in the future. However, due to the high computational costs it is at present not feasible to perform this analysis. In addition, such a study would require using observational data with realistic year to year variability as forcing, but also for the model validation, which would in turn require a sensitivity study for each sediment trap/plankton tow by itself.

Based on the sensitivity analysis of Fraile et al. (2008) and also on our own results it seems that temperature has the strongest influence on the foraminiferal distribution regarding both the seasonal and vertical habitat. In particular, the distribution of each individual foraminiferal species seems to react most sensitively to changes in the individual temperature tolerance ranges (see Fraile et al., 2008). However, to further assess the sensitivity of the model to the chosen parameters especially in regard to the vertical distribution of the foraminiferal species a thorough sensitivity analysis should be performed in an independent study, which we will bear in mind for the future. Nevertheless, even after a further tuning based on such a sensitivity analysis the model will be far from perfect and discrepancies between the model data and the observations may always be present, as the caveats mentioned in section 4.2 will still be valid.

Presentation quality: good/fair

Although the scientific results and conclusions are presented in a relatively clear and well-structured way it is not easy to grasp why the model underestimates e.g peak amplitude. What would happen if growth in the equation is increased or mortality is decreased? I sometimes wondered why the authors didn't play more with the model or used statistical techniques to quantify data-model mismatch (this is the reason for the "fair" mark).

As already mentioned, due to the long runtime of the model and, hence, the high computational costs we were not able to perform a thorough sensitivity analysis and just performed some very preliminary and short test runs to evaluate the model performance. In addition, since PLAFOM2.0 is based on PLAFOM, which has been tested and validated thoroughly (e.g., Fraile et al., 2008; Kretschmer et al., 2016), and since our aim was to demonstrate the applicability and the usability of PLAFOM to simulate the vertical distribution of individual foraminiferal species when combined with a complex 3D model configuration (such as CESM1.2(BGC)) without explicitly parameterizing the vertical dimension, we on purpose decided to not test what would happen if we change the given parameter setting. However, to better quantify the model-data-mismatch, we calculated the Bray-Curtis index of similarity between the model and the core-top data. This way, we can provide some measure of confidence regarding the general model performance. In addition, we also extended the discussion regarding the model-data-comparison by also considering potential mismatches due to the ocean model (p. 19-20, lines 23-5). Nevertheless, we are not entirely able to unequivocally differentiate between the different model components (i.e., POP2, BEC or PLAFOM2.0) and their individual share likely leading to the model-data-mismatch.

The number and quality of figures/tables is good and the supplementary material is very appropriate. The English language is very good.

Thank you!

Minor corrections:

On page 2 line 18-20: “............the lunar cycle and/or the structure of the water column), which influence the species-specific depth habitats (including their mean living depth and vertical migration) (e.g., Fairbanks and Wiebe, 1980; Fairbanks et al., 1982; Schiebel et al., 2001; Simstich et al., 2003; Field, 2004; Salmon et al., 2015; Rebotim et al., 2017), the only attempt to model the vertical habitat is by Lombard et al. (2011).”, and on page 17 line 20-23: “Several studies from different areas also showed that the main habitat depth of some species increases from the surface to deeper water layers during shell growth (Peeters and Brummer, 2002; Field, 2004; Iwasaki et al., 2017). Although I appreciate all the references that you list for ontogenetic migration and lunar cycle, there are only a few papers that specifically deal with very detailed population dynamics, lunar cyclicity and ontogenetic migration of planktonic forams that could/should be mentioned here (it was one of the first topics I studied when starting to work on planktonic foraminifera): Bijma et al., 1990; Bijma, 1991; Bijma and Hemleben, 1994; Bijma et al., 1994; Hemleben and Bijma, 1994; Schiebel et al., 1997. In my opinion, these references would fit best on p. 19 line 32-34: “........and by explicitly parameterizing the ontogeny of each individual planktonic foraminifera, thus, by considering the changes in the species’ life cycles with depth, could considerably improve the model.”.

Thank you for pointing this out. We added the mentioned references accordingly (see p. 22, lines 17-18).

P. 9 line 27-30: “Although seasonal changes in the modeled foraminiferal peak fluxes with temperature are evident, all five species exhibit an almost constant peak amplitude (i.e., the maximum concentration divided by the annual mean) in their preferred habitat, which is, i.a., limited by temperature. Outside their preferred living conditions the peak amplitudes increase for most of the species considerably (Figure 3).”. It has not become clear to me what it means when “peak amplitude” is large or small in terms of real population dynamics (“bloom”?) and what it means in terms of model performance?

The maximum seasonal abundance or flux in itself is not a very useful parameter that can be compared among different regions/studies. Population dynamics can be much better (if not only) described in terms of deviations from the mean conditions, for instance, it would be impossible to recognize a bloom event in the absence of knowledge about the mean conditions. Moreover, any seasonal or vertical weighting of the proxy signal – and constraining this was the main motivation to develop the model – varies as a function of the relative departure from the mean. To be more clear about this, we rewrote this paragraph and provided a better explanation (p. 10, lines 21-26):

"To allow for a global comparison of the modeled and observed flux seasonality, we standardized peak amplitudes for each foraminiferal species, i.e., the species' maximum concentration divided by its annual mean. This reveals that the timing of the modeled foraminiferal peak abundances varies with temperature, but all five species exhibit an almost constant peak amplitude in their preferred thermal habitat. Outside their preferred living conditions, modeled peak amplitudes considerably increase for most of the species(Figure 3), thus, the species experience a strong deviation from their annual mean living conditions and likely occur only at times when the ambient conditions are (close to) their optima."

P. 14 line 26-28: "This would explain why the highest modeled concentrations of T. sacculifer occur at shallower depths compared to G. ruber (white) (see Figures 4d-e and 5d-e).". Strictly speaking this doesn't explain it because this is what you put into the model in the first place (see my comments above).

Actually, this is a perfect example how the habitat emerges from the model. We only prescribe the light sensitivity and still obtain the right depth ranking. Throughout the model code, we specifically did not specify the depth ranking. We rewrote this sentence to avoid confusion (p. 16, lines 8-11):

"This is to some degree also indicated in our results, as on average the highest modeled concentrations of T. sacculifer occur at shallower depths compared to G. ruber (white) (see Figures 4d-e and 5d-e). However, at some locations both model and observations show the reverse (see Figure S4 and, e.g., Rippert et al., 2016; Rebotim et al., 2017), indicating that this depth ranking is not globally valid. "

P. 16 line 18: "G. bulloides, however, is found year-round close to the surface along the.....". Write the genus name full at the beginning of a sentence.

Done and applied throughout the manuscript.

References:

- Bijma, J., Erez, J. and Hemleben, C. (1990) Lunar and semi-lunar reproductive cycles in some spinose planktonic foraminifers. Journal of Foraminiferal Research 20, 117-127.
- Bijma, J. (1991) Lunar pulses of carbonate output by spinose planktonic Foraminifera, in: Reid, P.C., Turley, C.M., Burkill, P.H. (Eds.), Protozoa and Their Role in Marine Processes. NATO ASI Series G: Ecological Sciences. Elsevier, Plymouth, pp. 353-354.
- Bijma, J. and Hemleben, C. (1994) Population dynamics of the planktic foraminifer Globigerinoides sacculifer (Brady) from the central red sea. Deep-sea research part I: oceanographic research papers 41, 485-510.
- Bijma, J., Hemleben, C. and Wellnitz, K. (1994) Lunar-influenced carbonate flux of the planktic foraminifer Globigerinoides sacculifer (Brady) from the central red sea. Deep-sea research part I: oceanographic research papers 41, 511-530.
- Hemleben, C. and Bijma, J. (1994) Foraminiferal population dynamics and stable carbon isotopes., in: Zahn, R., Pedersen, T.F., Kaminski, M., Labeyrie, L. (Eds.), Carbon Cycling in the Glacial Ocean: Constraints on the Ocean's Role in Global Change. Elsevier, Fellhorst, pp. 145-166.
- Longhurst, A. (1995) Seasonal cycles of pelagic production and consumption. Progress in Oceanography 36, 77-167.
- Longhurst, A. (1998) Ecological Geography of the Sea ACADEMIC PRESS
- Schiebel, R., Bijma, J. and Hemleben, C. (1997) Population dynamics of the planktic foraminifer Globigerina bulloides from the North Atlantic. Deep Sea Research 44, 1701-1713.
- Fraile, I., M. Schulz, S. Mulitza, and M. Kucera (2008), Predicting the global distribution of planktonic foraminifera using a dynamic ecosystem model, *Biogeosciences*, *5*, 891-911.
- Kretschmer, K., M. Kucera, and M. Schulz (2016), Modeling the distribution and seasonality of *Neogloboquadrina pachyderma* in the North Atlantic Ocean during Heinrich Stadial 1, *Paleoceanography*, *31*, 986-1010.
- Lombard, F., L. Labeyrie, E. Michel, L. Bopp, E. Cortijo, S. Retailleau, H. Howa, and F. Jorissen (2011), Modelling planktic foraminifer

growth and distribution using an ecophysiological multi-species approach, *Biogeosciences*, *8*, 853-873.

- Moore, J. K., S. C. Doney, J. A. Kleypas, D. M. Glover, I. Y. Fung (2002a), An intermediate complexity marine ecosystem model for the global domain, *DSR II*, *49*, 403-462.
- Schmidt, D. N., S. Renaud, J. Bollmann, R. Schiebel, and H. R. Thierstein (2004), Size distribution of Holocene planktic foraminifer assemblages: biogeography, ecology and adaptation, *Marine Micropaleontology*, *50*, 319-338.

Response to Referee #4:

We would like to thank the reviewer for the constructive comments and suggestions, which helped us to greatly improve our manuscript. Please find, in the following, the original comments in black and our responses in light blue; the indicated page and line numbers refer to the revised manuscript.

Referee #4 comments:

This paper builds upon preexisting work modeling planktonic foram distributions in the global oceans via a coupling to CESM's ocean model. The goal is to better understand how the vertical distribution of foraminifera species varies seasonally and throughout larger climatic changes in the ocean. The paper is generally well written, clear, and broadly does a fine job demonstrating the usefulness of the model. It is also very thorough in its examination of the model's performance against available data. The methods seem robust and I can recommend that with some minor revisions (mostly grammar and clarity) the paper be published in Biogeosciences.

I must acknowledge that I am not an expert on the biogeochemistry of planktonic forams in any way and hope the other reviewers can address the methods and parameterizations employed in this paper in particular. I can instead comment on the benefit of this work and the need for such proxy system models for the robust interpretation of paleoceanographic records via the use of PLAFOM2.0 + CESM1.2. To that end, my first major comment is that the authors can focus more in the introduction and conclusion on the body of literature developing forward models, or proxy system models, for understanding paleoclimate proxies and introduce this work as a part of this group of literature. A major effort has been underway to build proxy system models, link them with GCMs, and make these models publicly available, and this paper is absolutely in this category and should make as much clear.

See for example:

- Dee, S., et al. "PRYSM: An open-source framework for PRoxY System Modeling, with applications to oxygen-isotope systems." Journal of Advances in Modeling Earth Systems 7.3 (2015): 1220-1247.
- Evans, Michael N., et al. "Applications of proxy system modeling in high resolution paleoclimatology." *Quaternary Science Reviews* 76 (2013): 16-28.
- Schmidt, Gavin A. "Forward modeling of carbonate proxy data from planktonic foraminifera using oxygen isotope tracers in a global ocean model." *Paleoceanography* 14.4 (1999): 482-497.

We agree that over the last decades proxy system/formation models have become more and more important for understanding paleoclimate proxies and that PLAFOM2.0 belongs to a series of different proxy system/formation models. We briefly introduced PLAFOM2.0 as part of this large group of proxy system models in section 2.1 (page 3, lines 22-24): *"Thus, PLAFOM2.0, as belonging to a suite of proxy system models (e.g., Pollard and Schulz, 1994; Schmidt, 1999; Fraile et al., 2008; Evans et al., 2013; Dee et al., 2015; Völpel et al., 2017), will aid the interpretation of paleoclimate reconstructions."*

You might also consider mentioning (in the intro or discussion) the potential for PLAFOM to assist in data assimilation exercises for periods extending back further than the last millennium, for example. A number of papers look at the impacts of using process-based models in the DA framework and this is another application of your model. See work of Hugues Goosse's lab (e.g. Goosse, Hugues, et al. "Reconstructing surface temperature changes over the past 600 years using climate model simulations with data assimilation." *Journal of Geophysical Research: Atmospheres* 115.D9 (2010)), as well as:

- Steiger, Nathan J., et al. "Assimilation of time-averaged pseudoproxies for climate reconstruction." *Journal of Climate* 27.1 (2014): 426-441.

- Dee, Sylvia G., et al. "On the utility of proxy system models for estimating climate states over the common era." *Journal of Advances in Modeling Earth Systems* 8.3 (2016):
- Hakim, Gregory J., et al. "The last millennium climate reanalysis project: Framework and first results." *Journal of Geophysical Research: Atmospheres* 121.12 (2016): 6745-6764

Thank you for pointing this out. We agree that PLAFOM2.0 has the potential to be used in the data assimilation framework and we added a statement in this regard to section 2.1 (p. 3, lines 24-26):

"In addition, PLAFOM2.0 has the potential to be used in a 25 paleoclimate data assimilation framework (see, e.g., Goosse et al., 2010; Steiger et al., 2014; Dee et al., 2016; Hakim et al., 2016)."

In Section 4, it would be nice if the authors could provide a more quantitative data-model comparison technique—you identify areas where the model does not well simulate the observations and Figure 2 summarizes this to some extent, but perhaps you could include an additional table or figure or even compute something like the RMSE for each oceanic province? Or the mean RMSE for each species over all of the locations where core-top data exist?

Please refer to our response to a similar comment by reviewer #1 regarding a more quantitative model-data-comparison.

Finally, in the discussion, you assert (correctly) that your new model is a powerful tool for separating the independent influences of habitat and climate on foram reconstructions. I think this paper would be greatly strengthened by a demonstration of this. Can you take a well-known and vetted reconstruction and apply this model in a meaningful way to reassess the climatic interpretation? I think this would show the power of forward modeling in this field to make more robust assessments of uncertainties in oceanic climate changes... And I think having this demonstration would add weight to the assertions you make in your Discussion section.

This is a good point and we agree that such a demonstration would add to a better understanding of climate change. In a next study, we plan on performing a model run with, e.g., Last Glacial Maximum climate conditions to test the applicability of our modeling approach. Here, in this study we simply wanted to test if the existing planktonic foraminifera model is able to reproduce species-specific habitats when combined with a model configuration that resolves the vertical.

Minor / Line by Line comments: (Page-Line)

2-10 awkward paragraph break, consider revising

We agree and deleted the paragraph break.

2-13 comma after perspective,

Done.

2-20 Have you investigated/reviewed Schmidt et al., 1998, 1999? These papers I believe address vertical migration of foram species in the water column—worth checking/citing if appropriate.

- Schmidt, Gavin A. "Oxygen-18 variations in a global ocean model." *GRL* 25.8 (1998): 1201-1204.
- Schmidt, Gavin A. "Forward modeling of carbonate proxy data from planktonic foraminifera using oxygen isotope tracers in a global ocean model." *Paleoceanography* 14.4 (1999): 482-497.

Thank you for referring to those two studies. In both studies, Schmidt does unfortunately not address the vertical migration of foraminifera. Schmidt (1998, 1999) investigates the distribution of oxygen isotopes in seawater and subsequently calculates equilibrium calcite values based on different temperature equations. This, however, is beyond the scope of our present study and, hence, citing those studies is not appropriate.

2-26 need comma after behavior.

Done.

Check for needed commas and small grammatical errors throughout text.

Done.

3-6 comma after estimate,

Done.

3-13 this phrase is awkward, revise (“with the biogeochemical model being enabled”)

We revised the phrase as follows (p. 3, lines 9-11):

“[…] as an off-line module into the ocean component of the Community Earth System Model, version 1.2.2 (CESM1.2; Hurrell et al., 2013), with active ocean biogeochemistry (which is denoted as CESM1.2(BGC) configuration).”

3-15 change “aimed for” to ‘aimed to’

Done.

3-16 change “at geologic timescales” to “ON geologic timescales”

Done.

Check for similar awkward language throughout.

Done.

3-23 comma after configuration,

Done.

3-30 no paragraph break.

Done.

4-9 what do you mean by ‘data models’ for the atmosphere, etc.? Are you not using the fully coupled simulations and using some kind of statistical representation of the other components?

The CESM data models are “non-active” model components that read external data, modify that data (e.g., interpolate that data in time and space), and subsequently return the final data fields to the coupler. In this study, we did not perform a fully coupled simulation. Here we analyze an ocean-ice-only simulation with active ocean biogeochemistry coupled to data models for the atmosphere, land, and river routing. Since “data model” is a common term in the CESM model community, we also used it to be consistent with other publications using the CESM1.2(BGC) configuration. However, for a better understanding, we revised the sentence as follows (p.4, lines 10-12):

“Here we performed an ocean-ice-only simulation with active ocean biogeochemistry, whereby the ocean model is coupled to both the sea ice model and data models for the atmosphere, land, and river routing, which provide the required input data for the simulation.”

Heading 2.4 consider changing this to “Coupled GCM Setup” ?

Since our results are based on an ocean-ice-only simulation, a heading change to “Coupled GCM setup” is not appropriate. Nevertheless, we changed heading 2.4 to “Model simulation”, which is more accurately describing this section.

7-15 missing space before new sentence.

Done.

8-21 comma after ‘life cycle,’

Done.

Throughout section 3, be extremely clear about whether you are referring to observations vs. the model simulation of foram distributions/abundances etc. The reader gets a bit lost in the data-model comparison here unless that’s super clear.

In section 3, we actually just describe model results and do not provide a model-data-comparison. To be more concise and clear about that, we revised this section accordingly. In addition, we also revised section 4 to be more clear about when we refer to observations and/or model output.

16-29 no comma after ‘data’

Done.

16-30 this is a run-on sentence—consider shortening/rewriting

We revised this run-on sentence by splitting it into two parts (p. 18, lines 29-31):

“The emergence of seasonal and vertical habitat patterns consistent with observational data provides important support for our modeling approach. Nevertheless, a more detailed comparison with observations is warranted to gain further insight into the model behavior.”

I appreciate the thorough discussion of the model – data comparison limitations on page 17.

Thank you!

Figure 5 has some strange cropping issues along top margin.

Thank you for pointing this out. We checked for this and adjusted Figure 5 accordingly.

References:

- Fraile, I., M. Schulz, S. Mulitza, and M. Kucera (2008), Predicting the global distribution of planktonic foraminifera using a dynamic ecosystem model, *Biogeosciences*, *5*, 891-911.
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Modeling seasonal and vertical habitats of planktonic foraminifera on a global scale

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Abstract. Species of planktonic foraminifera exhibit specific seasonal production patterns and different preferred vertical habitats. The seasonality and vertical habitats are not constant throughout the range of the species and changes therein must be considered when interpreting paleoceanographic reconstructions based on fossil foraminifera. However, ~~A~~accounting for the effect of vertical and seasonal habitat tracking on foraminifera proxies at times of climate change from proxy data alone is difficult because it requires independent fossil evidence. An alternative that could reduce the bias in paleoceanographic reconstructions is to predict species-specific habitat shifts under climate change using an ecosystem modeling approach. To this end, we present a new version of a planktonic foraminifera model, PLAFOM2.0, embedded into the ocean component of the Community Earth System Model, version 1.2.2. This model predicts monthly global concentrations of the planktonic foraminiferal species: *Neogloboquadrina pachyderma*, *N. incompta*, *Globigerina bulloides*, *Globigerinoides ruber* (white), and *Trilobatus sacculifer* throughout the world ocean, resolved in 24 vertical layers to $250\,\mathrm{m}$ depth. The resolution along the vertical dimension has been implemented by applying the previously used spatial parameterization of carbon biomass as a function of temperature, light, nutrition, and competition on depth-resolved parameter fields. This approach alone results in the emergence of species-specific vertical habitats, which are spatially and temporally variable. Although an explicit parameterization of the vertical dimension has not been carried out, the seasonal and vertical distribution patterns predicted by the model are in good agreement with sediment trap data and plankton tow observations. In the simulation, the colder-water species *N. pachyderma*, *N. incompta*, and *G. bulloides* show a pronounced seasonal cycle in their depth habitat in the polar and subpolar regions, which appears to be controlled by food availability. During the warm season, these species preferably occur in the subsurface (below $50\,\mathrm{m}$ water depth), while towards the cold season they ascend through the water column and are found closer to the sea surface. The warm-water species *G. ruber* (white) and *T. sacculifer* exhibit a less variable shallow depth habitat with highest carbon biomass concentrations within the top $40\,\mathrm{m}$ of the water column. Nevertheless, even these species show vertical habitat variability and their seasonal occurrence outside the tropics is limited to the warm surface layer that develops at the end of the warm season. The emergence in PLAFOM2.0 of species-specific vertical habitats that are consistent with observations indicates that the population dynamics of planktonic foraminifera species may be driven by the same factors in time, space, and with depth, in which case the model can provide a reliable and robust tool to aid the interpretation of proxy records.

1 Introduction

Planktonic foraminifera are found throughout the open ocean, where they inhabit roughly the top 500 m of the water column (Fairbanks et al., 1980, 1982; Kohfeld et al., 1996; Kemle-von Mücke and Oberhänsli, 1999; Mortyn and Charles, 2003; Field, 2004; Kuroyanagi and Kawahata, 2004; Bergami et al., 2009; Wilke et al., 2009; Pados and Spielhagen, 2014; Iwasaki et al., 2017; Rebotim et al., 2017). Their calcareous shells, preserved in ocean sediments, are widely used to reconstruct past climate conditions. To do so, information about their habitat including their horizontal and vertical distribution are needed. It is known from observational data that the prevailing environmental conditions, such as temperature, stratification, light intensity, and food availability, affect the growth and distribution of the individual planktonic foraminifera (Fairbanks et al., 1980, 1982; Bijma et al., 1990b; Watkins et al., 1996; Schiebel et al., 2001; Field, 2004; Kuroyanagi and Kawahata, 2004; Žarić et al., 2005; Salmon et al., 2015; Rebotim et al., 2017).

Based on stratified plankton tow and sediment trap data the seasonal succession of planktonic foraminifera species has been assessed on a local/regional scale (e.g., Fairbanks and Wiebe, 1980; Kohfeld et al., 1996; Wilke et al., 2009; Jonkers et al., 2013; Jonkers and Kučera, 2015), whereas for a broader regional/global perspective, modeling approaches have been used to study the seasonal variations in the surface (mixed) layer of the ocean (Žarić et al., 2006; Fraile et al., 2008, 2009a, b; Lombard et al., 2011; Kretschmer et al., 2016). Comparatively less is known about the depth habitat of planktonic foraminifera species and how it varies seasonally. Although previous studies identified different environmental and ontogenetic factors (i.a., temperature, chlorophyll *a* concentration, the lunar cycle and/or the structure of the water column), which influence the species-specific depth habitats ~~(~~including their mean living depth and vertical migration~~)~~ (e.g., Fairbanks and Wiebe, 1980; Fairbanks et al., 1982; Schiebel et al., 2001; Simstich et al., 2003; Field, 2004; Salmon et al., 2015; Rebotim et al., 2017), the only attempt to model the vertical habitat is by Lombard et al. (2011).

It is well known that species-specific habitats vary seasonally and spatially depending on the prevailing climatic conditions (Mix, 1987; Mulitza et al., 1998; Ganssen and Kroon, 2000; Skinner and Elderfield, 2005; Jonkers and Kučera, 2015). Yet, despite this evidence for a variable habitat, it is often assumed in paleoceanographic studies that the habitat of planktonic foraminifera is constant, i.e., it does not change in time and space, potentially leading to erroneous estimates of past climate conditions. Jonkers and Kučera (2017) recently highlighted how foraminifera proxies are affected by habitat tracking and showed that by not accounting for this behavior, spatial and temporal trends in proxy records may be underestimated. Given the habitat variability in planktonic foraminifera, it is more than likely that a climate-dependent offset from mean annual sea surface conditions results not only from a seasonal, but also from depth habitat variability due to changes in ambient conditions. Such vertical habitat variability was shown by Rebotim et al. (2017), who investigated parameters controlling the depth habitat of planktonic foraminifera in the subtropical eastern North Atlantic. In line with studies from other regions of the world ocean (e.g., Fairbanks et al., 1982; ~~Ortiz et al., 1995;~~ Bijma et al., 1990a; Ortiz et al., 1995; Schiebel et al., 2001; Field, 2004; Salmon et al., 2015), Rebotim et al. (2017) identified distinct species-specific depth habitats, but they also showed that the habitats vary on lunar and seasonal time scales and in response to temperature, chlorophyll *a*, and other environmental factors. Evidence for variable depth habitats at least on a regional scale has emerged from studies in other regions (Watkins et al., 1998; Peeters and Brummer, 2002; Kuroyanagi and Kawahata, 2004).

These observations underline the necessity to consider species-specific habitats and their variability on a global scale to increase the reliability of paleoceanographic reconstructions. However, a global assessment of species-specific depth habitat variability in time and space and the potential underlying control mechanisms is lacking. Since the observational data coverage of the global ocean is too sparse to provide in this regard a broad general estimate, we apply an ecosystem modeling approach to predict the vertical and seasonal distribution of planktonic foraminifera on a global scale.

2 Methods

2.1 Approach

To predict the seasonally varying global species-specific depth habitat of planktonic foraminifera, we modified the previously developed PLAFOM model (Fraile et al., 2008; Kretschmer et al., 2016), which is implemented as an ~~on~~off-line ~~planktonic foraminifera~~ module ~~embedded~~ into the ocean component of the Community Earth System Model, version 1.2.2 (CESM1.2; Hurrell et al., 2013), with ~~the biogeochemical model being enabled~~ active ocean biogeochemistry (~~i.e., the~~ which is denoted as CESM1.2(BGC) configuration). This model system simulates the monthly concentrations of five modern planktonic foraminiferal species, which are widely used in paleoceanographic reconstructions. The original approach of Fraile et al. (2008) and Kretschmer et al. (2016) aimed ~~for~~ to predict~~ing~~ the distribution of planktonic foraminifera in the surface mixed layer ~~at~~ on geological time scales. This model version has been successfully used to assess the effect of changing environmental conditions on species distributional patterns in time and space (Fraile et al., 2009a, b; Kretschmer et al., 2016) and to aid in interpreting paleoceanographic records regarding seasonal production shifts in the geological past (Kretschmer et al., 2016), but could not provide any information about depth. To implement the vertical dimension, we used an approach, in which we first updated PLAFOM (hereafter referred to as PLAFOM2.0) by including light dependency for symbiont-bearing planktonic foraminifera and then applied the previously used spatial parameterization of carbon biomass as a function of temperature, nutrition, and competition, together with light, on depth-resolved parameter fields. By combining PLAFOM2.0 with the CESM1.2(BGC) configuration (hereafter referred to as CESM1.2(BGC+PLA) configuration), the vertical dimension can be resolved throughout the ocean, with 24 layers in the top 250 m. Thus, PLAFOM2.0, as belonging to a suite of proxy system models (e.g., Pollard and Schulz, 1994; Schmidt, 1999; Fraile et al., 2008; Evans et al., 2013; Dee et al., 2015; Völpel et al., 2017), will aid the interpretation of paleoclimate reconstructions. In addition, PLAFOM2.0 has the potential to be used in a paleoclimate data assimilation framework (see, e.g., Goosse et al., 2010; Steiger et al., 2014; Dee et al., 2016; Hakim et al., 2016).

2.2 CESM1.2(BGC) configuration

We used the CESM1.2(BGC) configuration (Moore et al., 2013; Lindsay et al., 2014) as code base. This configuration includes the Biogeochemical Elemental Cycling (BEC) model (Moore et al., 2004, 2006; Krishnamurthy et al., 2007; Moore and

Braucher, 2008), which is based on the upper ocean ecosystem model of Moore et al. (2002a, b) coupled to a biogeochemistry model based on the Ocean Carbon Model Intercomparison Project (OCMIP; Doney et al., 2006).

The BEC model includes various potentially growth-limiting nutrients (nitrate, ammonium, phosphate, dissolved iron, and silicate), three explicit phytoplankton functional types (diatoms, diazotrophs, pico/nano phytoplankton), a partial calcifier class (representing coccolithophores), a single adaptive zooplankton class, dissolved organic matter, sinking particulate detritus, and full carbonate system thermodynamics (Moore et al., 2004, 2013). Phytoplankton growth rates are controlled by temperature, light, and available nutrients (Moore et al., 2002b, 2004). The single zooplankton pool grazes on all phytoplankton types, whereby the routing of grazed material varies depending on the type of prey (Moore et al., 2004, 2013). For further details, we refer to Moore et al. (2002b, 2004, 2013).

The BEC model has been embedded into the ocean component of CESM, version 1.2.2. CESM1.2 is a fully coupled climate model consisting of several components including the atmosphere, ocean, land, and sea ice (Hurrell et al., 2013), whereby the geophysical fluxes among the components are exchanged through a central coupler (Craig et al., 2012). Here we performed an ocean-ice-only simulation~~s~~ with active ocean biogeochemistry, whereby ~~using~~ the ocean model is coupled to both the sea ice model and data models for the atmosphere, land, and river routing, which provide the required input data for the simulation.

The CESM1.2 ocean component is the Parallel Ocean Program, version 2 (POP2; Smith et al., 2010; Danabasoglu et al., 2012), ~~which is a z-level hydrostatic primitive equation model. Here we use the coarse-resolution configuration of POP2 (Shields et al., 2012), where the longitudinal~~ with a zonal resolution ~~amounts to 3.6°~~ of 1° and ~~the latitudinal~~ an increased meridional resolution ~~varies between 1° and 2°, with a finer resolution~~ of 0.27° near the equator. POP2 employs a non-uniform dipolar grid with the North Pole being displaced into Greenland. With a total number of 60 vertical levels, the grid spacing is fine near the surface (10 levels in the top 100 m) and increases with depth to 250 m near the bottom. The sea ice component of CESM1.2 is the Community Ice Code, version 4 (CICE4; Hunke and Lipscomb, 2008; Holland et al., 2012), which uses the same horizontal grid as the ocean model.

2.3 PLAFOM2.0

This new model version, PLAFOM2.0, considers the polar species *Neogloboquadrina pachyderma*, which is supplemented by the subpolar species *N. incompta* (sensu Darling et al., 2006) and *Globigerina bulloides* as well as by the warm-water algal symbiont-bearing species *Globigerinoides ruber* (white) and *Trilobatus sacculifer* (sensu Spezzaferri et al., 2015). Those species have been chosen as they can be considered to represent a large portion of the planktonic foraminiferal biomass in the surface ocean (for further details see Kretschmer et al., 2016). The different planktonic foraminifera species were added to the ocean component of CESM1.2 as optional passive tracers with the requirement that the BEC model is active.

PLAFOM2.0 is driven by temperature, the available food sources (including zooplankton, diatoms, small phytoplankton, and organic detritus), and also light availability, whereby the latter only matters with regard to the growth of the two algal symbiont-bearing species (Erez, 1983; Jørgensen et al., 1985; Gastrich, 1987; Gastrich and Bartha, 1988) and *G. bulloides*, which according to the latest findings hosts the picocyanobacterium *Synechococcus* as a photosynthesizing endobiont (Bird et al., 2017). *Synechococcus* is known to be important for cyanobacterial photosynthesis in marine and freshwater ecosystems (Ting et al., 2002; Jodłowska and Śliwińska, 2014).

The food preferences and temperature tolerance limits for each species have been derived from sediment trap data and culturing experiments (see Fraile et al., 2008, for details). Changes in the foraminifera carbon concentration for each species are determined as follows:

$$\frac{dF}{dt} = (GGE \cdot TG) - ML \qquad (1)$$

where F is the foraminifera carbon concentration (in $\mathrm{mmol\,C\,m^{-3}}$), GGE (gross growth efficiency) is the portion of grazed matter that is incorporated into foraminiferal carbon biomass, TG represents total grazing (i.e., the growth rate in $\mathrm{mmol\,C\,m^{-3}s^{-1}}$), and ML denotes mass loss (i.e., the mortality rate in $\mathrm{mmol\,C\,m^{-3}s^{-1}}$). To properly simulate the vertical distribution of each considered planktonic foraminifera, we included light dependency and modified parts of the parameterizations of the foraminiferal species concentration. Therefore, we extended the growth rate equation by not only considering food availability and temperature sensitivity, but also light intensity to define growth. Additionally, we adjusted parts of the mortality rate equation to improve the model accuracy. In the following, the performed modifications are described in detail in regard to the growth and mortality rates. The modifications compared to the earlier model version are summarized in Table 1.

2.3.1 Growth rate

The growth rate depends on the available food and temperature sensitivity of each foraminiferal species as well as on light for the species with algal symbionts and/or cyanobacterial endobionts. To account for the light dependence with depth influencing the growth of *G. bulloides* and of the spinose species *G. ruber* (white) and *T. sacculifer*, we included a photosynthetic growth rate. As a first-order estimate, ~~W~~we applied a similar approach as Doney et al. (1996) and Geider et al. (1998), who determined phytoplankton growth rates based on ~~by~~ available light and nutrient~~s~~ conditions, which have been accordingly ~~as~~ used in the BEC model (Moore et al., 2002b, 2004). We are aware that a phytoplankton response to light is not directly transferable to planktonic foraminifera, but we argue that as a first approximation this is a valid approach.

Photosynthesis depends on light availability and temperature. This co-dependency can be expressed as follows:

$$P_{F,photo} = P_{F,max} \cdot \left[1 - \exp\left(\frac{-\alpha_{PI} \cdot I_{PAR}}{P_{F,max}}\right)\right]$$

where $P_{F,photo}$ is the foraminiferal specific rate of photosynthesis (in $\mathrm{s^{-1}}$) and $P_{F,max}$ is the maximum value of $P_{F,photo}$ at temperature T (in $\mathrm{s^{-1}}$), calculated as:

$$P_{F,max} = P_{F,0} \cdot T_{func}$$

α_{PI} is the initial slope of the photosynthesis-light curve (in $\mathrm{m^2\,W^{-1}s^{-1}}$) (Table 1), I_{PAR} is the average irradiance over the mixed layer depth provided by the ecosystem model (in $\mathrm{W\,m^{-2}}$), $P_{F,0}$ represents the maximum foraminiferal growth rate at a specific temperature T_0 (in $\mathrm{s^{-1}}$) (Table 1), and T_{func} is the temperature response function (dimensionless). The temperature function is defined as:

$$T_{func} = q_{10}^{\frac{T-T_0}{10}} \tag{2}$$

with a q_{10} value of 1.5 (Sherman et al., 2016) and T being the ambient ocean temperature (in K) and T_0 the reference temperature of $303.15\,\mathrm{K}$.

The photosynthetic growth rate, P_F~~,~~ (in $\mathrm{mmol\,C\,m^{-3}s^{-1}}$), can finally be determined as follows:

$$P_F = P_{F,photo} \cdot F \cdot p_{\%}$$

where $p_{\%}$ represents the fraction of photosynthesis contributing to growth (see Table 1).

2.3.2 Mortality rate

The mortality rate is determined by respiration loss, predation by higher trophic levels, and competition among species. To improve the seasonal patterns in the foraminiferal carbon biomass for low temperatures, we followed Moore et al. (2004) and adjusted the temperature dependence of the predation term (ML_{pred} in $\mathrm{mmol\,C\,m^{-3}s^{-1}}$):

$$ML_{pred} = f_{mort2} \cdot T_{func} \cdot F_p^2$$

where f_{mort2} represents the quadratic mortality rate ~~in~~ (in $\mathrm{s^{-1}(mmol\,C\,m^{-3})^{-1}}$), T_{func} is the temperature response function (dimensionless) used for scaling, and F_p (in $\mathrm{mmol\,C\,m^{-3}}$) is used to limit the planktonic foraminifera mortality at very low carbon biomass levels. Compared to Fraile et al. (2008), here predation is scaled by Eq. (2), a temperature function using a q_{10} value of 1.5 (Sherman et al., 2016).

Additionally, we included a stronger competitive behavior of *G. bulloides* by adjusting the free parameters in the competition term. In PLAFOM2.0, competition (ML_{comp} in $\mathrm{mmol\,C\,m^{-3}s^{-1}}$) is defined as follows:

$$ML_{comp} = \sum_i \left[F_p \cdot \frac{cl_{ij} \cdot F_i \cdot d}{F_i \cdot d + 0.1} \right]$$

with F_i being the concentration of the foraminiferal species exerting competition, cl_{ij} the maximum competition pressure of species i upon species j, and d the constant controlling the steepness of the Michaelis-Menten relationship for competition. In comparison with Kretschmer et al. (2016), we only modified the parameter cl_{ij} for *N. incompta*, *G. bulloides*, and *G. ruber* (white) (Table 1).

We added the present implementation of PLAFOM2.0 to the code trunk of POP2 as a separate module. Additionally, the food sources for the planktonic foraminifera species are computed in the ecosystem model and instantly passed to PLAFOM2.0 to calculate the foraminifera carbon concentration. A parameter sensitivity assessment for PLAFOM was carried out by Fraile et al. (2008) and since PLAFOM2.0 is based on the same underlying formulation, we consider an extensive new sensitivity assessment not essential at this stage. For a more detailed description of the planktonic foraminifera model and its behavior on a regional/global scale in the surface mixed layer, we refer to Fraile et al. (2008) and Kretschmer et al. (2016).

2.4 Model ~~setup~~ simulation

To test the model, we performed a preindustrial-control experiment. Therefore, we derived the initial ocean and sea ice states from an ocean-ice-only simulation, which did not include the BEC ocean biogeochemistry. This model integration was spun-up from rest for ~~1250~~ 300 years to approach a quasi-steady state by using a climatological forcing (based on atmospheric observations and reanalysis data) as repeated normal year forcing. Heat, freshwater, and momentum fluxes at the sea surface are based on the atmospheric data sets developed by Large and Yeager (2004, 2009) and implemented following the CORE-II-protocol (Coordinated Ocean-ice Reference Experiment) suggested by Griffies et al. (2009).

The oceanic and sea ice tracer fields (such as potential temperature, salinity, and ice area) resulting from the end of this 300-year-long spin-up run were used to initialize the CESM1.2(BGC+PLA) preindustrial-control simulation. The biogeochemical tracer fields (such as nutrients) were, i.a., initialized from ~~data-based~~ climatologies. For instance, initial nutrient (phosphate, nitrate, silicate) distributions were taken from the World Ocean Atlas 2009 (WOA09; Garcia et al., 2010), initial values for dissolved inorganic carbon and alkalinity are from the Global Ocean Data Analysis Project (GLODAP; Key et al., 2004), whereas zooplankton, phytoplankton pools, and dissolved organic matter have been initialized uniformly at low values (Moore et al., 2004). Additionally, each planktonic foraminiferal species was also initialized uniformly at low values assuming the same (vertical) distribution as the zooplankton component of the BEC model. Furthermore, the atmospheric deposition of iron and dust is based on the climatology of Luo et al. (2003).

The CESM1.2(BGC+PLA) preindustrial-control simulation was integrated for ~~2~~300 years to reach stable conditions in the ocean biogeochemistry in the upper $500\,\mathrm{m}$ of the water column (see Figure S1 in the Supplement). Since this simulation has been forced and/or initialized based on climatologies, inter-annual variability and forcing trends can be excluded and, therefore, we focus our analysis on the model output of only one year, here of year ~~2~~300.

2.5 Comparison to observations

To validate the model performance, we compare the simulated spatial and temporal distributions of the considered planktonic foraminiferal species with data from core-tops, sediment traps, and plankton tows (Figure 1). Based on data availability, we focus our analysis on distinct regions distributed over the world ocean covering all climate zones from the poles to the tropics.

2.5.1 Core-top data

To examine the spatial pattern of the five considered planktonic foraminiferal species, we compared the model predictions with fossil data by using in total ~~2844~~ 2896 core-top samples distributed over all oceans (Figure 1a). We combined the Brown University Foraminiferal Database (Prell et al., 1999) with the data assembled by the MARGO project (Kucera et al., 2005), and the data sets provided by Pflaumann et al. (1996, 2003). For the comparison, we recalculated the relative abundances of the faunal assemblages by only considering those five species used in PLAFOM2.0. Similarity between the simulated and observed abundances was quantified using the Bray-Curtis index of similarity (b_{jk} in %) between the relative abundances of the core-top data and the modeled data at the respective sample locations:

$$b_{jk} = \left(1 - \frac{1}{2} \cdot \sum_{i=1}^{5} |x_{ji} - x_{ki}|\right) \cdot 100\%$$

Here x_{ji} and x_{ki} are the modeled and observed relative abundances (with values between 0 and 1) of each species i at the given core-top locations, respectively. Note that for the calculation of the modeled relative abundances, we accounted for the different sizes of each individual species by multiplying the modeled annual mean concentration of each species with an estimate of their relative sizes (Table 2).

2.5.2 Sediment trap data

To compare modeled and observed seasonal production patterns, several sediment traps (Table S1 in the Supplement, Figure 1b) have been examined. Those can provide foraminiferal shell fluxes continuously collected over several months or even years. However, some sediment traps comprise only of a few months (i.e., less than a year) and might have just recorded local short-term processes of a particular season/year and can, thus, not provide a long-term/climatological mean.

Here we use the same approach as in Jonkers and Kučera (2015) and present the observed fluxes for multiple years from every location on a $\log_{10}$ scale versus day of year, whereby the zero fluxes have been replaced by half of the observed minimum flux to be able to visualize the results. In this way, we can directly compare the peak timings of the measured fluxes at each location with the model, whereby we assume that the flux through the water column (in $\#\,\mathrm{m}^{-2}\,\mathrm{day}^{-1}$) is proportional to the volume integrated model concentrations (in $\mathrm{mmol\,C\,m}^{-3}$).

2.5.3 Plankton tow data

To analyze the vertical distribution, plankton net hauls from different sites distributed across the world ocean (Table S2 in the Supplement, Figure 1b) have been used for a comparison with the simulated vertical distributions. Plankton tow samples have been collected by means of a multiple opening-closing net with a vertical resolution differing between 5 depth levels (one haul) and up to 13 depth levels (two or more consecutive hauls) resolving the upper 100s of meters of the water column. Since the plankton tow data has been collected during a particular time (i.e., a specific day/month) (Table S2), the same month has been considered for the simulated vertical planktonic foraminifera profile for the model-data comparison.

Here we followed the same approach as Rebotim et al. (2017) and calculated an average living depth (ALD) and the vertical dispersion (VD) around the ALD to provide a direct comparison with the modeled depth profile. The ALD (in m) is defined as follows:

$$ALD = \frac{\sum_i C_i \cdot D_i}{\sum_i C_i}$$

with C_i being the foraminiferal species concentration (in $\#\,\mathrm{m}^{-3}$) in the depth interval D_i and VD (in m) is calculated as:

$$VD = \frac{\sum_i (|ALD - D_i| \cdot C_i)}{\sum_i C_i}$$

For further information, we refer to Rebotim et al. (2017).

3 Results

3.1 Modeled horizontal distribution patterns

The modeled global spatial distribution patterns based on the depth integrated annual mean relative abundances of the five considered foraminiferal species (Figure 2) correspond to the five major provinces of the modern ocean (i.e., polar, subpolar, transitional, subtropical, and tropical) known to be inhabited by those species (Bradshaw, 1959; Bé and Tolderlund, 1971; Hemleben et al., 1989; Kucera, 2007). Note that since the core-top data used for comparison ~~can neither~~ provides ~~any~~ information ~~about~~ neither on the depth habitat of the planktonic foraminiferal species nor ~~about~~ on their life cycle, the modeled annual mean relative abundances have been obtained by integrating the individual foraminiferal concentrations over the whole water column and by subsequently calculating the percentage of each species relative to the modeled total foraminiferal carbon biomass, whereby we also accounted for the different sizes of each species (Table 2).

For a direct comparison of the observed (i.e., the core-top data) and modeled foraminiferal community composition the Bray-Curtis index of similarity was used. The comparison reveals generally a good fit between the simulated and sedimentary assemblage composition with median Bray-Curtis similarity of $\sim 68\%$. The fit is particularly good in the high latitudes and in the tropics (Bray-Curtis similarity $> 80\%$) and only a few regions (off South America and southern Africa, in the equatorial and North Pacific, and in the eastern North Atlantic) reveal a poorer agreement with similarities of $< 50\%$ (Figure 2a).

In the simulation, ~~T~~the cold-water species *N. pachyderma* is confined to the high latitudes dominating the polar waters of both hemispheres. *Neogloboquadrina~~.~~ pachyderma* shows the highest modeled annual mean relative abundances ($> 90\%$) north of the Arctic ~~c~~Circle and south of the Antarctic Convergence, whereas toward the subtropics the species' occurrence in the model reduces gradually (Figure 2~~a~~b). *Neogloboquadrina~~.~~ incompta* ~~is~~ occurs mainly ~~found~~ in the subpolar to transitional water masses of the world ocean in the simulation. This species shows highest modeled annual mean relative abundances in the latitudinal belt at around $45\,^\circ$N and/or $45\,^\circ$S ~~($> 30\%$) in the subantarctic belt as well as in the upwelling region of the equatorial Pacific and in the coastal upwelling systems associated with the cold eastern boundary currents of the Atlantic and Pacific Oceans~~ (Figure 2~~b~~c). *Globigerina~~.~~ bulloides* also ~~exhibits a similar distribution pattern as *N. incompta*. It is present~~ occurs in the subpolar to transitional waters of the world oceans with the highest modeled annual mean relative abundances (>~~30~~ 60%) occurring in the Southern Ocean~~, the upwelling areas of the Pacific Ocean,~~ and in the subpolar gyres (Figure 2~~c~~d). In the upwelling region of the equatorial Pacific and in the coastal upwelling systems associated with the cold eastern boundary currents of the Atlantic and Pacific Oceans, *G. bulloides* is found with modeled annual mean relative abundances of $< 40\%$. In the simulation, ~~T~~the warm-water species *G. ruber* (white) is mostly confined to the subtropical and tropical regions of both hemispheres, whereby the highest modeled annual mean relative abundances of up to 60% are reached in the subtropical gyres (Figure 2~~d~~e). Lowest modeled annual mean relative abundances can be found in the ocean's upwelling areas, especially in the equatorial Pacific cold tongue, where *G. ruber* (white) appears to be almost absent. The modeled distribution pattern of *T. sacculifer* is limited to the warm waters of the subtropics and tropics and is similar to the one of *G. ruber* (white). *Trilobatus~~.~~ sacculifer* shows highest modeled annual mean relative abundances (>~~50~~ 60%) in the equatorial Pacific between $15\,^\circ$N and

15 °S and exhibits low modeled annual mean relative abundances (<~~20~~ 30%) in the coastal upwelling regions of the ocean basins (Figure 2~~e~~f).

3.2 Modeled seasonal distribution

For each foraminiferal species, the month of modeled maximum production changes on average with temperature and consequently with latitude (Figure 3, Figure S2 in the Supplement). In the simulation, ~~T~~there is a general tendency for the maximum production peak of the cold-water species *N. pachyderma* to occur later in the year (i.e., during summer) for lower annual mean temperatures (Figures 3a and S2a). With increasing mean annual temperatures, however, the modeled peak timing occurs earlier in the year (i.e., during spring) (Figure 3a). For *N. incompta*, modeled maximum production is reached during late summer in the midlatitudes at lower temperatures and is shifted towards spring/early summer when temperatures increase (Figure S2b). In the low latitudes at high temperatures, however, ~~peak fluxes of~~ *N. incompta* ~~occur~~ exhibits a constant~~ly~~ flux pattern throughout the year (Figure 3b). The modeled peak timing of *G. bulloides* is similar to the modeled peak timing of *N. incompta*, where the highest modeled fluxes are reached later (earlier) in the year in the midlatitudes at lower (higher) temperatures (Figure S2c). In the warm waters (of the tropics)~~, the maximum production of~~ *G. bulloides* ~~occurs~~ exhibits year-round a rather uniform flux pattern (Figure 3c). In the model, ~~B~~both *N. incompta* and *G. bulloides* show indications of a double peak in their timing that is shifted towards the first half of the year when temperatures rise (Figures 3b and 3c). This earlier-when-warmer pattern is also indicated in the modeled peak timing of *N. pachyderma* (Figure 3a). ~~The maximum in the modeled flux of~~ *Globigerinoides*~~.~~ *ruber* (white) ~~occurs~~ shows a uniform flux pattern all year~~-~~round in the warm waters of the world ocean in the subtropical/tropical regions (Figure S2d). In colder waters (e.g., towards higher latitudes)~~, the maximum production~~ modeled peak fluxes of *G. ruber* (white) ~~is~~ are reached in late summer/fall (Figure 3d). A similar seasonal pattern in the modeled peak timing is evident for the tropical species *T. sacculifer* with ~~peak~~ constant fluxes occurring year-round at high temperatures in the low latitudes (Figure S2e). ~~and in fall when the~~ At lower ambient temperatures, ~~are lower~~ modeled peak fluxes of *T. sacculifer* occur during fall (Figure 3e). ~~The peak timing of~~ For both *G. ruber* (white) and *T. sacculifer*, the modeled peak timing is shifted to later in the year when the surroundings become colder (Figures 3d and 3e).

To allow for a global comparison of the modeled and observed flux seasonality, we standardized peak amplitudes for each foraminiferal species, i.e., the species' maximum concentration divided by its annual mean. ~~Although seasonal changes in~~ This reveals that the timing of the modeled foraminiferal peak ~~fluxes~~ abundances varies with temperature ~~are evident~~, but all five species exhibit an almost constant peak amplitude ~~(i.e., the maximum concentration divided by the annual mean)~~ in their preferred thermal habitat~~, which is, i.a., limited by temperature~~. Outside their preferred living conditions, ~~the~~ modeled peak amplitudes considerably increase for most of the species ~~considerably~~ (Figure 3), thus, the species experience a strong deviation from their annual mean living conditions and likely occur only at times when the ambient conditions are (close to) their optima. For the warm-water species *G. ruber* (white) and *T. sacculifer*, peak amplitudes rise when the ambient temperatures fall below 20 °C (Figures 3d and 3e). The peak amplitude~~s~~ of ~~both *N. incompta* and~~ *G. bulloides* increases noticeably with mean annual temperatures falling below ~~5~~ 10 °C (Figure~~s 3b and~~ 3c). ~~Additionally, with~~ By contrast, when ambient temperatures exceed~~ing~~

25 °C, the peak amplitude of *N. incompta* increases (Figure 3b). For the cold-water species *N. pachyderma*, the relation between peak amplitudes and mean annual temperatures is more complex (Figure 3a).

3.3 Modeled vertical distribution

Among the three major ocean basins the modeled vertical distribution of each considered planktonic foraminiferal species shows similar patterns in the annual mean (Figure 4). The temperate/cold-water species (i.e., *G. bulloides*, *N. incompta*, and *N. pachyderma*) occur ~~in~~ from the surface down ~~to subsurface layers up~~ to about 200 m water depth (Figures 4a, 4b and 4c). *Neogloboquadrina*~~.~~ *pachyderma* is consistently present in the top few 100 m of the water column in the high latitudes and absent in the subtropical/tropical regions. In the polar waters of the three ocean basins, modeled maximum annual mean concentrations are found ~~close to~~ at the surface and ~~subsequently descend with depth~~ deeper toward lower latitudes. The highest modeled annual mean concentrations of *N. pachyderma* are, however, located in the subpolar gyres between 0 and ~~80~~ 75 m water depth (Figure 4a). *Neogloboquadrina*~~.~~ *incompta* is in general present between 60 °N and 60 °S with the modeled annual mean concentration reaching its maximum at around 100 m water depth. In the mid- to higher latitudes, *N. incompta* is found ~~in~~ from the surface to ~~subsurface of~~ ∼ 200 m water depth in the Atlantic, Indian, and Pacific Oceans, but seems to be ~~largely absent~~ rarely present in the respective ~~surface~~ uppermost water layers (i.e., between 0 and ∼ 75 m) of the tropics. However, the modeled annual mean concentration increases with depth especially from the subpolar regions toward the equator (Figure 4b). As for *N. incompta*, *G. bulloides* has been consistently found from the surface to ∼ 200 m water depth between about 60 °N and 60 °S (Figure 4c). Depending on the ocean basin, modeled maximum annual mean concentrations of *G. bulloides* are either mainly reached at the surface (i.e., in the Indian and Pacific Oceans) or at depth (i.e., in the Atlantic Ocean), but also ~~subsurface~~ at around 100 m water depth in the subpolar regions of the three chosen transects~~ (Figure 4c)~~. Both, *N. incompta* and *G. bulloides*, show highest modeled annual mean concentrations between 30° and 60° latitude (Figures 4b and 4c).

The warm-water species, *G. ruber* (white) and *T. sacculifer*, are found between the surface of each ocean basin and ∼100 ~~150~~ m water depth, thus occurring in a shallower depth range compared to *N. pachyderma*, *N. incompta*, and *G. bulloides* (Figures 4d and 4e). Among all five planktonic foraminiferal species, *G. ruber* (white) exhibits on average the highest modeled annual mean concentrations along the transects (Figure 4). This species is confined to the subtropical/tropical regions of the ocean basins with the highest modeled annual mean concentrations occurring between ∼15 ~~20~~° and 30° latitude and the lowest around the equator (Figure 4d). Along the three chosen transect~~s of the Atlantic Ocean,~~ modeled maximum annual mean concentrations of *G. ruber* (white) are almost consistently reached at ~~depth between 50 and 80 m, whereas in the Indian and Pacific Oceans the annual mean concentrations of *G. ruber* (white) reach their maximum at~~ the surface in the low latitudes and at around 60 m water depth ~~at~~ in those ~~locations~~ areas, where the highest modeled abundance of this species occurs~~ is found (Figure 4d)~~. *Trilobatus*~~.~~ *sacculifer* also occurs predominantly between 30 °N and 30 °S with modeled annual mean concentrations gradually decreasing with depth. Compared to the other planktonic foraminiferal species, *T. sacculifer* exhibits a rather uniform distribution pattern along the different transects (Figure 4e) with ~~the~~ modeled maximum annual mean concentrations being primarily located at the surface~~ (Figure 4e)~~.

3.4 Modeled seasonal variability of habitat depth

In the model, the depth of maximum production of each considered planktonic foraminifera changes over the course of a year (Figure 5). Towards higher latitudes, *N. incompta* and *N. pachyderma* show in ~~general~~ the model maximum abundances at lower depth levels compared to low and midlatitudes. In the polar regions, *N. pachyderma* occurs close to the surface during winter and descends through the water column from spring to summer with modeled maximum abundances being reached at ~ 40 m water depth ~~mid-depth~~ in summer. In the subpolar regions, *N. pachyderma* is generally found at deeper depths between 50 and 100 m for almost the entire year except for the winter season, where highest modeled concentrations are reached close to the surface (Figure 5a). The modeled depth habitat of *N. incompta* increases from spring to summer and is shallower in winter in the subpolar regions (Figure 5b). In the subtropics and tropics, however, *N. incompta* shows year-round highest modeled concentrations consistently below 90 m water depth ~~year-round~~.

Globigerina~~.~~ bulloides exhibits a relatively shallow habitat (i.e., up to ~ 50 m water depth) along the equator throughout the year (Figure 5c). In the subpolar regions, the depth of modeled maximum production of *G. bulloides* varies seasonally and, similar to *N. incompta*, is shallower during winter and deepest during summer. The modeled depth habitat of *G. ruber* (white) is mostly confined to the top 60 m of the water column and seems to be less variable compared to the temperate and cold-water species (Figure 5). In the midlatitudes and near the equator, highest modeled concentrations of *G. ruber* (white) occur close to the surface during almost the entire year, whereas in the subtropical/tropical regions, this species is most abundant below 20 m and shows a weak seasonal cycle, occurring deeper in late summer/early fall (Figure 5d). *Trilobatus~~.~~ sacculifer* exhibits the least variable depth habitat in the simulation among the five considered species and is consistently found close to the surface above 20 m water depth throughout the year (Figure 5e).

4 Discussion

4.1 Large-scale patterns

4.1.1 Geographical range of planktonic foraminifera species

The predicted global distribution patterns of the five considered planktonic foraminiferal species are in good agreement with the core-top data (Figure 2a). This is remarkable, considering the simplifications that had to be used to facilitate the comparison, such as the use of a constant biomass to size scaling within a species and a constant size scaling among the species.

Neogloboquadrina~~.~~ pachyderma is most abundant in the polar-subpolar waters of the northern and southern hemispheres both in the model and in the core-top samples (Figure 2~~a~~b). This cold-water species dominates the waters north of the Arctic ~~c~~Circle and south of the Antarctic Convergence with relative abundances exceeding 90% and is very rarely found in subtropical/tropical waters, which is also seen in the model output. Bé (1969), Bé and Tolderlund (1971), and Bé and Hutson (1977) showed that *N. pachyderma* mainly occurs in regions with sea surface temperatures (SSTs) below 10 °C, but is also present in the cold-temperate waters of, e.g., the subpolar gyres with relative abundances being reduced to 30-50%. Thus, in areas, which are influenced by warmer waters the abundance of this species decreases gradually. This is especially evident in the eastern North Atlantic Ocean, where the abundance of *N. pachyderma* is reduced to about 50% due to the influence of the warm Atlantic Water, which is transported northward by the North Atlantic Current (NAC) (Husum and Hald, 2012). In line with the observations, the modeled annual mean relative abundances of *N. pachyderma* also decrease with decreasing latitude and, hence, get reduced towards warmer surface waters (Figure 2~~a~~b). ~~However~~ Additionally, PLAFOM2.0 is able to reproduce the observed ~~overestimates this~~ species' abundance pattern in the ~~eastern~~ North Atlantic with a reduced relative abundance of <30% ~~(i.e.,~~ in the area, which is influenced by the NAC~~) compared to the core-top data~~. Similar to PLAFOM (see Fraile et al., 2008) a slight deviation between the simulated and observed relative abundances of *N. pachyderma* at the edge of the species' distribution pattern is observed in the northern hemisphere. It has been shown that distinct genotypes discovered within this morphologically defined species exhibit different ecological preferences (Darling et al., 2006; Morard et al., 2013). Thus the above mentioned ~~This model-data-mismatch~~ minor discrepancy might partly arise due to the underlying model parameterizations, which are mainly based on the environmental preferences (i.e., temperature tolerance limits) of the *N. pachyderma* genotypes found in the Southern Ocean (for more details see Fraile et al., 2008), which differ~~s~~ genetically from the ~~single~~ genotypes found in the North Atlantic and North Pacific Oceans (Darling et al., 2004, 2006, 2007). ~~It has been hypothesized that distinct genotypes seem to have different ecological preferences (de Vargas et al., 1999; Darling et al., 2000; Darling et al., 2006; Stewart et al., 2001; Bauch et al., 2003).~~

The modeled global distribution patterns of *N. incompta* and *G. bulloides* agree ~~in general~~ to a broad extent with the observations (Figures 2~~b~~c and 2~~c~~d). Both species are predominantly ~~occur~~ found in the subarctic/-antarctic and transitional waters of the world oceans (with relative abundances >50%), where ~~the~~ SSTs range~~s~~ between 10° and 18 °C (Bé and Tolderlund, 1971; Bé and Hutson, 1977). They are also highly abundant in the cool eastern boundary currents off Africa and South America (e.g., Bé and Tolderlund, 1971; Giraudeau, 1993; Darling et al., 2006) as well as in the eastern North Atlantic and occur continuously in a subantarctic belt between 30 °S and the Antarctic Convergence (Bé, 1969; Bé and Tolderlund, 1971; Boltovskoy et al., 1996). In addition, high abundances (>40%) of *N. incompta* ~~are evident~~ have been observed in the equatorial Pacific upwelling system and of *G. bulloides* in the Arabian Sea. In the model, *N. incompta* is confined to the subpolar belts at around 45° latitude, which matches the general distribution pattern seen in the core-top data, but the relative abundance is underestimated (here *N. incompta* accounts for <20% of the modeled assemblage compared to up to 50% in the observations; Figure 2c). The model prediction~~s~~ for ~~both *N. incompta* and~~ *G. bulloides* ~~also~~ shows in accordance with the core-top samples higher abundances in the subantarctic belt (here ~~both~~ the species accounts ~~together~~ for up to ~~90~~ 80% of the modeled assemblage) and in the (coastal) upwelling regions of the Atlantic and Pacific Oceans Figure 2d. PLAFOM2.0, however, ~~seems~~ fails to fully capture ~~constantly underestimate~~ the relative abundances in those areas, where the assemblages are usually dominated by ~~those two species~~ *N. incompta* and *G. bulloides* ~~according to the core-top data~~ (Figures 2~~b~~c and 2~~c~~d). For instance, in the Benguela upwelling system, *N. incompta* and *G. bulloides* together account locally for >60% of the total planktonic foraminifera population (Bé and Tolderlund, 1971; Giraudeau, 1993), whereas in the model, both species ~~only~~ account for ~~∼~~ <40% of the assemblage~~, which is, however, still of the same order of magnitude~~. In fact, *N. incompta* is almost absent in the model simulation outside of the subpolar belts. Furthermore, in the western Arabian Sea, the modeled annual mean relative abundance of *G. bulloides* ranges between 10 and 20%, which corresponds to the lower end of the observed range varying between 20 and $\sim 50\%$ (Naidu and Malmgren, 1996). Additionally, it is evident that the model slightly overestimates the ~~species'~~ relative abundance of *G. bulloides* in the central subtropical/tropical waters of the ocean basins ~~as they are infrequently (<10%) found in the faunal records~~ (Figure~~s 2b and~~ 2~~e~~d). The~~se~~ apparent discrepancies between the observations and PLAFOM2.0 arise, ~~on the one hand~~ firstly, due to an overestimation of the modeled annual mean relative abundances of *G. bulloides*, in particular in the subpolar belt at around 45°N, and of *G. ruber* (white) and *T. sacculifer* especially in the upwelling regions, and/or due to the overall underestimation of the occurrence of *N. incompta*, outside the subpolar belts. Secondly, since the model parameterizations are performed on a global scale, distinct genotypes (possibly having different environmental preferences) of *N. incompta* and especially *G. bulloides* (~~see,~~ e.g., Kucera and Darling, 2002; ~~Darling and Wade, 2008~~ Morard et al., 2013) cannot be included in detail in the model, potentially resulting in the model-data-mismatch.

The simulated global distribution patterns of *G. ruber* (white) and *T. sacculifer* compare favorably with the core-top samples (Figures 2~~d~~e and 2~~e~~f). Both species dominate the subtropical and tropical waters of the global ocean, together accounting for 75-100% of the total planktonic foraminiferal fauna (Bé and Tolderlund, 1971; Bé and Hutson, 1977). *Globigerinoides~~.~~ ruber* (white) is the most abundant species in the subtropical areas, where SSTs range between 21° and 29°C, whereas *T. sacculifer* shows highest relative abundances (>50%) in the tropics with SSTs between 24° and 30°C (Bé and Hutson, 1977). Additionally, *G. ruber* (white) is also highly abundant (>50%) compared to *T. sacculifer* along the continental margins of the low latitudes (Figures 2~~d~~e and 2~~e~~f). However, in the coastal upwelling regions, *G. ruber* (white) and *T. sacculifer* are rarely found as cooler water masses influence their usual habitat (e.g., Thiede, 1975). Since both species ~~prefer~~ thrive~~ing~~ in warmer waters, their (relative) abundance gradually diminishes when transported towards the higher latitudes, thus being absent in the subpolar/polar regions of the ocean basins. The model predictions for *G. ruber* (white) and *T. sacculifer* show in general similar patterns as the observations with higher loadings in the subtropical and tropical regions and a gradual decrease in the occurrence toward the poles (Figures 2~~d~~e and 2~~e~~f). PLAFOM2.0 is also able to reproduce the dominance of *G. ruber* (white) in the subtropics and of *T. sacculifer* around the equator; and together both species ~~largely~~ account for >70% of the modeled assemblage in the warm waters of the world ocean. Additionally, the reduction in the (relative) abundances in the upwelling regions (i.e., ~~in~~ along the equatorial Pacific and ~~along~~ the coasts of South America and Africa) is likewise captured by the model. However, in those provinces dominated by *G. ruber* (white) and *T. sacculifer*, the relative abundances are underestimated in the model, whereas in the coastal upwelling regions, the species' abundances are slightly overestimated compared to the observations. Such deviations may result from the over- and/or underestimation of *G. bulloides* and *N. incompta* in the tropical/subtropical or upwelling regions (Figures 2~~b~~c and 2~~e~~d) or from the ~~coarse~~ 1° model resolution ~~resulting in~~ leading to an inadequate ~~mis~~representation of the coastal upwelling regions.

Thus, we consider that part of the model-data-mismatch may arise from uncertainty in the conversion of biomass to (relative) abundance, which is based on constant offsets approximated from sparse data (cf. Schmidt et al., 2004). Likely an even larger part of the discrepancies between the model and core-top data stems from the underlying model parameterizations applied on a global scale, which do not distinguish between distinct genotypes of the different species with potentially varying ecological preferences. Theoretically, this problem could be solved by parameterizing all known genotypes individually and approximating the total morphospecies abundance as the sum of its constituent genotypes. This would allow a comparison with sediment data, but not a diagnosis, since the sediment data provide no information on which genotypes are contained in the assemblages. Interestingly, the generally fair fit between the model and observations suggests that ecological differences between cryptic species are likely limited and that the model provides a useful first-order approximation of global species distribution.

4.1.2 Seasonality of planktonic foraminifera species

The meta-analysis of Jonkers and Kučera (2015), which is based on sediment trap data, revealed that the (spatially varying) seasonality of individual planktonic foraminifera is predominantly related to either temperature or the timing of primary productivity. For the temperate and cold-water species, such as *G. bulloides*, *N. incompta*, and *N. pachyderma*, one or two flux maxima have been observed, which occur earlier in the year at higher temperatures. This seasonal pattern is also to a large degree evident in the model results (Figures 3a-c and S2a-c). At lower temperatures (below 5 °C), the modeled season of maximum production for the cold-water species *N. pachyderma* is predominantly reached in (late) summer, whereas in the comparatively warmer subpolar and transitional waters, the modeled peak season is shifted towards spring (Figures 3a and S2a). A similar pattern can be observed for *N. incompta* and *G. bulloides*. In line with Jonkers and Kučera (2015), none of the three species shows a clear dependency of the peak amplitude with temperature (Figure 3a-c). In the model, ~~T~~the temperate and cold-water species exhibit a shift in their peak timing, but do not considerably change their peak amplitude (except for *G. bulloides* when temperatures fall below 5 °C). Hence, the observed and predicted earlier-when-warmer pattern can most likely be sought to a large extent in the timing of the primary productivity rather than in a temperature dependence. Several studies showed that the seasonality of the temperate and cold-water planktonic foraminiferal species is closely tied to phytoplankton bloom events leading to an increased food supply (e.g., Fairbanks and Wiebe, 1980; Donner and Wefer, 1994; Wolfteich, 1994; Kohfeld et al., 1996; Mohiuddin et al., 2002, 2004, 2005; Northcote and Neil, 2005; Asahi and Takahashi, 2007; Storz et al., 2009; Wilke et al., 2009; Jonkers and Kučera, 2015). In particular, the flux of *G. bulloides* reaches highest values in response to an increased food supply to a large extent associated with open ocean and/or coastal upwelling (e.g., Thiede, 1975; Curry et al., 1992; Wolfteich, 1994; Naidu and Malmgren, 1996; Kincaid et al., 2000; Mohiuddin et al., 2004, 2005; Storz et al., 2009). The warm-water species *G. ruber* (white) and *T. sacculifer* exhibit relatively uniform annual flux patterns with almost no seasonal peak in the subtropical/tropical regions of the ocean basins (e.g., Deuser et al., 1981; Jonkers and Kučera, 2015). Similar to observations, the modeled timing of the low-amplitude peaks is random during the year in warm waters (Figures 3d-e and S2d-e). However, in colder waters, peak fluxes are concentrated towards fall and peak amplitudes increase considerably both in the observations and in the model (Figures 3d-e and S2d-e). This shift in the seasonality can most likely be linked to temperature. In the low latitudes, optimum temperatures prevail all year round, whereas further north-/southward those optimum thermal conditions occur only during a short period later in the year. Thus, those species focus their flux into the warm season in colder waters (Figure 3d-e). This emerging behavior is consistent with observations from sediment traps (Jonkers and Kučera, 2015) and suggests that the seasonality of the warm-water species is driven by temperature rather than food availability, which is in agreement with observational studies (e.g., Wolfteich, 1994; Eguchi et al., 1999, 2003; Kincaid et al., 2000; Kuroyanagi et al., 2002; Mohiuddin et al., 2002, 2004; Storz et al., 2009; Jonkers and Kučera, 2015).

4.1.3 Spatial and temporal variability of depth habitats of planktonic foraminifera species

The modeled depth habitats of *N. pachyderma*, *N. incompta*, *G. bulloides*, *G. ruber* (white), and *T. sacculifer* differ ~~among each other~~ and show (distinct) spatial and temporal variability in response to different environmental conditions (Figures 4 and 5). Plankton tow studies have shown that the vertical distribution of planktonic foraminifera is mostly affected by temperature, primary productivity, light availability, and thermal/density stratification of the upper water column (e.g., Fairbanks et al., 1982; Ortiz et al., 1995; Schiebel et al., 2001; Field, 2004; Kuroyanagi and Kawahata, 2004; Salmon et al., 2015; Rebotim et al., 2017).

In line with the observations, the modeled depth distribution patterns indicate that the warm-water species *G. ruber* (white) and *T. sacculifer* ~~preferably~~ occur at shallower depths compared to the temperate and cold-water species *G. bulloides*, *N. incompta*, and *N. pachyderma* (see Figures 4 and 5). In the model, both *G. ruber* (white) and *T. sacculifer* have been consistently found from the surface to $\sim 100\,\mathrm{m}$ water depth in the subtropical/tropical regions of the ocean basins (Figure 4d-e). In the tropics, they are most abundant close to the surface, which agrees well with the observations. In the Arabian Sea and in the central tropical Pacific Ocean, both species have been mostly found in the upper $60\,\mathrm{m}$ (Peeters and Brummer, 2002; Watkins et al., 1996, 1998). In the transitional and subtropical waters, however, PLAFOM2.0 slightly underestimates the depth habitat of *G. ruber* (white) and *T. sacculifer* (Figures 4d-e and 5d-e) as they inhabit the upper $125\,\mathrm{m}$ in the western North Atlantic (Fairbanks et al., 1980) and/or consistently occur from 0 to $200\,\mathrm{m}$ water depth in the subtropical eastern North Atlantic (Rebotim et al., 2017) or in the seas surrounding Japan (Kuroyanagi and Kawahata, 2004). Nevertheless, both species typically live close to the surface (above $100\,\mathrm{m}$) (e.g., Bé and Hamlin, 1967; Fairbanks et al., 1982; Kemle-von Mücke and Oberhänsli, 1999; Schiebel et al., 2002; Wilke et al., 2009; Rippert et al., 2016), thus being associated with a shallow depth habitat, which is reproduced by the model. Since *T. sacculifer* and *G. ruber* (white) are algal symbiont-bearing species, they are most abundant in the photic zone, where light intensities are highest, but also chlorophyll *a* concentrations and temperature control their habitat. Light intensity is especially important for the growth of *T. sacculifer* (Caron et al., 1982, 1987; Jørgensen et al., 1985; Bijma et al., 1990b; Watkins et al., 1998), whereas *G. ruber* (white) seems to be more affected by food availability (Peeters and Brummer, 2002; Field, 2004; Kuroyanagi and Kawahata, 2004; Wilke et al., 2009) rather than light. This is to some degree also indicated in our results, ~~would explain why~~ as on average the highest modeled concentrations of *T. sacculifer* occur at shallower depths compared to *G. ruber* (white) (see Figures 4d-e and 5d-e). However, at some locations both model and observations show the reverse (see Figure S4 and, e.g., Rippert et al., 2016; Rebotim et al., 2017), indicating that this depth ranking is not globally valid. In comparison with the temperate and cold-water species, *G. ruber* (white) and *T. sacculifer* are most abundant in the model in waters with temperatures above $22\,^{\circ}\mathrm{C}$ and absent, where temperature values drop below $15\,^{\circ}\mathrm{C}$ (see Figure 4), reflecting the different temperature tolerance limits of the two species.

Neogloboquadrina~~.~~ pachyderma, *N. incompta*, and *G. bulloides* generally thrive in cold to ~~transitional~~ temperate waters. In the model, the depth habitat of those species decreases with increasing latitude (Figure 4a-c), indicating a preferred habitat in the subsurface (see Figure 5a-c). This is consistent with the observations from several locations, where the three species have typically been found between 50 and $200\,\mathrm{m}$ water depth (e.g., Kohfeld et al., 1996; Mortyn and Charles, 2003; Kuroyanagi and

Kawahata, 2004; Bergami et al., 2009; Wilke et al., 2009; Pados and Spielhagen, 2014; Iwasaki et al., 2017; Rebotim et al., 2017). In the subtropical to subpolar regions, the highest modeled concentrations of *G. bulloides* occur, however, between 60 and 100 m, whereas in the tropics, maxima are reached close to the surface (Figures 4c and 5c). This agrees well with the observations: *G. bulloides* has been found to be tightly linked to phytoplankton bloom events occurring either at deeper depth layers associated with a deep chlorophyll maximum (DCM) (Fairbanks and Wiebe, 1980; Mortyn and Charles, 2003; Wilke et al., 2009; Iwasaki et al., 2017) or in the coastal and equatorial upwelling regions, where a shoaling of the species' habitat towards the near-surface can also be related to high chlorophyll *a* concentrations (Ortiz et al., 1995; Watkins et al., 1998; Peeters and Brummer, 2002; Field, 2004; Kuroyanagi and Kawahata, 2004). *Neogloboquadrina~~.~~ incompta* is also highly abundant, where chlorophyll *a* concentrations are high, but, nevertheless has most often been observed at mid-depth (Ortiz et al., 1995; Mortyn and Charles, 2003; Field, 2004; Kuroyanagi and Kawahata, 2004; Iwasaki et al., 2017; Rebotim et al., 2017). In the model, *N. incompta* shows also highest concentrations between 30 and 120 m (Figures 4b and 5b), clearly inhabiting the subsurface. This is especially evident in the tropics, where *N. incompta* is virtually absent in the near-surface layers, but present, albeit in low numbers, around 100 m water depth. The predictions show, in general, that *N. incompta* prefers warmer waters compared to *N. pachyderma* and, where the species co-exist, *N. incompta* inhabits for this reason shallower depths (Figures 4a-b and 5a-b). This agrees with the observations from the subarctic Pacific and the seas around Japan (Iwasaki et al., 2017; Kuroyanagi and Kawahata, 2004). *Neogloboquadrina~~.~~ pachyderma* is confined to the high latitudes with peak abundances occurring in the upper 100 m of the water column (Kohfeld et al., 1996; Stangeew, 2001; Mortyn and Charles, 2003; Kuroyanagi and Kawahata, 2004; Bergami et al., 2009; Pados and Spielhagen, 2014) (partly associated with high chlorophyll *a* concentrations), which agrees well with the model results. Although *N. pachyderma* has been classified as a "deep dweller" in different studies (Bé, 1960; Boltovskoy, 1971; Hemleben et al., 1989; Simstich et al., 2003), this species appears to be more surface-restricted at higher latitudes (Carstens and Wefer, 1992; Kohfeld et al., 1996; Mortyn and Charles, 2003), which is also evident in the model results (Figures 4a and 5a).

Several studies showed that the depth habitat of planktonic foraminifera varies throughout ~~a~~the year in response to changing environmental conditions. Rebotim et al. (2017) identified an annual cycle in the habitat of *T. sacculifer* and *N. incompta* in the subtropical eastern North Atlantic. Both species appear to descend in the water column from winter to spring and reach their deepest habitat in spring to summer before ascending again to a shallower depth towards winter (Rebotim et al., 2017). It has been associated that *N. incompta* is affected by chlorophyll *a* concentrations, hence, the seasonal shift in its habitat depth could be related to food availability as a DCM develops in the summer months. In the Canary Islands region, *G. ruber* (white) and *G. bulloides* have been found at lower depth levels during winter, and during summer/fall, shell concentrations w~~h~~ere highest at deeper depths associated with the DCM (Wilke et al., 2009). However, *G. ruber* (white) did occur at moderate abundance levels throughout the year, whereas *G. bulloides* was only present in low numbers during wintertime in the study area of Wilke et al. (2009). Peeters and Brummer (2002) investigated the influence of a changing hydrography on the habitat of living planktonic foraminifera in the northwest Arabian Sea. During the southwest monsoon (occurring in summer), strong coastal upwelling associated with low SSTs and a near-surface chlorophyll maximum leads to high abundances of *G. bulloides* dominating the species assemblage in the uppermost part of the water column (Peeters and Brummer, 2002). In comparison, during the northeast monsoon (occurring in winter), a relatively warm nutrient-depleted surface mixed layer as well as a DCM develop resulting in high concentrations of *G. ruber* (white) and *T. sacculifer* near the surface, whereas the concentrations of *G. bulloides* are low and show a subsurface maximum between the DCM and the thermocline (Peeters and Brummer, 2002). Based on their findings, Peeters and Brummer (2002) conclude that the habitat depth of individual foraminifera strongly depends on the local hydrography controlling, i.a., the food availability. Watkins et al. (1998) also found high abundances of *G. bulloides* in the equatorial surface waters of the Pacific Ocean associated with higher primary productivity due to an intensified upwelling, but also with the zonal advection by the South Equatorial Current during La Niña conditions. In contrast, during El Niño conditions, *G. bulloides* has been absent in the central tropical Pacific (Watkins et al., 1996) due to unfavorable living conditions.

The change in the depth of modeled maximum production of each considered planktonic foraminifera throughout a year (Figure 5) agrees to a large extent with the observations. *Neogloboquadrina~~.~~ pachyderma* is almost constantly found ~~in the subsurface (~~below 50 m~~)~~ except during winter, where highest modeled concentrations occur close to the surface (Figure 5a). The shift in the simulated habitat depth most likely indicates that *N. pachyderma* is highly dependent on food availability (cf. Figure 5a), which coincides with observational studies, where ~~as~~ this species has been extensively found at mid-depth during summer associated with the chlorophyll maximum (Kohfeld et al., 1996; Mortyn and Charles, 2003; Bergami et al., 2009; Pados and Spielhagen, 2014). The simulated change~~s~~ from a deeper to a shallower depth habitat of *N. incompta* in the subpolar regions over the course of a year could be strongly affected by the food supply by potentially following the seasonal distribution of phytoplankton. In the low latitudes, modeled maximum concentrations of *N. incompta* are constantly reached ~~in the subsurface~~ below 90 m water depth, which might be attributed to the presence of a permanent DCM (Figure 5b), being a characteristic feature throughout the low latitudes (Mann and Lazier, 1996). *Globigerina~~.~~ bulloides*, however, is found year-round close to the surface along the equator in the model (Figure 5c), which, in line with the observations, can be associated with equatorial upwelling, but also the inclusion of the photosynthetic growth rate in the model could explain the occurrence of modeled maximum concentration values at lower depth levels due to higher light requirements compared to *N. incompta*. In the subpolar regions, the simulated depth habitat of *G. bulloides* varies seasonally, most likely following the chlorophyll maximum (Figure 5c). The model simulation indicates that the seasonal occurrence of both *G. ruber* (white) and *T. sacculifer* in colder regions, where they face suboptimal environmental conditions, is limited to the warm surface layer during the warm season (Figure 5d-e). Even in the low latitudes, both species exhibit a weak seasonal cycle in their simulated depth habitat, which is more pronounced for *G. ruber* (white) ~~constantly occurs close to the surface in the midlatitudes due to the prevailing temperature conditions, but in the low latitudes this warm-water species exhibits a weak seasonal cycle in its depth habitat~~ (Figure 5d), indicating ~~its dependence on~~ come influence of primary productivity, which also agrees with the observations (Peeters and Brummer, 2002; Field, 2004; Kuroyanagi and Kawahata, 2004; Wilke et al., 2009). In line with Kuroyanagi and Kawahata (2004), our results suggest that *T. sacculifer* seems to prefer living in warmer waters than *G. ruber* (white) year-round (Figure 5e) and is most abundant at shallow depths, where the light intensity is highest. Our results, thus, confirm the observations by Jonkers and Kučera (2015) that both *G. ruber* (white) and *T. sacculifer* adapt to changing environmental conditions by adjusting their seasonal and vertical habitat to local circumstances. This emerging behavior can have important implications for paleoceanographic reconstructions (Jonkers and Kučera, 2017).

We find that the modeled depth habitats of the five considered foraminiferal species are in agreement with the relative ranking of their apparent calcification depths, but the inferred absolute values of calcification depth are often deeper or show a broader range of depths (e.g., Carstens and Wefer, 1992; Kohfeld et al., 1996; Ortiz et al., 1996; Bauch et al., 1997; Schiebel et al., 1997; Ganssen and Kroon, 2000; Peeters and Brummer, 2002; Anand et al., 2003; Simstich et al., 2003; Nyland et al., 2006; Jonkers et al., 2010, 2013; van Raden et al., 2011). This is not surprising, because PLAFOM2.0 does not model species' ontogeny and cannot capture processes related to ontogenetic depth migration (e.g., Fairbanks et al., 1980; Duplessy et al., 1981). The same limitation applies to estimates of living depth derived from plankton tow data, which often appears to deviate from apparent calcification depths (e.g., Duplessy et al., 1981; Rebotim et al., 2017). Nevertheless, as a first essential step in understanding the variability in calcification depths, PLAFOM2.0 provides a powerful tool that can aid the interpretation of proxy records.

4.2 Detailed ~~C~~comparison with ~~local~~ observations

The emergence of seasonal and vertical habitat patterns consistent with observational data~~,~~ provides important support for our modeling approach. Nevertheless, ~~yet~~ a more detailed comparison with observations is warranted to gain further insight into the model behavior. However, when comparing observational data and model output, one has to bear in mind several caveats. These can be broadly categorized into ~~three~~ four groups: i) model resolution, ii) model parameterization, iii) model hierarchy, and iv~~ii~~) analytical constraints on the observations.

i) The model resolution has limits on temporal and spatial scales when compared to sediment trap and plankton tow data. Most sediment trap time series span at most a few years and hence represent ~~snapshots~~ short time series that are potentially aliased/biased by inter-annual, seasonal, and/or monthly variability~~, depending on the deployment time~~. Similarly, plankton tow samples represent snapshots (of one particular day) and the prevailing environmental conditions during their actual sampling time cannot be fully captured by the model. In fact ~~T~~the model~~, on the other hand,~~ is forced using climatological data, thus representing a long-term average response that ignores such short-term variability. ~~Similarly, plankton tow samples represent even shorter (i.e., daily) snapshots, thus, not being able to reflect a long-term mean, such that the prevailing environmental conditions during their actual sampling time cannot be fully captured by the model.~~ Additionally, because of the ~~rather coarse~~ employed 1° model resolution, ~~of the employed model configuration~~ only the nearest model grid points rather than the exact locations of the sediment traps and plankton tows (especially along the coast lines) can be considered. This~~us,~~ potentially results~~ing~~ in different environmental conditions influencing the seasonality and depth habitat of planktonic foraminifera compared to the observations. The observational records are, additionally, affected by sub-grid phenomena (such as mesoscale eddies and/or steep gradients~~ in particular near the coast~~). For instance, Gulf Stream cold core rings transport large planktonic foraminiferal assemblages into the generally nutrient-poor Sargasso Sea (Fairbanks et al., 1980). In addition, Beckmann et al. (1987) found that an increase in zooplankton (including planktonic foraminifera) productivity coincided with an increase in phytoplankton biomass in a cold-core eddy in the eastern North Atlantic. ~~Due to t~~The ~~coarse~~ 1° resolution of the underlying model configuration leads to an inadequate representation of such sub-grid processes ~~are not resolved~~ and, thus, their impact cannot be fully reflected by ~~PLAFOM2.0~~ the CESM1.2(BGC+PLA) configuration.

ii) The underlying model parameterizations used in PLAFOM2.0 are limited in regard to taxonomic resolution and species' ontogeny. Different ~~morphotypes~~ genotypes of one species could exhibit different habitat preferences (e.g., Kuroyanagi and Kawahata, 2004), which is not captured by PLAFOM2.0 since the model parameterizations do not resolve the different known ~~morphotypes~~ genotypes of ~~some of~~ the considered planktonic foraminiferal species. Several studies from different areas also showed that the main habitat depth of some species increases from the surface to deeper water layers during shell growth (Peeters and Brummer, 2002; Field, 2004; Iwasaki et al., 2017). This vertical migration of planktonic foraminifera during ~~their~~ ontogeny cannot be reproduced by PLAFOM2.0 as the model parameterizations do not include the individual species' life cycles.

iii) The underlying complex model configuration consists of three major model components (i.e., the POP2 ocean model, the BEC ecosystem model, and PLAFOM2.0), which follow a certain model hierarchy by interacting differently with each other. Both the BEC model and PLAFOM2.0 run within POP2 (see Moore et al., 2013; Lindsay et al., 2014; this study), which provides the temperature distribution used to determine, i.a., the phytoplankton, zooplankton, and/or foraminifera carbon concentrations. It was shown that POP2 exhibits several temperature biases (e.g., Danabasoglu et al., 2012, 2014). These include large warm SST biases originating in the coastal upwelling regions of North and South America and of South Africa, colder-than-observed subthermocline waters in the equatorial Pacific as well as cold temperature biases of up to 7 °C in the North Atlantic emerging throughout the water column (see Figure S5 and Danabasoglu et al., 2012, 2014). These temperature biases influence the foraminiferal distributions directly and indirectly by affecting the distributions of their food sources in the BEC model. In addition, the BEC model also exhibits several biases, such as higher-than-observed (lower-than-observed) surface nutrient and chlorophyll concentrations at low (high) latitudes (Moore et al., 2013), implying potential misrepresentations of the modeled phytoplankton and zooplankton distributions, likely influencing the foraminiferal carbon concentrations. The inferred importance of temperature and food availability (estimated by POP2 and/or the BEC model) in PLAFOM (see Fraile et al., 2008; Kretschmer et al., 2016), on the distribution of planktonic foraminifera implies that each model component is important for an accurate representation of the foraminifera distribution. Therefore, it is difficult to unequivocally differentiate between the different model components of the CESM1.2(BGC+PLA) model configuration and their individual share likely leading to the model-data-mismatch.

iv~~ii~~) The analytical constraints regarding the observational records include drift due to (sub-grid) ocean processes, distinction between live and dead specimens, collection depths, and taxonomic agreement among different studies. For instance, a few sediment trap ~~data~~ samples might be compromised due to the collection of sinking particles derived from different regions of the surface ocean, being transported through eddies and/or ocean currents (Mohiuddin et al., 2004). Strong current velocities sometimes associated with eddies could lead to a tilt in the moored sediment trap, resulting in fewer material being collected by the trap (Yu et al., 2001). The impact of eddies might, thus, hamper the observed season of maximum production of planktonic foraminifera as well as their average living depth. A further uncertainty in the plankton tow data arises from the identification of living cells, because dead cells with cytoplasm collected at depth still appear as living and lead to a shift in the average living depth to greater depth (Rebotim et al., 2017). Uneven sampling intervals of the tows also result in a bias in the observed depth habitat (cf. Figure S4). Additionally, a taxonomic consistency within the observational data is assumed, which cannot be guaranteed as different researchers have been responsible for the data collection (see Tables S1 and S2).

With these caveats in mind, we compare the results of PLAFOM2.0 with 26 sediment trap records and 45 plankton tow samples from all oceans (Figure 1b, Tables S1 and S2). Note that the results of the point-by-point comparative analysis for each site and species are given in the Supplement (see Figures S3 and S4).

The peak season of the temperate and cold-water species (*G. bulloides*, *N. incompta*, and *N. pachyderma*) is shifted from late summer in the higher latitudes towards spring at the more equatorward directed locations in the subpolar and transitional water masses both in the model and in the sediment trap records (Figure 6a, Table S3a). The modeled peak amplitudes of those species remain almost constant at rather low values independent of the considered region. In the sediment traps, however, the peak amplitude values are higher and more diverse and also no clear pattern is evident neither for the species nor for the provinces changing with latitude (Figure 6b, Table S3b). In line with the plankton tow samples, *N. pachyderma*, *N. incompta*, and *G. bulloides* occur to a large extent ~~in the subsurface~~ below 50 m water depth from the cold high latitudes to the warmer provinces. However, the modeled ALDs (ranging between ~~50~~ 20 and 100 m) are considerably lower than the observed ALDs, which spread over 250 m (Figure 6c, Table S4). The warm-water species *G. ruber* (white) and *T. sacculifer* occur year-round in the subtropical/tropical regions with no distinct preference for a particular season both in the observations and in the model simulation (Figure 6a, Table S3a). In the transitional waters, however, their peak fluxes are consistently concentrated into fall, leading to higher peak amplitude values at least in the model (Figure 6b, Table S3b). Throughout the tropics and subtropics, the modeled peak amplitudes remain constant at low values. In the sediment trap records, however, the peak amplitudes are higher (compared with PLAFOM2.0) and vary within both species and within each province (Figure 6b). In the tropics, *G. ruber* (white) and *T. sacculifer* occur primarily close to the surface with ALDs below 50 m both in the model simulation and in the plankton tow records (Figure 6c, Table S4). In fact, the predicted ALD values (consistently ranging between the surface and 55 m) are lower in comparison with the observations in the transitional and subtropical waters and, accordingly, do not exhibit a similar value range as the plankton tow records.

In general, the point-by-point comparison between the observations and the model simulation reveals that the peak seasons are well predicted by PLAFOM2.0. The predicted peak amplitudes and average living depths also show realistic trends, but the model tends to underestimate the magnitude of these trends (cf. Figure 6). Additionally, some sediment trap flux time series of the temperate and cold-water planktonic foraminiferal species show two seasonal peaks a year (cf. Jonkers and Kučera, 2015) (see Figures S3 and 7a). PLAFOM2.0 is, however, not always able to faithfully reproduce this bimodal pattern (cf. Figures S3 and 7a). In the following, we try to identify the causes of discrepancies between the observations and predictions by comparing the model output with exemplarily chosen sediment trap records and/or plankton tow samples of three different locations in each case (Figure 7).

The timing of flux pulse(s) of the temperate and cold-water species has, in general, been linked to the timing of the peak in primary productivity (e.g., Fairbanks and Wiebe, 1980; Donner and Wefer, 1994; Wolfteich, 1994; Kohfeld et al., 1996; Mohiuddin et al., 2002, 2004, 2005; Northcote and Neil, 2005; Asahi and Takahashi, 2007; Storz et al., 2009; Wilke et al., 2009; Jonkers and Kučera, 2015). It is known from studies of the North Atlantic Ocean that phytoplankton seasonality changes with latitude, featuring a single spring bloom in the polar and subpolar Atlantic, a bimodal pattern (one large peak in spring, one smaller peak in fall) in the temperate North Atlantic, a single fall/winter bloom in the subtropical Atlantic, and no prominent seasonal cycle in the tropical Atlantic (e.g., Colebrook, 1979, 1982; Taboada and Anadón, 2014; Friedland et al., 2016). The ecosystem model (providing the food information for PLAFOM2.0), however, does not faithfully reproduce the observed seasonal cycle in the primary productivity (cf. Figure 4 in Moore et al., 2002b). The simulated (depth integrated) chlorophyll concentration, used as an indicator for productivity, does ~~not~~ only in parts show two cycles per year (Figure 7a-c). Nevertheless, the peak timings of the (depth integrated) foraminifera concentration follow the maxima in the primary productivity. For instance, the modeled maximum production peak of *N. pachyderma* at site PAPA ~~is preceded by~~ coincides with a peak in the diatom concentration (Figure 7a), *N. incompta* reaches its maximum in the simulation more likely at depth at site CP following a DCM (Figure 7b), and the predicted spring and/or fall peak of *G. bulloides* ~~predicted peak value~~ at site ~~JGOFS34~~WAST occurs slightly after the peak in the main food concentration or the maximum in the chlorophyll concentration (Figure 7c). However, the ecosystem model seems to underestimate the seasonality in the primary productivity, which most likely leads to the model-data-mismatch in the seasonal pattern of the planktonic foraminifera concentration. Additionally, the variability of planktonic foraminifera carbon biomass produced by PLAFOM2.0 is in general too low compared to the observations. This mismatch can either be explained by misrepresentations of the foraminiferal carbon biomass or of the foraminifera response (to the environmental forcing) in the model parameterizations or by an underestimation of the driving factors (i.e., especially the main food sources as outlined above). The depth habitat of planktonic foraminifera depends on several environmental and ontogenetic factors (e.g., Fairbanks and Wiebe, 1980; Fairbanks et al., 1982; Schiebel et al., 2001; Simstich et al., 2003; Field, 2004; Salmon et al., 2015; Rebotim et al., 2017). The simulated vertical distribution patterns can also be related to food availability and temperature (Figure 7d-f). For instance, at station ~~PS78-44~~PS55-063, peak abundances of *N. pachyderma* are reached in the top $50\,\mathrm{m}$ in the model corresponding to the highest diatom concentrations (Figure 7d). At station MOC1-28, the predicted depth profile of *G. ruber* (white) coincides with the vertical distribution pattern of zooplankton with ~~both their~~ maximaum concentrations ~~being reached at 55 m~~ occurring over the top $50\,\mathrm{m}$ of the water column (Figure 7e). At station SO225-21-3, the modeled species' concentration of *T. sacculifer* decreases gradually with depth following the zooplankton distribution, but also temperature (Figure 7f). However, the simulated depth profiles differ from the observations, which is also indicated by the differences in the ALDs. In PLAFOM2.0, the foraminiferal species do not occur below $200\,\mathrm{m}$ water depth (cf. Figures 4 and 7d-f) most likely being restricted through food availability and the ambient temperatures. Thus, depending on the vertical resolution of the sampling intervals of a plankton tow sample the predicted ALD is very likely lower by several meters than the observed ALD. In summary, PLAFOM2.0 is able to reproduce the observed species' behavior with regard to time and depth on a local scale, but is strongly dependent on the input variables (e.g., temperature and the different food sources) provided by both the ocean and the ecosystem model and is, thus, limited in its capability to match the observations.

Keeping the caveats regarding the model resolution, model parameterizations, model hierarchy, and analytical constraints on the observations in mind, the model-data-mismatch might, however, be reduced by a higher model resolution (in time and space), which would in turn increase the computational costs. A higher taxonomic resolution of the considered species (resulting in an increased number of passive tracers and likewise degrees of freedom) and by explicitly parameterizing the ontogeny of each individual planktonic foraminifera, thus, by considering the changes in the species' life cycles with depth (e.g., Bijma et al., 1990a; Bijma, 1991; Bijma and Hemleben, 1994; Bijma et al., 1994; Hemleben and Bijma, 1994; Schiebel et al., 1997), could considerably improve the model. The discrepancies between the model and the observations could, additionally, be minimized by including better ecological constraints on planktonic foraminifera species and their habitat, e.g., by introducing more phytoplankton and zooplankton functional groups in the ecosystem model to better resolve species' food preferences, which would, however, result in an increased computational cost. Nevertheless, additional knowledge about the factors controlling the habitat of planktonic foraminifera in time and space based on culturing experiments and field studies are needed for an optimization and better validation of the current model version. In addition, due to the model complexity it is not trivial to determine which model component (i.e., POP2, BEC or PLAFOM2.0) contributes to what extent to the model-data-mismatch. Determining this would require a suite of sensitivity experiments with each model component, which should be considered for future work. The model produces, nonetheless, seasonal and vertical abundance patterns that are consistent with our current understanding and which emerge from the model without an explicit parameterization of abundance in time and space. PLAFOM2.0, ~~however~~ thus, represents a major step forward from the previous model version and can be used to assess paleoclimate information in a better way.

5 Conclusions

A new version of the dynamic planktonic foraminifera model PLAFOM (PLAFOM2.0)~~,~~ has been developed and combined with the CESM1.2(BGC) model configuration to simulate species-specific seasonal and depth habitats for *N. pachyderma*, *N. incompta*, *G. bulloides*, *G. ruber* (white), and *T. sacculifer* on a global scale. In comparison with the original approach, where only species' concentrations in the surface mixed layer were predicted, PLAFOM2.0 includes a vertical component and, thus, predicts species' distribution patterns in space and time more realistically.

PLAFOM2.0 produces spatially and temporally coherent abundance patterns, which agree well with available observations. The model configuration faithfully reproduces the areal extent of the species. In line with core-top data, the modeled global distribution of each foraminifera changes with latitude. Additionally, PLAFOM2.0 successfully predicts the patterns in the timing of peak fluxes of planktonic foraminiferal species on a global scale. The earlier-when-warmer pattern for the temperate and cold-water species and the flux focusing at low temperatures of warm-water species, as inferred from observations by Jonkers and Kučera (2015), have emerged from the model.

Although an explicit parameterization of the vertical dimension is lacking, the model successfully predicts the preferred habitat depth of the individual planktonic foraminiferal species as well as the spatial and temporal variability in the vertical abundance. In accordance with the available observations, the warm-water species *G. ruber* (white) and *T. sacculifer* consistently occur close to the sea surface year-round in the tropics/subtropics, whereas the depth habitat of the colder-water species *N. pachyderma*, *N. incompta*, and *G. bulloides* changes seasonally in the polar/subpolar regions. During the cold season these species occur near-surface, while during the warmer season they descend in the water column to be found up to 120 m water depth or even below ~~at mid-depth~~ most likely following the chlorophyll maximum.

In general, paleoceanographic reconstructions based on planktonic foraminifera are hampered by the fact that the environmental signal preserved in their shells is the result of both habitat and climate change. The two effects are difficult to separate without independent data. PLAFOM2.0 presents a powerful tool to address this issue and can contribute to more meaningful comparisons of climate model results and paleoclimate reconstructions, ultimately aiding to the understanding of mechanisms of climate change.

Code and data availability. All model data can be obtained from the PANGAEA database (www.pangaea.de). The model code is available upon request from the corresponding author (Kerstin Kretschmer, kkretschmer@marum.de).

Competing interests. The authors declare that they have no conflict of interest.

Acknowledgements. This paper has benefited from the constructive comments and suggestions of Inge van Dijk, Jelle Bijma and two anonymous reviewers as well as of the handling associated editor Lennart de Nooijer. We are grateful to Graham Mortyn for providing the plankton tow data from the Atlantic sector of the Southern Ocean. We would like to thank Gerlinde Jung and Jeroen Groeneveld for their helpful advice. The model integration has been performed at the North-German Supercomputing Alliance (HLRN). This project was supported by the DFG (Deutsche Forschungsgemeinschaft) through the International Research Training Group IRTG 1904 ArcTrain and the DFG Research Center/Cluster of Excellence “The Ocean in the Earth System”.

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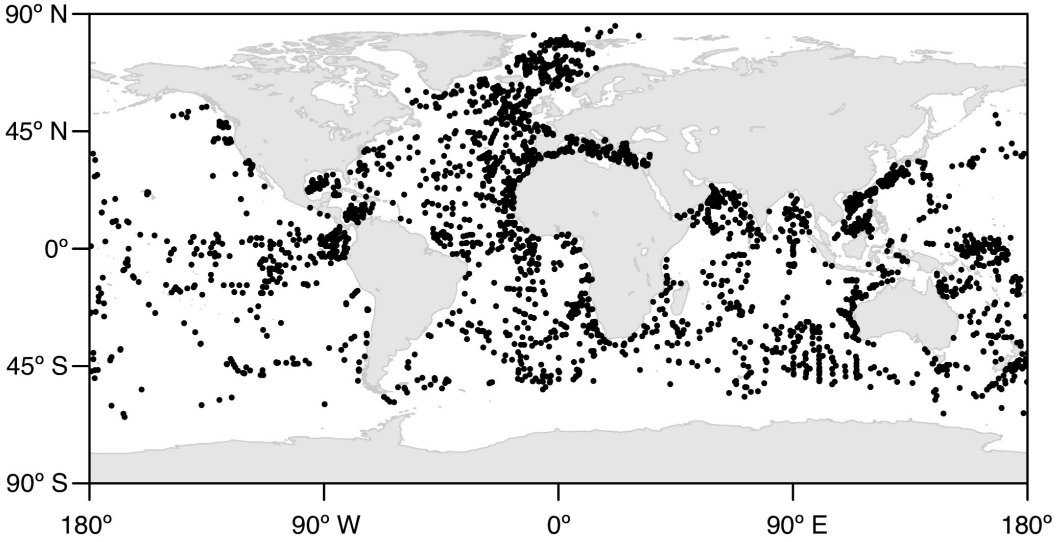
(a) Core-top samples



(b) Sediment trap & plankton tow samples

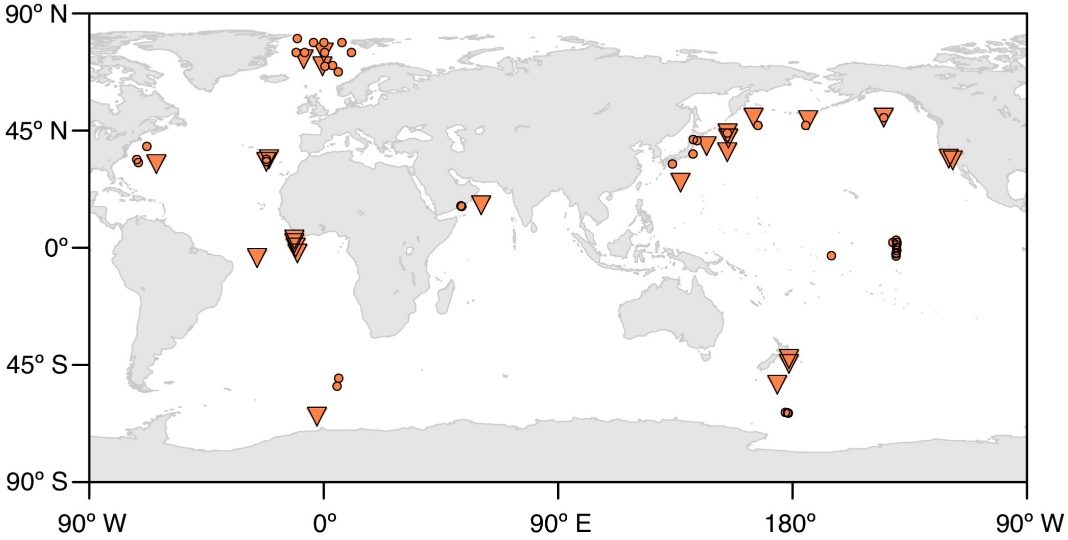


Figure 1. Locations of (a) the core-top samples with planktonic foraminifera counts and (b) the plankton tow (orange circles) and sediment trap (orange triangles) samples used for the model validation. The map in Figure 1a shows a combination of the data sets of Prell et al. (1999), Pflaumann et al. (1996, 2003), and Kucera et al. (2005). The respective information on the sediment trap and plankton tow data shown in Figure 1b is given in Tables S1 and S2 in the Supplement.

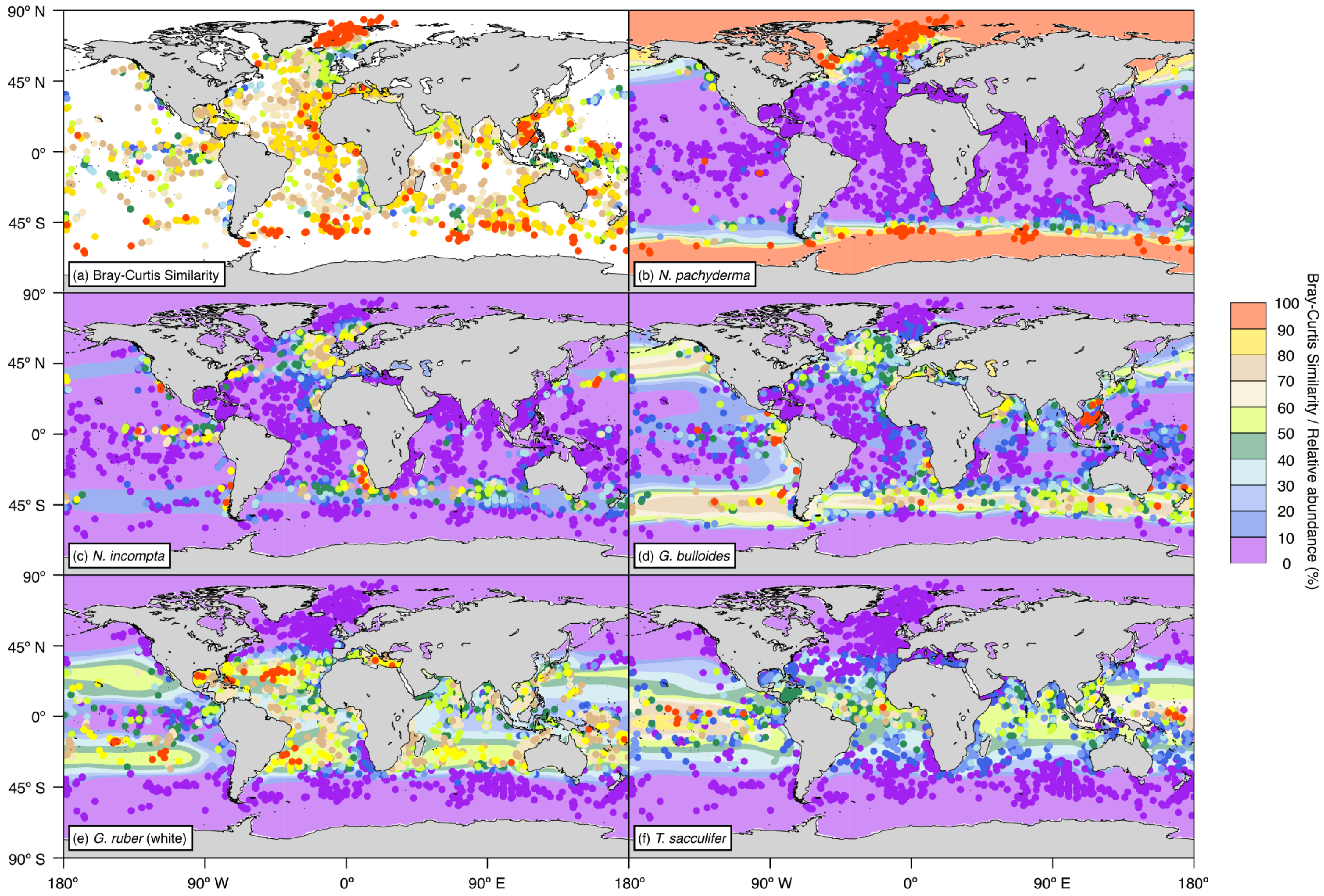


Figure 2. (a) Bray-Curtis index of similarity (in %) between the relative abundances of the modeled and core-top data as well as ~~R~~relative abundances of the depth integrated modeled annual mean concentration (pale-colored contours; in % carbon biomass) and of the core-top samples (circles; in % individuals) for (~~a~~b) *N. pachyderma*, (~~b~~c) *N. incompta*, (~~c~~d) *G. bulloides*, (~~d~~e) *G. ruber* (white), and (~~e~~f) *T. sacculifer*. The relative abundances consider only the five foraminiferal species included in PLAFOM2.0. In addition, to account for the different sizes of each foraminiferal species, we multiplied the modeled annual mean concentration of each species with their relative size (Table 2) and subsequently calculated the depth integrated species' annual mean concentrations relative to the total modeled foraminiferal carbon biomass. Note that we are aware that for a small number of core-top samples the relative abundances of the individual planktonic foraminiferal species are overestimated due to the recalculations by only considering *N. pachyderma*, *N. incompta*, *G. bulloides*, *G. ruber* (white), and *T. sacculifer* rather than the whole assemblage. However, the overall general pattern does not change and can, thus, be used for the model-data comparison.

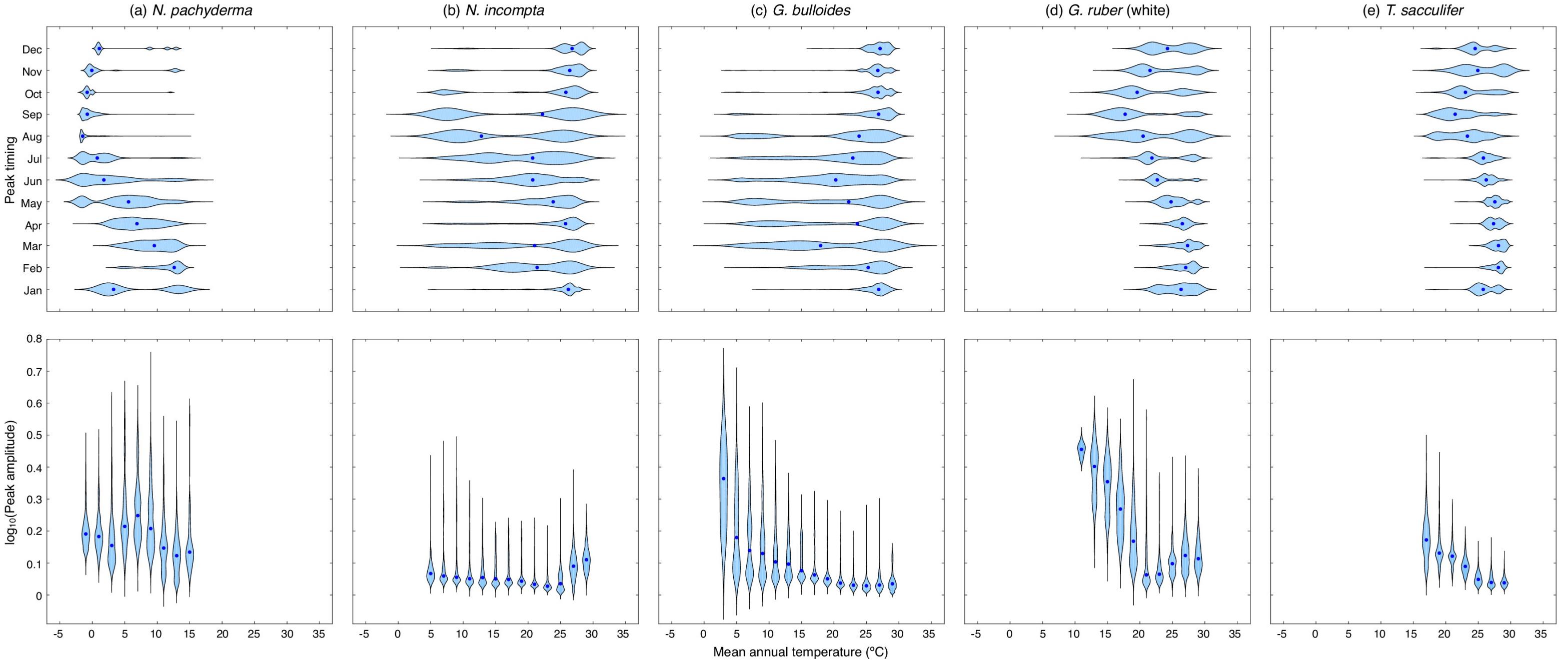


Figure 3. Violin plots showing the dependence of the modeled peak timing (top row) and/or the modeled peak amplitude (bottom row) on the annual mean temperature (in $^\circ\mathrm{C}$) averaged over the top $55\,\mathrm{m}$ of the water column for (a) *N. pachyderma*, (b) *N. incompta*, (c) *G. bulloides*, (d) *G. ruber* (white), and (e) *T. sacculifer*. The blue dots represent the respective median values. The modeled peak timing is given in months and the modeled peak amplitude has been log-transformed. Note that the peak timings of each species from the southern hemisphere have been transformed to northern hemisphere equivalents by adding or subtracting 6 months.

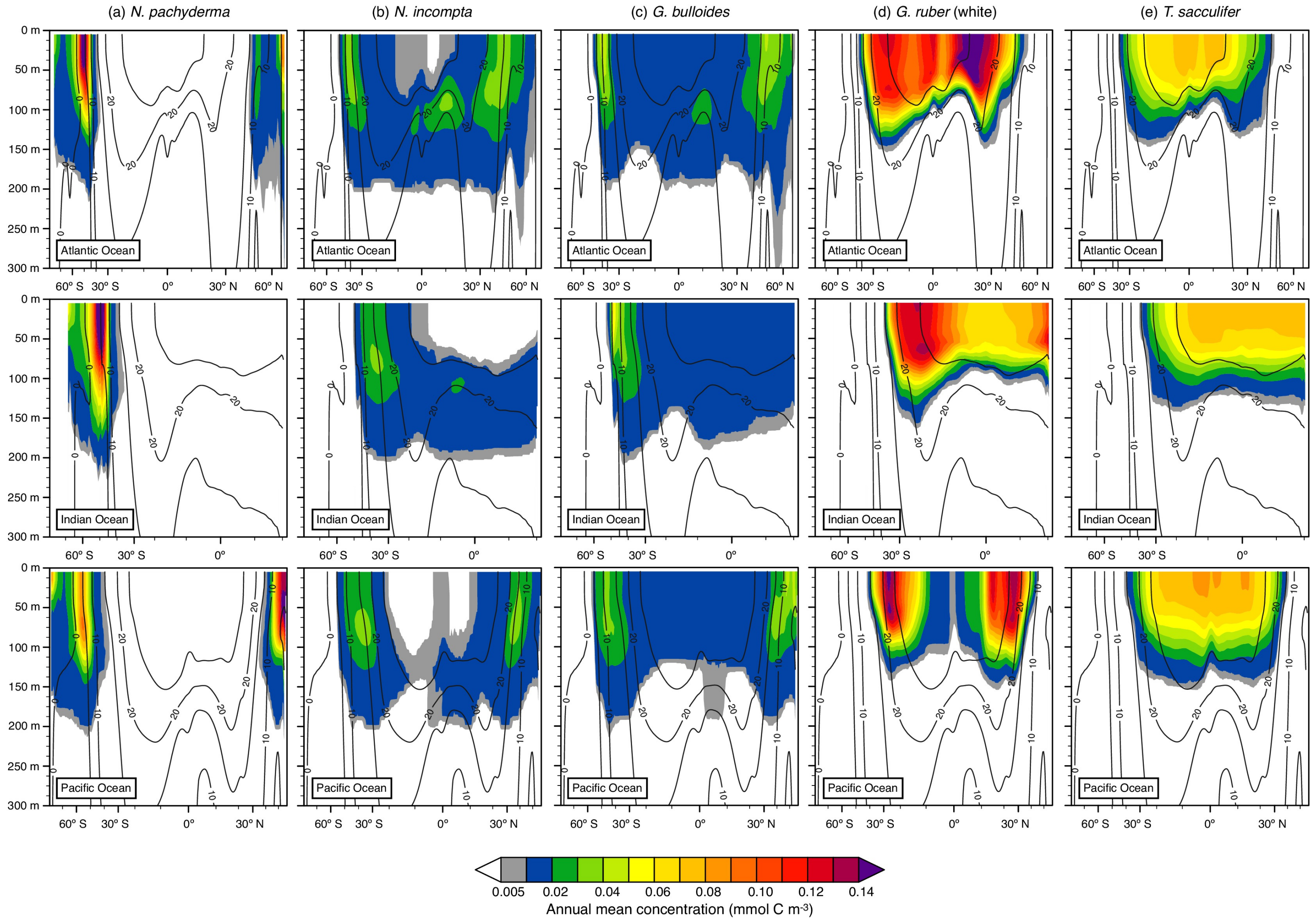


Figure 4. Depth transects of the modeled annual mean concentration (in $\mathrm{mmol\,C\,m^{-3}}$) along $\sim 27\,^{\circ}\mathrm{W}$ in the Atlantic Ocean (top row), $\sim 71\,^{\circ}\mathrm{E}$ in the Indian Ocean (middle row), and $\sim 162\,^{\circ}\mathrm{W}$ in the Pacific Ocean (bottom row) over the top ~~250~~ 300m for (a) *N. pachyderma*, (b) *N. incompta*, (c) *G. bulloides*, (d) *G. ruber* (white), and (e) *T. sacculifer*. ~~The dashed grey lines mark the depth of the maximum modeled annual mean production for each planktonic foraminiferal species respectively.~~ The black contour lines indicate the annual mean temperature estimates. The blank areas denote where a species is absent.

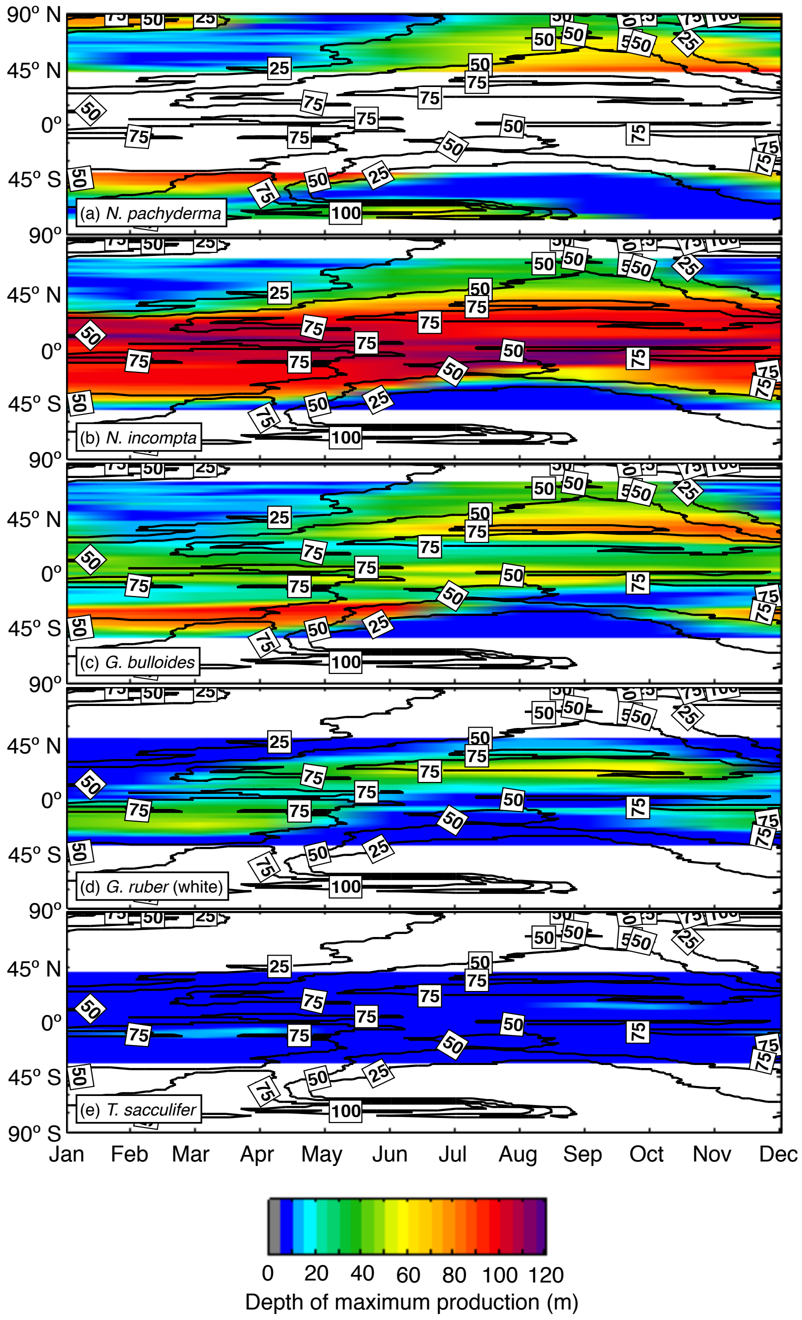


Figure 5. Zonal average of the depth (in m) at which the modeled maximum production of (a) *N. pachyderma*, (b) *N. incompta*, (c) *G. bulloides*, (d) *G. ruber* (white), and (e) *T. sacculifer* occurs over time. The ~~grey~~ black contour lines indicate the zonal average of the (seasonally varying) depth of the chlorophyll maximum (in m). The blank areas denote where a species is absent.

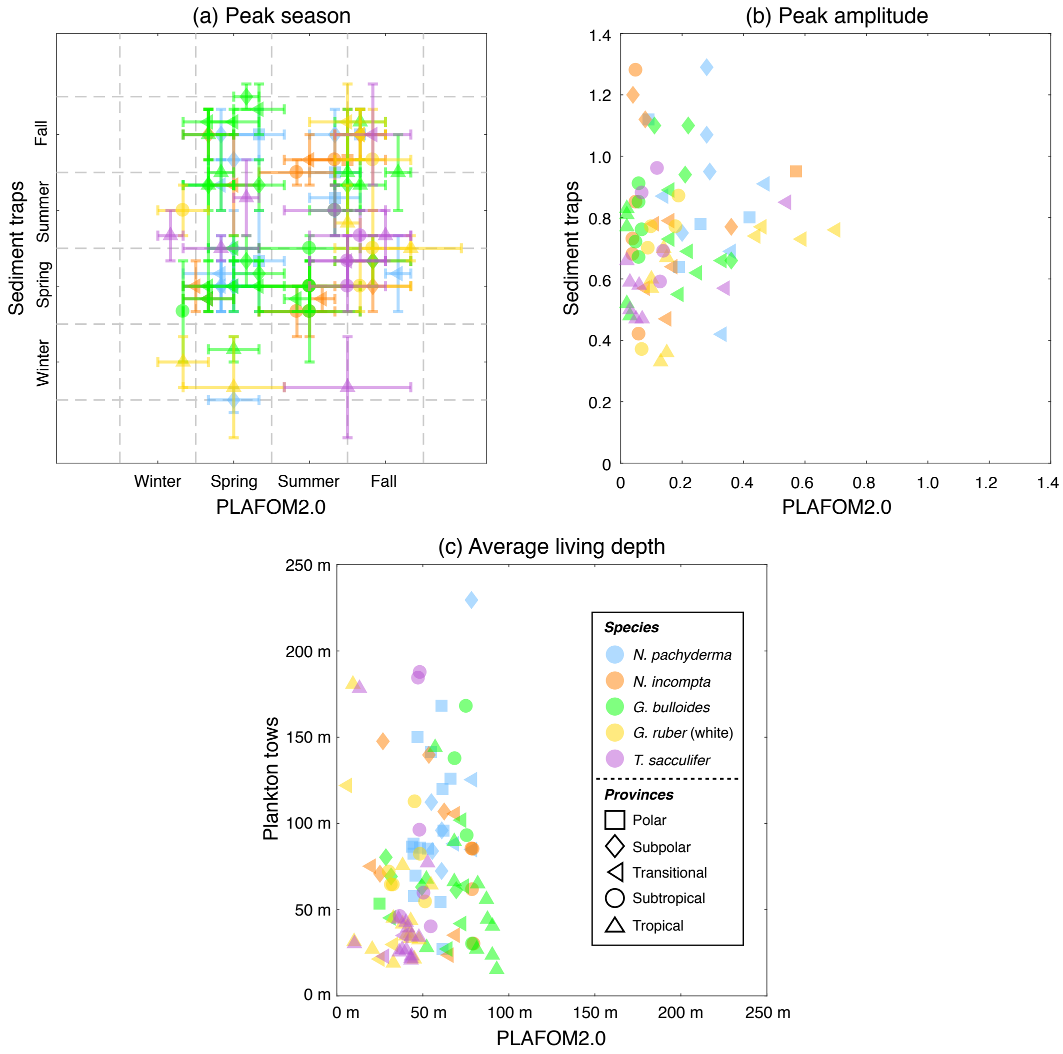


Figure 6. (a) Peak seasons (i.e., caloric season of the maximum production), (b) peak amplitudes (i.e., maximum production divided by annual mean), and (c) average living depths (in m) for *N. pachyderma* (light blue), *N. incompta* (orange), *G. bulloides* (green), *G. ruber* (white) (gold), and *T. sacculifer* (orchid) based on either the sediment trap data (given in Table S3) or the plankton tow data (given in Table S4) vs. PLAFOM2.0. The symbols represent the polar (squares), subpolar (diamonds), transitional (left-pointing triangles), subtropical (circles), and tropical (upward-pointing triangles) provinces of the ocean, respectively. The symbols in (a) indicate the month corresponding to the mid-season and the error bars refer to the overall time frame given in Table S3a. Note that the observed and modeled peak amplitudes in (b) have been log-transformed.

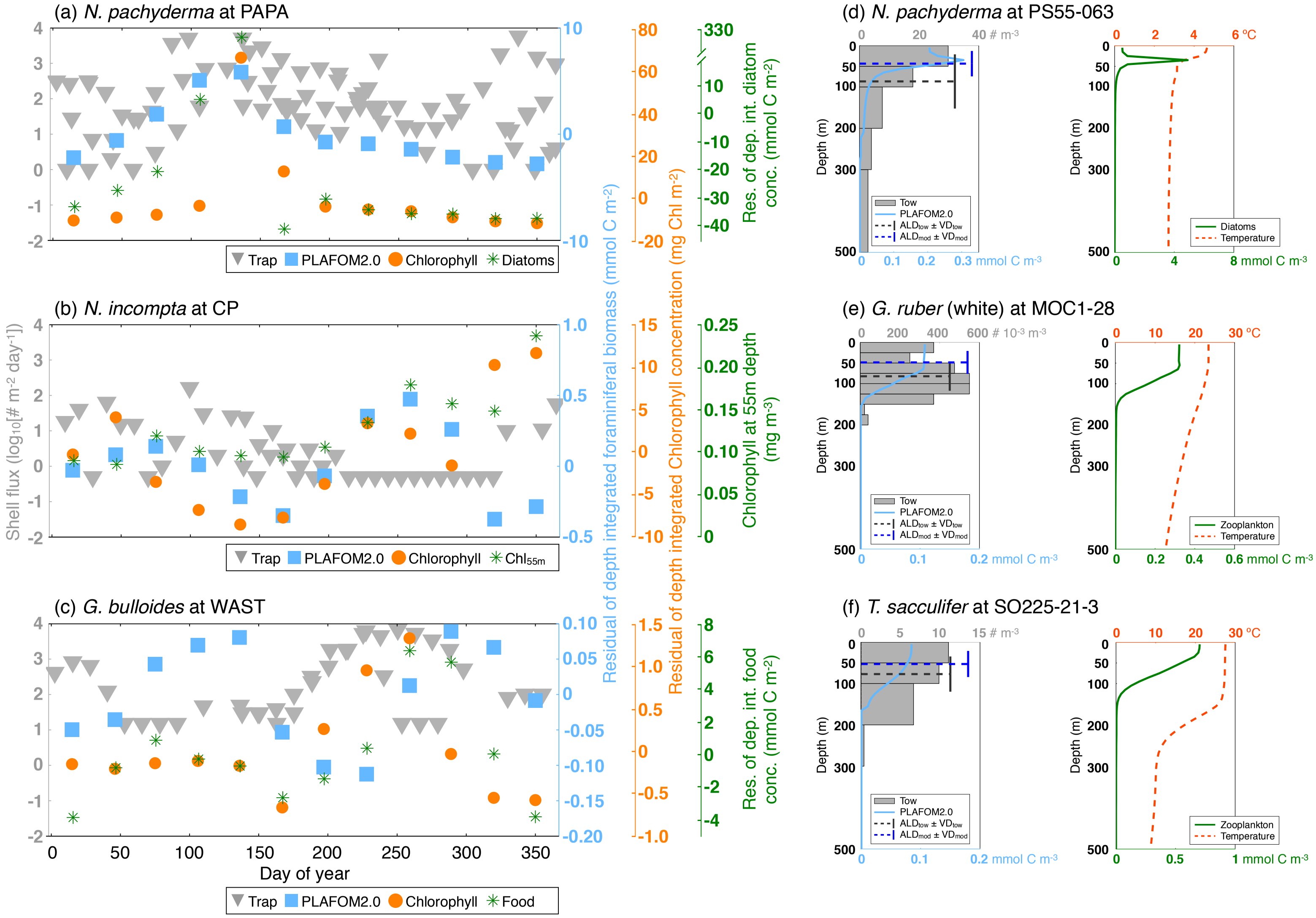


Figure 7. (a-c) Comparison of export planktonic foraminiferal shell fluxes in sediment traps (grey triangles) with the residuals (i.e., the deviation from the mean) of the depth integrated modeled foraminiferal carbon biomass (light blue squares). Note that the difference in the units between sediment trap data (in $\log_{10}[\#\,\mathrm{m}^{-2}\,\mathrm{day}^{-1}]$) and model output (in $\mathrm{mmol\,C\,m^{-2}}$) does not affect the assessment of peak timing. The orange circles denote the residuals of the depth integrated modeled chlorophyll concentration (in $\mathrm{mg\,Chl\,m^{-2}}$), and the dark green asterisks indicate in (a) the residuals of the depth integrated modeled diatom concentration (in $\mathrm{mmol\,C\,m^{-2}}$), ~~and/or~~ in (b) the modeled chlorophyll concentration (in $\mathrm{mg\,m^{-3}}$) at 55 m water depth, and/or in (c) the residuals of the sum of the depth integrated modeled diatom and large detritus (i.e., main food) concentrations (in $\mathrm{mmol\,C\,m^{-2}}$). (d-f) Comparison of the vertical distribution of live specimens in plankton tows (in $\#\,\mathrm{m}^{-3}$; grey bars) with the modeled foraminiferal concentration over depth (in $\mathrm{mmol\,C\,m^{-3}}$; light blue profiles). The dashed dark grey and blue lines indicate the average living depth (in m) and vertical dispersion calculated for the plankton tows ($\mathrm{ALD_{tow} \pm VD_{tow}}$) and PLAFOM2.0 ($\mathrm{ALD_{mod} \pm VD_{mod}}$), respectively. The dashed red lines denote the predicted temperature profiles (in °C), whereas the dark green lines correspond to the modeled vertical distribution of (d) diatoms (in $\mathrm{mmol\,C\,m^{-3}}$) and/or (e-f) zooplankton (in $\mathrm{mmol\,C\,m^{-3}}$). Data series of (a) *N. pachyderma* at site PAPA, (b) *N. incompta* at site CP, and (c) *G. bulloides* at site ~~JGOFS34~~WAST. Depth profiles of (d) *N. pachyderma* at station ~~PS78-44~~PS55-063, (e) *G. ruber* (white) at station MOC1-28, and (f) *T. sacculifer* at station SO225-21-3. The ~~respective~~ locations of each sediment trap and plankton tow sample are given in Tables S1 and S2, respectively.

Table 1. Model parameter and their modifications relative to Fraile et al. (2008) and/or Kretschmer et al. (2016). The original value is given in parentheses.

Species	*N. pachyderma*	*N. incompta*	*G. bulloides*	*G. ruber* (white)	*T. sacculifer*
$P_{F,0}$	- (-)	- (-)	2.6 (-)	2.6 (-)	2.6 (-)
α_{PI}	- (-)	- (-)	0.012 (-)	0.01 (-)	0.07 (-)
$p_{\%}$	- (-)	- (-)	0.3 (-)	0.3 (-)	0.4 (-)
T_{thres}	18.0 (24.0)	3.0 (-0.3)	3.0 (-0.3)	10.0 (5.0)	15.0 (15.0)
$cl_{N.pachyderma,j}$	- (-)	0.2 (0.2)	0 (0)	0 (0)	0 (0)
$cl_{N.incompta,j}$	- (-)	- (-)	0.1 (0.1)	0.2 (0.8)	0 (0)
$cl_{G.bulloides,j}$	- (-)	0.8 (0.5)	- (-)	0.8 (0.8)	0.8 (0.8)
$cl_{G.ruber(\mathrm{white}),j}$	- (-)	0.2 (0.8)	0.1 (0.5)	- (-)	0.2 (0.2)
$cl_{T.sacculifer,j}$	- (-)	0 (0)	0.1 (0.5)	0.2 (0.2)	- (-)

$P_{F,0}$ – maximum foraminiferal growth rate (in day^{-1}) at $30\,^{\circ}\mathrm{C}$ (derived from the maximum zooplankton growth rate at $20\,^{\circ}\mathrm{C}$ given by Doney et al. (1996)).

α_{PI} – initial slope of the photosynthesis-light (PI) curve (in $\mathrm{m}^2\,\mathrm{W}^{-1}\mathrm{day}^{-1}$) (derived from PI-curve of *Synechococcus* given in Jodłowska and Śliwińska (2014) for *G. bulloides* and of endosymbiotic dinoflagellates given in Jørgensen et al. (1985) for *T. sacculifer*).

$p_{\%}$ – fraction of photosynthesis contributing to foraminiferal growth rate.

T_{thres} – minimum (for *N. pachyderma*) or maximum (for all other species) threshold temperature at which foraminiferal species can thrive (in $^{\circ}\mathrm{C}$).

cl_{ij} – competition pressure of species i upon species j.

Table 2. Relative sizes of the analyzed planktonic foraminifera species based on estimates of species size ranges from Schmidt et al. (2004) averaged over the sample locations in that study.

Species	Size (in μm)
N. pachyderma	321.50
N. incompta	321.50
G. bulloides	553.14
G. ruber (white)	541.00
T. sacculifer	661.44

Supporting Information for “Modeling seasonal and vertical habitats of planktonic foraminifera on a global scale”

Contents of this file

Figure S1 (page 2): 50-year (left panel) and ~~200~~ 300-year (right panel) time series of the year-to-year difference (in $\mathrm{mmol\,m^{-3}}$) of the modeled carbonate ion concentration ($\mathrm{CO_3^{2-}}$; grey), dissolved inorganic nitrate ($\mathrm{NO_3^-}$; light blue), small phytoplankton concentration (orange), zooplankton concentration (magenta), and the concentration of *N. pachyderma* (black) at the surface ocean, $105\,\mathrm{m}$, $250\,\mathrm{m}$, and $530\,\mathrm{m}$ water depth. Note that the left panel only shows a zoom for the latter three mentioned concentrations.

Figure S2 (page 3): Modeled peak timing (top row) and/or modeled peak amplitude (bottom row) vs. annual mean temperature (in $^\circ\mathrm{C}$) averaged over the top $55\,\mathrm{m}$ of the water column for (a) *N. pachyderma*, (b) *N. incompta*, (c) *G. bulloides*, (d) *G. ruber* (white), and (e) *T. sacculifer*. The color coding corresponds to latitude. Modeled peak timing is given in months and modeled peak amplitudes have been log-transformed. Note that peak timings of each species from the southern hemisphere have been transformed to northern hemisphere equivalents by adding or subtracting 6 months. For a better visualization the peak timing data has been offset along the ordinate axis to avoid that overlapping points plot on top of each other (this has been achieved by adding a small amount of white noise to the peak timing data). The grey shadings in the top row panels show the data density, i.e., where most of the data points occur.

Figure S3 (pages 4-14): Comparison of export planktonic foraminiferal shell fluxes in sediment traps (in $\log_{10}[\#\,\mathrm{m^{-2}\,day^{-1}}]$; grey triangles) with the residuals (i.e., the deviation from the mean) of the volume integrated modeled biomass (in $\mathrm{mmol\,C\,m^{-3}} \times 10^{-4}$; light blue squares). The respective location of each sediment trap is given in Table S1.

Figure S4 (pages 15-26): Comparison of the vertical distribution of live specimens in plankton tows (in $\#\,\mathrm{m^{-3}}$; grey bars) with modeled concentrations over depth (in $\mathrm{mmol\,C\,m^{-3}}$; light blue profiles). Dashed dark grey and blue lines indicate average living depth (in m) and vertical dispersion calculated for the plankton tows ($\mathrm{ALD_{tow} \pm VD_{tow}}$) and PLAFOM2.0 ($\mathrm{ALD_{mod} \pm VD_{mod}}$), respectively. The respective location of each plankton tow sample is given in Table S2.

Figure S5 (page 27): Difference in potential temperature (in $^\circ\mathrm{C}$) between the Community Earth System Model, version 1.2.2 (CESM1.2) and the World Ocean Atlas 2013 (WOA13; Locarnini et al., 2013) averaged over the top (a) $55\,\mathrm{m}$ and (b) $250\,\mathrm{m}$ of the water column.

Table S1 (page ~~27~~ 28): Information on sediment trap data.

Table S2 (pages ~~28-~~29-30): Information on plankton tow data.

Table S3 (pages ~~30-~~31-32): (a) Peak season (i.e., season of maximum production) and (b) peak amplitude (i.e., maximum in production divided by the annual mean) for each planktonic foraminiferal species at the locations of the sediment traps shown in Figure 1b in the main text. Empty cells indicate absence of species in either the sediment trap data or the model output.

Table S4 (page ~~32~~33): Average living depths for each planktonic foraminiferal species at the locations of the plankton tows shown in Figure 1b in the main text. Empty cells indicate if species has been absent in either the plankton tow data or the model output.

References (pages ~~33-~~34-36)

Figure S1.

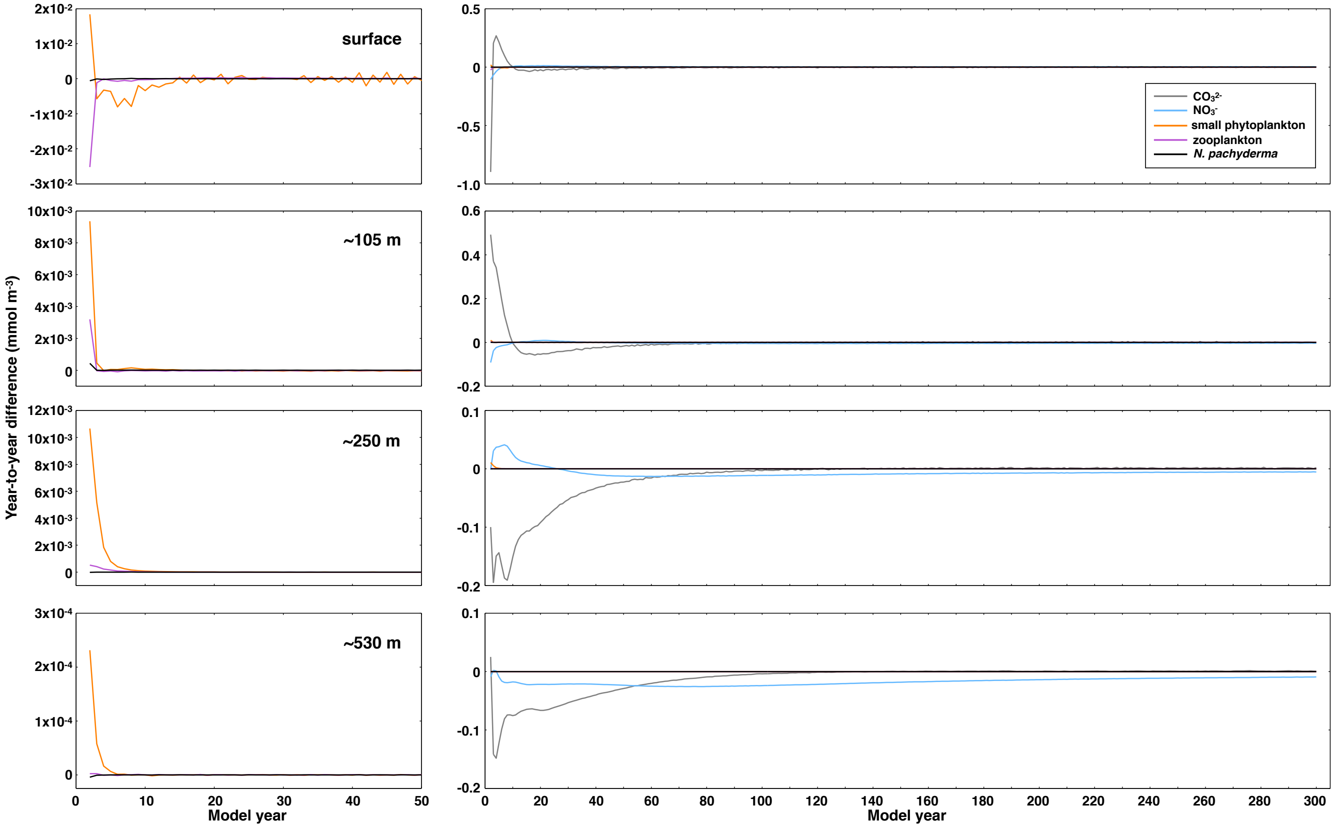
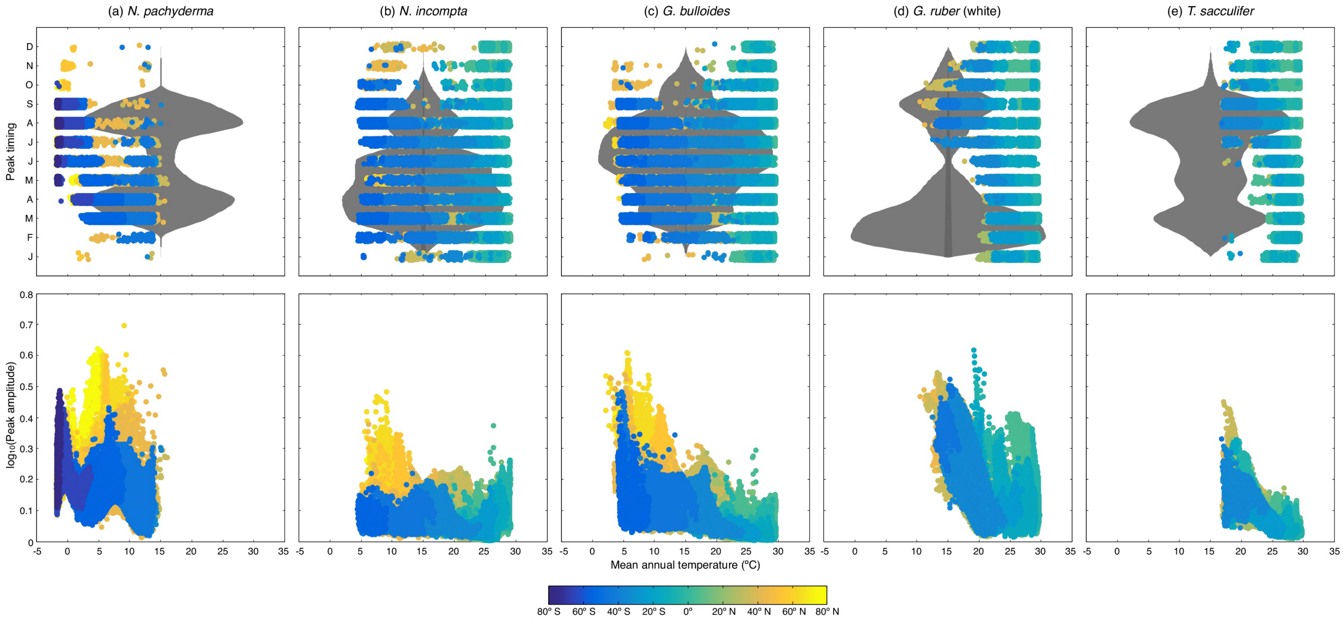

surface
~105 m
~250 m
~530 m
Year-to-year difference (mmol m-3)
2x10-2
1x10-2
0
-1x10-2
-2x10-2
-3x10-2
10x10-3
8x10-3
6x10-3
4x10-3
2x10-3
12x10-3
3x10-4
2x10-4
1x10-4
0.5
-0.5
-1.0
0.6
0.4
0.2
-0.2
0.1
-0.1
0
10
20
30
40
50
Model year
60
80
100
120
140
160
180
200
220
240
260
280
300
Model year
CO3 2-
NO3 -
small phytoplankton
zooplankton
N. pachyderma

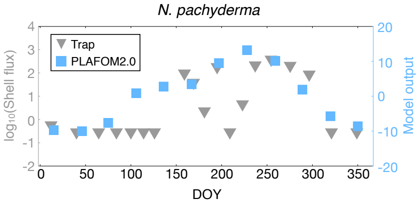
Figure S2.



(a) *N. pachyderma*
(b) *N. incompta*
(c) *G. bulloides*
(d) *G. ruber* (white)
(e) *T. sacculifer*
Peak timing
D
N
O
S
A
J
J
M
A
M
F
J
log10(Peak amplitude)
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-5
0
5
10
15
20
25
30
35
Mean annual temperature (°C)
80° S
60° S
40° S
20° S
0°
20° N
40° N
60° N
80° N

Figure S3.

Site GS2



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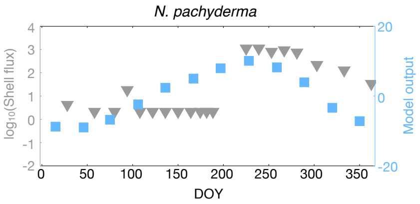
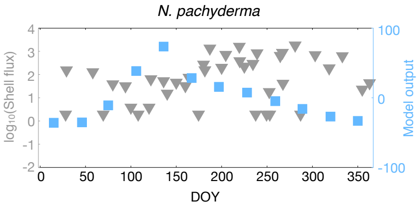
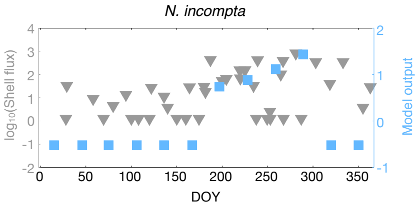


Site NB6/7





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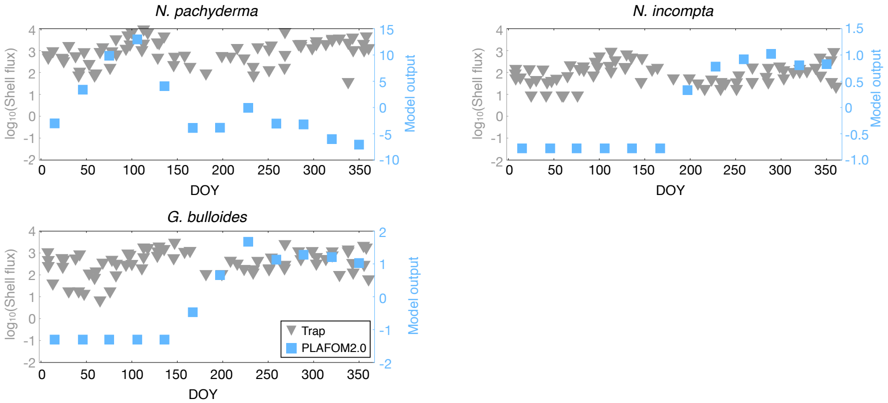

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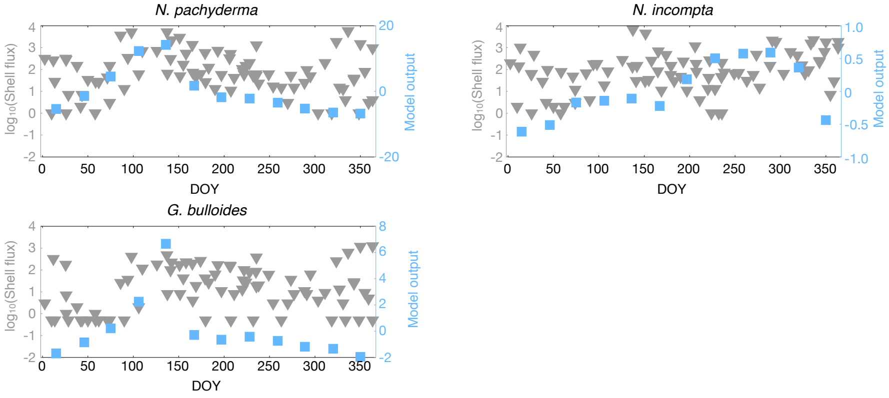
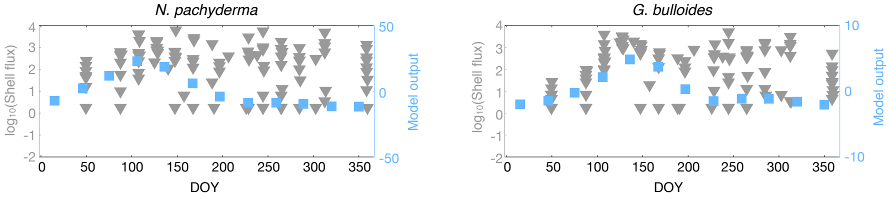
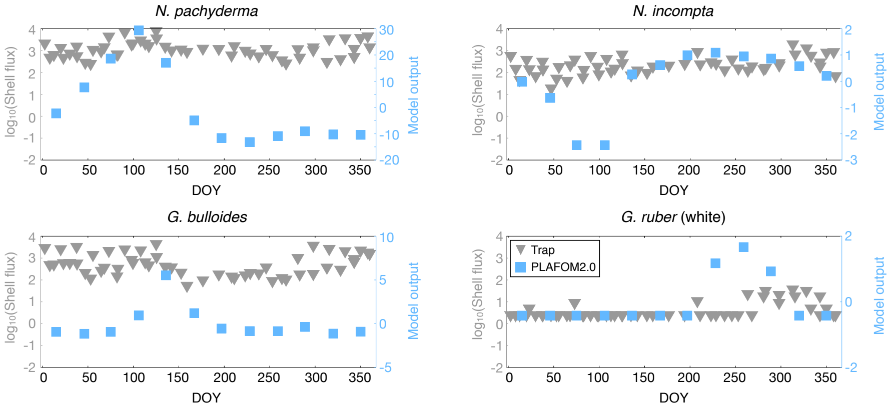


Site SA



Site KNOT



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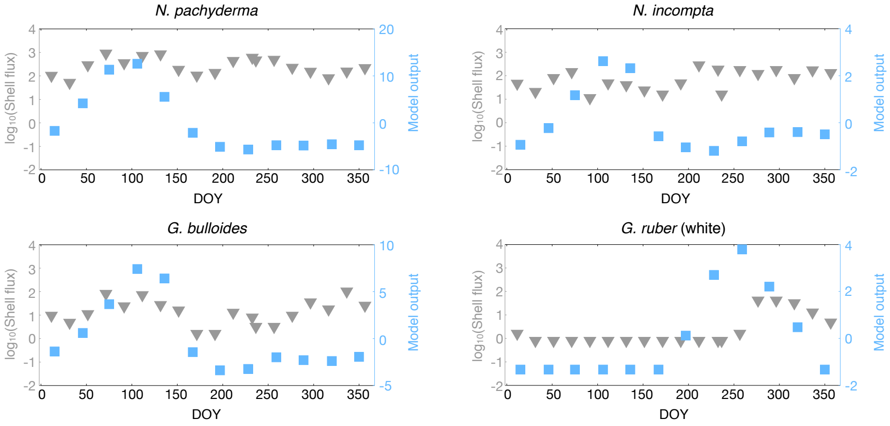

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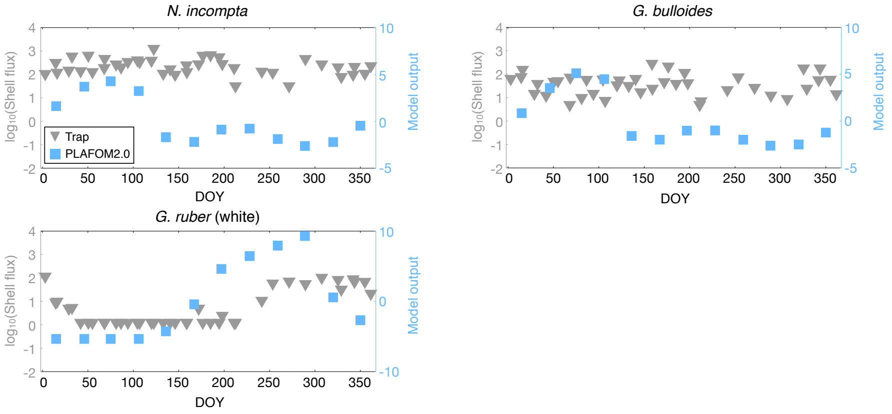

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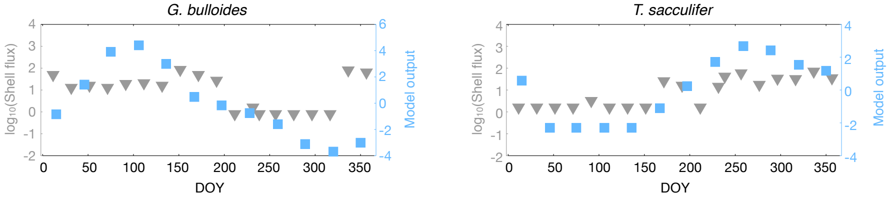

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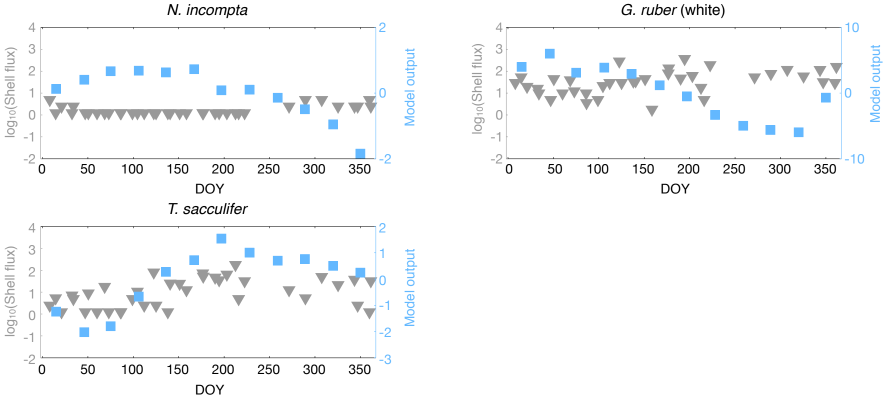

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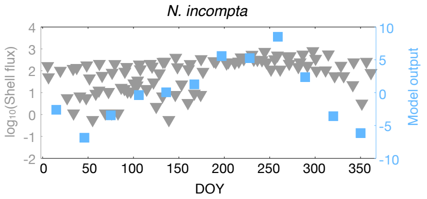

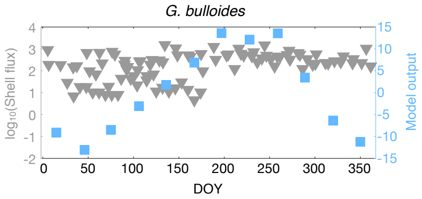

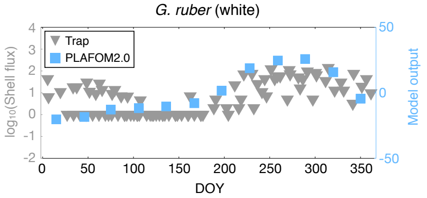

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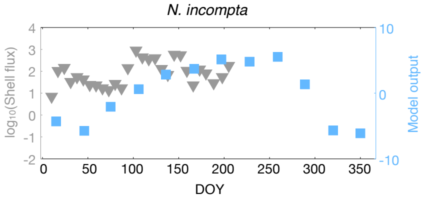

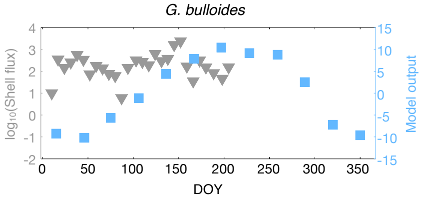

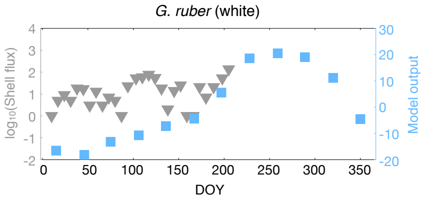

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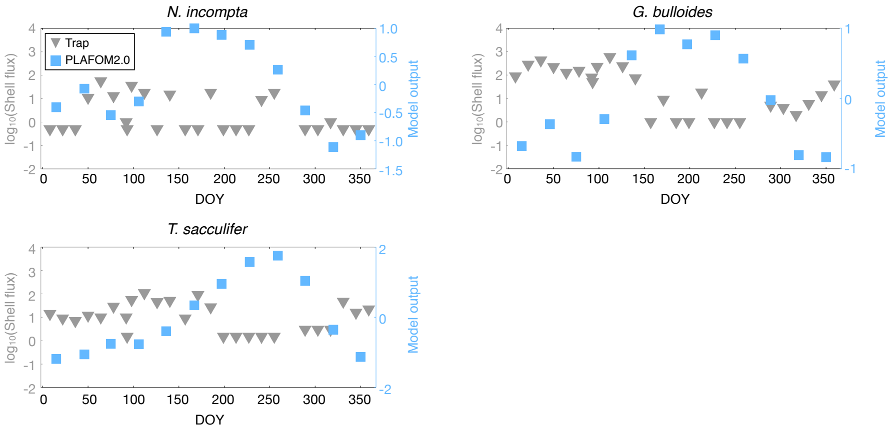

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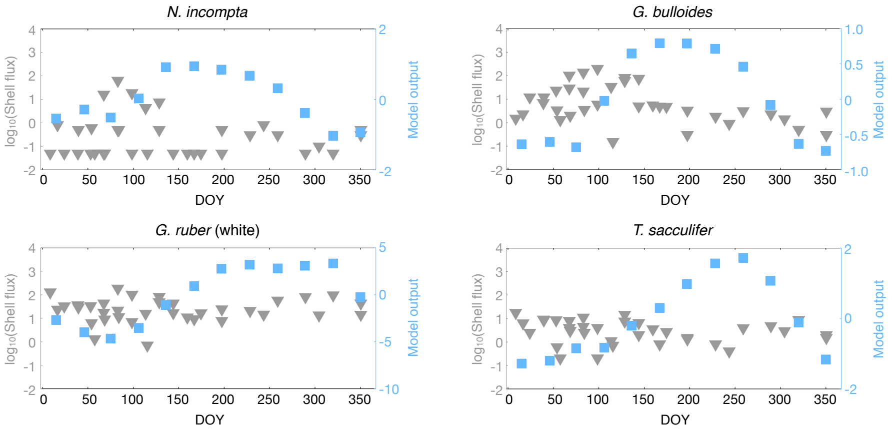

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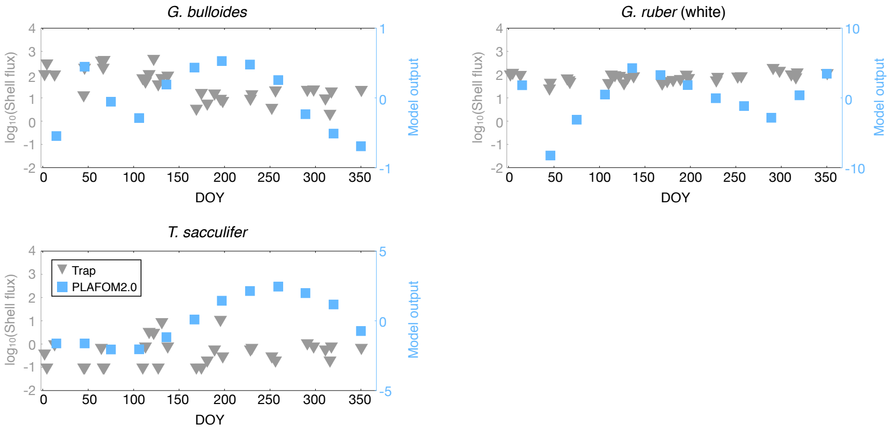

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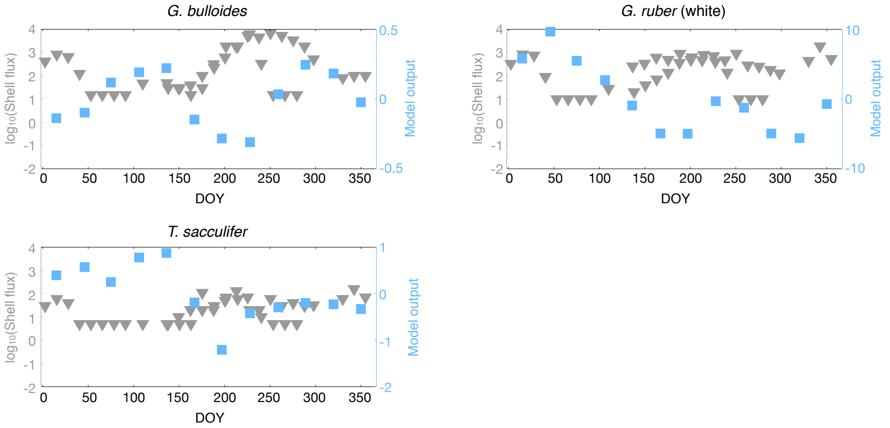

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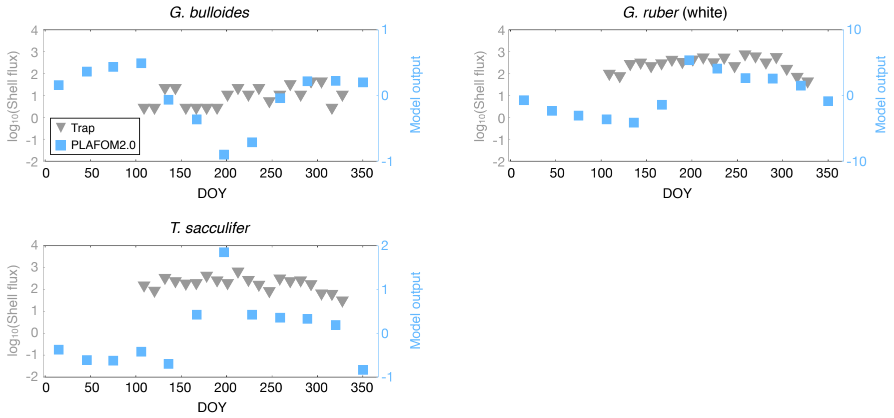

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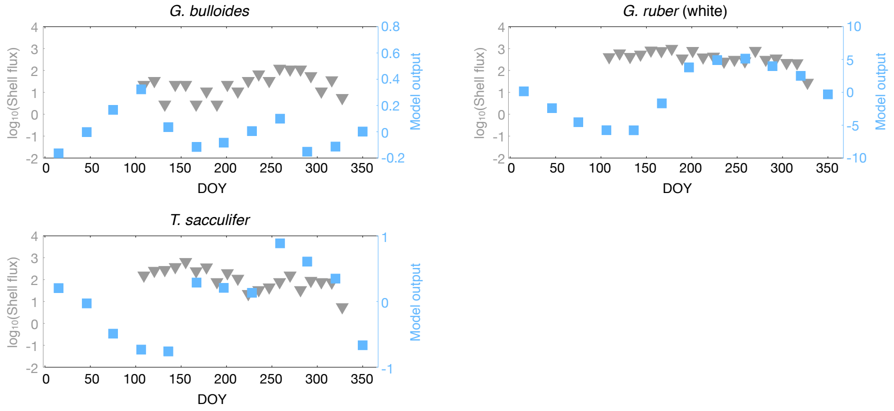

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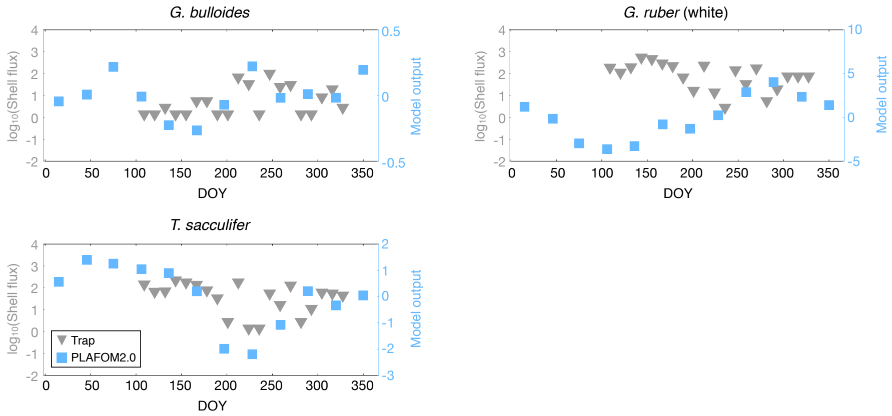

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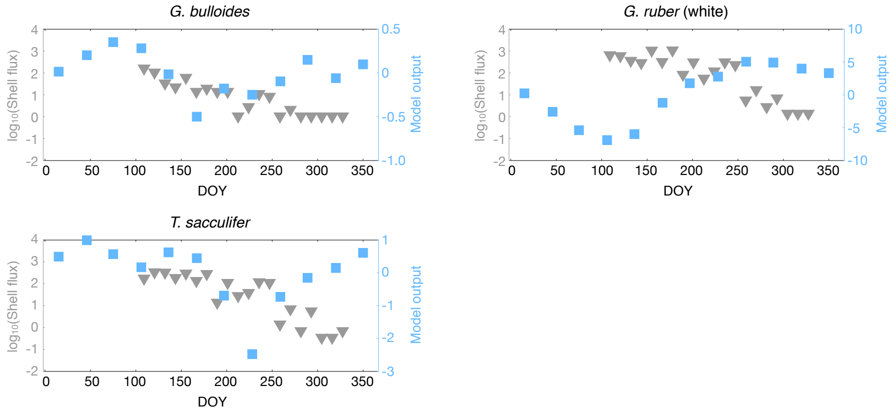

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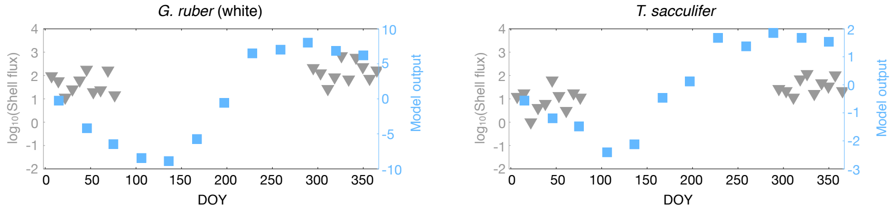

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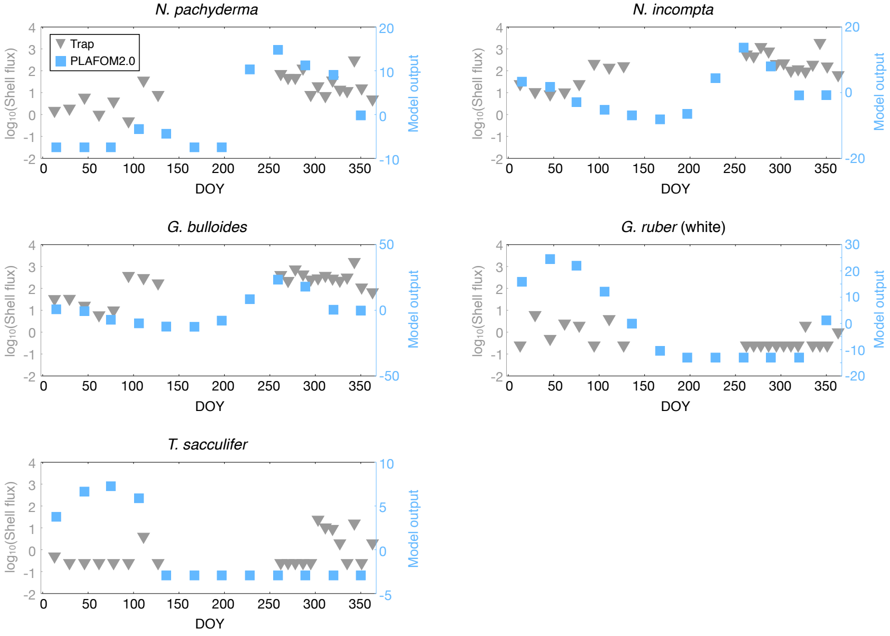

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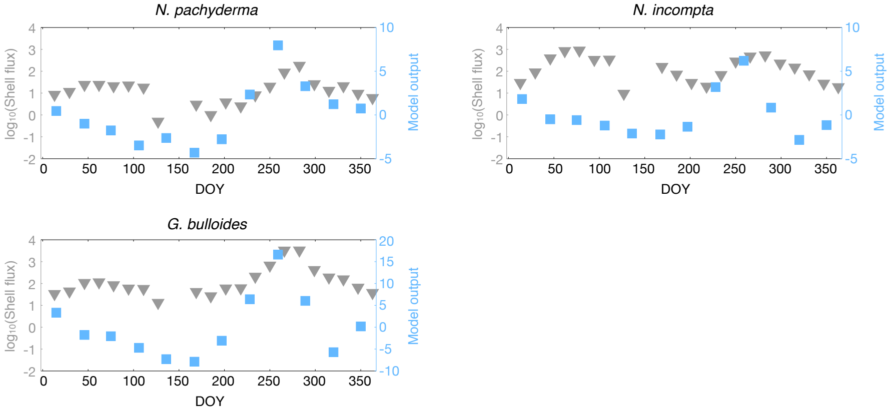

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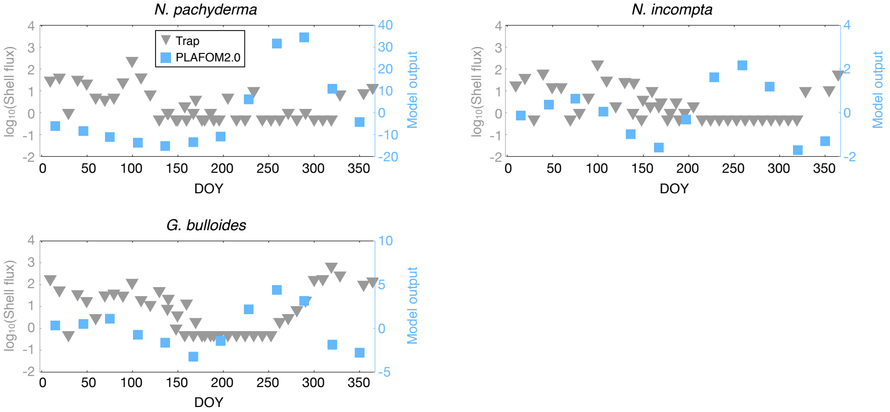

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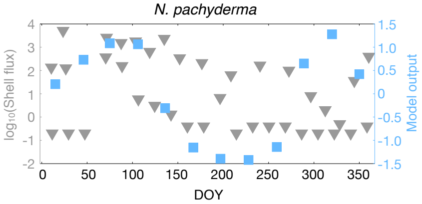
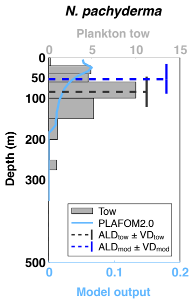


Figure S4.

Station 93-36



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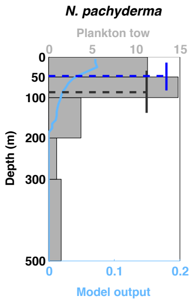

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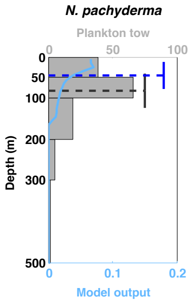

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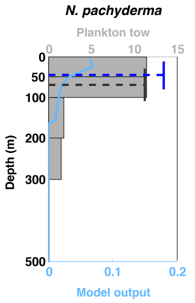

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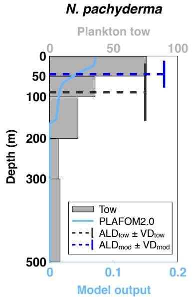

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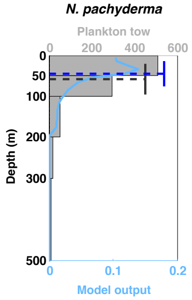

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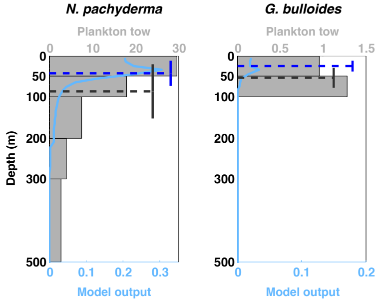

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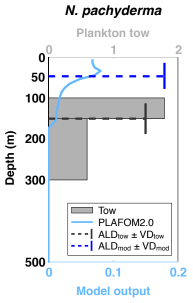

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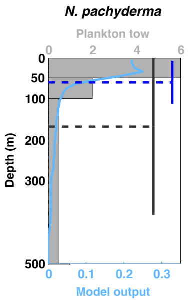

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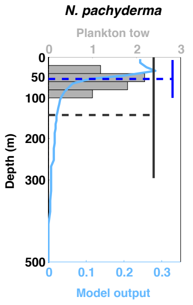

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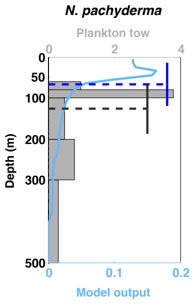

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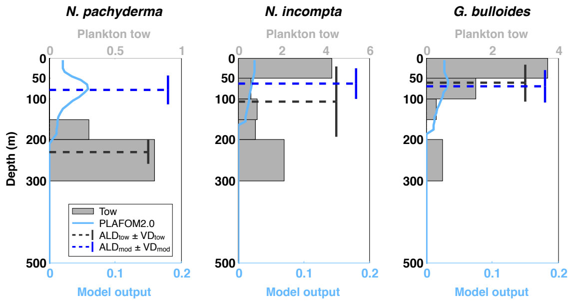

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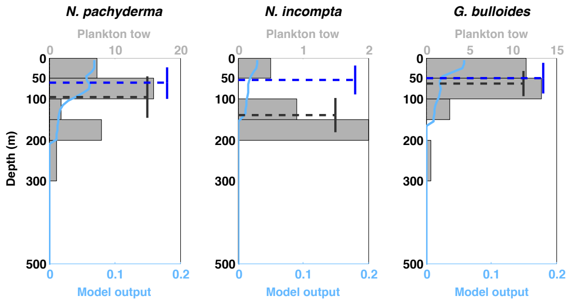

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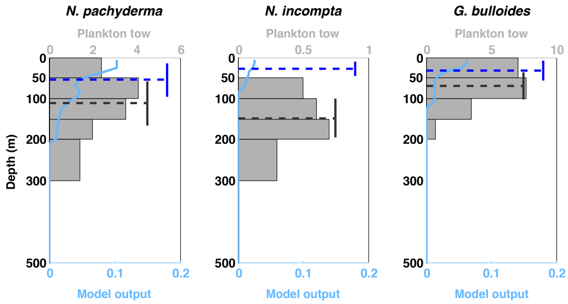

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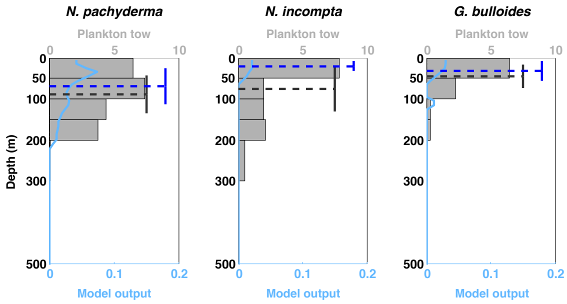

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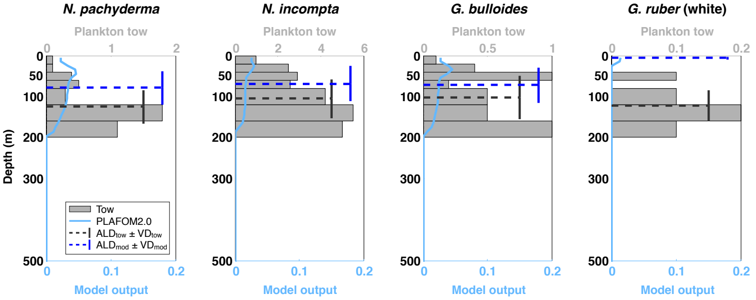

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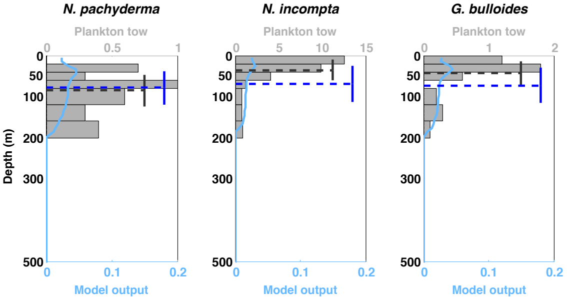

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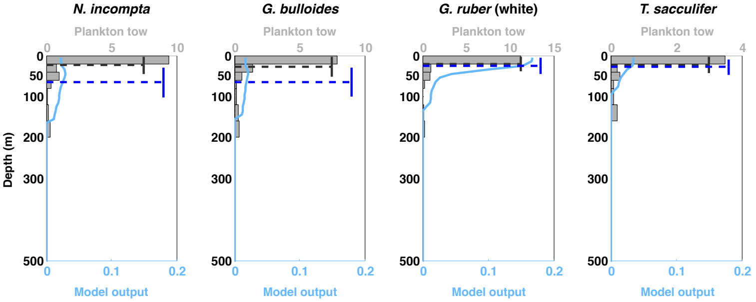

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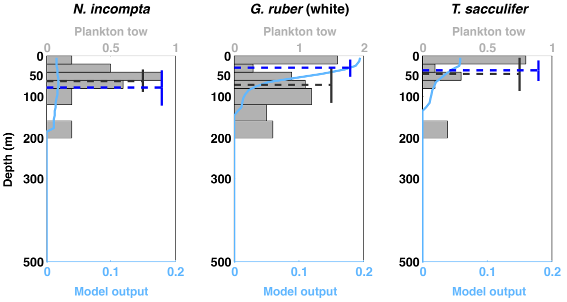
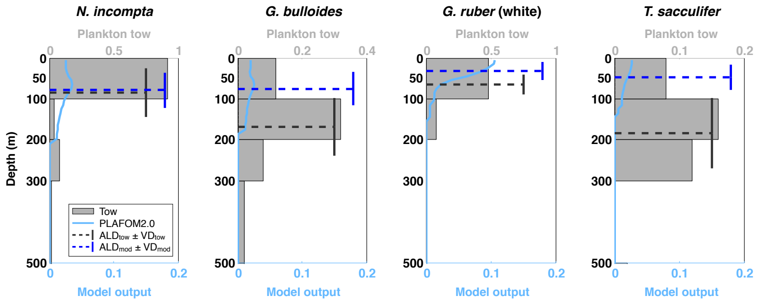


Station POS383-165



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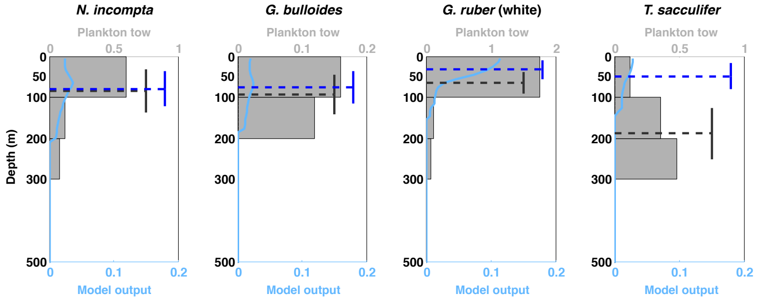

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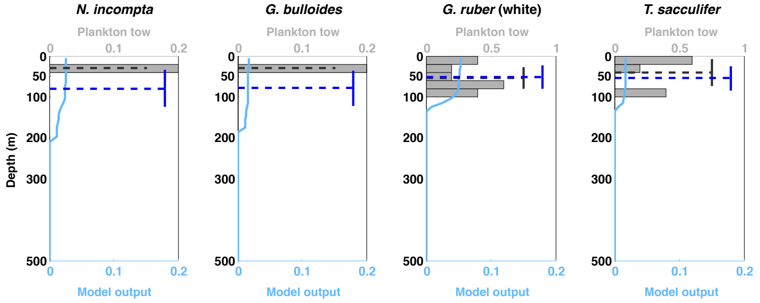

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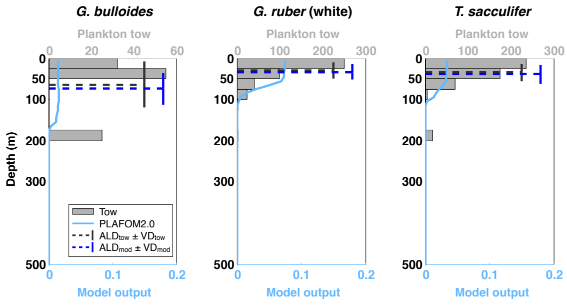

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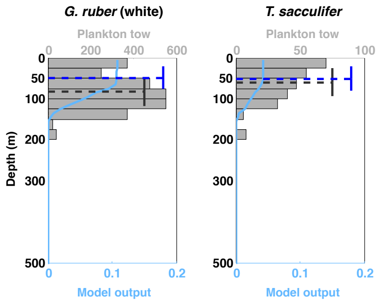

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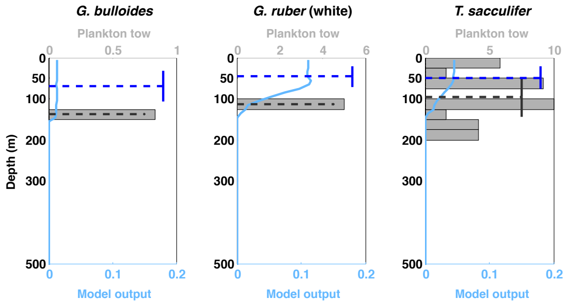
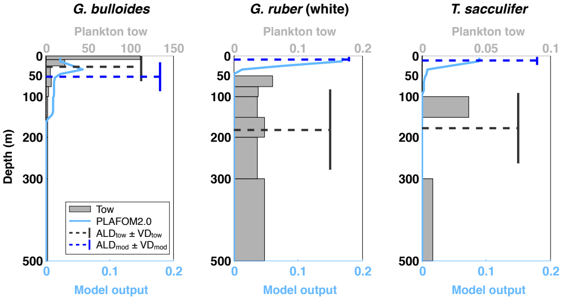


Station 310



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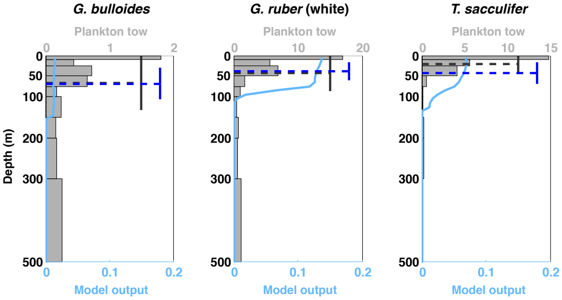

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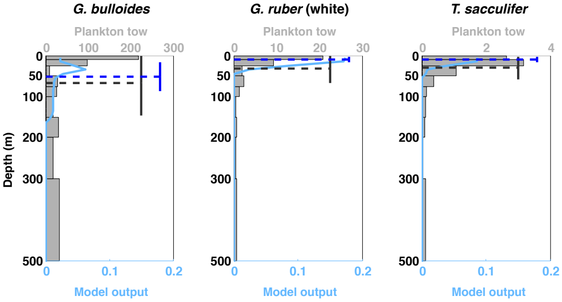

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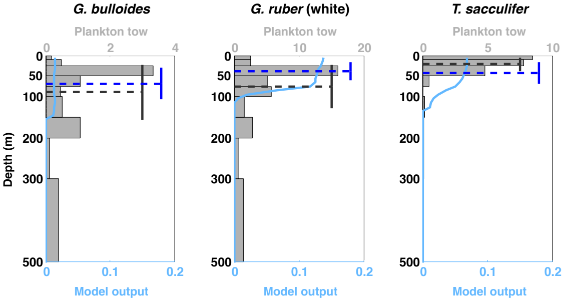

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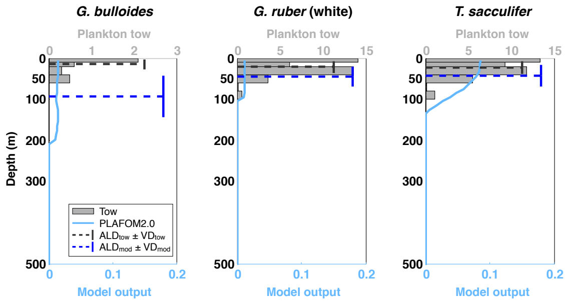

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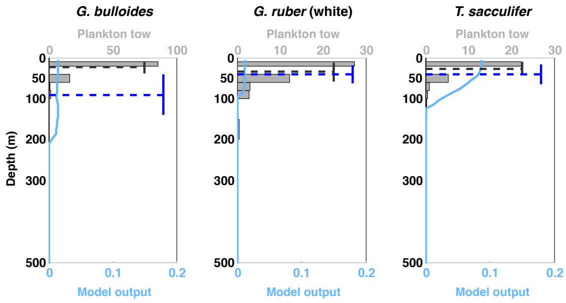

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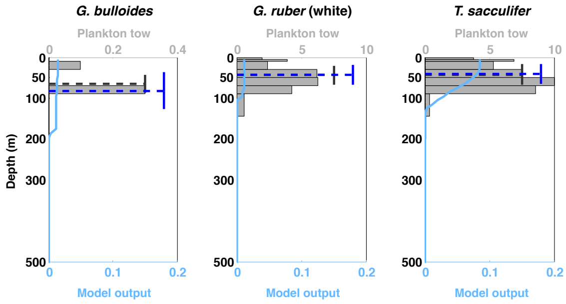

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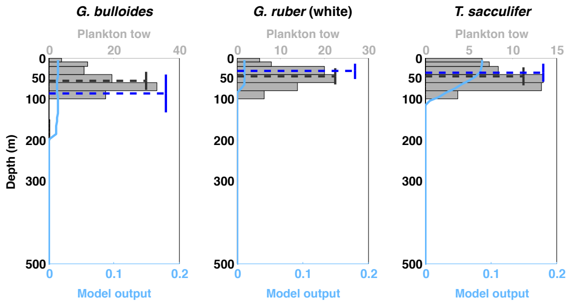

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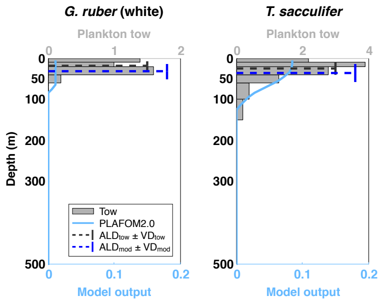
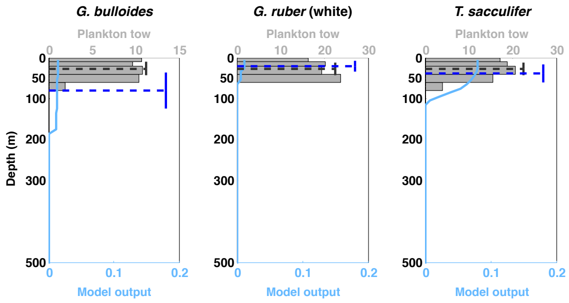
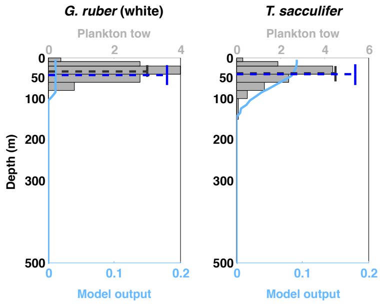


Station MOC69



Station MOC20



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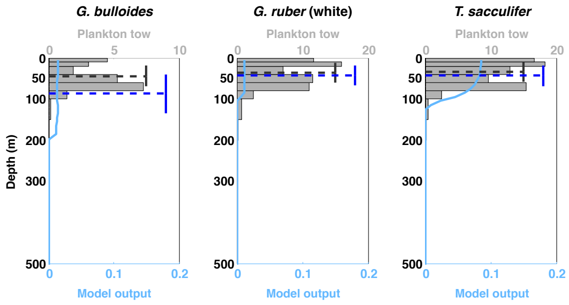

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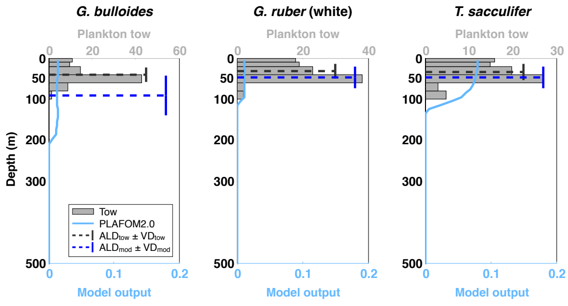

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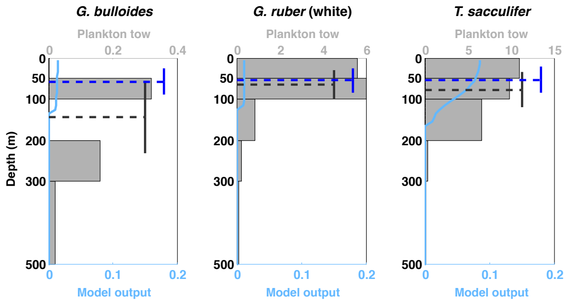

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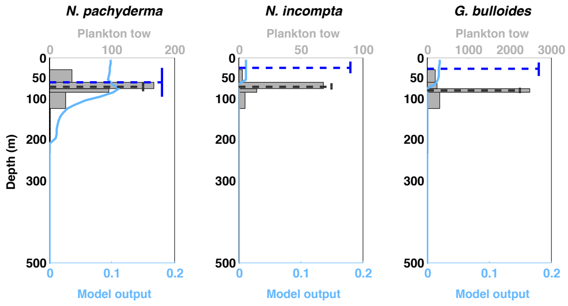

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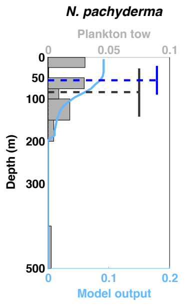
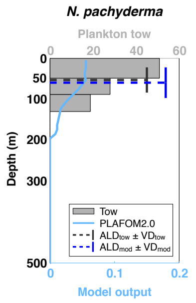
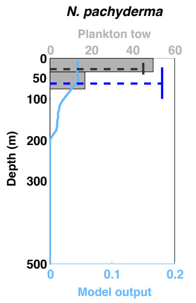


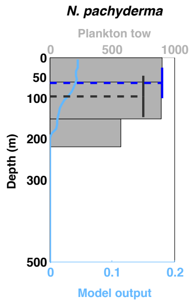
Station AN98-O



Station AN99-O



Station AN00-O



Station AN01-O

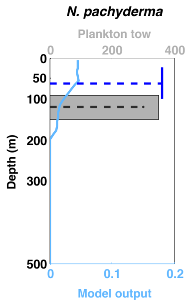
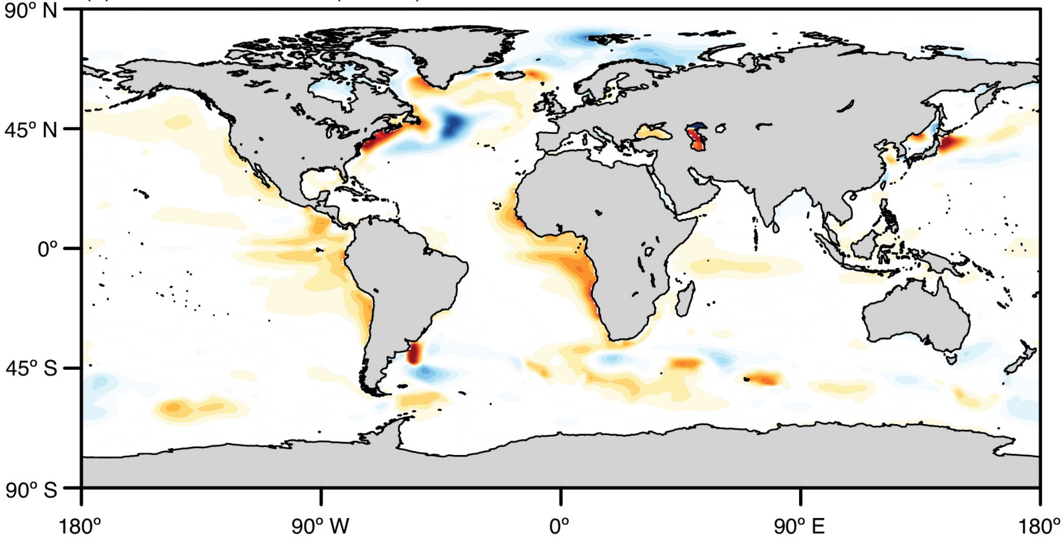


Figure S5.

(a) CESM1.2 - WOA13 (0-55 m)



(b) CESM1.2 - WOA13 (0-250 m)

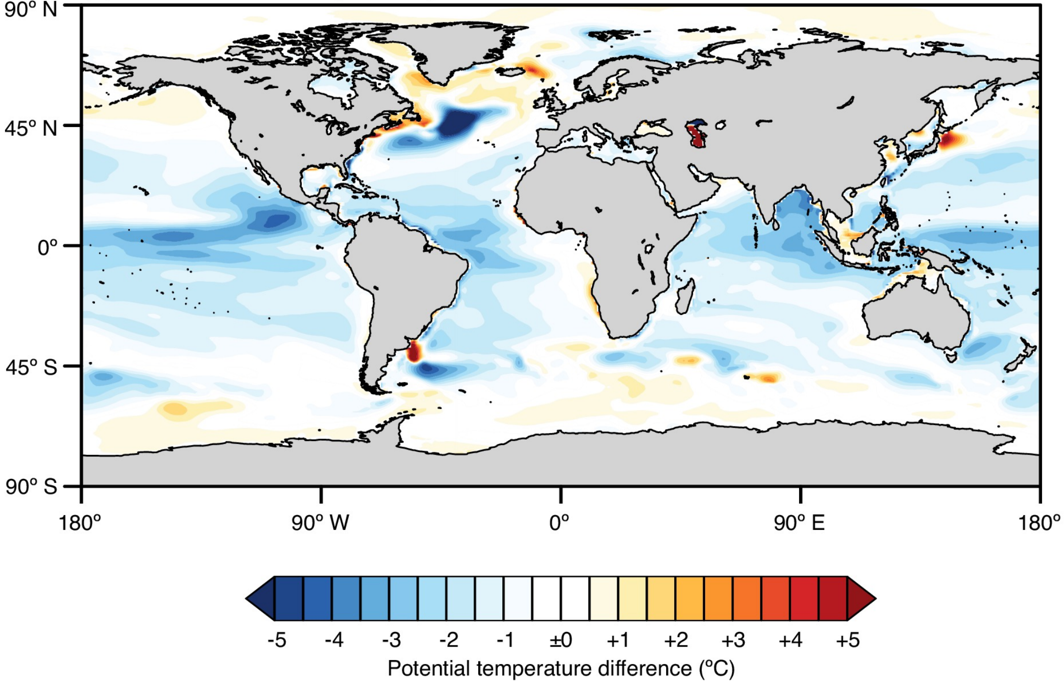


Table S1.

#	Site	Latitude (°N)	Longitude (°E)	Water Depth (m)	Trap Depth (m)	Deployment Time (day/month/year)	Duration (days)	Species	Fraction (μm)	Source
1	GS2	75.00	0.00	3720	300	03/06/1994 to 11/05/1995	342	Np	63-500	Jensen (1998)
2	OG5	72.40	-7.70	2624	500	06/08/1991 to 10/07/1992	339	Np	63-500	Jensen (1998)
3	NB6/7	69.69	0.47	3273	500	06/08/1991 to 02/10/1993	780	Np, Ni	63-500	Jensen (1998)
4	PAC50	50.01	165.03	5570	3260	01/12/1997 to 10/06/2001	1091	Np, Ni, Gb	>125	Kuroyanagi et al. (2002)
5	PAPA	50.00	-145.00	4240	3800	23/09/1982 to 30/08/1986	1122	Np, Ni, Gb	>125	Sautter and Thunell (1989)
6	SA	49.00	-174.00	5406	4812	23/08/1990 to 03/08/1999	2702	Np, Gb	>125	Asahi and Takahashi (2007)
7	KNOT	43.97	155.06	5370	2957	01/12/1997 to 12/05/2000	799	Np, Ni, Gb, Gr	>125	Kuroyanagi et al. (2002)
8	WCT6	42.00	155.34	5578	1091	15/08/1999 to 31/08/2000	382	Np, Ni, Gb, Gr	>125	Mohiuddin et al. (2005)
9	WCT2	39.00	147.00	5356-5322	1371; 1586	19/11/1997 to 10/08/1999	608	Ni, Gb, Gr	>125	Mohiuddin et al. (2002)
10	WCT7	36.68	154.94	5578	5034	19/08/1999 to 29/08/2000	376	Gb, Ts	>125	Mohiuddin et al. (2004)
11	WCT1	25.00	136.99	4905-5308	917; 1388	07/12/1997 to 12/08/1999	560	Ni, Gr, Ts	>125	Mohiuddin et al. (2002)
12	SBB	34.23	-120.03	650	590; 470	12/08/1993 to 26/06/1999	1015	Ni, Gb, Gr	>125	Kincaid et al. (2000) Darling et al. (2003)
13	SPB	33.55	-118.50	880	500	07/01/1988 to 26/07/1988	199	Ni, Gb, Gr	>125	Sautter and Thunell (1991)
14	JGOFS34	34.00	-21.00	n.a.	2000	03/04/1989 to 16/04/1990	378	Ni, Gb, Ts	>150	Wolfteich (1994)
15	L1	33.00	-22.00	5300	3000	24/02/2002 to 01/04/2004	764	Ni, Gb, Gr, Ts	>125	Storz et al. (2009)
16	BATS	32.08	-64.25	4200	3200	06/04/1978 to 17/05/1984	1848	Gb, Gr, Ts	>125	Deuser et al. (1981) Deuser and Ross (1989)
17	WAST	16.32	60.47	4016	3026	10/05/1986 to 21/10/1987	506	Gb, Gr, Ts	>150	Curry et al. (1992)
18	EA1	3.17	-11.25	4524	984	13/04/1991 to 29/11/1991	230	Gb, Gr, Ts	>150	Fischer and Wefer (1996)
19	EA2	1.78	-11.25	4399	953	13/04/1991 to 29/11/1991	230	Gb, Gr, Ts	>150	Fischer and Wefer (1996)
20	EA3	0.08	-10.77	4141	1097	13/04/1991 to 29/11/1991	230	Gb, Gr, Ts	>150	Fischer and Wefer (1996)
21	EA4	-2.19	-10.09	3906	1068	13/04/1991 to 29/11/1991	230	Gb, Gr, Ts	>150	Fischer and Wefer (1996)
22	WA1	-4.00	-25.57	5530	652	17/10/1992 to 21/03/1993	155	Gr, Ts	>150	Fischer and Wefer (1996)
23	NCR	-42.70	178.63	1500	1000	14/09/1996 to 15/05/1997	243	Np, Ni, Gb, Gr, Ts	>150	King and Howard (2001)
24	SCR	-44.62	178.62	1500	1000	09/06/1996 to 15/05/1997	340	Np, Ni, Gb, Gr, Ts	>150	King and Howard (2001)
25	CP	-52.62	174.15	n.a.	442; 362	14/05/1998 to 13/07/1999	368	Np, Ni, Gb	>150	Northcote and Neil (2005)
26	WS34	-64.90	-2.60	5053	360	16/01/1988 to 26/02/1990	745	Np	>125	Donner and Wefer (1994)

Np – *N. pachyderma*; Ni – *N. incompta*; Gb – *G. bulloides*; Gr – *G. ruber* (white); Ts – *T. sacculifer*
n.a. – not available (i.e., not given in data set)

Table S2.

#	Station	Latitude (°N)	Longitude (°E)	Water Depth (m)	Depth Intervals	Date (season)	Species	Fraction (μm)	Source
1	93-36	80.36	-10.14	n.a.	0-20, 20-40, 40-60, 60-100, 100-150, 150-200, 200-250, 250-275	27/07/1993 (summer)	Np	n.a.	Kohfeld et al. (1996)
2	PS78-25	78.83	7.00	1465	0-50, 50-100, 100-200, 200-300, 300-500	26/06/2011 (summer)	Np, Ni, Gb	100-250	Pados and Spielhagen (2014)
3	PS78-44	78.83	0.08	2636	0-50, 50-100, 100-200, 200-300, 300-500	29/06/2011 (summer)	Np, Ni, Gb	100-250	Pados and Spielhagen (2014)
4	PS78-75	78.83	-3.92	1978	0-50, 50-100, 100-200, 200-300, 300-500	04/07/2011 (summer)	Np, Ni, Gb	100-250	Pados and Spielhagen (2014)
5	PS55-025	75.00	-10.58	3084	0-50, 50-100, 100-200, 200-300, 300-500	11/07/1999 (summer)	Np, Ni, Gb	125-250	Stangeew (2001)
6	PS55-043	75.00	0.36	3789	0-50, 50-100, 100-200, 200-300, 300-500	14/07/1999 (summer)	Np, Ni, Gb	125-250	Stangeew (2001)
7	PS55-063	75.00	10.65	2542	0-50, 50-100, 100-200, 200-300, 300-500	16/07/1999 (summer)	Np, Ni, Gb	125-250	Stangeew (2001)
8	MN116	75.00	-7.31	3393	0-50, 50-100, 100-150, 150-300	21/08/1994 (summer)	Np	125-250	Simstich et al. (2003)
9	MN2	70.00	3.40	3261	0-50, 50-100, 100-500, 500-1000, 1000-2000	10/07/1994 (summer)	Np	125-250	Simstich et al. (2003)
10	MN323	69.69	0.47	3290	0-20, 20-40, 40-60, 60-80, 80-100, 100-200, 200-300, 300-500, 500-700, 700-1000, 1000-1500, 1500-2000, 2000-2500	07/07/1992 (summer)	Np	125-250	Simstich et al. (2003)
11	MN314	67.54	5.58	1438	0-20, 20-40, 40-60, 60-80, 80-100, 100-200, 200-300, 300-500, 500-700	28/06/1992 (summer)	Np	125-250	Simstich et al. (2003)
12	PAPA	49.98	-144.97	4253	0-50, 50-100, 100-150, 150-200, 200-300	16/08/2015 (summer)	Np, Ni, Gb	>100	Iwasaki et al. (2017)
13	101	47.00	-174.95	5790	0-50, 50-100, 100-150, 150-200, 200-300	05/08/2015 (summer)	Np, Ni, Gb	>100	Iwasaki et al. (2017)
14	79	46.98	166.73	5957	0-50, 50-100, 100-150, 150-200, 200-300	31/07/2015 (summer)	Np, Ni, Gb	>100	Iwasaki et al. (2017)
15	KNOT	44.08	154.98	5335	0-50, 50-100, 100-150, 150-200, 200-300	25/07/2015 (summer)	Np, Ni, Gb	>100	Iwasaki et al. (2017)
16	#B	41.57	141.90	1000	0-20, 20-40, 40-60, 60-80, 80-120, 120-160, 160-200	03/06/2002 (summer)	Np, Ni, Gb, Gr, Ts	125-1000	Kuroyanagi and Kawahata (2004)
17	#b	41.15	143.38	2077	0-20, 20-40, 40-60, 60-80, 80-120, 120-160, 160-200	04/06/2002 (summer)	Np, Ni, Gb, Gr, Ts	125-1000	Kuroyanagi and Kawahata (2004)
18	#A	36.02	141.78	2220	0-20, 20-40, 40-60, 60-80, 80-120, 120-160, 160-200	25/05/2002 (spring)	Np, Ni, Gb, Gr, Ts	125-1000	Kuroyanagi and Kawahata (2004)
19	#E	32.17	133.88	2660	0-20, 20-40, 40-60, 60-80, 80-120, 120-160, 160-200	27/05/2002 (spring)	Np, Ni, Gb, Gr, Ts	125-1000	Kuroyanagi and Kawahata (2004)
20	POS383-165	34.00	-22.00	5288	0-100, 100-200, 200-300, 300-500, 500-700	23/04/2009 (spring)	Np, Ni, Gb, Gr, Ts	>100	Rebotim et al. (2017)
21	POS383-175	33.15	-22.00	5232	0-100, 100-200, 200-300, 300-500, 500-700	26/04/2009 (spring)	Np, Ni, Gb, Gr, Ts	>100	Rebotim et al. (2017)
22	POS247-1389	33.08	-22.00	5226	0-20, 20-40, 40-60, 60-80, 80-100, 100-200, 200-300, 300-500, 500-700	24/01/1999 (winter)	Np, Ni, Gb, Gr, Ts	>100	Rebotim et al. (2017)
23	MOC1-38	38.92	-67.90	n.a.	0-25, 25-50, 50-75, 75-100, 100-125, 125-150, 150-175, 175-200	11/1975 (fall)	Gb, Gr, Ts	n.a.	Fairbanks et al. (1980)
24	MOC1-28	33.91	-71.78	n.a.	0-25, 25-50, 50-75, 75-100, 100-125, 125-150, 150-175, 175-200	11/1975 (fall)	Gr, Ts	n.a.	Fairbanks et al. (1980)
25	MOC1-23	32.73	-71.16	n.a.	0-25, 25-50, 50-75, 75-100, 100-125, 125-150, 150-175, 175-200	11/1975 (fall)	Gr, Ts	n.a.	Fairbanks et al. (1980)
26	310	16.02	52.73	n.a.	0-10, 10-25, 25-50, 50-75, 75-100, 100-150, 150-200, 200-300, 300-500	20/08/1992 (summer)	Np, Gb, Gr, Ts	>125	Peeters and Brummer (2002)
27	920	16.09	52.70	n.a.	0-10, 10-25, 25-50, 50-75, 75-100, 100-150, 150-200, 200-300, 300-500	27/02/1993 (winter)	Np, Gb, Gr, Ts	>125	Peeters and Brummer (2002)
28	313	15.91	53.02	n.a.	0-10, 10-25, 25-50, 50-75, 75-100, 100-150, 150-200, 200-300, 300-500	21/08/1992 (summer)	Np, Gb, Gr, Ts	>125	Peeters and Brummer (2002)
29	917	15.89	52.97	n.a.	0-10, 10-25, 25-50, 50-75, 75-100, 100-150, 150-200, 200-300, 300-500	25/02/1993 (winter)	Np, Gb, Gr, Ts	>125	Peeters and Brummer (2002)
30	MOC63	2.92	-140.20	n.a.	0-10, 10-20, 20-40, 40-60,	22/08/1992	Gb, Gr, Ts	>150	Watkins et al. (1998)

Continued on next page

#	Station	Latitude (°N)	Longitude (°E)	Water Depth (m)	Depth Intervals	Date (season)	Species	Fraction (μm)	Source
					60-80, 80-100, 100-150, 150-200	(summer)			
31	MOC65	2.05	-141.49	n.a.	10-20, 40-60, 60-80, 80-100, 100-150, 150-200	26/08/1992 (summer)	Gb, Gr, Ts	>150	Watkins et al. (1998)
32	MOC12	2.01	-139.88	n.a.	0-5, 5-10, 10-30, 30-50, 50-70, 70-90, 90-145, 145-200	17/02/1992 (winter)	Gb, Gr, Ts	>150	Watkins et al. (1996)
33	MOC66	1.13	-140.01	n.a.	0-10, 10-20, 20-40, 40-60, 60-80, 80-100, 100-150, 150-200	27/08/1992 (summer)	Gb, Gr, Ts	>150	Watkins et al. (1998)
34	MOC15	0.00	-140.07	n.a.	0-10, 10-20, 20-40, 40-60, 60-100, 100-150	23/02/1992 (winter)	Gr, Ts	>150	Watkins et al. (1996)
35	MOC69	-1.05	-139.97	n.a.	0-10, 10-20, 20-40, 40-60, 60-80, 100-150, 150-200	01/09/1992 (fall)	Gb, Gr, Ts	>150	Watkins et al. (1998)
36	MOC20	-2.02	-140.16	n.a.	0-10, 10-20, 20-40, 40-60, 60-80, 80-100, 100-150, 150-200	29/02/1992 (winter)	Gr, Ts	>150	Watkins et al. (1996)
37	MOC71	-2.33	-140.32	n.a.	0-10, 10-20, 20-40, 40-60, 60-80, 80-100, 100-150, 150-200	04/09/1992 (fall)	Gb, Gr, Ts	>150	Watkins et al. (1998)
38	MOC72	-3.21	-140.25	n.a.	0-10, 10-20, 20-40, 40-60, 60-80, 80-100, 100-150, 150-200	06/09/1992 (fall)	Gb, Gr, Ts	>150	Watkins et al. (1998)
39	SO225-21-3	-3.05	-165.06	5188	0-50, 50-100, 100-200, 200-300, 300-500	08/12/2012 (winter)	Gb, Gr, Ts	>150	Rippert et al. (2016)
40	TNO57-16	-50.12	5.75	3761	0-30, 30-60, 60-75, 75-85, 85-125, 125-235, 235-300, 300-440	24/02/1996 (winter)	Np, Ni, Gb	>150	Mortyn and Charles (2003)
41	TNO57-13	-53.18	5.13	2851	0-25, 25-50, 50-75, 75-100, 100-150, 150-200, 200-300, 300-400, 400-500	21/02/1996 (winter)	Np, Ni, Gb	>150	Mortyn and Charles (2003)
42	AN98/O	-63.25	177.25	4100	0-50, 50-90, 90-130	20/01/1998 (winter)	Np, Ni, Gb	>100	Bergami et al. (2009)
43	AN99/O	-63.40	178.05	4074	0-35, 35-70	09/01/1999 (winter)	Np, Ni, Gb	>100	Bergami et al. (2009)
44	AN00/O	-63.53	178.38	3548	0-60, 60-150, 150-220	11/01/2000 (winter)	Np, Ni, Gb	>100	Bergami et al. (2009)
45	AN01/O	-63.43	178.10	3964	0-90, 90-150	09/01/2001 (winter)	Np, Ni, Gb	>100	Bergami et al. (2009)

Np – *N. pachyderma*; Ni – *N. incompta*; Gb – *G. bulloides*; Gr – *G. ruber* (white); Ts – *T. sacculifer*
n.a. – not available (i.e., not given in data set)
Here the season refers to those of the Northern Hemisphere.

Table S3a.

Province	Sediment Trap Details			*N. pachyderma*		*N. incompta*		*G. bulloides*		*G. ruber* (white)		*T. sacculifer*	
	Site	Latitude (°N)	Longitude (°E)	Trap	PLAFOM2.0	Trap	PLAFOM2.0	Trap	PLAFOM2.0	Trap	PLAFOM2.0	Trap	PLAFOM2.0
Polar	GS2	75.00	0.00	Jun-Sep	Jul-Sep	-	-	-	-	-	-	-	-
	OG5	72.40	-7.70	Aug-Sep	~~Aug~~ Jul-Sep	-	-	-	-	-	-	-	-
	NB6/7	69.69	-0.47	Jun-Nov	~~Mar~~ Apr-~~Jul~~ Jun	Jul-Nov	~~Sep~~ Jul-Oct	-	-	-	-	-	-
Subpolar	PAC50	50.01	165.03	Mar-May Sep-Nov	Feb-~~Apr~~ May ~~Jun~~ Jul-~~Aug~~ Sep	Mar-May	~~Sep~~ Aug-~~Dec~~ Nov	Apr-Jun	~~Oct~~ Aug-~~Dec~~ Nov	-	-	-	-
	PAPA	50.00	-145.00	Mar-May Nov-Dec	Mar-May	Apr-Jun	~~Jul~~ Aug-Nov	Apr-Jun Nov-Dec	~~Jun~~ Apr-~~Aug~~ May	-	-	-	-
	SA	49.00	-174.00	Apr-Jul Aug-Oct	~~Feb~~ Mar-May	-	-	Apr-May Jul-Sep	~~Aug~~ Apr-~~Oct~~ Jun	-	-	-	-
Transitional	KNOT	43.97	155.06	Mar-May	Mar-May	none	~~Oct~~ Jul-~~Dec~~ Oct	Mar-May Oct-Dec	Apr-~~May~~ Jun	Sep-Nov	Aug-Oct	-	-
	WCT6	42.00	155.34	Mar-May Jul-Sep	~~Mar~~ Feb-~~Apr~~ May	Jun-Oct	~~Oct~~ Mar-~~Dec~~ May	Mar-May Oct-Nov	~~Apr~~ Mar-May	Sep-Nov	Aug-~~Sep~~ Oct	-	-
	WCT2	39.00	147.00	-	-	none	Jan-~~Mar~~ Apr ~~Aug-Oct~~	none	Jan-~~Mar~~ Apr ~~Aug-Sep~~	Sep-Dec	~~Aug~~ Jul-Oct	-	-
	WCT7	36.68	154.94	-	-	-	-	May-Jun	~~Feb~~ Mar-~~Mar~~ May ~~Jul-Aug~~	-	-	Aug-Dec	~~Jul~~ Aug-Nov
Subtropics	SBB[a]	34.23	-120.03	-	-	Aug-Oct	~~May~~ Jul-Sep	Jun-Aug	~~May~~ Jul-Sep	Jul-Nov	~~Jul~~ Aug-Nov	-	-
	JGOFS34	34.00	-21.00	-	-	Feb-Apr Aug-Sep	May-Aug	Mar-May	May-Sep	-	-	Apr-Jun	~~Jun~~ Jul-Oct
	SPB	33.55	-118.50	-	-	Mar-May	May-Sep	May-Jun	May-Sep	Apr-Jul	~~Jul~~ Aug-Nov	-	-
	L1	33.00	-22.00	-	-	Feb-Apr	May-~~Aug~~ Sep	Mar-May	May-Sep	Mar-May	~~Jun~~ Jul-~~Sep~~ Nov	Mar-May	~~Jun~~ Jul-Oct
	BATS	32.08	-64.25	-	-	-	-	Jan-May	~~Jun-Sep~~ Feb May-Sep	none	May-Jul Nov-Jan	May-Jul	~~Jun~~ Jul-~~Oct~~ Nov
	WCT1	25.00	136.99	-	-	none	~~Mar~~ Feb-~~May~~ Jun	-	-	Jun-Aug	Jan-~~Apr~~ Mar	Jun-Aug	Jun-~~Sep~~ Oct
Tropics	WAST	16.32	60.47	-	-	-	-	Jan-Feb Jul-Oct	~~Oct~~ Mar-~~Dec~~ May Oct-Nov	Dec-Feb May-Aug	Jan-~~Apr~~ Mar Aug-Sep	Jun-Sep	~~Mar~~ Apr-May
	EA1	3.17	-11.25	-	-	-	-	Sep-Nov	~~Oct~~ Feb-~~Nov~~ Apr	none	Jul-~~Oct~~ Sep	none	Jun-Aug
	EA2	1.78	-11.25	-	-	-	-	Jul-Oct	~~Feb~~ Mar-Apr ~~Nov~~ Aug-~~Dec~~ Sep	none	Jul-~~Oct~~ Nov	May-Jul	~~Jul~~ Jan-~~Oct~~ Feb Sep-Nov
	EA3	0.08	-10.77	-	-	-	-	Jul-Sep	~~Mar~~ Feb-Apr ~~Oct~~ Aug-~~Dec~~ Oct	May-Jun	~~Jul~~ Sep-~~Oct~~ Jan	May-Jun	~~Jan~~ Feb-~~Mar~~ May ~~Sep-Oct~~
	EA4	-2.19	-10.09	-	-	-	-	Apr-May	~~Mar~~ Feb-~~May~~ Apr	Apr-Aug	~~Jul~~ Aug-~~Oct~~ Dec	Apr-Aug	~~Jun~~ Dec-~~Sep~~ May
	WA1	-4.00	-25.57	-	-	-	-	-	-	none	Aug-Dec	none	Aug-~~Oct~~ Dec
Tran-sitional	NCR	-42.70	178.63	Sep-Dec	~~Aug~~ Apr-~~Sep~~ May Aug-Nov	Sep-Oct	~~Aug~~ Jan-~~Sep~~ Feb ~~Dec~~ Aug-~~Feb~~ Oct	Apr-May Sep-Nov	~~Jul~~ Aug-~~Sep~~ Oct ~~Dec-Feb~~	none	Jan-Apr	Oct-Dec	Jan-Apr
	SCR	-44.62	178.62	Sep-Oct	Aug-Oct	Feb-Apr Sep-Nov	~~Sep~~ Aug-~~Oct~~ Sep Dec-~~Jan~~ Feb	Sep-Oct	~~Sep~~ Aug-~~Jan~~ Oct Dec-Jan	-	-	-	-
Sub-polar	CP	-52.62	174.15	Mar-May	Aug-Nov	Mar-May	~~Aug~~ Feb-~~Oct~~ Apr Aug-Oct	Nov-May	~~Aug~~ Feb-~~Oct~~ Mar Aug-Oct	-	-	-	-
Polar	WS34	-64.90	-2.60	Mar-May	Feb-Apr Oct-Dec	-	-	-	-	-	-	-	-

[a] The nearest model grid point for site SBB fell onto land. Therefore, we used the nearest model grid point in the ocean to perform a consistent model-data-comparison.

Table S3b.

Province	Sediment Trap Details			*N. pachyderma*		*N. incompta*		*G. bulloides*		*G. ruber* (white)		*T. sacculifer*	
	Site	Latitude (°N)	Longitude (°E)	Trap	PLAFOM2.0	Trap	PLAFOM2.0	Trap	PLAFOM2.0	Trap	PLAFOM2.0	Trap	PLAFOM2.0
Polar	GS2	75.00	0.00	0.78	~~0.21~~ 0.26	-	-	-	-	-	-	-	-
	OG5	72.40	-7.70	0.64	~~0.17~~ 0.19	-	-	-	-	-	-	-	-
	NB6/7	69.69	-0.47	0.80	~~0.23~~ 0.42	0.95	~~0.84~~ 0.57	-	-	-	-	-	-
Sub-polar	PAC50	50.01	165.03	0.75	~~0.12~~ 0.20	0.77	~~0.37~~ 0.36	0.66	~~0.22~~ 0.36	-	-	-	-
	PAPA	50.00	-145.00	1.07	~~0.11~~ 0.28	1.20	0.04	1.10	~~0.07~~ 0.22	-	-	-	-
	SA	49.00	-174.00	0.95	~~0.15~~ 0.29	-	-	0.94	~~0.08~~ 0.21	-	-	-	-
Transitional	KNOT	43.97	155.06	0.69	~~0.28~~ 0.36	0.79	~~0.07~~ 0.16	0.66	~~0.14~~ 0.33	0.76	~~0.62~~ 0.70	-	-
	WCT6	42.00	155.34	0.42	~~0.28~~ 0.33	0.47	~~0.07~~ 0.15	0.62	~~0.14~~ 0.25	0.73	~~0.62~~ 0.59	-	-
	WCT2	39.00	147.00	-	-	0.64	~~0.06~~ 0.17	0.69	~~0.11~~ 0.22	0.74	~~0.43~~ 0.44	-	-
	WCT7	36.68	154.94	-	-	-	-	0.55	~~0.08~~ 0.19	-	-	0.57	~~0.40~~ 0.34
Subtropics	SBB[a]	34.23	-120.03	-	-	0.68	~~0.03~~ 0.04	0.67	0.06	0.87	~~0.16~~ 0.19	-	-
	JGOFS34	34.00	-21.00	-	-	0.85	~~0.02~~ 0.05	0.76	~~0.03~~ 0.07	-	-	0.69	~~0.12~~ 0.14
	SPB	33.55	-118.50	-	-	0.73	~~0.03~~ 0.04	0.85	0.06	0.77	~~0.16~~ 0.18	-	-
	L1	33.00	-22.00	-	-	1.28	~~0.02~~ 0.05	0.91	~~0.03~~ 0.06	0.70	~~0.08~~ 0.09	0.59	~~0.11~~ 0.13
	BATS	32.08	-64.25	-	-	-	-	0.72	0.05	0.37	~~0.09~~ 0.07	0.96	~~0.13~~ 0.12
	WCT1	25.00	136.99	-	-	0.42	~~0.08~~ 0.06	-	-	0.77	~~0.14~~ 0.10	0.88	~~0.06~~ 0.07
Tropics	WAST	16.32	60.47	-	-	-	-	0.77	~~0.04~~ 0.02	0.70	~~0.11~~ 0.14	0.66	~~0.03~~ 0.02
	EA1	3.17	-11.25	-	-	-	-	0.48	~~0.04~~ 0.03	0.36	~~0.08~~ 0.15	0.47	~~0.03~~ 0.07
	EA2	1.78	-11.25	-	-	-	-	0.52	0.02	0.33	~~0.12~~ 0.13	0.59	~~0.04~~ 0.03
	EA3	0.08	-10.77	-	-	-	-	0.81	~~0.01~~ 0.02	0.57	~~0.07~~ 0.10	0.47	~~0.02~~ 0.05
	EA4	-2.19	-10.09	-	-	-	-	0.83	~~0.04~~ 0.02	0.60	~~0.12~~ 0.10	0.50	~~0.02~~ 0.03
	WA1	-4.00	-25.57	-	-	-	-	-	-	0.67	~~0.09~~ 0.15	0.58	~~0.04~~ 0.06
Transitional	NCR	-42.70	178.63	0.91	~~0.26~~ 0.47	0.78	~~0.07~~ 0.11	0.73	~~0.12~~ 0.16	0.77	~~0.39~~ 0.46	0.85	0.54
	SCR	-44.62	178.62	0.87	~~0.12~~ 0.14	0.57	~~0.06~~ 0.08	0.89	~~0.10~~ 0.16	-	-	-	-
Sub-polar	CP	-52.62	174.15	1.29	0.28	1.12	~~0.11~~ 0.08	1.10	~~0.15~~ 0.11	-	-	-	-
Polar	WS34	-64.90	-2.60	1.12	~~0.13~~ 0.09	-	-	-	-	-	-	-	-

[a] The nearest model grid point for site SBB fell onto land. Therefore, we used the nearest model grid point in the ocean to perform a consistent model-data-comparison.

Table S4.

Province	Plankton Tow Details			*N. pachyderma*		*N. incompta*		*G. bulloides*		*G. ruber* (white)		*T. sacculifer*	
	Site	Latitude (°N)	Longitude (°E)	Tow[a] (m)	PLAFOM2.0[a] (m)	Tow[a] (m)	PLAFOM2.0[a] (m)	Tow[a] (m)	PLAFOM2.0[a] (m)	Tow[a] (m)	PLAFOM2.0[a] (m)	Tow[a] (m)	PLAFOM2.0[a] (m)
Polar	93-36	80.36	-10.14	85±35	55±~~40~~ 35	-	-	-	-	-	-	-	-
	PS78-25	78.83	~~0.08~~ 7.00	~~80~~ 85±~~40~~ 55	~~55~~ 50±~~40~~ 35	-	-	-	-	-	-	-	-
	PS78-44	78.83	~~7.00~~ 0.08	~~85~~ 80±~~55~~ 40	~~50~~ 45±~~40~~ 35	-	-	-	-	-	-	-	-
	PS78-75	78.83	-3.92	70±40	~~50~~ 45±~~40~~ 35	-	-	-	-	-	-	-	-
	PS55-025	75.00	-10.58	90±70	~~50~~ 45±35	-	-	-	-	-	-	-	-
	PS55-043	75.00	0.36	60±40	~~55~~ 45±~~40~~ 30	-	-	-	-	-	-	-	-
	PS55-063	75.00	10.65	85±65	~~50~~ 45±~~40~~ 30	-	-	55±25	25±15	-	-	-	-
	MN116	75.00	-7.31	150±40	~~55~~ 45±~~40~~ 30	-	-	-	-	-	-	-	-
	MN2	70.00	3.40	170±215	~~55~~ 60±~~35~~ 50	-	-	-	-	-	-	-	-
	MN323	69.69	0.47	140±155	55±~~35~~ 45	-	-	-	-	-	-	-	-
	MN314	67.54	5.58	125±60	65±~~35~~ 55	-	-	-	-	-	-	-	-
Sub-polar	PAPA	49.98	-144.97	230±30	80±35	105±85	~~65~~ 60±35	60±45	70±40	-	-	-	-
	101	47.00	-174.95	95±50	~~70~~ 60±~~30~~ 40	140±40	55±35	65±30	~~65~~ 50±~~40~~ 35	-	-	-	-
	79	46.98	166.73	110±55	~~65~~ 55±~~30~~ 40	150±50	~~50~~ 25±~~35~~ 15	70±35	~~65~~ 30±~~35~~ 25	-	-	-	-
Transitional	KNOT	44.08	154.98	90±45	~~65~~ 70±~~25~~ 45	75±55	~~60~~ 20±~~35~~ 10	45±30	~~65~~ 30±~~35~~ 25	-	-	-	-
	#B[b]	41.57	141.90	125±40	~~60~~ 80±~~45~~ 40	105±45	~~65~~ 70±~~40~~ 45	100±55	75±45	122±40	5±5	-	-
	#b	41.15	143.38	85±40	~~85~~ 80±~~20~~ 40	35±25	~~65~~ 70±~~40~~ 45	40±30	75±45	-	-	-	-
	MOC1-38	38.92	-67.90	-	-	-	-	65±55	~~85~~75±~~45~~40	30±20	~~25~~ 35±~~15~~ 20	35±20	~~25~~ 40±~~15~~ 20
	#A	36.02	141.78	-	-	25±20	~~55~~ 65±~~30~~ 35	25±25	~~55~~ 65±35	20±20	~~15~~ 25±~~10~~ 20	25±20	~~10~~ 30±~~10~~ 20
Subtropics	POS383-165	34.00	-22.00	-	-	85±60	~~85~~ 80±45	170±70	~~85~~ 75±~~45~~ 40	65±25	~~50~~ 30±~~35~~ 25	185±85	50±30
	MOC1-28	33.91	-71.78	-	-	-	-	-	-	80±35	~~45~~ 50±~~25~~ 30	60±35	50±30
	POS383-175	33.15	-22.00	-	-	85±55	~~90~~ 80±~~45~~ 40	95±50	~~85~~ 75±~~45~~ 40	65±25	~~50~~ 35±~~30~~ 25	190±65	50±30
	POS247-1389	33.08	-22.00	-	-	30±0	~~85~~ 80±45	30±0	~~85~~ 80±45	55±25	~~55~~ 50±30	40±35	55±30
	MOC1-23	32.73	-71.16	-	-	-	-	140±0	~~75~~ 70±~~40~~ 35	115±0	45±25	95±50	~~45~~ 50±30
	#E	32.17	133.88	-	-	60±30	~~85~~ 80±~~45~~ 40	-	-	70±45	30±20	45±40	~~40~~ 35±~~30~~ 25
Tropics	920	16.09	52.70	-	-	-	-	65±65	~~75~~ 70±~~45~~ 40	40±45	40±20	20±20	45±25
	310	16.02	52.73	-	-	-	-	30±35	~~70~~ 50±35	180±100	~~15~~ 10±~~10~~ 5	180±85	~~30~~ 15±~~20~~ 10
	313	15.91	53.02	-	-	-	-	70±80	~~70~~ 50±35	30±35	~~15~~ 10±~~10~~ 5	30±30	~~30~~ 10±~~20~~ 5
	917	15.89	52.97	-	-	-	-	90±65	~~75~~ 70±~~45~~ 40	75±50	40±20	20±15	45±25
	MOC63	2.92	-140.20	-	-	-	-	15±10	95±50	20±15	45±25	25±15	~~40~~ 45±25
	MOC65	2.05	-141.49	-	-	-	-	25±15	90±50	35±25	~~45~~ 40±~~25~~ 20	25±15	40±25
	MOC12	2.01	-139.88	-	-	-	-	65±25	~~85~~ 80±45	45±25	45±25	45±25	~~35~~ 40±~~20~~ 25
	MOC66	1.13	-140.01	-	-	-	-	55±25	85±45	45±20	35±20	45±25	35±20
	MOC15	0.00	-140.07	-	-	-	-	-	-	20±10	35±20	25±15	35±20
	MOC69	-1.05	-139.97	-	-	-	-	25±15	~~85~~ 80±45	25±15	~~30~~ 20±15	25±15	~~35~~ 40±20
	MOC20	-2.02	-140.16	-	-	-	-	-	-	35±15	~~50~~ 45±25	40±20	40±25
	MOC71	-2.33	-140.32	-	-	-	-	45±25	~~85~~ 90±45	35±25	45±25	35±25	~~40~~ 45±25
	SO225-21-3	-3.05	-165.06	-	-	-	-	145±90	55±30	65±35	~~50~~ 55±~~25~~ 30	75±45	~~50~~ 55±30
	MOC72	-3.21	-140.25	-	-	-	-	40±20	90±50	35±15	50±25	35±20	~~45~~ 50±25
Sub-polar	TNO57-16	-50.12	5.75	70±10	~~65~~ 60±35	70±10	25±15	80±5	30±15	-	-	-	-
	TNO57-13	-53.18	5.13	85±60	~~60~~ 55±35	-	-	~~75±25~~	~~25±15~~	-	-	-	-
Polar	AN98-O	-63.25	177.25	55±30	60±35	-	-	-	-	-	-	-	-
	AN99-O	-63.40	178.05	25±15	~~65~~ 60±40	-	-	-	-	-	-	-	-
	AN01-O	-63.43	178.10	120±0	~~65~~ 60±40	-	-	-	-	-	-	-	-
	AN00-O	-63.53	178.38	95±50	~~65~~ 60±40	-	-	-	-	-	-	-	-

[a] ALD±VD (in m) of the planktonic foraminiferal species calculated after Rebotim et al. (2017) for the plankton tow samples and for PLAFOM2.0 (obtained at the nearest model grid points of the given plankton tow locations). Note that the values have been rounded to the nearest 5 m.

[b] The nearest model grid point for site #B fell onto the shelf. Therefore, we used the nearest model grid point in the open ocean to perform a consistent model-data-comparison.

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