Response to Reviewer #1

We would like to take this opportunity to thank the anonymous reviewer for their helpful comments on our manuscript. Below we provide a detailed response to their comments (in italics), indicating the changes that have been made. Line numbers refer to those of the revised manuscript that includes all tracked changes.

With kind regards,

Mattia Greco (on the behalf of all co-authors)

Greco et al. present an interesting study on the variability of depth habitat of the planktonic foraminifera N. pachyderma, the most important species in the Arctic. Due to the ubiquity of N. pachyderma both in paleo-records and in present-day Arctic and the significance of its depth habitat for paleoreconstructions, the authors address a relevant scientific question within the scope of BG. The presented results can be used in paleoreconstructions as long as there are proxy on chlorophyll and sea-ice concentration available. The authors compile new and existing data from the Arctic and the North Atlantic Ocean and the substantial conclusions that they come up with are also novel. The scientific methods and assumptions are valid and clearly outlined and the results are sufficient to support the interpretations and conclusions. The authors compare the observational data with a numerical model though this comparison only shows that the model does not perform very well. The methods are described sufficiently precisely. However, as I am not an expert on statistics, I cannot evaluate this aspect of the manuscript. The authors give proper credit to related work and clearly indicate their own contributions. The title clearly reflects the contents of the paper and the abstract provides a concise and complete summary. The MS is well-structured and written and the language is fluent and precise. Therefore I find the MS suitable for publication in Biogeosciences after minor revisions according to general, specific and technical comments listed below. I am looking forward for the authors' response and further discussion.

General Comments

The authors use the term 'habitat depth' along with 'depth habitat (DH)', which is a bit confusing. Are these two different terms? If so, what is the difference between them? Wouldn't it be better to stick to only one of these terms? I don't see a significant difference between them.

The reviewer rightly mentions that this is confusing, the two terms refer to the same parameter; we will correct and homogenize the terminology adopting only the term "depth habitat".

A table listing all the published profiles used in the study and/or a more detailed location map would be useful, at least as an appendix or supplementary material. Now it is completely unclear what published data are you using.

We appreciate this comment. Due to the size of such a table we prefer to make it available as supplementary material at zenodo.org, where long-term storage is guaranteed. We would like to point out that the link to the table with the complete metadata and environmental data was already provided in the "Data availability" section in the original manuscript.

A weak, though unavoidable, point of the study is that it compiles data with different sampling depth intervals which might bias the calculated DHs. The authors should stress and discuss this issue a bit more.

The reviewer rightly points out that the precision with which the DH can be determined depends on the vertical resolution of the individual casts. By mixing casts with different vertical resolution we unavoidably lose some precision, but we would argue that this introduces random noise, rather than a

systematic bias. This is probably part of the reason why our predictive models do not explain all the variability in DH. We will add some discussion on this in the method section at page 6, lines 7-9:

'Anyway, since the accuracy with which the DH is determined is linked to the vertical resolution of the single profiles, mixing casts with different vertical resolution causes unavoidably the loss of some precision and the introduction of random noise in the data.'

Specific comments

2.3 (page 2, line 3) and 2.20: I know that 'climate change' is a catchy phrase but N. pachyderma is a marine species and so it doesn't directly react to climate changes but rather to changes in marine environment (which, of course, are usually related to climate changes). Please be more precise in your wording!

We will change the sentence to 'To assess the reaction of this species to a future shaped by climate change and to be able to interpret the paleoecological signal contained in its shells…'

2.22: Please change 'Arctic and its marginal seas' to either 'Arctic Ocean and its marginal seas' or just 'Arctic' (or 'Arctic seas').

We will change 'Arctic and its marginal seas' to Arctic Ocean and its marginal seas.

4.3: similar as above

We will change Eurasian Arctic and its marginal seas to Eurasian Arctic Ocean and its marginal seas.

4.30-32: It is not clear whether the satellite data were used only for data generated by the authors or also for the data from the literature. Please explain.

We rewrote the sentence to avoid confusion 'In addition to the in-situ data, daily sea ice concentrations for each location of all the 104 sites included were extracted from 25 × 25 km resolution passive microwave satellite raster imagery obtained from the National Snow and Ice Data Centre'

7.8: In the text the adjusted r2 = 0.32, while in Table 3 it's 0.336 - 0.34. Please correct or explain the difference.

We apologise for this mistake, the number referred to in the table is correct and we have changed the text accordingly.

8.27: It might not be clear to a reader whether 'lowering the DCM' means lowering the value of the DCM, i.e. moving it up the water column (shallowing) or lowering it 'geometrically', i.e. moving it down the water column (deepening, which I guess is the case). Please clarify.

We modified the sentence replacing 'lowering' with 'deepening'.

9.26: 'at the depth of DH' please rephrase.

We rewrote the sentence using 'at the level of DH'.

24: The small diagrams in Fig. 4b (normalized density profiles?) need more explanation.

These profiles only serve to illustrate the meaning of loadings of the first principle component. To make this clearer we rewrote the sentence in the caption: 'The density profiles based on the standardized counts in the plot show examples of shape of the vertical distribution of N. pachyderma at three PC1 loadings.'

Technical comments

2.32: I'm not sure about the rules concerning citing of papers with three authors in Biogeosciences but shouldn't it be just 'Ding et al., 2014'?

The reviewer is correct and we have changed it accordingly.

5.9: Table 2 is referenced in the text before Table 1. Again I am not sure about the rules in BG, but I guess you should change the numeration.

We will correct the reference to Table 1 as we refer to the DVM results.

5.14: I suppose 'Fig. 2d' was meant.

Correct and amended.

5.33 & 6.1-2: You already introduce the DVM abbreviation so use it!

Done.

6.14: Use 'DH' instead of 'depth habitat'

Done.

9.2: 'sea-surface' instead of 'seas-surface'

Done.

10.27: An unnecessary 'the' after 'mismatch'.

Done.

Response to Robert F. Spielhagen

We would like to take this opportunity to thank Robert F. Spielhagen for his helpful comments on our manuscript. Below we provide a detailed response to his comments (in italics), indicating the changes that have been made. Line numbers refer to those of the revised manuscript that includes all tracked changes.

With kind regards,

Mattia Greco (on the behalf of all co-authors)

General comments

Planktic foraminifera of the species Neogloboquadrina pachyderma are a major carrier of paleoenvironmental information in Arctic and sub-Arctic marine sediments and widely used to reconstruct properties of the upper water column, namely sea-ice coverage, salinity, and temperature. The variability of their geochemical composition (e.g., stable isotopes, Mg/Ca) can be very large within an investigated sediment core. In particular to interpret this variability it is important to know which factors may determine the habitat depth of the species. A number of studies have determined the depth distribution of N. pachyderma under a large variety of boundary conditions (oceanic parameters). A synoptic study involving all the available depth distribution data plus oceanic data from the same sites was much needed but still lacking. The manuscript by Greco et al. fills this gap with a statistical evaluation of mostly published data from the Arctic Ocean and its neighboring seas, amended by some new data from Baffin Bay and results from a numerical model. The combination of biological, physical oceanographic, biochemistry and modelling data results in a novel approach to determine the habitat depth of N. pachyderma on a larger scale and is thematically well suited for the journal Biogeosciences. It is well-written in very good English. The structure of the manuscript follows standard principles of scientific publications. The abstract gives a good overview of the topic, the methodological approach, the major results and the main conclusions. The Introduction chapter gives a good overview of the present knowledge and thereby manifests the problem of defining the factor(s) determining the depth habitat of N. pachyderma. It also describes the general approach applied here and which environmental factors are considered as potentially responsible for the variability in habitat depth. The Material and Methods chapter describes in detail the origin of the data sets used for the following evaluation, the methods to obtain the new data from Baffin Bay, and the statistical methods applied to evaluate and weight the environmental factors determining the habitat depth. I am not an expert on such statistical methods and can therefore not evaluate whether proper attention has been paid to significance levels. The Results chapter lists briefly but in sufficient detail the major outcome of the statistical evaluations, in particular the correlation of habitat depth to individual and combined environmental parameters and how the results from statistical evaluations compare to the model results. The Discussion chapter puts the results of statistical evaluations in context and elaborates which environmental factors are determining the habitat depth. The outcome is discussed with respect to previous hypotheses on which parameters have forced N. pachyderma to live shallower or deeper in the water column. Interestingly, some of these published hypotheses (which in most cases were based on regional studies) are not supported by the conclusions of Greco et al.. The very large data base of the present study (I cannot see that relevant published data sets were left out) is the advantage of the present study and adds significantly to the credibility of the conclusions presented here. To me, the discussion appears to the point and overall sound, and I cannot see that systematic errors may bias the conclusions. These are compiled in the Conclusion chapter which lists the major findings but also open questions which may trigger further research in this field. The figures and tables are mostly clear and easy to understand (see comments below for minor exceptions). Overall, I think this paper is already in a mature state and does not need significant changes. Publication in Biogeosciences is recommended after some minor revision in response to the points listed below.

Specific comments to the authors

Title and manuscript text: Regarding the use of "planktonic" (instead of "planktic") in this manuscript I suggest to read the advice of the Godfather of Paleoceanography, Cesare Emiliani, which can be found here: https://www.cambridge.org/core/journals/journalof-paleontology/article/planktic planktonic-nekticnektonicbenthicbenthonic/CDF06242F0F9130B7A5A082DFDDFC425

We agree with the reviewer that the correct expression would be "planktic" as explained in the referred paper. However, the expression "planktonic foraminifera" is more common in the literature than "planktic foraminifera" (up to about 5 times more- as a quick search in Scopus revealed). For practical reasons we therefore prefer to keep using the term "planktonic".

You use both "habitat depth" and "depth habitat" in the manuscript. The latter is defined on page 5 (line 17ff), the first not. Do these terms have different meanings? If yes, you should explain this. I note that even at the end of the manuscript, in the Conclusion chapter, you still use both terms (page 10, lines 17/18). That is confusing!

Reviewer 1 also pointed out that we used these two terms interchangeably in the manuscript. We will correct and homogenize the terminology adopting only the term "depth habitat".

It will be helpful for the reader to receive a bit more information on the PLAFOM2.0 model. As it stands, we just learn that it can predict the seasonal and vertical habitat of N. pachyderma. For those readers who have not studied the Kretschmer et al. (2018) paper in detail, you should use 2-3 lines to explain what the model is based on and which boundary conditions are used.

We added the following information about PLAFOM2.0 in the text:

'This model is driven by temperature, food concentration, and light availability (which matters only for species with symbionts). The species-specific food concentrations are simulated by the Community Earth System Model, version 1.2.2 (CESM1.2, Hurrell et al., 2013) at every time step and are subsequently used by PLAFOM2.0 to calculate the monthly carbon concentration of N. pachyderma and four other species of planktonic foraminifera.'

Many readers may not be acquainted with all the statistical parameters applied to determine correlations, anticorrelations, significance limits etc.. Those terms used widely throughout the manuscript (e.g., r, p, R, F-test, t-test) should be explained in the manuscript, including a comment on what higher or lower values mean.

We will add some explanatory notes at page 6 lines 14-16. However, these are all standard statistical concepts that we feel should be familiar to readership of Biogeosciences and we have hence not provided a detailed explanation.

I suggest not to mix British and American spelling. Either use "paleo" and "...ize" or "palaeo" and "...ise". Please check the entire manuscript for other language cases (e.g., "metres" vs. "meters").

We will check the manuscript and correct the language inconsistencies.

Comments by page and line numbers (page/line)

2/1: Better write "dominant plankt(on)ic foraminifer species"

Done

2/8: Arctic and North Atlantic oceans

Done.

2/10: Here and in other places you mention "chlorophyll a", later you also just write "chlorophyll". Be precise in what you mean.

We re-checked the usage of the two expressions and specified the data we refer to in the method section.

2/23-24: "When the organism dies, its calcite shells sink to the seafloor and when preserved in the sediments, they serve ..." Do not mix singular and plural.

Corrected.

3/10-14: You are discussing the issue of diel vertical migration again on page 7, lines 18ff, largely repeating what is said here. I suggest to shorten this part in the introduction and put the discussion where it belongs.

We think that this part is important to highlight why there is still a need for more analyses on the influence of DVM on the DH of N. pachyderma even in the presence of previous investigations.

3/22: drivers

Done.

3/22-26: Very long sentence, hard to read. Split it into two.

Done.

4/17: with a conductivity

Done.

 4/18: obtain vertical profiles

Done.

4/19: for all stations

Done.

4/20: chlorophyll a concentration profiles

Done.

4/21: from the PANGAEA

Done.

5/1: all stations

Done.

5/2: time of collection

Done.

5/11: related to SST

Done.

6/23: neither in the complete data

Done.

8/21: relationship between DH and environmental parameters

Done.

8/21-23: Three sentences starting with "This...". Maybe rephrase?

Done.

8/25ff: Better write "In the model, this overestimation of the MLD affects..."

Done.

8/34: matter

Done.

9/1: depth of

Done.

9/2 sea surface

Done.

9/6: tolerance limit

Done.

9/5-7: Split long sentence into two.

Done.

10/2-3: ...evidence ... indicates

Done.

10/6-7: compromise between ... and ...

Done.

10/22-25: Split long sentence into two.

Done.

10/27: mismatch in the

Done.

11/6: gratefully acknowledged

Done.

12/3-4: Delete blanks!

Done.

12/10: ocean

Done.

12/13: Carstens, J.

Done.

12/13: Sarnthein

Done.

13/4: Delete "(Ehrenberg 1861)"

Done.

16: A word is missing in the table caption!

Done.

Fig. 2c/d: Several symbols are hidden. Possibly use open symbols with no filling?

We have tried this solution, but even though some symbols overlap we think that the original figure with transparent symbols is clearest and prefer to keep it. It is important to note that the purpose of the figure is not primarily to show each individual point, but the overall absence of a linear trend between sea ice concentration and sea surface temperature, which allows us to investigate their effect on DH independently.

Fig. 9: Why is "Productivity" related to a filled symbol in the legend while the triangle is open in the figure?

Corrected.

Response to Antje Voelker

We would like to thank Antje Voelker for her helpful comments on our manuscript. Below we provide a detailed response to her comments (in italics), indicating the changes that have been made. Line numbers refer to those of the revised manuscript that includes all tracked changes.

With kind regards,

Mattia Greco (on the behalf of all co-authors)

Greco and co-authors compiled new and published vertical abundance data from multi-net tows to evaluate – using statistical approaches – the habitat depth of polar foraminifera N. pachyderma and its relationship to environmental parameters. The study provides new and important insights into a species widely used in paleoceanographic reconstructions, but still with limited information on its living conditions. The authors compare their evidence also to the outcome of the PLAFOM2.0 model (with limited success). With the environmental changes currently occurring in the subpolar North Atlantic and Arctic Ocean this study is for sure timely and relevant for any future studies. The manuscript is well written, the data well presented and deserves to be published in Biogeosciences after minor revision. The following are more general comments that might help improve the manuscript, but are not essential for accepting the manuscript:

1) There exists a very nice study (PhD thesis) [in German] on "The planktonic foraminifera Neogloboquadrina pachyderma (Ehrenberg) in the Weddell Sea, Antarctica" by Doris Berberich published as Berichte zur Polarforschung 195, in 1996. Although this is a different genotype than in the northern hemisphere, it seems that some aspects of the Greco et al. and Berberich observations are similar. So I urge the authors to have a look at this work. I do not know, if the authors could verify with their data is the deeper depth habitat in their data is also related to more adult/ terminal stage specimens and thus potentially to the reproduction cycle. Berberich is also discussing influence of phytoplankton abundance (i.e., food supply) on the foraminifera abundance and sees similar changes in depth as discussed on p. 9 lines 17 to 30. She is referring to Arikawa (1983) when discussing the relationship between N. pachyderma abundance and the deep chlorophyll a maximum. So the Arikawa study is another one the current authors should look into as support for their observation that the depth habitat of their genotype of N. pachyderma appears to be below the chlorophyll maximum. Arikawa, R. (1983), Distribution and taxonomy of Globigerina pachyderma (Ehrenberg) off the Sanriku Coast, Northeast Honshu, Japan. Tohoku Euniv. Sci. Repts., Ser. 2 (Geol.), 53, p. 103-157

Thank you for these suggestions. Our dataset does not allow for an extensive investigation of differences in DH among size classes of N. pachyderma. For the limited number of stations where we have size data, we found that specimens of smaller size show a deeper depth habitat than the bigger ones. Our subset thus shows the opposite pattern reported by Berberich's. Whether this pattern is real or not requires more detailed size distribution data that we currently do not have.

We also thank the reviewer to point us at the interesting work of Arikawa. In his paper, he describes ecological and taxonomical features of the pacific genotype of N. pachyderma (Type VII) collected with horizontal tows from two stations off the Sanriku Coast (Japan). At page 113, lines 1 to 9, Arikawa discusses the general distribution pattern of the planktonic foraminifera concentrations:

'At each station, the population density of each species in water columns broadly corresponds to the value of chlorophyll a, which indicates a standing crop of phytoplankton, producer. At both stations, the shallower maximum exists at a depth of 50m and 75m (around or just below the maximum of chlorophyll a concentration).'

Our data on type I shows a different pattern and indicates no link between DH and the DCM (Figs 5a and 9). These contrasting observations suggest distinct ecological patterns among the different

genotypes of N. pachyderma. However, our study aims to explore the DH of genotype I and we think that a detailed comparison with all other genotypes would require more data and we hence refrain from a rather ad-hoc comparison. We consider this a potential avenue for future research.

2) p. 4 line 29: did the authors inquire at the AWI oceanography group if the CTD data collected during the ARK campaigns might have been stored there? Since I participated in ARK-X/2, I verified the cruise report and it clearly says on page 95 that at most stations with plankton sampling hydrographic information was obtained with a CTD probe.

We queried PANGAEA data repository to retrieve the CTD data from the ARK X-2 station and did not find the data for this station. However, we used the counts from that station to investigate the effects of lunar day and DVM on the DH of N. pachyderma.

More detailed comments to the manuscript itself:

1) throughout the manuscript you are referring to the North Atlantic, even though your samples are actually limited to the subpolar and polar regions of the North Atlantic. If you do not want to use the term Nordic Seas (for the area between Iceland, Greenland, Norway and Svalbard), you could use "northern North Atlantic" to better describe the geographical range of your samples.

We follow the suggestion and will refer to our sampling area using more precise geographical ranges.

2) p. 3 line 26: why is food source/supply not mentioned here -although one could argue that this could be a consequence of the change in the environmental conditions?

We mention the food source at page 3 line 23 where we introduce the environmental drivers of the depth habitat of N. pachyderma.

3) Material: please provide a table with the stations, date/ year of collection, data source for published data. From your figures one can deduce the season etc., but not how the samples are distributed over the years. Please also provide the name of the station excluded from the Jensen (1998) data set.

Reviewer 1 also suggested to implement the table in the manuscript. However, due to the size of such a table we prefer to make it available as supplementary material at zenodo.org, where long-term storage is guaranteed. We would like to point out that the link to the table with the complete metadata and environmental data was already provided in the "Data availability" section in the original manuscript. .

4) p. 4 line 18: please provide the depth until which pigment concentrations were measured. Were the profiles also done down to 300 m?

We will provide the range of the measurement of the pigment concentrations. The submersible fluorospectrometer recorded data from the surface until 300 m.

5) p. 5 line 11: small English correction; it should say "related to"

Done.

6) p. 7 line 15: it would be good if you could provide the reader with the information how and in which geographical resolution sea ice and chlorophyll are presented in the earth system model, from which PLAFOM2.0 derives its environmental conditions. I wonder if the poor relationship between observations and model might be a resolution problem or sea ice itself not being presented in the model.

The disagreement is not due to sea ice not being modelled. The here analysed model simulation was an ocean-ice-only simulation of CESM1.2 with active ocean biogeochemistry, whereby the ocean model was coupled to the sea ice model. However, the reviewer rightly points out that the coarse resolution of climate models is often a challenge in model-data comparison. Here, both the ocean

component and the sea ice component of CESM1.2 have a zonal resolution of 1° and an increased meridional resolution of ~0.3° near the Equator. However, here we avoid this complication of the relatively coarse resolution of the model by simply looking at modelled versus observed relationships between DH and environmental variables. We will add the following explanation to the text:

'By comparing modelled with observed ecological patterns, rather than individual observations, we ensure a more consistent evaluation of the model performance.'

We will also make it more explicit that Fig.8 compares modelled DH with modelled sea ice and chlorophyll a concentration. The comparison is thus entirely in model space and not a strict data-model comparison.

7) p. 9 line 14: if the authors would like to include a study more concentrated on isotopic evidence from the Arctic Ocean they could add the following reference: could also look into Hillaire-Marcel, C., 2011. Foraminifera isotopic records: : : with special attention to high northern latitudes and the impact of sea-ice distillation processes. IOP Conference Series: Earth and Environmental Science 14, doi:10.1088/1755-1315/14/1/012009

Done.

8) p. 9 line 30: although the authors write on p 10 line 18 that the species is likely not grazing on fresh phytoplankton, I wonder if type of food source might not be a driver with a preference for "fresh food" during period with a shallower DH and more refracted organic matter during periods when the species prefers the depths below the chlorophyll maximum.

This is an interesting point. In our data, we observe that the depth habitat is in virtually all cases located below the chlorophyll maximum (Fig. 9), thus N. pachyderma consistently feeds below the DCM, where fresh phytoplankton is rare. Hence, we do not observe indications for food source as a driver of DH. Assuming that N. pachyderma has specific food preferences, such proposed change in its diet also seems unlikely. However, we agree with the reviewer that more investigations on the diet of this species are needed for a better understanding of its ecology.

Response to Caterina Bergami

We would like to take this opportunity to thank Caterina Bergami for her helpful comments on our manuscript. Below we provide a detailed response to her comments (in italics), indicating the changes that have been made. Line numbers refer to those of the revised manuscript that includes all tracked changes.

With kind regards,

Mattia Greco (on the behalf of all co-authors)

The paper provides interesting paired planktonic foraminfera and environmental data from an important oceanographic region both from new and yet published data in order to better understand the habitat depth preferences of N. pachyderma. This type of studies can help to better understand in which way environmental parameters control the habitat depth and behaviour of this important planktonic calcifier and has an impact on future palaeoecological and palaeoceanographic studies in this area and in other high latitude environments. The authors also compare their evidence to the outcome of the PLAFOM2.0 model, with limited results. The manuscript is well structured and the data well presented and relevant for future studies on the same issues. The amount of figures and tables is adequate to illustrate the results discussed in this paper. The paper deserves to be published in Biogeoscience after some minor revisions that I listed below and in the attached pdf file.

I also suggest to the author a further check of the English language.

Technical points:

- please check the use of the acronyms along the text. Once you define them the first time, please use the same along the text (check in particular DVM, SST and SSS).

We will make corrections in the text to ensure the correct use of the acronyms once introduced in the text.

- choose between the term "habitat depth" and "depth habitat (DH)" as definied in the text and use it accordingly. - please check along the text the use of the term "compilation". I would prefer dataset.

Reviewer 1 and Robert Spielhagen also pointed out that we used these two terms interchangeably in the manuscript. We will correct and homogenize the terminology adopting only the term "depth habitat".

Since our analyses are based on an array of data pulled from different sources (PANGAEA, NSIDC, and digitization of existing data from literature), we believe that the term 'compilation' better describes the nature of our dataset.

- Material and methods sections (from page 5/line 16 to page 6/line 11: In this part of the text some results are mixed with M&M. Please, check and move the results to the following section.

This is a valid point. However, we consider that part of the methods section more as an evaluation of the methods employed in the analyses and not results. We therefore prefer to keep it in the methods section.

- Page 4/line 3-4: "We retained all other profiles, despite the differences in the mesh size, counted size fraction and vertical resolution". This phrase is not clear, please re-phrase. What do you mean?

We refer to the differences in sampling design (mesh size of the nets and sampled depth intervals) and in size fraction analysed. We re-wrote the sentence to increase the clarity:

'We retained all other profiles, despite the differences in the sampling design (mesh size and vertical resolution of the sampled depth intervals,) and in the counted size fraction and vertical resolution.'

- page 9/line 11-12: "sedimentary and plankton specimens". Do you mean fossils and living specimens?

We use the terms 'sedimentary' and 'plankton' to refer to the source from where the specimens analysed in the cited studies were collected (sediment/cores, water column/sediment traps-plankton hauls). We feel that the distinction suggested by the reviewer is incorrect for two reasons, i) strictly speaking specimens from recent sediments are not fossil or fossilised and ii) dead specimens can also be collected from the water column. However, the distinction is not entirely necessary here and we will delete it.

Response to Katrine Husum

We would like to take this opportunity to thank Katrine Husum for her helpful comments on our manuscript. Below we provide a detailed response to her comments (in italics), indicating the changes that have been made. Line numbers refer to those of the revised manuscript that includes all tracked changes.

With kind regards,

Mattia Greco (on the behalf of all co-authors)

General comments

The manuscript BG_2019_79 by Greco et al. study which factors that influence the depth habitat of the planktic foraminifera Neogloboquadrina pachyderma using both published and new data together with a suite of statistical methods. The scope of the study is very timely as the regions where this species dominates are subject to climate-ocean changes, hence in order to evaluate current changes and establish robust natural baseline values a better understanding of this species' depth habitat is necessary. The manuscript is well-written and in an advanced state.

Specific comments

1. Figure 10: Introduce this information and figure early on?

We understand the comment from the reviewer. However, the structure of the paper builds on previously proposed drivers of DH of N. pachyderma and we started with investigating these variables first. The fact N. pachyderma does not appear to track specific temperature, salinity or density (Fig. 10), shows that its habitat is not controlled directly by these environmental variables, lending support to our proposed model. We therefore prefer to keep the original order in which the information is presented.

2. It would be beneficial to define what is a good correlation/a correlation/a weak correlation, e.g. what is the difference between the r- values of -0.28; -0.38 and -0.60. I am not an expert on statistics but +/- 0.28 seems like a weak correlation? It would also be good to point out that it seems that the correlation improves with a smaller number of observations (e.g. 21 samples without sea-ice)?

We agree with the reviewer that our model does not explain all observed variability in DH and have discussed the potential reasons for why this is the case on page 8 lines 7-10.

To avoid ambiguity, we will reword cases where we used subjective adjectives to describe the correlation (page 7, lines 27-30).

'Contrary to observations, the modelled DH shows the highest correlation with the depth of the mixed layer (r = 0.57, p <0.01). Moreover, the observed relationship between the modelled DH and the modelled sea-ice and chlorophyll concentration is lower and of opposite sign compared to the observations (Figs.8a-b).'

With regard to the second point raised, we would like to point out that, contrary to the impression of the reviewer, the correlations actually improve both in strength and in significance when more samples are included in the analyses for the subsets of profiles with and without sea ice. (page 7 lines 27-29, Figs 5c and 5d).

3. The PLAFOM2.0 model is introduced somewhat superficially; more information would be useful.

A more detailed description of PLAFOM2.0 was also suggested by Robert Spielhagen, so we integrated the following text in the introduction section:

'This model is driven by temperature, food concentration, and light availability (which matters only for species with symbionts). The species-specific food concentrations are simulated by the Community Earth System Model, version 1.2.2 (CESM1.2, Hurrell et al., 2013) at every time step and are subsequently used by PLAFOM2.0 to calculate the monthly carbon concentration of N. pachyderma and four other species of planktonic foraminifera.'

Technical comments

1. Overall: The use of "planktonic" vs "planktic". Please refer to Emiliani 1991: https://doi.org/10.1016/0377-8398(91)90003-O

We agree with the reviewer that the correct expression would be "planktic" as explained in the referred paper. However, the expression "planktonic foraminifera" is more common in the literature than "planktic foraminifera" (up to about 5 times more- as a quick search in Scopus revealed). For practical reasons we therefore prefer to keep using the term "planktonic".

2. Overall: There are many acronyms in the paper. Except for SST, SSS, DVM and DH they do not help reading the paper.

We will check the use of the acronyms and make sure that each is properly introduced and used consistently in the text.

3. Page 5, lines 6-15 and lines 20-32 ("Materials and methods"): This seem more like a description of results, which it may benefit to move to the start of "Results".

Caterina Bergami also suggested this change in her review. However, we consider that part of the methods section more as an evaluation of the methods employed in the analyses and not results. We therefore prefer to keep it in the methods section.

~~Variable habitat depth~~ Depth habitat of the planktonic foraminifera *Neogloboquadrina pachyderma* in the northern high latitudes explained by sea-ice and chlorophyll concentration

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Abstract. *Neogloboquadrina pachyderma* is the ~~dominant~~ dominant planktonic foraminifera species in the polar regions. In the northern high latitude ocean, it makes up more than 90% of the total ~~planktonic foraminifera~~ assemblages, making it the dominant pelagic calcifier and carrier of paleoceanographic proxies. To assess the reaction of this species to a future shaped by climate change and to be able to interpret the paleoecological signal contained in its shells, its ~~habitat depth~~depth habitat must be known. Previous work showed that *N. pachyderma* in the northern polar regions has a highly variable depth habitat, ranging from the surface mixed layer to several hundreds of met~~r~~ers below the surface, and the origin of this variability remained unclear. In order to investigate the factors controlling the ~~habitat depth~~depth habitat of *N. pachyderma*, we compiled new and existing population density profiles from 104 stratified plankton tow hauls collected in the Arctic and the North Atlantic ~~oO~~ceans during 14 oceanographic expeditions. For each vertical profile, the Depth Habitat (DH) was calculated as the abundance-weighted mean depth of occurrence. We then tested to what degree environmental factors (mixed layer depth, sea surface temperature, sea surface salinity, ~~Cc~~hlorophyll a concentration and sea ice concentration) and ecological factors (synchronised reproduction and daily vertical migration) can predict the observed DH variability and compared the observed DH behaviour with simulations by a numerical model predicting planktonic foraminifera distribution. Our data show that the DH of *N. pachyderma* varies between 25 m and 280 m (average ~100 m). In contrast with the model simulations, which indicate that DH is associated with the depth of chlorophyll maximum, our analysis indicates that the presence of sea-ice together with the concentration of chlorophyll a at the surface have the strongest influence on the vertical habitat of this species. *N. pachyderma* occurs deeper when sea-ice and chlorophyll concentrations are low, suggesting a time transgressive response to the evolution of (near) surface conditions during the annual cycle. Since only surface parameters appear to affect the vertical habitat of *N. pachyderma,* light or light-dependant processes might influence the ecology of this species. Our results can be used to improve predictions of the response of the species to climate change and thus to refine paleoclimatic reconstructions.

Introduction

Neogoboquadrina pachyderma is the most abundant planktonic foraminifera in the Arctic Ocean and its marginal seas, where it also dominates the pelagic calcite production (Schiebel et al., 2017; Volkmann, 2000). When the organism dies, its calcite shells sink to the seafloor and when preserved in the sediments, ~~they~~ it serves as a source of information on the physical state of the ocean in the past (Eynaud, 2011; Kucera, 2007). To understand the origin of the paleoceanographic proxy signal and to predict the production of the species under varying physical conditions, including projected future change scenarios, it is important to constrain the factors that determine its vertical habitat. Previous work has shown that the seasonality of *N. pachyderma* production follows the timing of food availability, which is tightly linked with temperature (Jonkers and Kucera, 2015; Tolderlund and Bé, 1971). On the other hand, the vertical habitat of the species is variable and appears hard to predict (Xiao et al., 2014).

Previous studies proposed different abiotic factors as drivers of *N. pachyderma* vertical distribution including temperature (Carstens et al., 1997; Carstens and Wefer, 1992; ~~X.~~ Ding et al., ~~R. Wang, H. Zhang,~~ 2014), density stratification (Simstich et al., 2003) and the depth of the subsurface chlorophyll maximum indicating food availability (Kohfeld and Fairbanks, 1996; Pados and Spielhagen, 2014; Volkmann, 2000). Next to environmental factors, the behaviour of the species itself, such as its ontogenetic vertical migration (Bijma et al., 1990; Erez, 1991) and day/night migration (Field, 2004), or morphologically hidden cryptic diversity (Weiner et al., 2012) , could also influence the vertical habitat observed in a single profile. However, the Arctic and the North Atlantic are inhabited by a single *N. pachyderma* genotype (Type I) (Darling et al., 2007), indicating that the variable depth habitat of the species cannot be attributed to cryptic diversity. On the other hand, analysis of the size distribution of *N. pachyderma* shells in the Arctic by Volkmann (2000) suggested a synchronised reproduction around the full moon, with sexually mature individuals descending towards a deeper habitat to release gametes. Similarly, diel vertical migration (DVM) is known to confound observations of vertical distributions patterns of Arctic plankton (Berge et al., 2009). Although the only study on DVM in polar waters on *N. pachyderma* showed no evidence of this phenomenon (Manno and Pavlov, 2014), it was based on observations during the midnight sun with relatively weak changes in light intensity and the existence of DVM in *N. pachyderma* during other times of the year cannot be firmly ruled out. Therefore, the influence of the two ecological patterns on the depth habitat of *N. pachyderma* has to be considered in the analysis of our compilation of vertical profiles.

The lack of consensus on potential drivers of habitat variability in *N. pachyderma* calls for a systematic approach synthesizing new and existing observations into the same conceptual framework. In addition, there is now an opportunity to compare observations with predictions of a numerical model in the same framework. This opportunity arises from the recently extended model PLAFOM2.0, which can predict the seasonal and vertical habitat of *Neogloboquadrina pachyderma* (Kretschmer et al., 2018). This model is driven by temperature, food concentration, and light availability (which matters only for species with symbionts). The species-specific food concentrations are simulated by the Community Earth System Model, version 1.2.2 (CESM1.2,(Hurrell et al., 2013)) at every time step and are subsequently used by PLAFOM2.0 to calculate the monthly carbon concentration of *N. pachyderma* and other four species of planktonic foraminifera.

~~To this end~~Here, we assembled existing vertical population density profiles of this species from the Arctic and North Atlantic, combined these with new observations from the Baffin Bay and associated the observations with oceanographic data. Based ~~on~~ an analysis of th~~is~~e ~~resulting~~ dataset, we present a new concept that explains ~~habitat~~ depth habitat~~depth~~ variability in this important high-latitude marine calcifier. Next to three previously proposed environmental drivers of habitat variability (temperature, stratification, food availability), we also consider chlorophyll concentration at the surface as a measure of productivity, as well as salinity and sea-ice concentration. These parameters were included in order to test i) ~~testing for~~ the possibility that the foraminifera are attracted to food at the surface, ~~salinity, testing for~~ ii) the possibility of the foraminifera evading low salinity surface layers, ~~and sea-ice concentration,~~ and iii) ~~testing for~~ the possibility that the foraminifera habitat responds to sea-ice related variability in light, atmospheric exchange and/or mixing.

2 Material and methods

Our analysis is based on a synthesis of existing and new vertical ~~density~~ abundance profiles of *N. pachyderma* from the high-northern latitudes. We exclude the Pacific Ocean because it is inhabited by a distinct genetic type of *N. pachyderma* with potentially different ecology (Darling et al., 2007). We compiled 97 population density profiles of *N. pachyderma* collected during 13 oceanographic expeditions between 1987 and 2011 (Fig.1). We excluded one profile from Jensen (1998), station 37/6, where the abundance maximum occurred anomalously deep (below 500 m) and which we thus suspect to reflect an error (i.e. due to sample mislabelling). We retained all other profiles, despite the differences in the sampling design (~~-~~mesh size and vertical resolution of the sampled depth intervals,) and in ~~-~~counted size fraction ~~and vertical resolution~~. The ~~remaining~~ compilation is representative of the Eurasian Arctic Ocean and its marginal seas, as well as of the North Atlantic, but contains no data from the oceanographically distinct Baffin Bay. To ~~close~~ fill this gap, we extended the compilation by generating new data from eight plankton tow profiles collected during the MSM09 cruise in 2008 (Fig.1). At all stations sampling was carried out down to 300 m using a multiple closing plankton net (HydroBios, Kiel) with a 50 × 50 cm opening and a 100 μm mesh (Kucera et al., 2014). The vertical distribution of planktonic foraminifera was resolved to nine levels by conducting two casts at each station (300–220 m, 220–180 m, 180–140 m, 140–100 m, 100–80 m, 80–60 m, 60–40 m, 40–20 m, 20–0 m). After collection, net residues from each depth were concentrated on board, settled and decanted, filled up with 37% formaldehyde to a concentration of 4% and buffered to pH 8.5 using pure solid hexamethylenetetramine ($C_6H_{12}N_4$) to prevent dissolution, and refrigerated. Specimens of planktonic foraminifera were picked from the wet samples under a binocular microscope and air-dried. All individuals in the fraction above 100 μm were counted and identified to species level following the classification of Hemleben et al. (1989) and Brummer and Kroon (1988). Full (cytoplasm-bearing) tests were counted separately and considered as living at the time of sampling. Counts were converted to concentration using the volume of filtered water determined from the product of towed intervals height and the net opening (0.25 m²).

For the new profiles from the Baffin Bay, water temperature and salinity were measured with a conductivity–temperature– depth (CTD) device deployed before each plankton tow. ~~In order to obtain the vertical profiles of algae pigment concentrations, A~~a ~~-~~submersible fluorospectrometer (bbe Moldaenke) was used for ~~all~~ the stations MSM09/457, MSM09/458, MSM09/460 and MSM09/462 to obtain vertical profiles of algae pigment concentrations from the surface to 300 meters depth (Kucera et al., 2014). For the remaining profiles from the literature, physical oceanographic data and chlorophyll a concentration~~s~~ profiles for each station were, if available, obtained from CTD profiles retrieved from the PANGAEA data repository using the R package "pangaear" (Simpson and Chamberlain, 2018, R Core Team, 2017). Sea surface parameters, sea surface temperature (SST), sea surface salinity (SSS) and surface chlorophyll concentration, were obtained from CTD profiles and Niskin bottles by averaging all the values from the first 5 meters. The depth of the chlorophyll maximum (DCM) was determined from vertical profiles of chlorophyll concentration obtained from either water column profiles or discrete measurements from Niskin bottles. The depth of the mixed layer (MLD), defined as the depth

where in situ water density varied by more than 0.03 kg/m^3 as in De Boyer Montegut *et al.* (2004), was calculated from the CTD profile of each station using a custom function in R. No vertically resolved profiles of environmental variables were available for plankton net hauls collected during the expeditions NEWP93, ARK-IV/3, ARK-X/1, ARK-X/2, M36/3, and M39/4. These profiles could thus only be used for the analysis of ontogenetic and diel vertical migration. In addition to the in-situ data, daily sea ice concentrations for the location of ~~each~~ all the 104 ~~profiles~~sites included were extracted from 25 × 25 km resolution passive microwave satellite raster imagery obtained from the National Snow and Ice Data Centre (Boulder, Colorado, USA) for 1979–2011 using a custom function in R ~~(R Core Team, 2017)~~. We used the data to determine sea-ice concentration at the time of collection and also to retrieve the time after sea-ice break for all ~~the~~ stations that were sea-ice free at the moment of sampling. The date of the most recent sea-ice concentration maximum was used to retrieve the time by subtracting the days until the ~~sampling~~ time of collection~~date~~. Finally, the time of the collection was compared to the time of sunrise and sunset for each station determined using the R package "SunCalc" (Agafonkin and Thieurmel, 2018) to distinguish day-time and night-time collections. The sampling date was used to determine the lunar day using the R package "lunar" (Lazaridis, 2015).

The cross plots in Fig. 2 show how the final compilation of 104 profiles covers the environmental space and how the observations are spread across the seasons and the lunar cycle. The sampling is strongly biased towards the summer but the lunar cycle is completely covered. Most of the profiles were collected under midnight sun conditions, leaving only 28 profiles that could be used to test the diel vertical migration (Table 1~~2~~). The profiles cover SST conditions between -2 and 7°C and contain profiles taken across the entire range of sea-ice concentrations. Since sea-ice concentration at the studied profiles was not linearly related ~~with~~ to SST, the compilation should allow to assess the effect of the two variables independently (Fig.2c). Productivity, expressed as surface chlorophyll a concentration, is neither correlated with temperature. The most productive stations were located in the Baffin Bay and in the Fram Strait with surface chlorophyll concentrations ranging between 2 and 4 mg m^{-3} (Fig. 2b~~d~~). Surface salinity was mostly around 33 PSU, only in the Laptev Sea ~~we observed~~ values dropped below 30 PSU.

To facilitate the analysis of ~~habitat~~ depth habitat~~depth~~ across density profiles with observations at different depth intervals, the density profiles were summarized into a single parameter, ~~depth habitat (~~DH (depth habitat)~~)~~, which is the abundance-weighted mean depth calculated using the mid points of the collection intervals (Fig.3), as in Rebotim et al. (2017). The precision with which the DH can be determined is linked to the vertical resolution of the profiles. The combined analysis of casts with different vertical resolution therefore unavoidably introduces some random noise in the DH estimates, but this does not compromise the first order results of our study. Since counts of living and dead specimens were not available for all the stations, total counts were considered. However, where possible, we also derived the average living depth (ALD) to assess possible biases deriving from using total counts to constrain depth habitat. This comparison showed that ALD was highly correlated with DH and on average 11 meters shallower than DH, which thus represents a slight systematic overestimation of the actual living depth of *N. pachyderma* (Fig.4). Exceptions are stations MSM09/466, 55/84, and 36/069 where the observed ALD was deeper than DH due to the high number of dead specimens in the upper catch

intervals. The appropriateness of a single parameter (DH) as an indicator of the distribution of *N. pachyderma* in the water column was further tested using a multivariate approach. We determined profile-standardized concentrations calculated for 5 depths (0-50, 50-100, 100-200, 200-300, 300-500) for all the stations and performed a principal component analysis (PCA) on the relative abundances in the sampling intervals using the R package "vegan" (Oksanen et al., 2018). The two first principle components explained 43% and 32% of the total variance in the relative abundance in the water column. The first axis exhibited negative loadings for the deeper intervals (100-200, 200-300, 300-500) and positive loadings for shallow intervals 0-50 and 50-100, indicating that it describes a depth-changing unimodal distribution (Fig 4b). Mapped on the PC1 loadings, DH showed a significant correlation (Pearson r = -0.88, p-value <0.01) indicating that all profiles had a single maximum and the depth distribution can be collapsed into a single variable (Fig 4b).

We start our analysis by considering the potential effect of ~~diel~~ DVM ~~vertical migration~~ and the possibility of synchronised vertical ontogenetic migration associated with the lunar cycle. Despite its potential importance (Rebotim et al., 2017), we cannot analyse seasonal variation in depth habitat because only a single season was sampled. The influence of ~~diel DVM~~~~vertical migration~~ on DH was assessed by dividing samples in two groups based on whether they were collected during the day or during the night. The two groups were tested for homoscedasticity (homogeneity in variances) using an F- test and then a t-test was performed to verify if there was a significant difference in the DH of day and night populations. To investigate the effects of the lunar cycle on the depth habitat of *N. pachyderma,* we used a periodic regression following the approach described in Jonkers and Kucera (2015). In the next step, we analysed the relationship between DH and sea surface temperature, sea surface salinity, mixed layer depth, surface chlorophyll concentration, depth of chlorophyll maximum and sea-ice concentration. We use linear regression to assess if any of the variables individually predicts a significant part of the DH variability and the variables that showed significant correlation with DH were used to construct a multiple linear regression model allowing interactions. The use of linear regression assumes normality, which was tested, and linearity in the relationship, which is assumed, but prevents overfitting and therefore all estimates of goodness of fit in our models can be considered conservative.

3 Results

The ~~depth habitat~~ DH values derived from the abundance profiles ranged from 26 m to 283 m with an average of 100 m (IQR= 54.95). The deepest observation comes from the Fram Strait, the shallowest from the Baffin Bay.

An independent-samples t-test revealed no evidence for an effect of diel vertical migration on the observed *N. pachyderma* vertical distribution (Table 1). Similarly, the periodic regression showed no significant effect of lunar phase on DH (p = 0.17, adjusted r^2 ~~Adjusted R^2~~ = 0.029) (Table 2). In the subsequent analyses we could thus focus on abiotic factors in explaining vertical habitat variability in *N. pachyderma*. Bivariate linear regressions against DH carried out on a subset of 66 profiles for which all of the tested environmental parameters were available yielded a significant relationship only for

chlorophyll concentration at the surface (Fig. 5a). However, we noticed that profiles from stations where sea-ice was present appeared to show a relationship with sea-ice concentration and we thus carried out separate analyses for profiles with and without sea-ice. We found no significant correlation between DH and the variables SST, SSS, MLD and DCM neither in the complete data set nor in the subsets (Fig.5a). Chlorophyll concentration at the surface appeared to be the only parameter

5 showing significant negative correlation in both the complete dataset ($r = -0.28$, $p < 0.05$) and the sea-ice free subset ($r = -0.60$, $p < 0.01$). A negative correlation between DH and sea-ice concentration was observed in the subset including ice-covered stations ($r = -0.38$, $p < 0.05$). Following the initial variable selection, where only profiles for which all variables were available were considered, we then extended the analyses to all profiles where sea-ice concentration and/or chlorophyll concentration at the surface were available. These analyses confirm the significance of the relationships (Figs. 5b and c).

10   In the Arctic, the break-up of the sea-ice is normally followed by a pulse of productivity (Leu et al., 2015), making the two tested variables potentially causally connected in a time-transgressive manner. To test for the presence of such a relationship, we tested the relationship between DH and the number of days since sea-ice break-up. To decrease the collinearity between sea-ice and productivity, the analysis was restricted to 18 profiles from stations with chlorophyll concentrations <0.5 mg m^{-3}. This analysis shows that DH significantly increases with time after the sea-ice break-up ($r =$

15 0.65, $p < 0.01$) (Fig. 6). In the final step, we combined the three variables that individually showed significant effect on DH for at least one subset of the profiles and constructed a multiple regression model to predict the depth habitat of *N. pachyderma* based on sea-ice concentration and the interaction between chlorophyll concentration at surface and days after the sea-ice break. A linear formulation of the model is significant (p < 0.01) and the model explains 29 % of the depth habitat variability in *N. pachyderma* (adjusted $r^2 = 0.29$). Next, we tested a non-linear relationship, considering the log-

20 normal nature of the DH. This model leads to a marginal improvement (adjusted $r^2 = 0.3\frac{4}{2}$) (Table 3).

       Finally, we evaluate how PLAFOM2.0 (Kretschmer et al., 2018) captures the observed patterns in *N. pachyderma* depth habitat. To this end, we assess the relationship between modelled DH of *N. pachyderma* and modelled SST, SSS, MLD, DCM and chlorophyll concentration for summer months in the geographic area covered by the compilation (Fig.1). By comparing modelled with observed ecological patterns, rather than individual observations, we ensure a more meaningful

25 evaluation of the model performance that does not rely in the simulation of individual profiles. Although PLAFOM2.0 simulations also indicate a dominantly subsurface summer depth habitat of *N. pachyderma*, the modelled DH is shallower than observed, with values ranging between 9 and 127 meters (Fig.7). Contrary to observations, the modelled DH shows the ~~strongest~~ highest correlation with the depth of the mixed layer ($r = 0.57$, $p < 0.01$). Moreover, the observed relationship between the modelled DH and the modelled sea-ice and chlorophyll concentration is ~~weak~~ lower and of opposite sign to the

30 observations (Figs.8a-b).

4 Discussion

Previous research indicated the absence of DVM in *N. pachyderma* in the Fram Strait (Manno and Pavlov, 2014) but the fact that the sampling was carried out during the midnight sun led the authors to concede that the species still could engage in

DVM in the presence of a diurnal light cycle. Indeed, studies on copepods in the Arctic showed that natural patchiness rather than DVM is responsible for shifts in vertical distribution in periods of midnight sun, while in late summer/early autumn, when changes in the diurnal light cycle are apparent, DVM can be observed (Blachowiak-Samolyk et al., 2006; Rabindranath et al., 2011). Our compilation allowed us to assess the behaviour of *N. pachyderma* under changing light

5   condition, ~~revealing~~ but showed no evidence for DVM (Table 1). Similarly, a recent investigation on the presence of DVM in planktonic foraminifera from the tropical Atlantic found no evidence for this phenomenon in any of the analysed species (Meilland et al., 2019). Our observations thus add to the existing consensus that planktonic foraminifera are unlikely to participate in DVM. Although we cannot rule out DVM on a very small vertical or geographical scale, we conclude that the observed variability in habitat depth of *N. pachyderma* in our compilation is likely not biased by DVM, allowing us to

10 investigate other potential drivers.

The reproduction of many species of planktonic foraminifera appears synchronized on lunar or semi-lunar cycle (Bijma et al., 1990; Jonkers et al., 2015; Rebotim et al., 2017; Schiebel et al., 1997; Spindler et al., 1979), with sexually mature individuals descending towards a deeper habitat to release their gametes (Bijma et al., 1990; Erez, 1991). Volkmann (2000) analysed size distribution of *N. pachyderma* in the Arctic and found an indication for a synchronised descent of adult

15 individuals below 60 m during full moon. In our analysis of 104 density profiles, including those from Volkmann (2000), we found no evidence of a systematic shift towards deeper habitat associated with lunar periodicity (Table 2). Our analysis cannot resolve whether or not the reproduction in *N. pachyderma* is synchronised nor can we rule out an irregular ontogenetic vertical migration. However, the absence of a systematic relationship between DH and lunar cyclicity in our compilation indicates that a potential ontogenetic vertical migration would likely only contribute a noise component to the

20 DH variability.

Considering all potential sources of noise, including the possibility of an irregular ontogenetic vertical migration, differences in the vertical resolution of the profiles and the counted size fractions, and the large geographical and temporal coverage of the data, it is remarkable that we observe a highly significant relationship between DH and three environmental parameters that collectively explain almost a third of the variance (Table 3). This indicates that the vertical habitat of *N.*

25 *pachyderma* in the Arctic and North Atlantic changes systematically in response to sea-ice and chlorophyll concentration at the surface. The absence of a systematic relationship with any other of the previously considered environmental drivers, like the position of the DCM or thickness of the mixed layer is surprising. It implies that the ecophysiology of the species is not yet completely understood and this lack of understanding is also mirrored in the contrast between the environmental drivers inferred from observations and assumed in PLAFOM2.0 (Fig.8).

30 There is general consensus that *N. pachyderma* grazes on phytoplankton and it would thus seem reasonable to assume that food availability primarily influences its vertical distribution (Bergami et al., 2009; Carstens et al., 1997; Kohfeld and Fairbanks, 1996; Pados and Spielhagen, 2014; Taylor et al., 2018; Volkmann, 2000). Surprisingly, our analysis yielded no significant correlation between the position of the subsurface chlorophyll maximum and DH. Instead, the DH of the species is always located below DCM and thus most specimens of the population do not appear to be grazing at the

DCM. This observation is also in contrast with the modelled relationship ~~of~~ between DH ~~with~~ and the environmental parameters. As also noted by Kretschmer et al. (2018), ~~T~~this is because the strong relationship between DH and MLD in the model reflects a strong link between MLD and the position of the subsurface chlorophyll maximum, ~~as also noted by Kretschmer et al. (2018)~~. This strong link likely results from a bias in the ocean component of the Community Earth System

5 Model (CESM1.2) propagated in PLAFOM2.0. The CESM1.2 model is known to overestimate the mixed layer depth in the Arctic by 20 to 40 metr~~er~~s (Moore et al., 2013). ~~This~~ In the model, this overestimation of the MLD ~~in the model~~ affects ocean biogeochemistry and the light regime experienced by the phytoplankton. Specifically, a deeper mixed layer equates to a thicker layer of nutrient depletion, ~~lowering~~ deepening the DCM. Consequently, the simulated depth of the chlorophyll maximum reaches 60 to 95 meters, whereas a recent survey of vertical chlorophyll profiles in the post-bloom period (May-

10 September) in the Arctic indicated that subsurface chlorophyll maxima occur in the top 50 meters (Ardyna et al., 2013), which is also in line with the range of DCM among the studied profiles (Fig.9). Clearly, the observed preference of *N. pachyderma* for a habitat below the DCM (Fig.9) indicates that the species may not primarily feed on fresh phytoplankton. The possibility of other species of *Neogloboquadrina* feeding on marine snow particles (hence below the DCM) has been recently suggested by Fehrenbacher et al. (2018) and a similar food source, related to degraded organic matter is thus not

15 unlikely for *N. pachyderma*.

Among the other previously considered abiotic drivers of depth habitat ~~depth in~~ of *N. pachyderma*, our analysis provides no evidence for the effect of sea~~s~~-surface temperature, salinity and stratification (Fig. 4). Surface water temperature is the main controller of *N. pachyderma* abundance and it defines its geographic range (Bé and Tolderlund, 1971; Duplessy et al., 1991). Temperature could therefore also be expected to influence the vertical habitat of the species. However, we

20 found no link with surface temperature and *N. pachyderma* depth habitat. This is probably because the temperature range sampled by our compilation remains well within the tolerance limit~~s~~ of the species (Žarić et al., 2005). ~~and t~~Thus, temperature does not represent a limiting factor for this species and does not affect its vertical distribution. Previous research has suggested that *N. pachyderma* may avoid low salinities and preferentially occur deeper in the water column when the surface is fresh (Volkmann, 2000, see also the discussion in Schiebel et al., 2017). Like Carstens and Wefer (1992), we did

25 not find a significant correlation between surface salinity and DH indicating that the inferred response of *N. pachyderma* to surface layer freshening only applies to situations where the salinity reaches values below 30 PSU (below the limit covered by the observations in our compilation). Finally, geochemical analyses of ~~sedimentary and plankton~~ *N. pachyderma* specimens were interpreted as evidence for calcification depth of the species being controlled by the position of the pycnocline (Hillaire-Marcel, 2011; Hillaire-Marcel et al., 2004; Kozdon et al., 2009; Simstich et al., 2003; Xiao et al., 2014).

30 In our data, we found DH always situated below the MLD, within the pycnocline. Thus, our observations confirm that a significant part of the calcification is likely to occur within the pycnocline, but the depth habitat of the species is not reflecting the depth of the local pycnocline.

Our observations indicate that *N. pachyderma* resides closer to the surface when sea ice and/or surface chlorophyll concentrations are high. The DH also increases with time since sea-ice break-up. This suggests that the DH of *N.*

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pachyderma is controlled by multiple, interacting variables, likely connected in the temporal dimension. The scheme in Fig. 9 summarizes our conceptual model: when either sea-ice cover or surface chlorophyll concentrations reach high values, *N. pachyderma* prefers shallower depths, while in open waters with low productivity levels, it lives deeper. While the relationship with sea-ice has been observed repeatedly (Carstens et al., 1997; Pados and Spielhagen, 2014), the relationship

5   with surface chlorophyll at the surface is unexpected. Intuitively, rather than sea-ice and chlorophyll at the surface, the DH should reflect ambient conditions at depth. The DH does not appear to reflect the DCM (Fig. 9), but it could be that the species vertical abundance reflects the local depth at which a specific temperature or salinity optimum occur or where a given density is realised. We have thus extracted data on temperature, salinity and density at the ~~depth~~ level of DH in all profiles where CTD data were available. The analysis reveals a large variability in all parameters, indicating that the DH is

10 not tracking specific temperature, salinity or density (Fig.10). The observation that the subsurface depth habitat of *N. pachyderma* appears to be best predicted by surface parameters is counter-intuitive and points to an indirect relationship to the inferred surface drivers.

A possible link between surface properties and conditions at the DH could be light (or light-related processes). Increasing sea-ice cover and higher chlorophyll at the surface both act to reduce light penetration, potentially explaining why

15 *N. pachyderma* habitat is shallow when either sea-ice or surface chlorophyll are high (Fig. 9). The exact mechanism by which the species would respond to light intensity is not clear. So far, there is no evidence that the species would possess photosynthetically active symbionts. On the other hand, a recent molecular study indicated the presence of symbionts in a closely related species *Neogloboquadrina incompta* (Bird et al., 2018), and evidence for potential symbiosis with cyanobacteria in *Globigerina bulloides* (Bird et al., 2017) indicate~~s~~ that the range of symbioses in planktonic foraminifera

20 may be more diverse than previously thought. However, half the observed DH values are > 100 m, indicating that a substantial part of the population of the species inhabits depth where in the Arctic light for photosynthesis is not available (Ardyna et al., 2013). Alternatively, it could be that the vertical habitat of *N. pachyderma* reflects a compromis~~ing~~ between living close to the DCM (finding food)~~, but~~ and remaining in darkness (protected from predation). In many places of the ocean, heterotrophic protists are known to be metabolically more active at night (Hu et al., 2018), and predator evasion by

25 remaining in darkness is the leading hypothesis explaining DVM in marine zooplankton (Hays, 2003). These hypotheses are at present speculative and more investigations on the diet of *N. pachyderma* are needed for a better understanding of the process regulating its vertical distribution.

5 Conclusion

30 We compiled a dataset of 104 vertically resolved profiles of *N. pachyderma* concentration in the Arctic and North Atlantic and analysed the relationship of the observed depth habitat to a range of potential biotic and abiotic drivers. The analysis confirms that *N. pachyderma* inhabits a wide portion of the water column, but its maximum concentration is typically found

in the subsurface. The ~~habitat depth~~depth habitat is variable but most of the population is consistently found below the subsurface chlorophyll maximum. This indicates that the species is likely not grazing on fresh phytoplankton. The depth habitat of *N. pachyderma* as recorded by the vertically resolved plankton tow profiles shows no evidence for diel vertical migration or a synchronised change in depth habitat with lunar cycle. Temperature, salinity and density alone (at the surface or at depth) do not show significant relationship with the ~~habitat~~ depth habitat. Instead, sea-ice and chlorophyll concentration at the surface, in combination with the time since sea-ice break up explain almost a third of the variance in the depth habitat data. Most of the population of *N. pachyderma* resides between 50 and 100 m under dense sea-ice coverage and/or high surface chlorophyll concentration. When sea-ice cover is reduced and/or ~~when~~ chlorophyll at the surface is ~~and the~~low, the habitat deepens to 75 – 150 m ~~when sea-ice cover is reduced and/or when chlorophyll in the surface is low~~. This pattern reflects a response to an unknown primary driver acting below the DCM and likely reflecting trophic behaviour of the species, which is still poorly constrained. The knowledge gap on the ecological preferences of *N. pachyderma* is reflected in the mismatch ~~the~~ in the behaviour of *N. pachyderma* between observations and predictions by the PLAFOM2.0 model. Our findings can serve as a basis to calibrate new ecosystem models and refine paleoclimatic reconstructions based on *N. pachyderma* in the Arctic and its adjacent seas. Our analysis rejects the hypothesis that the vertical habitat of the species is tied to the DCM and the existence of a significant relationship with sea ice and surface chlorophyll allows us to derive a model that can predict the depth habitat ~~depth~~ of the species across the Arctic realm.

Author contributions. MK, LJ, and MG designed the study. KK provided the PLAFOM2.0 data. MG generated the data and carried out the analyses. All authors contributed to writing the paper.

Data availability: Total concentrations and filtered volumes will be made available on request to the main author until their online publication on PANGAEA (https://pangaea.de/). The table complete with data source and derived environmental data of the stations included in the study is available on Zenodo (DOI:~~10.5281/zenodo.2585796~~ 10.5281/zenodo.2653733)

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Table 1 Results of the *t*-test ~~to~~ performed on the samples collected in normal day/night conditions to assess the effects of DVM on DH.

Time of the day	n	Mean DH (m)	Std. Deviation	t-value	p-value
Night	19	99.069	46.762	-1.82	0.08
Day	9	66.949	35.401		

Table 2 Results of the periodic regression performed to asses the influence of the lunar cycle on DH.

	Depth habitat (m)	
Predictors	*Estimates*	*p*
sin (Lunar day [R])	-8.41	0.171
cos (Lunar day [R])	-10.39	0.071
Observations	104	
R^2 / adjusted R^2	0.047 / 0.029	

Table 3 Results of the multiple regression model including sea-ice concentration, chlorophyll concentration at surface and time since sea-ice break-up as predictors.

Predictors	DH (m)			log₁₀(DH) (m)		
	Estimates	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	110.76	80.37 – 141.15	**<0.001**	2.03	1.89 – 2.18	**<0.001**
Sea-ice (%)	-0.04	-0.08 – -0.00	**0.033**	0	-0.00 – -0.00	**0.021**
Chlorophyll at surface (mg m⁻³)	10.94	-10.82 – 32.71	0.329	0.06	-0.04 – 0.16	0.263
Days after sea-ice break-up	0.71	0.22 – 1.20	**0.007**	0	0.00 – 0.01	**0.005**
Interaction (Chlorophyll and sea-ice break-up timing)	-0.81	-1.25 – -0.37	**0.001**	0	-0.01 – -0.00	**<0.001**
Observations		52			52	
R² / adjusted R²		0.343 / 0.287			0.388 / 0.336	

Figure captions

Figure 1. Plankton net stations with vertically resolved *N. pachyderma* counts that were used in this study. Background colour indicates the mean summer sea surface temperature (SST) (data from World Ocean Atlas 2013~~(Locarnini et al., 2013)~~).

Figure 2. Temporal and environmental coverage of the vertical profiles of *N. pachyderma* concentration included in the study. The distribution of (a) the months and (b) days of the synodic lunar cycle of sample collection, showing a summer bias but even coverage of the lunar cycle. The relationship between the environmental conditions during sample collection (c-d) indicate the extent of the sampled environmental space.

Figure 3. Example of vertical profiles from three stations included in the study displaying shallow (left), intermediate (centre) and deep (right) depth habitat (DH).

Figure 4. a) Relationship between the depth habitat (DH) and the average living depth (ALD). The dashed red line shows the linear fit while the solid line represent the 1:1 relationship between the two variables. b) Relationship between the DH and the PC1 resulted from the PCA calculated on the normalized counts. The abundance profiles based on the standardized counts in the plot show examples of the shape of the vertical distribution of *N. pachyderma* for three values of PC1 loadings~~The normalized density profiles in the plot show the relationship between the loadings on the PC1 and the shape of the distribution.~~ The dashed red line shows the linear fit.

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Figure 5. a) Correlation between depth habitat (DH) and the environmental variables calculated in all the sites, in the subset with sea-ice and without sea-ice (only sites where all the tested variables were available were considered). Chl= Chlorophyll concentration at surface, Sea_ice= Sea-ice coverage, DCM= Depth of Chlorophyll maximum, SST= sea surface temperature, MLD = depth of the mixed layer and SSS= sea surface salinity. b) Relationship between DH and sea-ice concentration in the stations covered by sea-ice (all the sites with available sea-ice data are shown, n=65). c) Relationship between DH and chlorophyll concentration at the surface for the sea-ice free stations (all the sites with available chlorophyll data are shown, n=22).The dashed red lines show the linear fit.

Figure 6. Relationship between depth habitat (DH) and the time (days) after the sea-ice break-up. The dashed red line shows the linear fit.

Figure 7. Comparison of observed DH and the PLAFOM2.0 predictions relative to the~~.~~ summer months in the same geographic area covered by our compilation.

Figure 8. a) Relationship between the DH predicted by PLAFOM2.0 and a) sea-ice concentration in the stations covered by sea-ice and b) between DH predicted by PLAFOM2 and chlorophyll concentration at the surface for the sea-ice free stations (values averaged for the months June, July, August and September). The dashed red lines show the linear fit.

5   **Figure 9.** Data-based scheme of the final model: samples are displayed in descending order for sea-ice concentration (light-blue fading bar) and ascending chlorophyll concentration (green fading triangle) to simulate the time dimension. The green star symbols (*) represent the depth of the chlorophyll maximum and the dashed red line show the smooth fit of the data.

Figure 10. Conditions of a) temperature, b) salinity and c) density at the DH (top) and in the first 600 meters of water 10   column (bottom) for all the sites with available CTD data.