

Dear reviewers, Dear Lisa Levin (Editor),

thank you very much for the feedback to this review paper. I am really glad that three experienced specialists from this field provided such detailed constructive revisions to the manuscript. Of course, a review article will strongly benefit from discussing different opinions and different points of view of several experts. I revised my manuscript thoroughly regarding the feedback to all three reviewers. Below you can find a detailed point by point response to the review by Frans Jorissen.

Reviewer: The review paper of Glock addresses concerns an exciting and rapidly evolving field of research. It comes very timely, and presents a good overview and perfect starting point for all scientists that want to know more about foraminifera living in anaerobic environments.

However, this first version is not perfect yet, and in my opinion, several points need to be addressed:

1. The taxonomy used in this paper.

Although taxonomy is not a central topic here, in order to avoid confusion, justice should be done to the important recent advances, largely resulting from the contribution of molecular studies. One of the problems is the treatment of species of the genus *In* some parts of the text, the author talks about *A. tepida*, a species name that was often used in the past for a complex of cryptic and pseudocryptic species that has only been sorted out recently. On lines 189-200 the author gives more detailed information and says that in that case, the text concerns "*Ammonia* sp. (T6)", which is an informal name of a phylotype previously placed in the *A. tepida* morphocomplex. According to the most recent revision of this group of species (Hayward et al., 2021, *Micropaleontology*, 67; p. 109-313) the correct name of this phylotype is *Ammonia confertitesta*. I think that in the whole text, the taxonomy of *Ammonia* should be standardized, according to the 2021 revision of Hayward and coauthors.

A very similar case concerns the morphospecies *Uvigerina peregrina*. Also here, we are very probably confronted with a pseudocryptic species complex, but in case, things haven't been sorted out yet. The consequence is that it is impossible to treat *U. peregrina* as a single biological species, as the author is doing. When the author writes (lines 86-87) "*Also, the NO₃ - storage in U. peregrina shows a high variability, depending on the environment.*", it is very well possible that different biological species are concerned, and that the differences in nitrate storage are species-specific and have nothing to do with the environmental conditions.

A very similar situation, of species complexes with a multitude of cryptic and pseudocryptic species can be expected in the genera *Nonionella* and *Globobulimina*.

Although there is no ready solution for this problem, the author should take it into account, and realise that different species may be designed by the same species name, or inversely, different species names may indicate the same biological species. The author should show in the text that he is aware of this potential problem, and some of the conclusions should be reconsidered and be formulated with somewhat more reserve.

Reply: This is indeed a complex problem and it might be complicated to find a ready solution how to deal with older literature that considered these morphogroups as single species with ecophenotypic plasticity. I tried to address this topic in several parts of the revised manuscript and also tried to adapt the latest revision of the *Ammonia tepida* taxonomy. When *A. tepida* is mentioned in tables, I mark them with a * and add into the figure caption:

“*Ammonia tepida* is a morphogroup of pseudocryptic species that recently had a revision. Specimens earlier identified as *A. tepida* are likely either *A. aberdoveyensis* or *A. confertitesta* according to Hayward et al. (2021).”

When *A. tepida* is mentioned in the text, I also tried to address this problem:

“However, not all benthic foraminifera are able to denitrify, even if they live in environments that are periodically exposed to anoxia such as representatives of the intertidal species morphogroup *Ammonia tepida* (either *Ammonia venata*, *Ammonia aberdoveyensis* or *Ammonia confertitesta* according to Hayward et al., 2021), which neither store NO_3^- nor show any denitrification activities (Piña-Ochoa et al., 2010b).”

“LeKieffre et al. (2017) did a feeding experiment with specimens from the *Ammonia tepida* morphogroup (*A. confertitesta* according to Koho et al., 2018 and Hayward et al., 2021) using a ^{13}C -labeled diatom film as food source.”

Also, I wrote a paragraph, where I discuss, that this problem might concern other taxa, too:

“The observations that some species store NO_3^- and denitrify in some environments and in others not might have two reasons. One reason could be that these species belong to an opportunistic group of foraminifera that can well adapt to both oxygenated environments where they respire O_2 and do not denitrify and O_2 depleted environments where they switch to denitrification. The other reason could be that some of these foraminifera belong to morphogroups that are identified as a single species but indeed are a mixture of cryptic and pseudocryptic species that include denitrifying and non-denitrifying species. An example for such a morphogroup that has recently had a revision is *A. tepida*. This morphogroup includes three species (*Ammonia venata*, *A. aberdoveyensis* or *A. confertitesta*) that now can be morphologically distinguished (Richirt et al., 2019; Hayward et al., 2021). A similar case concerns the morphogroup *Nonionella stella*, where representatives have been found to denitrify (Høgslund et al., 2008; Choquel et al., 2021) but also consists out of several cryptic to pseudocryptic species (Deldicq et al., 2019). The situation might be similar with other *Nonionella* species and the widespread species *U. peregrina*.”

Reviewer:

2. The synonymising of microhabitat and metabolic categories.

Both in lines 146-165 and in figure 4, the author states that epifaunal taxa are aerobic, shallow infaunal taxa are facultative anaerobes whereas deep infauna are facultative aerobes. Although this is certainly partly true, this seems to be a major oversimplification, for which the author gives insufficient justification.

Reply: This section indeed suffered a bit from overgeneralizations by my side. I tried to clarify, that there definitely are exceptions from this concept within each category of microhabitat. Detailed examples are discussed in each of the microhabitat sections. Before the individual microhabitat sections I added the following sentence:

“Due to our increasing understanding about the anaerobic metabolism of foraminifera we can now assume that NO_3^- availability is another controlling factor (Fig.4). This is also indicated by a study coupled early diagenetic modeling with foraminiferal ecology to model the microhabitats of benthic foraminifera (Jorissen et al., 2022). According to their metabolic preference for NO_3^- or O_2 as electron acceptors many benthic foraminifera species that typically occupy a certain microhabitat (epifauna, shallow infauna and deep infauna) might **partly** be assigned to three different attributes (Aerobe,

facultative anaerobe and facultative aerobe). **Most likely there are exceptions to these classifications that will be discussed below. Another controlling factor on the microhabitat is most likely the trophic strategy of the foraminiferal species, which is further discussed in section 3.**"

Reviewer: First, it is not evident that all "epifauna" have necessarily an aerobic metabolism. In cases where bottom waters are strongly hypoxic, some typically epifaunal taxa may very well be facultative anaerobes or even facultative aerobes. As an example, I think of *Epistominella smithi* from the California foreland basins and the Peruvian margin. This large-sized species, which has never been described from well oxygenated sites, can reach high densities in strongly hypoxic settings, and its morphology very strongly suggests an epifaunal lifestyle.

Reply: This is a good point. I already discussed in the original part of this section that certain *Cibicides* spp. might be able to denitrify under certain circumstances. Now, I tried to integrate the example suggested by the reviewer and another epifaunal species *Planulina limbata* that also seems to be restricted to low oxygen environments. Also I adapted the first sentence of this section to prevent overgeneralization:

"Many **epifaunal species** can most likely be considered as **aerobes** that typically occur at the sediment-water interface or on elevated surfaces."

This is the new part that describes examples of epifaunal species that are restricted to low oxygen environments:

"In the same way as for the other microhabitats, not all species with an epifaunal lifestyle should be automatically considered as aerobes. There are examples of epifaunal benthic foraminifera that have not been found in well oxygenated environments but reach high abundances in O₂ depleted environments. One example is *Epistominella smithi*, which has been described in low O₂ environments, such as the Santa Barbara Basin (Harman, 1964) or the Peruvian OMZ (Erdem and Schönfeld, 2017). Nevertheless, the morphology of *E. smithi* strongly suggests an epifaunal lifestyle. Another example is the epifaunal species *Planulina limbata*. This species is abundant only in O₂ depleted environments on continental margins within the East Pacific (Natland, 1938; Erdem and Schönfeld, 2017; Glock et al., 2022). Recent *P. limbata* specimens are present in severely O₂ depleted water masses within the Peruvian OMZ ([O₂] = 3 - 12 μmol/kg, Glock et al., 2022). Nevertheless, *P. limbata* adapts its pore density to the availability of O₂ (Glock et al., 2022), which might indicate that it has an aerobic metabolism, despite that its presence appears to be limited to low O₂ environments. Another possibility is that species such as *E. smithi* or *P. limbata* may denitrify under certain circumstances and therefore can also be considered as facultative anaerobes. Hopefully, measurements of metabolic rates, intracellular nutrient content and enzymatic activity might bring further evidence in the future, if at least some epifaunal species can switch to an anaerobe metabolism, when O₂ is too depleted."

Reviewer: Next, it is not evident either that all shallow infaunal taxa are facultative anaerobes, some definitely are not. Representatives of the *Ammonia tepida* morphogroup (*A. aberdoveyensis*, *A. confertitesta*) are good examples. Until to date, all tests trying to show anaerobic metabolism were negative for these taxa. Nevertheless, they are found massively in deeper sediment layers in estuarine mudflats, where they may survive the most adverse conditions by dormancy. But I would definitely consider them as shallow infaunal taxa with an aerobic metabolism.

Reply: Again, this is a good point and overgeneralizations are certainly not very helpful. Within the revised manuscript I tried to clarify that, of course, we cannot generalize that all shallow infaunal species are facultative anaerobes. Regarding the *Ammonia tepida* morphogroup: It is true that they neither can store nitrate nor denitrify, but it might be that they have other adaptations to withstand O₂ depletion. Recent genetic studies indicated that some foraminifera have the capacity for anaerobe metabolism by using fermentation. Other recent studies revealed that several foraminifera species store large amounts of phosphate, which is likely another adaptation to O₂ depletion. Actually, I found that specimens of the *Ammonia tepida* morphogroup from tidal mudflats

have the highest intracellular phosphate concentrations of more than 20 species I analyzed from various environments. Since these are unpublished results for a manuscript in preparation, I cannot discuss those in this review but there is actually a lot of evidence that these *Ammonia* species have adaptations to stay mobile, even within anoxia. I adapted the first sentence of this paragraph to prevent overgeneralization and added several sentences, where I discussed possible exceptions:

“Shallow infauna can **in many cases** be considered as facultative anaerobes that are well adapted to the presence of low O₂ concentrations but can switch to denitrification if they are exposed to anaerobic conditions or need to enter the deeper sediment parts to find food or avoid competitive stress.”

And the text that discusses the exceptions:

“Of course, it cannot be generalized that all foraminifera from a shallow infaunal habitat are indeed facultative anaerobes. At least some species that can be considered shallow infaunal have been shown neither to be able to store NO₃⁻ nor to denitrify. As mentioned above all specimens from the *Ammonia tepida* morphogroup that have been analyzed so far lack an intracellular NO₃⁻ storage and cannot denitrify (Piña-Ochoa et al., 2010b). Nevertheless, these taxa are often exposed to anoxia and can sometimes even be found alive in 4 to 26 cm sediment depth (Alve and Murray, 2001; Thibault de Chanvalon et al., 2015). It is possible that these foraminifera indeed only have an aerobic metabolism and just become dormant under exposure to anoxia (dormancy is discussed in another section). Though, another possibility is that intertidal species such as *A. venata*, *A. aberdoveyensis* or *A. confertitesta* have other adaptations to anoxia than denitrification. Recent studies revealed other possible anaerobic metabolic pathways in foraminifera such as fermentation or dephosphorylation of creatine phosphate which are discussed in section 2.1.4 (Orsi et al., 2020; Goma et al., 2021). Eventually, studies on the transcriptome of non-denitrifying species from infaunal environments might be able to show, if some of these species can switch an alternative anaerobe metabolism under exposure to anoxia.”

Reviewer: Third, I have the least problems with considering deep infaunal taxa as facultative aerobes. But there is actually not a lot of evidence for the fact this. You would expect this, but it would be good if the author could give some arguments to strengthen this point.

Reply: I extended this part significantly to provide more arguments (new parts are marked in red):

“**Deep infaunal** species can most likely be considered as **facultative aerobes** that have a metabolic preference of NO₃⁻ over O₂ (Glock et al., 2019c) and try to avoid trace amounts of O₂. **They cannot be accounted as obligate anaerobes, though, since they can withstand periods of oxygenation. Many experiments show that denitrifying foraminifera can switch to O₂ respiration, if they are exposed to O₂ (i.e. Piña-Ochoa et al., 2010b). Still, they follow the oxycline in the sediments to avoid the inhibition of denitrification by trace amounts of O₂. The δ¹³C signature of shells of deep infaunal globobuliminids also indicates that they calcify in sediment depth where the pore water O₂ level reaches zero or even deeper in the sediments. The offset between δ¹³C of *Globobulima* spp. tests and δ¹³C of epifaunal foraminifera or of bottom water dissolved inorganic carbon (DIC) is nearly equal to the offset between DIC at the zero O₂ layer and the bottom water (Schmiedl and Mackensen, 2006) and often can be even higher (Costa et al., 2023), indicating that many globobuliminids live even below the oxycline. Even though they can switch to O₂ respiration (Piña-Ochoa et al., 2010b), these species most likely would try to avoid crossing the oxycline since denitrification would be already inhibited by nM O₂ concentrations (Dalsgaard et al., 2014) and the O₂ concentration slightly above the oxycline is not high enough to fulfil their metabolic demands. Indeed, the model by Jorissen et al. (2022) describes the distribution of deep infauna very well, by using the presence of O₂ as an inhibiting factor, which also promotes that they can rather be considered **facultative aerobes instead of facultative anaerobes**. Taxa belonging to the deep infaunal group that might be considered as facultative aerobes that prefer NO₃⁻ over O₂ include for example *Valvulineria inflata* and *bradyana*,**

Bolivina seminuda, *Globobulimina pyrula* and *Cancris carmenensis* (e.g. Jorissen et al., 1995; Mojtahid et al., 2010; Glock et al., 2019c).“

Reviewer: Finally, I strongly regret that the author doesn't mention "intermediate infauna". The maximum abundance of these taxa is systematically found in the nitrate maximum zone; *Melonis barleeanus* is a typical example. These taxa are interesting, because most of them do not store nitrate (maybe because there is no reason to do so when you live in the nitrate maximum), but appear to be capable to denitrify.

Reply: In the revised version, I will add a small paragraph about the intermediate infauna. I also discuss now that they live close to the NO_3^- maximum, since NO_3^- increases by remineralization before it decreases again due to denitrification (Jorissen et al., 2022). Though, denitrification would be likely inhibited by the presence of O_2 in these depths. It could be a possibility that it simply does not store NO_3^- but denitrifies the NO_3^- directly after the uptake from the seawater, when O_2 decreases below the inhibition threshold. This definitely provides some questions for future research. I added the following paragraph to the revised manuscript:

“The **intermediate infauna** is somehow an exceptional case. Common representatives of intermediate infaunal taxa are *Melonis barleeanus* or *Pullenia* spp. (Corliss, 1991). The typical example for intermediate infaunal species *M. barleeanus* is interesting, since it either stores no or only very small amounts of NO_3^- (See table 2 and 3). Still, several studies indicate that *M. barleeanus* lives deeper in the sediments than some *Uvigerina* spp. (Corliss, 1991; Ní Fhlaithearta et al., 2018) although many *Uvigerina* species have been shown to store NO_3^- and denitrify (Tab. 1&2). This might give room to speculate if *M. barleeanus* has other metabolic adaptations to O_2 depletion than denitrification or if it simply does not store large amounts of NO_3^- but denitrifies NO_3^- directly after the uptake from the seawater. Indeed, a recent study predicted the microhabitats of infaunal benthic foraminifera using an early diagenetic model and showed that the intermediate infauna clusters around the NO_3^- maximum in the pore water (Jorissen et al., 2022). Future perspectives on understanding the biology of intermediate infauna might include transcriptome analyses to decipher other anaerobe metabolic pathways and testing the denitrification capacity after incubation in NO_3^- -free and NO_3^- -containing seawater.”

Reviewer: And a detail: the legend of figure 4 is way too long, and repeats the running text.

Reply: Agreed. The figure caption was indeed too long. I shortened it for the revised version. In addition, I removed the terms "aerobic", facultative

3. Chapter 5: Applications in paleoceanography

Reviewer: This chapter didn't convince me. The texts are very concise, and repeatedly the reader refers to the paper of Hoogakker et al., who treats this topic in much more detail. As it is, this chapter doesn't add anything useful. I think the author should delete it altogether and expand some of the topics that would become more robust with a more deep-going treatment.

Reply: This is a good point. I deleted chapter 5 and condensed the whole chapter to one paragraph, that is now moved into the introduction:

“Benthic foraminifera from low O_2 environments have also been established as an invaluable archive for paleoceanography. However, I will touch on summarizing redox proxies based on benthic foraminifera only briefly, since there is work in progress to give a comprehensive review about proxies for O_2 concentrations in paleoceanography (Hoogakker et al., in prep). Due to their ability to precipitate their calcitic tests even under anoxic conditions, fossil benthic foraminifera became routine tools in paleoceanography to reconstruct past redox conditions (Nardelli et al., 2014; Orsi et al., 2020). Some

morphological adaptations are very common for benthic foraminifera that thrive in O₂ depleted habitats. Small, more elongated and flattened morphologies are often characteristic for O₂ depletion, while more spherical forms can indicate oxygenated conditions (Bernhard, 1986; Bernhard et al., 1997). In addition, high porosity and thin test walls seem to be characteristic for foraminifera that live in low O₂ environments (Kaiho, 1994). The porosity, including pore size and pore density, of foraminiferal tests recently received more attention as possible paleoceanographic tool. Different foraminiferal species seem to adapt their pore characteristics in a different way to environmental conditions. *Cibicides* spp. for example mainly thrive in well oxygenated environments (Mackensen et al., 1995) and the porosity in epifaunal *Cibicides* spp. and *Planulina* spp. is significantly negatively correlated to the O₂ concentrations in the bottom water (Rathburn et al., 2018; Glock et al., 2022). If O₂ is too depleted, these foraminifers increase their porosity to optimize the O₂ uptake. Furthermore, the mechanism of biomineralisation in foraminifera can preserve the chemical signature of ambient seawater in their test calcite. These species precipitate their test calcite directly from vacuolized seawater (Erez, 2003; de Nooijer et al., 2014; Toyofuku et al., 2017)) and thus the chemical composition of the test calcite reflects the chemical composition of the surrounding water in their habitats. Different element/Ca ratios are used as proxy for various parameters. Over the past decades several redox sensitive element/Ca ratios in foraminiferal calcite were identified as potential O₂ proxies, where Mn/Ca (Reichart et al., 2003; Barras et al., 2018; Brinkmann et al., 2021) and I/Ca (e.g. Zhou et al., 2014, 2022; Lu et al., 2016; Glock et al., 2019d; Winkelbauer et al., 2021; Cook et al., 2022) are amongst the most prominent examples. The offset of the stable carbon isotope fractionation ($\delta^{13}\text{C}$) between the tests of epifaunal and deep infaunal benthic foraminifera can also be used as a quantitative [O₂]_{BW} proxy (e.g. McCorkle and Emerson, 1988; Schmiedl and Mackensen, 2006; Hoogakker et al., 2014, 2018). Finally, species compositions of benthic foraminifera assemblages are used to reconstruct past environmental conditions. Kaiho et al. (1994) developed the first benthic foraminifera O₂ index (BFOI). Further development of this index is still going on with recent developments by Tetard et al., 2021 and Kranner et al., 2022.”

4. Minor points:

Reviewer: The title: I think that it is somewhat overdone: I don't understand the plural form of the first words, and I would say that a review is always a synthesis. I would recommend something like : “Foraminifera from anaerobic environments - survival strategies, biogeochemistry and ecology – an overview” .

Reply: A similar recommendation has been given by anonymous reviewer #2. To be honest, I agree with these statements and did not have “Reviews and syntheses” in my original title. Though, after submission to Biogeosciences as a review paper, I had the request by the editorial office to change my title accordingly. “Reviews and syntheses” is mandatory in the title of review papers that are submitted to Biogeosciences.

Reviewer: The cartoons presented in figures 1 and 6: these drawings are very nice (although somewhat simplistic), would be perfect in a text for a larger public, but are in my opinion not suitable for a scientific review paper.

Reply: I disagree in this point and actually corresponded with some other colleagues about exactly this point before submitting the paper. A review paper is often a starting point for either early career scientists or scientists that have to become acquainted with a new topic in their field. For both groups it is much easier to memorize context by looking at figures that are easy to follow and not too sterile. There are enough original papers out there that show SEM images of foraminifera, which are surely aesthetic but can also be very sterile. Nevertheless, I tried to keep the “cartoons” scientifically

correct. If the reviewers find anything in the figures misleading or plain wrong: Please let me know and I correct everything accordingly.

Reviewer: Tables 2 and 3: these two tables are really the heart of this review paper. First, it is essential that the authors make it very clear that these tables are exhaustive, that they contain ALL published info available today. For me this became only progressively clear when reading the text. Next, unlike table 3, which is perfect, table 2 is a mess, all taxa are mixed without any visible order. Like for table 3, the taxa should be presented in alphabetical order. Finally, the signs used to indicate the different studies from which the data are taken are certainly artistic, but also unreadable. My mind is totally unfit to memorise such symbols, and I think it will be the same with many of our colleagues.

Reply: In table 2 the taxa were already in alphabetical order but they were not in table 1. I changed this and the taxa are sorted in alphabetical order in table 1, too. In addition, I substituted the cryptic signs that indicate the references with superscripted letters in brackets behind the species names. Every reference got its own letter, which has been kept in all the different tables. For example: Piña-Ochoa et al., 2010b is now indicated as “^(a)” in all the tables.

Reviewer: On several places the author is going too quickly, simply backs up a statement with a reference, but doesn't tell on what evidence the statement is based. Some examples:

Lines 118-119: “It is noteworthy that denitrifying foraminifera from the Peruvian OMZ show a metabolic preference of NO₃⁻ over O₂ as an electron acceptor (Glock et al., 2019c).”

Reply: This part has been extended for clarification:

“It is noteworthy that denitrifying foraminifera from the Peruvian OMZ show a metabolic preference of NO₃⁻ over O₂ as an electron acceptor (Glock et al., 2019c). These foraminifera show an increasing cell volume with increasing ambient NO₃⁻ and decreasing O₂ concentrations. Similar observations have been made at the Californian Borderlands, where some benthic foraminifera increase their cell volume with decreasing ambient O₂ concentrations (Keating-Bitonti and Payne, 2017). Additional evidence for the metabolic NO₃⁻ preference came from comparing denitrification and O₂ respiration rates and scaling them to their cell volume (Glock et al., 2019c). The scaling is lower for O₂ respiration than for denitrification, indicating that the NO₃⁻ metabolism during denitrification is more efficient than the O₂ metabolism during aerobic respiration in foraminifera from the Peruvian OMZ. This might explain, why some infaunal denitrifying foraminifera follow the oxycline within sediments (Linke and Lutze, 1993; Duijnsteet et al., 2003).”

Reviewer: Lines 125-126: “Larger amounts of O₂ might supply this demand but also harm the cell.”

Reply: Added a bit text for clarification:

“Larger amounts of O₂ might supply this demand but also harm the cell. For example, O₂ can inhibit the growth of some obligate anaerobes poison enzymes that are important for their metabolism (Lu and Imlay, 2021). Also for aerobes O₂ can be harmful. “Hyperoxia”, an excess supply of O₂, leads to damaging effects by highly-reactive metabolic products of O₂ (free O₂ radicals) that inactivate enzymes in the cell, damage DNA and destroy lipid membranes (Frank and Massaro, 1980).”

Reviewer: Lines 134-135: “The fact that some foraminifera prefer NO₃ over O₂ as electron acceptor (Glock et al., 2019c)”.

Reply: See above.

Reviewer: Line 147: “since they are also able to respire O₂.”

Reply: Deleted this part of the sentence and added the following two sentences for clarification:

“They cannot be accounted as obligate anaerobes, though, since they can withstand periods of oxygenation. Many experiments show that denitrifying foraminifera can switch to O₂ respiration, if they are exposed to O₂ (i.e. Piña-Ochoa et al., 2010b).”

Reviewer: In none of these cases the author explains on what evidence these statements are based. Many similar examples are present in the text.

In all these cases, I would like that the author explains what evidence these important conclusions are based on. Since this is a review paper, the author should not oblige the reader to find such important information in another paper.

Reply: For all examples that have been addressed by the reviewer I added some sentences and references for further clarification.

Reviewer: Lines 116-117: I feel that there is a slight contradiction here. On lines 92-94 the author indicates that foraminifera can denitrify without bacterial symbionts, whereas from lines 110-117 I understand that complete denitrification is not possible without bacterial symbionts.

Reply: That’s again a valid point. Bernhard et al. (2012b) did not measure N₂ production after the antibiotic treatment but nitrate consumption. This is not a proof for complete denitrification but a strong evidence, since the rate was similar as in the species that have been shown to denitrify. To discuss this controversy, I added the following text:

“Recent metagenomics and transcriptomics results of denitrifying foraminifera indicate that bacterial symbionts might perform the missing steps in the foraminiferal denitrification pathway or that they at least partly contribute to the amount of NO₃⁻ that is denitrified within foraminiferal cells (Woehle & Roy et al., 2022). This seems contradictory to the results by Bernhard et al. (2012b) who showed that *B. argentea* consumed its intracellular NO₃⁻ storage (likely for denitrification) even after the antibiotics treatment. Gomaa et al. (2021) confirmed that *B. argentea* also lacks the first and last denitrification step in its transcriptome, although it lacks intracellular bacterial symbionts (Bernhard et al., 2012b). Future studies might decipher, if indeed bacteria are responsible for the missing denitrification step and be immune to such antibiotic treatment, if an oxygenic nitric oxide dismutase skips the last denitrification step as discussed by Woehle & Roy et al. (2018) and/or if foraminifera have unknown enzymes that catalyze the missing steps as suggested by Gomaa et al. (2021).”

Reviewer: Lines 207-208: “*it is likely that dormancy is a common survival strategy under anoxia for foraminiferal species that don’t have an anaerobic metabolism*”. I agree that dormancy is a logical alternative in case of absence of anaerobic metabolism, like in the various species of the *A. tepida* morphogroup. However, on line 182, as examples of dormancy, the author mentions *Bulimina marginata*, *Stainforthia fusiformis* and *Adercotryma glomerata*. The first two species have been shown to concentrate intracellular nitrate, and *Stainforthia* sp. has been shown to be able to denitrify. This would mean that we have also indications of dormancy in species which can denitrify. What makes the addition “*that don’t have an anaerobic metabolism*” in the line cited above, incorrect, or at least incomplete. The author has to clarify this!

Reply: This is a very good point, since this basically provides solid evidence that even denitrifying foraminifera can get dormant under unfavorable conditions. I rewrote this part as follows:

“Considering all these studies, it is likely that dormancy is a common survival strategy for foraminiferal species that either get exhausted of suitable electron acceptors (i.e. O₂ or NO₃⁻) or are exposed to periods of extreme environmental conditions. Since there is evidence for dormancy in both *S. fusiformis* and *B. marginata* (Bernhard and Alve, 1996), it is likely that even denitrifying species can get dormant under unfavorable conditions. Another *Stainforthia* sp. has been shown to denitrify and *B. marginata* stores NO₃⁻ in some environments (Piña-Ochoa et al., 2010b).”

Reviewer: Lines 225-227: “Intertidal foraminifera are often exposed to hypoxic or even anoxic conditions, when water stagnates during low tide or if they are transported to deeper anoxic sediment layers by bioturbation (Rybarczyk et al., 1996; Cesbron et al., 2017)”. These lines suggest that the author is not very familiar with intertidal environments. Things are much worse: on most intertidal mudflats, oxygen penetration is less than 1 mm, so that all forams are confronted with anoxia.

Reply: I added the following sentence to clarify, that intertidal foraminifera are often exposed to anoxia, even within the first cm of the sediment column: “Oxygen penetration depths in tidal flats can vary between a few mm during low tide to several cm during high tide (Jansen et al., 2009). Thus, intertidal foraminifera are often exposed to anoxia, even within the first cm of the sediment column.”

Reviewer: Lines 211-231: It should perhaps be useful to explain here that *Haynesina germanica* is very often found together with taxa of the *Ammonia tepida* morphogroup (*Ammonia aberdoveyensis* or *Ammonia confertitesta*), taxa which don’t have the ability to keep the ingested chloroplasts active.

Reply: The following sentence has been added to this part: “*H. germanica* often shares the habitat with species from the *Ammonia tepida* morphogroup (*Ammonia aberdoveyensis* or *Ammonia confertitesta* according to Hayward et al., 2021) which also tend ingest chloroplasts but these chloroplasts do not show any photosynthetic activity anymore (Jauffrais et al., 2016).”

Reviewer: Lines 308-310: “It is remarkable that there is so much evidence for phagotrophy on or by benthic foraminifera under anaerobic conditions and future studies might shed more light on predator prey interactions of benthic foraminifera in O₂ depleted environments.” I think this is very much exaggerated. As far as I can see, evidence for foraminiferal phagotrophy under anaerobic conditions is very scarce. It seems to be limited to (rather indirect) evidence of Orsi et al. (2020).

Reply: This chapter will get an extended overhaul according to the review by Andrew Gooday. It will briefly all kinds of trophic strategies of benthic foraminifera, summarize what is known about the forams from O₂ depleted environments and show that predation is more an exception, but possible.

Reviewer: As a final remark, although I appreciated the review, and found it very useful, I also think it emphasizes what we (think to) know, but doesn’t talk too much about the things we don’t know (yet). It would be good if the author could from time to time indicate some unsolved resolved questions, and, if possible, research strategies to answer these questions.

Reply: In the revised manuscript I will address some unsolved questions in several parts of the paper. Some of these statements are already mentioned above in my responses to the reviewer’s previous points of revision. Here are some examples of such sentences which I added to the revised MS:

“Future perspectives on understanding the biology of intermediate infauna might include studying the transcriptome to decipher other anaerobe metabolic pathways and testing the denitrification capacity after incubation in NO₃⁻-free and NO₃⁻-containing seawater.”

“Eventually, studies on the transcriptome of non-denitrifying species from infaunal environments might be able to show, if some of these species can switch an alternative anaerobe metabolism under exposure to anoxia.”

“Hopefully, measurements of metabolic rates, intracellular nutrient content and enzymatic activity might bring further evidence in the future, if at least some epifaunal species can switch to an anaerobe metabolism, when O₂ is too depleted.”

“Future studies might decipher, if indeed bacteria are responsible for the missing denitrification step and be immune to such antibiotic treatment, if an oxygenic nitric oxide dismutase skips the last denitrification step as discussed by Woehle & Roy et al. (2018) and/or if foraminifera have unknown enzymes that catalyze the missing steps as suggested by Gomaa et al. (2021).”

“In general, future metabarcoding studies to identify food sources of deep infauna or foraminifera that inhabit anoxia might shed more light on trophic strategies in O₂ depleted environments.”