

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 Andy Gooday.

Reviewer: This manuscript gives a very useful review of biology of foraminifera that live where oxygen is absent or scarce. I found the section on survival strategies(1.3), together with the data summarized in Tables 1-3 and the figures, very interesting and informative. Section 1.5 on the role of foraminifera in nutrient cycling and biogeochemistry is also useful (although see the comment below). However, sections 1.4 and 1.6 need some thought. Section 1.4 is headed 'ecology' but that's misleading. It's actually a very brief and rather confusing treatment of diets/feeding. The final section about palaeoceanography is rather superficial and somewhat redundant, since a more detailed review is on the way.

Reply: Thanks a lot for the detailed, constructive feedback to this manuscript. The paleoceanography section has been deleted and condensed to a short paragraph in the introduction according to the feedback of another reviewer (see response to Frans Jorissen). The “ecology” part has been carefully rewritten according to your suggestions. Below you can find a detailed point by point response to all points of revision.

Reviewer: Specific comments

Reviewer: line 79, Table 2. Since the paper is about foraminifera, you should mention somewhere in the text that gromiids are not foraminifera but a separate group of protists within the Rhizaria.

Reply: This is a good point and has also been addressed by another reviewer. I adapted the part in the text, where gromiids are mentioned for the first time accordingly:

“Other studies showed that bacterial endobionts likely perform denitrification in some allogromiid foraminifera and gromiid species (Bernhard et al., 2012a; Høgslund et al., 2017). Gromiida are a separate group of protists within the Rhizaria and closely related to foraminifera.”

Reviewer:

1. 8. Section 1.4 Ecology.

This is a brief and selective section about feeding, not a review of foraminiferal ecology. I would change the title to ‘Trophic interactions in oxygen-depleted environments’ or something similar. At the beginning, you might want to cite a few general reviews of feeding and diets in foraminifera, such as those of Lipps (1973, cited elsewhere) and Gooday et al. (1993, 2008). This would provide some context for feeding and diets in general. I have several other comments.

Reply: This is a very helpful and constructive feedback. I rewrote the whole section and took the new title as suggested. This section now synergizes much better with the rest of the manuscript, since the different feeding strategies can also be used to discuss the microhabitat preferences that have been discussed in the section about survival strategies. The text of the reworked section can be found below:

“Trophic interactions in O₂ depleted environments

In general, benthic foraminifera show a wide range of trophic strategies. Gooday et al. (2008) suggested that they can be separated according to their main trophic types: A: Selective herbivores, which include phytophagous species that consume only phytodetritus; B: Seasonal herbivores, which feed on fresh phytodetritus, when available and consume sedimentary organic matter at other times; C: Detrivores that non-selectively ingest sediment and consume the present degraded organic matter, bacteria and/or other organisms; D: Selective bacterivores, that consume only bacteria; and E: Suspension feeders, that either erect from the sediments or occur on elevated substrates. The latter two are not discussed in detail, since they mainly apply to abyssal species that inhabit more oxygenated environments. Nevertheless, some *Cibicides* and *Planulina* species, can also inhabit environments with relatively low O₂ concentrations (Erdem and Schönfeld, 2017; Rathburn et al., 2018; Hoogakker et al., 2018b; Glock et al., 2022) and at least some of these *Cibicides* species are certainly suspension feeders (Wollenburg et al., 2018, 2021). The trophic types that have been introduced above suggest that foraminifera mainly feed on a low trophic level and it has been suggested that they constitute a trophic link to higher levels in the food chain (Lipps and Valentine, 1970; Gooday et al., 1992; Nomaki et al., 2008).

There are a few studies that specifically focused on trophic interactions of foraminifera in environments where O₂ is scarce or absent. Early observations have been documented by Nomaki et al. (2006), who conducted an *in situ* feeding experiment at central Sagami Bay (1450 m), Japan, using ¹³C labeled algae and bacteria. Bottom water O₂ concentration at this location is usually less than 60 μM and O₂ penetration depth in the sediments are less than 5 mm (Glud et al., 2005). Nomaki et al. (2006) described three different feeding strategies by benthic foraminifera in this environment. Since the O₂ concentrations at central Sagami Bay are not extremely low, these observations likely apply to more oxygenated environments as well, especially for the shallow infaunal species. *Uvigerina akitaensis*, *Bolivina spissa* and *Bolivina pacifica* selectively ingest fresh phytodetritus and thus can be described as phytophagous species (selective herbivores). *Bulimina aculeata*, *Textularia kattegatensis* and *Globobulimina affinis* ingest fresh phytodetritus selectively but feed on sedimentary organic matter instead, when fresh phytodetritus is unavailable (seasonal herbivores). The species *Cyclammina cancellata* and *Chilostomella ovoidea* ingest sedimentary organic matter at random and can thus be described as detrivores. A later study confirmed these trophic types for most of the species at Sagami Bay by measuring the nitrogen isotope fractionation (δ¹⁵N) of their amino acids, which is commonly used to trace the trophic position of an organism in the food chain (Nomaki et al., 2015). Another feeding experiment at Sagami Bay by Nomaki et al. (2011) revealed that all of the analyzed benthic species assimilated carbon from ¹³C labeled glucose and thus can effectively utilize also dissolved organic carbon. The same study indicated that even the deep infaunal detrivores can be selective regarding their food source. Four of the five analyzed species, except *C. cancellata*, incorporated proportionally more ¹³C-labeled organic matter from the green algae *Dunaliella* sp. than from other carbon sources, while *C. cancellata* preferentially incorporated carbon from *Chlorella* sp. (Nomaki et al., 2005, 2006, 2011). Additional feeding experiments have been conducted at the Arabian Sea OMZ, where benthic foraminifera from locations with different bottom water O₂

concentrations have been supplied with ^{13}C and ^{15}N labeled algae (Enge et al., 2014, 2016). Nine out of nine analyzed species took up labeled phytodetritus during the four days experimental phase (Enge et al., 2014). The foraminifera took up the highest amount of labeled carbon in the OMZ center and the uptake decreased with distance from the OMZ (Enge et al., 2016). The authors hypothesized that either the foraminifera from the core OMZ have a higher carbon demand or that there was less food competition with macrofauna at the O_2 depleted locations. Similar to the studies by Nomaki et al. at Sagami Bay, the experiments by Enge et al. (2014 & 2016) showed a more or less selective ingestion at the Arabian Sea OMZ depending on the foraminiferal species. For example, several several *Uvigerina* species took up large amounts of carbon from the labeled algae and are thus either selective or seasonal herbivores, while *Globobulimina* spp. took up either no or only small amounts of the labeled carbon indicating their detritivore behavior (Enge et al., 2016). Further examples for selective herbivores, opportunistic omnivores, which include seasonal herbivores, and sediment detritivores are discussed by Gooday et al. (2008). It appears that many of the species that are considered to be selective herbivores (e.g. *B. spissa*, *U. akitaensis*, *Eponides pusillus* or *Cassidulina carinata*) are living epifaunal or shallow infaunal, although the selective herbivore *B. pacifica* can be also considered as intermediate infauna (Gooday et al., 2008). The seasonal herbivores (or opportunistic omnivores; e.g. *U. peregrina*, *G. affinis* or *G. pacifica*) can be found in a relatively wide range of microhabitats from shallow to deep infauna (Gooday et al., 2008). Species that are considered to be sediment deposit feeders (or detritivores, e.g. *C. ovoidea* or *M. barleeianum*) are usually found in the deeper habitats and belong to intermediate to deep infauna (Gooday et al., 2008). This indicates that the selective herbivores must live closer to the source of fresh food supply, while the less selective species can also feed on degraded organic matter or bacteria deeper in the sediments. Thus, the specific trophic type is another control on the microhabitat of benthic foraminifera in addition to the availability of O_2 , NO_3^- and the metabolic adaptations discussed in section 2. Indeed, the coupled diagenetic and ecologic model of Jorissen et al. (2022) successfully uses different types of food particles as a controlling factor to simulate the microhabitats of benthic foraminifera.

Although benthic foraminifera feed mainly on detritus and minute organisms there is also (less common) evidence for carnivorous behavior when foraminifera prey on meiofauna (e.g. Lee, 1980; Bowser et al., 1986, 1992; Hallock and Talge, 1994). These observations have mainly been done on species that usually live in oxygenated environments. Dupuy et al. (2010) documented carnivorous behavior in a laboratory experiment also for the *Ammonia tepida* morphogroup (*A. aberdoveyensis* or *A. confertitesta* according to Hayward et al., 2021), which is not uncommon in anoxic layers of tidal mudflats. A study on the trophic behavior of intertidal foraminifera, using metabarcoding brought up evidence that *A. confertitesta* is actively preying on small eukaryotes (e.g. nematodes) even in their natural environment (Panagiotou-Chronopoulou et al., 2019). The intracellular eukaryotic community in *A. confertitesta* varies with sediment depth but even up to 10 cm depth the metabarcoding indicates freshly ingested eukaryotic prey in this species (Panagiotou-Chronopoulou et al., 2019). Still, the main eukaryotic prey of *A. confertitesta* appear to be diatoms (Panagiotou-Chronopoulou et al., 2019). Recently, new evidence came up indicating ingestion of nematodes by *Globobulimina auriculata* from the O_2 depleted Alsbäck Deep in Gullmar Fjord, Sweden (Glock et al., 2019a). The species *G. auriculata* denitrifies and lives under O_2 depleted conditions (Woehle & Roy et al., 2018). It is inconclusive, though, if the foraminifer preys on the nematode or vice versa but the nematodes have most likely been ingested in the natural O_2 depleted habitat (Glock et al., 2019a). Although predation is the main type of interaction in aerobic communities, it usually plays a much smaller role in anoxic communities (Fenchel and Finlay, 1995). This is related to the low growth yields associated

with the anaerobic metabolism, which results in very short food chains. Thus, the decrease in energy flow along the anaerobic food chains is higher than along the aerobic food chain (Fenchel and Finlay, 1995). The predatory isopod *Saduria entomon* for example strongly reduces its predatory activity under hypoxia in comparison to aerobic conditions (Sandberg, 1994) and the predator/prey biomass ratio has been shown to be 4 times lower in anoxic environments compared to oxic environments (Fenchel and Finlay, 1995). There is evidence that foraminifera from the Namibian shelf can perform phagocytosis (vacuolic ingestion of food particles) even under anoxic conditions, which usually requires bursts of energy (Orsi et al., 2020). This study provides further evidence that the Namibian foraminifera express enzymes for lysing digested prey cells inside food vacuoles after phagocytosis (schematic representations for phagocytosis and predation on meiofauna shown in fig. 6). The evidence for phagotrophy and predation on or by benthic foraminifera under O₂ depleted conditions, although it is rare, is thought-provoking and future studies might shed more light on predator-prey interactions of benthic foraminifera in O₂ depleted environments. 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.”

Reviewer: 1) The Sagami Bay habitat is not strongly hypoxic, at least in terms of bottom water, and the observations of Nomaki probably apply to more oxygenated settings as well, particularly for the shallow infaunal species (*Uvigerina akitaensis* and *Bolivina spissa*).

Reply: This is a valid point and I tried to clarify this in this part of the review by adding the following sentence:

“Since the O₂ concentrations at central Sagami Bay are not extremely low, these observations likely apply to more oxygenated environments as well, especially for the shallow infaunal species.”

Reviewer: 2) In lines 325-326, you say that predation (‘phagotrophy’) is the main type of interaction in aerobic communities. Is phagotrophy synonymous with predation? I thought it applied to any ingested particle, not necessarily prey?

Reply: Of course, the reviewer is totally right that phagotrophy is not synonymous with predation. This sentence was formulated in a very misleading way. I deleted the “phagotrophy” from the brackets in this sentence. In addition, to avoid further misunderstanding, I adapted the end of the paragraph accordingly:

“There is further evidence by Orsi et al. (2020) that foraminifera from the Namibian shelf can perform phagocytosis (vacuolic ingestion of food particles) even under anoxic conditions. They provide further evidence that the Namibian foraminifera express enzymes for lysing digested prey cells inside food vacuoles after phagocytosis (schematic representations for phagocytosis and predation on meiofauna shown in fig. 6).”

Reviewer: 3) The same sentence seems to imply that foraminifera are mainly predators, which to me gives the impression that they are carnivores (as discussed in lines 319-324). I don’t believe this is correct. It’s true that there is increasing evidence that some foraminifera eat metazoans or other foraminifera, at least sometimes (e.g., review of Culver and Buzas, 2003), but in general, most forams seem to feed most of the time at a low trophic level on algae such as diatoms, bacteria, and decaying organic material, and form a link to higher trophic levels (Gooday et al., 1993; Nomaki et al., 2008). By predation you seem to mean consumption of mainly algae, bacteria, and sediment/degraded material (as described by

Nomaki et al., 2005), which I would call herbivory, bacterivory and deposit feeding. Also, lines 325-333 are apparently about benthic communities generally, not specifically about forams, but the meaning is not clear and may give the wrong impression. I found this whole paragraph rather confusing.

Reply: As stated above, the whole section has been completely reworked. It should be clear now, that foraminifera aren't mainly predators but that some species can show predatory behavior (text changes see above).

Reviewer: 4) What about dissolved organic matter (DOM)? This may also be important, including in Sagami Bay (Nomaki et al., 2011).

Reply: The possible utilization of DOM is now discussed in the revised MS:

“Another feeding experiment at Sagami Bay by Nomaki et al. (2011) revealed that all of the analyzed benthic species assimilated carbon from ¹³C labeled glucose and thus can effectively utilize also dissolved organic carbon.”

Reviewer: Culver S J, Buzas MA (2003). Predation on and by foraminifera. In *Predator-Prey Interactions in the Fossil Record*, ed. Patricia H. Kelley, Michael Kowalewski & Thor A. Hansen Kluwer Academic/Plenum Publishers, New York; pp. 7-32.

Gooday, AJ, Levin LA, Linke P, Heeger T. (1992b) The role of benthic foraminifera in deep-sea food webs and carbon cycling. In: Rowe GT and Pariente V (eds) *Deep-Sea Food Chains and the Global Carbon Cycle*. Kluwer Academic Publishers, p. 63-91.

Gooday, A.J., Nomaki, H. & H. Kitazato. 2008. Modern deep-sea benthic foraminifera: a brief review of their biodiversity and trophic diversity. In: Austin, W. E. N. & James, R. H. (eds) *Biogeochemical Controls on Palaeoceanographic Environmental Proxies*. Geological Society, London, Special Publications, 303, 97–119. DOI: 10.1144/SP303.8 0305-8719/08/

Nomaki, H., Ogawa, N.O., Ohkouchi, N., Suga, H., Toyofuku, T., Shimanaga, M., Nakatsuka, T., Kitazato, H., 2008. Benthic foraminifera as trophic links between phytodetritus and benthic metazoans: carbon and nitrogen isotopic evidence. *Mar. Ecol. Prog. Ser.* 357: 153–164, 2008

Nomaki, H., Ogawa, N.O., Takano, Y., Suga, H., Ohkouchi, N., Kitazato, H., 2011. Differing utilization of glucose and algal particulate matter by deep-sea benthic organisms of Sagami Bay, Japan. *Mar. Ecol. Prog. Ser.* 431, 11–24.

Reviewer: Section 1.5 Lines 376-379. Are the pristine shells live and those filled with phosphorite dead? Or are they dead in both cases? If the shells are dead, it might suggest that the phosphorite was deposited by some inorganic process. I thought that modern phosphorites in anoxic sediments were precipitated from interstitial porewater (e.g., Kolodny, 1981, Phosphorites. In: *The Sea v. 7, The Oceanic Lithosphere*). Please explain further or delete.

Reply: This section might indeed have been a bit too short and some important information was missing. There have been several studies that showed that the large intracellular polyphosphate enrichments in sulfur bacteria can facilitate phosphorite formation at the upper boundary of the Peruvian OMZ that is rich in bacterial mats and phosphorite deposits. The phosphorite deposits at the lower boundary of the Peruvian OMZ are different, because these

bacterial mats are usually not present and the phosphorite grains have a similar size and shape of foraminifera. These phosphorite grains are also abundant in the surface fraction of the sediments. In the Peruvian OMZ, living foraminifera abundances are very high. The sediments are thus a mixture of living forams, phosphorite grains with a coarse shape and size of a foram and every intermediate step in between. It is likely that their high intracellular phosphate storage, together with the calcium storage to precipitate their tests results in a supersaturated apatite microenvironment within their shells and initiates apatite formation. This has been also suggested for other organisms before. All this is discussed in detail in my 2020 GCA paper (“A hidden sedimentary phosphate pool inside benthic foraminifera from the Peruvian upwelling region might nucleate phosphogenesis”). To address these issues and avoid further misunderstandings, I extended the text in this section:

“In addition, there is evidence that the intracellular phosphate storage in foraminifera facilitates phosphogenesis in some environments, similar to the intracellular polyphosphate enrichments in some sulfur bacteria (Schulz and Schulz, 2005). The release of phosphate after breakdown of these polyphosphates to harvest energy in times of electron acceptor depletion results in apatite supersaturation and initiates phosphogenesis (Schulz and Schulz, 2005). Sediments at the lower boundary of the Peruvian OMZ contain many small phosphorite grains with similar size and shape of foraminifera (Manheim et al., 1975; Glock et al., 2020). The sand fraction of the surface sediments in this region is a mixture of pristine living foraminifer shells with dead tests that show a transition from shells that are filled with phosphorites until small phosphorite grains that only retain the size and coarse shape of a foraminifer. It is likely that a *post mortem* release of the intracellular phosphate storage results in a supersaturated microenvironment within the shells that initiates apatite formation (Glock et al., 2020) in a similar way as it has been suggested for other organisms (Kulakovskaya, 2014).”

Reviewer: Subsection 1.5.1, p. 9-10. You finish this subsection rather abruptly with equations for estimating cell biovolume, denitrification rates, and P content. You precede these equations by presenting a regression between intracellular NO₃⁻ and cell volume (Fig. 7). It would make more sense to present Fig. 7 after you have outlined the equations, since the regression depends on equation 1. This would give the subsection a more logical structure.

Reply: I understand that this subsection ends rather abruptly, especially since the following section is cut out in the revised version of the paper (see next comment below). Nevertheless, I thoroughly read through this section again and I think it is important to present figure 7 before the equations or at least before equation 1, which might be moved further down in the paper. Equation 1 is a result from the power regression that is shown in figure 7. Equations 2 & 3 are equations that are independent from this regression and have been published before in the cited papers. Since the reviewer is totally right with the abrupt ending, I added two more general sentences to the end, that adjust the whole section into a bit of a bigger context:

“With an increasing amount of data about metabolic rates and intracellular nutrient storage more accurate models and equations might become available in the future that describe the role of benthic foraminifera within marine biogeochemistry. Similar models and equations might be also very helpful for exploring the role of planktonic foraminifera in pelagic biogeochemistry.”

Reviewer: Section 1.6.3. Obviously, this is a very extensive topic that a short paragraph cannot do justice to. If you want to keep it, then there are reviews that you could cite (e.g., Gooday 2003, Jorissen et al. 2007). The OMZ review of Levin (2003), which deals with benthos as whole but includes foraminifera, is also relevant. Please note that it's not just the

taxonomic composition that reflects oxygen concentrations. Other assemblage attributes, such as diversity and dominance, are also strongly influenced. However, I would agree that the problem of disentangling the relative effects of organic matter and oxygen on the composition, diversity, dominance etc of foraminiferal assemblages in hypoxic settings is an important point to make.

Reply: According to the suggestions of another reviewer I completely cut the part about applications in paleoceanography in this paper and only provide a brief summary of all three subsections in the introduction of the paper. As mentioned in the original draft by my paper there is a larger community review paper in progress that focuses on the paleo-applications (Hoogakker et al., *in prep*). This paper in preparation will also provide more details regarding the ecology and paleoceanographic application of foraminiferal assemblages from O₂ depleted environments.

Gooday, A.J. (2003). Benthic foraminifera (Protista) as tools in deep-water palaeoceanography: a review of environmental influences on faunal characteristics. *Advances in Marine Biology*, **46**, 1-90.

Levin, L.A. (2003) Oxygen minimum zone benthos: adaptation and community response to hypoxia. *Oceanography and Marine Biology: An Annual Review* 41: 1-45

Jorissen, F., Fontanier, C., and Thomas, E. 2007. Paleoceanographical proxies based on deep-sea benthic foraminiferal assemblage characteristics. in: Hillaire-Marcel, C., and de Vernal, A.: *Proxies in Late Cenozoic Paleocanography*, Elsevier, Amsterdam, Boston, Heidelberg, London, New York, Oxford, Paris, San Diego, San Francisco, Singapore, Sydney, Tokyo, 263-325.

Editing suggestions

Some parts of the text are well written, but others are not and need careful editing, for which suggestions are made below.

Abstract and Introduction

Reviewer: Line 12. Delete ‘ongoing’

Reply: Done.

Reviewer:

1. ‘Since several species....’ (no need to repeat foraminifera)

Reply: Done.

Reviewer: 23, 24. Delete the repetitions of ‘even’.

Reply: Done.

Reviewer: 24-25. ‘Finally, since foraminifera can calcify under anaerobic conditions, I will briefly review proxies for O₂ based on their shell composition and assemblage composition.

Reply: The structure of the abstract has slightly been changed according to the changes in the manuscript.

Reviewer:

1. ‘More than a decade later.....published...’

Reply: Done.

Reviewer:

2. ‘Nevertheless, advances in methods to analyse the metabolic rates, intracellular nitrate storage and molecular genetics of foraminifera has changed our understanding of strategies such as anaerobic metabolism that help them to withstand O₂ depletion.’

Reply: Done.

Reviewer:

3. Are foraminifera really ‘microeukaryotes? This term would be more appropriate for eukaryotic microbes such as flagellates. Better to just call them ‘small eukaryotes’ or ‘meiofaunal eukaryotes’ (although not all are meiofaunal or particularly small).

Reply: “Microeukaryotes” has been deleted.

Reviewer:

4. ‘...2021). As a result, G. hexagonus has...’

Reply: Done.

Reviewer:

43-44. ‘Benthic foraminiferahave also been established ..’

Reply: Done.

Reviewer:

1. However, I will touch onbenthic foraminifer only briefly, since...’

Reply: Done.

Reviewer:

48-52. ‘The first part of this paper reviews recent advances in our understanding of the diverse strategies that foraminifera use to withstand O₂ depletion, focussing mainly on denitrification, dormancy and kleptoplasty. I also incorporate denitrification into the

conceptual TROX model of Jorissen et al. (1995), which explains the sediment microhabitats of benthic foraminifera in terms of an interplay.....’

Reply: Done.

Reviewer:

1. Next, I briefly discuss....’
2. ‘foraminifera in marine...’
3. You’ve already mentioned foraminifera as oxygen proxies in paleoceanography in lines 44-47

Reply: All done.

Reviewer:

Section 1.3

60-65. You’ve already explained some of this paragraph in the Introduction. I think you can limit it to the first sentence (but please change ‘examples see’ to ‘see examples’).

Reply: Done.

Reviewer:

1. ‘first evidence emerged...’
2. ‘can store substantial amounts of...’
3. ‘of the presence..’

Reply: All done.

Reviewer:

4. ‘storage capacity’

Reply: I am not completely sure, which part of this paragraph is meant, because the nitrate storage is mentioned several times.

Reviewer:

108-109. ‘This indicates that foraminifera use other enzymes to catalyze these steps, or they rely on...., or.....’ (you can only use ‘either...or’ for two alternatives, not three)

Reply: Done.

Reviewer:

1. Woehle & Roy et al, 2022. Is this the same as Woehle et al 2022?

Reply: Yes, it is. Both papers Woehle & Roy et al. 2018 & 2022 were papers with doubled first authorships. I wanted to do the second first author justice, because otherwise, mainly the

first name will be shown as citation in other papers. Unfortunately, this was not uniform along my manuscript, due to the use of a reference manager. I corrected this and now use “Woehle & Roy” all along the manuscript.

Reviewer:

2. Replace second ‘likely’ with ‘possibly’ or ‘probably’.
3. Better to delete ‘Furthermore’ and start sentence with ‘The’.

Reply: All done.

Reviewer:

149, 154. ‘epifaunal’ (not ‘Epifaunal’ – you are not starting a new sentence).

168 ‘its shallow infaunal...’ (not ‘their’)

1. ‘certain circumstances’

Reply: All done.

Reviewer:

182-186. These last two sentences can be simplified – ‘Research to measure denitrification rates in different benthic foraminiferal species continues. This will add to the scarce available data and contribute to estimates of the role of foraminifera in’

Reply: Done.

Reviewer:

195-196. ‘some studies suggested that some foraminifera may become dormant when ...’

1. ‘putative anoxic habitats
2. ‘had’ (not ‘has’)
3. Delete ‘own’
4. ‘fended’

Reply: All done.

Reviewer:

247-248. Insert commas after brackets.’

1. No comma after ‘test’
2. Delete ‘rest’.

Reply: All done.

Reviewer:

277-281. You could condense these two sentences as follows – ‘Several recent publications based on advances in molecular biological methods.....have revealed some other metabolic adaptations of foraminifera that thrive under.....’

281-283. Again, this could be simplified - ‘In *N. stella* and *B. argentea*, Goma et al. (2021) found evidence for the expression of proteins, including pyruvate.....hydrogenase, that are characteristic of anaerobic metabolism. The PFOR sequences.....’

1. ‘already came from a study by Nardelli...’

Reply: All done.

Reviewer:

297-299. This sentence more or less repeats the previous one in lines 295-296. I suggest you run together the next two sentences to say – ‘These processes (calcification and the ingestion of prey cells by phagocytosis) require bursts of high energy, which the authors suggest is generated by dephosphorylation of....to generate ATP.’

1. ‘metatranscriptonomes’ (spelling)

303-304. ‘might serve as a’

Reply: All done.

Reviewer:

305-307. ‘Orsi also found evidence for an anaerobic metabolism....’. I may not be understanding correctly, but isn’t anaerobic metabolism what you describe on line 300? If so, perhaps you should run these two sentences together – ‘Orsi et al. (2021) also found evidence that foraminifera on the Namibian shelf metabolize hydrolyzed.....’

Reply: Not really. The previous part describes the dephosphorylation of creatine phosphate, which is more like a “lifeline” for the forams, when conditions are really bad. They use it as a reservoir to generate ATP, when electron acceptors are depleted. The anaerobic metabolism, described at the end of the paragraph describes the “typical” anaerobic metabolism that is based on fermentation and is happening all the time and not only, when the conditions are “bad”.

Reviewer:

1. ‘conducted’ (not ‘made’)

Reply: Done.

Section 1.4.

Please see comments above.

Reviewer:

Section 1.5

339-342. These two opening sentences more or less repeat lines 74-76. I would start this section instead with the third sentence ('Pina-Ochoa et al. (2020b) pointed out the possible importance of...').

1. 'due partly to their high abundances...'
2. 'Globobuliminids' is not a genus. If you want to use italics, then this should be 'Some species of *Globobulimina*...'
3. Add comma after 'foraminifera'.

Reply: All done.

Reviewer:

363-365. These equations are the subject of subsection 1.5.1, so perhaps they should not be mentioned here. Also, '.....to calculate estimated denitrification rates,....'

1. 'data' (not 'Data').

Reply: All done.

Reviewer:

372-373. 'Hypotheses include...' (Delete 'about the use of the stored phosphate' – you've said this already)

1. 'contain' (not 'bear').

Reply: All done.

Reviewer:

389-390. '...are typically shallow infaunal and ...'

394-395. This could be reworded for clarity, e.g. – 'Given this variation in NO₃- storage capability, the reliability of estimates for the foraminiferal contribution to NO₃- budgets depends crucially on the availability of data. The more data there is, the better'

1. '...including the contribution of species with....'

404, 412. Maybe remove the comma at the beginning of the line. It looks odd.

Reply: All done.

Reviewer:

Section 1.6

1. 'This section (not chapter) briefly discusses morphological and geochemical aspects of benthic foraminiferal tests, and foraminiferal assemblage attributes, that can be used..... A more extensive review will summarize...'
2. 'that live in deep infaunal microhabitats below....' Also 'spp., for example, are....' (spp. is not in italics).

434-5. 'Though, Globobuliminidae.....' Delete this sentence. You already said this a few lines earlier. Also please note that although species of *Globobulimina* (and *Praeglobobulimina*) are large and are not flattened, none of them are actually spherical. I would say that members of this genus tend to have an ovate or globular shape, sometimes with a pointed proximal end.

Reply: According to the remarks by another reviewer (Frans Jorissen) the whole section about paleoceanographic applications has been deleted and there is only a brief summary of this section left in the introduction (see response to review by Frans Jorissen).

Reviewer:

1. 'is the porosity, including pore size and pore density, of foraminiferal tests.'
2. '...characteristics began in the 1950s...'
3. '...the first attempts were made to use the test porosity of PLANKTONIC foraminifera...'
4. 'Here, I focus on the...'

451-452. '...environments withand fossil specimens from periods of..'

1. Delete comma after 'known'
2. 'were identified as potential...'

481-482. 'This offset depends on the vertical separation of the species within the sediment column...'

Reply: According to the remarks by another reviewer (Frans Jorissen) the whole section about paleoceanographic applications has been deleted and there is only a brief summary of this section left in the introduction (see response to review by Frans Jorissen).

Reviewer: Table 2 caption. Foraminifera and gromiids (or *Gromia*, but not 'gromiida') are mentioned separately, which is correct, but in the table itself it might be clearer to put them in a separate section, just to be clear.

Reply: Done.

Reviewer:

Table 3 caption line 1. 'foraminifera'

Fig. 4 caption line 5. Delete 'supply'.

Fig. 4 caption line 8. '..when they have to, although if the food supply is too low, they ...'

Reply: All done.

Reviewer:

Fig. 6 caption, bottom line. 'Foraminifera in hypoxic'

Reply: I am not really sure, which part you mean because this phrase does not really fit into the bottom line of the Fig. 6 caption.