

Comments on:

Reviews and syntheses: Review of proxies for low-oxygen paleoceanographic reconstructions Hoogakker et al. (50+ authors)
by Ellen Thomas

Overall, this manuscript is a great resource for the community working on (paleo)oxygenation of the oceans, with the large numbers of authors clearly contributing to the highly various (and complex- aspects of oxygenation proxies, ranging from sedimentology to chemistry to biology. I think this review is a great service to the broader community, but despite my overall appreciation I have suggestions/recommendations. In view of the length and breadth of the paper (with only some topics within my expertise) I will not comment on the text in detail, but highlight some sections which from my personal point of view could be improved. In addition, I think that the paper would become easier to follow (important for such a complex and long paper) with reorganization of some of the sections. In addition, and maybe hard to prevent in a very long and multi-authored paper, in my opinion there are - specifically where foraminifera are discussed (or maybe also in the biomarker section) - basically too many sections in which overlapping information is discussed (morphology, pores, wall thickness, shape, carbon isotopes). In my opinion there should be an introduction section for foraminifera in which shared information can be presented just once (e.g., denitrification is now discussed in various sections) before the proxies are debated, and the later sections should be simplified through reintegration.

Response: we are grateful for the in depth review of our manuscript and the useful comments proposed by Professor Thomas. We are happy to adopt the proposed changes in terms of reorganizing some of the sections where possible, and adding an introduction section for foraminifera where information is shared once before the proxies are debated, and simplify the denitrification sections.

List of proxies: one fairly new proxy for OMZs are biogenic magnetic particles (e.g., Chang, Hoogakker et al., 2023, Indian Ocean glacial deoxygenation and respired carbon accumulation during mid-late Quaternary ice ages, NatureComm 14, 4841. Might be nice to mention at least shortly as another potential/beginning proxy?

Response: agreed, we will add this to our Concluding summary statement and future direction section.

Line 94: OMZs and/or ODZs? ODZs used in e.g., lines 866, 987, 1083, 1127, 1249, 1301, 1374, 1515 and more; please define both acronyms. Are they used for the same phenomenon or are they used specifically to distinguish between oxygen **minimum** and oxygen **deficient** zones? In 1521 ODZ seems to be defined as Oxygen Minimum Zone (OMZ)?

Response: this is discussed in Figure 1. We will refer back to this figure when mentioning the acronyms, and check what nomenclature was used where (thanks for carefully checking).

Lines 185- 209: Figure 1 (and 3): This is a good figure to include to the introduction to the paper. However, I think it misses some important information on 2 topics, relevant especially for 'older' literature (including papers cited later on in the ms), despite the text above this figure, explaining that there has been inconsistent and confusing nomenclature.

Topic 1: In marine science, oxygen levels used to be expressed in ml/L (however unfortunate), and terms for different levels of oxygenation such as 'dysoxic' have been defined in ml/L units. Even in recent publications we see data in ml/L, e.g., oxygenation as derived from ichnofossil assemblages (e.g., Rodriguez-Tovar, 2022; 2021-Earth Sci Rev 216, 103579: oxic - 8-2 ml/L; dysoxic 2-0.2 ml/L; suboxic 0.2->0 ml/L; anoxic 0 ml/L, i.e. as in Tyson & Pearson, 1991, see figure below).

Topic 2: Authors (e.g., chemists and biologists) have used (very) different definitions of terminology (see figure below, from Jorissen et al. 2007). Quite a few papers cited in this manuscript (e.g. Kaiho, 1994; Bernhard & Gupta, 1999) used different definitions of, for instance, 'dysoxic', and a commonly used term (suboxic) is not mentioned.

True, the caption to Figure 1 says it provides the values for 'Anoxic', 'Dysoxic/hypoxic' and 'Oxic' as '**most often** associated with specific terms of oxygen concentration', but how often we see which term depends upon the date of publication and the field of expertise, and it is easy to find examples of a different use of terms. As is, the text suggests to the unwary reader by its use of the terms placed along the vertical black bar of varying thickness (what does the thickness indicate?) that the sequence 'oxic-dysoxic/hypoxic-anoxic' provides the terms generally used, and that these terms mean the same in most cited papers. But the terms do not mean the same in various papers cited in section 6.6.2 (see figure below). and the excellent review by Glock 2023 (one of the co-authors of this ms) uses 'anoxia: $O_2 < 0\mu M$; suboxic conditions: $O_2 \sim 1-10 \mu M$; hypoxia $O_2 < 62.5 \mu M$, which is not as shown in fig. 1.

Therefore I think that this manuscript aiming at a broad audience should make its audience familiar with the fact that there is confusion in terminology, and should provide a definition of terms (with reference to authors who used these terms), explaining that different definitions are used in the literature. An approximate scale for ml/L (at standard conditions, not calibrated for temperature/pressure, as e.g. shown in the values in line 2004) should be added to figure 1 (maybe also 3).

	Tyson and Pearson, 1991	Bernhard and Sen Gupta, 1999	Kaiho, 1994	
8 ml/l	Oxic	Oxic	High oxic	3 ml/l
2 ml/l			Low oxic	
	Dysoxic		1 ml/l	Suboxic
0.2 ml/l	Suboxic	Dysoxic	Dysoxic	0.3 ml/l
0 ml/l	Anoxic	Microoxic	Anoxic	0.1 ml/l
0 ml/l		Anoxic/Postoxic		

Response: Oxygen boundaries differ between different authors and disciplines, and trying to have a consistent scheme across all the different proxies is too challenging. This is one of the reasons that we used fading colors to represent uncertain thresholds. It would be ok to include other terminology used (e.g. suboxic) in the revised manuscripts, but we'd need to point out the issues that are associated with this term, geochemists are especially weary about using it. The varying thickness for the black line (next to ODZ) doesn't mean anything, it is just a way of indicating the zones in relation to other terminology. We can modify the figure and caption to make the terminology and uncertain thresholds clearer. In addition we can add some numbers and definitions in

[this sections 3. Also see comment by reviewer 3.](#)

After reading much of the text, I also wonder about the organization: would it not be better to have the discussion on oxygenation in the water column somewhere here, early on in the discussion? In my opinion that would make more sense, and then the concept of wanting to have planktic as well as benthic proxies can be placed upfront rather than very late in the paper. It could then also be mentioned here that benthic proxies work where the seafloor is within an ODZ/OMZ, but that we need planktic proxies to get an idea of the spatial extent of such zones. In addition, this discussion of the water column structure is highly relevant to the sections on Nitrogen-based proxies (6.4) and on Biomarkers (6.3), which now are placed before the section on water column structure (early part of 6.5). In my opinion this is rather important, since it could make the paper much easier to follow for people from outside the direct oxygenation-community.

[Response: excellent idea which we will follow up on for the revised manuscript.](#)

Lines 215-220: the manuscript is said to be *'limited to proxies that can be applied through the Cenozoic'...* although we briefly touch upon some well-studied earlier examples, such as Cretaceous oceanic anoxic events (OAEs). I agree with these statements, but think that there should be more explanation, because the reasons for time limitation are not just age of sea floor/recovery by drilling projects, or average state of preservation. This manuscript deals extensively with proxies based on foraminifera, i.e., their test morphology or chemistry. By far the most diverse and abundant living group of Foraminifera are the Rotaliida, which differ in morphology (test growth) and mode of calcification - thus also trace metal incorporation - from other groups (e.g., Miliolida and Nodosariida; de Nooijer et al., 2023, 500 million years of foraminiferal calcification, Earth Sci Rev 243, 104484; and references therein). The Rotaliida mainly diversified (arguably during the Mid Mesozoic Revolution) somewhere between the start of the Albian (~113) through the Santonian (~84), though the rate of diversification is not well constrained (e.g., Tappan & Loeblich, 1988, Foraminiferal Evolution, Diversification, and Extinction, Journal of Paleontology, 62 (5), 695-714; Kaiho, 1994, Phylogeny of deep-sea calcareous trochospiral benthic foraminifera: evolution and diversification. Micropaleontology 44 (3), 291-311). In my opinion, the authors should mention that the proxies linked to foraminifera are limited through the evolutionary processes of benthic foraminifera and can be used from the latest part of the Cretaceous (~Campanian-Maastrichtian) on to Recent. For earlier times we may have problems in using an actualistic approach: benthic foraminifera across the Cretaceous OAEs were not necessarily analog to modern forms (e.g., bolivinids as we know them did not yet exist), thus potentially limiting proxy use.

[Response: we agree wholeheartedly with this suggestion and will add text reflecting this to the revised manuscript.](#)

Lines 239-on: SecEon 6.1: Sediments as Proxy Carriers.

6.1.1. Historical based sedimentary redox/bottom water oxygen reconstructions.

This section discusses laminations. Of course, absence of laminations is commonly due to a lack of bioturbation, and I would have liked to see a clear discussion of ichnofossils/bioturbation as tracers (quantitatively) of oxygen levels. There is a large

literature on this topic, as e.g. reviewed by Rodriguez-Tovar in 2021 (Ichnology of the Toarcian Oceanic Anoxic Event: An underestimated tool to assess palaeoenvironmental interpretations, Earth Sci Rev 216, 103579) and the cited Rodriguez-Tovar 2022. This topic is important not just for reconstruction of oxygen levels with a proxy that can be used back into deep time, but also for understanding oxygenation of sediment and its spatial heterogeneity, thus for the discussion in section 6.2.

Bioturbation is mentioned in the following section 6.1.2, but there the emphasis is on methodology (non-destructive), and ichnological reconstruction of oxygen levels has been done for many years before the availability of CT scanning (e.g. Francus, 2001, J Sed Res 71 (3), 501- 507; Nicolo et al., 2010, Paleoceanography 25, PA4210; Rodriguez-Tovar 2021). I thus think that a section on ichnofossils should be inserted in 6.1.1, or - alternatively- the authors could consider trace fossils as fossils and insert text in section 6.1.3.

As to CT scanning- see also Salas et al., 2022, J Petr Sci Engin 208, 109251.

[Response: thanks for this suggestion, we will add this to the text.](#)

Line 546: 6.2.3.2 typo - race rather than Trace

[Response: we will change that in the revised manuscript.](#)

Line 605-secEon 6.2.4: in my opinion this section is not optimally placed - it breaks up the chemical discussion by getting into Ba as a tracer for productivity (not directly relevant to oxygenation proxies), and the organic carbon supply is a confusing proxy for both chemical and biological oxygenation proxies. Might it not be better to have a separate section on organic matter supply / effects on oxygenation of bottom/pore waters maybe before starting to talk about geochemical proxies, i.e. after the introduction in section 6.1?

[Response: yes this is a good idea, and we will change this in the revised manuscript.](#)

Line 622: 6.2.5.4 - particulate shuttles; I wonder whether placement of this section is optimal. It refers back to the earlier section on trace element proxies, i.e. before the section on diagenesis i.e., directly after section 6.2.3.2?.

Response: We think it is fine where it is; and not sure that directly after section 6.2.3.2 would be a better place for it.

Line 782: 'Towards more quantitative oxygen proxies..' text is not unequivocal, i.e. does 'more' refer to quantitative (i.e. get truly quantitative rather than semiquantitative proxies (which is what I think is meant) or does 'more' refer to proxies? we need more proxies?

Response: this refers to transitioning a qualitative proxy to semi-quantitative or fully quantitative proxy. We will make sure the text is unequivocal.

Lines 896-889: factor b)- mention the words 'biological pump'? that is what is described here, right

Response: the processes we summarize under factor b) are more diverse and broader than the biological pump. For example, they also include the availability and composition of ballast material, lateral transport/advection, and heterotrophic remineralization during export through the water column. We will add this context to the sentence.

Lines 1377-1380: *'When foraminifera build their chambers, they form an organic sheet between calcite layers to facilitate the calcification process'* - First, this would be valid for rotaliid foraminifera, not miliolids (see e.g. de Nooijer et al., 2009, Foraminifera promote calcification by elevating their intracellular pH, PNAS 106, 15374-15378a0, or lagenids (de Nooijer et al., 2023). Then, rotaliid foraminifera first produce an organic layer - the primary organic sheet (in the shape of the chamber to be formed), then precipitate the calcite (or aragonite) on that organic layer (e.g., de Nooijer et al., 2009, 2014, Biomineralization in perforate foraminifera, Earth Sci Rev 135, 48-58). This text reads as if the forams put the organic layer between the calcite layers. Line 1379 *'are encased within the shells after calcification'* also reads a bit 'off' - they are 'encased DURING calcification, I would say. Oscar et al. 2016 missing from reference section.

Response: in our revised manuscript we will add those details and change the wording to better communicate that the calcite is precipitated onto the organic sheet rather than formed between calcite layers; thanks for spotting that.

Line 1401: ..'protective as in foraminifera tests' - in my opinion it is not necessarily generally accepted that foraminiferal tests are for 'protection'- against what?. Most organisms that eat forams take them up, test and all, indiscriminately (benthics by deposit feeders such as holothurians and Dentalium, plankton by suspension feeders).

Response: this is meant to be a reflection of the organic matter from the primary organic sheet being protected, not the foraminifera cytoplasm, and we will change this in the revised text.

Lines 1490-on:

The whole first part (through lines 1664) should, in my opinion, be given a different title, and placed elsewhere in the paper. It is a solid description of elemental behavior in the water column, without foraminifera being considered. Should this section not go to the beginning of the whole paper, i.e. BEFORE section 6.2.3? Maybe even directly after, or integrated within section 3? After all, this section is also relevant to the discussion of N proxies and the discussion of organic proxies earlier on.

Response: We prefer to keep this in section 6.2, and can include further references in the other sections.

Figure 8: once again, a very good explanatory figure. However, there is no vertical scale. Could we see at least a suggestion of what the depth range is of 'deep', 'intermediate' and 'shallow'? Is the latter used for shelf sites, the middle one for continental margin sites, or what? Are these indeed 'ODZ' = oxygen deficient zones? or could they be OMZ 'Oxygen minimum zones.?

Response: All ODZs are OMZs but not visa versa. The ODZ term comes from the nitrogen literature and tends to imply (sometimes explicitly defined as such, but not always) an OMZ where denitrification occurs. Agree that our usage should be better defined throughout and also that OMZ might be the better term here. Shelf= shallow, slope = intermediate, and abyssal plain = deep.

Line 1497: maybe mention that benthic proxies can be used over a large part of the Phanerozoic, planktic proxies only after the Jurassic/Cretaceous?

Response: we will add those constraints to the revised paper.

Line 1555 and on: I think that section **6.5 Foraminifera trace elements** might be better placed after section **6.6 Foraminifera assemblages**, since in that section foraminifera are generally described. **What I am missing**, before a discussion of trace element incorporation and vital effects, is a section broadly on **foraminiferal calcification**. We are now starting with planktic foram elemental incorporation without the reader being made aware of any knowledge of foraminiferal calcification processes, and of the fact that planktic forams have been evolutionarily derived from benthos many times, but only from the group Rotaliida, and that their calcification thus is limited to what we see in one group of benthos (e.g., Morard et al., 2022, Renewal of planktonic foraminifera diversity after the Cretaceous Paleogene mass extinction by benthic colonizers, Nature Comms 13, 7135). Reference to the broad overview in de Nooijer et al., 2023, 500 million years of foraminiferal calcification on Earth Sci Reviews 243, 104484 would be a good start to such a section (with many references in that paper). In my opinion an introduction on foraminiferal calcification is absolutely needed, e.g., before the text in line 1642-1675. The text in lines 1846-1858 could be incorporated in the section on calcification.

Response: we will add an introductory section about foraminifera with a short section about calcification.

In my opinion it would be better to re-organize the text on elemental/Ca values, so that all text is organized by element, rather than hopping from I/Ca to Mn/Ca to U/Ca several times.

Response: It is our preference to maintain an integrative discussion of the proxies. Each of the proxies have already been previously reviewed on their own in other places. The significance here is that we reviewed them together in a way that allowed us to compare and contrast. To some extent, these proxies have similarities that warrant mentioning them together. The paragraphs have a clear structure each time looking at I/Ca, Mn/Ca and then U/Ca, so that the "hopping" is systematic and the reader should not have difficulties to what the information useful for him/her. That said, we also interpret this feedback as indicating that some aspects of the current organization make the sections difficult to follow. In response, we will give the section a careful edit to ensure to improve readability and integration of the proxies into the same section.

Line 1567-1572: Winkelbauer et al., 2023 - but see comment on this paper, Lu et al., 2023, *Frontiers of Marine Sciences*, 10, 1095570.

Response (check with Dalton, Sha, Babette): we are not sure what is being referred to here. The comment by Lu et al. (2023) mainly reiterates what is being discussed in the Winkelbauer et al. (2023) manuscript. We could add this sentence "Lu et al., (2023) confirm that proxy data from plankton tows and sediment core top samples may not necessarily agree with each other because of the complexity of foraminiferal calcification and postdepositional overprints in marine surface sediments."

Line 1589: please see my notes at the end of the next section - the genus *Ammonia* is a very shallow water taxon (inner neritic - intertidal), has been recorded as living infaunally (see below), and it remains a question how relevant its biology is for deeper water taxa.

Response: we will add additional information reflecting this.

Line 1865-on: SecEon 6.6: Foraminifera Assemblages.

I greatly appreciate the work by many authors starting with Kaiho (1994, 1999) through Kranner et al 2022 to develop a foraminifera assemblage -based, quantitative proxy for oxygenation, but in my opinion this proxy (broadly, BFOI-based) needs more discussion. Authors including Buzas et al 1993 (A statistical evaluation of the microhabitats of living (stained) infaunal benthic foraminifera, Mar Micropal 20 (3-4), 311-320), Gooday (2003) and (Jorissen et al. 2007) - and more - discussed various problems/uncertainties with the BFOI (some of which are in my opinion not resolved in the EBFOI), but their arguments are not represented in this paper.

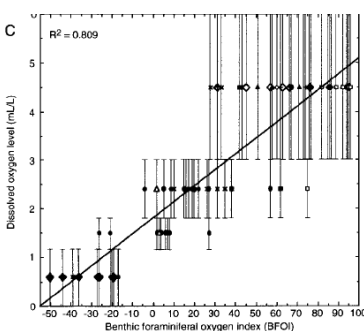
Response: we can add a comment that the EBFOI resolves some, but potentially not all uncertainties associated with the BFOI (and add some examples and references).

What problems can there be with this widely used (and modified/improved, e.g., Kranner et al., 2022) proxy? After all, numerous authors (since e.g., Smith 1964 and earlier) observed a correlation between 'morphotype' (size, thickness of wall, chamber arrangement - shape, porosity) and oxygenation levels, with species indicating lower oxygen levels more commonly living infaunally. Kaiho (1994, 1999, Effect of organic carbon flux and dissolved oxygen on the benthic foraminiferal oxygen index (BFOI), Mar Micropal 37, 67-76) defined the BFOI by assigning taxa to be indicators of oxic, suboxic or dysoxic conditions: '**Dysoxic** (0.1-0.3 mL/L), **Suboxic** (0.3-1.5 mL/L), and **Oxic** (>1.5 mL/L) indicators based on the basis of the relationship between specific morphologic characteristics (or species composition) and oxygen levels' (cited from Kaiho 1994), with dysoxic and suboxic species living deeper in the sediment than oxic indicators. In order to calculate the BFOI, we thus assign an indicator status to all (in Kaiho's case, all calcareous) species present in samples.

But how do we assign species to the D, S or O group? Lists of species indicating whether each is D, S or O usually do not always contain a reference with species names provided with a reference showing on which data the assignment is based. For living species, one can use direct observations (though these are limited for the deep sea), for extinct species we can use stable carbon isotope or trace element data. However, such direct observations are not available for all the ~ 2000+ living species of benthic foraminifera (Murray, 2007, Biodiversity of living benthic foraminifera: How many species are there?. Mar Micropal 64 [3-4], 163-176), let alone for extinct species. In practice, therefore, assignment for many taxa is based on **morphological similarity to species for which data are available**. However, the link between morphology and microhabitat - thus oxygenation - (epifaunal-shallow infaunal-deep infaunal) showed an accuracy of only 75% (Buzas et al., 1993). These authors (and others, e.g., Jorissen & Sen Gupta, 2003, Benthic foraminiferal microhabitats below the sediment-water interface, in 'Modern Foraminifera', 161-179) show evidence that there are few to none actual 'epifaunal taxa' in soft sediments - foraminifera cannot live on top of soft, sloppy sediment, except for these that live on objects sticking out above the sediment as reported for *C. wuellerstorfi*. However, even the widely used epifaunal 'oxic indicator' *C. wuellerstorfi* survives under low oxygen conditions (e.g., Venturelli et al., 2018, Frontiers Mar Sci 5; Rathburn et al., 2018). Then, 'small specimens' (<350 µm) of 'oxic indicators' are defined 'suboxic A indicators' (Kaiho, 1994, 1999), but how certain are we about

placing the boundary between 'large' and 'small' at 350 μm ? I thus think that the assignment of species to 'indicator groups is not that simple, and we do not know the errors involved. Therefore, what error bars should we consider in calculating a BFOI, especially at somewhat higher oxygenation levels (e.g., Kaiho's 'suboxic indicators A, B and C are not that clearly defined, see Kranner et al., 2022)? Kaiho 1999's figure 2C (see below) indicates error bars which are quite large at somewhat higher oxygenation levels (and that is where we see the differences with EBFOI, Kranner et al., 2022, making BFOI more semiquantitative than quantitative. This is even more so since we now have ample evidence (not available when Kaiho wrote the BFOI papers) that many species of benthic foraminifera can survive and flourish at very low oxygenation/no oxygen and many practice denitrification (broad literature cited in this ms and in Glock 2023).

What I want to argue is that one should consider that BFOI and similar proxies are empirical, i.e., we do not really know WHY (for instance) a large trochospiral foraminifer should indicate higher oxygenation levels than a small, flat biserial foraminifer: correlation is not causation. We do not really know what (if any) limitations a test form imposes: after all, both trochospiral and biserial tests are represented in planktic and benthic species. There are speculations as to volume/surface, but the fact remains that some large trochospiral foraminifera in some habitats have no problems with anoxia: **Ammonia species are large trochospiral species** (much used in studies of calcification and ecology) living in shallow coastal waters (neritic into intertidal), and they survive and even calcify under anoxic conditions (Nardelli et al., 2014, Biogeosciences 11, 4029-4038), and have been observed living infaunally down to 35 cm in the sediment (Moodley & Hess, 1992; Tolerance of infaunal benthic foraminifera for low and high oxygen conditions, Biol. Bull. 183, 94-98). Note that the remarks in line 2061 on circular foraminifera, and in lines 2170-2171 on large spirally arranged tests, and the discussion small/large foraminifera (section 6.7.2.2) thus are not universally valid, even in the present world. We should probably question more clearly (as for chemical proxies) under which specific conditions our biotic proxies work - in agreement to what the authors say in lines 1937-1940. I do **not** think, that the statement that '**All of these indices are considered valid (line 1936)**' is evidence based - how has that been tested? For me personally, Figure 13 is quite discouraging, if we want to consider



the 'assemblage proxies' as quantitative: the compared proxies agree as to where oxygenation values are higher or lower (i.e. qualitative agreement), but the actual values - plotted on a logarithmic scale! - show very large differences, with some plotting at around 20 for the present value - which should be around correct, but others at >100 micromolar for the same sample (hypoxic and oxic in figure 1); lower values for the same samples are around 2 micromolar for the BFA method (dysoxic to anoxic), around 70 for the BFOI method dysoxic to oxic). I would therefore say that the biotic proxies, like the chemical incorporation proxies, need a considerable amount of work. Possibly - but this is looking far into the future, probably, we might do better work in both biotic and chemical proxies if we were to gain actual understanding of the 'vital effect' and its genetic/metabolic base, nowadays pretty much a black box. Such papers as Ujie et al 2023 (Unique evolution of foraminiferal calcification to survive global changes, Sci Adv

9, eadd3584) point towards potential developments, and collaboration with biologists working at understanding calcification processes might also offer new insights (e.g., Davila-Hernandez et al., 2023, Directing polymorph specific carbonate formation with de novo protein templates, Nature Comm, 14, 8191).

In addition, I think that we should consider to what extent models defined for foraminifera living at below-shelf depth conditions are useable for intertidal-neritic dwellers. Possibly, trochospiral *Ammonia* differs from trochospiral *Cibicides* through its possession of an internal canal system, so we should look carefully at how we characterize taxa. These food-replete environments might not be well understood through the TROX model. This could be important, since shallow-water taxa are much easier kept in the lab, and we thus might wonder whether observations on such taxa are valid for their deep-sea relatives. I thus agree with the authors (line 1950) that '*different approaches are appropriate for different environments and questions*'.

Response: we thank professor Thomas for these comments and will add additional information and discussions to this section, as discussed in the comment. We understand the criticism that *Ammonia* spp. do not fit into the general morphology approach, due to its trochospiral shape. Nevertheless, it is usually endemic in very shallow coastal environments, especially intertidal mudflats, which are usually not the aimed locations for the morphology based reconstructions. We will include this issue into the discussion and emphasize that the choice of the environment for the paleoreconstruction matters. Also, we will be more critical regarding the contrasting results in fig.13, since despite the different approaches are showing the same trends, they significantly differ quantitatively.

Line 1954: At the end of this section, I want to mention that I also missed any reference to Jorissen et al., 2022. The 4GFOR model - coupling 4G early diagenesis and benthic foraminiferal ecology. Mar Micropal 170, 102078. In this paper we see a first effort to link benthic assemblages not just to oxygenation, but to the several regimes mentioned 'redox ladders' in the sediment (e.g., Figure 3). In my opinion this is a highly significant paper that should be mentioned. This could go in the section 6.6.6, as well.

Response: Good point, we will add information about the 4GFOR model of Jorissen et al. 2022 in the revised manuscript.

Line 2002 (section 6.6.6 Proxy drivers): I think that this section could be placed in a separate, much earlier section, e.g. placed just before a section on foram calcification, and BEFORE the proxies are discussed. This is information we should have had before discussing the proxies. Line 2053-2054: In my opinion, the reference to Glock's 2023 review paper should have come much earlier in the text, which text then could have been guided by this recent review.

Response: we will consider this for the revised version of the manuscript. This section can be moved to the introduction part about foraminifera, which will come before the different proxy sections.

Line 2022: an early and important paper on environmental controls on benthic foraminifera including *Uvigerina* (organic carbon - oxygen) that should be cited is was Lutze & Coulbourn, 1984, Recent benthic foraminifera from the continental margin of northwest Africa: Community structure and distribution, Mar Micropal 8, 361-401.

Response: we will add this to the revised version of the manuscript.

Line 2058-on, secEon 6.6.6.2. This short section is not very useful, and gives no description of planktonic foraminifera in low oxygen environments. In fact, relevant text is presented in the section on porosity, lines **2208-2016**). I suggest to either remove this section, or just refer to] section 6.7.2, where important references are provided.

Response: We disagree with this suggestion. The text following 2208 is about porosity of planktic foraminifera, while the paragraph from 2058 discusses planktic species that might be able to survive under low O₂ conditions. Of course, there is not so much information in this paragraph compared to the benthics. But this is the whole point of this section: To mention our gaps of knowledge about planktic forams from low O₂ habitats. We can add some further references. We will also remove subheaders referring to benthic and planktic foraminifera to reduce complexity.

Line 2076: an important early review paper on morphology (including thin-walled tests): Boltovskoy et al., 1991, Morphological variations of benthic foraminiferal tests in response to changes in ecological parameters: a review, J of Paleontol 65, 175-185.

Response: We will add this reference to the revised version of the manuscript.

Line 2083-2084: excellent examples of evidence for such sediment mixing are papers by Hupp et al., 2022, PNAS 119, e2115561119; Hupp & Kelly, 2020, Paleoc PaleoCI 35, 1-19; Hupp et al., 2019, Geology).

Response: We will add these references at the appropriate sections to the revised version of the manuscript.

Lines 2095-2100: fairly superficial; paragraph. Presence of non-analogue fauna of course in the first place is due to evolution/extinction. One factor that is not mentioned specifically: coexistence of taxa in samples that lived in different seasons (e.g. seasonal anoxia is. common phenomenon); see e.g. Stassen et al., 2015 Mar Micropal 115, 1-23; or Wagner et al., 2023 Paleoc PaleoCI 37, e2022PA004502.

Response: Fair point, we will add information about coexistence of taxa that lived in different seasons.

Line 2155: secEon 6.6.9.

This text could have been helped with an earlier general introduction to foraminifera, their calcification and evolution, as mentioned above (line 1555). Calcareous hyaline foraminifera (Rotaliida) outnumber other groups since the Late Cretaceous. Specific taxa nowadays more common in oxygen rich environments (Nodosariida) are not necessarily so in deep-time (including the time of OAEs).

Response: yes, we follow up on Prof. Thomas' earlier suggestion of having an earlier general introduction to foraminifera, which will address this (+ include the comment here).

Line 2160: note that these (*Dentalina*, *Lagena*, *Nodosaria*- and *LenEculina*) are all

Nodosariidae, which use a different mode of calcification (de Nooijer et al., 2023, and Pacho et al., 2023, Element/Ca ratios in Nodosariida (Foraminifera) and their potential application for paleoenvironmental reconstructions, Biogeosciences 20, 4043-4056).

Response: Good point, we will add this detail. It will be mentioned in the about foraminiferal calcification that will be added.

Line 2161: as mentioned above, the statement on more circular foraminifera dominating on oxygenated environments is not valid generally even in the present world: in inner neritic- intertidal settings: large trochospiral *Ammonia* species are among the most anoxia-surviving taxa in the world. I greatly like Tetard et al.'s 2017 work and think that it is extremely useful, but it should be kept in mind (as mentioned in this paper) that one can use such shape analysis only in specific settings. Also relevant to circularity in Table 2 (lines around 2220). As long as we do not know **why** large trochospiral taxa in deeper water setting are more common in oxygen-rich settings, we cannot use this observation for all environments.

Response: We will add these caveats to the text.

Line 2164-2166, 2070-2071: here again - test shape and size cannot that simply be understood in a universal way - see notes on *Ammonia*.

Response: We will add this caveat.

Line 2175: see notes above- morphology is not that simply/universally a reaction to environment.

Response: we will address this. Maybe not universally interspecifically but intraspecifically it usually reflects phenotypic plasticity, which should reflect the environment. Otherwise: Why should forams put energy into morphologic adaptation, if not due to changes in the environment?

Line 2204: the important word here, in discussing porosity, is 'conspecifics'. Porosity has been used successfully to look at oxygenation in shallow waters (e.g. various cited papers by Richirt et al), but pore size in *Ammonia* species is an interplay between its genetic identity and environmental factors (e.g. Hayward et al., 2021. Molecular and morphological taxonomy of living *Ammonia* and related taxa (Foraminifera) and their biogeography, *Micropaleontology* 67, 109-313). this thus might become a problem if the 'conspecificity' is not that easily worked out, as e.g. in *Ammonia*. Note that similar problems can be predicted for other neritic/intertidal taxa such as *Elphidium clavatum* (Table 2- note typo in *Elphidium*). Table 2: circularity in plankton: by far the most plankton (presently) are circular, and occurrence of biserials/triserials is generally linked to high food (rather than low oxygen) conditions.

Response: We do not think this comment helps to improve the review. Most plankton lives in better oxygenated environments and round forms typically have lower surface to volume ratios, which could represent this. If this refers to planktics then it could only be the meroplanktic bolinivids that are being referenced here. We certainly find them in both the high-productivity, low-oxygen California borderlands and the low-productivity, relatively low-oxygen North Atlantic gyre. Plus the Mediterranean. So, I'm not sure they're either canonical or functionally indicative of either... In benthic environment if there is high food, there is most likely also lower O₂. In addition, non-circular forams often are found in low-oxygen environments. Take bolinivids for example. They are conical and have a very high surface to volume ratio, which is considered to be an adaptation to low O₂ conditions. They are also often found under low O₂ conditions. The *Ammonia* problem is something completely different. Of course we get problems, if we can not distinguish species properly because they look so similar.

Line 2239-on: Size and Morphotype. Would be nice to cite Schmidt et al. 2004 paper in Science: Abiotic forcing of Plankton Evolution in the Cenozoic (303, 207-210), for a more long-term view of size of planktonic forams.

Response: We will add this citation to the revised version of the manuscript.

Line 2300: as to acidification/dissolution see also Foster et al., 2013, Surviving rapid climate change in the deep-sea during the Paleogene hyperthermals. *PNAS*, 110: 9273-9276, and Schmidt et al., 2018.

Response: We will add this reference to the revised version of the manuscript.

Line 2434: for ostracods, oxygen morphology linkages have been very long discussed - whether one thinks these linkages are correct or not. See e.g. McKenzie et al., 1989, The *KRITHE* problem — first test of Peypouquet's hypothesis, with a redescription of *KRITHE PRAETEXTA PRAETEXTA* (rustacea, Ostracoda), *Palaeo*³ 74, 343-354.

Response: We will discuss this paper at the appropriate section in the revised version of the manuscript.

Line 2477: SecEon 6.8.1: in my opinion this section could also benefit from a general benthic foram introduction.

Response: We are happy to add this.

Lines 2559-2562: There is discussion (various papers co-authored by Jorissen et al.) whether 'epifaunal' is a correct term for many species, with the exception of species living on hard substrate sticking out above the sediment/water interface; see discussion of use of 'Average Living Depth). Many species of *Cibicidoides* are biconvex, thus do not live attached to surfaces, and thus may not be truly 'epifaunal'. This is further discussed in section 6.8.5 (lines 2606 on); in my opinion this discussion - what is infaunal and what not - should have been provided before the $\delta^{13}\text{C}$ proxy was discussed.

Response: We will make these changes to the revised version. The terms epifaunal and infaunal will be introduced and discussed according to reviewers suggestions in the foram section.

Line 2560: *C. mundulus* is the correct name, *C. kullenbergi* is the junior synonym (see book by Holbourne et al. on benthic foraminifera), not the other way around.

Response: We will change this around.

Line 2621-on: not mentioned, but in my opinion the most important limiting factor for use of the $\delta^{13}\text{C}$ proxy is the fact that we see common deep infaunal taxa ONLY if the food supply is sufficiently high (see TROX model, Jorissen et al 1995), whatever

species it is. The use of this proxy is thus limited to regions and depths where there is such a sufficient food supply.

Response: Yes, this is absolutely true. We will mention this in the revised manuscript.