Rebuttal letter

Title: Living (Rose Bengal stained) benthic foraminiferal faunas along a strong bottom-water oxygen gradient on the Indian margin (Arabian Sea)

Authors: C. Caulle; M. Mojtahid; A. J. Gooday; F. J. Jorissen and H. Kitazato

doi:10.5194/bgd-12-3245-2015

Dear Editor,

Hereby we resubmit the revised version of the manuscript "Living (Rose Bengal stained) benthic foraminiferal faunas along a strong bottom-water oxygen gradient on the Indian margin (Arabian Sea)" by Caulle et al.

We would like to acknowledge Tony Rathburn and anonymous referees #1 and #3 for their comments and suggestions which much helped to improve the manuscript. We considered the comments with care and acted on the majority of the points raised by the reviewers. Only in a few cases we have decided not to follow the suggested changes. Below, please find our answers to all referees comments, presented in the same order as in the review.

Thank you for considering our manuscript for publication in the Biogeosciences special issue on "Low oxygen environments in marine, fresh and estuarine waters".

Yours sincerely,

Clémence Caulle (also on behalf of the co-authors)

1- Anonymous Referee #1

Received and published: 1 March 2015

This is a well-constructed, detailed and articulate piece of research into the living foraminifera of the Arabian Sea - across a major OMZ gradient. The authors investigated living fauna in upper 1-cm of sediment across five sites. The identification of the fauna in this work is done exceedingly carefully, and the biotic snapshot of community structure and species occurrences is really interesting. I found this a very interesting documentation of foraminiferal community ecology. Additionally, the manuscript is well written, organized and referenced. I agree with the principle finding: the community shows primary affinity to hypoxia, and calls into question the importance of primary productivity in shaping subsurface community composition.

1-1- **Referee # 1:** I am curious with the authors position on the community structure data. While I find the conclusion regarding BWO and surface productivity to be compelling, I also am interested in the community-scale patterns of diversity, evenness and marker species abundance/dominance (a term I think should probably be incorporated into the discussion).

Author response: *We added in the manuscript these specific ecological terms (see annotated manuscript, lines 322-325, 419-420).*

1-2- **Referee # 1:** Some of the diversity patterns do not reflect the existing paradigm of low O2/low diversity and high O2/high diversity. This is interesting - and worthwhile of a broader integration into the conclusions of the manuscript. The authors do discuss these findings, and they mention two particularly appropriate rationales for this diversity question. One is the influence of high-frequency climate and oceanographic variability. The other is endemism and, essentially, the unique community structure of Arabian Sea foraminifera. Ultimately, there may be a need to reframe the ecological interpretation of foraminiferal community diversity across gradients of hypoxia - the existing paradigm may be too simple or not well-suited to the collection methods we have at hand.

Author response: *We agree with reviewer 1 that the existing paradigm may be too simple to describe our data on the Indian margin. We rephrased this part of conclusion by putting more weight into this statement (See annotated manuscript, page 19 lines 594-597).*

1-3- **Referee # 1:** There are clear interpretations to paleocommunities from this research. However, I found the discussion of this facet of the research to be slightly disorganized. I would recommend considering the toolkits commonly used in paleocommuntiy ecology, and directly addressing each: marker species, community-scale parameters (diversity, evenness), density.

Author response: *We added in the discussion part a separate paragraph about paleoceanographic implications (See annotated manuscript, page 19 lines 571-587).*

1-4- **Referee # 1:** This may be beyond the scope of this investigation, however it would be really interesting to see this data analyzed using multivariate statistical software (such as Primer). It would be interesting to see the 2-D projections of community similarity - and this kind of analysis would provide very defensible descriptive statistics with which to make statements and conclusions from.

Author response: *The authors decided not to use descriptive statistical as a tool for discussion. Data clearly support our statement and conclusions. In view of the very low number of stations (five), we do not believe that adding multivariate statistics in the present manuscript will significantly improve this study. In a future study comparing all recent benthic foraminiferal data collected from all over the Arabian Sea, we intend to use descriptive statistics which are more appropriate regarding the large number of stations.*

1-5- **Referee # 1:** I think a more fleshed-out conversation about community density is also needed....not much, but because it's so critical in paleocommunity interpretation, it's worth some discussion.

Author response: *Community densities have already largely been discussed in previous papers on the Arabian Sea OMZ (e.g. Jannink et al., 1998; Gooday et al., 2000; Schumacher et al., 2007; Larkin et al., 2009; Caulle et al., 2014). For that reason, we decided first not to insist on this point. However, we do agree with the referee that it should be mentioned briefly. We added a small paragraph in the discussion (see annotated manuscript, page 11, lines 325-330)*

1-6- **Referee # 1:** In the methods section there needs to be a sentence clearly stating the sampling depths for each station through the OMZ.

Author response: *Sampling depths for each station are added in the methods section (see annotated manuscript, page 5, lines 126-128)*

Line-edit critique:

1-7- **Referee # 1:** Consistency in sentence structure should be evaluated across the manuscript. In particular, there are many instances of independent clauses joined by simply a comma. Also known as a comma splice (admittedly a common error in science writing). Look up the acronym FANBOYS - and use these coordinating conjunctions.

Author response: *Sentence structure has been corrected when necessary.*

1-8- **Referee # 1:** Consistency in reference formatting needs attention. I noted the following references that need reformatting, on lines: 580, 609, 626, 630, 634, 655, 658, 661, 664, 701, 716, 730, 733, 818, 838.

Author response: *These references have all been reformatted.*

1-9- **Referee # 1:** I am not familiar with bio-volume (line 375). This term either needs a clear explanation (with units) or to be omitted for a more general term entirely.

Author response: *We added a short definition of bio-volume: estimation of the cytoplasmic volume by assuming that the internal test volume corresponds to 75% of the total foraminiferal test volume (Hannah et al., 1994) and that the internal test volume of the shell is entirely filled with cytoplasm (See annotated manuscript, page 13, lines 404-407)*

1-10- **Referee # 1:** Line 484: potentially change to: "It is not clear how these indices describe..."

Author response: *Done (See annotated manuscript, page 18, lines 541-542)*

1-11- **Referee # 1:** Paragraph starting on line 488: I would consider using the term "marker species" to describe fauna associated with a narrow and paleoceanographically-relevant environmental variable.

Author response: *The term "marker species" has been added (See annotated manuscript, page 18, lines 551).*

1-12- Referee # 1: Line 540: the sentence starting on this line is awkward - it could be rewritten for clarity.

Author response: *The sentence has been changed into "The same foraminiferal species are found on the Indian margin and in previously described study areas from the Arabian Sea (Fig. 7)." (pages 18, lines 548-549)*

1-13- Referee # 1: Additional line edits to be addressed: Line 23, 34, 287, 304.

Author response: *We edited these lines.*

2- A. Rathburn (Referee)

trathburn@gmail.com

Received and published: 17 March 2015

This paper presents engaging discussion about the relationship between oxygen availability and the distribution and percentage of agglutinated taxa in foraminiferal assemblages living on the Indian Margin. The methodology is sound and the paper is well written and of high quality. Although I do not necessarily agree with all of the conclusions, I found the results and discussion to be quite interesting.

Specific Comments

2-1- **Referee # 2:** I suggest that the abstract include the size fractions examined (>300 and >150 microns). Although the authors make a case for the likelihood that the <150 micron assemblage does not differ substantially from the >150 micron assemblage, the abstract should make it clear that the conclusions are based on examination of >150 micron assemblages.

Author response: *The size fractions examined have been added in the abstract (See annotated manuscript, page 1; lines 17 and 23)*

2-2- **Referee # 2:** Do not use the term "successions" (line 23, page 3255 and elsewhere) when referring to microhabitats or transect assemblage patterns. In ecology this term refers to something else entirely.

Author response: *The term "successions" is deleted (See annotated manuscript, page 10; lines 280-282)*

2-3- **Referee # 2:** Page 3256, line 20: The <150 micron assemblage contains not just small species, but small individuals of large species. In oxygen-poor environments, the percentage of <150 micron individuals can be quite high. Although the 63-150 micron assemblage may be similar in species composition and diversity as suggested in lines 25-27, abundances and percentages of species (and hence designations of dominance) can be quite different when comparing >63 micron and >150 micron assemblages.

Author response: *The sentence has been clarified by adding* "*However, adding the small size fraction may indeed add some small-sized taxa, and induce slight changes in absolute and relative abundance*" *(See annotated manuscript, page 11; lines 313-315).*

2-4- **Referee # 2:** I agree that the data clearly show that some agglutinated taxa can tolerate strong oxygen depletion. This is an important finding. While I understand the reasoning behind the suggestion that these assemblages are controlled by oxygen availability, I do not think that this is necessarily the case. Given that many, though admittedly, not all, previous studies have concluded that agglutinated taxa were less able to tolerate oxygen-poor conditions compared to calcareous taxa, it seems to me that we need to look at the global data set for insights into the ecology of these agglutinates. In many oxygen-poor habitats, organic-rich sediments tend to be "soupy," while under more oxygenated conditions, sediments tend to be coarser and less thixotropic. In soupier sediments, fewer grains would be available for agglutinated tests, and it would be more difficult for an agglutinated individual to remain near the sediment-water interface. This idea coupled with the presence of winnowed sediments (line 15 on page 3258) suggests to me that sediment characteristics might account for the dominance of agglutinates in this region as compared to those from other OMZ regions. Were sediment characteristics measured? The presence of abundant soft-walled taxa in some oxygen-poor environments (lines 20-28, page 3259) is consistent with this hypothesis. To me, the dominance of agglutinated taxa and the presence of *H. elegans* in the OMZ study area suggest that sediment characteristics enable these low-O2 tolerant taxa to thrive in this OMZ habitat compared to other, more typical, oxygen-poor sediments.

Author response: *Grain size analyses were performed at each of the sampled stations and the results are published in Levin et al. (2013) and Cowie et al. (2014). We do agree that sediment granularity might influence agglutinated species and especially hormosinacean species. For instance the 535m-site is characterized by 44% of sand compared to 9.6% at 800m (Levin et al., 2010), where agglutinated fauna have a lower abundance. However, in the core of the OMZ (885 and 1013m; BWO ~2µM) on the Murray Ridge where the sediments are fine (63-70% of silt, Koho et al., 2013) agglutinated species (mainly Reophax species) were largely dominant (> 150µm) (Caulle et al., 2014). Moreover, sediment grain size was nearly constant between the OMZ core and deeper sites (below the OMZ from 1495 to 3010m; Caulle et al., 2014), suggesting that sites on the Murray Ridge were not submitted to strong currents removing sediments. However, these sites also had a large contribution of agglutinated taxa.*

We conclude then that the strong dominance of hormosinacean species in the OMZ of the Murray Ridge and the Indian margin suggest that other factors than sediment grain size play a role, such as

the quality and availability of the organic matter or pH and carbonate saturation. We added a short paragraph in the discussion suggesting that presence of agglutinated species might be related to sediment grain size characteristics (See annotated manuscript, page 14; lines 426-440).

3- Anonymous Referee #3

Received and published: 31 March 2015

3-1- **Referee # 3:** The paper by Caulle et al presents data on living (Rose Bengal stained) benthic foraminifera across an OMZ bottom water gradient on the Indian Margin. The paper is generally well constructed and data is well organized. However, I do not agree with the main conclusions that the authors make here.

Author response*: We regret that we didn't convince the reviewer of our ideas. However, we paid much attention into his/her arguments, which in general helped moderating our statements but didn't change our main conclusions. Whenever possible, we tried to strengthen our arguments and present counter-arguments when we do not agree with the reviewer.*

3-2- **Referee # 3:** The authors suggest (abstract lines 14-15 and conclusion) that the foraminiferal assemblage and the dominance of agglutinated foraminifera are linked to relatively low surface water productivity and associate lower Corg flux at the area. The authors base this argument on satellite productivity estimates, which indeed show lower productivity in the study area in comparison to the other OMZ areas in the Arabian Sea. Yet, they have no actual flux data and the sedimentary Corg content and amino acid index seems to suggest otherwise, showing relatively high values in the OMZ. In addition, in the paper Cowie et al (2014), where organic geochemistry of the study region is discussed in detail, shows that the organic matter distribution at the Indian margin is tightly coupled to hydrodynamic processes and oxygen availability. Therefore, I suspect that the local hydrodynamic region coupled to BWO, and/or alternatively the carbonate chemistry and associated lower pH may restrict the distribution of larger calcareous foraminifera and favoring agglutinated taxa. The carbonate chemistry was also suggested to be a factor in Murray Ridge where agglutinated foraminifera were abundant in >125 um fraction (Caulle et al. BGD 10, 15257–15304, 2013). All statements about organic fluxes should be deleted, as there is no data to support them.

Author response*: We do not suggest that the foraminiferal assemblage and the dominance of agglutinated foraminifera are linked to relatively low surface water productivity and low fluxes of organic matter. However, we do suggest that in the Arabian OMZ, the faunas can't be considered as "high productivity faunas", and low oxygen concentration appears to be the dominant control on benthic foraminiferal fauna. We based our statement by comparing sea-surface productivity, Corg at the sediment surface and bottom oxygen concentration of different areas of the Arabian Sea. Similar*

calcareous species were observed at a similar range of oxygen concentration, probably under very different organic flux regimes. Organic matter fluxes are often believed to be the main factor structuring BF abundance and assemblage composition. Surprisingly, our finding does not support this hypothesis, which we think is an important finding. We do agree that using satellite productivity images can be approximate but, in our opinion, it gives the necessary information about primary production in the area. This is even truer when knowing that chlorophyll-a is measured on a daily basis generating a large data set whereas organic fluxes measurements give only punctual values. Consequently, we carefully reconsidered all statements about organic matter fluxes, and where necessary added some more explanation. The work of Cowie et al. (2014) is cited (See annotated manuscript, page 17; lines 531-535).

3-3- **Referee # 3:** The study is also based on surficial sediments (0-1 cm) and >150 um fraction, although sediment was sampled down to 10 cm depth. I wonder why the deeper intervals were not investigated? Or alternatively, why did the authors did not investigate the smaller size fraction, if only the surficial sediments were studied? In the paper the authors state that the small fraction was not studied as it is very time consuming, yet this study has 5 stations, where only surficial sediments (10 samples in total) where studied. Furthermore, as authors state in section 4.1, this could cause a bias, as especially in low oxygen setting foraminifera are generally smaller. Furthermore, this size dependence seems to be especially the case for calcareous foraminifera as shown in the study of Caulle et al (2013) in the Arabian Sea OMZ. Similarly in the study of Schumacher et al (2007) agglutinated foraminifera are abundant at deeper sites (at similar water depths to this study) and calcareous foraminifera are only abundant in the small size class.

Author response: *The authors choose to not investigate smaller size fraction as well as deeper sediment layers because our analyses were especially time-consuming in view of our decision to consider very fragile agglutinated and soft-bodied species as well. Usually, these taxa are not studied. Consequently, we spent about 4 full working months into picking and taxonomical identification of the 5815 specimens sorted out in this study. Of course, we agree that considering only the 0-1 cm and the > 150µm fraction may bias the ecological interpretation. But basically all benthic foraminifera studies decide to study only a selection of the total fauna, and thereby introduce some bias. Also studies of the >63 µm exclude a part of the fauna, and the big majority of studies does not include soft-walled foraminifera. We chose to focus on fragile agglutinated and soft-shelled foraminifera. Finally, a major advantage of working on the >150 µm size fraction is that it allows direct comparison with paleo-oceanographic studies, which are mainly based on the >125 or >150 µm*

fractions. However, we better indicated the potential bias due to this choice at several places in the text. (See annotated manuscript, page 10-11; lines 300-317).

3-4- **Referee # 3:** I also do not agree that the small size class only consists of juveniles as authors suggest in section 4.1 (lines 28-29). Especially in low O2 settings, adults may not just grow as large due to environmental reasons. I would think this study would improve significantly if small size class would be examined as well. This could then potentially provide confidence to the current arguments, or alternatively lead to new different outcomes.

Author response: *Dr. Rathburn made the same remark. Of course, both reviewers are right, and we corrected the text accordingly (See our response to comment 2-3).*

We agree that the addition of the 63-150 µm would make a valuable addition. Unfortunately because of the amount of time needed for such an analysis, this will have to the scope of a future study.

3-5- **Referee # 3:** The abundance of agglutinated taxa in low oxygen setting is indeed interesting but I do not think this is totally new. The study of Pina-Ochoa et al. (2010) showed that at least some species of agglutinated foraminifera also collect nitrate. For *Reophax* no nitrate pool was measured but only very limited number of specimens was measured (4 in total). Thus further investigation is required. These parts of the discussion should be rewritten and work of Pina-Ochoa et al cited.

Author response: *Part of the discussion on the abundance of agglutinated taxa has been rewritten and the work of Piña-Ochoa et al. (2010) have been cited. We also added the suggestion that hormosinacean species living in the core of the OMZ stock nitrate and use denitrification as an energetic pathway (See annotated manuscript, page 15; lines 452-459).*

3-6- **Referee # 3:** Other notes Census data should be presented as an appendix, and counts of all species shown even if not discussed in detail.

Author response: *Census data are now presented in an appendix.*

3-7- **Referee # 3:** Authors also comment on the extreme low-oxygen content of the core of the Indian margin OMZ in context of species diversity and compare it to other studies in the

region (this study 0.3 uM, around 2 uM Murray Ridge, around 4 uM Pakistan Margin; Section 4.2 lines 12-15; and Section 4.5). I indeed agree that the high diversity may be related to careful taxonomy of this study, and hence I would not place this much emphasis on the topic. Firstly, as the authors note in the start of section 2.1. core of OMZ is where O2 content is <2uM, this would then leave out the Pakistan margin complete. Secondly the position of the core of the OMZ is slightly different in different regions, for example, at Murray Ridge the shallowest OMZ core sample comes from over 800 m water depth unlike in this study where it is from 535m depth. Thirdly it may be relevant to take into account differences in the measuring techniques and what their O2 detection limits and errors may be. For example, sensors are continually developing. The unisense O2 detection limit now is 0.3 uM, although in the past there has been a problem especially at very low concentrations. Further other studies may have used other approaches like Winkler titration to measure bottom water O2 content.

***Author response**: As suggested, we insisted more in the discussion on the fact that the high diversity we observed compared to the other sites in the Arabian Sea could be partly due to a more careful observation technique (See annotated manuscript, page 12; lines 356-360). We added in the discussion a section about the precision of oxygen measurements (page 11 lines 327-330) and about the OMZ in different area of the Arabian Sea (See annotated manuscript, page 17; lines 524).*

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3-8- **Referee # 3:** p. 3250 lines 12 add weight % or wt. % in front of Corg content. Check everywhere for this as units are missing in other places too.

***Author response**: The unit wt. % has been added in front of Corg content.*

3-9- **Referee # 3:** p. 3250 line 6 you mean lower boundary of the OMZ core?

***Author response**: Yes. We corrected it (See annotated manuscript, page 5; lines 139).*

3-10- **Referee # 3:** p.3255 line 26 Caulle et al 2014 does show some infaunal foraminiferal species. For example at the OMZ core site highest abundances where at 1-2 cm depth in sediment. Also at the transition towards more oxygenated conditions foraminifera are present at

relatively high numbers from 1-3 cm depth and at more oxygenated sites *M. barleeanus* is also found.

***Author response**: We do agree that studying only the top surface (0-1 cm) may induce some bias in the sense that we may have omitted some infaunal species. However, as we mentioned in the text, the compression of redox profiles in such hypoxic settings, leads to an absence of a well vertical suite of classical microhabitats and a concentration of deep-infaunal taxa close to the sediment surface. Intermediate and deep infaunal taxa were scarce on the Indian margin, and have rarely been reported in the OMZ in previous Arabian Sea studies. In Caulle et al. (2014) most of the fauna was concentrated in the top first cm of sediment (0-1 cm), expect in the core of the OMZ With the exception of the core of the OMZ. However, in the core of the OMZ, the soupy nature of the sediment was supposed to be the main factor of this peculiar foraminiferal distribution (maximum abundance at 1-2 cm) because the volume of the first two slices was very imprecise, and the maximum density in the 1-2 cm layer may be a sampling artifact. So, in view of our results and those from previous studies from the Arabian Sea, studying only the 0-1 cm layer does not induce a major bias.*

3-11- Referee # 3: p.3259 Lines 16-18. Why only mention dormancy? What about denitrification. Do authors have any data on bottom and pore-water nitrate concentrations?

***Author response**: We do not have data for bottom and pore-water nitrate concentrations. These parameters have not been measured. Denitrification has been added (See annotated manuscript, page 12; lines 407-411).*

3-12- Referee # 3: p. 3261 line 24 you mean the OMZ core? Add OMZ for clarity.

***Author response**: The term OMZ has been added (See annotated manuscript, page 16; lines 487).*

3-13- Referee # 3: p. 3264 line 16. No E. trigona and C. oolina in Fig 7. Please check Figure is ok and contains all appropriate data.

***Author response**: Part of the Fig. 7 with Ehrenbergina trigona and Chilostomella oolina was missing. The complete figure has been uploaded now.*