We thank the anonymus reviewer for his critical comments concerning several issues in our original manuscript which might have been misleading to the readers. After having adressed the critical issues we think our manuscript has significantly improved from the comments of the anonymous reviewer. In particular, we now think that there are no further misunderstandings in the text.

Below we comment in detail the points of revision.

Anonymus reviewer 2:

AR2: General comments: The article by Glock et al. titled "The role of benthic foraminifera in the benthic nitrogen cycle of the Peruvian oxygen minimum zone" brings awareness to the understudied and relatively recently discovered aspects of denitrification, namely examining the role of benthic foraminifera in the nitrogen cycle. Although the topic of the study is highly interesting and relevant to BG journal I feel that the actual study presented here was not executed in very accurate manner and data is relatively speculative. Part of this may be due to sampling scheme (may be this study was not the focus of original cruise) and this study/manuscript has been put together mainly using exiting published data without real additional measurements to support the foraminiferal denitrification rates and/or nitrate pool.

Reply: We understand the critic of the reviewer that we do not present real measurements of foraminiferal denitrification rates or foramiferal nitrate pool, but this was not the intention of the manuscript. Several aspects contributed to the origin of this study. The first and most important point is that all the authors come from different fields in science working together in a collaborative research project (SFB754) about oxygen minimum zones, in this case focusing on the Peruvian OMZ. This brings the opportunity to combine the taxonomic studies about foraminifera, *in-situ* nitrate flux measurements done in benthic lander chambers, pore-water nitrate profiles and data from previous published modeled denitrification rates (Bohlen et al., 2011) all from the same sampling area and the same cruises to one study. Furthermore, we wanted to present a method how to estimate foraminiferal denitrification based on the limited amount of yet published measured rates. With our assumptions (indicated in the manuscript as A&B) we tried to include the whole living fauna into our calculations while previously published estimations of total benthic foraminiferal denitrification rates are usually based only on very few species (Hogslund et al., 2008; Pina-Ochoa et al., 2010; Bernhard et al., 2012). Due to the high number of benthic foraminiferal species (2140; Murray, 2007) it will take some time till the rates for all of these species will be measured (12 measured rates have been published in total over the last 7 years) and approximations to estimate the contribution of foraminifera to the benthic nitrogen cycle are important. The comparison of our estimations with the *in-situ* fluxes and the modeled total benthic denitrification rates (from Bohlen et al., 2011, these rates are based on porewater profiles, those nitrate fluxes that are presented in the MS are based on actual in situ measurements using flux chambers) showed that these results are in the right order of magnitude. Definitely additional "real" measurements will support the quality of such estimations and we hope we will bring

awareness on the (as the reviewer already stated) “understudied” role of foraminifera in the nitrogen cycle. This is also reflected in our conclusions (page 17792; line 14-17 in the original manuscript):

“However, data on nitrate respiration rates and the knowledge of individual storage capacities of more species are required in order to better constrain the contribution of foraminifera to the nitrate budget of the world oceans.”

AR2: Below some more detailed comments why I question the scientific impact of this manuscript: Methods: The study presents data on foraminifera, in situ fluxes and pore water profiles. To me it is currently unclear if the data for these different components actually came from exactly the same sample sites, or close by sites? I.e. do you have a flux measurement, pore water profile and foraminifera counts for each site? Or is some of your environmental data from near by sites? In your Table 1 you only list the sample locations for your foraminifera but not for the other parameters. Also if I look at the appendix with the pore water data, all of the station names do not seem to match with the foraminiferal station names. The same is for the in situ flux data.

Reply: This might indeed have been confusing due to the different station names listed in our tables. The station names differ for the different devices used on the cruise (for example BIGO; for the biogeochemical lander chambers or MUC for the multiple corer device). In the revised manuscript we added a map with the sampling sites (figure 1) which should bring more transparency into this topic. Furthermore we added a column into table 5 indicating which MUC station coincides with BIGO station. Indeed, we have consistent data sets with *in-situ* fluxes, pore water data, modeled denitrification rates (Bohlen et al., 2011) and foraminifera counts for each site with two exceptions:

The 248 m site (M77/1-583/MUC-65) for foraminiferal counts coincides in our study with the 259 m site (M77/1-583/BIGO-T6) for *in-situ* flux measurements, but is actually located 0°07´ (approx. 11 km) south of that location. In the revised manuscript this is now clearly marked (see table 5) but these stations are characterized by similar bathymetric, topographical and redox-conditions.

The fact that the 248 m MUC station is located 0°06´south of the coinciding BIGO station is marked in the figure captions of figure 1 in the revised manuscript:

“*At 248 m the MUC site for foraminiferal studies and pore water profiles is about ~0°07´ south of the corresponding lander station.”*

and also in the table captions of table 5:

“*Italic letters mark that the multicorer for the foraminiferal studies has been taken at a closeby site at the same water depth which is ~0°07´ south of the lander station.”*

The other exception is the 465 m site (M77/1-456/MUC-22). Since we do not have *in-situ* flux data from this water depth we did not compare foraminiferal denitrification with the *in-situ* fluxes at this site at all. What we did for comparison is to intrapolate the modeled denitrification rates from the two closest sites from Bohlen et al. (2011) for a comparison to foraminiferal denitrification. This has already been marked in the discussion of the original manuscript (17790; line 9-12):

"*If the calculated foraminiferal denitrification is compared to the total benthic denitrification as intrapolated from the two closest sites where model data were available (Bohlen et al., 2011), foraminifera only account for 5% to the total benthic denitrification.*"

For further clarification we also added the following part to the results in the revised manuscript:

"*Since no total benthic denitrification rate was available for the 465 m site we intrapolated it from the the rates of the two closest sites (Bohlen et al., 2011).*"

AR2: Is all the insitu flux data taken from the paper of Bohlen et al. 2011? Or are the date new, which are reported here? In your results section p. 17785 line 13 you refer to some model calculations. These calculations are not explained anywhere in the manuscript. Are these the modelled data of Bohlen et al?

Reply: Indeed *in-situ* fluxes that were measured in benthic flux chambers of the BIGO lander are shown in the paper by Bohlen et al. (2011) in figure 4 for comparative purposes. However, with regard to these data, a clear reference in the figure captions was made to another paper of Sommer et al. (submitted) which has not been published and is presently not submitted to any other publisher. Hence the nitrate fluxes measured in the benthic flux chambers presented in this MS are original data. This mixture of total (flux chamber) and diffusive rates might be indeed confusing, however the Bohlen et al. (2011) publication is based on modeled diffusive fluxes that were exclusively and originally derived from pore-water gradients which is also described in their methods section. The *in-situ* fluxes we present in our study are real measured data not modeled fluxes! To avoid further confusions we changed the legend of figure 4 (figure 3 in the original manuscript) in the revised manuscript:

"Nitrate loss from lander measurements"

Has been changed to:

"*Total in-situ nitrate loss*"

AR2: Pore water pressing: I would think that a large proportion of the cell bound nitrate is actually due to presence of *Beggiatoa* and *Thioploca* sulfur bacteria as outlined in Bohlen et al. I think it will be very difficult to try to separate the cell bound nitrate content of forams vs sulfur bacteria based on this method.

Reply: We agree with the reviewer that it is not possible to separate the cell bound nitrate content of forams vs sulfur bacteria with this method and we did not suggest anything different in the original manuscript. We already stated, that also *Beggiatoa* and *Thioploca* can contribute to the cell bound nitrate squeezed out with the pore water press in the original manuscript:

"However, another fraction of the excess nitrate might be contributed from squashed *Thioploca* and *Beggiotoa* cells which were common in these habitats (Mosch et al., 2012)." (page 17791; Line 18-20)

For clarification and to explain our reasons why we believe that some amount of squeezed out cell stored nitrate has to come from foraminifera we changed this part of the discussion of the revised manuscript:

"Some amount of cell stored nitrate could be squeezed out of squashed foraminiferal and Thioploca or Beggiotoa cells which were also common in these habitats (Mosch et al., 2012). The spatial extend of the bacterial mats is higher at the shallower shelf station (79 m) and the mats are rather threadlike at 319 m (Mosch et al., 2012), while the foraminiferal abundance is much higher at 319 m. Since the pore water nitrate concentration from the pore water press is much lower at the 79 m site than at the 319 m site it is reasonable to assume that some amount of the nitrate has been squeezed out of foraminiferal cells."

Furthermore, we added the following sentence to the table captions of table 4:

"The elevated pore water nitrate concentrations at samples from the pore water press most probably resulted from squashed foraminiferal as well as Thioploca and Beggiotoa cells."

AR2: Foraminiferal nitrate pool calculations. I think (unfortunately) that it is not possible to calculate such an average nitrate pool as presented here. From previous studies we know that the nitrate pool of foraminifera is highly variable (e.g. Pina-Ochoa et al. 2010 MEPS and Koho et al. 2011 FEMS) and taking an average value and multiplying this by number of living population is thus not correct, or very speculative. The values reported for average nitrate pool/per species of foraminifera in Pina-Ochoa et al. 2010 PNAS are also often based on very few individuals so the averages are probably not completely representative. Furthermore, the standard error reported in Pina-Ochoa et al. 2010 (PNAS) also illustrates this high variability in the intracellular nitrate content. More actual measurements are needed on the size of the foraminiferal nitrate pools to better estimate this, including various species.

Reply: The reviewer is right that the nitrate storage in foraminiferal cells is highly variable even within single species and that our estimations in this case show uncertainties. We tried to clarify in the manuscript that our calculations are just estimations rather absolute values. As we stated in the beginning of this letter the big opportunity of our study is the possibility of combining very different data from the same locations obtained during our collaborative research project SFB 754 with literature data to estimate the influence of foraminifera in the benthic nitrogen cycle of Peru. In this case these are the pore water nitrate concentrations measured with different methods, the compositions of the foraminiferal assemblages at these

sites and the literature data of cell stored nitrate (Piña-Ochoa et al., 2010). We are convinced that it is reasonable to use the literature data for rough estimations because it would neither change the discussion nor the conclusions of this manuscript if the "real" values are 40% higher or lower. To clarify that our estimations have high uncertainties we added the following part to the discussion part 4.3:

"The foraminiferal nitrate storage shows high variability even within the same species. Standard-deviations of nitrate stored in 49 species reported by Piña-Ochoa et al., (2010a) varied from 2% to (in a single case) 179% with an average of 40%. Thus, we assume also for our estimations high uncertainities."

AR2: I think that rose Bengal staining is a valid method for identifying the numbers of living foraminifera in ecological studies. But as authors must be aware a care should be taken when working with specimens from low oxygen sites. I think authors should at least acknowledge this potential over estimation in the size of the living population. The overestimation in the size of the living population would also lead to overestimation in the foraminiferal denitrification rates and nitrate storage.

Reply: To acknowledge that rose bengal staining might overestimate the size of living fauna we added the following part into the methods section (2.1) of the revised manuscript:

"*Staining with rose bengal is a valid method for the identification of the foraminiferal living fauna but might also overestimate its size: Decaying protoplasm of foraminifera that have ceased their metabolic activity, and which is degrading slowly under anoxic conditions, can also be stained (Walker et al., 1974; Bernhard, 1988; Murray and Bowser, 2000; Bernhard, 2000; Schönfeld et al., 2012).*"

AR2: The approximation A and B used in the study sound reasonable but they should be reported more clearly. A supplementary appendix should be added to the manuscript were denitrification rates for each taxa are shown and explained where the value came from.

Reply: We already included all denitrification rates we used for each taxa without approximation or derived from approximation A (mean values for one genus) in table 2 of the original manuscript. In the table captions we already explained where these values came from. We did not apply specific rates for single Taxa within approximation B, thus it is not possible to them. In approximation B we added the percentage of all species from genera with no available denitrification rates to the total denitrification rate from all other species at the same sampling site. For example: If 90% of all foraminifera at one site are covered without approximation and approximation A, 10% is added to the overall results. To report approximation B more clearly we changed the following part of the methods (2.3):

"In the second approximation B, the proportions of species from genera with no available denitrification rates were added. The average denitrification rate of all other species was

applied for this cumulative percentage of the species for which denitrification rates are not available." (Page 17781; Line 10-13 in the original manuscript)

has been changed to:

"*In the second approximation B, the proportions of species from genera with no available denitrification rates were added. The totaldenitrification rate of all other species at a sampling site was applied for this cumulative percentage of the species for which denitrification rates are not available. To give an example for approximation B: If 90% of all foraminifera at one site are covered without approximation and approximation A, 10% is added to the overall results.*"

AR2: I can appreciate that in the OMZ sites where the bottom water oxygenation is very low <2uM foraminifera rely on denitrification. However, it becomes very difficult to estimate how much they contribute towards denitrification when oxygen content increases even a little bit. We do not know at which oxygen concentration forams switch to denitrifcation. Perhaps they continue to respire on oxygen even when the amount is very little, for example couple of micromolar or even less?

Reply: We understand the critic of the reviewer in this point but the conditions in the Peruvian OMZ are very extreme. Indeed, oxygen fluctuations at the upper (Gutiérrez et al. 2008) as well as on the lower boundary of the OMZ below 500 m water depth (Sommer et al. unpubl. data) were reported. As now mentioned in the revised MS, at the upper boundary periodical oxygen intrusions occur caused by coastal trapped waves (Guitierrez et al., 2008) reaching water depths of 100 and more. However, towards greater water depths i.e. towards the core of the OMZ the probability of such oxygen intrusion events becomes increasingly low, and beyond 300 m the centre of the OMZ essentially stays anoxic and usually is not influenced by oxygen intrusions (Noffke et al. 2012). The fact that parts of the Peruvian OMZ are essentially anoxic has already been addressed briefly in the original manuscript (page 17788; line 13-15). Furthermore, most of the foraminiferal species at the Peruvian OMZ live infaunal and oxygen concentrations in the pore waters are even more depleted.
At 1000 m water depth where fluctuations of bottom water O_2 in the range of 30 to 44 µM were recorded (Sommer et al., unpublished data) in situ micro-profiling revealed that O_2 penetration depth into the sediments only reached a maximum of 5 mm. Closer to the lower OMZ boundary oxygen in the pore waters was not even measurable at all.
Hence, given such rather stable low O_2 < 2µM conditions within the core of the OMZ down to 500 to 600 m, we assume that at least within the core of the OMZ the forams depend very much on denitrification. At the upper boundary these organisms might indeed switch periodically to an aerobic metabolism. But even there low oxygen conditions prevail for longer time periods (cf. Gutiérrez et al. 2008) which suggest that the forams also at least partially depend on denitrification there. Please note that during our cruise the bottom water O_2 level at the shallowest station was less than 2µM. Within the year 2008, where our cruise took place (end Oct. to Dec.) only one O_2 intrusion event was recorded in June / July in about 125 m water depth off Callao (Noffke et al. 2012. Apart from this bottom water levels were low.
As mentioned above the following part has been added to the revised manuscript:

"Periodical oxygen intrusions due to coastal trapped waves are known for the water column and bottom waters at upper boundary of the OMZ (Guitierrez et al., 2008) but the centre of the OMZ essentially stays anoxic and usually is not influenced by oxygen intrusions (Noffke et al. 2012). Oxygen concentrations of the pore waters are even more depleted."

AR2: Data in table 4 and section 3.2 is very confusing and somewhere must be a mistake. You report 3 columns of data for foraminiferal denitrification rates, and if I add up approx A and B together I get the values you report in the text in the section 3.2 but these are not the values reported in your table 4 as the total foraminiferal denitrification!

Reply: Thanks a lot for this comment! Indeed there has been a mistake at the column for the foraminiferal denitrification rates. The denitrification rates discussed in the text were the right ones. All tables were checked again for mistakes and the errors have been corrected in the revised manuscript.

AR2: Section 4.2 First sentence. Its not true that foraminiferal denitrification has only been estimated in Sagami Bay. And you also contradict this sentence several times later in this section. For example, Pina-Ochoa et al. 2010 (PNAS) also estimated foraminiferal denitrification in Skagerrak, Bay of Biscay and Arabian Sea OMZ. Also Hogslund et al (2008) has estimated foraminiferal denitrifcation in the OMZ off the coast of Chile.

Reply: This is probably a misunderstanding. We did not write that foraminiferal denitrification at Sagami has only been estimated. Indeed we wanted to state that it is the only location where it had been measured quantitatively and not been estimated. To clarify this we changed the following part in the revised manuscript:

"Despite the novel pathway of nitrogen loss due to foraminiferal denitrification, so far the contribution of foraminiferal denitrification to the total benthic N2 production has been only **determined** for a single sampling site in 1450m water depth at Sagami Bay, Japan (Glud et al., 2009)." (Page 17788; Line 4-7 in the original manuscript)

has been chaged to:

"*Despite the novel pathway of nitrogen loss due to foraminiferal denitrification, so far the contribution of foraminiferal denitrification to the total benthic N_2 production has been only **measured** for a single sampling site in 1450 m water depth at Sagami Bay, Japan (Glud et al., 2009).*"

AR2: Conclusions section from lines 19 to end of paragraph. Nowhere before this have the nitrogen isotopes been discussed in the manuscript and no data is presented on this. How can you conclude about something you have no data on?

Reply: It is right that we do not have data about nitrogen isotopes but we internally discussed a lot about the potential influence of foraminifera on possible benthic nitrogen isotope fractionation within our collaborative research project (the SFB 754). We did not want to conclude about this topic but we wanted to provide some interesting implications which we felt is fine based on the interpretation of our data presented in this study (the caption of this part was "Conclusions and implications"). Thus, we kept the paragraph about the nitrogen isotopes in our revised manuscript but we will not hesitate to remove it if we have to.

AR2: Some other smaller commenst/issues that I feel should be revised and/or addressed. Abstract: In the first sentence you imply that foraminifera use nitrate as an energy source. Is this true? I thought that foraminifera are heterotrophic organisms. They can use nitrate/oxygen for their respiration but for as their primary energy source.

Reply: We apologize for our lax formulation in the abstract. To clarify that foraminifera use nitrate for respiration and not as food we changed the following part of the abstract:

"The discovery that foraminifera are able to use nitrate instead of oxygen as energy source for their metabolism has challenged our understanding of nitrogen cycling in the ocean." (Page 17776; Line 2-5 in the original manuscript)

has been changed to:

"*The discovery that foraminifera are able to use nitrate instead of oxygen as electron acceptor for respiration has challenged our understanding of nitrogen cycling in the ocean.*"

AR2: Abstract, line 3: elsewhere in article you also mention that diatoms are also able to denitrify? I also though some flagellates are also known to use nitrate, although they do not reduce all the way to N2. If you mention one example here you should mention them all?

Reply: It is true that some flagellates are known to survive anaerobic conditions (Müller et al., 2012) but as far as we know no flagellate has been reported to denitrify. We would be glad for a reference here because this is an interesting topic.

AR2: I would constantly refer to your stations with water depth. Rather than sometimes saying the shallowest, deepest etc. Use names consistently and it is much easier for a reader follow the text.

Reply: In the whole text of the revised manuscript we now refer all our stations with water depth, even if we sometimes are speaking from the shallowest, deepest etc. .

AR2: I would add bottom water oxygen content in Table 1. Also if your environmental data is not from these sites they should also be listed. And the implication of this should be explained and whether you can then actually compare the data?

Reply: We included bottom water oxygen concentrations ($[O_2]_{BW}$) in table 1. For two locations (465 m and 697 m) winkler calibrated measurements with an oxygen sensor at a CTD where available from Glock et al. (2011). For the other stations oxygen measurements were taken from nearby CTD-stations at the same water depths. Actually for all these stations a value <2 µmol/kg was measured which is below the detection limit of the CTD-sensor. We know that the CTDs were from nearby CTD-Stations (maximum difference W-S of ~0°01´´) but in all water depths (except for the two deepest stations) were essentially anoxic conditions during sampling time. Pore waters should be even more oxygen depleted (if it is even possible

to be more oxygen depleted than anoxic). We added the following part to the table captions of table 1 to explain where $[O_2]_{BW}$ come from:

"*Bottom water oxygen concentrations $[O_2]_{BW}$ in italic letters are taken from Glock et al. (2011). All other $[O_2]_{BW}$ are derived from closeby CTD-Stations. Note that detection limit for the CTD oxygen sensor was ~2 µmol/kg.*"

AR2: p.17781 line 15. Reference to Murray 2001? This sentence should be modified or reference changes. I doubt Murray discusses nitrate utilisation in his article from 2001?

Reply: Indeed this sentence might have been confusing because Murray did not speak about nitrate utilization in his study from 2001, of course. Murray made the ecological consideration that in environments where one factor is dominating and limiting it affects all species. To clarify this misunderstanding we changed the following part in the revised manuscript:

"The basic argument for this approach was that in a nitratelimited and chemical stable environment having a considerable faunal diversity a single species will not outcompete all others by exceptional high nitrate utilisation (Murray, 2001)." (Page 17781, Line 13-16 in the original manuscript)

has been changed to:

"*The basic argument for this approach was the ecological consideration that in environments having a considerable faunal diversity and where one factor is dominating and limiting, in this case nitrate, it will affect all species.(Murray, 2001). Thus, a single species will not outcompete all others by exceptional high nitrate utilisation.*"

AR2: I feel that the reference to "approximations A and B" in the results and discussuin is a chaotic. I feel that if this is well explained in the methods, it may not be necessary to confuse the reader with these assumptions throughout the text. Alternatively, a study limitations paragraph where this limitation is explained could be added and it would not need to be discussed more than that. I also think that "assumption" would be a better word than "approximation" to describe these study limitations.

Reply: As the reviewer suggested we changed the term "approximation A and B" to "assumption A and B" in the revised manuscript. These "assumptions" are described only in in the methods and there is a small paragraph about the total influence in the results section with reference to table 3 the revised manuscript. We did not take the "assumptions" out of the discussion in our manuscript completely because part 4.1 is mainly dealing with the "study limitiation" by these two assumptions. The only part where these assumptions are mentioned elsewhere in the manuscript is one small sentence in section 4.2:

"*Bolivina costata* was the dominant species at this station. The individual denitrification rate for this species is yet unknown and has been obtained by using approximation A. Hence, foraminiferal denitrification could be overestimated in our calculations at this site." (Page 17788, Line 25-28 in the original manuscript)

We think this sentence is important in this part of the discussion thus it was the only part mentioning the assumptions elsewhere in the manuscript we kept. To clarify that part 4.1 is evaluating the assumptions in respect to the calculated foraminiferal denitrification rates we changed the caption of this part in the revised manuscript:

"4.1 Evaluation of calculated foraminiferal denitrification rates" (Page 17787, Line 2 of the original manuscript)

has been changed to:

"*4.1 Evaluation of calculated foraminiferal denitrification rates and influence of assumption A and B.*"

AR2: p. 17786 lines 22-24. I do not understand the link with the rest of the paragraph.

Reply: This sentence has been deleted in the revised manuscript.

AR2: p. 17789 lines 17-26. I don't know how relevant the discussion of Globobulimina is here as it is not present in the study region.

Reply: It is true that *Globobulimina turgida* was not found in the study region. But the closely related and morphological similar *Globobulimina pacifica* was recorded. Although it has not been proven by comparison of genomes that both were the same species and hence synonyms, the discussion about *Globobulimina* is still reasonable at this point. Thus, we decided to keep this part in the discussion but we will not hesitate to remove it if we have to.

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AR2: p. 17789 lines 27-29. As this sentence reads now it implies to me that Bohlen et al modelled foraminiferal denitrification rates. I think this is not true so sentence should be modified.

Reply: We changed this part in the revised manuscript:

"At the 317 and 319-m stations in the centre of the Peruvian OMZ, foraminifera still cover 30–50% of the total denitrification as predicted by model calculations (Bohlen et al., 2011)." (Page 17789, Lines 27-29 of the original manuscript)

has been changed to:

"*At the 317 and 319-m stations in the centre of the Peruvian OMZ, foraminifera still cover 30-50% of the total benthic denitrification modeled by Bohlen et al. (2011).*"

AR2: p. 17790 line 6-7. I would think that denitrifying bacteria are the dominant denitrifiers at these sites!

Reply: We changed this part in the revised manuscript:

"It is yet unknown which organisms take over the baton from foraminifera as dominant denitrifiers at the deeper stations." (Page 17790, Lines 6-7 of the original manuscript)

has been changed to:

"*Denitrifying bacteria are probably also the dominant denitrifiers at the deeper stations (465 m and 697 m).*"

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