GENERAL ANSWER

The two referees asked for an improvement of the structure of the manuscript, especially concerning the discussion section 4.4 of the original submission. We agree with the two referees that the structure of submitted manuscript could be improved. Consequently, we reorganised the manuscript following the referees' comments and suggestions.

List of corrections made to improve the structure of the manuscript highlighted by the two referees:

1- The whole section about size distribution (section 3.3 in the original submission) was moved to the supplementary material. Since the data do not allow us to make conclusive observations about the foraminiferal population dynamics, we now use the size data only as an additional argument corroborating our hypothesis of interspecific differences in preferred food sources (last section of the discussion). We state very clearly that these results should be considered with care in the Material and Methods (2.5) section.
2- Section 4.4 of the discussion in the original submission (now 4.2) was completely reorganised (mainly the order of the different paragraphs within the section) and renamed, to make our discussion about species-specific responses to 1) anoxia/sulphide and 2) food sources clearer.
3- In the same manner, in section 4.3 of the original submission (now 4.1), we moved the second paragraph (about previous studies investigating the foraminiferal response to the presence of sulphides) to a later part of the same section, and used it for comparison with our results.
4- The first paragraph of section 4.3 of the original submission (now 4.1), about previous publications investigating the response of foraminifera to low oxygen concentration/anoxia and presence of sulphide was moved to the introduction.
5- The third paragraph of section 4.4 of the original submission (now 4.2), about previous publications investigating the species-specific responses of foraminifera to low oxygen concentration/anoxia and presence of sulphide was also moved to the introduction.
6- The original section 4.1 (discussion) about Rose Bengal and CTG was shortened and incorporated in the introduction, as suggested by the two referees.
7- A new section 2.1 "Study area", which contains section 2.1 and 4.2 of the original submission presents the general environmental setting of Lake Grevelingen and the environmental parameters measured in the Den Osse Basin (where our studied stations are located).
8- In section 2.2 (about field sampling methodology) we added many methodological details as asked by both referees.
9- The first paragraph and a part of the second paragraph of section 3.4 of the original submission, about encrusted forms of E. magellanicum was moved, to a new section (2.6) in the Material and Methods part of the revised manuscript. The second part of the last paragraph of section 3.4 of the original submission about encrusted forms of *E. magellanicum* was enlarged and moved to discussion section 4.2.

Referee #1

Review of the manuscript bg-2019-382.

General comments

The manuscript entitled "Foraminiferal community response to seasonal anoxia in Lake Grevelingen (the Netherlands)" by Richirt et al. consists of a field study which aims to analyze the benthic foraminiferal community characteristics during 1.5 years, during when seasonal hypoxia/anoxia occurs together with presence of H2S. The results are very interesting and will be useful for the community, and the figures are clear and informative. However, the paper is poorly structured, and some statements need to be taken more carefully. Therefore, I suggest the following revisions before publication in Biogeosciences.

A restructuration of the material and methods section seems necessary. I suggest to create a studied area section, separated from the material and methods, with a description of the lake and the Den Osse Basin. It would be especially interesting as, as the authors say in the introduction, "a large amount of environmental data is available" (Line 64). This section should include all the references cited in the second part of section 2.1 (which should then be deleted) and in section 4.2 from the discussion. This section 4.2 is a description of already published results, not a discussion of the results from this paper. I suggest moving this paragraph to the studied area section.

Done, see general answer point 7.

The CTG method and a comparison with the Rose Bengal method was published in 2006, which is thirteen years ago. Since then, many studies have successfully used CTG to label their samples. I do not think that this part of the discussion about why the authors have chosen this method is necessary. The whole section 4.1 is a repetition of what you say in the introduction and does not bring anything new, it should be removed.

Done, see general answer point 6.

The discussion needs to be restructured as well. The first two paragraphs of section 4.3 are a description of the literature, not a discussion. I would move them in the introduction section, and cite these references where they are relevant, later in the discussion. Similarly in section 4.4, the 3rd paragraph is literature description that should or go in the introduction and/or be included later when discussing the results of the paper.

Done, see general answer points 4 and 5.

I strongly suggest to reconsider the whole structure of the section 4.4, which I find not easy to read in the current state.

Done, see general answer point 2.

The authors should be very careful about the reaction times they give in the discussion and conclusion. For example, line 329, the "two months after" cannot be assed for sure, as we do not have information about the fauna in October. Picking does take a lot of time, and I understand that picking all the months was not possible, but I recommend using more

approximate times, especially for station 1. Moreover, for me at station 1 on Fig. 11, the foraminiferal response to H2S appears immediate, as their abundance is lower already in July. Could the authors explain?

We agree with the reviewer, and changed the text accordingly (lines 305–309):

"However, the fact that foraminiferal abundances reached almost zero only in September (about two months after the first occurrence of anoxic and sulphidic conditions in the upper sediment, in July) suggests that the presence of H_2S did not cause instantaneous mortality, but that the disappearance of the foraminiferal community was a delayed response, probably caused by inhibited reproduction and, eventually, increased mortality."

In the results, a full paragraph is dedicated to encrusted forms, together with a full plate of pictures, and two detailed graphs. I suggest to strongly develop this part in the discussion, which now consist of 4 lines, to include the information from the second paragraph of section 3.4 – and explanation given by these authors -, and the following references: Cedhagen 1996 (Phuket Marine Biological Center), and Heinz et al. 2005 (Marine Biology Research).

Done, see general answer point 9.
Because our results are merely an additional observation of this phenomenon, and do not allow us to draw any further conclusions about the function of these cysts, we do not want to develop this aspect much further in the discussion. However, we moved one sentence from the result section to the discussion section, and added some details about these cysts following the referee's suggestion.

Please also explain the current statements, do you suggest that the feeding cysts only get formed when *P. globosa* is blooming?

We found abundant encrusted forms (representing more than half of the specimens of *E. magellanicum*) only from May onwards, when the bloom of *P. globosa* occurs. This may of course be a coincidence, but it is also possible that the formation of feeding cysts (and then the proportion of encrusted individuals) is enhanced by the presence of suitable food, such as *P. globosa* may be for *E. magellanicum*.
In view of the lack of firm arguments in support of our rather speculative idea, we prefer not to develop it any further.

Please find below minor suggestions and text comments.
Minor comments

Abstract

Line 19: early diagenesis and organic matter recycling are mentioned here but never again in the paper. Please explain.

We think this is not really needed. However, we modified this sentence to underline the impact of these processes of the functioning of benthic ecosystems (lines 18–20):

"These hypoxic events have large consequences for the functioning of benthic ecosystems. They profoundly modify early diagenetic processes involved in organic matter recycling, and in severe cases, they may lead to complete anoxia and presence of toxic sulphides in the

sediment and bottom water, thereby severely affecting biological compartments of benthic marine ecosystems."

To:

"Hypoxic events have large consequences for the functioning of benthic ecosystems. In severe cases, they may lead to complete anoxia and presence of toxic sulphides in the sediment and bottom-water, thereby strongly affecting biological compartments of benthic marine ecosystems."

Line 30: This is in contradiction with your conclusion, is there not a "drop in standing stocks" for station 2?

We changed this sentence to clarify the relation between faunal density and euxinia (lines 28–30).

"Conversely, at the shallower site (23 m), where the duration of anoxia and free H_2S was shorter (one month or less), a dense foraminiferal community was found throughout the year."

By:

"Conversely, at the shallower site (23 m), where the duration of anoxia and free H_2S was shorter (one month or less), a dense foraminiferal community was found throughout the year excepted for a short period after the stressful event."

Line 34-35: The two sentences are in contradiction, please rephrase.

We do not see what is contradictory in our text.

Line 32: Replace "H2S" by "H2S".

Done

Introduction

Please shortly explain what are foraminifera, what are their place and role in these types of environment, and why you chose them for your study.

We do not think it is necessary to explain what are foraminifera; the aim of our study is explained in lines 82–83 and 97–98.

Line 43-46: This sentence is long and confusing, please rephrase.

We agree with the referee and rephrased it lines 42–45:

"The combination of global warming and eutrophication is strengthening seasonal stratification of the water column, decreasing oxygen solubility, and enhancing benthic oxygen consumption in response to increased primary production, resulting from increased anthropogenic nutrient and/or organic matter input (i.e. eutrophication, Diaz and Rosenberg,

2008).”

By:

“This is due to the combination of (1) global warming, which is strengthening seasonal stratification of the water column and decreasing oxygen solubility and (2) eutrophication resulting from increased anthropogenic nutrient and/or organic matter input, which is enhancing benthic oxygen consumption in response to increased primary production (Diaz and Rosenberg, 2008).”

Line 46: Could you give some examples of these consequences?

In view of the fact that the introduction is already very long, and that the biological response is widely known, we prefer to cite Riedel’s review paper (line 46).

Line 50: I suggest to specify which ones of these references are field or culture studies, and to reconsider the sentence accordingly.

In order to answer together with the reviewer suggestion from lines 77–78, we replaced this list of references (which were moved lines 77–79) by a review from Koho et al., (2012) line 49:

“Many foraminiferal taxa are able to withstand seasonal hypoxia/anoxia (e.g. Alve and Bernhard, 1995; Moodley et al., 1997; Moodley et al., 1998a; Geslin et al., 2004; Pucci et al., 2009; Koho et al., 2011; Langlet et al., 2013), and consequently can play a major role in carbon cycling in ecosystems affected by seasonal low oxygen concentrations (Woulds et al., 2007).”

By:

“Many foraminiferal taxa are able to withstand seasonal hypoxia/anoxia (see Koho et al., 2012 for a review), and consequently can play a major role in carbon cycling in ecosystems affected by seasonal low-oxygen concentrations (Woulds et al., 2007).”

Line 52: Could you explain why/how anoxia and H2S are linked?

In Lake Grevelingen, the relation between anoxia and sulphide is very complex, because of the interference of cable bacteria. Explaining this here would take a lot of place, and would be somewhat superfluous. We added some references in which the relationship is treated in detail (Jørgensen 1982, Seitaj et al., 2015) line 51.

Lines 77-78: These references are already cited earlier. Please restructure.

All these references are now used once in the introduction in lines 77–79. See our answer to the reviewer suggestion line 50 just above.

We modified the sentence in order to specify if the study was from field or culture study lines 76–80:

"Although the tolerance of foraminifera to low DO contents and long term anoxia (from weeks to 10 months) has been well documented for many species from different types of environments in laboratory culture (e.g. Moodley and Hess, 1992; Alve and Bernhard, 1995; Bernhard and Alve, 1996; Moodley et al., 1997; Duijnstee et al., 2003; Geslin et al., 2004; Duijnstee et al., 2005; Ernst et al., 2005; Pucci et al., 2009; Koho et al., 2011; Geslin et al., 2014) as well as in field studies (e.g. Piña-Ochoa et al., 2010b ; Langlet et al., 2013; 2014), their tolerance to free H_2S is still debated."

Line 81: Please add references, even if they are "sparse".

We removed this sentence, which concerns population dynamics. See general response, point 1.

Line 82: Is there not any previous foraminiferal studies in the lake itself?

There are only some previous reports (e.g. Donders et al. 2012), not published in peer-reviewed journals.

Lines 82-92: Please shorten this part, the CTG method is well known already.

In agreement with the second referee, we decided not to discuss Rose Bengal/CTG in the discussion section but rather to explain in the introduction why CTG is important particularly in environments where OM degradation may be very slow, lines 99–113.

Lines 96-97: This belongs to the method section, please remove.

This explains what we did so we think that it deserves to be mentioned at the end of the introduction. However, to take into account the reviewer's suggestion we changed the two sentences in lines 117–118:

"Foraminiferal assemblages were studied in the top 1 cm layer. For each dominant species, size distributions were determined in order to get insight into the population dynamics."

To:

"Living foraminiferal assemblages were studied in the uppermost sediment and size distributions were determined in order to get insight into the possible moment(s) of reproduction or accelerated growth in test size."

Line 100: example of these indices?

We think that adding this information would not be relevant.

Material and Methods

The description of the lake is not a part of the method. See also my general comments.

We agree with the reviewer. We added a "Studied area" section to the revised manuscript, see general answer point 7.

Please specify that SEM pictures were taken for the four dominant species including encrusted specimens, with which microscope and where were they taken.
We thank the reviewer for this comment. We added this in the Acknowledgements section in lines 500–502:

"We are grateful to Romain Mallet and the team of the SCIAM imaging facility at the University of Angers."
We also added T. Jauffrais and C. LeKieffre in acknowledgments.
"We acknowledge Jassin Petersen for his help with recovering some of the environmental data ***and Thierry Jauffrais and Charlotte LeKieffre for discussion about alternative metabolisms****."*

Lines 112-114: This paragraph should be moved to the field sampling section.

Done, see lines 148–150.

Line 114: I guess a map is available in the cited paper? Maybe you can precise it here?

We modified the sentence in agreement with the reviewer's suggestion line 149.
We also changed the reference here for an earlier one (Hagens et al., 2015):
"Both station 1 (51°44.834' N, 3°53.401' E) and station 2 (51°44.956' N, 3°53.826' E) are located in the main channel, at 34 and 23 m depth, respectively (see map in Hagens et al, 2015)."

Line 118: "similarly", by who?

We now precise it lines 155–156:

"The data for station 2 (Supplementary Table 1) were acquired similarly and during the same cruises but never published, for further details about the sampling method, see Seitaj et al. (2015)."

Line 120: Please give more details about the sampling. I see in the acknowledgments that the r/v Luctor was involved. What kind of corer was used? How long where the cores? Were some environmental data taken at the same time?

Done, see general answer point 8.

Line 123: I know that CTG labelling happens on the field. But after that you talk about picking. As this is not a field sampling event, I would move this to the sample treatment section.

Done, this sentence was moved to the section 2.3 (Sampled Treatment) on lines 171–173.

Line 127: Add "finally" before "investigated". See my comment about Table 1.

We changed the caption of Table 1 to make it clearer:

"Sampling dates for stations 1 and 2. x = one core investigated, o = no core investigated"

By:

"Sampling dates of the samples which were investigated for living foraminifera for stations 1 and 2. x = one core investigated, o = no core investigated"

Line 133: "previous studies", where were they? Please add references.

This is a generality. We took this value because it is easier to compare standardised volume with other studies. To make it clearer we changed line 176:
"Abundances were then standardised to a volume of 10 cm^3 in order to facilitate comparison with previous studies."
By:
"Abundances were then standardised to a volume of 10 cm^3."

Line 166: On which species was this done, and how many specimens were used?

Added in section 2.5 on lines 208–209:
"The measurements were made for all species, which represent together 4176 individuals for station 1 and 19624 individuals for station 2."

Results

Line 178-179: Remove this sentence. You already explain it in the method, and the Figure 2 has a caption.

Done.

Line 179: Please check if you mean total or mean abundances here.

We replaced *"Total abundances"* by *"Averaged total abundances"* line 241.

Line 183: I would be careful with the use of "early" and "late", talking about the seasons. July is not early summer. Line 433, March is not winter. Please check through the paper, maybe giving the months is the most accurate solution.

In the submitted version, we used astronomical seasons, in which March is late winter and July is early summer. As suggested by the reviewer, in order to avoid any confusion, we replaced and/or specified references to seasons in the manuscript with months in all necessary cases.

Lines 194-195: Please remove this sentence, you have already explained in the method.

Done.

Line 197: Replace "Fig.4" by "Figure 4". This sentence should be moved to the method section.

Done in line 257.

Lines 203-204: I suggest to remove this sentence, it does not bring anything new.

We don't really agree, even if the dominant species for both stations are given before, this sentence summarises the faunal difference between stations 1 and 2. We think it is a useful addition.

Line 206: Add "and Table 2" after Fig. 4.

Done in lines 265–266.

Line 211: Remove "(fairly low)"

We removed the brackets. We changed this paragraph accordingly to the reviewer next comment.

Line 213: We know that *T. inflata* was absent in 2011, as you said it line 205. Please rephrase. I think the way you described the results for the station 2 is clearer than for station 1. I suggest to also describe the station 1 species by species, instead of year by year.

The sentence in line 205 in the original submission is a general comparison between the two stations for all the species. Sentence line 213 in the original submission is dedicated to station 1 and only *Trochammina inflata*. We think that the two sentences have to remain in the manuscript.
We restructured the paragraph about station 1 and now describe densities species by species as suggested by the reviewer (lines 265–275).

Line 225: Please remove "Conversely to station 1", this is confusing here.

Done.

Lines 230-233: This should be moved to the methods section.

This part was moved to Supplementary material. See general answer point 1.

Line 234: Please add "(Fig. 6)" after "station 2".

Done.
This part was moved to Supplementary material. See general answer point 1.

Lines 256 and 258: same information, please modify.

Done.
This paragraph was modified following the general answer point 9.

Line 260: "Similar observations", where?

This paragraph was modified following the general answer point 9.
It is now in Discussion section lines 469–472.
To follow the reviewer comment we added the locations between the brackets:

"Concerning the cysts of E. magellanicum described here, very similar observations have been made for Elphidium incertum at different locations (Norwegian Greenland Sea and

Baltic Sea in Linke and Lutze, 1993; Koljö Fjord in Gustafsson and Nordberg, 1999; Kiel Bight in Polovodova et al., 2009).”
Line 260-262: This part should go to the discussion section.

It is now in Discussion section lines 469–472.
See general answer point 9 and previous comment.

Line 263: Please remove this sentence and cite the Figure 9 in the following sentence.

To take into account the reviewer’s suggestion, we modified the sentence in line 293–295: *“At station 1, encrusted forms of E. magellanicum were present in moderate proportions in May (26.8 % of the total E. magellanicum population, Fig. 9) and July (47.6 %); the species disappeared thereafter. At station 2, encrusted forms strongly dominated the E. magellanicum population from May (72.3 %) to December (88 %, Fig. 9).”*

Discussion

I think the section 4.1 should be removed from the paper. See also my general comments.

See general discussion point 6.

The information given in the 4.2 section are not results from this paper, they are a description of the site citing already published papers. This should go in the studied area section. See also my general comments.

See general discussion point 7.

In section 4.3, the actual discussion starts on line 321. See also my general comments.

See general discussion point 3.

Line 337: Do you have information about why the 2011 hypoxia was so severe compared to the 2012 one?

We do not have information about this.

Line 339: I know that this study only focus on living fauna, but it would have been interesting to check the dead fauna further down in the cores, to see if standing stocks were indeed higher before the 2011 severe hypoxia.

This is a part of another paper about a long core studying dead fauna at station 1. Because the work is still in progress, we cannot say anything about this yet.

Line 345: Could you explain how you deduced these “6 months” of recovery? As the hypoxia event was much more severe in 2011, how could we know if the H2S stayed longer in the upper sediment compared to 2012, and thus how long it affected the fauna? Please explain.

We assumed that H_2S front in the sediment migrated according to bottom water hypoxia in 2011 like in 2012 for stations 1 and 2: when bottom water hypoxia (or anoxia) occurred, H_2S in the upper part of the sediment occurred also. See lines 337–340 in original submission and

now lines 315–318.
We estimated a recovery time of about 6 months because this is the time between the resurgence of oxic conditions in the bottom water in September 2011 and presence of foraminifera in March 2012.

Line 366: Please remove "(i.e. like station 1)".

We removed this as suggested by the reviewer in line 355.

Line 365: This paragraph and the following one are very similar. I suggest to merge them.

In the first paragraph (lines 365-370 in original submission) we discuss the delayed response which also probably occurred in 2011.
In the second one (371-374 in original submission) we discuss the fact that repeated short events are probably more harmful than one short event (comparison 2011–2012).
Since these two ideas/suggestions are different, we prefer to keep the two paragraph as they are now in the discussion in lines 355–364.

Line 379: We cannot be sure about that, as there are no available data. Please modify this statement.

We want to point out that there are available data in November 2011 and January 2012 for station 1.
However, we slightly changed the sentence to make clearer that this is an assumption on lines 367–369:

"However, at station 2, foraminiferal abundances increased again in December 2012, suggesting a recovery time of about two months, much shorter than at station 1, where standing stocks in the >125 µm fraction only increased 6 months after the presence of anoxia and free sulphides."

By:

"However, at station 2, foraminiferal abundances increased again in December 2012, suggesting a recovery time of about two months, ***which is likely*** *much shorter than at station 1, where standing stocks in the >125 µm fraction only increased 6 months after the presence of anoxia and free sulphides."*

Line 386: Remove "(in contrast to station 2)".

We think it is a relevant comparison at this point in the discussion and we would like to keep this sentence as in original submission. Now in line 377.

Line 387: "by the nearby sites", I thought the water circulation was weak in the lake? Is transportation then possible? Please check.

This transport can happen because we are in one of the deepest channel of the lake, and could take place by under-water landslides.
Even in the case of weak water circulation, we cannot exclude completely transport of propagules from nearby sites for example.

We added *"possibly"* between the brackets on line 378:

"(e.g. ***possibly*** *by nearby sites or by the remaining few individuals)"*

Lines 395-396: This sentence belongs to the results section, please remove.

See general answer point 2.

Line 437: But no diatoms?

This information is not specified in Hagens et al. 2015.

Line 438: Which *Elphidium*? Elphidiids?

We refer to the genus *Elphidium* in general. For further information, see Pillet et al., 2011 as mentioned in the original submission.

Line 440-441: Remove this sentence, it is confusing there, and you talk about this aspect just after.

We think that this sentence has its place in the manuscript in its new form (see general discussion point 2) and that it should be conserved.

Line 470: What about *T. inflata*?

We decided not to discuss this species in this paragraph because we have no clue of its food source. To our knowledge, the general ecology is less known that that of the hyaline species of this study. Moreover, this species, although considered as dominant species based on subjective criteria (>1%), is less represented than the others. For these reasons we prefer not to discuss this species extensively in our manuscript.

Lines 476-479: This part should be developed. See also my general comments.

See general answer point 9. We developed this aspect in the discussion lines 466–475 as requested by the reviewer. However, we prefer not to discuss these encrusted forms in our manuscript further than this.

Conclusion

I would add a short introductory sentence or add details to the first sentence, to quickly remind the reader what you did.

We added a sentence in lines 473–474.
"In this study we examined the foraminiferal community response to different durations of seasonal anoxia coupled with the presence of sulphide in the uppermost layer of sediment at two stations in Lake Grevelingen."

References

Biogeosciences is very careful with bibliography details. Please go through your references list: ~10 papers miss doi, some miss page range, etc.

We carefully checked the references list as asked by the reviewer.

Figures
Table 1: You say in the text that the sampling happened every month, but that you only analyzed specific months. Thus, it the title correct here?

We corrected the caption, see previous referee comment about line 127.
We changed the caption of Table 1:
"Sampling dates for stations 1 and 2. x = one core investigated, o = no core investigated"
By:
"Sampling dates of the samples which were investigated for living foraminifera for stations 1 and 2. x = one core investigated, o = no core investigated"

Figure 1: In the caption, remove "This figure shows" in the first sentence, and add somewhere "for size measurement" as well as "ImageJ software".

We replaced:
"This figure shows the different steps of the numerical treatment of each image. The left figure shows the untreated image, the middle figure presents the next step, when all individual foraminifera are depicted. Finally, the figure on the right shows the individual foraminiferal outlines which were measured."
By:
"Numerical treatment used for the size measurement for each image performed with ImageJ software. The left figure shows the untreated image, the middle figure presents the next step, when all individual foraminifera are depicted. Finally, the figure on the right shows the individual foraminiferal outlines which were measured."

Figure 2: I don't think "Total living assemblage" is necessary below Station 1 and Station 2. Instead, it would be better to have this as the vertical axis title, with the unit (ind. 10 cm-3) into brackets. In the caption, replace "for which" by "where" to be consistent with other captions.

We replaced *"for which"* by *"where"* in the caption of figure 2.

However, we prefer not to remove *"Total living assemblage"* from the figure itself and place it as vertical axis title, because we think it helps the understanding and this is consistent with figures 11 and 12. We think that the figure is already clear enough when also considering caption.

Figure 4: Vertical axis title?

We think that the figure is already clear enough when also considering the caption.

Figure 5: Vertical axis title? Also, I guess you mean "station 1" in the last sentence. Please check the months in bold.

We think that the figure is already clear enough when also considering the caption.

We replaced *"station 2"* by *"station 1"* in the last sentence of the caption, as pointed out by the reviewer.

Figure 9: Vertical axis title? It would be informative to have the percentage of encrusted specimens on top of each bar.

We added the % of encrusted form specimens on top of each bar. We also changed the vertical axis legend *"ind. / 10 cm^{-3}"* by *"ind. 10 cm^{-3}"* to stay consistent with other figures. We think that the figure is already clear enough when also considering the caption concerning the vertical axis title.
The caption was modified accordingly:
"Figure 9: Mean abundances (ind. 10 cm^{-3}) of non-encrusted (grey) and encrusted forms (black) of Elphidium magellanicum in 2012, at station, 1 (left) and 2 (right), with proportion of encrusted forms above each bar (in %). Investigated months are indicated in bold."

Figure 11: You use the word "suboxic" in the caption, it's not coherent with the rest of the paper. Please check the months in bold.

We corrected the reference in the caption of figure 10 by replacing "Sulu-Gambari et al., 2015" by "Seitaj et al., 2015".
The term suboxic is used in Seitaj et al. 2015, the original publication where the data where published. We changed the caption as following:
"The middle panel represents the depth (in mm) distribution of the oxic (blue), absence of oxygen and sulphides (orange) and sulphidic (black) zones within the sediment in 2012, from Seitaj et al. (2015)."
The term "suboxic" does not appear anymore in the manuscript.

Figure 12: "Figure 12".

We changed *"Figure Discussion3"* by *"Figure 11"* (because figure 10 in the original submission was removed as asked by the second reviewer).

I hope my comments will be taken by the authors in a spirit of constructive criticism with only intention to further improve their manuscript.

Sincerely, Laurie M. Charrieau

Referee #2

Comments to the Author
Manuscript ID: bg-2019-382
The manuscript of Richirt and coauthors on "Foraminiferal community response to seasonal anoxia in Lake Grevelingen (the Netherlands)" represents the assemblage fluctuation of benthic community in response to hypoxic/anoxic environments. These analyses are important to understand the foraminiferal tolerance to hypoxia/anoxia and hydrogen sulfide, and to understand life histories under the extreme environments. However, the structure of manuscript is very poor and experimental design and data validations are problematic. Therefore, I strongly suggest reconstructing throughout the manuscript, and also data validation is needed.
The biggest problem is that authors only used specimens of 125µm or more. Juvenile specimens have the size smaller than 125µm. If you are looking at population dynamics, you must deal with juvenile specimens.

See general answer point 1.

We agree with the reviewer that the use of only the >125µm fraction (due to time limits) is a strong limitation and consequently, we cannot draw any firm conclusions about the population dynamics of the different species.

However, we already made very clear statements in the original submission itself that we use these data only to get insights and not to determine the population dynamics exhaustively.

In original submission section 2.5 line 165:

"In order **to gain insight** into the foraminiferal population dynamics, size measurements were performed on all samples of 2012"

We also already explained how we considered these results and emphasized the caution the reader must take when considering these data in the original submission section 2.5 lines 174-175:

"As we only examined the size fractions >125 µm, our analysis mainly concerns adult specimens, and does not include juveniles. **This limitation should be kept in mind when interpreting the results**."

Also in section 3.3 in the original version (now lines 223–230), we detailed what is possible or not possible to assess with our data and that we get only some clues concerning population dynamics in lines 245-251:

"Our tentative to distinguish cohorts by using a deconvolution method to separate the total size distributions into a sum of Gaussian curves was not conclusive. **The main problem was the fact that we did not have any information concerning individuals smaller than 125 µm**, so that our size distributions were systematically skewed on the left side (i.e. toward small individuals). An additional problem was the large number of smaller specimens which were always present. Because the identification of individual cohorts was not successful, **parameters like reproduction rate, growth rate or lifespan were not assessable**.

Nevertheless, **the size distribution data give some clues** concerning the population dynamics of the two dominant species."

However, we agree that the term "population dynamics" for the foraminiferal size distribution in our study should not be used in the manuscript because it can be confusing, and we modified the manuscript accordingly.

In the methods section, the authors should explain more detailed procedures. I also found several methods sentences in the result and also in the discussion. Also, in the section 3.4, the authors described methods, although this paragraph is in the results section. These explanations should be move to appropriate section.

See general answer points 2, 8 and 9.

In the first section of the discussion (4.1), the author described both advantages and disadvantages of both CTG methods and Rose Bengal staining respectively. However, the CTG method has already described in Bernhard et al. (2006), and therefore it is not necessary to explain in detail.

See general answer points 6.

In the Section 4.2, I strongly suggest that the author should describe environmental setting of the sampling points. However, these descriptions must be explained in the beginning of this article. The authors also should explain vertical profile of oxygen in the water column and in the sediment in the "environmental settings of Den Osse Basin" section. This information can help readers to understand the habitat where foraminifera live in.

See general answer points 7.

In the section 4.3, I cannot understand what you want to discuss about. The authors referred (quoted) about previous studies in the first two paragraphs. The authors should move these paragraphs to the introduction, Ah...you would like to discuss relationship between sulfidic condition and foraminiferal assemblages? The discussion starts from line 321... I strongly recommend to make clear and re-structure throughout the manuscript.

See general answer points 3.

Other comments.

Line 34, "Elphidium selseyense and Elphidium magellanicum are much less affected by anoxia and free H2S than Ammonia sp. T6"
Is the light reaching the lake bottom? Is it not necessary to consider the photosynthesis of kleptoplasts?

We added the fact that light is not likely reaching the bottom of the lake in the discussion section 4.2 in lines 411–413:
"As Hagens et al. (2015) observed that the light penetration depth in the Den Osse Basin never exceeded 15 m in 2012, and therefore photosynthesis by kleptoplasts (Bernhard and Alve, 1996) appears unlikely for both our aphotic stations (34 and 23 m depth)."

Ammonia T6 has a nitrate pool in the cell. Nomaki et al. (2014, Limnol. Oceanogr., 59, 1879–1888) points out that this species potentially use an anaerobic respiration.

We now discuss about alternative metabolisms and symbiont bearing in introduction lines 93–96 and in discussion section 4.2 lines 395–403.

Line 47-, "Benthic faunas are strongly impacted by these events (Diaz and Rosenberg, 1995) although the meiofauna, especially foraminifera, appears to be less sensitive to low Dissolved Oxygen (DO) concentrations than the macrofauna"

Virgulinella, Bulimina, etc. may be sensitive to anoxic environments. Cannariato et al (1999, Geology, 27, 63-66) has analyzed community changes over the last 60,000 years at Santa Barbara Basin. As a result, low-oxygen torelant species are clearly replaced. Bolivina tumida, Buliminella tenuata and Globobulimina auriculata are low oxygen torelant species (dysoxic species). Interestingly, the response to hypoxia varies from species to species. Buliminella tenuata increase at the beginning of dysoxic. On the other hand, Bolivina tumida increases toward to the end of the dysoxic period.

We agree with the referee, this sentence is a general statement, and is completed by the next sentence which specifies that not all foraminiferal taxa are able to withstand with hypoxia/anoxia using also a reference (Koho et al., 2012) in lines 46–50:

"Benthic faunas are strongly impacted by these events (Diaz and Rosenberg, 1995) although the meiofauna, especially foraminifera, appears to be less sensitive to low dissolved oxygen (DO) concentrations than the macrofauna (e.g. Josefson and Widbom, 1988). ***Many foraminiferal*** *taxa are able to withstand seasonal hypoxia/anoxia (****see Koho et al., 2012 for a review****), and consequently can play a major role in carbon cycling in ecosystems affected by seasonal low-oxygen concentrations (Woulds et al., 2007)."*

Bolivina tumida has symbiotic microbes in its cells. Bolivina pacifica, Uvigerina peregrina, and Loxostomum pseudoberyichi retain microbes outside (in the pore) (Bernhard et al. 2018, Mar. Micropal. 138, 33-45). Based on these phenomena, it is expected that the response pattern to anoxia will differ depending on the symbiotic mode. The authors should explain/discuss this phenomenon in introduction and discussions.

We now discuss alternative metabolisms and symbiont bearing in the introduction in lines 93–96 and in the discussion in section 4.2 in lines 395–403.

Line53-, "Neutral molecular H2S can diffuse through cellular membranes and inhibits the functioning of cytochrome c oxydase (a mitochondrial enzyme involved in ATP production), finally inhibiting an aerobic respiration (Nicholls and Kim, 1982; Khan et al., 1990; Dorman et al., 2002)."
What do you think about an anaerobic respiration? The authors should explain about an anaerobic repiration.

We now discuss alternative metabolisms and symbiont bearing in the introduction in lines 93–96 and in the discussion in section 4.2 in lines 395–403.

Line 89, "In order to avoid this problem, we used CellTracker™ Green (CTG) to recognise living foraminifera. CTG is a fluorescent probe which marks only living individuals with

cytoplasmic (i.e. enzymatic) metabolic activity (Bernhard et al., 2006)"
This method is not new. The authors should only mention that CTG staining was used to distinguish live benthic foraminifera populations.

See general answer point 6.

Line 115-, "Measurements of oxygen concentrations in the bottom water (1 m above the sediment-water interface using a CTD) for 2011 are from Donders et al. (2012), whereas the 2012 data are from Hagens et al. (2015) and Seitaj et al (2017). Oxygen Penetration Depth (OPD) and depth of free H2 S detection were determined using O2 and H2S microsensors by Seitaj et al., (2015) for station 1, and the data for station 2 were acquired similarly (Supplementary Table 1)."
The authors should explain about environmental settings both station 1 and 2 in the beginning. This information can help reader to understand faunal assemblage changes (and population dynamics). This information is in the end of this manuscript.

See general answer point 7.

Line 121-, "The uppermost centimetre of each core was labelled with CellTracker™ Green CMFDA (CTG, 5-chloromethylfluorescein diacetate, final concentration of 1µM following Bernhard et al., 2006) and fixed in 5 % sodium borate buffered formalin after 24 h of incubation."
Where did you done this experiment? What kind of tools did you use? Did you sliced top 1cm and then put in the petri dish or some other container for CTG incubation? or jut put CTG directly onto the top of core? Need detailed experimental procedures.

See general answer point 8.

Line 129, "125µm"
As the authors mention about juvenile specimens, it is important point. Juvenile specimens have smaller than 125µm in size in many cases. If you are looking at population dynamics, you should deal with juvenile specimens. For this reason, it is difficult to see when the juvenile specimens have been reproduced.

See general answer point 1.

Line 145, "Supplementary Figure 1 shows…"
I found there are two types in these specimens. Specimens #145 and 152 have a larger proloculus than specimens #147 and #155. In my opinion, these differences in morphology correspond to different generations, megarospheric and microspheric. It is important points to find these generations to understand population dynamics. I strongly recommend to check which generations are abundant in each month.

Unfortunately, the scale bar in the previous version of the Supplementary Figure 1 was wrong for 3 of the 4 specimens. We corrected this, and measured a proloculus size of 43 to 61 µm, meaning that these are all megalospheric specimens. In fact, when we checked several of our microscopic slides, we found that the assemblages were always strongly dominated (>95%) by megalospheric specimens. In view of this, it doesn't seem useful to pay further attention to this point. All the more so, since we substantially diminished our discussion of population dynamics, with the few remaining elements now being presented as supplementary material.

Line 145, “the penultimate chamber”
Are there any differences in the pore size for each month (season)?

There is in fact a difference in pore size between stations 1 and 2, previously described by Petersen et al. (2016). We don’t mention this, because we consider it to be outside the scope of the present paper.

Line 165, “population dynamics”
Need juvenile specimens for analyze.

Agree, see general answer point 1.

Line 169, “Fig. 1”
I think the authors should explain much more detail in this paragraph. Detailed procedures were written in figire1 caption!

Agree, see general answer point 8.

Line 175, “>125 μm, our analysis mainly concerns adult specimens, anddoes not include juveniles. This limitation should be kept in mind when interpreting the results”
If the authors discuss about population dynamics, it is necessary to check juveniles.

Agree, see general answer point 1.

Section3.1
Any statistical analyses?

We think that statistical analyses are not relevant/meaningless in view of the number of replicates and values (only 2).

Line 185, “very low in January”
I strongly suggest that the author should describe environmental setting of the sampling points. However, these descriptions must be explained in the beginning of this article. The authors also should explain vertical profile of oxygen in the water column and in the sediment in the "environmental settings of Den Osse Basin" section. This information can help readers to understand the habitat where foraminifera live in.

Agree, see general answer point 7.

Line 193, section 3.2
It is better to explain one by one. The authors should explain about station 1 and then explain about station 2.

This is already the case in original submission, lines 194–204: general statement
Lines 205–214: station 1
Lines 215–228: station 2

Line 221-, “then progressively decreased until the end of 2012 (= 48.1 ± 26) in November 2012). Trochammina inflata showed a similar pattern as Ammonia sp. T6”

It is necessary to indicate statistical analyses. Statistically significant?

In view of the low number of replicates, we think that inferential statistics will be not meaningful. We prefer to use descriptive statistics as the mean and standard deviation. However, we changed the word *"similar"* by *"analogous"* to soften this statement in line 283.

Line 237, "of larger individuals (>400 µm)"
Are there any ecological meanings?

Our discussion of the size distribution has been shortened and moved to supplementary material. In view of this, it doesn't seem useful to us to speculate about the ecological meaning of size differences.

Line 239-, "The low number of Ammonia sp. T6 individuals at station 1 does not allow us to draw any firm conclusion concerning the size distribution at this station"
In the result section, the authors should describe "results" in detail. For example, there are several large sized individuals in May, simultaneously 200~250 µm-sized individuals are there. How about propagules? Alve and Goldstein (2002, Journal of Micropaleontology, 21, 95-96; 2003, Limnology and Oceanography, 28, 2163-2170) discussed about propagules in their literatures.

See general comment point 1. This part was moved to the supplementary data. Therefore, it doesn't need more details.
Propagules are the same problematic than the fact that we do not look at specimens smaller than 125 µm. We also want to point out that looking at propagules in situ is very difficult because of taxonomical issues that arise when looking at very small individuals.

Line 243, "but started to diminish in December"
Are there any data? Please provide.

See general answer point 1.
Yes, see figure 7 right panel where the data are shown in original submission for station 2. Now moved in supplementary as Supplementary Figure 2.

Line 244, "decrease of the median to 339 µm"
Ammonia has two generations, asexual and sexual phases. These two generations are commonly found in spring and autumn. The authors have to think about the life cycle of foraminifera.

See our answer to the previous comment about micro/megalospheric alternance generation. There is no evidence of seasonal changes between megalospheric and microspheric generations in our material.

line 245-, "Our tentative to distinguish cohorts by using a deconvolution method to separate the total size distributions into a sum of Gaussian curves was not conclusive"
Please indicate in the methods section.

This paragraph was moved to the section 2.5 in lines 220–223:

"In an attempt to recognize the different cohorts for each species in each of the bimonthly samples, we assumed that the size distribution was a sum of Gaussian curves, each of them representing a cohort. In order to identify the approximate mode for the Gaussian curves (i.e. cohorts), we used the changes in slope (i.e. inflexion points) of the second-order derivative of the total size distribution (Gammon et al., 2017)."

Line 246-251,
It is not a result. If the goal is to evaluate foraminiferal behavior in an anaerobic environment, an experimental desing that analyzes small individuals should be considered. Objective 2 cannot be achieved.

We reformulated objective 2 in order to clarify that the aim of the paper is not to describe or explain population dynamics but rather the species-specific response to seasonal anoxia coupled with sulphide in lines 120–121:
"to obtain information about the life histories of the various species under adverse conditions"
By:
"to obtain information about the responses of the various species to adverse conditions."

Line 255, "thin (Fig. 8c– e) and rather coarse"
Are there any data? To explain how it differs from the normal case, the authors should show the data.

Unfortunately, we don't have data concerning the thickness of the cysts. Since these cysts have only on very few occasions been described, and never in great detail, it is impossible to define what a "normal" cyst is.

Line 257-, "Because the crust stayed cohesive after exposition to 0.1 M of EDTA (EthyleneDiamineTetraacetic Acid) diluted in 0.1 M cacodylate buffer (acting as a carbonate chelator)"
This sentence should be moved to the methods section.

This sentence was moved to the Method section in lines 234–236:
"In order to determine if the crust matrix is constituted of carbonate, we placed some specimens in microtubes and exposed them to 0.1 M of EDTA (EthyleneDiamineTetraacetic Acid) diluted in 0.1 M cacodylate buffer (acting as a carbonate chelator)."

Line 259-,
This sentence should be move to the discussion section.

See also general answer point 9.
These sentences were modified and moved to the discussion section 4.2, lines 467–472.

Line 269-281,
It is not necessary to explain detailed about disadvantages of Rose Bengal staining method and advantages of CellTracker Green. Yes, the CellTracker Green labeling is suitable and reliable method to identify live specimens. However, incubation is required for the CTG method. I think this method includes some artifacts. During the staining, samples were transferred to petri dishes or bottles for 24 hours. The specimens were exposed different environmental condition from their habitat. This paragraph can be more shorten. Because this

method was already described in Bernhard et al (2006), so the authors do not need a detailed description of this method.

See general answer point 6.

Line 291, Fig. 10
You can omit this figure. Because, this is not your data. You can mark the timing of blooming on your figures 11 and 12.

We removed this figure from the manuscript and adapted the figure numbers in accordance with this change throughout the manuscript.

Line 328-,
In the case of symbiontic bacteria-bearing foraminifera, oxic condition is not suitable. Because symbiotic bacteria cannot consume hydrogen sulfide, methane or nitrate in an oxic condition, and the host foraminifera cannot use organic matter and/or anaerobic respiration from microbes.

We now discuss alternative metabolisms and symbiont bearing foraminifera in the introduction in lines 93–96 and in discussion section 4.2 lines 395–403.

Line 368-
There is little data in 2011. This sentence is overstatement. At both stations 1 and 2, low oxygen was observed from May to August. This situation is totally different from 2012. This characteristic situation will affect next year's (2012) assemblages.

In order to underline the speculative nature of our sentence, we modified lines 356-358 as follows:
"If we assume that, like in 2012, rich foraminiferal faunas were present in spring 2011 at both stations, the low faunal densities observed in August and November 2011 could suggest that also in 2011, foraminifera show a delayed response to sulphidic conditions."
To:
"If we assume that, like in 2012, rich foraminiferal faunas were present in May–July 2011 at both stations, the low faunal densities observed in August and November 2011 could suggest that foraminifera ***may have also shown*** *a delayed response to sulphidic conditions in 2011."*

We agree with the reviewer, that the succession of hypoxia was very different between the 2 years, but unfortunately, our faunal sampling in late 2011 is too scarce to compare the responses to the 2011 and 2012 hypoxia in detail.

Line 381-, "leading ultimately (in November) to almost complete disappearance of the foraminiferal fauna."
I'm worried about incubation time (duration) for CTG staining. For example, oxygen penetration depth is about 4mm in October at station 1, but sulfide layers still existed in the deep layer below 4mm. When the authors used top 1cm of the sediment for incubation, sulfidic conditions will be constructed in the experimental bottle (or other gear). For this reason, when living specimens still exist in top 4mm in October, sulfidic conditions may affect living ones. However, the authors did not explain detailed procedures of CTG staining methods. Long time exposure of sulfidic condition may affect living specimens. How did you evaluate for this effect in your experiment?

Immediately after sampling, and before adding the CTG stain, the sediment sample was carefully mixed with an equal volume of oxygenated water, and sample recipients were left unclosed in contact with the atmosphere. This treatment should be sufficient to oxidize all available sulphides.
The implicit question of the referee, whether in sulphidic conditions the metabolic activity of the foraminifera is still sufficient to be labelled with the CTG stain, is important. The answer may be different for different species, and can't be answered here.
We added details about sampling method as pointed out in the general answer point 8.

Line 384-, "inhibited reproduction, and eventually, increased mortality"
Need juvenile data.

See general answer point 1.
To take into account the reviewer's comment we changed this statement and slightly altered the sentence lines 373–375:
"The delayed response at both stations shows that mortality has not been instantaneous, and suggests that the decreasing standing stocks are the result of inhibited reproduction, and eventually, increased mortality."
By:
"The delayed response at both stations shows that instantaneous mortality was limited, and suggests that the decreasing standing stocks might rather be the result of inhibited reproduction, and eventually, increased mortality."

Line 390, Section 4.4
It is not appropriate section title. Need improvement. This section includes many topics related to environmental characteristics and food availability for foraminiferal responses. The authors should rearrange and clarify what authors want to discuss. This paragraph also includes the results. Need reconstruction.

We agree with the reviewer. We restructured this section as indicated in general answer point 2. We renamed the section as asked by the reviewer, which is now:
"4.2 Species-specific response to anoxia, sulphide and food availability in Lake Grevelingen"

Line 391-, 1st paragraph
Is this a topic sentence in this section? I think this information should be move to the Materials & Methods section.

See general answer point 2. The sentence was removed from the manuscript.

This section is also long and confusing. The authors have to reconstruct.

See general answer point 2.

Line 413, "take place throughout the year"
Are there any evidences that reproduction took place throughout the year? The authors should describe detailed results in the Result section. There exist relatively small-sized specimens that increased in May and September-October-November. In my opinion, it looks reproduction occurred twice in 2012. However, it is difficult conclude that there are no three or four chambered juveniles.

The suggestion of the reviewer is based on the increased number of Ammonia T6 specimens of 180 to 240 µm. However, these are already young adults. Unfortunately, we do not have any data for the 63-125 µm fraction, so that we can't draw firm conclusions about reproduction periods, as indicated by both referees.

Foraminiferal community response to seasonal anoxia in Lake Grevelingen (the Netherlands)

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Abstract. Over the last decades, hypoxia in marine coastal environments ha~~ve~~s become more and more widespread, prolonged and intense. ~~These hypoxic~~Hypoxic events have large consequences for the functioning of benthic ecosystems. ~~They profoundly modify early diagenetic processes involved in organic matter recycling, and in~~In severe cases, they may lead to complete anoxia and presence of toxic sulphides in the sediment and bottom ~~-~~water, thereby ~~severely~~strongly affecting biological compartments of benthic marine ecosystems. Within these ecosystems, benthic foraminifera show a high diversity of ecological responses, with a wide range of adaptive life strategies. Some species are particularly resistant to hypoxia/anoxia and consequently, it is interesting to study the whole foraminiferal community as well as species specific responses to such events. Here we investigated the temporal dynamics of living benthic foraminiferal communities (recognised by CellTracker™ Green) at two sites in the saltwater Lake Grevelingen in the Netherlands. These sites are subject to seasonal anoxia with different durations and are characterised by the presence of free sulphide (H_2S) in the uppermost part of the sediment. Our results indicate that foraminiferal communities are impacted by the presence of H_2S in their habitat, with a stronger response in case of longer exposure times. At the deepest site (34 m), in summer 2012, one to two months of anoxia and free H_2S in the surface sediment resulted in an almost complete disappearance of the foraminiferal community. Conversely, at the shallower site (23 m), where the duration of anoxia and free H_2S was shorter (one month or less), a dense foraminiferal community was found throughout the year~~.~~ excepted for a short period after the stressful event. Interestingly, at both sites, the foraminiferal community showed a delayed response to the onset of anoxia and free H_2S, suggesting that the combination of anoxia and free H_2S does not lead to increased mortality, but rather to strongly decreased reproduction rates. At the deepest site, where highly stressful conditions prevailed for one to two months, the recovery time of the community takes about half a year. In Lake

Mis en forme : Indice

Grevelingen, *Elphidium selseyense* and *Elphidium magellanicum* are much less affected by anoxia and free H_2S than *Ammonia* sp. T6. We hypothesise that this is not due to a higher tolerance ~~of~~for H_2S, but rather related to the seasonal availability of food sources, which could have been less suitable for *Ammonia* sp. T6 than for the elphidiids.

1 Introduction

Hypoxia affects numerous marine environments, from the open ocean to coastal areas. Over the last decades, a general decline in oxygen concentration was observed in marine waters (Stramma et al., 2012), with an extent varying between the concerned regions. In coastal areas, oxygen concentrations have been estimated to decrease 10 times faster than in the open ocean, with indications of a recent acceleration, expressed by increasing frequency, intensity, extent and duration of hypoxic events (Diaz and Rosenberg, 2008; Gilbert et al., 2010). ~~The~~ This is due to the combination of (1) global warming ~~and eutrophication~~ , which is strengthening seasonal stratification of the water column~~, and~~ decreasing oxygen solubility~~, and~~ and (2) eutrophication resulting from increased anthropogenic nutrient and/or organic matter input, which is enhancing benthic oxygen consumption in response to increased primary production~~, resulting from increased anthropogenic nutrient and/or organic matter input (i.e. eutrophication, (~~Diaz and Rosenberg, 2008). Bottom water hypoxia has serious consequences for the functioning of all benthic ecosystem compartments (see Riedel et al., 2016 for a review). Benthic faunas are strongly impacted by these events (Diaz and Rosenberg, 1995) although the meiofauna, especially foraminifera, appears to be less sensitive to low ~~Dissolved Oxygen~~dissolved oxygen (DO) concentrations than the macrofauna (e.g. Josefson and Widbom, 1988). Many foraminiferal taxa are able to withstand seasonal hypoxia/anoxia (~~e.g. Alve and Bernhard, 1995; Moodley et al., 1997, 1998a; Geslin et al., 2004; Pucci et al., 2009;~~see Koho et al., ~~2011; Langlet et al., 2013~~2012 for a review), and consequently can play a major role in carbon cycling in ecosystems affected by seasonal low ~~-~~oxygen concentrations (Woulds et al., 2007). Anoxia is often accompanied by free sulphide (H_2S) in pore and/or bottom ~~waters,~~ waters (e.g. Jørgensen, 1982; Seitaj et al., 2015), which is considered very harmful for the benthic macrofauna (Wang and Chapman, 1999). Neutral molecular H_2S can diffuse through cellular membranes and inhibits the functioning of cytochrome *c* oxydase (a mitochondrial enzyme involved in ATP production), finally inhibiting aerobic respiration (Nicholls and Kim, 1982; Khan et al., 1990; Dorman et al., 2002).

Lake Grevelingen (southwestern Netherlands) is a former branch of the Rhine-Meuse-Scheldt estuary, which was closed in its eastern part (riverside) by the Grevelingen Dam in 1964 and in its western part (seaside) by the Brouwers Dam in 1971. The resulting saltwater lake, with a surface of 115 km², is one of the largest saline lakes in Western Europe. Lake Grevelingen is characterised by a strongly reduced circulation (even after the construction of a small sluice in 1978) with a strong thermal stratification occurring in the main channels in summer, leading ~~-~~to seasonal bottom ~~-~~water hypoxia/anoxia in late summer and early autumn (Bannink et al., 1984). This situation ~~leads~~results in to a rise of the H_2S front in the uppermost part of the sediment, sometimes up to the ~~water~~ sediment ~~-~~water interface.

These observations especially concern the Den Osse Basin (i.e. one of the deeper basins, maximum depth 34 m; Hagens et al., 2015), which has been intensively monitored over the last decades, so that a large amount of environmental data is available

(e.g. Wetsteijn, 2011; Donders et al., 2012). The annual net primary production in the Den Osse Basin (i.e. 225 g C m^{-2} y^{-1}, Hagens et al., 2015) is comparable to other estuarine systems in Europe (Cloern et al., 2014). However, there is almost no nutrient input from external sources, thus primary production is largely based on autochthonous recycling (>90 %, Hagens et al., 2015), both in the water column and in the sediment, with a very strong pelagic/benthic coupling (de Vries and Hopstaken, 1984). The benthic environment is characterised by the presence of two antagonistic groups of bacteria, with contrasting seasonal population dynamics (i.e. cable bacteria in winter/spring and *Beggiatoaceae* in autumn/winter), which have a profound impact on all biogeochemical cycles in the sediment column (Seitaj et al., 2015; Sulu-Gambari et al., 2016a, 2016b). The combination of hypoxia/anoxia with sulphidic conditions, which is rather unusual in coastal systems without external nutrient input, and the activity of antagonistic bacterial communities make Lake Grevelingen ~~(and especially the Den Osse Basin)~~ a very peculiar environment. In the Den Osse Basin, seasonal anoxia coupled with ~~H_2S~~the presence of H_2S at or very close to the ~~water~~ sediment-water interface occurs in summer~~.~~ (i.e. between July–September). However, euxinia (i.e. diffusion of free H_2S in the water column) does not occur, because of ~~the~~ cable bacterial activity (Seitaj et al., 2015).

Although the ~~large~~ tolerance of foraminifera to low DO contents ~~is~~and long term anoxia (from weeks to 10 months) has been well ~~known~~documented for many species from different types of environments in laboratory culture (e.g. Moodley and Hess, 1992; Alve and Bernhard, 1995; Bernhard and Alve, 1996; Moodley et al., 1997; Duijnstee et al., 2003; Geslin et al., 2004; Duijnstee et al., 2005; Ernst et al., 2005; Pucci et al., 2009; Koho et al., 2011; Geslin et al., 2014) as well as in field studies (e.g. Piña-Ochoa et al., 2010b ; Langlet et al., 2013; 2014), their tolerance to free H_2S is still debated. In the vast majority of previous studies, no decrease in the total abundances of living foraminifera (i.e. strongly increased mortality) was observed during anoxic events. ~~Unfortunately (Bernhard, 1993; Moodley et al., 1998b; Panieri and Sen Gupta, 2008; Langlet et al., 2014). Moreover~~, studies on foraminiferal ~~population dynamics~~response in systems affected by seasonal hypoxia/anoxia with sulphidic conditions are still very sparse. The few available observations are not conclusive, but suggest that H_2S could be toxic for foraminifera even on fairly short time scales (Bernhard, 1993; Moodley et al., 1998b; Panieri and Sen Gupta, 2008; Langlet et al., 2014).

To our knowledge, all earlier studies show that the foraminiferal response to hypoxia/anoxia is species-specific (e.g. Bernhard and Alve, 1996; Ernst et al., 2005; Bouchet et al., 2007; Geslin et al., 2014; Langlet et al., 2014). However, this species-specific response generally follows the same scheme (usually decrease in density, reduction of growth and/or reproduction), with different response intensities. Duijnstee et al. (2005) suggested that oxic stress leads to an increased mortality and an inhibited growth and reproduction. The suggestion of inhibited growth is supported by LeKieffre et al. (2017) who observed that the morphospecies *Ammonia tepida* (probably *Ammonia* sp. T6) showed minimal or no growth under anoxia. Conversely, Geslin et al. (2014) and Nardelli et al. (2014) suggested that, in the same morphospecies, reproduction was strongly reduced, but growth would not be affected by hypoxic and/or short anoxic events. Additionally, under low-oxygen conditions, some species are able to shift to anaerobic metabolism (i.e. denitrification, Risgaard-Petersen et al., 2006; Piña-Ochoa et al., 2010a), to sequester chloroplast (i.e. kleptoplastidy, Jauffrais et al., 2018), to associate with bacterial symbionts (Bernhard et al., 2010) or to enter into a state of dormancy (Ross and Hallock, 2016; LeKieffre et al., 2017).

The highly peculiar environmental context of Lake Grevelingen offers an excellent opportunity to study this still poorly known aspect of foraminiferal ecology.

The conventional method to discriminate between live and dead foraminifera uses Rose Bengal, a compound which stains proteins (i.e. organic matter). This method was proposed for foraminifera by Walton (1952) and is based on the assumption that "*the presence of protoplasm is positive indication of a living or very recently dead organism*". The author already noted that this assumption implied that the rate of degradation of organic material should be relatively high. Previous studies of living benthic foraminifera in environments subjected to hypoxia/anoxia were almost all based on Rose Bengal stained samples (e.g. Gustafsson and Nordberg, 1999, 2000; Duijnstee et al., 2004; Panieri, 2006; Schönfeld and Numberger, 2007; Polovodova et al., 2009; Papaspyrou et al., 2013). However, foraminiferal protoplasm may remain stainable from several weeks to months after their death (Corliss and Emerson, 1990), especially under low dissolved oxygen concentrations where organic matter degradation may be very slow (Bernhard, 1988; Hannah and Rogerson, 1997; Bernhard et al., 2006). The Rose Bengal staining method is therefore not suitable for studies in environments affected by hypoxia/anoxia. Consequently, the results of foraminiferal studies in low-oxygen environments based on this method have to be considered with reserve. In order to avoid this problem, we used CellTracker™ Green (CTG) to recognise living foraminifera. CTG is a fluorescent probe which marks only living individuals with cytoplasmic (i.e. enzymatic) metabolic activity (Bernhard et al., 2006). Since metabolic activity stops after the death of the organism, CTG should give a much more accurate assessment of the living assemblages at the various sampling times, and thereby avoid over-estimation of the live foraminiferal abundances.

In this study, samples were collected in August and November 2011 and then every month through the year 2012, at two different stations in the Den Osse Basin, with two replicates dedicated to foraminifera. The two stations were chosen in contrasted environments regarding water depth (34 m and 23 m, respectively) and duration of seasonal hypoxia/anoxia and sulphidic conditions. ~~Foraminiferal~~Living foraminiferal assemblages were studied in the ~~top 1 cm layer. For each dominant species,~~uppermost sediment and size distributions were determined in order to get insight into the ~~population dynamics~~possible moment(s) of reproduction or accelerated growth in test size. The seasonal variability study of the foraminiferal community allows us (1) to better understand the foraminiferal tolerance to seasonal hypoxia/anoxia with presence of free H_2S in their microhabitat and (2) to obtain information about the ~~life histories~~responses of the various species ~~under~~to adverse conditions. This knowledge will be useful for the development of indices assessing environmental quality (i.e. biomonitoring) and may also improve paleoecological interpretations of coastal records (e.g. Murray, 1967; Gustafsson and Nordberg, 1999).

2 Material and Methods

2.1 Studied area – environmental settings in the Den Osse Basin.

Lake Grevelingen is a part of the former Rhine-Meuse-Scheldt estuar~~iney~~, in the southwestern Netherlands. This former estuarine branch was turned into an artificial saltwater lake during the Delta Works project. ~~Due to~~In Lake Grevelingen, the ~~thermal stratification~~water circulation is strongly limited by the construction of dams (in the early 1970s) and only a small

sluice allows water exchanges with open sea waters (i.e. very weak hydrodynamics). ~~high oxygen consumption in the benthic compartment~~In the Lake, development of bottom–~~-~~water hypoxia/anoxia occurs in the deepest part of the basin in summer (i.e. July–September) to early autumn (i.e. October–December, Bannink et al., 1984; Hagens et al., 2015). In the literature, the terminology and threshold values used to describe oxygen depletion are highly variable (e.g., oxic, dysoxic, hypoxic, suboxic, microxic, postoxic; see Jorissen et al., 2007; Altenbach et al., 2012). In this study we defined hypoxia ~~by~~as a concentration of oxygen <63 µmol L^{-1} (1.4 mL L^{-1} or 2 mg L^{-1}) whereas anoxia is defined as no detectable~~d~~ oxygen (following Rabalais et al., 2010).

~~2.1 Environmental parameters~~

In Den Osse Basin, the nutrient input from external sources is very low and pelagic/benthic coupling is essential, as already noted by de Vries and Hopstaken (1984). In 2012, phytoplankton blooms occurred in April-May and July (Hagens et al., 2015, Fig. 10) in response to the increasing solar radiation and nutrient availability in the water column following organic matter recycling in winter. This led to an increased food availability in the benthic compartment in the same periods. In general, Chl *a* concentrations in Den Osse Basin are below 10 µg L^{-1}, excluding very short peaks during blooms in April–May and July which did not exceed 30 µg L^{-1} in 2012 (Hagens et al., 2015). Thermal stratification of the water column and increased oxygen consumption due to organic matter input (i.e. from phytoplankton blooms) both are responsible for the development of seasonal bottom-water hypoxia/anoxia in summer (i.e. July–September). Although euxinia (i.e. the presence of free H_2S in the water column) does not occur in the Den Osse Basin due to cable bacterial activity in winter, free H_2S is present in the uppermost layer of the sediment in summer (Seitaj et al., 2015). Summarising, in the benthic ecosystem, increased food availability in summer is counterbalanced by strongly decreasing oxygen contents, sometimes accompanied by the presence of free sulphides in the topmost sediment.

2.2 Field Sampling

The two studied sites are located along a depth gradient in the Den Osse Basin of Lake Grevelingen. Both station 1 (51°44.834' N, 3°53.401' E) and station 2 (51°44.956' N, 3°53.826' E) are located in the main channel, at 34 and 23 m depth, respectively (see ~~Petersen~~map in Hagens et al., 201~~9~~5).

Measurements of bottom-water oxygen (BWO) concentrations ~~in the bottom water (1~~were performed at 2 m above the sediment-water interface ~~using a CTD) for 2011~~ and are from Donders et al. (2012), whereas the data for 2012 ~~data are from~~ were published in Hagens et al. ~~(2015) and~~ (2015). Sediment cores were collected monthly in 2012 using a single core gravity corer (UWITEC, Austria) using PVC core liners (6cm inner diameter, 60cm length). All cores were inspected upon retrieval and only visually undisturbed sediment cores were used for further analysis (Seitaj et al ~~(~~., 2017). Oxygen ~~Penetration Depth~~ penetration depth (OPD) and depth of free H_2S detection were determined ~~using O_2 and H_2S microsensors~~ by Seitaj et al., (2015) using profiling microsensors for station 1~~, and the~~. The data for station 2 (Supplementary Table 1) were acquired

similarly ~~(Supplementary Table 1~~and during the same cruises but never published, for further details about the sampling method, see Seitaj et al. (2015).

~~**2.2 Field Sampling**~~

Two replicate sediment cores ~~(inner diameter 6 cm)~~ dedicated to the foraminiferal study were sampled in August and November 2011 using the same gravity corer (UWITEC, Austria) and then monthly throughout the year 2012. ~~The~~ at the same sampling time as for BWO concentration and OPD and H_2S measurements in the sediment (see Seitaj et al., 2015). Consequently, for 2012 at station 1 and 2, OPD and H_2S were measured in the sediment column at the same time as foraminifera were sampled (Seitaj et al., 2015). For each replicate, the uppermost centimetre of ~~each~~the core was ~~labelled~~then transferred on board in a vial of 250 mL, and 30 mL of seawater (at the same temperature than *in situ*) was added in the vial. Then we labelled the samples with CellTracker™ Green CMFDA (CTG, 5-chloromethylfluorescein diacetate, final concentration of ~~1µM~~1µmol L^{-1} following Bernhard et al., 2006) and slowly agitated manually to allow the CTG diffusion in the whole sample. Samples were then fixed in 5 % sodium borate buffered formalin after 24 h of incubation. ~~in the dark~~ ~~Since picking foraminifera under an epifluorescence stereomicroscope is particularly time-consuming, we decided to study samples only every two months for the year 2012. At a later stage, in view of the large differences in foraminifera abundances between the samples of September and November 2012 at station 2, we decided to study the October and December 2012 samples as well for this station. The sampling dates investigated in this study are listed in Table 1~~.

2.3 Sample Treatment

All samples were sieved over 315, 150, 125 µm meshes, and foraminiferal assemblages were studied in all three size fractions. Individuals were picked wet under an epifluorescence stereomicroscope (Olympus SZX12, light fluorescent source Olympus URFL-T, excitation/emission wavelengths: 492 nm/517 nm) and placed on micropalaeontological slides. Only specimens that fluoresced brightly green were considered as living and were identified to the (morpho-)species level when possible. Since picking foraminifera under an epifluorescence stereomicroscope is particularly time-consuming, we decided to study samples only every two months for the year 2012. At a later stage, in view of the large differences in foraminiferal abundances between the samples of September and November 2012 at station 2, we decided to study the October and December 2012 samples as well for this station. The sampling dates investigated in this study are listed in Table 1.

Abundances were then standardised to a volume of 10 cm^3 ~~in order to facilitate comparison with previous studies~~. The abundances of living foraminifera for each sampling time and replicate are listed in Supplementary Tables 2 and 3. The mean abundance and standard deviation $(\bar{x} \pm sd)$ for the two replicates for each sampling date were calculated both for the total living assemblage and the individual species, as an indication of spatial patchiness.

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2.4 Taxonomy of dominant species

Four dominant species (>1 % of the total assemblage) were present in our material: *Ammonia* sp. ~~(~~T6~~),~~ *Elphidium magellanicum* (Heron-Allen and Earland, 1932), *Elphidium selseyense* (Heron-Allen and Earland, 1911) and *Trochammina inflata* (Montagu, 1808). As we identified these species on the basis of morphological criteria, we will use them as "morphospecies".

Concerning the genus *Ammonia*, two living specimens collected at Grevelingen ~~-~~station 1 were molecularly identified (by DNA barcoding) as phylotype T6 by Bird et al. (2019). At the same site, we genotyped seven other living *Ammonia* specimens, which were all T6. Their sequences were deposited on GenBank (accession numbers MN190684 to MN190690) and Supplementary Figure 1 shows Scanning Electron Microscope (SEM) images of the spiral side and of the penultimate chamber at 1000x magnification for four individuals. A morphological screening based on the criteria proposed by Richirt et al. (2019) confirmed that T6 accounts for the vast majority (>98 %) of *Ammonia* individuals, whereas phylotypes T1, T2, T3 and ~~*Ammonia falsobeccarii*~~T15 are only present in very small amounts (Supplementary Table 3).

The specimens of *Elphidium magellanicum* were identified exclusively on the basis of morphological criteria, as there are no molecular data available yet. This morphospecies, although rare, is regularly recognised in ~~b~~Boreal and ~~l~~Lusitanean provinces of Europe (e.g. Gustafsson and Nordberg, 1999; Darling et al., 2016; Alve et al., 2016). However, as the type species was described from the Magellan strait (Southern Chile), the European specimens may represent a different species and further studies involving DNA sequencing of both populations are needed to confirm or infirm this taxonomic attribution (see Roberts et al., 2016).

In the past, *Elphidium selseyense* has often been considered as an ecophenotype of *Elphidium excavatum* (Terquem, 1875) and has been identified as *E. excavatum* forma *selseyensis* (e.g. Feyling-Hanssen, 1972; Miller et al., 1982). Recently, Darling et al. (2016) showed that the various ecophenotypes recognised in *E. excavatum* are in fact genetically separated and therefore represent different species. Four living specimens of the *E. excavatum* group sampled at station 1 for DNA analysis were all identified as *E. selseyense* (phylotype S5, Darling et al., 2016). We only observed minor morphological variations in our material, especially concerning the number of small bosses in the umbilical region, which we considered as intraspecific variability. Consequently, we identified all our specimens as *E. selseyense*.

The specimens attributed to *Trochammina inflata* were also identified exclusively on the basis of morphological criteria, as no molecular data are available yet.

2.5 Size distribution measurement

In order to ~~gain insight into the foraminiferal population dynamics~~detect periods of increased growth and/or reproduction, size measurements were performed on all samples of 2012. The measurements were made for all species, which represent together 4176 individuals for station 1 and 19624 individuals for station 2. Prior to measurements, trochospiral species were all orientated in the same way (spiral side up). High-resolution images (3648*2736 pixels) of all micropalaeontological slides

were taken with a stereomicroscope (Leica S9i, 10x magnification). In order to obtain measurements for all individual specimens, images were processed using ImageJ software (Schneider et al., 2012, Fig. 1).

The three size fractions (125–150, 150–315, >315 µm) were analysed together for the size distribution analyses. ~~For each~~Each individual~~,~~ was isolated on the image (Fig. 1) and its maximum diameter was measured (i.e. Feret's diameter). We represented all size distributions using histograms with 20 µm classes (the best compromise between the total number of individuals and the size range~~)~~. (Supplementary Figure 2). In order to compare more easily months and species, the median and the mode (associated with the numbers of individuals) were calculated for each size distribution. As we only examined the size fractions >125 µm, our analysis mainly concerns adult specimens, and does not include juveniles. This limitation should be kept in mind when interpreting the results.

In an attempt to recognize the different cohorts for each species in each of the bimonthly samples, we assumed that the size distribution was a sum of Gaussian curves, each of them representing a cohort. In order to identify the approximate mode for the Gaussian curves (i.e. cohorts), we used the changes in slope (i.e. inflexion points) of the second-order derivative of the total size distribution (Gammon et al., 2017). Unfortunately, this tentative to distinguish cohorts by using a deconvolution method was not conclusive. The main problem was the lack of information concerning individuals smaller than 125 µm, so that our size distributions were systematically skewed on the left side (i.e. toward small individuals). An additional problem was the large number of smaller specimens which were always present. Because the identification of individual cohorts was not successful, parameters like reproduction rate, growth rate or lifespan were not assessable, and therefore a study of population dynamics was not possible. For this reason, the data are shown in the supplementary material (Supplementary Figures 2). Nevertheless, the size distribution data give some clues concerning the possible moment(s) of reproduction or intensified test growth for the different species.

2.6 Encrusted forms of *E. magellanicum*

In our samples, we found abundant encrusted forms of *E. magellanicum* at station 1 (May 2012) and station 2 (May, July, September and December 2012, Fig. 8). Most individuals were totally encrusted (Fig. 8a), others only partly (Fig. 8b). These crusts were hard, firmly stuck to the shell (difficult to remove with a brush), thin (Fig. 8c–e) and rather coarse. In order to determine if the crust matrix is constituted of carbonate, we placed some specimens in microtubes and exposed them to 0.1 M of EDTA (EthyleneDiamineTetraacetic Acid) diluted in 0.1 M cacodylate buffer (acting as a carbonate chelator). After an exposition of 24h, we checked under a stereomicroscope if the crust was still cohesive (no carbonate in the crust) or was disaggregated (crust contains carbonate).

3 Results

3.1 Total abundances of foraminiferal assemblages

Figure 2 shows the total living foraminiferal abundance for each replicate, and the mean and standard deviation computed for the two replicates ($\overline{x} \pm sd$) of the 0–1 cm depth interval for the two studied stations. TotalAveraged total abundances varied between 1.1 $\pm$ 1.5 and 449.9 $\pm$ 322.1 ind. 10 cm^{-3} for station 1, and between 91.1 $\pm$ 25 and 604.8 $\pm$ 3.5 ind. 10 cm^{-3} for station 2. (Figure 2 and Table 2). For every studied month, the total density was higher at station 2 than at station 1. The seasonal succession is very different between the two sites. (Figure 2). Station 1 shows very low total foraminiferal abundances for most months, contrasting with a much higher densityies in late spring (May) and early summer (July). Conversely, station 2 shows high total foraminiferal abundances throughout the year, with somewhat lower values in late autumn (i.e. November 2011, and October and November 2012 (Figure 2).

At station 1, almost no individuals were present in August ($\overline{x} = 3.4 \pm 1.3$) and November 2011 ($\overline{x} = 1.1 \pm 1.5$). In 2012, total abundances were very low in January ($\overline{x} = 11.5 \pm 9.3$), showed a slight increase in March ($\overline{x} = 62.1 \pm 19.3$) and reached a maximal abundance in May ($\overline{x} = 449.9 \pm 322.1$). Total abundances then progressively decreased from May to September ($\overline{x} = 34 \pm 17$) and almost no foraminifera were present in November ($\overline{x} = 1.6 \pm 0.3$).

At station 2, total abundances were comparatively low in August and November 2011 ($\overline{x} = 174 \pm 48$ and $\overline{x} = 128.7 \pm 25$ ind. 10 cm^{-3}, respectively). In 2012, total abundances were relatively high and stable from January to September (between $\overline{x} = 523.6 \pm 30.7$ to $\overline{x} = 604.8 \pm 3.5$), then decreased in October ($\overline{x} = 211.5 \pm 8$) and November ($\overline{x} = 91.1 \pm 25.3$) and finally increased again in December ($\overline{x} = 377.9 \pm 38.8$).

3.2 Dominant Species

In this section, we will only consider the dominant morphospecies, which individually represent at least 1 % of the total assemblage for the total assemblage sampled for each station (all samples taken together, Table 2).

At station 1, the major species were, in order of decreasing abundances, *Elphidium selseyense* (Fig. 3a–b), *Elphidium magellanicum* (Fig. 3c–d) and *Ammonia* sp. T6 (Fig. 3e–g). In Fig.ure 4, we added *Trochammina inflata* (Fig. 3h–j) to facilitate comparison with station 2, where this species is among the dominant ones. The "Other species" account only for 2.2 % of the total assemblage at station 1. The fact that they are well represented in some months (e.g. 26.3 % of the assemblage in August 2011) is due to the extremely low number of individuals (see Fig. 2 and Table 2). At station 2, the dominant species, in order of decreasing abundances, were *E. selseyense*, *Ammonia* sp. T6, *E. magellanicum* and *T. inflata* (Table 2). Here, "Other species" account only for 2.6 % of the total assemblage.

Whereas *E. selseyense* and *E. magellanicum* were dominant species at both stations, both *Ammonia* sp. T6 and *T. inflata* were present in much higher abundances at station 2 compared to station 1, where the latter species was almost absent (Fig. 4–5).

At station 1, only some very scarce individuals of *E. selseyense* and *Ammonia* sp. T6 were observed in August and November 2011 (Fig. 4 and Table 2). In 2012, *E. selseyense* and *E. magellanicum* together account always for 60 % or more of the fauna,

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except in January. The abundances of these two species were very low in January, started to increase in March ($\overline{x} = 23.9 \pm 6.8$ and $\overline{x} = 21.6 \pm 11$) to reach maximal values in May ($\overline{x} = 336.5 \pm 275.8$ and $\overline{x} = 96.4 \pm 47.3$).). In July, values for *E. selseyense* were still high ($\overline{x} = 162 \pm 121.5$), whereas *E. magellanicum* had strongly decreased) and($\overline{x} = 3.7 \pm 0.3$). Both species further decreased until an almost total absence in November 2012. No specimen of *E. magellanicum* was observed in 2011 (Fig. 4 and Table 2). The abundance of *E. magellanicum* was very low in January 2012*Ammonia* sp. T6, started to increase in March ($\overline{x} = 21.6 \pm 11$) to reach maximal values in May ($\overline{x} = 96.4 \pm 47.3$), then strongly decreased in July ($\overline{x} = 3.7 \pm 0.3$). The species was absent from samples in September and November 2012. *Ammonia* sp. beT6 was almost absent in August and November 2011 and present with low abundances very few specimens in January 2012 ($\overline{x} = 3.2 \pm 3.5$), to reach (fairly low) maximum). Maximum abundances were reached between March and July 2012 (ranging between $\overline{x} = 9.2 \pm 6.5$ and $\overline{x} = 12.9 \pm 1.3$). Then abundances rapidly decreased until the species was almost absent in November. *Trochammina inflata* was absent in 2011 and was only present with very low abundances from January to May and in NovSeptember 2012. At station 2, the two dominant major species were *E. selseyense* and *Ammonia* sp. T6, which together always represented at least 70 % of the total assemblage (Fig. 5 and Table 2). These two species showed a different seasonal pattern over the considered period. Abundances of *E. selseyense* were comparable in August ($\overline{x} = 74.8 \pm 29.8$) and November 2011 ($\overline{x} = 52.3 \pm 27$) then showed a progressive increase until a maximum in September 2012 ($\overline{x} = 365.5 \pm 70.3$). Abundances then showed a sharp decrease in October and November (respectively $\overline{x} = 98.7 \pm 8.5$ and $\overline{x} = 30.9 \pm 2.3$) to increase again in December ($\overline{x} = 252.2 \pm 41$). For *Ammonia* sp. T6, abundances strongly increased between November 2011 ($\overline{x} = 60.8 \pm 1.5$) and January 2012 ($\overline{x} = 226.2 \pm 52.3$) and then progressively decreased until the end of 2012 ($\overline{x} = 48.1 \pm 26$ in November 2012). *Trochammina inflata* showed a similaran analogous pattern asto *Ammonia* sp. T6. Abundances strongly increased between November 2011 ($\overline{x} = 11.8 \pm 1.8$) and January 2012 ($\overline{x} = 121.5 \pm 29.8$), and then progressively decreased until very low abundances were found in November ($\overline{x} = 3.7 \pm 3$). *E. magellanicum* was completely absent in August and November 2011, almost absent in January 2012 ($\overline{x} = 0.9 \pm 0.3$) and then suddenly increased until a maximum of $\overline{x} = 116 \pm 6.5$ in May. Conversely to station 1, abundancesAbundances stayed relatively high in July ($\overline{x} = 37.8 \pm 2.5$) and September ($\overline{x} = 72 \pm 35.8$), and then drastically decreased until minimum numbers in October and November. Finally, like all other species, *E. magellanicum* abundances increased again in December ($\overline{x} = 25.5 \pm 13$).

3.3 Size distribution

In order to base our analysis on a sufficiently high number of specimens, we will here focus on *E. selseyense* and *Ammonia* sp. T6. As explained before, we will consider only specimens retained on a 125 µm mesh, which means that juvenile specimens are not represented. Only the samples taken in 2012 were considered.

The size distribution of *E. selseyense* was relatively similar between the two stations regarding the median, ranging from 253 µm (in May) to 295 µm (in November) at station 1 and from 261 µm (in October) to 290 µm (in March) at station 2. At both stations, we observed the presence of an abundant group of smaller specimens, with a mode that never exceeded 250 µm,

except in March at station 2, when it is difficult to separate this subpopulation from the larger specimens (Fig. 6). The main difference between the two stations is the higher proportion of larger individuals (>400 µm) at station 2, which is visible through the better developed tails at the right side of the distribution graphs (Fig. 6).

The low number of *Ammonia* sp. T6 individuals at station 1 does not allow us to draw any firm conclusion concerning the size distribution at this station. At station 2, a group of individuals with smaller diameters (< 300 µm) was always present (Fig. 7). The overall size distribution showed a clear shift to higher diameters between March (median = 279 µm) and May (median = 373 µm, Fig. 7), which is also evidenced by the much higher proportion of larger individuals. Specimens larger than 400 µm were abundantly found until November (median = 378 µm), but started to diminish in December, as is also shown by the decrease of the median to 339 µm.

Our tentative to distinguish cohorts by using a deconvolution method to separate the total size distributions into a sum of Gaussian curves was not conclusive. The main problem was the fact that we did not have any information concerning individuals smaller than 125 µm, so that our size distributions were systematically skewed on the left side (i.e. toward small individuals). An additional problem was the large number of smaller specimens which were always present. Because the identification of individual cohorts was not successful, parameters like reproduction rate, growth rate or lifespan were not assessable. Nevertheless, the size distribution data give some clues concerning the population dynamics of the two dominant species.

3.4 Encrusted forms of *Elphidium magellanicum*

In our samples, during May at station 1 and May, July, September and December at station 2, we found abundant encrusted forms of *E. magellanicum* (Fig. 8). Most individuals were totally encrusted (Fig. 8a), others only partly (Fig. 8b). These crusts were hard, firmly stuck to the shell (difficult to remove with a brush), thin (Fig. 8c–e) and rather coarse (the crust seemed composed of sediment particles cemented by a rather homogenous matrix).

Because the crust stayed cohesive after After exposition to 0.1 M of EDTA (EthyleneDiamineTetraacetic Acid) diluted in 0.1 M cacodylate buffer (acting as a carbonate chelator), it appears that this crust, the crusts remained cohesive, indicating that it does not consist of carbonate, and suggesting that it is composed of sediment particles cemented by an organic matrix. In view of the fact that the crusts consist mainly of organic matter, the encrusted individuals probably are specimens with preserved feeding cysts. Similar observations have been made for *Elphidium incertum* (Linke and Lutze, 1993; Gustafsson and Nordberg, 1999) and also in Flensburg Fjord, where partial cysts remained attached to the tests of *E. incertum* (Polovodova et al., 2009), similar to our observations (Fig. 8a).

Figure 9 shows the quantitative occurrence of encrusted specimens for the successive samples. At station 1, encrusted forms of *E. magellanicum* were present in moderate proportions in May (26.8 % of the total *E. magellanicum* population, Fig. 9) and July (47.6 %); the species disappeared thereafter. At station 2, encrusted forms strongly dominated the *E. magellanicum* population from May (72.3 %) to December (88 %). %, Fig. 9).

4 Discussion

4.1 UseTolerance of CellTracker™ Green

The conventional method to discriminate between live and dead foraminifera uses Rose Bengal, a compound which stains proteins (i.e. organic matter). This method was proposed for foraminifera by Walton (1952) and is based on the assumption that "*the presence of protoplasm is positive indication of a living or very recently dead organism*". The author already noted that this assumption implied that the rate of degradation of organic material should be relatively rapid. However, it appears that protoplasm degradation may be relatively long (from weeks to years, Corliss and Emerson, 1990), especially in hypoxic or anoxic conditions deeper in the sediment (Bernhard, 1988; Hannah and Rogerson, 1997). In these conditions, it can therefore not be excluded that dead individuals become stained as well. Bernhard et al. (2006) showed that abundances of living individuals recognised on the basis of Rose Bengal staining could be overestimated by a factor of two. The use of more trustworthy criteria is even more crucial in environments where organic matter may degrade very slowly, such as under low oxygen conditions. In this study, we used CellTracker™ Green (CTG), a fluorogenic probe (i.e. the substance becomes fluorescent after modification of the original molecule) which labels the enzymatic (esterase) activity in the foraminiferal cytoplasm (Bernhard et al., 2006). CTG allowed us to discriminate efficiently between living and dead foraminifera at the time of sampling, and to avoid over-estimation of the live foraminifera abundances.

4.2 Environmental setting of Den Osse Basin

At Lake Grevelingen, the water circulation was strongly limited by the construction of dams (in the early 1970s) and only a small sluice allows water exchanges with oceanic waters (i.e. very weak hydrodynamics). Nevertheless, in 2012, the salinity ranged from 30 to 33. Consequently, Lake Grevelingen is euhaline and salinity variations are not likely to affect foraminiferal communities, since the dominant species (i.e. *E. selseyense*, *E. magellanicum* and *Ammonia* sp. T6) are known to be euryhaline (i.e. highly tolerant to salinity variations) and typically live in this salinity range (e.g. Bradshaw, 1957; Gustafsson and Nordberg, 2000; Murray and Alve, 2000; Darling et al., 2016; Mojtahid et al., 2016).

In Den Osse Basin, the nutrient input from external sources is very low and pelagic/benthic coupling is essential, as already noted by de Vries and Hopstaken (1984). In 2012, phytoplankton blooms occurred in April-May and July (Hagens et al., 2015, Fig. 10) in response to the increasing solar radiation and the nutrient availability in the water column following organic matter recycling in winter. This led to an increased food availability in the benthic compartment in the same periods. In general, Chl *a* concentrations in Den Osse Basin are below 10 µg L^{-1}, excluding very short peaks during blooms in late spring (April–May) and summer (July) which didn't exceed 30 µg L^{-1} in 2012 (Hagens et al., 2015). Thermal stratification of the water column and increased oxygen consumption due to organic matter input (i.e. from phytoplankton blooms) are together responsible for the development of seasonal bottom water hypoxia/anoxia in summer. Although euxinia (i.e. diffusion of free H_2S into the water column) does not occur in the Den Osse Basin due to cable bacterial activity in winter, free H_2S is present in the uppermost layer of the sediment in summer (Seitaj et al., 2015). Summarising, in the benthic ecosystem, increased food

~~availability in summer is counterbalanced by strongly decreasing oxygen contents, sometimes accompanied by the presence of free sulphides in the topmost sediment.~~ ~~The tolerance of individual species to these conditions will influence their competitive success, which will ultimately control the community characteristics.~~

~~4.3 Foraminiferal tolerance~~ to anoxia and free sulphide

At station 1, bottom-waters were hypoxic in July 2012 and became anoxic in August (Fig. 10). Both in July and August, oxygen penetration into the sediment was null, whereas it was 0.7 ± 0.1 mm depth in September. In all three months (July to September 2012), sulphidic conditions were observed very close to the sediment-water interface (1 mm or less, Fig. 10 and Supplementary Table 1). In view of these results, the duration of anoxic and sulphidic conditions in the uppermost sediment layer can be estimated as one to two months (in July and August, Fig. 10).

After the strong increase of foraminiferal densities in May 2012, there was a decrease starting in July, leading to a near-absence of foraminifera at station 1 in November (Fig. 10). The most probable cause of the strong decline of the foraminiferal community appears to be a prolonged presence of sulphides in the foraminiferal microhabitat. However, the fact that foraminiferal abundances reached almost zero only in September (about two months after the first occurrence of anoxic and sulphidic conditions in the upper sediment, in July) suggests that the presence of H_2S did not cause instantaneous mortality, but that the disappearance of the foraminiferal community was a delayed response, probably caused by inhibited reproduction and, eventually, increased mortality. Inhibited reproduction has previously been suggested as a response to hypoxic/short anoxic (Geslin et al., 2014) and sulphidic conditions (Moodley et al., 1998b).

Such a time lag between a change in foraminiferal abundances and changes in environmental parameters affecting reproduction and/or growth of foraminifera has been suggested previously by Duijnstee et al. (2004). These authors highlighted that the density patterns of some foraminiferal species showed a higher correlation with measured environmental parameters (e.g., oxygenation or temperature) when a time lag of about three months was applied.

~~Tolerance to long term anoxia (i.e. from weeks to 10 months) has been shown for many species of foraminifera from different types of environments (e.g. Bernhard, 1993; Bernhard and Alve, 1996; Moodley et al., 1997; Duijnstee et al., 2003, 2005; Ernst et al., 2005; Pucci et al., 2009; Piña-Ochoa et al., 2010b; Langlet et al., 2013; Geslin et al., 2014). In the vast majority of these studies, no decrease in the total abundances of living foraminifera (i.e. strongly increased mortality) was observed during anoxic events. Unfortunately, observations concerning the foraminiferal tolerance to the presence of H_2S in the sediment are much scarcer. The few available observations are not conclusive, but suggest that H_2S could be toxic for foraminifera even on fairly short time scales.~~

~~Bernhard (1993) exposed diverse faunas collected at 23 m depth in Explorer's cove in Antarctica to euxinic conditions by using sealed flasks~~For 2011, at station 1, no pore-water O_2 and H_2S measurements are available. However, severe hypoxia was observed in the bottom-waters from May to August, with anoxia in June 2011 (Fig. 10). We therefore assume that like in 2012, anoxic and probably co-occurring sulphidic conditions were responsible for the very low standing stocks in August and November 2011 and January 2012.

~~seawater flushed with nitrogen and with a H_2S concentration of 500 µmol L^{-1}. The author found that foraminiferal activity (as determined by ATP content) was not significantly~~Our observations confirm the suggestion in previous studies that the foraminiferal community is severely affected by a long-term presence of H_2S in its habitat, but does not show instant mortality. In fact, after ~~30 days (32.6 ± 8.6 % of 174 ind. in control conditions and 29.5 ± 6.2 % of 173 ind. in sulphidic conditions). Conversely, for complete faunas from a 19 m deep site in the Adriatic Sea, Moodley et al. (1998a) found a strong decrease of Rose Bengal stained foraminifera over the course of the~~a 66 ~~-~~day~~s~~ incubation in euxinic conditions (a maximum of 11.9 ± 0.4 µmol L^{-1} of H_2S in the overlying water~~).~~) of foraminiferal assemblages collected at a 19 m deep site in the Adriatic Sea, Moodley et al. (1998a) found a strong decrease of the total density of Rose Bengal stained foraminifera. After 21 days, living specimens were still observed, whereas after 42 and 66 days, the live checks (based on protoplasm movement) gave only negative results. ~~Finally, during~~Langlet et al. (2013, 2014), performed an *in situ* ~~experience~~experiment with closed benthic chambers at a 24 m deep site in the Gulf of Trieste, in the Adriatic Sea~~, Langlet et al., (2013, 2014)~~. They observed a ~~decreased~~decrease of living foraminiferal density (labelled with CTG), but also found that almost all species survived after 10 months of anoxia ~~with~~and periodically co-~~occurrence of~~occurring H_2S in the ~~water column and~~ sediment~~.~~ and overlying water. However, the duration of sulphidic conditions, which was estimated to ~~last for~~ several weeks ~~but~~, could not be assessed precisely (Metzger et al., 2014). The suggestion that short-time exposure to euxinic conditions is not directly lethal for foraminifera is confirmed by the experimental results of Bernhard (1993), who found that foraminiferal activity (as determined by ATP content) was not significantly affected after 30-day exposure to euxinia (32.6 ± 8.6 % of active individuals, n=174. in control conditions versus 29.5 ± 6.2 %, n= 173 in sulphidic conditions).

~~In our study, at station 1, bottom waters were hypoxic in July 2012 and became anoxic in August (Fig. 11). Both in July and August, oxygen penetration into the sediment was null, whereas it was 0.7 mm in September. In all three months (July to September 2012), sulphidic conditions were observed very close to the sediment-water interface (1 mm or less, Fig. 11). In view of these results, the duration of anoxic and sulphidic conditions in the uppermost sediment layer can be estimated as one to two months (in July and August, Fig. 11).~~

~~After the strong increase of foraminiferal densities in spring 2012, there is a strong decrease starting in July, leading to a near-absence of foraminifera in November (Fig. 11). The most probable cause of the strong decline of the foraminiferal community appears to be a prolonged presence of sulphides in the foraminiferal microhabitat. However, the fact that foraminiferal abundances reached almost zero only in November (two months after the last stage of sulphidic conditions in the upper sediment, in September) suggests that the presence of H_2S did not cause instantaneous mortality, but that the disappearance of the foraminiferal community was a delayed response, probably caused by inhibited reproduction and, eventually, increased mortality.~~

~~Such a time lag between a drop or an increase in abundances in response to changes in environmental parameters affecting reproduction and/or growth of foraminifera was already suggested by Duijnstee et al. (2004). The authors highlighted that the dynamics of some foraminiferal species showed higher correlation with measured environmental parameters (e.g., oxygenation or temperature) when a time lag of about three months was applied.~~

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~~For 2011 at the same station, no pore-water O_2 and H_2S measurements are available. However, severe hypoxia was observed in the bottom waters from May to August, with anoxia in June 2011 (Fig. 11). We therefore assume that like in 2012, anoxic and probably co-occurring sulphidic conditions were responsible for the very low standing stocks in August and November 2011 and January 2012.~~

~~Our observations confirm the suggestion of Moodley et al. (1998a) that foraminifera cannot withstand a prolonged presence of H_2S in their habitat. Inhibition of reproduction has earlier been suggested as a response to hypoxic/short anoxic (Geslin et al., 2014) and sulphidic conditions (Moodley et al., 1998b).~~

After the 2011 hypoxia/anoxia, standing stocks at station 1 only started to increase in March 2012, indicating a very long recovery time (about 6 months) of the foraminiferal faunas after a temporary near-extinction due to anoxic and sulphidic conditions.

This confirms observations of relatively long recovery times in the literature (e.g. Alve, 1995, 1999; Gustafsson and Nordberg, 2000; Hess et al., 2005). For instance, Gustafsson & Nordberg (1999) showed that in the Koljö Fjord, at comparable water depths, foraminiferal populations responded with increased densities only three months after a renewal of sea-floor oxygenation following hypoxic conditions in the bottom waters. However, in that case, the disappearance of the foraminiferal ~~was~~population was only partial, and not nearly complete~~,~~ as in our study.

At station 2, in 2012, hypoxia was only observed in August, when the OPD was zero, and sulphidic conditions were observed in the superficial sediment (i.e. from 0.4 ± 0.2 mm downwards, Fig. ~~12).~~11, Supplementary Table 1). Both in July and September, oxygen penetrated more than one millimetre into the sediment. (1.3 ± 0.4 mm and 1.2 ± 0.2 mm, respectively). However, free H_2S was still detected at about ~~two millimetres~~one millimetre depth in the sediment. (1.1 ± 0.8 mm in July and 0.8 ± 0.2 mm in September). Although the sampling plan does not allow us to be very precise about the duration of anoxic and sulphidic conditions, we can estimate their duration to be 1 month or less (Fig. ~~12~~11).

Foraminiferal abundances showed a strong decrease in October and November 2012, about two months after the presence of anoxic and sulphidic conditions in the topmost part of the sediment (Fig. ~~12~~11). Like at station 1, this temporal offset ~~lag~~ between the presence of anoxia/sulphidic conditions at station 2 (in August) and the strong decrease of faunal densities may be explained as a delayed response, mainly due to inhibited reproduction during the anoxic/sulphidic event. If true, ~~in the months after the presence of H_2S in the uppermost sediment,~~ the mortality of adults did not strongly increase~~, but they were~~ in the months following the H_2S production in the uppermost sediment. Nevertheless, there was no ~~longer replaced (~~replacement in the >125 µm fraction~~)~~ by growing juveniles, probably because reproduction was interrupted when H_2S was present in the foraminiferal microhabitat. ~~Renewed~~A renewed recruitment after the last stage of sulphidic conditions somewhere in September would then explain why the faunal density in the >125 µm fraction increased again in December 2012. (Supplementary Figure 2).

In 2011, at station 2, bottom waters oscillated between hypoxic and oxic conditions between May and August (Fig. ~~12~~11). Although we have no measurements of H_2S in the pore waters for this year ~~(i.e. like at station 1),~~ it seems probable that bottom

-water hypoxia was accompanied by the presence of free H_2S very close to the sediment surface, strongly affecting the foraminiferal communities. If we assume that, like in 2012, rich foraminiferal faunas were present in ~~spring~~May–July 2011 at both stations, the low faunal densities observed in August and November 2011 could suggest that ~~also in 2011,~~ foraminifera ~~show~~may have also shown a delayed response to sulphidic conditions in 2011.

It is interesting to note that the foraminiferal densities observed at station 2 were lower in August 2011 ~~were lower~~ than in July or September 2012. This ~~might~~may be ~~attributable to~~a consequence of the repetition of short hypoxic events in the bottom-water between May and August 2011 (probably associated with anoxia and maybe H_2S in the uppermost part of the sediment), which possibly affected the foraminiferal community more substantially in 2011 than in 2012, when a hypoxic event was ~~only~~ recorded in August only.

The important decrease of total standing stocks at station 2 in October and November 2012~~,~~ (Fig. ~~12~~11) suggests that, in spite of the shorter duration of anoxia and sulphide conditions (compared to station 1; one month or less compared to one to two months), the foraminiferal faunas ~~had~~were still ~~been~~ strongly affected. However, at station 2, foraminiferal abundances increased again in December 2012, suggesting a recovery time of about two months, which is likely much shorter than at station 1, where standing stocks in the >125 µm fraction only increased 6 months after the presence of anoxia and free sulphides.

Summarising, the foraminiferal communities of both stations 1 and 2 seem ~~to be~~ strongly impacted by the anoxic and sulphidic conditions developing in the uppermost part of the sediment ~~developing~~ in ~~late~~ summer~~/early autumn.~~ (i.e. July–September). However, at station 1, where anoxic and sulphidic conditions lasted for one to two months, the response is much stronger, leading ultimately (in November) to almost complete disappearance of the foraminiferal fauna. The delayed response at both stations shows that ~~mortality has not been~~ instantaneous mortality was limited, and suggests that the decreasing standing stocks ~~are~~might rather be the result of inhibited reproduction, and eventually, increased mortality.

Recovery is much faster at station 2 (about two months) than at station 1 (about six months), probably because at station 1 (in contrast to station 2) the foraminiferal extinction was nearly complete, and the site had to be recolonised (e.g. possibly by nearby sites or by the remaining few individuals) after reoxygenation of the sediment. At station 2, a reduced but significant foraminiferal community remained present, explaining the faster recovery.

4.42 Species-specific response to ~~environmental conditions~~anoxia, sulphide and food availability in Lake Grevelingen

~~As species determinations are increasingly based on genetic evidence and studies based only on morphological identification may suffer of taxonomic bias (Pawlowski and Holzmann, 2014), the~~ The comparison ~~with earlier studies is difficult. Therefore, we have restricted our comparisons to studies with relatively similar environmental conditions and whenever possible, with clear SEM images.~~

~~The assemblages of Lake Grevelingen were dominated by *E. selseyense*, *E. magellanicum* and *Ammonia* sp. T6 at station 1 and the same three species plus *T. inflata* at station 2. *Elphidium selseyense*, *E. magellanicum* and *Ammonia* sp. T6 are very~~

~~commonly found in coastal intertidal mudflats and/or other shallow water environments (e.g. Gustafsson and Nordberg, 1999, 2000; Langer and Leppig, 2000; Murray and Alve, 2000; Armynot du Châtelet et al., 2011; Schweizer et al., 2011; Saad and Wade, 2016). *Trochammina inflata* is an estuarine species with a worldwide distribution, which is typically found in salt marshes in the upper estuary (Debenay et al., 2006; Horton and Murray, 2007). However, other species of *Trochammina* are also commonly found in low DO environment (Gupta, 2007).~~

~~To our knowledge, all earlier studies show that the foraminiferal response to hypoxia/anoxia is species-specific (e.g. Bernhard and Alve, 1996; Ernst et al., 2005; Bouchet et al., 2007; Geslin et al., 2014; Langlet et al., 2014). However, these species-specific responses generally follow the same scheme (usually decrease in density, reduction of growth and/or reproduction), with different response intensities. Duijnstee et al. (2005) suggested that an oxic stress led to an increased mortality and an inhibited growth and reproduction. The suggestion of inhibited growth is supported by LeKieffre et al. (2017) who observed that *Ammonia tepida* showed minimal or no growth under anoxia. Conversely, Geslin et al. (2014) and Nardelli et al. (2014) suggested that reproduction was strongly reduced, but growth would not be affected by hypoxic and/or short anoxic events. Additionally, it is known that under low oxygen conditions, many species are able to shift to an anaerobic metabolism, such as denitrification (Risgaard-Petersen et al., 2006; Piña-Ochoa et al., 2010a), or by entering into a state of dormancy (Ross and Hallock, 2016; LeKieffre et al., 2017).~~

~~Our study of the size distribution of *E. selseyense* and *Ammonia* sp. T6 shows an absence of clear cohorts, suggesting that reproduction takes place throughout the year. Continuous reproduction during the year has been described earlier for different foraminiferal genera, such as *Elphidium*, *Ammonia*, *Haynesina*, *Nonion* and *Trochammina* (e.g. Jones and Ross, 1979; Murray, 1983; Cearreta, 1988; Murray, 1992; Basson and Murray, 1995; Gustafsson and Nordberg, 1999; Murray and Alve, 2000). However, for *Ammonia* sp. T6, a rapid increase of overall test size between March and May could be indicative of a period of increased growth in spring (Fig. 7), possibly in response to a food input following phytoplankton blooms in April–May (Fig. 10, Hagens et al., 2015).~~

~~The comparison of the faunal dynamics at the two investigated stations and~~of the different seasonal patterns of the major species ~~allow~~at the two investigated stations allows us to draw some conclusions about interspecific differences in the response to seasonal anoxic and sulphidic conditions.

First, there is a clear faunal difference between the two stations. Station 1 is dominated by *E. selseyense* and *E. magellanicum* while at station 2, these two taxa are accompanied by *Ammonia* sp. T6 and *T. inflata*. The latter species is almost absent at station 1, where~~as~~ *Ammonia* sp. T6 is present with ~~very moderate~~low densities. At first view, ~~this would suggest that~~ the dominance of the two *Elphidium* species at station 1, would suggest that they have a greater tolerance to the seasonal anoxic and sulphidic conditions~~.~~

~~Furthermore, it~~, which lasted much longer there. It is interesting to note that the temporal evolution of standing stocks at station 1 is different ~~between~~for the two *Elphidium* species. *Elphidium magellanicum* shows a strong drop in absolute density in July 2012, at the onset of H_2S presence in the uppermost part of the sediment, whereas the diminution of *E. selseyense* is more progressive and the species disappears almost completely only in November (Fig. 4). This strongly suggests that *E.*

magellanicum is more affected by increased mortality than *E. selseyense* ~~due~~in response to the combined effects of anoxic and sulphidic conditions. This ~~conclusion~~hypothesis is confirmed by the patterns observed at station 2, where the drop in standing stock~~s~~ in October–November is also more drastic in *E. magellanicum* than in *E. selseyense* (Fig. 5).

As mentioned earlier, certain species of foraminifera can use an anaerobic metabolism (i.e. denitrification, Risgaard-Petersen et al., 2006; Piña-Ochoa et al., 2010a), sequester chloroplasts (i.e. kleptoplastidy, Jauffrais et al., 2018), host bacterial symbiont (Bernhard et al., 2010) or enter in dormancy (Ross and Hallock, 2016; LeKieffre et al., 2017) to deal with low-oxygen conditions. Concerning the species found in this study, although the presence of intracellular nitrate was shown for *Ammonia*, denitrification tests yielded negative results (Piña-Ochoa et al., 2010a; Nomaki et al. 2014). Similarly, the presence of active symbionts was previously suggested for *Ammonia* but never confirmed (Nomaki et al., 2016; Bernhard et al., 2018). To our knowledge, denitrification or the presence of bacterial symbionts was never shown for *Elphidium* either. In conclusion, a shift to an alternative anaerobic metabolism or an association with bacterial symbionts has never been shown conclusively for the dominant foraminiferal species found in Lake Grevelingen.

The greater tolerance of *E. selseyense* to low-oxygen conditions could be explained by the fact that it is able to sequester chloroplasts from ingested diatoms, and to keep them active for several days to weeks, conversely to *Ammonia* sp. T6 (Jauffrais et al., 2018). These active chloroplasts could serve as an alternative source of oxygen and/or food through photosynthesis (Bernhard and Alve, 1996) or another metabolic pathway (Jauffrais et al., 2019), and thereby increase the capability of this species to survive anoxic events. Although sequestration of chloroplasts was never investigated for *E. magellanicum*, its abundant spinose ornamentation in the umbilical region and in the vicinity of the aperture (Fig. ~~A~~3c–d) suggests that this species is capable to crush diatom frustules as some kleptoplastic species (Bernhard and Bowser, 1999; Austin et al., 2005). As Hagens et al. (2015) observed that the light penetration depth in the Den Osse Basin never exceeded 15 m in 2012, and therefore photosynthesis by kleptoplasts (Bernhard and Alve, 1996) appears unlikely for both our aphotic stations (34 and 23 m depth). However, other foraminifera from aphotic and anoxic environments such as deep fjords are kleptoplastic and use these kleptoplasts for a yet unknown purpose (Jauffrais et al. 2019).

Rather surprisingly, the drop in foraminiferal densities at station 2~~, it is also~~ in October–November, which we interpreted as a delayed response to sulphidic conditions, is less strong for *Ammonia* sp. T6 than for the two *Elphidium* species, suggesting that this species is less affected. However, this does not agree with our previous suggestion that the two *Elphidium* species would be more tolerant to anoxic and sulphidic conditions. As already proposed by LeKieffre et al. (2017), *Ammonia* seems to be able to deal with anoxia (up to 28 days, but with no sulphide) by reducing its metabolic activity, but this ability was never shown for *Elphidium* species. If *E. selseyense* and *E. magellanicum* are indeed unable to resist to anoxia by reducing their metabolism or by entering a dormancy state, this could explain their stronger decrease in densities at station 2 compared to

Ammonia sp. T6. Nevertheless, further studies about the ability and mechanisms of the two *Elphidium* species to resist to anoxic/sulphidic conditions are necessary.

Another remarkable ~~to see~~observation is that ~~both~~ *Ammonia* sp. T6 (and *T. inflata*) shows maximum densities in ~~winter (~~January–March~~),~~, contrasting with the two *Elphidium* species, which have their density maxima later in the year (May–September). This temporal offset could possibly be explained by a difference in preferential food ~~sources~~source, with food particles available in winter (January–March) being more suitable for *Ammonia* sp. T6 (and *T. inflata*), versus food particles available later in the year, resulting from phytoplankton blooms, being more favourable for *E. selseyense* and *E. magellanicum*. In our study, for *E. selseyense* (and *E. magellanicum*), the continuous presence of a high proportion of small sized specimens and progressively increasing densities between January and September 2012 strongly suggest ongoing and continuous reproduction (Supplementary Figure 2A). Continuous reproduction during the year has been described earlier for different foraminiferal genera, such as *Elphidium*, *Ammonia*, *Haynesina*, *Nonion* and *Trochammina* (e.g. Jones and Ross, 1979; Murray, 1983; Cearreta, 1988; Murray, 1992; Basson and Murray, 1995; Gustafsson and Nordberg, 1999; Murray and Alve, 2000). ~~Foraminifera~~Conversely, for *Ammonia* sp. T6, a decrease in densities coupled with a rapid increase of overall test size between March and May 2012 (small sized specimens remain present but in smaller proportions) could be indicative of a period of reduced recruitment (Supplementary Figure 2B).

In fact, foraminifera exhibit a large range of feeding strategies, ~~some are~~ with several species showing selective ~~feeders~~feeding with specific food particles (Muller, 1975; Suhr et al., 2003; Chronopoulou et al., 2019). Hagens et al. (2015) reported that in Lake Grevelingen the phytoplankton composition was different between ~~spring~~April–May and ~~summer~~July 2012. In April–May, the phytoplankton bloom was mainly composed of the haptophyte *Phaeocystis* ~~*globosa*~~,*globose* (Scherffel, 1899), whereas it was dominated by the dinoflagellate *Prorocentrum micans* (Ehrenberg, 1834) in July. *Elphidium* was reported to be able to feed on various food sources (e.g. diatoms, dinoflagellates, green algae; Correia and Lee, 2002; Pillet et al., 2011). However, diatoms ~~should be the~~are a major food source for kleptoplastic species (Bernhard and Bowser, 1999), such as *E. selseyense* (Jauffrais et al., 2018; Chronopoulou et al., 2019). *Ammonia* spp. seems able to feed on very diverse food sources including microalgae, diatoms, bacteria or even metazoans (Lee et al., 1969; Moodley et al., 2000; Dupuy et al., 2010; Jauffrais et al., 2016; Chronopoulou et al., 2019). Recently, Chronopoulou et al. (2019) showed different feeding preferences for *Ammonia* sp. T6 and *E. selseyense* in intertidal environments in the Dutch Wadden Sea. Although diatoms are ~~harv~~ingested by both species (but ~~in different proportions~~much more by *E. selseyense*), dinoflagellates were consumed by *E. selseyense* but not by *Ammonia* sp. T6~~, which feeds~~. The latter species is also capable to feed on metazoans by active predation (~~see also~~ Dupuy et al., 2010). ~~Jauffrais et al. (2018) showed that *E. selseyense* is able to sequester chloroplasts from ingested diatoms, and to keep them active for several days to weeks. These active chloroplasts could serve as an alternative source of oxygen and/or food through photosynthesis (if the amount of light is sufficient as shown at 45 m depth in a fjord for *Stainforthia fusiformis*, Bernhard and Alve, 1996) or another metabolic pathway (Jauffrais et al., 2019), and thereby increase the capability of this species to survive anoxic events. Although sequestration of chloroplasts was never shown in *E. magellanicum*, its~~

abundant spinose ornamentation in the umbilical region and in the vicinity of the aperture (Fig. 3c–d) strongly suggests that this species is capable to sequester chloroplasts as well (Bernhard and Bowser, 1999; Austin et al., 2005), which could partly explain its resilience to anoxia and sulphidic conditions.

The drop in foraminiferal densities These observations suggest that at station 2 in October–November, which we interpreted as a delayed response to sulphidic conditions, is less strong for *Ammonia* sp. T6, suggesting that this species is less affected than, the different seasonal density patterns of *Ammonia* sp. T6 and the two *Elphidium* species. This does are not agree with our earlier suggestion that *Elphidium* species would be more tolerant to anoxic and sulphidic conditions. An explanation for this apparent contradiction could be that food sources available in spring were more suitable for *E. selseyense and E. magellanicum* than for *Ammonia* sp. T6. At station 2, the decreasing densities of *Ammonia* sp. T6 between March and May 2012 may be due to a lack of recruitment, with a continuing size increase of the adult specimens (Fig. 7). Conversely, *E. selseyense* (and *E. magellanicum*) would continue to reproduce in spring, leading to progressively increasing densities, and an absence of clearly defined cohorts with a high proportion of small sized specimens (Fig. 6).

These observations seem to indicate that at station 2, the difference in population dynamics between *Ammonia* sp. T6 and the two *Elphidium* species does not denoteconsequence of a large difference in tolerance to anoxia/sulphides, but rather a different adjustment of *Ammonia* sp. T6 and the two *Elphidium* species with respect to the seasonal cycle of food availability.

The At station 1, the very low densities of *Ammonia* sp. T6 at station 1 could thenputatively be explained by a recolonization starting in (late) winter, with only a few individuals present in January, at the end of the late autumn/early winter season with January, when food conditions were favourable food conditions for this taxon (as testified by the very strong density increase in January 2012 at station 2). OnceHowever, once a more abundant pioneer population was presenthad developed (in early springMarch-May), food conditions weremay have been no longer favourable for *Ammonia* sp. T6, but wereT6, explaining why its density did not show a further increase. Conversely, the food conditions may have become optimal for the two *Elphidium* species, explaining their strong dominance of the latter two species at station 1density increase between March and May 2012. If true, this would mean that the lower densities of *Ammonia* sp. T6 would not be due to a lower resistance to anoxia and free sulphides, but rather due to an unfavourable seasonal succession of food availability.

Previous studies already suggested that hypoxic/anoxic conditions coupled with increased food input from autumnal phytoplankton blooms (composed of diatoms and dinoflagellates) would favour the development of *E. magellanicum* (Gustafsson and Nordberg, 1999). The fact that also at station 2, this species was mainly observed between March and September 2012 corroborates our conclusion of its dependence on a specific food regime.

Finally, encrusted forms of *E. magellanicum* were observed at both stations from May until the end of the year, but were absent in the samples of March 2012. The observation of abundant specimens covered by feeding cystsIn view of the fact that the crusts consist mainly of organic matter, the encrusted individuals appear to be specimens with preserved feeding cysts. The precise functions of cysts observed around foraminifera are not clear, and include feeding, reproduction, chamber formation, protection or resting (Cedhagen, 1996; Heinz et al., 2005). Concerning the cysts of *E. magellanicum* described here, very similar observations have been made for *Elphidium incertum* at different locations (Norwegian Greenland Sea and Baltic Sea

in Linke and Lutze, 1993; Koljö Fjord in Gustafsson and Nordberg, 1999; Kiel Bight in Polovodova et al., 2009). If we assume that encrusted specimens indeed present remains of feeding cysts, the observation of abundant encrusted specimens corroborates our conclusion that the surface water phytoplankton bloom in May 2012 (i.e. probably mainly *Phaeocystis globosa*) provided a food source particularly well suited to the nutritional preferences of this species.

5 Conclusion

In this study we examined the foraminiferal community response to different durations of seasonal anoxia coupled with the presence of sulphide in the uppermost layer of sediment at two stations in Lake Grevelingen. In both stations investigated, foraminiferal communities are highly impacted by the combination of anoxia and H_2S in their habitat. The foraminiferal response varied depending on the duration of adverse conditions, and led to a near extinction at station 1, where anoxic and sulphidic conditions were present for one to two months, compared to a drop in standing stocks at station 2, where these conditions lasted for one month or less. At both sites, foraminiferal communities showed a two-month delay in the response to anoxic and sulphidic conditions, suggesting that the presence of H_2S inhibited reproduction, whereas mortality was not necessarily increased. The duration of the subsequent recovery depended on the fact whether the foraminiferal community was almost extinct (station 1) or remained present with reduced effectivesnumbers (station 2). In the former case, about six months waswere needed for faunal recovery, whereas in the latter case, it took only two months. We hypothesize that the dominance of *E. selseyense* and *E. magellanicum* at station 1 is not due to a lower tolerance of *Ammonia* sp. T6 to anoxic and sulphidic conditions of *Ammonia* sp. T6, but is rather the consequence of a different adjustment between the two *Elphidium* species and *Ammonia* sp. T6 with respect to the seasonal cycle of food availability.

Data availability

Raw data are available in Supplementary Material.

Author contributions

J.R.: generated the size distribution data. B.R. and D.L. picked the foraminifera. D.S.: provided geochemical data. All authors contributed to the writing of the manuscript.

Competing interests

The authors declare that they have no conflict of interest.

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1000

Table 1: Sampling dates of the samples which were investigated for living foraminifera for stations 1 and 2. x = one core investigated, o = no core investigated.

Year	Month	Day	Station 1	Station 2
2011	August	22	x x	x x
2011	November	15	x x	x x
2012	January	23	x x	x x
2012	March	12	x x	x x
		31		

2012	May	30	x x	x x
2012	July	24	x x	x x
2012	September	20	x x	x x
2012	October	18	o	x x
2012	November	2	x x	x x
2012	December	3	o	x x

Table 2: Mean living foraminiferal abundances (ind. 10 cm^{-3}) and relative abundances (between brackets) of the dominant species and total assemblage in 2011 and 2012 for both stations 1 (top) and 2 (bottom).

STATION 1

Year	Month	*Elphidium selseyense*	*Ammonia* sp. T6	*Elphidium magellanicum*	*Trochammina inflata*	Others	Total assemblage

2011	**August**	1.2 (36.8%)	1.2 (36.8%)	0 (0%)	0 (0%)	0.9 (26.3%)	3.4 (100%)
2011	**November**	0.5 (50%)	0.4 (33.3%)	0 (0%)	0 (0%)	0.2 (16.7%)	1.1 (100%)
2012	**January**	5.1 (44.6%)	3.2 (27.7%)	0.2 (1.5%)	1.2 (10.8%)	1.8 (15.4%)	11.5 (100%)
2012	**March**	23.9 (38.5%)	12.9 (20.8%)	21.6 (34.8%)	1.4 (2.3%)	2.3 (3.7%)	62.1 (100%)
2012	**May**	336.5 (74.8%)	9.2 (2%)	96.4 (21.4%)	1.8 (0.4%)	6 (1.3%)	449.9 (100%)
2012	**July**	162 (90.2%)	10.3 (5.7%)	3.7 (2.1%)	0 (0%)	3.5 (2%)	179.5 (100%)
2012	**September**	29.7 (87.5%)	2.3 (6.8%)	0 (0%)	0.4 (1%)	1.6 (4.7%)	34 (100%)
2012	**November**	1.1 (66.7%)	0.4 (22.2%)	0 (0%)	0 (0%)	0.2 (11.1%)	1.6 (100%)
	Sum	560 (75.4%)	39.8 (5.4%)	121.8 (16.4%)	4.8 (0.6%)	16.4 (2.2%)	742.9 (100%)

STATION 2

Year	Month	*Elphidium selseyense*	*Ammonia* sp. T6	*Elphidium magellanicum*	*Trochammina inflata*	Others	Total assemblage
2011	**August**	74.8 (43%)	82.1 (47.2%)	0 (0%)	14.7 (8.4%)	2.5 (1.4%)	174 (100%)
2011	**November**	52.3 (40.7%)	60.8 (47.3%)	0 (0%)	11.8 (9.2%)	3.7 (2.9%)	128.7 (100%)
2012	**January**	161.8 (30.9%)	226.2 (43.2%)	0.9 (0.2%)	121.5 (23.2%)	13.3 (2.5%)	523.6 (100%)
2012	**March**	214.7 (38.2%)	214 (38.1%)	48.8 (8.7%)	75 (13.3%)	9.9 (1.8%)	562.3 (100%)
2012	**May**	288.2 (47.7%)	147.1 (24.3%)	116 (19.2%)	36.1 (6%)	17.3 (2.9%)	604.8 (100%)
2012	**July**	282.6 (53.2%)	158.4 (29.8%)	37.8 (7.1%)	31.5 (5.9%)	21.2 (4%)	531.6 (100%)
2012	**September**	365.5 (64.4%)	102.4 (18%)	72 (12.7%)	16.1 (2.8%)	11.5 (2%)	567.5 (100%)
2012	**October**	98.7 (46.7%)	99 (46.8%)	1.8 (0.8%)	7.4 (3.5%)	4.6 (2.2%)	206.9 (100%)
2012	**November**	30.9 (34%)	48.1 (52.8%)	4.1 (4.5%)	3.7 (4.1%)	4.2 (4.7%)	91.1 (100%)
2012	**December**	252.2 (66.7%)	78 (20.6%)	25.5 (6.7%)	12.7 (3.4%)	9.5 (2.5%)	368.4 (100%)
	Sum	1821.8 (48.3%)	1216.1 (32.2%)	306.8 (8.1%)	330.5 (8.8%)	83.6 (2.6%)	3758.9 (100%)

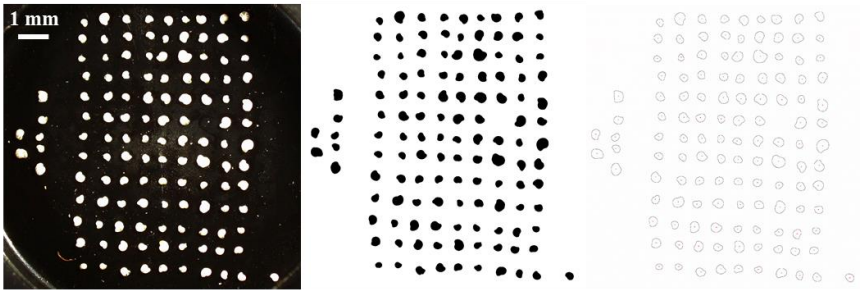

Figure 1: ~~This figure shows the different steps of the numerical~~Numerical treatment ~~of~~used for the size measurement for each image performed with ImageJ software. The left figure shows the untreated image, the middle figure presents the next step, when all

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individual foraminifera are depicted. Finally, the figure on the right shows the individual foraminiferal outlines which were measured.

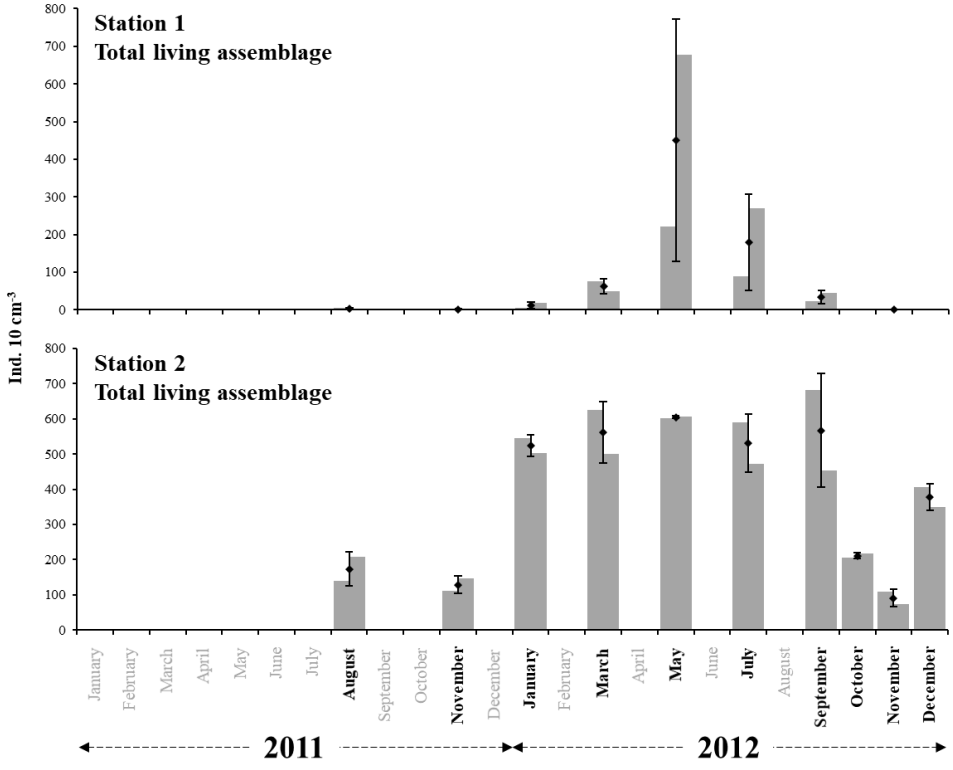


Figure 2: The grey bars represent the living foraminiferal abundances for the two replicates. The mean abundances (diamonds) and standard deviations (black error bars) were calculated for the two replicates for stations 1 (34 m depth, top panel) and 2 (23 m depth, bottom panel). All abundance values are for the 0–1 cm layer and were standardised to 10 cm^3. Months ~~for which~~where foraminiferal communities were investigated are indicated in bold. (excluding October and December at station 1).

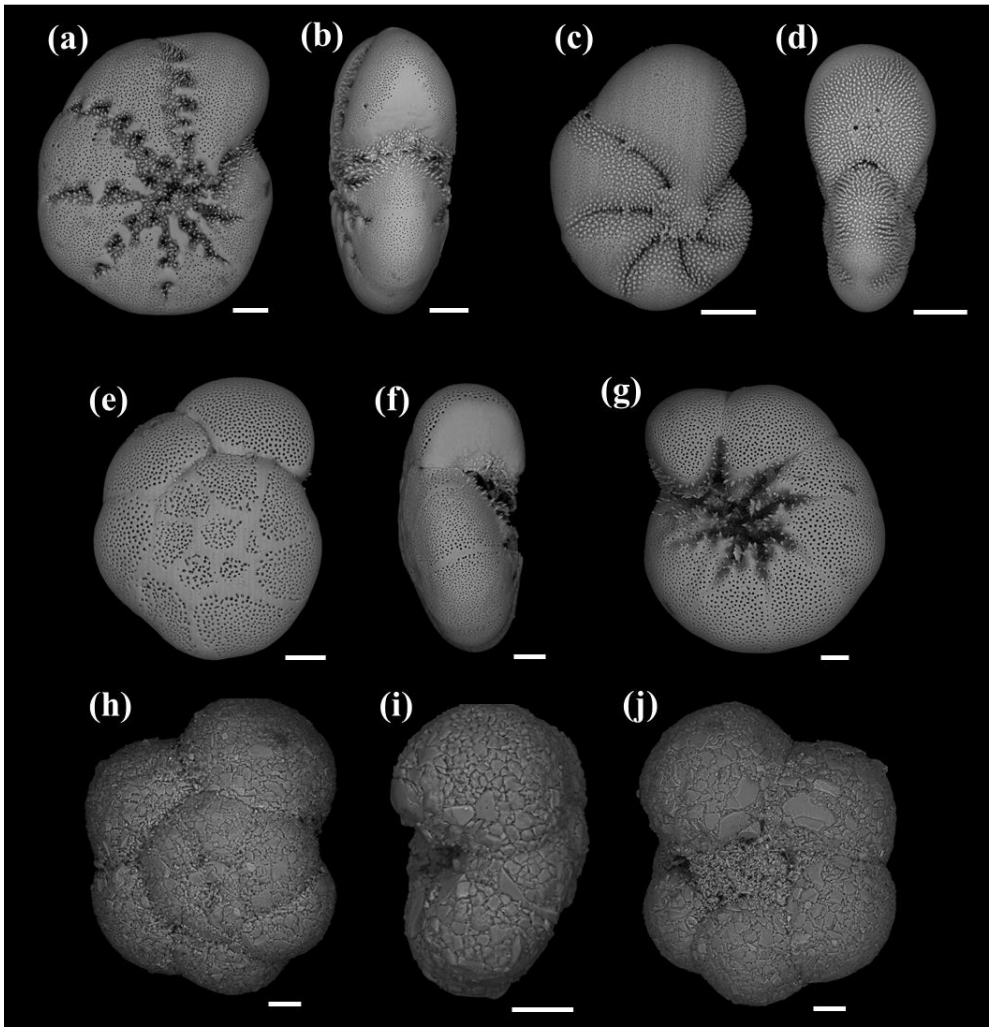


Figure 3: SEM images of *Elphidium selseyense* in lateral (a) and peripheral (b) view, *Elphidium magellanicum* in lateral (c) and peripheral (d) view, *Ammonia* sp. T6 in spiral (e), peripheral (f) and umbilical (g) view, and *Trochammina inflata* in spiral (h), peripheral (i) and umbilical (j) view. All scale bars are 50 µm.

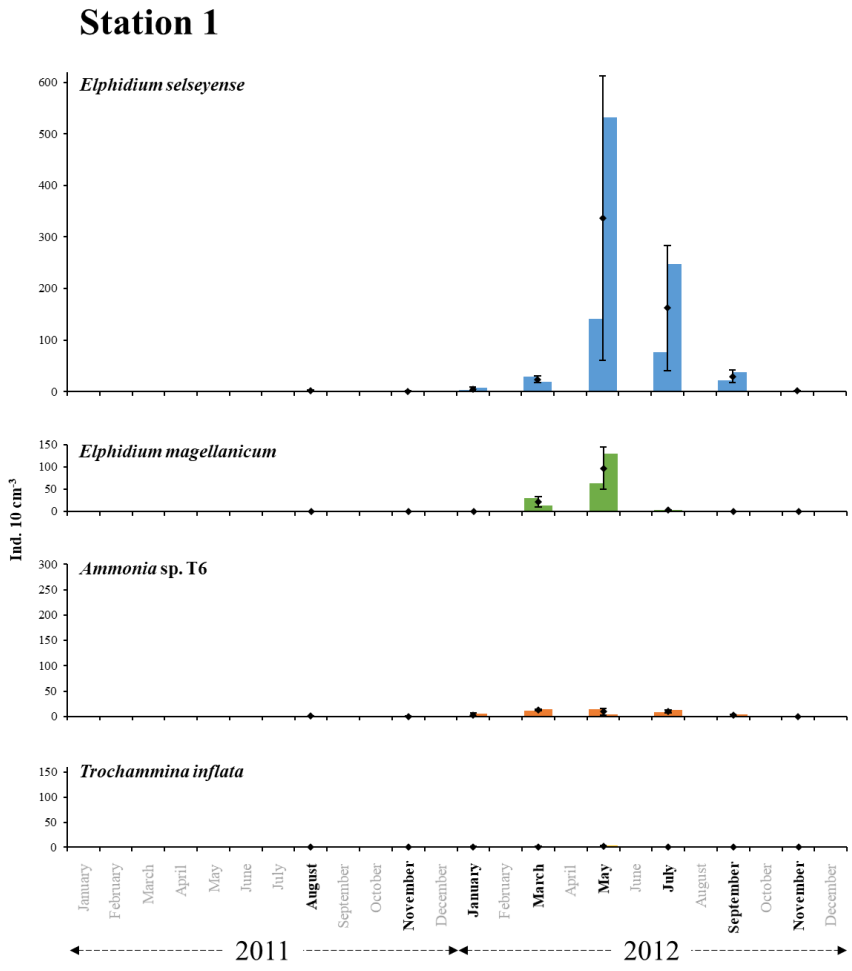
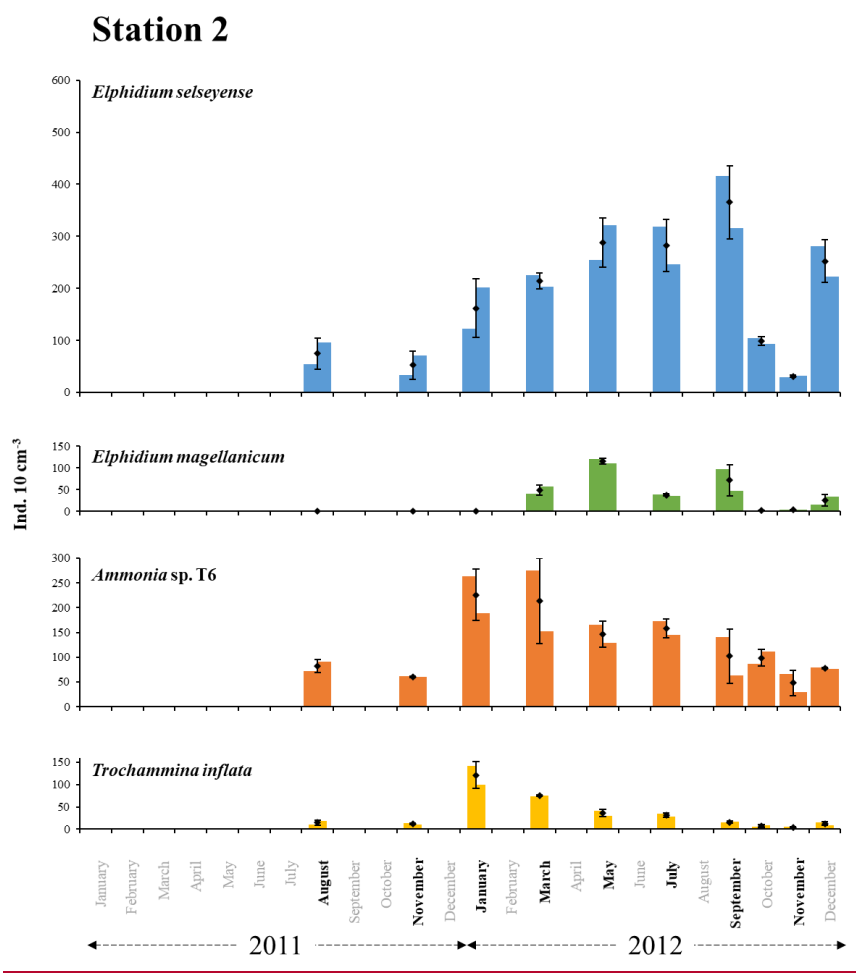


Figure 4: **The bars represent the living foraminiferal abundances for the two replicates for *Elphidium selseyense* (blue), *Elphidium magellanicum* (green), *Ammonia* sp. T6 (orange) and *Trochammina inflata* (yellow) at station 1 in 2011 and 2012. The mean abundances (diamonds) and standard deviations (black error bars) were calculated for the two replicates. All abundances values are for 0–1cm layer and were standardised to 10 cm^3. Months where foraminiferal communities were investigated are indicated in bold. Scales were chosen in order to facilitate comparison with station 2.**


Station 2
Elphidium selseyense
Elphidium magellanicum
Ammonia sp. T6
Trochammina inflata
Ind. 10 cm-3
January
February
March
April
May
June
July
August
September
October
November
December
2011
2012

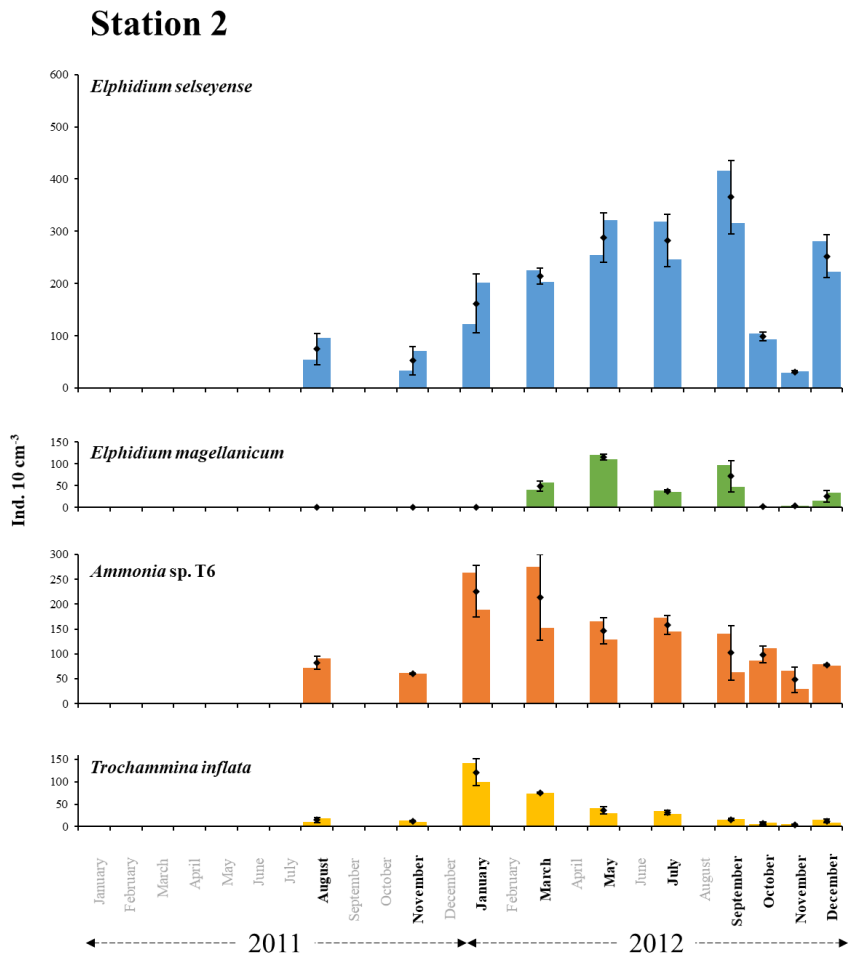
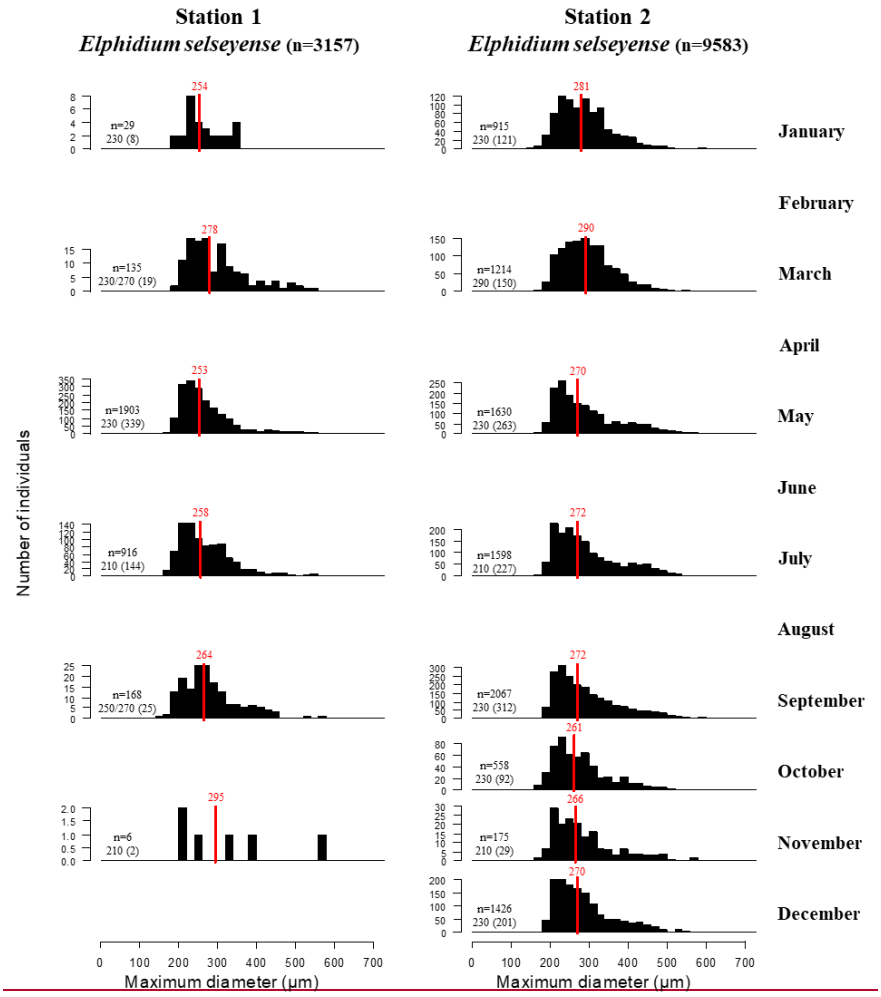
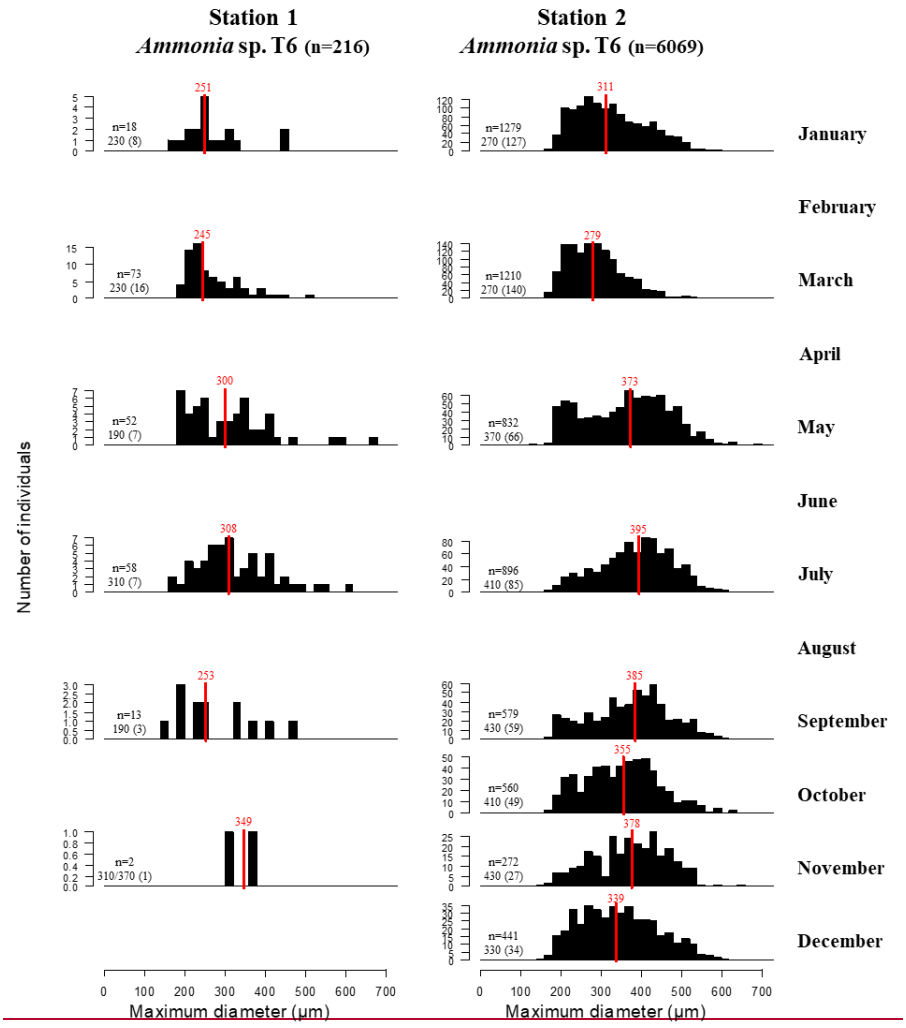


Figure 5: **The bars represent the living foraminiferal abundances for the two replicates for *Elphidium selseyense* (blue), *Elphidium magellanicum* (green), *Ammonia* sp. T6 (orange) and *Trochammina inflata* (yellow) at station 2 in 2011 and 2012. The mean abundances (diamonds) and standard deviations (black error bars) were calculated for the two replicates. All abundances values are for 0–1cm layer and were standardised to 10 cm^3. Months where foraminiferal communities were investigated are indicated in bold. Scales were chosen in order to facilitate comparison with station 21.**



~~**Figure 6: size distribution (maximum diameter for each individual in µm) of *Elphidium selseyense* for stations 1 (left) and 2 (right) in 2012. For each month, the number of individuals (n), the mode and the number of individuals associated to the mode (between brackets) are indicated in black. The medians are indicated by the red bars in each panel.**~~



~~Figure 7:~~ ~~size distribution (maximum diameter for each individual in µm) of *Ammonia* sp. T6 for stations 1 (left) and 2 (right) in 2012. For each month, the number of individuals (n), the mode and the number of individuals associated to the mode (between brackets) are indicated in black. The medians are indicated by the red bars in each panel.~~

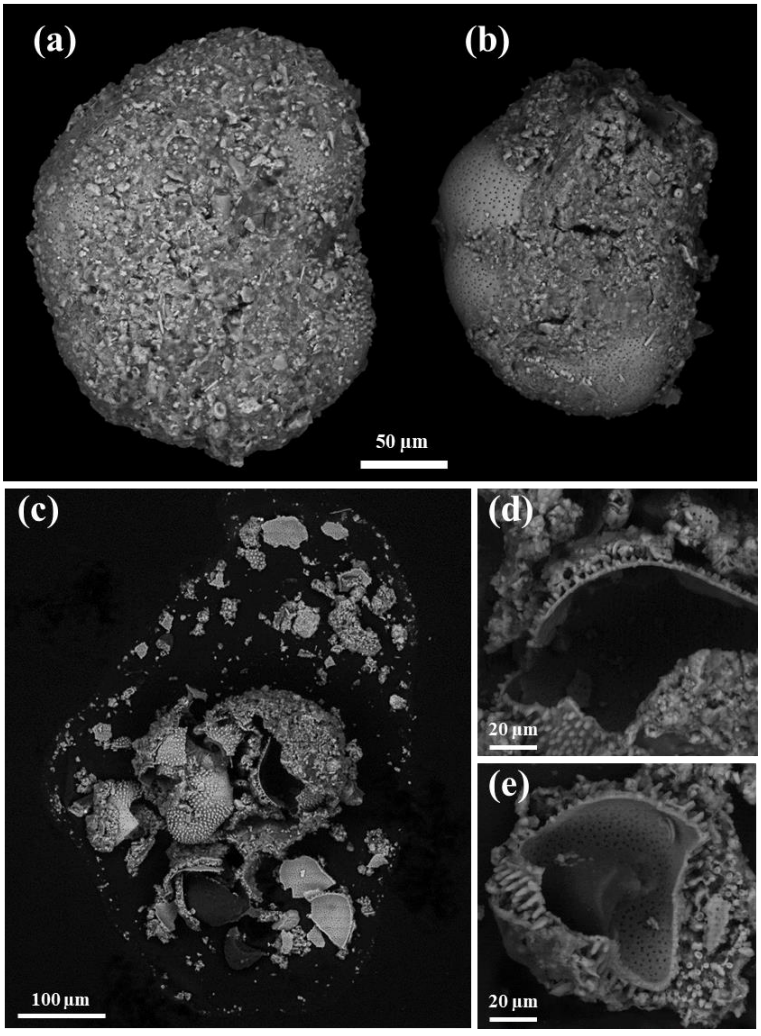


Figure 8: **SEM images of (a) fully encrusted specimen, (b) partially encrusted specimen, (c) crushed encrusted specimen of *Elphidium magellanicum*. Note the thinness of the crust and the spinose structures on (d) and (e).**

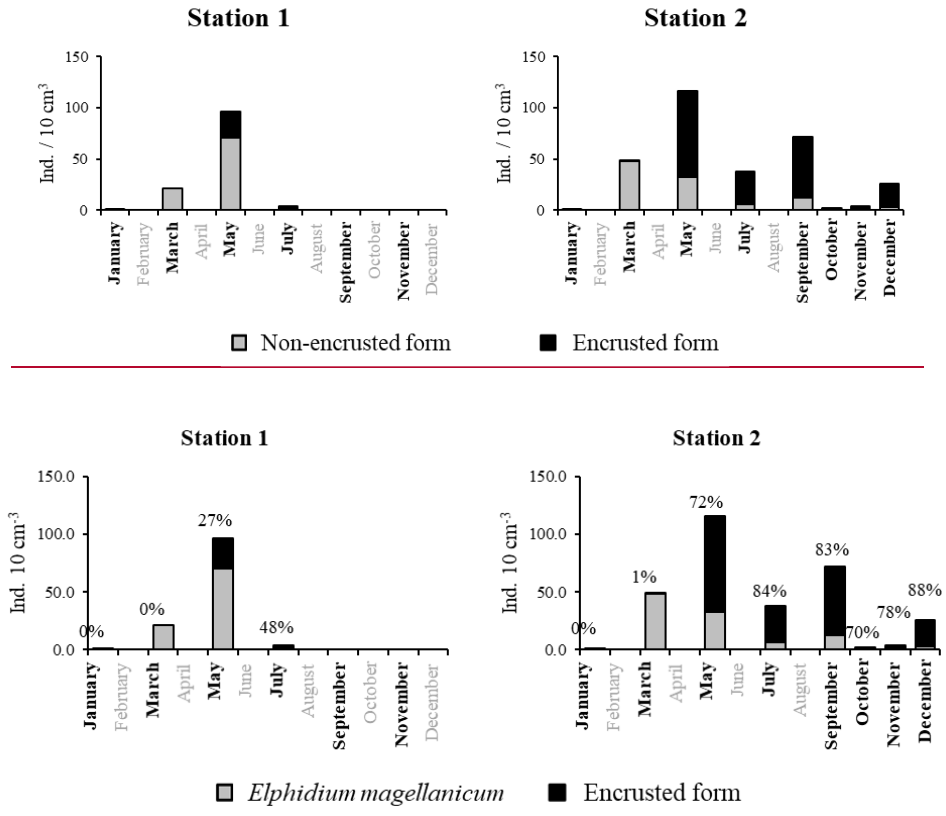
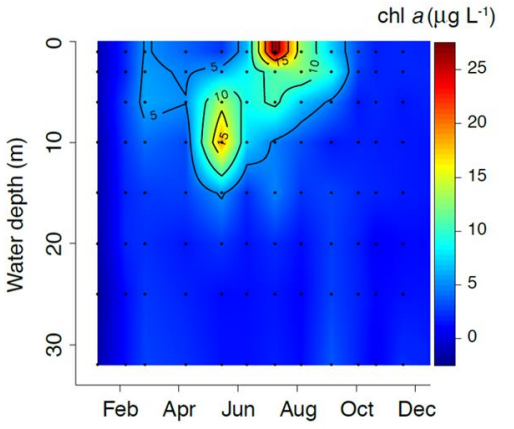


Figure 9: **Mean abundances (ind. 10 cm^{-3}) of non-encrusted (grey) and encrusted forms (black) of *Elphidium magellanicum* in 2012, at station, 1 (left) and 2 (right~~).~~, with proportion of encrusted forms above each bar (in %). Investigated months are indicated in bold.**


chl a (µg L-1)
Water depth (m)
0
10
20
30
Feb
Apr
Jun
Aug
Oct
Dec
25
20
15
10
5
0

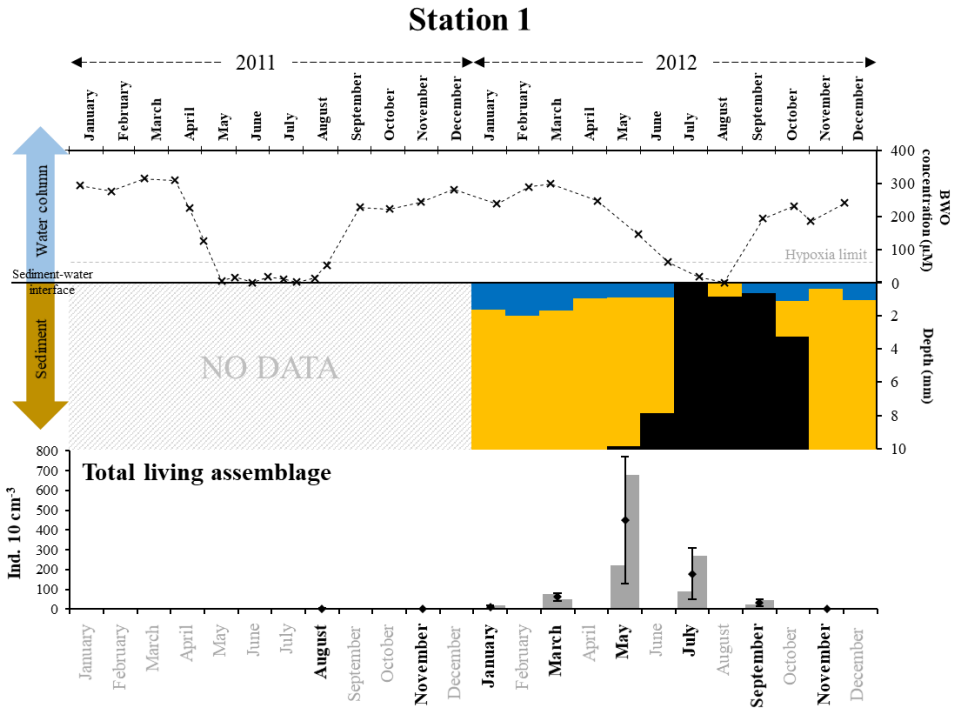
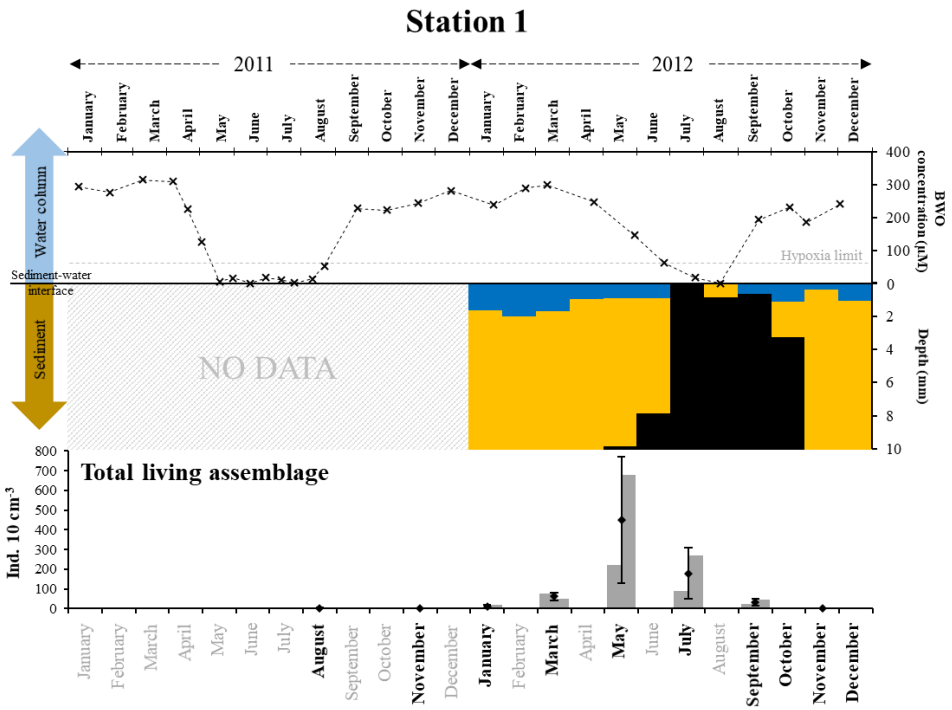


Figure 10: ~~Monthly Chl *a* concentrations (µg L^{-1}) in the water column in Den Osse Basin in 2012 – From Hagens et al. (2015).~~



~~Figure 11:~~ The top panel represents bottom–water oxygen concentrations (µmol L^{-1}) in 2011 and 2012 at station 1, from Donders et al. (2012) and Seitaj et al. (2017). The grey horizontal dotted line indicates the hypoxia limit (63 µmol L^{-1}). The middle panel represents the depth (in mm) distribution of the oxic (blue), ~~suboxic~~absence of oxygen and sulphides (orange~~),~~) and sulphidic (black) zones within the sediment in 2012, from ~~Sulu-Gambari~~Seitaj et al. (2015). The bottom panel shows the total living foraminiferal abundances for both replicates (grey bars), mean abundances (diamonds) and standard deviations (black error bars) calculated for the two replicates, for all investigated months (in bold) in 2011 and 2012.

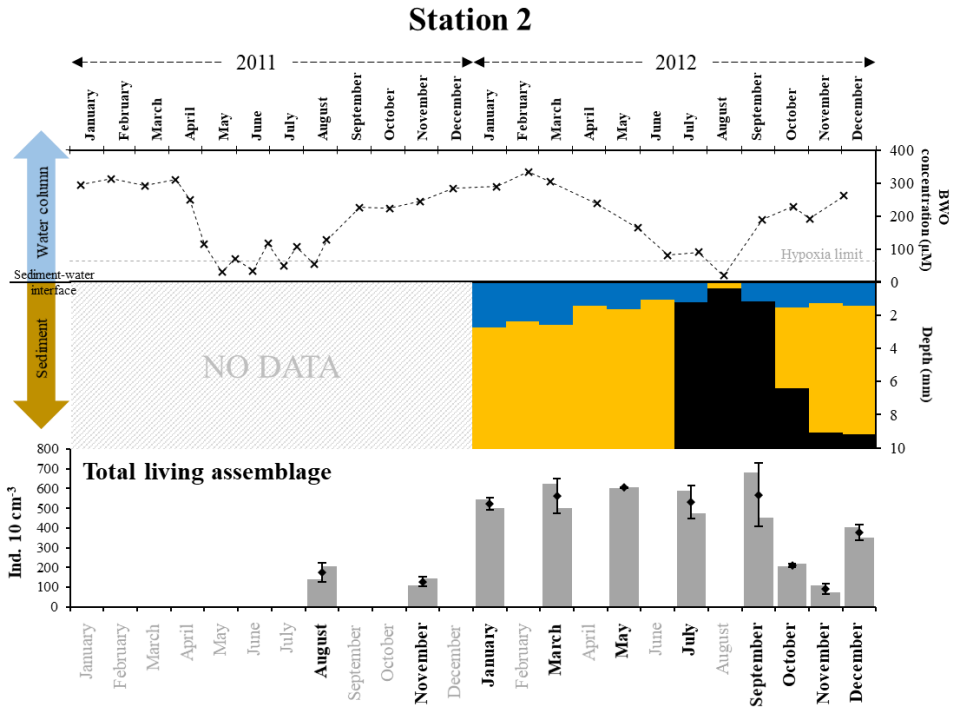


Figure ~~12~~11: The top panel represents bottom-water oxygen concentrations (µmol L^{-1}) in 2011 and 2012 at station 2, from Donders et al. (2012) and Seitaj et al. (2017). The grey horizontal dotted line indicates the hypoxia limit (63 µmol L^{-1}). The middle panel represents the depth (in mm) distribution of the oxic (blue), suboxic (orange, absence of oxygen and sulphides) and sulphidic (black) zones within the sediment in 2012. The bottom panel shows the total living foraminiferal abundances for both replicates (grey bars), mean abundances (diamonds) and standard deviations (black error bars) calculated for the two replicates, for all investigated months (in bold) in 2011 and 2012.

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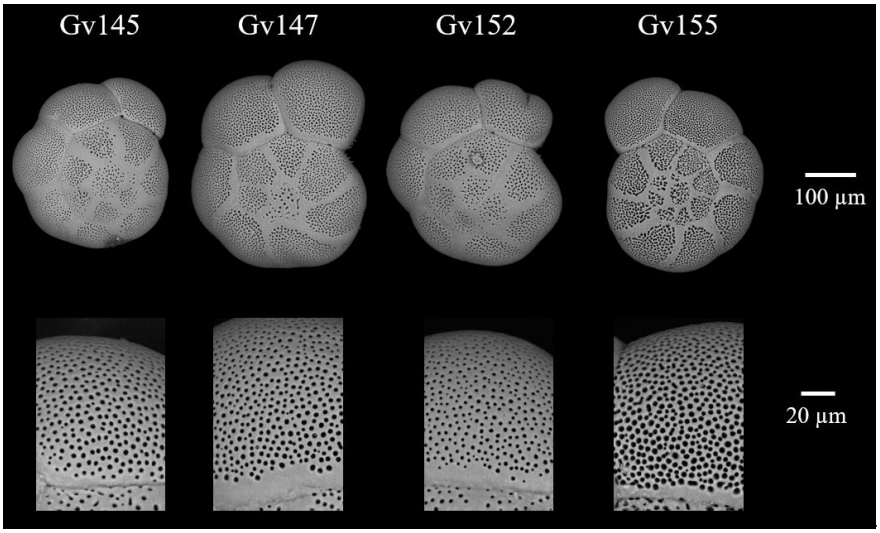
SUPPLEMENTARY MATERIAL



Associated with the manuscript:

Foraminiferal community response to seasonal anoxia in Lake Grevelingen (the Netherlands)

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~~**Supplementary figure 1. SEM images of spiral side and a 1000x magnification of the penultimate chamber for four individuals from Grevelingen station 1 identified T6 by molecular identification.**~~

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Supplementary Table 1. Oxygen Penetration Depth ± sd and free H_2S detection depth ± sd for each month in 2012 for both stations 1 and 2 (in mm).

Station	Month	OPD (mm)	H_2S depth (mm)
Station 1	January	1.7 ± 0.3	16.5 ± 3.2
	February	2 ± 0.4	17.1 ± 2.8
	March	1.7 ± 0.3	17.5 ± 0.7
	April	1 ± 0.2	18.6 ± 4.8
	May	1 ± 0.1	9.9 ± 2.2
	June	0.9 ± 0.1	7.9 ± 5.3
	July	0 ± 0	0.1 ± 0.1
	August	0 ± 0	0.9 ± 1.1
	September	0.7 ± 0.1	0.3 ± 0.2
	October	1.1 ± 0.1	3.3 ± 1.1
	November	0.4 ± 0	10.3 ± 1.9
	December	1.1 ± 0.2	13.4 ± 1.8
Station 2	January	2.8 ± 0	19.6 ± 2
	February	2.4 ± 0.2	15.8 ± 1.2
	March	2.6 ± 0.6	20.3 ± 3.3
	April	1.4 ± 0.2	23.3 ± 0.3
	May	1.6 ± 0	26.4 ± 1
	June	1.1 ± 0.4	17.1 ± 0.4
	July	1.3 ± 0.4	1.1 ± 0.8
	August	0 ± 0	0.4 ± 0.2
	September	1.2 ± 0.2	0.8 ± 0.2

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	October	1.6 ± 0.3	6.4 ± 2.9
	November	1.3 ± 0.2	9.1 ± 3.3
	December	1.5 ± 0.2	9.2 ± 0.7

Supplementary Table 2. Living foraminiferal abundances for each replicate for the dominant species and total assemblage (ind./10cm3).

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STATION 1

Species		***Elphidium selseyense***		***Ammonia* sp. *T6***		***Elphidium magellanicum***		***Trochammina inflata***		**Total assemblage**	
Year	**Month**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**
2011	August	2.1	0.4	1.4	1.1	0.0	0.0	0.0	0.0	4.2	2.5
2011	November	0.0	1.1	0.0	0.7	0.0	0.0	0.0	0.0	0.0	2.1
2012	January	2.8	7.4	0.7	5.7	0.0	0.4	0.4	2.1	5.0	18.0
2012	March	28.6	19.1	12.0	13.8	29.4	13.8	2.1	0.7	75.7	48.5
2012	May	141.5	531.6	13.8	4.6	63.0	129.8	0.4	3.2	222.1	677.6
2012	July	76.0	247.9	8.1	12.4	3.9	3.5	0.0	0.0	88.4	270.6
2012	September	21.2	38.2	0.7	3.9	0.0	0.0	0.0	0.7	21.9	46.0
2012	November	0.7	1.4	0.4	0.4	0.0	0.0	0.0	0.0	1.4	1.8

STATION 2

Species		***Elphidium selseyense***		***Ammonia* sp. *T6***		***Elphidium magellanicum***		***Trochammina inflata***		**Total assemblage**	
Year	**Month**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**
2011	August	53.8	95.8	72.5	91.6	0.0	0.0	10.6	18.7	140.1	208.0
2011	November	33.2	71.4	61.9	59.8	0.0	0.0	13.1	10.6	111.1	146.4
2012	January	122.0	201.6	263.1	189.2	1.1	0.7	142.5	100.4	545.4	501.9
2012	March	225.6	203.7	275.2	152.8	41.0	56.6	73.9	76.0	624.2	500.5
2012	May	254.6	321.8	165.9	128.4	120.6	111.4	42.1	30.1	602.3	607.3
2012	July	318.3	246.9	172.2	144.7	39.6	36.1	35.4	27.6	589.9	473.2
2012	September	415.2	315.8	141.1	63.7	97.3	46.7	14.9	17.3	681.2	453.8
2012	October	104.7	92.7	87.0	111.1	2.1	1.4	5.3	9.5	205.8	217.2

2012	November	29.4	32.5	66.5	29.7	3.9	4.2	5.0	2.5	108.9	73.2
2012	December	281.2	223.2	78.9	77.1	16.3	34.7	15.9	9.5	405.3	350.5

Supplementary Table 3. Living foraminiferal abundances for each replicate, year and month for all the species of the assemblage (ind./10cm3).

Year	Station	Replicate	Month	*Ammonia falsobeccarii* (T15)	*Ammonia* sp. T1	*Ammonia* sp. T2	*Ammonia* sp. T3	*Ammonia* sp. T6	*Bulimina denudata*	*Bulimina elongata*	*Bulimina marginata*	*Bulimina* sp.	*Cassidulina* sp.	*Elphidium selseyense*	*Elphidium magellanicum*	*Elphidium magellanicum* (encrusted)	*Elphidium margaritaceum*	*Elphidium* sp.	*Epistominella* sp.	*Haynesina depressula*	*Haynesina germanica*	*Hopkinsina* sp.	*Leptohalysis* sp.	Non determined	*Nonion* sp.	*Nonionella* sp.	*Quinqueloculina lamarckiana*	*Quinqueloculina* sp.	*Stainforthia* sp.	*Textularia* sp.	*Trochammina inflata*
2011	1	A	August	0.0	0.0	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.0	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.4	0.0	0.0	0.0
2011	1	A	November	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2012	1	A	January	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	2.8	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4
2012	1	A	March	0.4	0.0	1.1	0.0	12.0	0.4	0.0	0.0	0.0	0.0	28.6	29.4	0.0	0.0	0.4	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.4	2.1
2012	1	A	May	0.0	0.0	0.0	0.0	13.8	1.1	0.0	0.4	0.0	0.0	141.5	47.7	15.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.4	1.1	0.0	0.4	0.0	0.4
2012	1	A	July	0.0	0.0	0.0	0.0	8.1	0.0	0.0	0.0	0.0	0.0	76.0	1.8	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0
2012	1	A	September	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	21.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2012	1	A	November	0.0	0.0	0.4	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2011	1	B	August	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2011	1	B	November	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0
2012	1	B	January	0.0	0.0	0.7	0.0	5.7	0.0	0.0	0.0	0.0	0.0	7.4	0.4	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.4	0.0	0.0	2.1
2012	1	B	March	0.0	0.0	0.0	0.0	13.8	0.0	0.0	0.0	0.0	0.0	19.1	13.8	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.4	0.0	0.0	0.4	0.0	0.0	0.0	0.7
2012	1	B	May	0.0	0.0	0.0	0.0	4.6	0.4	0.0	0.0	0.0	0.0	531.6	93.4	36.4	0.4	0.0	0.7	0.4	0.0	0.0	0.0	2.1	0.0	0.4	0.4	1.1	2.5	0.4	3.2
2012	1	B	July	0.0	0.0	0.4	0.0	12.4	0.4	0.0	0.7	0.0	0.0	247.9	2.1	1.4	1.4	0.4	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.7	0.4	1.8	0.0	0.0
2012	1	B	September	0.0	0.0	0.0	0.0	3.9	0.0	0.0	0.0	0.0	0.0	38.2	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.5	0.4	0.7
2012	1	B	November	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2011	2	A	August	0.0	0.0	0.0	0.0	72.5	0.0	0.0	0.0	0.0	0.0	53.8	0.0	0.0	0.7	0.0	0.0	0.0	0.4	0.0	1.1	0.0	0.0	0.4	0.0	0.4	0.0	0.4	10.6
2011	2	A	November	0.0	0.0	0.0	0.0	61.9	0.0	0.0	0.0	0.0	0.0	33.2	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	1.1	0.0	0.0	13.1
2012	2	A	January	0.7	0.0	2.5	8.8	263.1	0.0	1.1	0.0	0.0	0.0	122.0	1.1	0.0	0.7	0.4	1.1	0.0	0.0	0.0	0.0	0.0	0.7	0.4	0.0	0.0	0.0	0.4	142.5
2012	2	A	March	0.0	0.0	1.4	0.0	275.2	0.0	0.0	0.0	1.8	0.0	225.6	40.0	1.1	0.4	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.7	0.7	0.0	1.4	0.0	1.8	73.9
2012	2	A	May	0.0	0.0	1.1	0.0	165.9	0.0	0.0	0.4	3.9	0.0	254.6	38.6	82.1	0.4	0.0	1.4	0.0	0.0	0.0	0.0	0.0	0.0	3.2	0.4	2.1	1.4	5.0	42.1
2012	2	A	July	0.0	0.0	1.8	0.0	172.2	6.0	2.1	0.4	0.4	0.0	318.3	3.9	35.7	1.4	0.0	0.4	0.7	0.0	0.0	0.0	0.0	0.0	0.4	0.0	7.1	1.8	2.1	35.4

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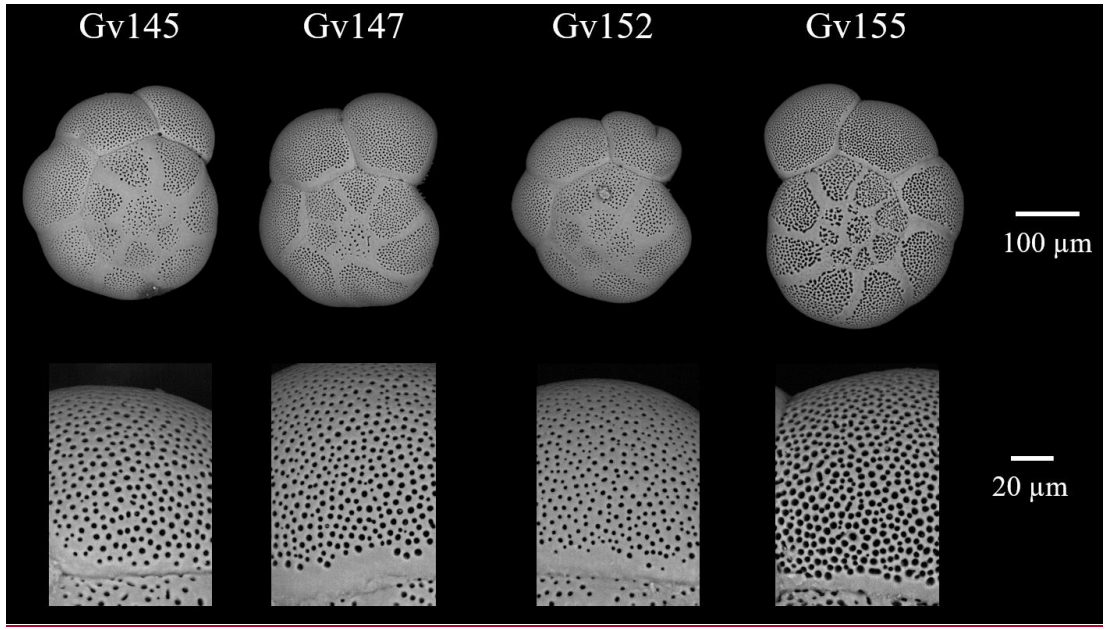
2012	2	A	September	0.0	0.7	0.0	0.0	141.1	0.0	1.4	0.4	0.0	0.0	415.2	16.3	81.0	0.4	0.4	3.2	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.0	0.4	1.4	3.2	14.9
2012	2	A	October	0.0	0.4	0.7	0.0	87.0	1.1	2.5	0.4	0.0	0.0	104.7	0.0	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	1.4	5.3
2012	2	A	November	0.0	0.0	0.0	0.0	66.5	0.7	0.0	0.4	0.0	0.0	29.4	0.0	3.9	0.4	0.0	0.0	0.0	0.0	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	5.0
2012	2	A	December	0.7	0.0	1.8	0.0	78.9	1.1	0.7	1.4	0.0	0.0	281.2	0.4	15.9	0.0	0.0	0.7	0.4	0.0	1.8	0.0	0.4	0.0	0.4	0.0	0.4	0.4	3.2	15.9
2011	2	B	August	0.0	0.0	0.0	0.0	91.6	0.0	0.0	0.0	0.4	0.0	95.8	0.0	0.0	0.0	0.0	0.0	0.7	0.4	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	18.7
2011	2	B	November	0.0	0.0	0.0	0.0	59.8	0.0	0.0	0.0	0.4	0.0	71.4	0.0	0.0	1.1	0.0	0.0	1.1	0.0	0.0	0.0	1.1	0.0	0.0	0.0	1.1	0.0	0.0	10.6
2012	2	B	January	0.0	0.4	2.1	0.0	189.2	0.0	0.4	0.0	0.0	0.0	201.6	0.7	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.7	0.0	0.4	100.4
2012	2	B	March	0.0	0.0	1.1	0.0	152.8	0.4	0.0	0.0	2.1	0.0	203.7	56.2	0.4	1.1	0.7	1.4	0.0	0.0	0.0	0.0	0.0	1.1	0.4	0.0	1.8	0.7	0.7	76.0
2012	2	B	May	0.0	0.0	1.4	0.0	128.4	2.1	0.0	0.7	0.0	0.4	321.8	25.8	85.6	0.0	0.0	0.4	0.4	0.0	0.0	0.0	1.8	0.0	2.8	1.1	0.7	1.1	2.8	30.1
2012	2	B	July	0.0	1.1	1.4	0.0	144.7	0.4	1.8	1.8	2.1	0.0	246.9	8.1	27.9	0.7	0.0	1.1	1.1	0.0	0.0	0.0	0.0	0.0	0.4	2.1	1.1	0.7	2.5	27.6
2012	2	B	September	0.0	0.0	0.4	0.0	63.7	1.8	0.7	0.0	0.0	0.0	315.8	8.1	38.6	1.4	0.4	2.1	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.4	1.4	1.4	17.3
2012	2	B	October	0.0	0.7	1.1	0.0	111.1	0.4	0.0	0.0	0.0	0.0	92.7	1.1	0.4	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	9.5
2012	2	B	November	0.0	0.0	0.4	0.0	29.7	1.1	0.0	0.4	0.0	0.0	32.5	1.8	2.5	0.4	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.4	0.7	2.5
2012	2	B	December	0.0	0.0	0.0	0.0	77.1	1.4	0.7	0.0	0.0	0.0	223.2	5.7	29.0	1.1	0.0	1.4	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.4	0.4	0.0	0.4	9.5



Supplementary figure 1. SEM images of spiral side and a 1000x magnification of the penultimate chamber for four individuals from Grevelingen station 1 identified T6 by molecular identification.

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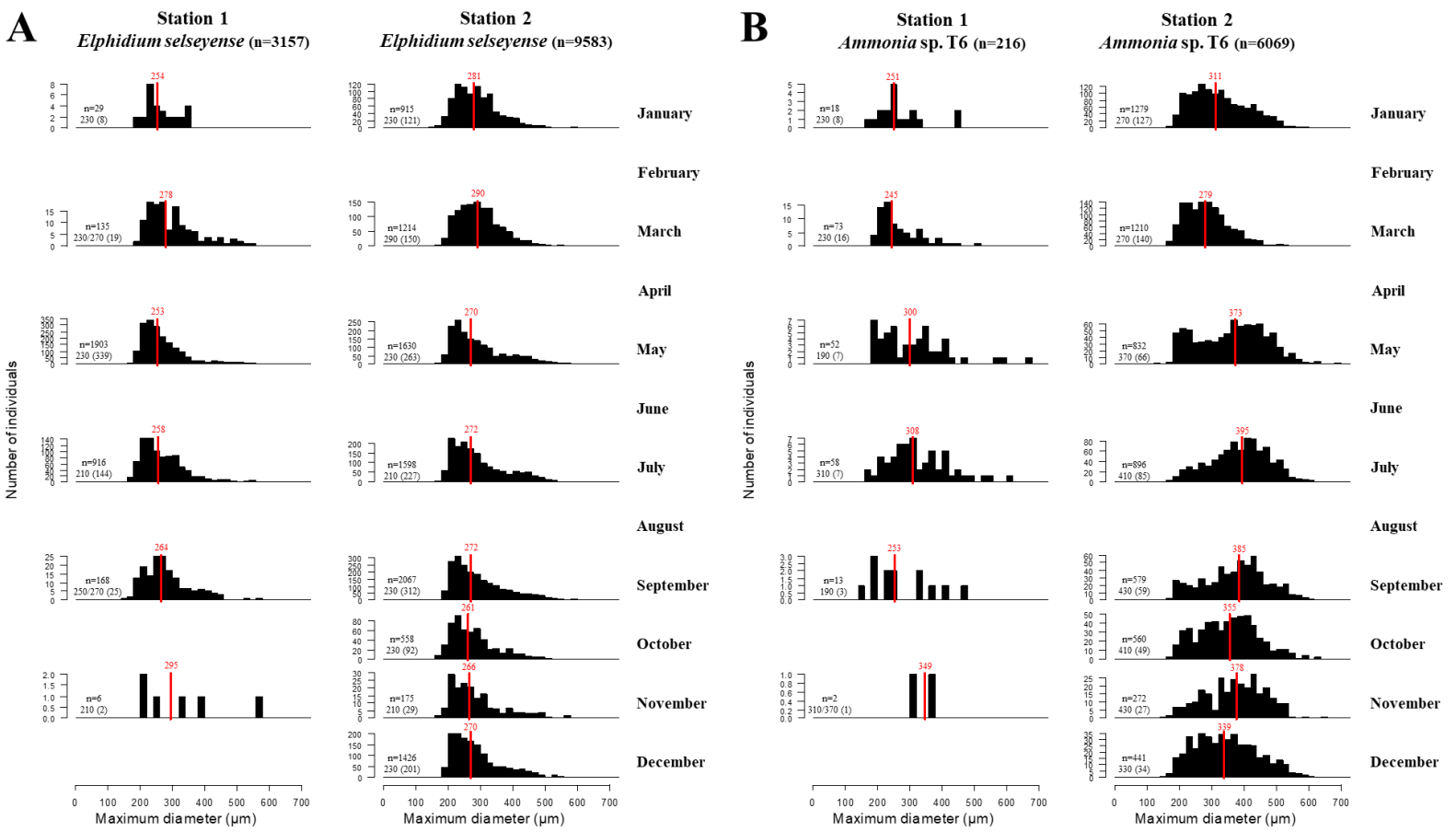

Supplementary Figure 2: A: size distribution (maximum diameter for each individual in µm) of *Elphidium selseyense* for stations 1 (left) and 2 (right) in 2012. B: size distribution (maximum diameter for each individual in µm) of *Ammonia* sp. T6 for stations 1 (left) and 2 (right) in 2012. For each month, the number of individuals (n), the mode and the number of individuals associated to the mode (between brackets) are indicated in black. The medians are indicated by the red bars in each panel. In order to base our analysis on a sufficiently high number of specimens, we focused on *E. selseyense* and *Ammonia* sp. T6. As explained before, we only considered specimens retained on a 125 µm mesh meaning that juvenile specimens are not represented. Only the samples taken in 2012 were considered. The size distribution of *E. selseyense* was relatively similar between the two stations regarding the median, ranging from 253 µm (in May) to 295 µm (in November) at station 1 and from 261 µm (in October) to 290 µm (in March) at station 2. At both stations, we observed the presence of an abundant group of smaller specimens, with a mode that never exceeded 250 µm, except in March at station 2, when it is difficult to separate this subpopulation from the larger specimens. The main difference between the two stations was the higher proportion of larger individuals (>400 µm) at station 2, which

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was visible through the better-developed tails at the right side of the distribution graphs. The low number of *Ammonia* sp. T6 individuals at station 1 did not allow us to draw any firm conclusion concerning the size distribution at this station (Supplementary Figure 3). At station 2, a group of individuals with smaller diameters (< 300 µm) was always present. The overall size distribution showed a clear shift to higher diameters between March (median = 279 µm) and May (median = 373 µm, Fig. 7), which is also evidenced by the much higher proportion of larger individuals. Specimens larger than 400 µm were abundantly found until November (median = 378 µm), but started to diminish in December, as is also shown by the decrease of the median to 339 µm. Our tentative to distinguish cohorts by using a deconvolution method to separate the total size distributions into a sum of Gaussian curves was not conclusive. The main problem was the fact that we did not have any information concerning individuals smaller than 125 µm, so that our size distributions were systematically skewed on the left side (i.e. toward small individuals). An additional problem was the large number of smaller specimens which were always present. Because the identification of individual cohorts was not successful, parameters like reproduction rate, growth rate or lifespan were not assessable. Nevertheless, the size distribution data give some clues concerning the population dynamics of the two dominant species.