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

Julien Richirt[1], Bettina Riedel[1,2], Aurélia Mouret[1], Magali Schweizer[1], Dewi Langlet[1,3], Dorina Seitaj[4], Filip J. R. Meysman[5,6], Caroline P. Slomp[7] and Frans J. Jorissen[1]

[1]UMR 6112 LPG-BIAF Recent and Fossil Bio-Indicators, University of Angers, 2 Boulevard Lavoisier, F-49045 Angers, France

[2]First Zoological Department, Vienna Museum of Natural History, Burgring 7, 1010 Vienna, Austria

[3]~~UMR~~ Univ. Lille, CNRS, Univ. Littoral Côte d'Opale, UMR 8187, LOG, Laboratoire d'Océanologie et de Géosciences~~, University of Lille, CNRS, University of Littoral Côte d'Opale~~, F 62930 Wimereux, France

[4]Department of Ecosystem Studies, Royal Netherlands Institute for Sea Research (NIOZ), Yerseke, the Netherlands

[5]Department of Biology, University of Antwerp, Universiteitsplein 1, BE-2610 Wilrijk, Belgium

[6]Department of Biotechnology, Delft University of Technology, 2629 HZ Delft, the Netherlands

[7]Department of Earth Sciences (Geochemistry), Faculty of Geosciences, Utrecht University, Princetonlaan 8a, 3584 CB Utrecht, the Netherlands

Correspondence to: Julien Richirt (richirt.julien@gmail.com)

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

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35 Grevelingen, *Elphidium selseyense* and *Elphidium magellanicum* are much less affected by anoxia and free H$_2$S than *Ammonia*
sp. T6. We hypothesise that this is not due to a higher tolerance ~~of~~for H$_2$S, 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
40 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
45 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~~
50 ~~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$_2$S) in pore and/or bottom ~~waters,~~ waters (e.g. Jørgensen, 1982; Seitaj et al., 2015), which is
55 considered very harmful for the benthic macrofauna (Wang and Chapman, 1999). Neutral molecular H$_2$S 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
60 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$_2$S front in the uppermost part of the
sediment, sometimes up to the ~~water-~~sediment-water interface.
65 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

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(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 H₂Sthe presence of H$_2$S 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$_2$S 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 isand long term anoxia (from weeks to 10 months) has been well knowndocumented 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$_2$S 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 dynamicsresponse 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$_2$S 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

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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.
135 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 detect~~ed~~able oxygen (following Rabalais et al., 2010).

140 **~~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
145 *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$_2$S in the water column) does not occur in the Den Osse Basin due to cable bacterial activity in winter, free H$_2$S is present in the uppermost
150 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'
155 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~~1~~95).
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
160 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$_2$S detection were determined ~~using O$_2$ and H$_2$S microsensors~~ by Seitaj et al., (2015) using profiling microsensors for station 1~~, and the~~. The data for station 2 (Supplementary Table 1) were acquired

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similarly (Supplementary Table 1and 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 eachthe core was labelledthen 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 1µM1µmol 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 darkSince 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 ($\overline{x} \pm sd$) 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*
195 *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,
200 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).
205 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
210 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
215 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.

220 **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

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225 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 eachEach 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

230 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

235 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

240 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.

245 **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

250 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

255 ~~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. Total~~Averaged 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

260 for most months, contrasting with ~~a~~ much higher densit~~y~~ies 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

265 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

270 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*

275 *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

280 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,

285 ~~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 ± 11~~) to reach maximal values in May ($\overline{x} = 336.5 \pm 275.8$ ~~and $\overline{x}$ = 96.4 ± 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 ± 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

290 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 ± 0.3)~~.~~. The species was absent from samples in September and November 2012. *Ammonia* sp. ~~be~~T6 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*

295 *inflata* was absent in 2011 and was only present with very low abundances from January to May and in ~~Nov~~Septe~~m~~ber 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 ± 27) then showed a progressive increase until a maximum in September 2012 ($\overline{x} = 365.5 \pm 70.3$). Abundances then

300 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 similar~~an analogous pattern ~~as~~to *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

305 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, abundances~~Abundances 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 ($\overline{x} = 25.5 \pm 13$).

310 **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~~

315 ~~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,~~

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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).

320 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

325 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

330 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

335 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 afterAfter 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

340 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).

345 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 ~~Use~~Tolerance 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$_2$S into the water column) does not occur in the Den Osse Basin due to cable bacterial activity in winter, free H$_2$S 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

385 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).

390 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,

395 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

400 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

405 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

410 using sealed flasksFor 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$_2$S concentration of 500 µmol L^{-1}. The author found that foraminiferal activity (as
415   determined by ATP content) was not significantlyOur observations confirm the suggestion in previous studies that the foraminiferal community is severely affected by a long-term presence of H$_2$S 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 thea 66 -days incubation in euxinic conditions (a maximum of 11.9 ± 0.4
420   µmol L^{-1} of H$_2$S 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, duringLanglet et al. (2013, 2014), performed an *in situ* experienceexperiment 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
425   decreaseddecrease of living foraminiferal density (labelled with CTG), but also found that almost all species survived after 10 months of anoxia withand periodically co-occurrence ofoccurring H$_2$S 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
430   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
435   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
440   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$_2$S 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
445   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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Mis en forme : Non Surlignage

Mis en forme : Non Surlignage

455 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
460 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 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
465 in the superficial sediment (i.e. from 0.4 ± 0.2 mm downwards, Fig. 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 H₂S was still detected at about 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. 11).
470 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. 11). Like at station 1, this temporal offset 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, the mortality of adults did not strongly increase
475 in the months following the H₂S production in the uppermost sediment. Nevertheless, there was no replacement in the >125 µm fraction by growing juveniles, probably because reproduction was interrupted when H₂S was present in the foraminiferal microhabitat. 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).
480 In 2011, at station 2, bottom waters oscillated between hypoxic and oxic conditions between May and August (Fig. 11). Although we have no measurements of H₂S in the pore waters for this year, it seems probable that bottom

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~~-~~water hypoxia was accompanied by the presence of free H$_2$S 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
485 ~~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$_2$S 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~~
490 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
495 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).
500 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
505 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.~~4~~2 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~~
510 ~~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~~

515 ~~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).~~

520 ~~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~~

525 ~~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).~~

530 ~~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~~

535 ~~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.

540 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, wherea~~s~~ *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~~.~~

545 ~~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.*

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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 stocks 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. ~~At~~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

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

585 Another remarkable ~~to see~~observation is that ~~both~~ *Ammonia* sp. T6 (and *T. inflata*) show~~s~~ 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*.

590 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).

595 ~~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

600 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.*

605 *selseyense* (Jauffrais et al., 2018; Chronopoulou et al., 2019). *Ammonia* sp~~p~~. 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 ~~harving~~ested by both species (but ~~in different proportions~~much more by *E. selseyense*), dinoflagellates were consumed by *E. selseyense* but

610 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~~

615 ~~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 denote~~consequence 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 ~~then~~putatively 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). ~~Once~~However, once a more abundant pioneer population ~~was present~~had developed (in ~~early spring~~March-May), food conditions ~~were~~may have been no longer favourable for *Ammonia* sp. ~~T6, but were~~T6, explaining why its density did not show a further increase. Conversely, the food conditions may have become optimal for the two *Elphidium* species, explaining the~~ir strong ~~dominance of the latter two species at station 1~~density 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 cysts~~In 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

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650 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

655 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
660 conditions lasted for one month or less. At both sites, foraminiferal communities showed a two-months 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
665 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.

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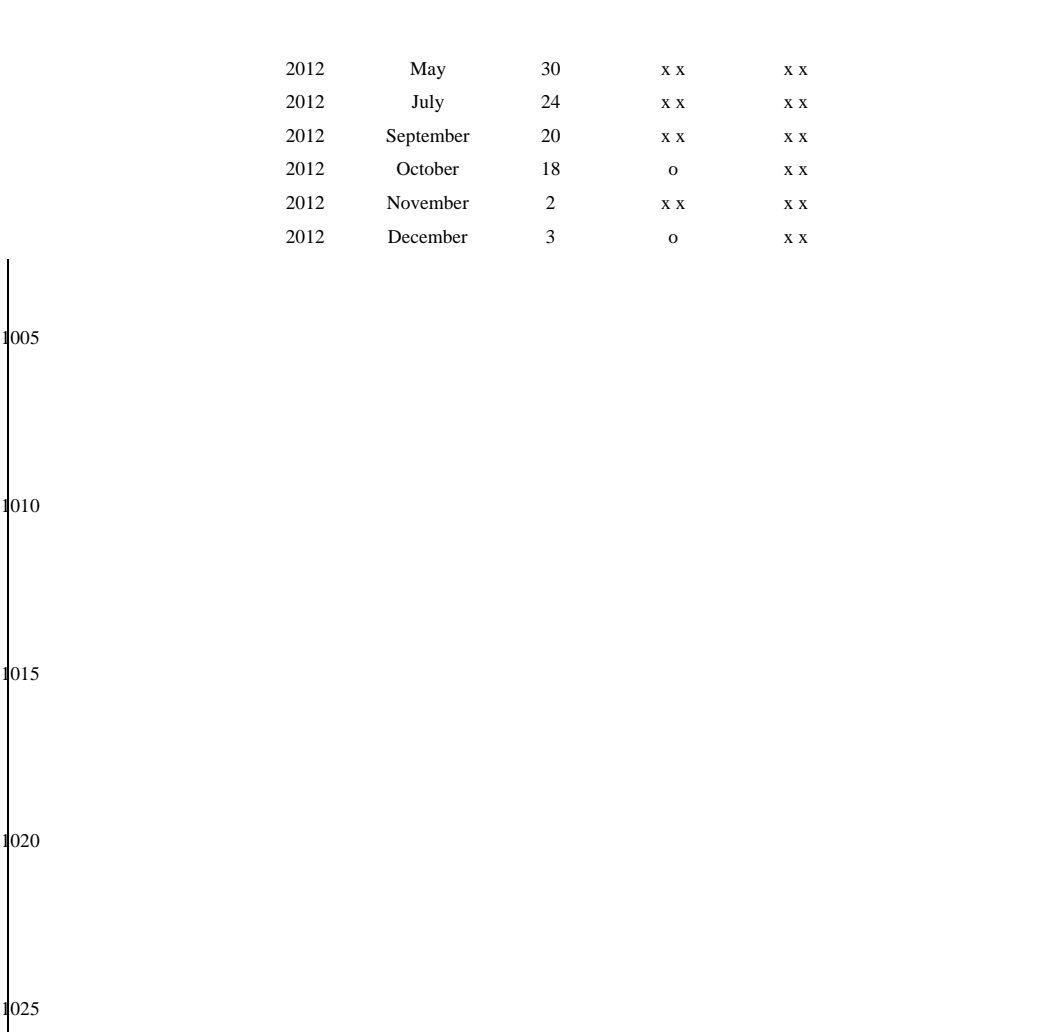**Table 1:** Sampling dates of the samples which were investigated for living foraminifera for stations 1 and 2. x = one core investigated, o = no core investigated.

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

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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

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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

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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%)

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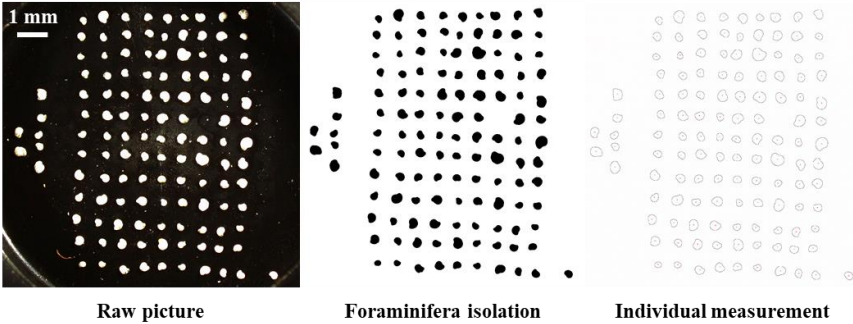
Figure 1: ~~This figure shows the different steps of the numerical~~Numerical treatment ~~of~~used for the size measurement for each image performed with ImageJ software. The left figure shows the untreated image, the middle figure presents the next step, when all

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individual foraminifera are depicted. Finally, the figure on the right shows the individual foraminiferal outlines which were measured.
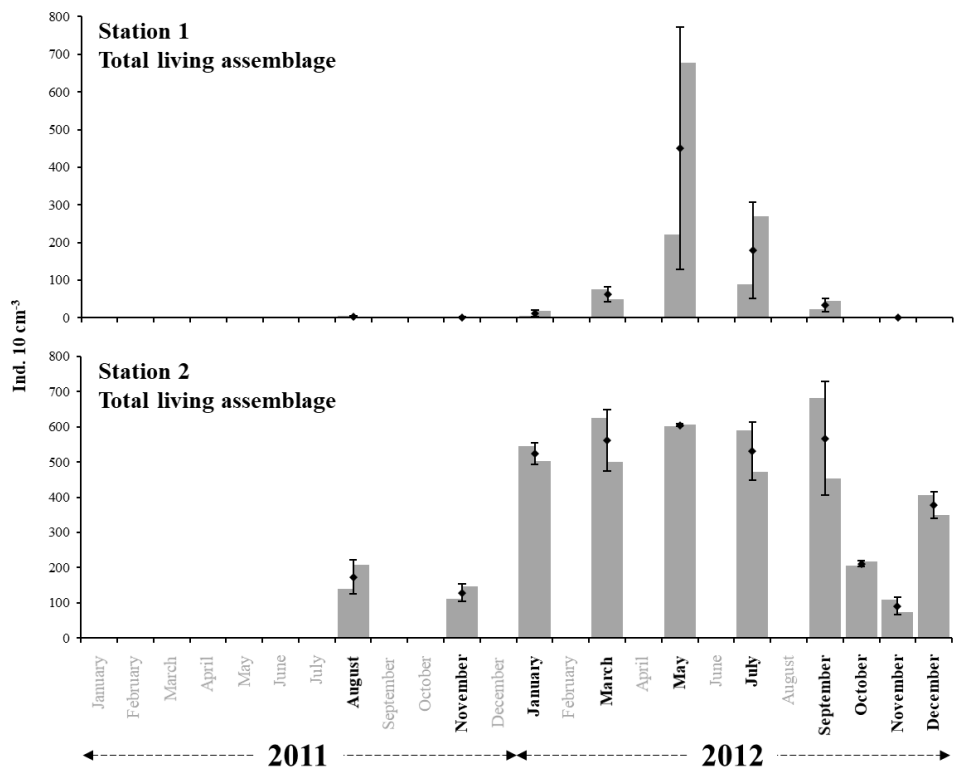
Figure 2: The grey bars represent the living foraminiferal abundances for the two replicates. The mean abundances (diamonds) and standard deviations (black error bars) were calculated for the two replicates for stations 1 (34 m depth, top panel) and 2 (23 m depth, bottom panel). All abundance values are for the 0–1 cm layer and were standardised to 10 cm³. Months ~~for which~~where foraminiferal communities were investigated are indicated in bold~~.~~ (excluding October and December at station 1).
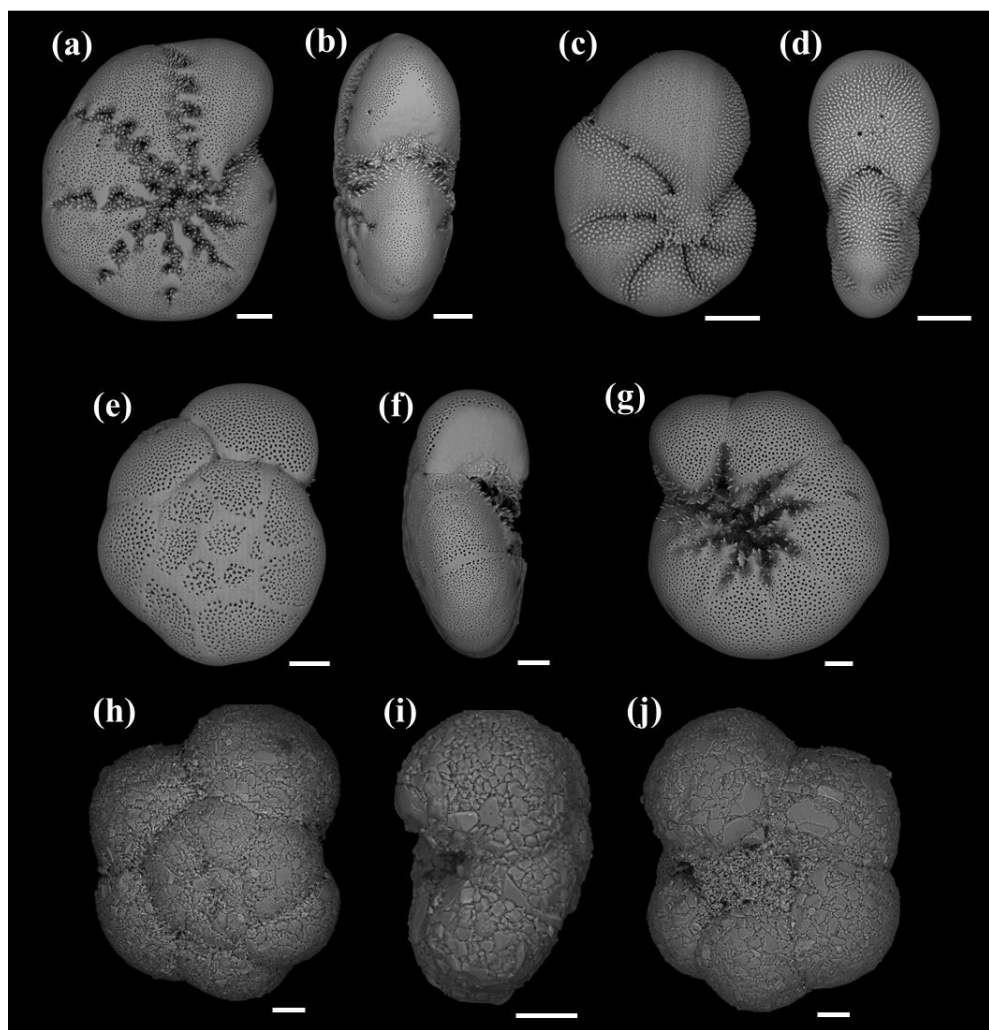
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Figure 3: SEM images of *Elphidium selseyense* in lateral (a) and peripheral (b) view, *Elphidium magellanicum* in lateral (c) and peripheral (d) view, *Ammonia* sp. T6 in spiral (e), peripheral (f) and umbilical (g) view, and *Trochammina inflata* in spiral (h), peripheral (i) and umbilical (j) view. All scale bars are 50 μm.
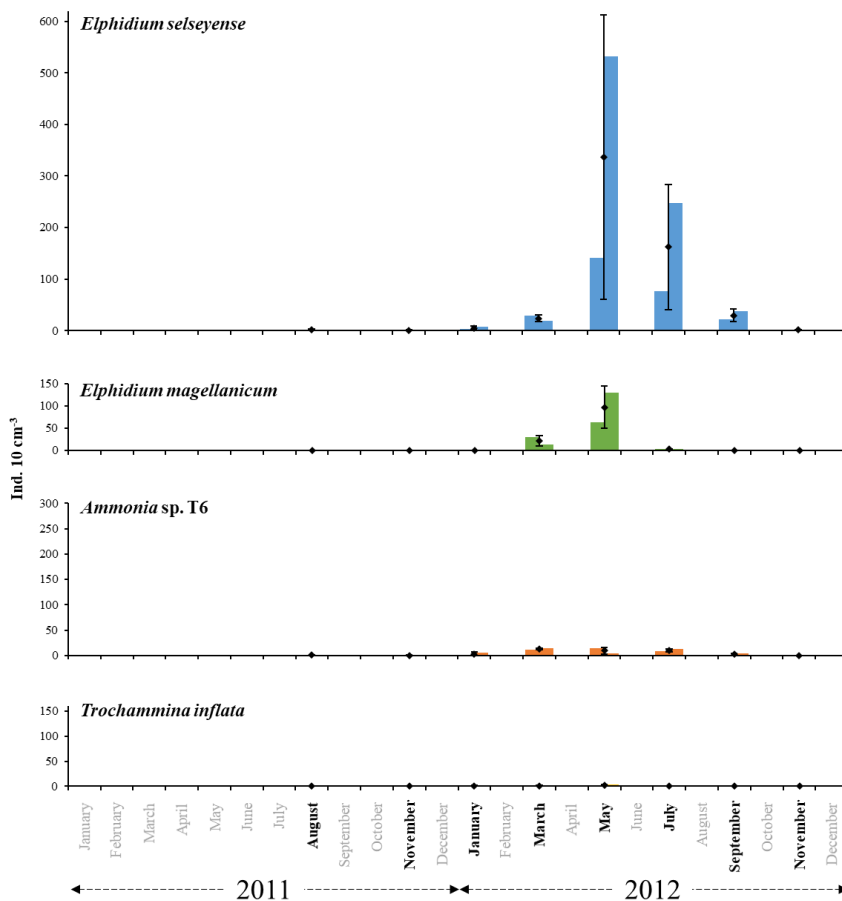
Station 1

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.

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Station 2

Station 2

Elphidium selseyense

Elphidium magellanicum

Ammonia sp. T6

Trochammina inflata

Ind. 10 cm^{-3}
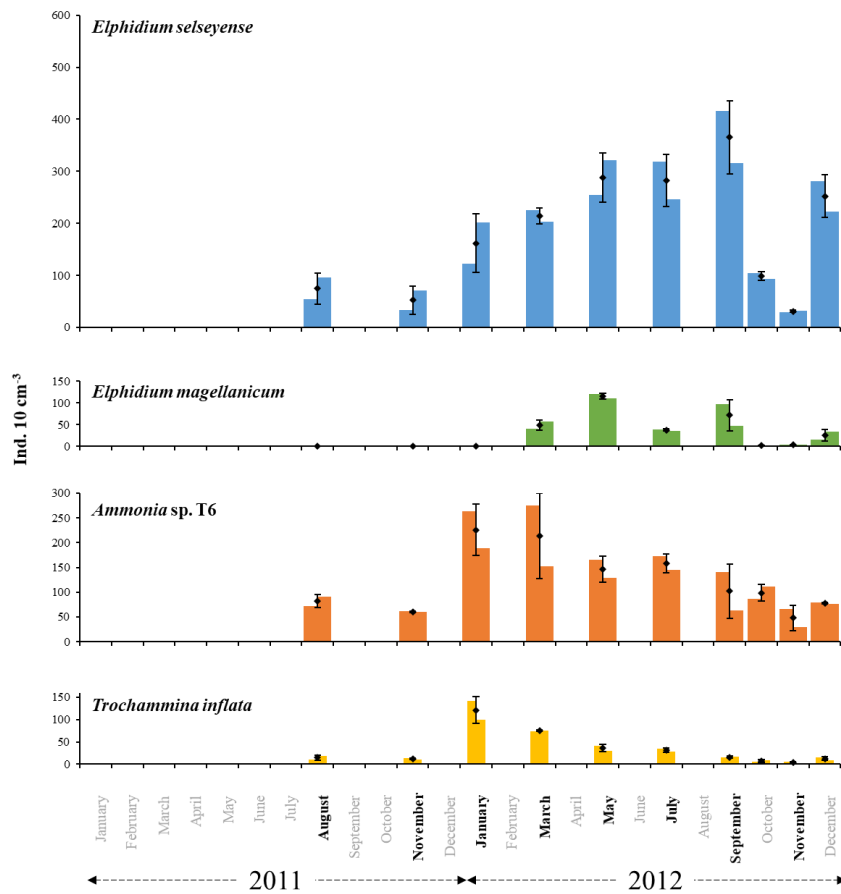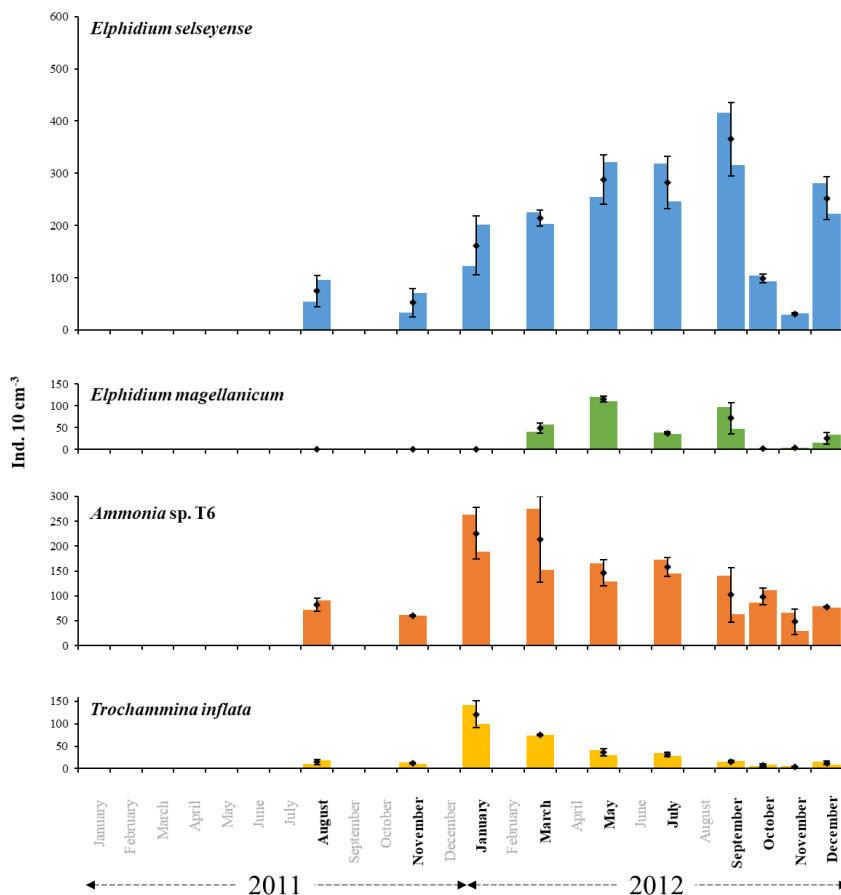
2011 — 2012

1050 **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.

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Station 1
Elphidium selseyense (n=3157)

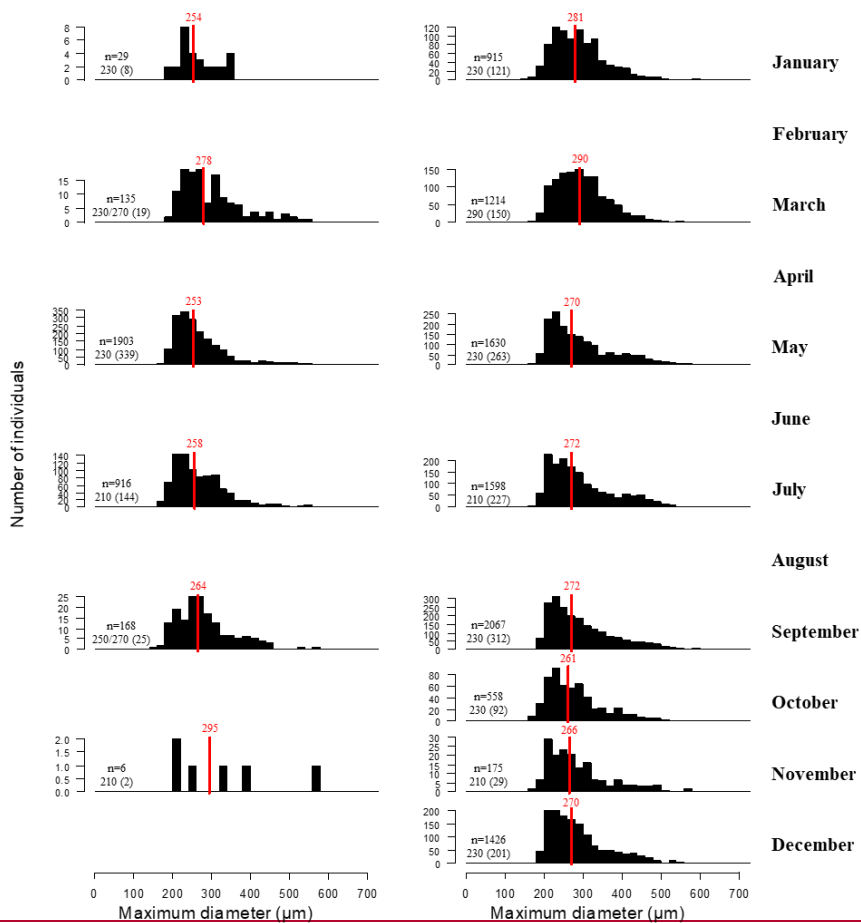**Station 2**
Elphidium selseyense (n=9583)

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.

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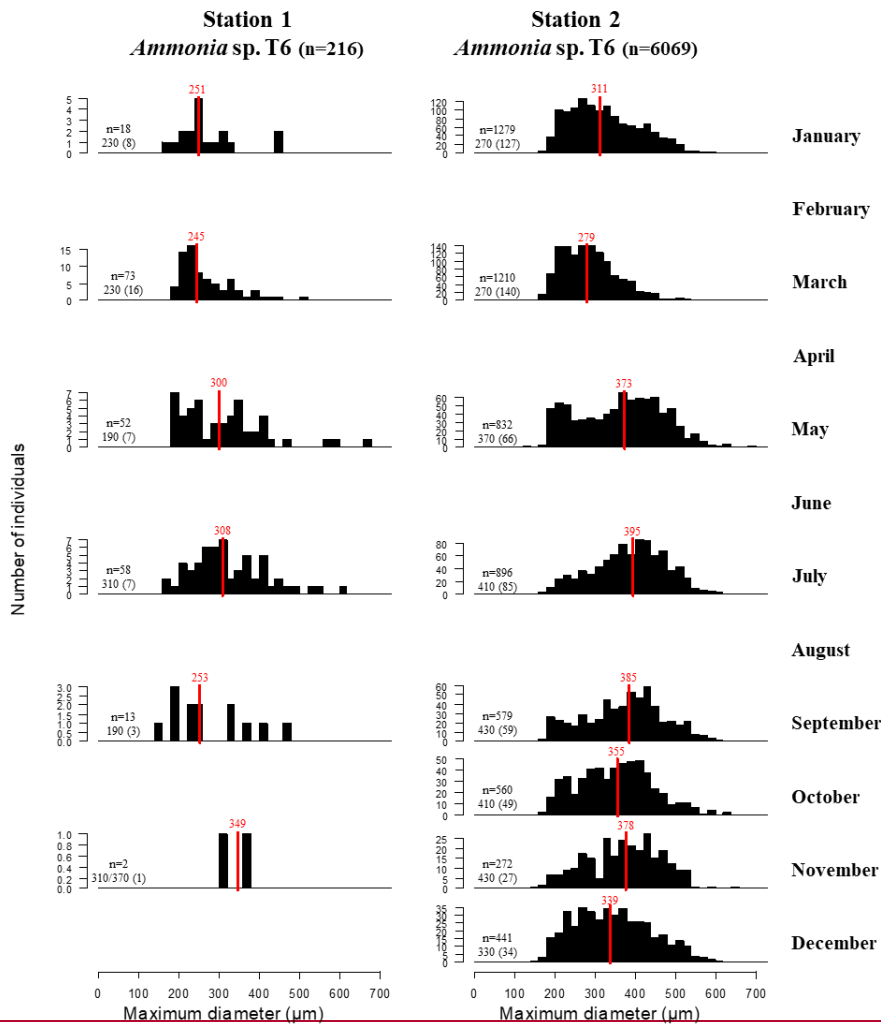
Figure 8: SEM images of (a) fully encrusted specimen, (b) partially encrusted specimen, (c) crushed encrusted specimen of *Elphidium magellanicum*. Note the thinness of the crust and the spinose structures on (d) and (e).
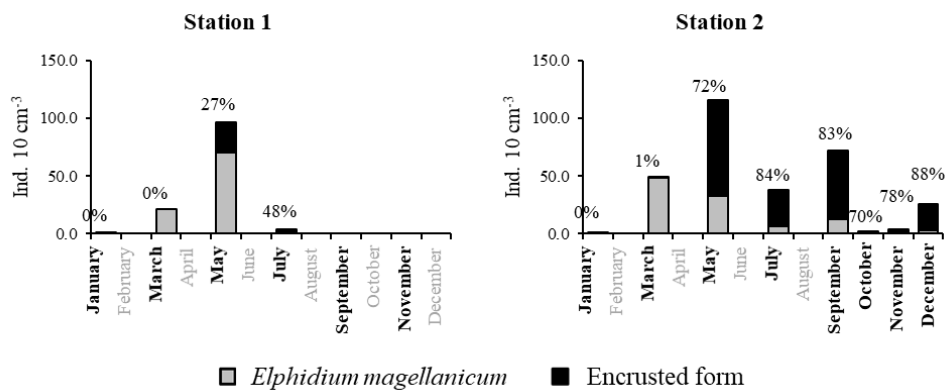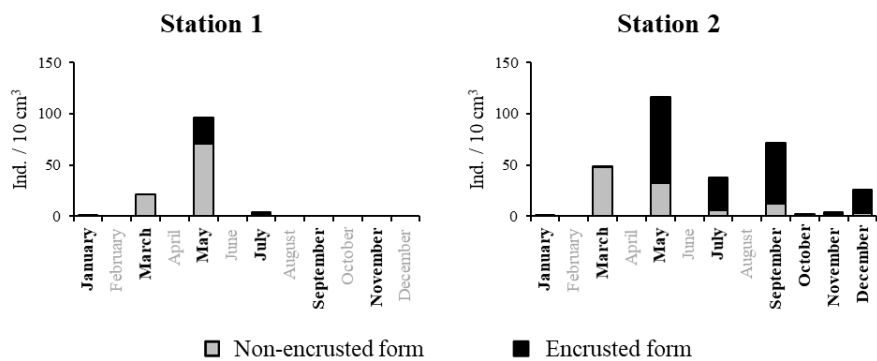
Figure 9: Mean abundances (ind. 10 cm⁻³) of non-encrusted (grey) and encrusted forms (black) of *Elphidium magellanicum* in 2012, at station, 1 (left) and 2 (right.), with proportion of encrusted forms above each bar (in %). Investigated months are indicated in bold.
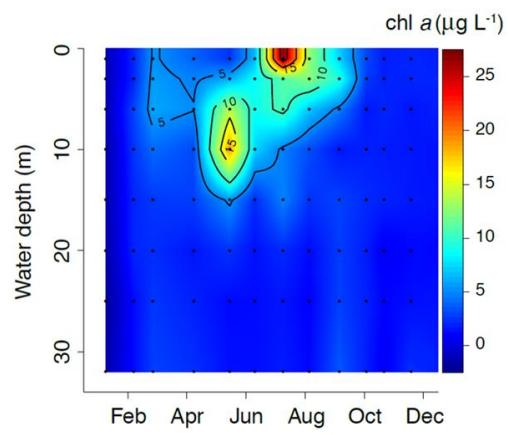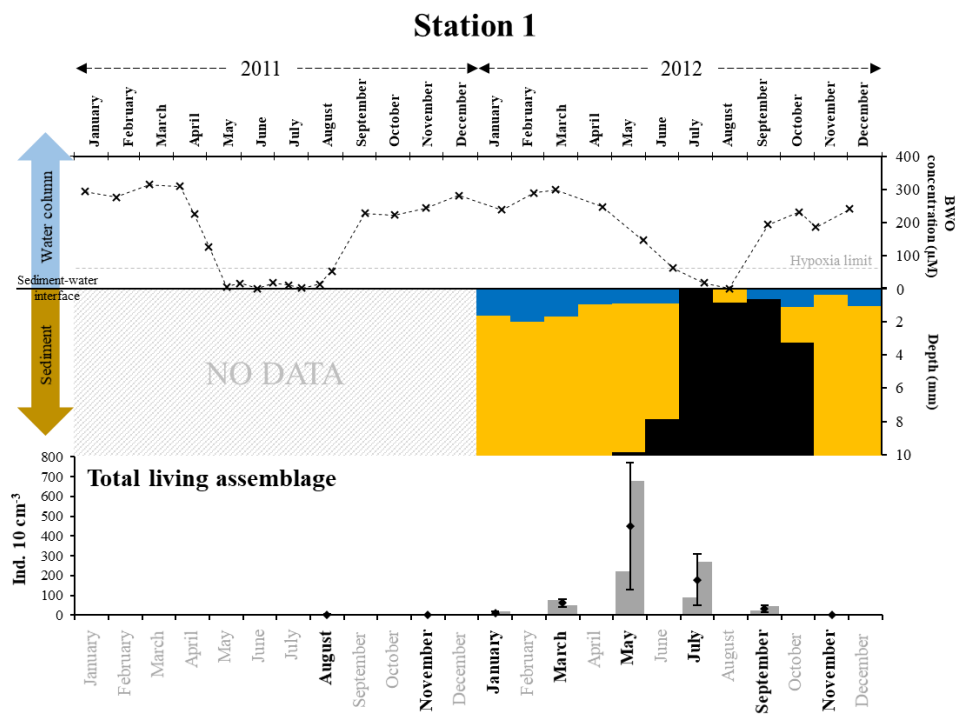
Figure 10: Monthly Chl *a* concentrations (µg L⁻¹) in the water column in Den Osse Basin in 2012 – From Hagens et al. (2015).
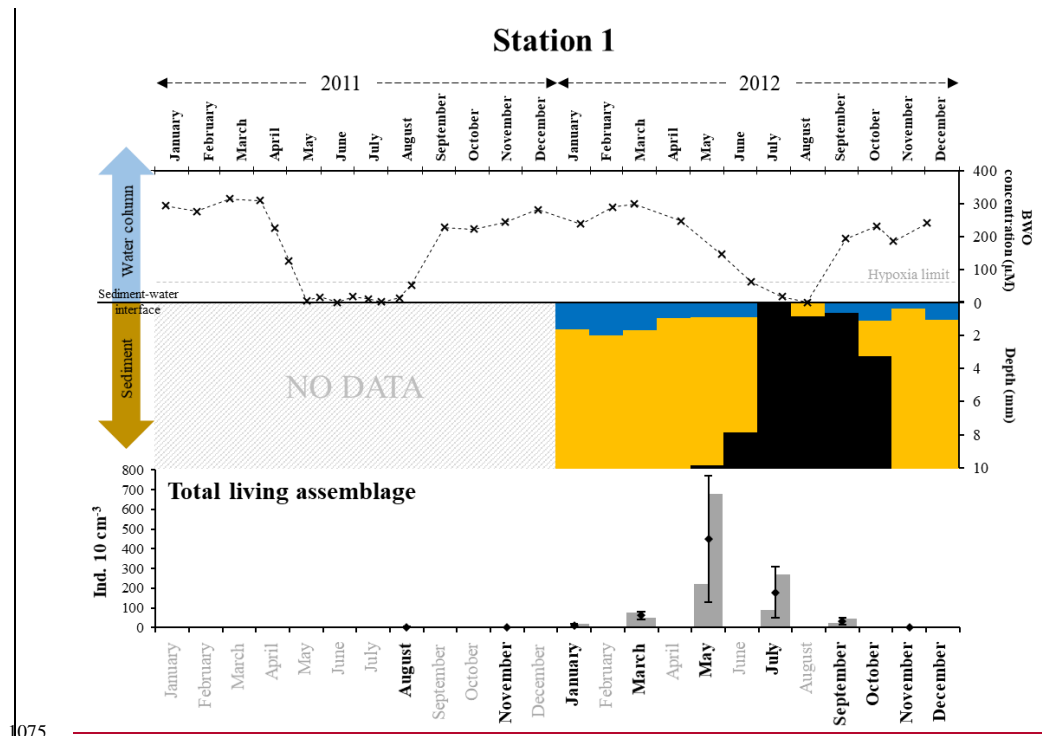
Station 1

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.

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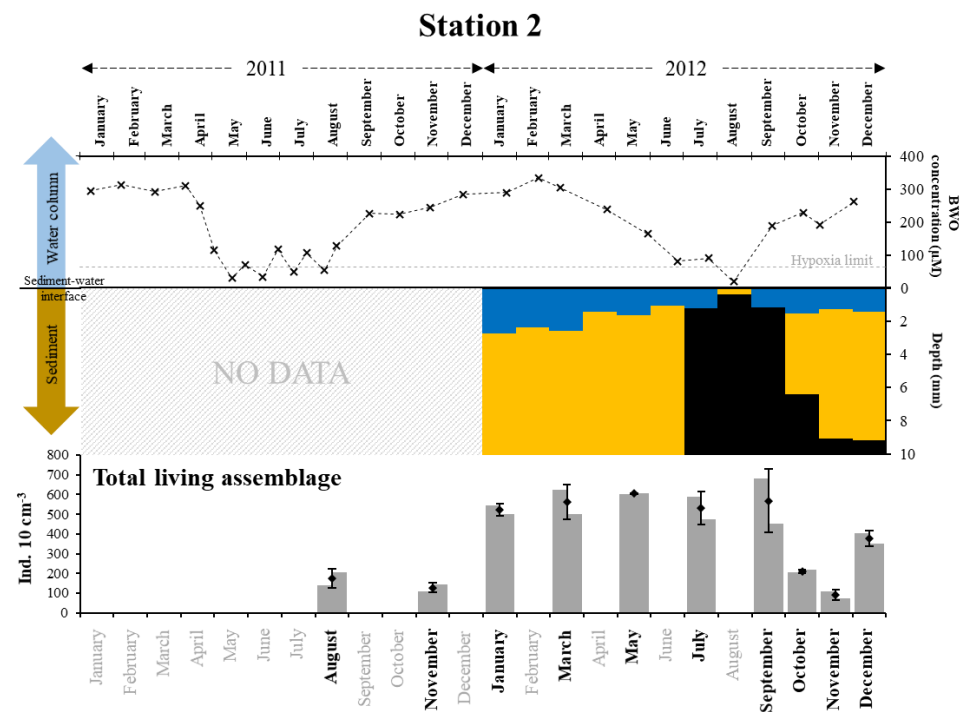
Figure ~~12~~11: The top panel represents bottom- water oxygen concentrations (µmol L^{-1}) in 2011 and 2012 at station 2, from Donders et al. (2012) and Seitaj et al. (2017). The grey horizontal dotted line indicates the hypoxia limit (63 µmol L^{-1}). The middle panel represents the depth (in mm) distribution 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.
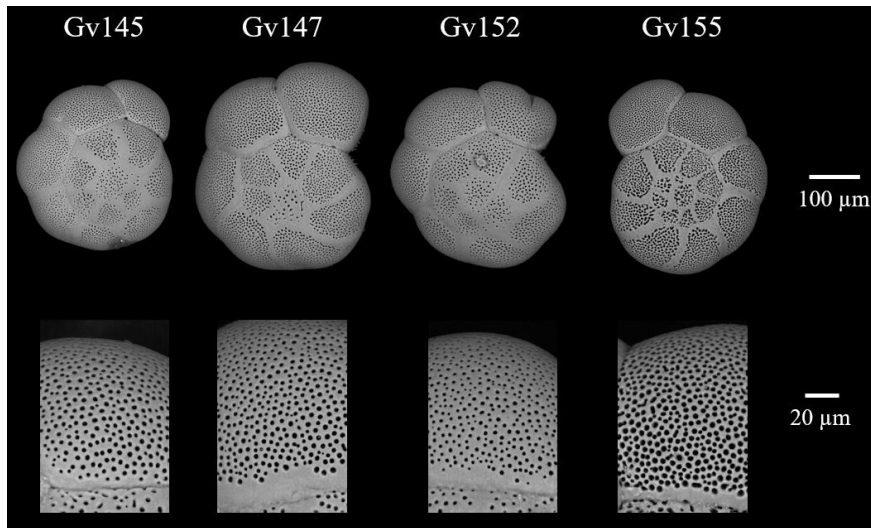
Associated with the manuscript:

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

Julien Richirt[1], Bettina Riedel[1,2], Aurélia Mouret[1], Magali Schweizer[1], Dewi Langlet[1,3], Dorina Seitaj[4], Filip J. R. Meysman[5,6], Caroline P. Slomp[7] and Frans J. Jorissen[1]

[1]UMR 6112 LPG-BIAF Recent and Fossil Bio-Indicators, University of Angers, 2 Boulevard Lavoisier, F-49045 Angers, France
[2]First Zoological Department, Vienna Museum of Natural History, Burgring 7, 1010 Vienna, Austria
[3]Univ. Lille, CNRS, Univ. Littoral Côte d'Opale, UMR 8187, LOG, Laboratoire d'Océanologie et de Géosciences, F 62930 Wimereux, France
[4]Department of Ecosystem Studies, Royal Netherlands Institute for Sea Research (NIOZ), Yerseke, the Netherlands
[5]Department of Biology, University of Antwerp, Universiteitsplein 1, BE-2610 Wilrijk, Belgium
[6]Department of Biotechnology, Delft University of Technology, 2629 HZ Delft, the Netherlands
[7]Department of Earth Sciences (Geochemistry), Faculty of Geosciences, Utrecht University, Princetonlaan 8a, 3584 CB Utrecht, the Netherlands

Correspondence to: Julien Richirt (richirt.julien@gmail.com)

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.

Supplementary Table 1. Oxygen Penetration Depth ± sd and free H2S detection depth ± sd for each month in 2012 for both stations 1 and 2 (in mm).

Station	Month	OPD (mm)	H$_2$S 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

Mis en forme : Légende

Mis en forme : Non Exposant/ Indice

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).

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 |

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 leavigata*	*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	0.0	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	0.7	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	0.0	0.4	0.0	1.1	0.0	0.0	0.4	0.0	0.4	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	1.1	0.0	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	0.7	0.4	0.0	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	0.7	0.7	0.0	1.4	0.0	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	0.0	3.2	0.4	2.1	1.4	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	0.0	0.4	0.0	7.1	2.1	35.4

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	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	0.4	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	0.4	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	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	0.4	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
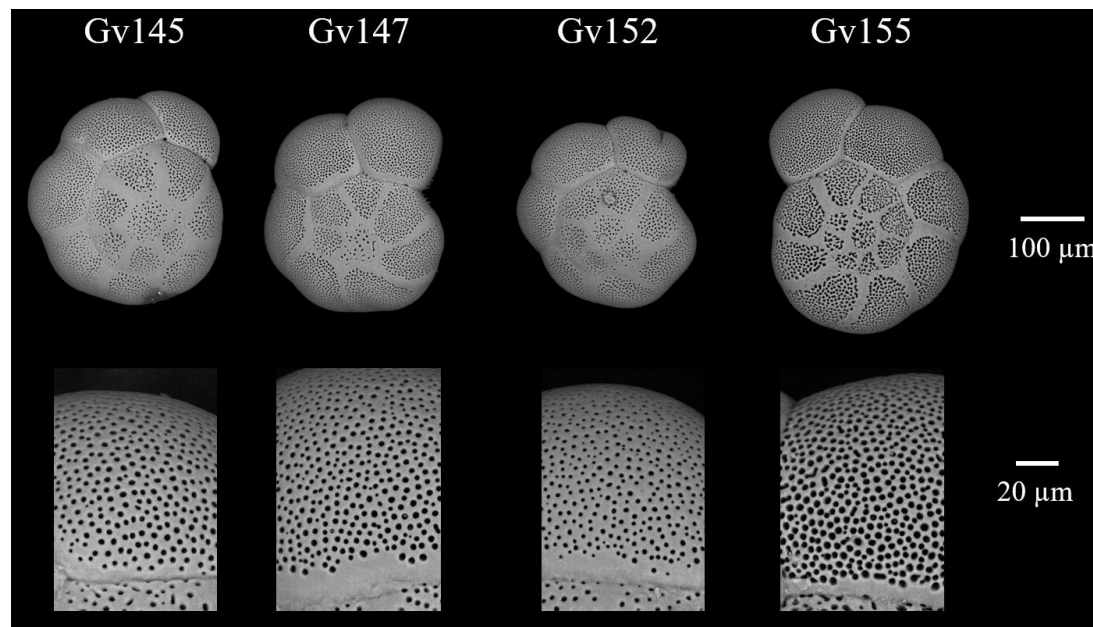
Supplementary figure 1. SEM images of spiral side and a 1000x magnification of the penultimate chamber for four individuals from Grevelingen station 1 identified T6 by molecular identification.
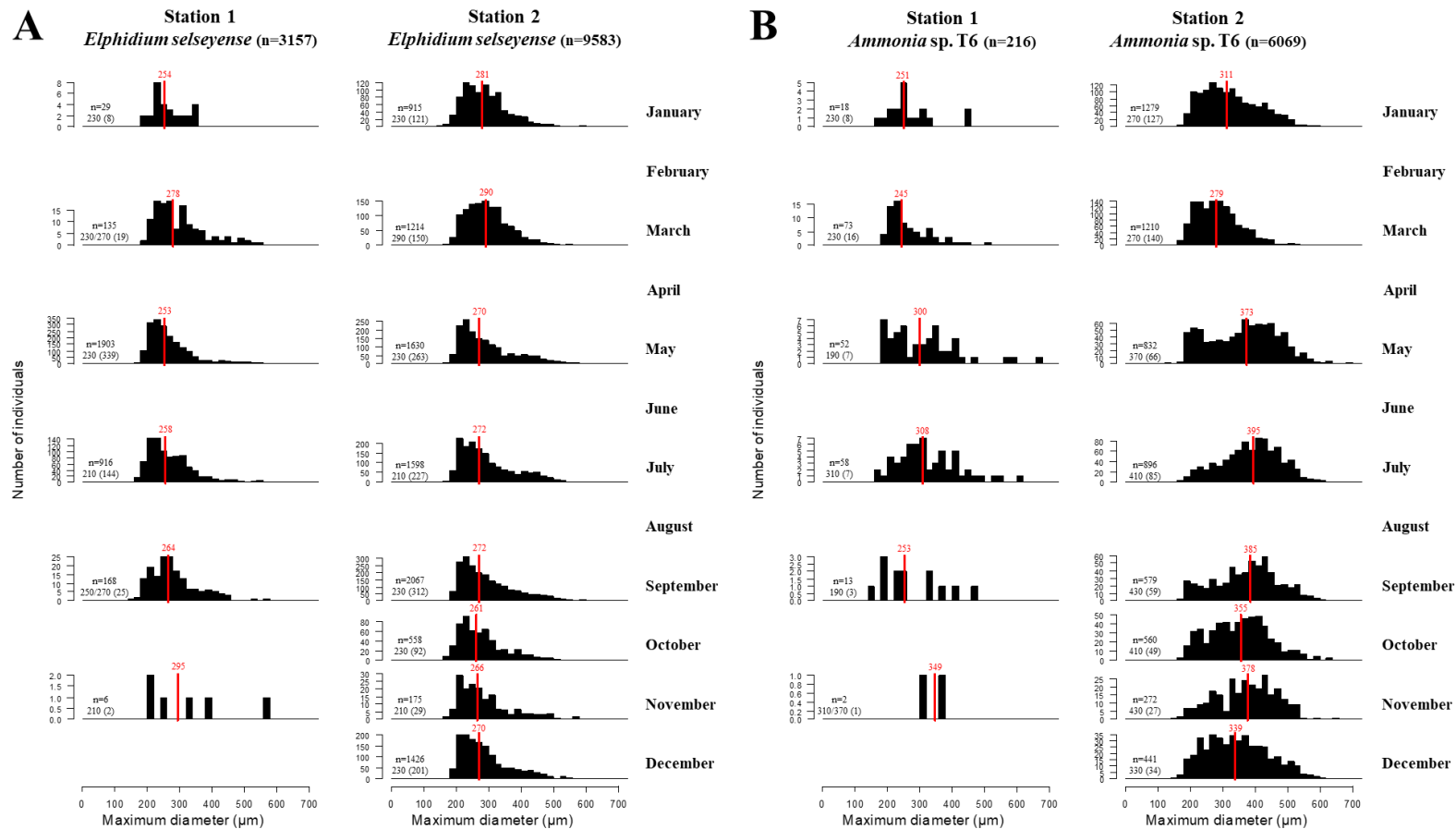
Supplementary Figure 2: A: size distribution (maximum diameter for each individual in μm) of *Elphidium selseyense* for stations 1 (left) and 2 (right) in 2012. **B:** size distribution (maximum diameter for each individual in μm) of *Ammonia* sp. T6 for stations 1 (left) and 2 (right) in 2012. For each 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

Mis en forme : Légende

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.