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To cite this version:

Julien Richirt, Anaïs Guihéneuf, Aurélia Mouret, Magali Schweizer, Caroline Slomp, et al.. A historical record of benthic foraminifera in seasonally anoxic Lake Grevelingen, the Netherlands. Palaeogeography, Palaeoclimatology, Palaeoecology, 2022, 599, pp.111057. 10.1016/j.palaeo.2022.111057 . hal-03925917

HAL Id: hal-03925917

https://hal.science/hal-03925917v1

Submitted on 8 Dec 2023

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A HISTORICAL RECORD OF BENTHIC FORAMINIFERA IN SEASONALLY ANOXIC LAKE GREVELINGEN, THE NETHERLANDS

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ABSTRACT

Lake Grevelingen is a former branch of the Rhine-Meuse-Scheldt estuary, which was artificially transformed into a salt-water lake by a dam in 1971. This transformation induced profound changes in the biological community of the basin, which have been described as an ecodisaster, with seasonal hypoxia/anoxia occurring in the deepest parts of the lake. Here, we investigate a sediment core sampled in 2012 in the Den Osse Basin (34 m depth) of Lake Grevelingen, recording the last ~ 50 years and including the transition from an estuary to a salt-water lake. Sediment molybdenum (Mo) concentrations were used to refine an existing age model based on ^{210}Pb, giving us an estimated precision of ± 3 years. The benthic foraminiferal succession reflects the anthropogenic modifications in Lake Grevelingen and allows four successive stages to be distinguished: 1) before 1971, when the system was estuarine; 2) from 1971 to 1978, when the system rapidly changed into an enclosed brackish water lake; 3) from 1978 to 1999, when a seaward sluice was opened during winter and 4) the period from 1999 to 2012, with a year-round opening of the sluice and doubling of water exchanges with the North Sea. The foraminiferal record, showing communities mainly dominated by *Elphidium selseyense*, also highlights the appearance of the putatively exotic *Ammonia confertitesta* in the mid-1980s, which thereafter progressively replaced the congeneric autochthonous *Ammonia aberdoveyensis*. Finally, we hypothesise that the activity of cable bacteria, S-oxidising prokaryotes present in the surface sediments of Den Osse Basin in winter and spring, causes dissolution of foraminiferal tests by decreasing the pore water carbonate saturation state in the sediments directly below the oxic zone. This explains the contrast between the abundant living populations and the very low numbers of foraminiferal shells preserved in the top ~ 15 cm of the sediment.

Keywords: foraminifera, historical record, Lake Grevelingen, anoxia, cable bacteria

1. INTRODUCTION

Foraminifera are among the most widespread groups of marine unicellular eukaryotes and constitute one of the most diverse groups of shelled organisms. They have a very rich fossil record and are widely used for palaeoenvironmental reconstructions and palaeoecological interpretations (Murray, 2006; Katz et al., 2010). Foraminifera are known to be relatively tolerant to low oxygen concentrations, anoxia and/or presence of sulphides in their habitat, on various timescales. This has been documented for many species from different types of environments in laboratory culture (e.g. Moodley and Hess, 1992; Bernhard, 1993; Alve and Bernhard, 1995; Moodley et al., 1998; Duijnstee et al., 2003; Geslin et al., 2004; Pucci et al., 2009) as well as in field studies (e.g. Piña-Ochoa et al., 2010; Langlet et al., 2013, 2014). Unfortunately, studies on the foraminiferal response in systems affected by seasonal hypoxia–anoxia with sulphidic conditions are still very sparse. 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. Recently, a study investigated the temporal response of living foraminiferal communities to recent seasonal anoxia in the Den Osse Basin of Lake Grevelingen (the Netherlands, Richirt et al. 2020). The authors highlighted that the deepest part of this basin shows a severe decline in foraminiferal populations in the months following late summer–early autumn seasonal anoxia. They explained this by the presence of sulphides in the foraminiferal habitat, that would inhibit foraminiferal reproduction and growth. In the shallower parts of the basin, where the duration of anoxia is shorter, there was not such a major decline in the foraminiferal community.

The Den Osse Basin is located in Lake Grevelingen, a former estuary of the Scheldt-Meuse-Rhine delta, in the Netherlands. After a storm in 1953, which caused large scale flooding and more than 1800 casualties, landward (1965) and seaward (1971) dams were constructed to avoid such disasters in future (Delta Plan, Bannink et al., 1984; Figure 1). Thanks to the preservation of shelled foraminifera in the sediment record, Lake Grevelingen provides a unique opportunity to study the benthic foraminiferal response to the progressive transformation of the ecosystem from an estuary to a salt water lake, especially regarding the development of seasonal hypoxia/anoxia.

The living foraminiferal community of the Den Osse Basin is largely dominated by *Elphidium selseyense* (phylotype S5, Darling et al., 2016), *Elphidium magellanicum*

(morphospecies not yet sequenced) and *Ammonia confertitesta* (*Ammonia* sp. T6 in Richirt et al., 2020; phylotype T6 in Hayward et al., 2021). The latter species, *A. confertitesta*, is often considered as an exotic and/or invasive species, originating from East Asia (e.g. Pawlowski & Holzmann, 2008; Schweizer et al, 2011; Bird et al., 2020). *Ammonia confertitesta*, which is almost the only representative of the genus *Ammonia* in the recent living assemblages (Richirt et al., 2020), is characterised by very large pores (Richirt et al., 2019a) compared to *Ammonia aberdoveyensis* and to a lesser extend *Ammonia veneta* (phylotypes T2 and T1, respectively, Hayward et al., 2021). Interestingly, a preliminary study of a long core sampled in the Den Osse Basin showed a clear shift from specimens with small pores to specimens with bigger pores in recent times (Petersen et al., 2016). This indicatess that in a recent past, *A. confertitesta* has progressively replaced *A. aberdoveyensis* (and/or *A. veneta*) in Lake Grevelingen. Richirt et al. (2019b), suggesting that an increase in overall porosity could be an adaptation to low oxygen concentrations. The putative replacement of *A. aberdoveyensis* (and/or *A. veneta*) by *A. confertitesta* could therefore be due to the larger tolerance of the latter species to hypoxia. The study of the sedimentary foraminiferal record should enable us to shed more light on this important species take-over.

In this study, we investigate foraminiferal assemblages of a 90 cm long sediment core sampled in the deepest part of the Den Osse Basin, representing the last ~ 50 years. We will especially address the following questions:

1) How did the foraminiferal community change in response to the closure of Lake Grevelingen in the 1970s and the subsequent management changes of the basin?

2) Has there been a substitution of the autochthonous *Ammonia* species (*A. veneta* and *A. aberdoveyensis*) by the putative allochthonous species *A. confertitesta*, and, if so, is it the result of an overall spreading of *A. confertitesta* across Europe, or rather of a better adaptation of this phylotype to seasonal hypoxia/anoxia?

2. STUDY AREA

In 1965, the former Grevelingen estuary was closed landward (Grevelingendam) and became a semi-enclosed embayment without river input. A second dam was constructed seaward in 1971 (Brouwersdam), closing the former Grevelingen estuary completely. This stopped the inflow of salt waters from the North Sea and increased the water residence time in the Grevelingen lake up to three to six years (instead of a few days, when the system was estuarine, Nienhuis, 1978; Bannink et al., 1984). The suppression of tidal currents and decrease

in salinity directly after the full closure strongly affected marine benthic animals (e.g. sponges, sea anemones, tunicates). Mass mortality of these animals contributed to increased food availability, accumulation of decomposition products and finally oxygen depletion. This "ecodisaster" induced a simplification of the ecosystem concerning both its structure and functioning (Nienhuis & Veld, 1984; Bannink et al., 1984). Within a few years after closure of the estuary, seasonal bottom water hypoxia/anoxia started to occur, followed by mass mortality of the remaining marine benthic animal populations (e.g. molluscs, worms), especially in the deeper parts of the basin (Nienhuis & Veld, 1984).

To remedy eutrophication phenomena and seasonal hypoxia by limiting water column stratification, the connection with the North Sea was partly reopened in 1978, by the construction of an underwater sluice in the Brouwersdam (capacity of about 100–140 $m^3 s^{-1}$, initially only opened in winter, Bannink et al. 1984; Muelen et al., 1984). This partial reopening improved the bottom water oxygenation in the Den Osse Basin and decreased water residence times to about half a year. Consequently, several species, which were common in the Grevelingen estuary but had disappeared when the estuary was closed, were observed again (e.g. some jellyfish and crab species; Nienhuis and Veld, 1984). A second, landward sluice (siphon) was opened in 1983 (at the Grevelingendam) to ensure a weak (compared to the natural situation without a dam) freshwater inflow (about 100 $m^3 s^{-1}$, Bannink et al., 1984; Muelen et al., 1984).

In 1999, the water exchanges between the Lake and the North Sea were doubled (from 1245–1255.10^6 m^3 to 2688–2864.10^6 m^3 per year, Wetsteijn, 2011) by opening the Brouwersdam sluice the whole year, except for a few weeks in autumn and during storm events. This allowed a further decrease of the average water residence time in the Lake from 164 to 72 days and limited water stratification due to high temperatures in summer (Wetsteijn, 2011). However, this situation was still very different compared to the estuarine situation before 1965, when the water residence time was estimated to be a few days (Nienhuis, 1978; Bannink et al., 1984) and average flood and ebb discharges at the location of the present Brouwersdam were about 126000.10^6 and 135000.10^6 m^3 per year, respectively (calculated for 1959, Louters et al., 1998), ~ 50 times higher than the current water exchanges.

Despite these management changes, seasonal bottom water oxygen depletion continued to occur every year, as is still the case today, especially in the deepest parts of Lake Grevelingen, such as in the Den Osse Basin that is investigated in this study (Wetsteyn, 2011; Sulu-Gambari et al. 2017). The transformation of Grevelingen from an estuary to a salt-water lake induced profound modifications at ecosystem (e.g. habitat losses, changes in trophic relationships),

community (e.g. decrease of biodiversity, replacement of marine by estuarine species) as well as species levels (e.g. disturbed or interrupted life cycles, change in densities, Nienhuis, 1978; Nienhuis & Veld, 1984).

To summarise, Lake Grevelingen, a former estuarine system, was completely closed in 1971. The ensuing strong increase of water residence time, bottom water stagnation and lower salinity caused a major biotope shift in Lake Grevelingen and led to strong modifications of its biological community (Nienhuis, 1978).

Today, two antagonistic groups of sulphur-oxidizing bacteria showing contrasting seasonal population dynamics are present in sediments of the Den Osse Basin: cable bacteria in January-May and *Beggiatoaceae* in September–December (Seitaj et al., 2015; Sulu-Gambari et al., 2016a). Cable bacteria activity is known to strongly impact biogeochemical cycles (e.g. of sulphur, iron or calcium) in the sediment, by promoting, for example, precipitation of iron oxide in the oxic layer and dissolution of iron sulphide and calcium carbonate in the anoxic layer (Risgaard-Petersen et al., 2012; Meysman et al., 2015). In the deepest part of the Den Osse Basin, where the maximum oxygen penetration depth in the sediment is about 2 mm (Seitaj et al., 2015), this was shown to occur seasonally, as a result of cable bacteria activity (Sulu-Gambari et al., 2016a, b). This phenomenon could play a major role in foraminiferal calcium carbonate test dissolution during taphonomic processes.

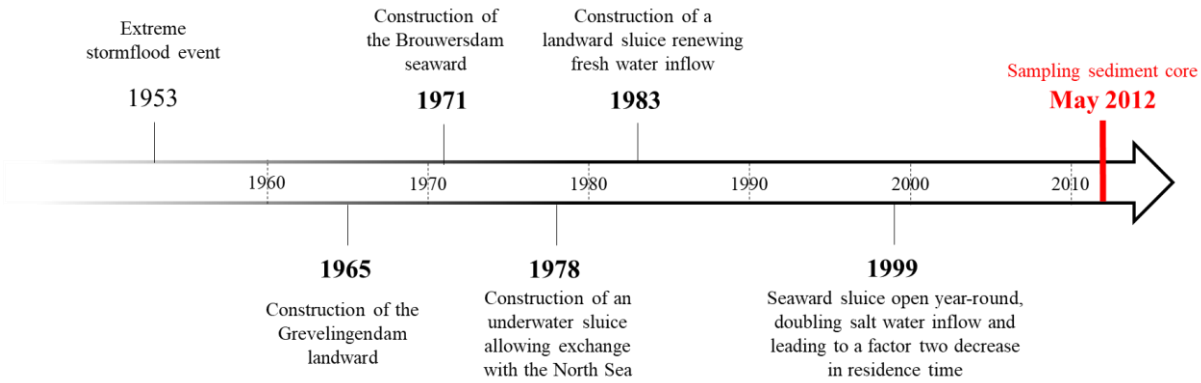

Figure 1. Timeline of the human-induced modifications following the Delta Plan at Lake Grevelingen. The sediment core used to investigate dead foraminiferal assemblages was sampled in May 2012 (red line).

3. MATERIALS AND METHODS

3.1. SAMPLING AND LABORATORY TREATMENT

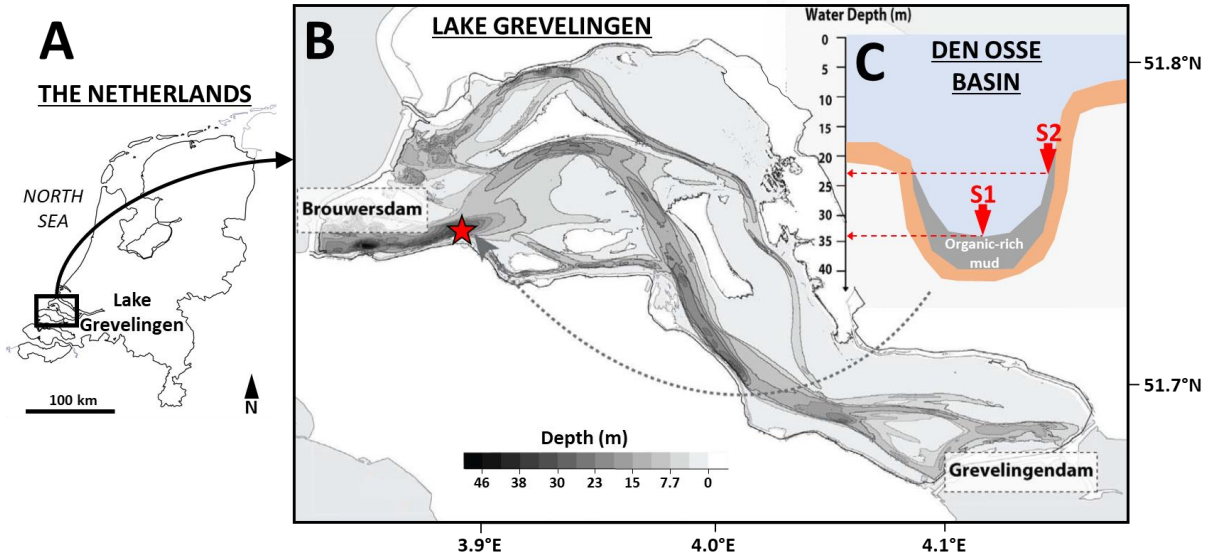

Figure 2. A. Map of The Netherlands (on the left) showing the location of Lake Grevelingen. B. Map of Lake Grevelingen (main panel) showing the location of the sediment sampling in the Den Osse Basin (red star). C. The transversal section of the Den Osse basin (top right) shows the depth at which the studied sediment core was sampled at Station 1 (S1, 34 m depth). Station 2 (S2, 23 m depth) was investigated for living assemblages by Richirt et al. (2020), as noted in the discussion. This figure was modified from Sulu-Gambari et al. (2016a).

The study site (station 1) is in the Den Osse Basin (51° 44.834'N, 3° 53.401'E), the main former channel of the Grevelingen estuary (The Netherlands), at 34 m depth (Figure 2). Our site is located at a distance of ~ 100 m from a location where water column oxygen was intensively monitored since the late 1970s by the Dutch Water Agency (DWA; e.g. Wetsteijn, 2011). Bottom water oxygen concentrations from 1978 to 2011 from the DWA database were summarised previously (Figure 3; Sulu-Gambari et al., 2017) and reveal recurring seasonal hypoxia and anoxia in bottom water. These bottom water data were collected up to about 3 m above the basin floor (and not at the sediment-water interface), which was at 37 m water depth at this location. Consequently, bottom water anoxia measured by the water column monitoring (Figure 3) is a reliable indicator of an anoxic sediment-water interface. However, oxic conditions in the water column (as frequently recorded from late 1990s to 2010, Figure 3), does not necessarily indicate that the basin floor was also oxic.

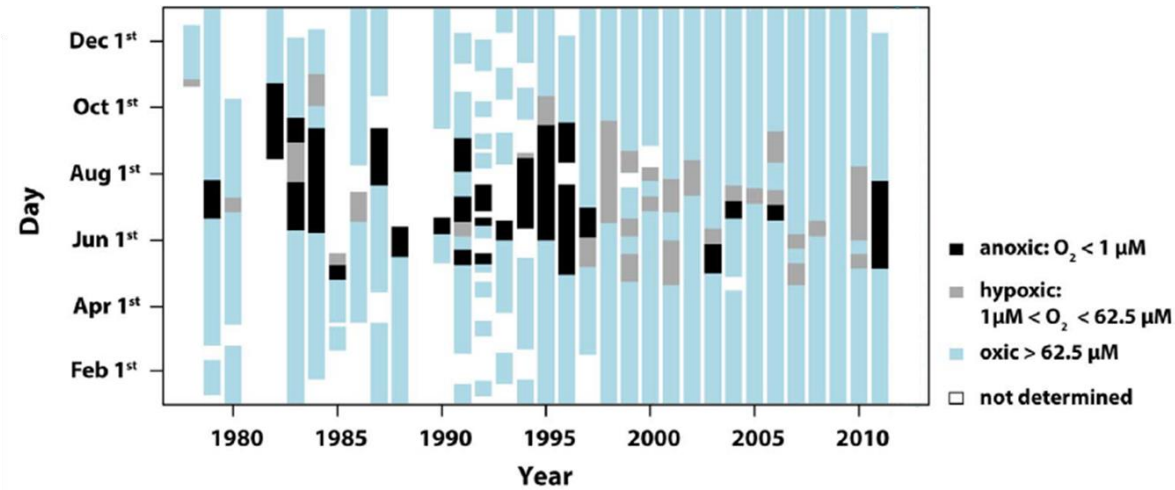

Figure 3. Periods of oxic (blue), hypoxic (grey) and anoxic (black) bottom water conditions from 1978 to 2011 at the DWA site, which is located at a distance of about 100 m from station 1 in this study (figure after Sulu-Gambari et al., 2017).

A sediment core of 90 cm length and 6 cm diameter was collected at station 1 in May 2012 with a UWITEC gravity interface corer. In the laboratory, the core was cut into 0.5 cm thick slices with an individual sample volume of ~ 14.1 cm^3. All samples were sieved at 63, 125, 150 and 315 µm, before being dried and stored in the laboratory. For this study, only foraminifera of the fraction > 125 µm (including all fractions above 125 µm) were picked and stored in micropalaeontological Plummer cells. Considering that picking foraminifera is very time-consuming, we decided to look at one sample every 2.5 cm (i.e., every fifth sample). Because the 54.5–55, 84.5–85 and 89.5–90 cm samples had a very high foraminiferal density (Suppl. Table 1), they were split into half (125–150, 150–315 and >315 µm for the first two, 125–150 µm fraction for the 89.5–90 cm sample) and complete splits were counted. Conversely, in the top 15 cm, many samples were very poor in foraminifera (Suppl. Table 1). Consequently, we decided to increase the resolution around these samples by picking adjacent samples. In all, the foraminiferal content of 40 samples was studied (Suppl. Table 1). When possible, determination was made to the species level using a stereomicroscope.

A major change in sediment composition was observed, from sandy deposits below 82.5 cm depth, very probably representative of the strong hydrodynamics of the former estuarine system to muddy/silty sediments above 82.5 cm depth, indicative of the much lower hydrodynamics of the salt lake environment.

3.2. FORAMINIFERAL ANALYSES

In cases where samples had very low foraminiferal abundances, two to three adjacent samples were merged (Table 1). This concerned samples in depth intervals 4.5–6, 6.5–8, 9–10.5, 11.5–13, 32–35, 57–60, 69.5–72.5 and 74.5–77.5 cm. We compromised between (1) maximising the number of individuals (to obtain a target value of at least 50 individuals) and (2) maximising sampling resolution. The total thickness of merged samples never exceeded 3 cm (Table 1).

To document temporal changes in assemblage composition, a Principal Component Analysis (PCA, non-standardised) was performed on the relative abundances of the dominant species. We considered only dominant taxa (i.e. taxa representing at least 5% of the total assemblage in at least one sample) to decrease the signal/noise ratio.

Data on living assemblages (0–1 cm depth interval) for our station 1 and additional station 2 (located at 23 m depth, impacted by a shorter seasonal oxygen depletion event; Figure 2) were taken from Richirt et al. (2020) and were computed as the sum of all seasonal samples of 2012. These samples were considered as supplementary individuals in the analysis, meaning that they did not contribute to the construction of the principal component axes. The data pre-treatment and multivariate analysis procedure are summarised graphically in Figure 4.

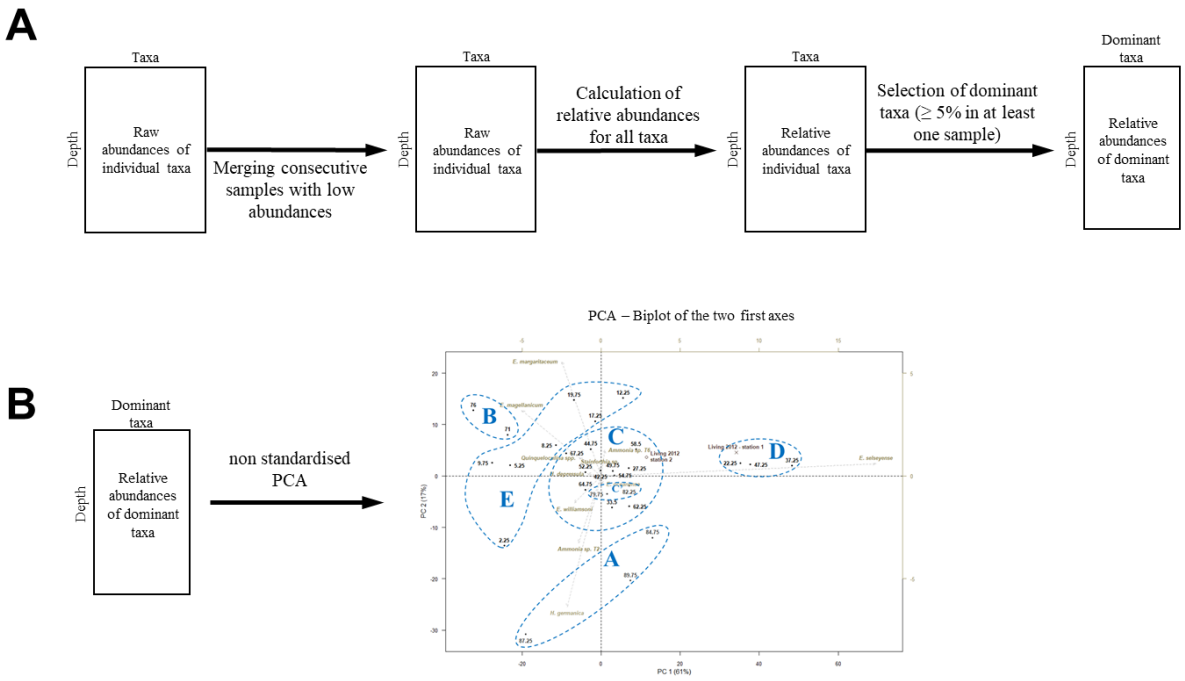

Figure 4. A: Data pre-treatment procedure performed from the initial data matrix, with data matrix lines representing samples (depth) and data matrix columns representing taxa. B: Principal Component Analysis (PCA) procedure.

3.3. AGE MODEL

For another 90 cm long core, sampled in May 2011 at station 1, an age model was developed using ^{210}Pb dating (Donders et al., 2012). This age model, which was not very well delimited, suggested an average sedimentation rate of 2.37 cm per year, meaning that the 90 cm long core covered about 37 years (1974 to 2011). This order of magnitude confirms our earlier hypothesis that the very abrupt shift in sediment composition at 82.5 cm core depth corresponds to the closure of the basin in 1971.

For a third core sampled at this site during the same cruise as the sediment core used in this study (in May 2012, Sulu-Gambari et al., 2017), molybdenum (Mo) concentrations were measured in the solid phase. Molybdenum is sequestered when sulphide is present in the porewater near the sediment-water interface (Crusius et al., 1996). Therefore, the successive Mo maxima in the sediment record should reflect the yearly seasonal hypoxia/anoxia coupled to the presence of sulphide (Seitaj et al., 2015), and can therefore be used to refine the age model based on ^{210}Pb levels. This principle was used earlier for a core from another site in Lake Grevelingen with an exceptionally high sediment accumulation rate (~ 13 cm y^{-1}), in the Scharendijke Basin, slightly further west of the Den Osse Basin (Egger et al., 2016).

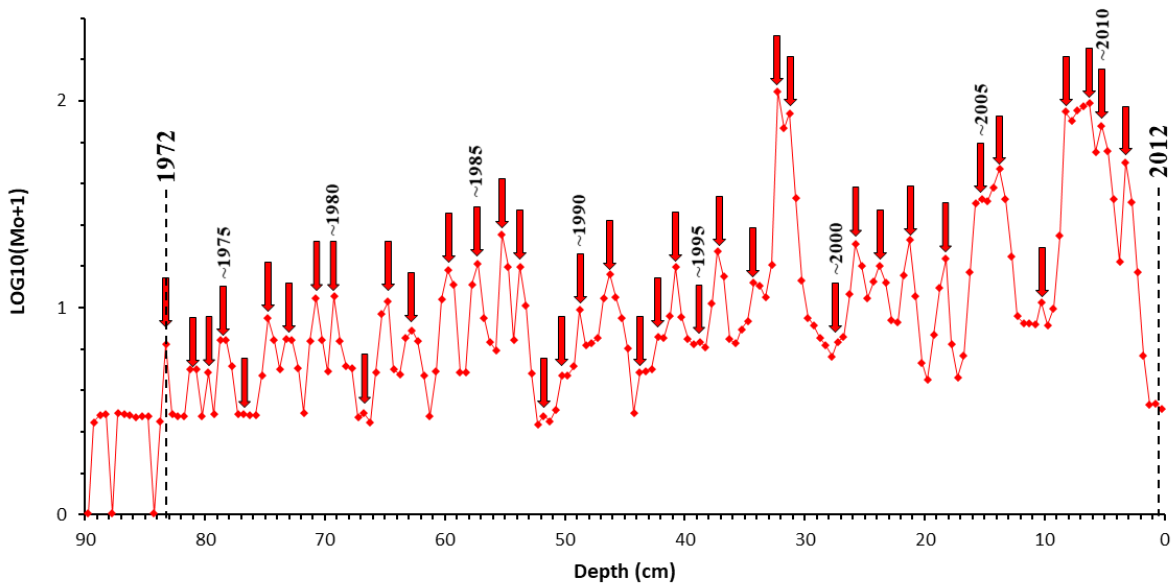

Figure 5. Molybdenum concentrations (ppm, detection limit = 0.06 ppm) as a function of core depth (cm), modified from Sulu-Gambari et al. (2017). All values were LOG10(x+1) transformed to better identify peaks. Each peak is highlighted with a red arrow and is assumed to represent a yearly summer hypoxia/anoxia event. Some additional yearly hypoxia/anoxia events have been added tentatively in case of broad peaks with shoulders (e.g., between 31 and 33 cm depth), or broad intervals without clear peaks (e.g., between 50 and 52 cm depth). Dotted lines represent the two constraints of the age model: the first observed Mo peak corresponding

to 1972 (first anoxic/sulphidic event assumed the year following the closure of the former estuary in 1971) and the surface layer corresponding to the sampling year in 2012.

In Figure 5, a very regular, apparently cyclic alternation of maximal and minimal Mo concentrations can be observed, where Mo maxima should correspond to late summer/early autumn anoxia. The first peak, at ~ 83 cm depth, which occurred after the closure of the estuary seaward in 1971, is assumed to represent a first anoxic/sulphidic event in summer/autumn 1972. Between this first peak at ~ 83 cm and the last peak, representing summer/autumn 2012, we tentatively placed 39 more annual peaks. In some years, seasonal anoxia may not have developed, or may have been very short, so that no Mo peaks developed. Another possible explanation for missing Mo peaks could be that in years with somewhat lower sedimentation rates, two seasonal Mo peaks may have merged. Consequently, our age model may be two to three years off.

A further potential issue is that Mo concentrations were not measured in the same core as the one used for the foraminiferal analysis. If we assume that the first Mo peak observed at ~ 83 cm is characteristic of the first anoxic/sulphidic event that occurred in 1972, the year following the transition from an estuary to a lake, the closure of the estuary in 1971 should have taken place directly before, corresponding to a core depth of ~ 84 cm. For the same core, based on a sedimentation rate of 2 cm y^{-1} proposed in Malkin et al. (2014), the transition from an estuary to a lake was estimated to have occurred at 82 cm depth by Sulu-Gambari et al. (2017; 2018). The same transition was found at 82.5 cm in the core used for foraminiferal analysis. Consequently, when applying our Mo-based age model on the foraminiferal record, there is an additional uncertainty of at most 1–2 cm, which could be the result of small differences in compaction between the cores. In conclusion, we consider that our age model is reliable with a precision of ± 3 years, which is sufficient for the aims of our study.

The average sediment accumulation rate calculated using the putative age model based on the Mo peaks is 2.06 cm y^{-1}. This is consistent with the average sediment accumulation rate of 2.37 cm y^{-1} obtained with the ^{210}Pb method by Donders et al. (2012).

3.4. CALCIUM CARBONATE SATURATION STATE

We used the CO2SYS software (Lewis and Wallace, 1998) to determine the variation of the calcium carbonate saturation state in the sediment at our station throughout the year. Monthly temperature and salinity data of 2012 are from Hagens et al. (2015) and were measured in the water column at 32 m depth. Monthly values for alkalinity and PO_4^{3-} concentrations in

the pore waters are from Sulu-Gambari et al. (2016a) and were measured in 0.5 cm thick sediment slices. The values of pH were obtained by profiling the first 2.5 cm of the sediment with a microsensor in three replicate cores (data from Seitaj et al., 2015). To compute the calcium carbonate saturation state, using alkalinity and PO_4^{3-} concentrations, pH values had to be averaged for 0.5 cm layers. Following Orr et al. (2015), we used the set of constant K_1 and K_2 from Lueker et al. (2000), the formula of Dickson (1990) for KSO_4 and the total boron-to-salinity ratio from Uppström (1974) for computation. The results of the calcium carbonate saturation state calculations will be presented in the discussion section because we will only use it to corroborate a hypothesis about the role of cable bacteria in the putative dissolution of foraminiferal shells.

4. RESULTS

4.1. FORAMINIFERAL COMMUNITIES

The black curve in Figure 6 represents the number of individuals per sample (Suppl. Table 1), whereas the red curve represents the number of individuals after merging of samples when we were below our target value of 50 individuals. However, even after this merging procedure, all samples in the top 17 cm of the core were still very poor in foraminifera, with less than 50 individuals (Figure 6 and Table 1).

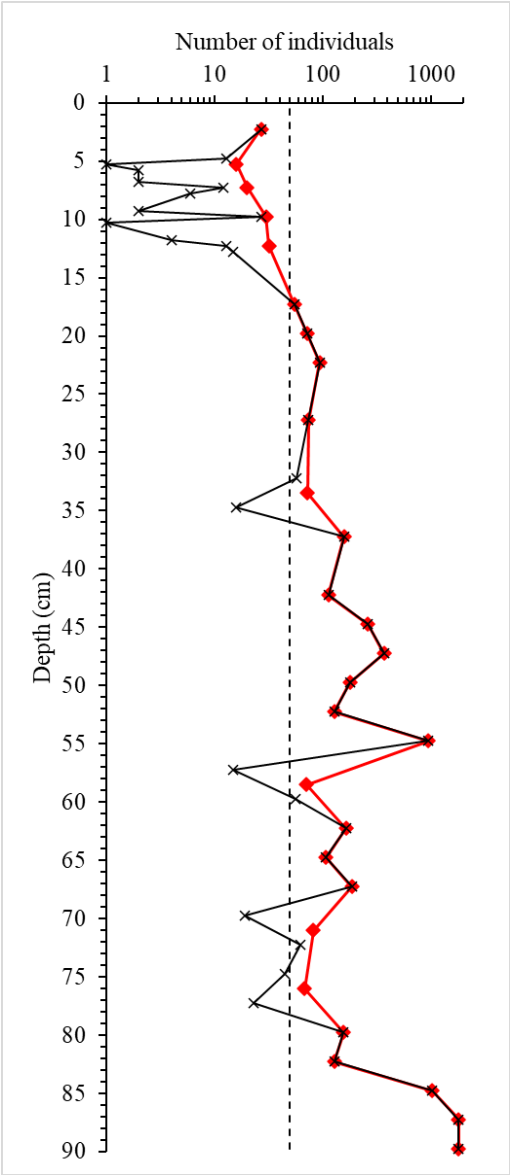

Figure 6. Total number of individuals in non-merged samples (black curve) and after merging samples to a maximum thickness of 3 cm (red curve). The dashed line represents the target value of 50 individuals per analysed sample.

Eleven of the 23 observed taxa were considered as dominant (≥ 5 % in at least one sample, Suppl. Table 1). Together, these 11 dominant taxa represent more than 90 % of the total assemblage in almost all samples (Table 1).

Total foraminiferal density was relatively high between 90 and 84.5 cm depth, ranging from 1033 to 1810 individuals per sample (of 14.1 cm^3; Figure 6 and Table 1). At 82.5 cm depth, the density abruptly decreased by one order of magnitude. Total densities between 82.5 and 17 cm depth oscillated between 15 (57–57.5 cm depth) and 950 individuals (54.5–55 cm depth) per sample, with an average of about 175 ind. per sample.

Finally, in the top 17.5 cm of the core, total densities were very low, between 1 and 27 individuals per sample (Figure 6 and Table 1).

Table 1. Census data for foraminifera >125 µm in the final reconstituted samples. Relative abundances of the dominant species of foraminifera (≥ 5 % of the total assemblage in at least one sample), total percentage of dominant taxa and total number of individuals in the recomposed samples (consisting of a single sample of 14.1 cm^3, or 2 or 3 merged samples). We also included *A. veneta* (not considered as a dominant species), because we discuss this species later in the manuscript. For raw data of all individual samples, see Suppl. Table 1.

Interval depth (cm)	*Ammonia aberdoveyensis*	*Ammonia confertitesta*	*Ammonia veneta*	*Elphidium magellanicum*	*Elphidium margaritaceum*	*Elphidium oceanense*	*Elphidium selseyense*	*Elphidium williamsoni*	*Haynesina germanica*	*Haynesina depressula*	*Quinqueloculina spp.*	*Stainforthia sp.*	Total dominant taxa (%)	Total number of individuals	Number of merged samples
2–2.5	7.4	0.0	3.7	11.1	14.8	0.0	18.5	11.1	25.9	3.7	0.0	0.0	96.3	27	1
4.5–6	6.3	0.0	0.0	18.8	6.3	0.0	18.8	12.5	0.0	0.0	12.5	0.0	75.0	16	3
6.5–8	0.0	15.0	0.0	15.0	10.0	0.0	30.0	20.0	0.0	0.0	5.0	0.0	95.0	20	3
9–10.5	0.0	0.0	3.3	26.7	10.0	0.0	16.7	6.7	10.0	6.7	6.7	0.0	86.7	30	3
11.5–13	0.0	12.5	0.0	9.4	25.0	0.0	46.9	3.1	0.0	3.1	0.0	0.0	100.0	32	3
17–17.5	0.0	0.0	0.0	10.9	21.8	0.0	40.0	0.0	3.6	1.8	5.5	5.5	83.6	55	1
19.5–20	2.8	8.3	0.0	5.6	29.2	1.4	33.3	0.0	0.0	8.3	1.4	4.2	90.3	72	1
22–22.5	1.1	1.1	2.1	0.0	11.7	0.0	74.5	2.1	3.2	1.1	0.0	0.0	96.8	94	1
27–27.5	4.1	6.8	2.7	8.1	12.2	2.7	47.3	5.4	5.4	0.0	0.0	0.0	94.6	74	1
32–35	11.0	15.1	0.0	0.0	9.6	2.7	41.1	6.8	8.2	1.4	0.0	0.0	95.9	73	2
37–37.5	0.0	0.0	0.6	0.0	6.3	0.0	87.3	3.2	0.6	1.3	0.0	0.0	99.4	158	1
42–42.5	7.1	0.9	0.9	3.5	21.2	0.9	40.7	4.4	8.8	7.1	0.0	0.0	95.6	113	1
44.5–45	6.1	2.3	3.4	6.8	19.8	0.0	38.0	3.4	3.8	7.2	1.1	0.0	92.0	263	1
47–47.5	1.4	3.8	0.5	2.4	6.8	0.0	77.0	2.4	1.4	1.6	1.6	0.0	98.9	370	1
49.5–50	2.8	3.3	0.6	3.3	20.0	1.7	43.3	2.2	11.1	5.6	0.0	0.0	93.9	180	1
52–52.5	7.0	0.8	2.3	1.6	20.3	1.6	35.9	5.5	7.0	10.9	0.8	0.0	93.8	128	1
54.5–55	6.1	1.1	0.6	4.0	14.7	0.6	43.6	5.1	5.9	10.5	1.7	0.0	93.9	950	1
57–60	1.4	0.0	2.8	14.1	9.9	0.0	50.7	1.4	2.8	11.3	4.2	0.0	98.6	71	2
62–62.5	8.5	0.0	1.2	0.6	12.1	2.4	46.7	6.1	9.7	4.8	1.8	0.0	93.9	165	1
64.5–65	10.2	0.0	0.9	4.6	14.8	2.8	36.1	4.6	7.4	7.4	0.9	0.0	89.8	108	1
67–67.5	11.2	0.0	0.5	4.3	23.0	0.5	32.1	7.0	2.7	8.0	4.8	0.0	94.1	187	1
69.5–72.5	11.0	0.0	1.2	7.3	31.7	1.2	18.3	6.1	4.9	6.1	2.4	0.0	90.2	82	2
74.5–77.5	4.4	0.0	1.5	35.3	19.1	0.0	14.7	4.4	4.4	5.9	5.9	0.0	95.6	68	2
79.5–80	5.7	0.0	0.6	3.8	15.3	4.5	42.0	5.1	11.5	6.4	1.9	0.0	96.8	157	1
82–82.5	3.9	0.0	0.0	9.4	7.8	6.3	47.7	5.5	6.3	6.3	0.8	0.0	93.8	128	1
84.5–85	10.2	0.0	1.7	3.4	0.8	1.5	52.3	6.4	10.2	4.5	1.0	0.1	91.9	1033	1
87–87.5	17.3	0.0	1.5	1.9	0.8	1.4	21.0	8.8	31.3	6.2	0.3	0.0	90.6	1810	1
89.5–90	13.6	0.0	1.3	0.9	0.2	0.9	46.9	7.1	18.8	3.5	0.5	0.0	93.7	1805	1

Elphidium selseyense was the dominant species in most of the samples, accounting for 15 to 87 % of the total assemblage (Figure 7, Table 1). The levels 47–47.5, 37–37.5 and 22–22.5 cm presented peak values for this taxon (>70 %), whereas the assemblages of the top 10.5 cm were rather poor in *E. selseyense* (between 17 and 30 %).

The relative abundance of *E. magellanicum* oscillated between 0 and 35 %. A major peak was present at 74.5–77.5 cm (35 %). This species showed relatively high percentages (9–27 %) in the low-density samples of the topmost 17.5 cm (Figure 7, Table 1).

Elphidium margaritaceum was nearly absent between 89.5–90 and 84.5–85 cm. Above these levels, relative abundances varied between 6 and 32 % with maxima around 70 cm depth, from 52–52.5 to 42–42.5 cm depth, and from 19.5–20 to 11.5–13 cm depth (Figure 7, Table 1).

The relative proportions of *H. germanica* fluctuated generally between 1 and 10 %. This species was abundant (19 and 31 %) in the first two samples (89.5–90 cm and 87–87.5 cm depth), whereas it was present in low numbers, or even absent, in the 20–4.5 cm interval. *Haynesina germanica* showed again an elevated percentage (26 %) in the most recent sample (2–2.5 cm depth, Figure 7, Table 1).

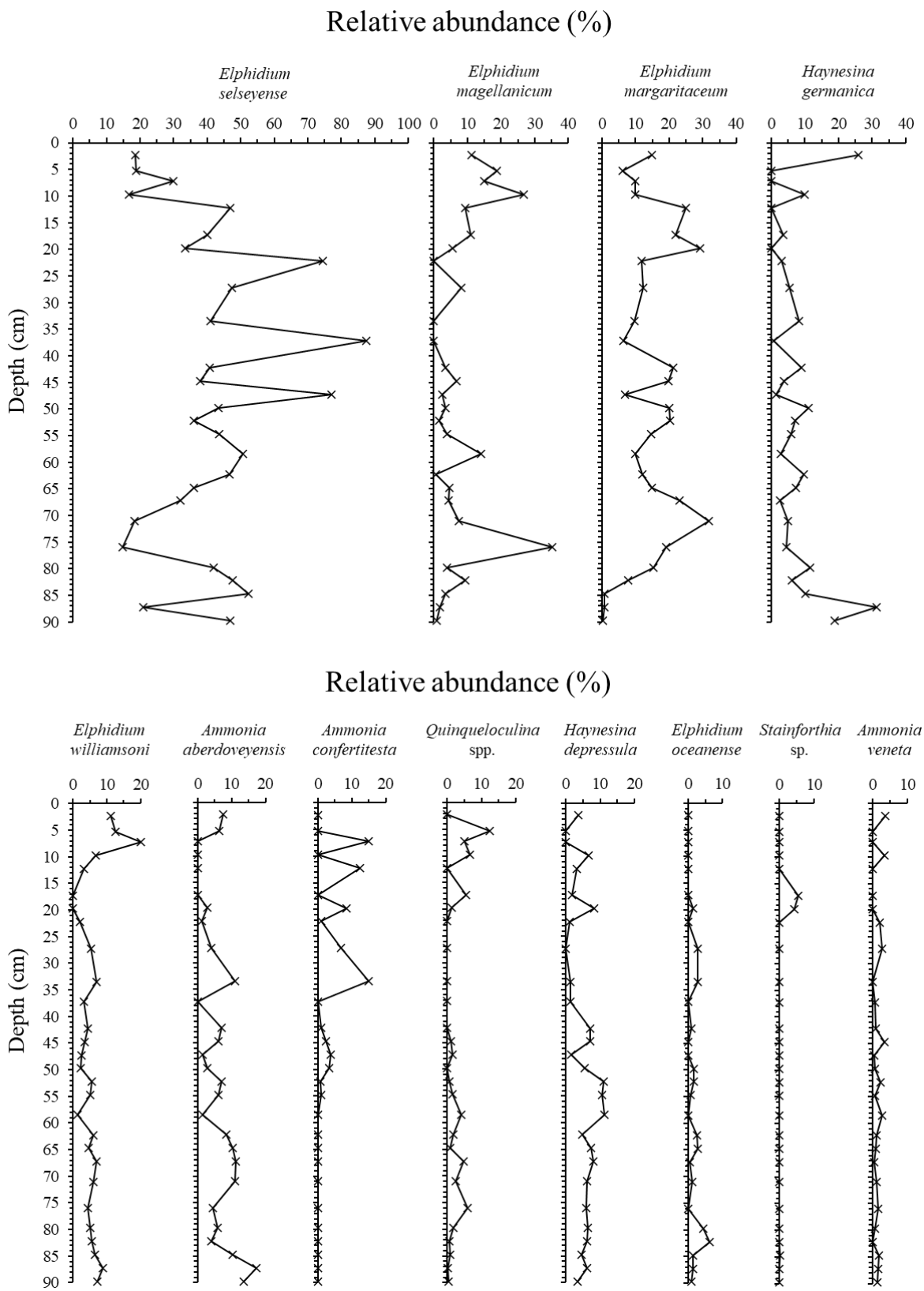

Figure 7. Relative abundances (%) of the dominant species as a function of depth (cm). We also included *A. veneta* (not considered as a dominant species), because we discuss this species later in the manuscript.

All other taxa only rarely contributed more than 10 % in the total assemblage (Figure 7, Table 1). *Elphidium williamsoni* showed maximum values (11–20 %) in the top 10 cm of the core, whereas *Elphidium oceanense* always accounted for only low percentages (0–6 %), slightly decreasing upward. This taxon was absent in the top 17.5 cm. *Ammonia aberdoveyensis* showed a general decrease from about 10–17 % at the bottom of the core to a near absence at about 20 cm depth. However, it showed higher percentages again (6–7 %) in the topmost two samples (4.5–6 and 2–2.5 cm depth). *Ammonia confertitesta* was totally absent until 55 cm core depth and fluctuated between absence and 15 % thereafter. *Ammonia veneta* was always present in low percentages, never exceeding 4 %, without a clear pattern. *Quinqueloculina* spp. showed two main presence intervals, between 80 and 44.5 cm (up to 6 %) and from 20 to 4.5 cm depth (up to 13 %). *Haynesina depressula* (up to 11 %) tended to be more abundant in the lower 40 cm of the core. Finally, *Stainforthia* sp. was absent in most samples, but was present at 19.5–20 and 17–17.5 cm depth (with 4 and 6 %, respectively).

4.2. MULTIVARIATE ANALYSIS

The first two axes of the non-standardised PCA based on relative abundance data account for 61 % and 17 % of the total variability of the dataset, respectively (Suppl. Table 2).

Table 2 presents the contributions of the dominant taxa to the first two PCs. *Elphidium selseyense* has a strong positive contribution to PC1, whereas *E. magellanicum* has a slight negative contribution to this axis. *Elphidium margaritaceum* and *E. magellanicum* have a positive contribution to PC2, whereas *H. germanica* and *A. aberdoveyensis* load negatively on this axis. Figure 8 presents a scatter plot for PC1 and PC2, in which we added the living assemblages of station 1 (same station as the long core) and of the nearby, shallower station 2 (water depth 23 m) which is less severely affected by seasonal hypoxia/anoxia (Richirt et al., 2020), as supplementary individuals.

Table 2. Taxa contributions to the first two PCs from the PCA. Values in bold are superior to the average contribution (|9.09|, if all species would contribute equally).

Species / PC contribution	PC 1	PC 2
Ammonia aberdoveyensis	-0.6	**-10.9**
Ammonia confertitesta	0.0	1.6
Elphidium selseyense	**87.5**	0.4
Elphidium magellanicum	-7.3	**10.4**
Elphidium margaritaceum	-1.8	**32.0**

Elphidium williamsoni	-0.8	-1.8
Elphidium oceanense	0.0	-0.2
Haynesina germanica	-1.3	**-41.8**
Haynesina depressula	-0.2	0.0
Quinqueloculina spp.	-0.5	0.8
Stainforthia sp.	0.0	0.2

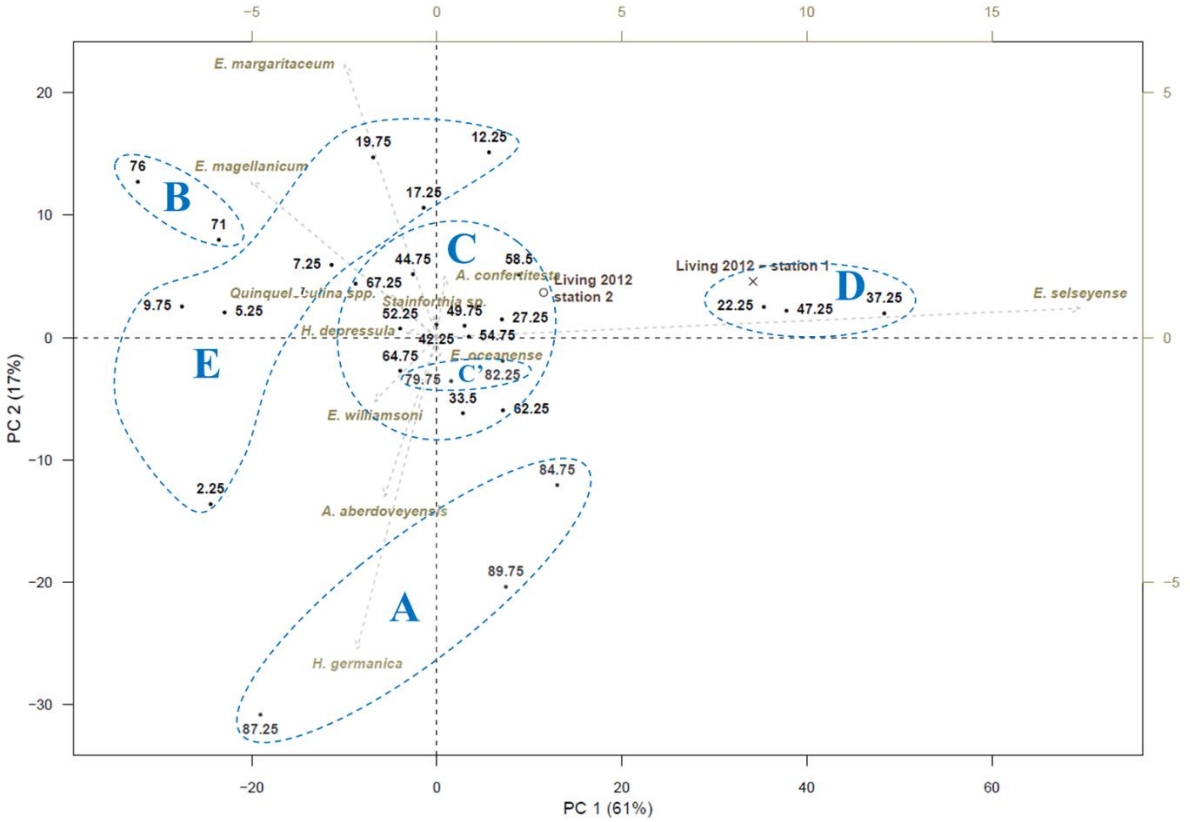

Figure 8. Scatter plot showing the taxa loadings and sample scores on the first two PCA axis. Core depth (cm) is indicated in black. Dominant taxa are represented by arrows. Supplementary individuals (living assemblages observed in 2012 from stations 1 and 2; Richirt et al., 2020) are indicated by a cross and a circle for stations 1 and 2, respectively. Blue dotted lines show the different, arbitrarily defined, groups of samples.

In Figure 8, five groups of samples have been recognised arbitrarily based on their position on the PCA scatter plot and their proximity in the core:

Group A is constituted of samples with high negative scores on PC2, reflecting high proportions of *A. aberdoveyensis* and *H. germanica*. This concerns the samples from 90 to 84.5 cm core depth.

Group B contains samples with strongly negative scores on PC1 and positive scores on PC2, characterised by high relative abundances of *E. magellanicum* and *E. margaritaceum* and relatively low percentages of *E. selseyense*. This concerns the 74.5–77.5 and 69.5–72.5 cm

samples, which are both merged samples because the number of individuals in the separate samples was very low.

Group C is composed of samples with low absolute scores on both PCs (i.e. centred on the scatter plot, Figure 8), indicative of average assemblages. These "typical" assemblages are dominated by *E. selseyense*, have a high percentage of *E. margaritaceum*, a lower percentage of *A. aberdoveyensis* and *H. germanica* (compared to group A), and contain *A. confertitesta* from 55 cm onward. This concerns most samples from 67.5 to 27 cm depth as well as the 82–82.5 and 79.5–80 cm samples (subgroup C'). The living community of station 2 (Den Osse Basin, 23 m water depth) plots together with this group.

Group D is composed of three samples with very high scores on PC1, reflecting uncommonly high percentages of *E. selseyense***.** This concerns the 22–22.5 cm, 37–37.5 cm and 47–47.5 cm samples. The living assemblage of station 1 is very similar, as shown by its proximity on the scatter plot (Figure 8).

Group E groups samples intermediate between groups B and C, mostly with negative scores on PC1, and positive scores on PC2. Assemblages in these samples are characterised by high relative abundances of *E. magellanicum* and *E. margaritaceum*, although lower than the samples of group B. Group E contains all samples between 20 and 2 cm core depth. The 2–2.5 cm sample is rather far away from the other samples of this group due to its high percentage of *H. germanica* (Table 1). However, most samples in group E show a low absolute total abundance, so that minor changes in the counts may lead to substantial changes in relative proportions.

5. DISCUSSION

5.1. TEMPORAL EVOLUTION OF THE FORAMINIFERAL COMMUNITY

Here we will focus on the temporal changes in foraminiferal densities and assemblage composition through time, and we will investigate whether it is possible to link the main assemblage changes to the anthropogenic modifications of Lake Grevelingen during the last 50 years (Figure 9). As we look at 0.5 cm thick layers in a context where the average sediment accumulation rate is about 2 cm y^{-1}, individual layers may represent a single season and not a complete year. Consequently, samples with high foraminiferal densities could be deposited during spring/early summer seasons, whereas samples with low foraminiferal densities could be representative of the late summer/autumn/winter seasons.

Additionally, we judge that vertical displacements of foraminiferal shells, either caused by the vertical migration of infaunal species (when alive) or by macrofaunal bioturbation (living as well as dead individuals), are strongly limited in the sedimentary environment studied here. The severe anoxic and sulphidic conditions at this site (sulphide was present in the pore water below 2 cm depth during the whole year in 2012, Seitaj et al., 2015) largely restrict the presence of macrofauna and probably limit their bioturbation to the top 2 cm at most (Seitaj et al., 2017; Hermans et al., 2020). For the same reason, living foraminifera are not expected to dwell deeper than the superficial oxic layer, being limited by the sulphidic conditions immediately below.

Finally, the high sedimentation rate (about 2 $cm.y^{-1}$) further decreases the possibility of mixing of sediment layers with different ages, suggesting that most samples contain contemporaneous assemblages, representing short periods of time (a single season to a year at most).

As explained before, the Principal Component Analysis allows us to recognise five groups of samples, each representing different vertical intervals from the sediment core, and therefore, successive stages of the evolution of the Lake Grevelingen.

Group A includes samples from 90 to 84.5 cm depth (estimated period ~ 1968 to 1971). They contain a sandy sediment, and are situated immediately below the shift to a much finer sediment at 82.5 cm. These samples represent the estuarine phase of the basin, before its seaward closure in 1971. The foraminiferal assemblages are characterised by high density (between 1000 and 2000 ind. per 14.1 cm^3 sample), and by high percentages of typical estuarine/mudflat species such as *H. germanica* and *A. aberdoveyensis* (e.g. Alve & Murray, 1994; 2001; Thibault de Chanvalon et al., 2015; Saad & Wade, 2016; 2017). In view of the location of station 1, in the middle of the Den Osse Basin at 34 m depth (the main former channel of the Grevelingen estuary), the sandy sediment reflects the strong hydrodynamics of this site, when it was still an estuary. Currents were too strong to allow deposits of clays and silts, so that the former channel floor was covered by a sandy lag deposit, with a very high foraminiferal density. The strong currents undoubtedly facilitated the transport of allochthonous foraminifera, such as the taxa cited above, which are typical of estuarine mudflats. However, *H. depressula*, a species typical of marine influence (Murray 1983; Darling et al., 2016) is present with substantial proportions as well, showing that foraminifera were not only transported from the inner to the outer estuary, but also from the North Sea into the outer estuary.

Subgroup C' of group C includes the next two samples, from 82.5 to 79.5 cm depth (estimated period ~ 1972 to 1975). The sediment is mainly composed of clay/silt, confirming

its deposition after the seaward closure of the basin, when hydrodynamics became much weaker. The strong drop of foraminiferal densities (from higher than 1000 to less than 100 ind. per sample) shows that these samples no longer constitute a lag deposit, but rather that the foraminiferal populations are diluted by supplies of fine-grained sediment (about 2 cm y^{-1}). The weaker hydrodynamics, together with the suppression of tides explain why the foraminiferal assemblage is much less affected by transport, and probably represents an autochthonous community.

The assemblages of these two samples show a strongly increased percentage of the more marine species *E. margaritaceum* and the euryhaline species *E. oceanense* (Darling et al., 2016), contrasting with a strong decrease of the percentages of the more estuarine species *H. germanica* and *A. aberdoveyensis*. This suggests that in the first years after the closure of the former estuary, the basin floor was still inhabited by species typical of marine influence (high salinity), whereas inner estuarine species were no longer living, or transported to the study area. Salinity, measured on surface waters, was consistently high (~ 30) in the years immediately following the closure of the basin (1972–1974, Bannink et al., 1984), allowing marine taxa to inhabit the former main channel.

Group B, which represents the 77.5 to 69.5 cm interval (estimated period ~ 1975–1980) contains only two merged samples (i.e. 74.5–77.5 and 69.5–72.5 cm). Their assemblage composition is somewhat peculiar, because of the high relative proportions of *E. magellanicum* and *E. margaritaceum,* contrasting with the relatively low, but still substantial contribution of *E. selseyense*.

In this period, surface water salinity showed a progressive decrease, from ~ 30 in 1974 to a minimum of ~ 23 in 1978, due to the input of rainwater (Bannink et al., 1984). In case these salinity values partly reflect conditions on the basin floor, this could suggest that *E. magellanicum* and *E. margaritaceum* are more tolerant to lower salinities than *E. selseyense*. Unfortunately, the ecology of these three species is still imperfectly known. In the literature, the European representatives of *E. magellanicum* are generally considered as euryhaline (20–30 in Fjords, Gustafsson & Nordberg, 1999; 2000; 10–20 in the western Baltic Sea, Schönfeld et al., 2018; shallow marine at Dunkirk beach, Lévy et al., 1969). *Elphidium selseyense* appears to be opportunistic and tolerant to a large range of salinity (Darling et al., 2016). Conversely, *E. margaritaceum* has been reported as a more marine species which tolerates only slight salinity variations (Alve & Murray, 1999; Darling et al., 2016).

The transition to a lacustrine system also strongly increased the average water residence in the lake, up to several years, compared to a few days when Grevelingen was an estuary. This

strongly modified the ecosystem structure and functioning of Lake Grevelingen (Nienhuis, 1978; Saeijs & Stortelder, 1982). The strengthened water column stratification and the much longer residence times led to a progressive increase of nutrient concentrations between 1971 and 1978 (Bannink et al., 1984). The opening of the Brouwersdam in late autumn 1978, resulting in limited salt water inflow, induced a further strengthening of the salinity stratification of the water column, which led to hypoxia/anoxia and mass mortality in the deepest parts of the basin in summer 1979 (Bannink et al., 1984).

The three *Elphidium* species that dominated the assemblages during this period were apparently more resistant to these rapidly changing conditions than other taxa. Their tolerance regarding low oxygen conditions is shown by their presence in the recent assemblages of this site (Richirt et al., 2020), but also by their presence in fjords affected by seasonal anoxia (Gustafsson & Nordberg, 1999; 2000).

The remaining samples of **Group C** represent the 67.5 to 27 cm interval (estimated period ~ 1980 to 2000). To remedy the increase of eutrophication phenomena observed in the 1970s, the basin was partly reopened by an underground sluice in 1978. This sluice was initially opened only in winter. Consequently, surface water salinity almost immediately rose to ~ 30 and nutrient concentrations showed a major decrease (Bannink et al., 1984). However, this did not solve the problem of bottom water oxygen deficiency, and in the next 20 years, an intermittent succession of major later summer/early autumn hypoxic/anoxic periods was observed, especially in the deepest parts of Lake Grevelingen (Figure 3). This is confirmed by the results of Lindeboom & Sandee (1984), who found anoxic conditions coupled with the presence of sulphide at a few mm depth in the sediment in May and June 1982, at much shallower stations, with depths < 10 m. In 1999, the sluice was opened year-round, to further increase water exchanges.

During this period (~ 1980 to 2000), the total foraminiferal density showed strong variations, between ~ 70 and 950 individuals per sample. This alternance of high and lower foraminiferal density could be due to differences between successive years regarding bottom water oxygen content (Figure 3; Seitaj et al., 2015; 2017), more specifically due to inter-annual variability in the intensity and duration of the summer hypoxia/anoxia (with or without sulphide in the topmost sediment). Richirt et al. (2020) showed that in case of prolonged summer anoxia combined with the presence of sulphides in the topmost sediment, the foraminiferal community almost completely disappears, and the site is recolonised the following winter, leading to low standing stocks the next spring. The strong Mo peak at ~ 32 cm (estimated age ~ 1998, Figure 9), could indicate particularly severe anoxic and sulphidic conditions in the sediment (anoxia

with presence of sulphides). This could explain why we observe a very low foraminiferal density (16 ind. per sample) at ~ 35 cm, immediately after this period. This apparent depth shift of ~ 3 cm between these two events could be explained by the fact that Mo concentrations and foraminiferal densities were measured on two different cores (see Materials & Methods section). Conversely, layers with high foraminiferal densities (such as sample at 54.5–55 cm, estimated age ~ 1986) could correspond to periods following weaker and/or shorter anoxic events, eventually without sulphides in the foraminiferal habitat.

All samples of group C are strongly dominated by *E. selseyense*, with *E. margaritaceum* being the second most dominant species. This seems to reflect increased salinity (more marine influence) and development of seasonal hypoxia favouring opportunistic species such as *E. selseyense*. The arrival of *A. confertitesta*, at about 55 cm core depth (~ 1986) corresponds to a progressive decrease of *H. depressula*, *Quinqueloculina* spp. and *A. aberdoveyensis*. It is interesting to note that the assemblage of group C is comparable to the composition of the living assemblage at the shallower station 2 (depth 23 m), as shown by the PCA scatter plot (Figure 8), suggesting that the environmental conditions may have been comparable, with a rather short anoxic event in summer (maximum of 1 month, Richirt et al. 2020).

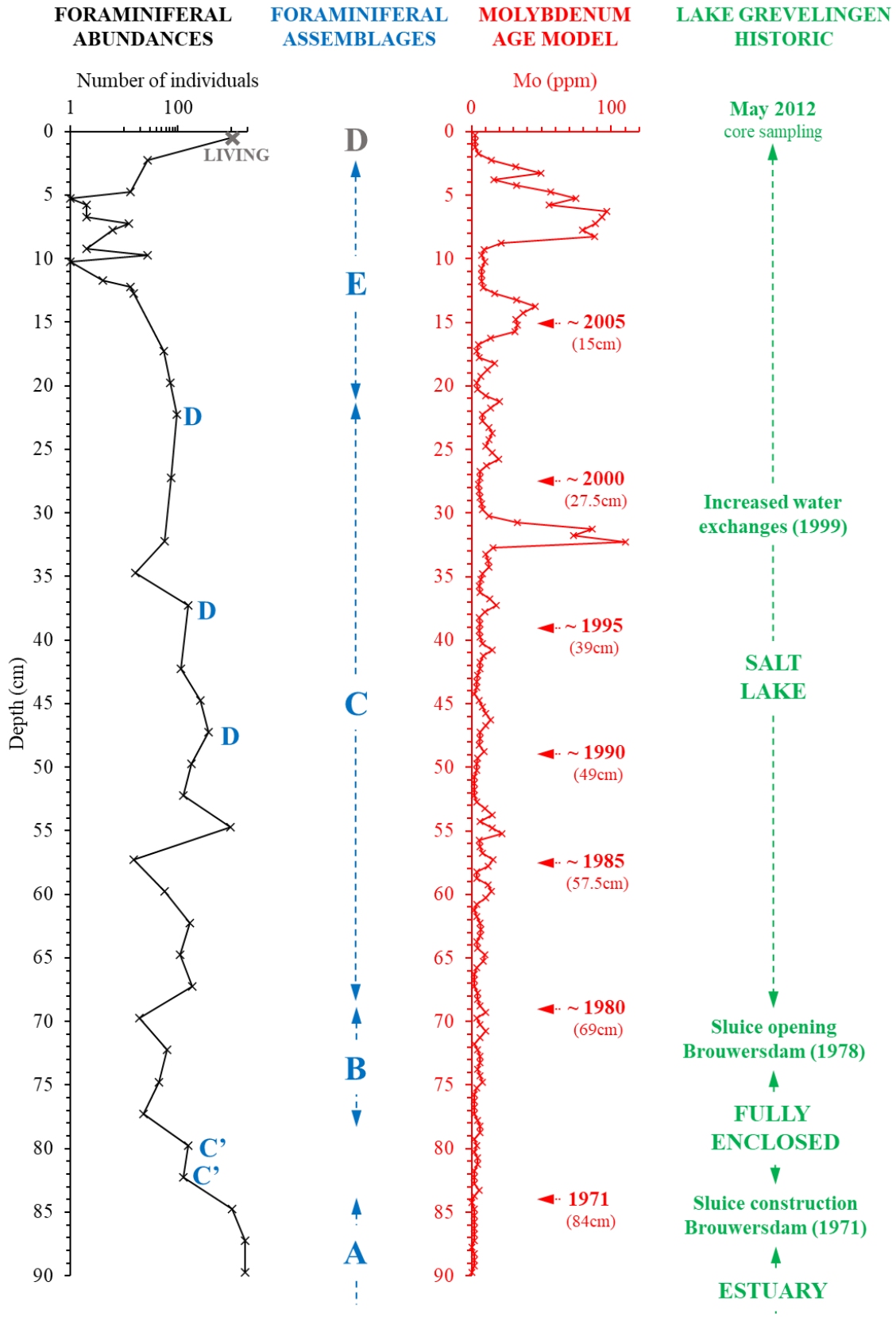

Figure 9. Timeline of the human-induced modifications following the Delta Plan at Lake Grevelingen. The sediment core used to investigate dead foraminiferal assemblage density record (black curve, excluding the top layer 0.5 cm showing living assemblage in grey) and the Mo record (red curve). Both long cores were sampled in May 2012. Blue letters emphasise the different groups of layers highlighted in the PCA scatter plot.

Group D contains only three samples (47–47.5, 37–37.5 and 22–22.5 cm core depth, deposited in ~ 1991, ~ 1996 and ~ 2003, respectively). The foraminiferal densities in these samples are comparable to densities from group C and range from 94 to 370 ind. per sample. The composition of these samples stands out by exceptionally high proportions of *E. selseyense* (> ~ 75 %). This is very similar to the composition of the living assemblage in 2012 at the same station (Richirt et al., 2020), as shown by their proximity on the PCA scatter plot. This suggests that the three samples of group D reflect similar conditions, which could be characterised by rather severe anoxic conditions with the presence of sulphides in the topmost sediment, as recorded in 2012 (Seitaj et al., 2015). It appears that *E. selseyense* could be particularly tolerant to such low oxygen conditions; this is confirmed by its strong dominance in the living community sampled at this site in 2012 (Richirt et al., 2020).

Finally, **Group E** comprises all samples in the top 20 cm of the core (estimated period ~ 2003 to 2011). This group of samples has been deposited in the years after the decision had been taken to open the seaward sluice year-round (in 1999), leading to a further decrease in water residence times. The total foraminiferal densities are extremely low in this interval (rarely exceeding 15 ind. per sample). Because of the low foraminiferal densities, several samples had to be merged. In spite of the merging procedure, relative proportions are still based on low numbers (from 16 to 72 specimens) and should be considered with caution. Even when taking into account the high sedimentation accumulation rate at this location, the unexpected very low densities strongly contrast with the elevated densities of living communities, which attained a maximum of 634 individuals per 14.1 cm^3 sample in May 2012 when the long core was sampled (recalculated from Richirt et al., 2020; Figure 9).

The foraminiferal assemblages of the samples from group E are relatively poor in *E. selseyense*, whereas the percentages of *E. margaritaceum*, *E. magellanicum* and *E. williamsoni* show a strong increase. *Quinqueloculina* spp. is also somewhat more frequent (Table 1). It is surprising that the taxonomic composition of the group E samples is very different from the year-averaged living assemblage from this site (Figure 8).

In view of the important density differences between the rich living populations and poor taphocoenoses, with a very different species composition, we suspect that the dead assemblages have suffered from important taphonomic losses during early diagenesis, specifically due to carbonate dissolution. In fact, in the deepest parts of Lake Grevelingen, two antagonistic bacterial populations occur: cable bacteria develop mainly between January and May, whereas *Beggiatoceae* mats occupy the sea floor from September to December (Seitaj et al., 2015). The reasons why these two filamentous S-oxidising bacteria show such an

antagonistic seasonal succession is not well understood yet (Seitaj et al. 2015), but it is clear that they strongly affect the geochemistry of the topmost sediment layer.

5.2. CABLE BACTERIA ACTIVITY RESPONSIBLE FOR FORAMINIFERAL TEST DISSOLUTION

Cable bacteria activity promotes carbonate precipitation in the oxic zone (maximum oxygen penetration depth about 2 mm at this site, even in winter, see Seitaj et al., 2015), and carbonate dissolution immediately below, where oxygen is absent (Risgaard-Petersen et al., 2012; Meysman et al., 2015). Consequently, the carbonate saturation state (ΩCa) is low in the first centimetres of the sediment (ΩCa < 1 at least down to 2 cm, see Table 3), which could result in the partial or complete dissolution of calcareous foraminiferal tests. In fact, for 2012, calculated ΩCa are < 1 from January (excluding in the top 0.5 cm) to April, when cable bacteria were active, indicating strongly increased calcium carbonate ($CaCO_3$) dissolution (Table 3). This is corroborated by a release of Ca^{2+} measured in the first centimetres in pore waters at the same station in January and March (Sulu-Gambari et al. 2016a).

Table 3. Values of calcium carbonate saturation state at station 1 at different depths in the sediment for each month of 2012. Red: ΩCa < 1, indicating increased carbonate dissolution. Blue: ΩCa > 1, indicating no carbonate dissolution. NA: data not available.

Depth (cm)	January	February	March	April	May	June	July	August	September	October	November	December
0.25	2.30	NA	NA	0.91	NA	1.93	3.08	NA	1.86	NA	2.81	3.06
0.75	0.54	0.90	0.68	0.70	NA	2.39	2.67	NA	2.30	7.46	9.62	14.68
1.25	0.29	0.41	NA	0.55	NA	2.41	2.87	NA	2.90	NA	14.76	22.66
1.75	0.20	0.27	0.24	0.51	NA	2.13	2.87	NA	NA	4.60	NA	21.11
2.25	NA	0.22	0.23	0.67	NA	1.99	2.75	NA	3.95	5.03	5.90	13.49
2.75	NA	0.21	NA	0.61	NA	2.40	2.78	NA	NA	NA	NA	7.75
3.25	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	4.29	6.98
3.75	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	4.68	NA

Living foraminifera have mechanisms to deal with a lower carbonate saturation state (e.g. active control of their internal and external pH during the calcification process, intracellular storage of Ca^{2+} ions, Toyofuku et al., 2008; de Nooijer et al., 2009; Toyofuku et al., 2017). When dwelling in environments with a lower carbonate saturation state, living specimens only rarely show serious signs of test dissolution (e.g. Charrieau et al., 2018). Hence, most dissolution is thought to occur after the death of the foraminifera. Furthermore, we note that the dense living populations, which are not much affected by carbonate dissolution,

predominantly live in the thin oxic zone (only a few mm), which is not affected by the strongly decreased ΩCa (Seitaj et al. 2015). Only when the tests of dead foraminifera passively cross this low ΩCa zone (due to sediment deposition at the sediment water interface), assemblages are probably affected by important losses due to carbonate dissolution. The very low foraminiferal densities in the top 20 cm of the core suggest that this situation has existed since about 2003, some years after the intensification of water exchanges. In the cartoon presented in Figure 10, the seasonal succession of events is illustrated.

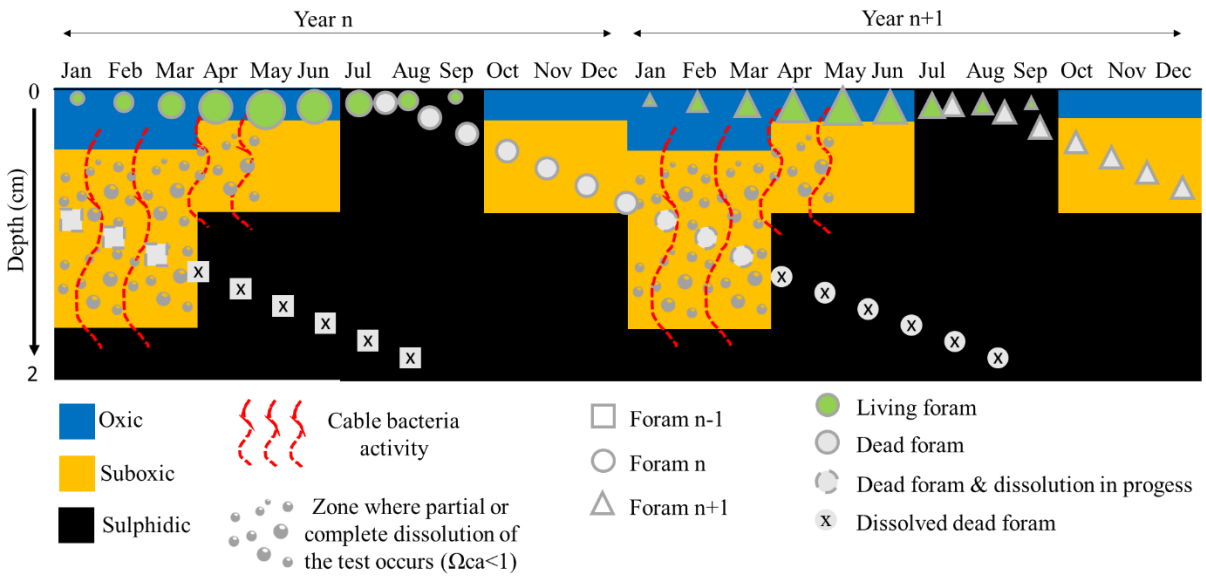

Figure 10. Conceptual scheme showing two consecutive years to explain the low density of dead foraminifera (in grey) in the first 20 cm of the core. The seasonal succession of oxic (blue), suboxic (orange) and sulphidic (black) zones and presence of cable bacteria (red dotted curves) are from Seitaj et al. (2015). Presence and densities (size of the signs) of living foraminifera (in green) are from Richirt et al. (2020). Squares, circles and triangles represent the yearly successive foraminifera generations.

If our hypothesis that the low density of foraminifera in the top 20 cm is due to dissolution resulting from cable bacteria activity is correct, this implies that cable bacteria activity in the Den Osse Basin started, or substantially increased between 2000 and 2005. This fits remarkably well with the year-round opening of the Brouwersdam sluice in 1999.

The increased inflow of saline, warm and well oxygenated water induced by the opening of the Brouwersdam sluice in 1999 should have improved the oxygenation and led to a reduction of the duration of anoxic events in the bottom waters compared to the situation before 1999 (Figure 3; Wetsteijn, 2011; Sulu-Gambari et al., 2017). However, the increased concentration and large peaks in the Mo record in the last ~ 30 cm of the core suggest the presence of increased sulphide concentrations in the pore waters during the same period. Sulu-Gambari et al. (2017) explained this contradiction (i.e. the better oxygenation of bottom waters

but development of more sulphidic conditions in sediment) by the introduction of large amounts of phytoplankton (mainly *Phaeocystis globosa*) into Lake Grevelingen from the North Sea (Hagens et al. 2015) since ~ 2000. The intensified remineralisation of organic matter induced by this extra input of dead algal material enhanced the sulphate reduction rate resulting in an increase of the porewater sulphide concentration. This process may have contributed to the exceptionally long hypoxia/anoxia in 2011 and 2012, compared to the period 1999–2010 (Sulu-Gambari et al. 2017).

The suggested increased cable bacteria activity resulting from the increased water flow in 1999 is corroborated by the fact that the presence of an oxygen-sulphide interface is a prerequisite for the development of S-oxidising bacteria, such as cable bacteria and *Beggiatocea* (Jørgensen, 1982).

5.3. TEMPORAL SUCCESSION OF *AMMONIA* SPECIES

The historical record for Lake Grevelingen presented here shows the arrival of *A. confertitesta* at 54.5–55 cm core depth (estimated year ~ 1986), and its subsequent progressive replacement of *A. aberdoveyensis* (Figure 11). It has already been suggested that *A. confertitesta* could be an exotic and/or invasive species originating from east Asia and introduced in the eastern Atlantic Ocean by anthropogenic activities (Pawlowski & Holzmann, 2008; Schweizer et al, 2011; Bird et al., 2020). Concerning the other two representatives of the *Ammonia* genus observed in our sediment core, *A. veneta* is considered cosmopolitan (Holzmann & Pawlowski, 2000; Hayward et al., 2021) whereas *A. aberdoveyensis* seems to be restricted to the north Atlantic (Hayward et al., 2004; Hayward et al., 2021). The latter two species are both assumed autochthonous in Europe and could at present be progressively replaced by the seemingly exotic *A. confertitesta* (Pawlowski & Holzmann, 2008; Schweizer et al. 2011).

This species replacement suggests that *A. confertitesta* is more resistant than *A. aberdoveyensis* to the seasonal hypoxia/anoxia found in Lake Grevelingen after the closure in 1971. This hypothesis is corroborated by the much higher test porosity measured in *A. confertitesta* compared to *A. aberdoveyensis* (22.45 ± 3.85 % versus 12.18 ± 3.8 %, respectively, Richirt et al. 2019a), suggesting that this phylotype could resist oxygen deficiency by increasing its gas exchanges with the surrounding environment. The fact that *A. confertitesta* is rather poorly represented (about 5 % of the total assemblage) in the living assemblages in 2012 was explained by a phase offset between: 1) the time of repopulation of the site in winter

2011–2012 after its decimation due to anoxic and sulphidic conditions in summer 2011, and 2) the availability of its preferred food sources, in spring 2012 (Richirt et al. 2020).

Alternatively, the rather poor density of *A. confertitesta* could also mean that this taxon tolerates hypoxia and short phases of anoxia but is not able to withstand prolonged periods of oxygen depletion, together with a presence of sulphides in its microhabitat. This could explain the much higher percentage of this taxon in the living assemblages of station 2 (shallower station in Den Osse Basin), where the duration of seasonal hypoxia/anoxia is shorter than at station 1 (Richirt et al. 2020).

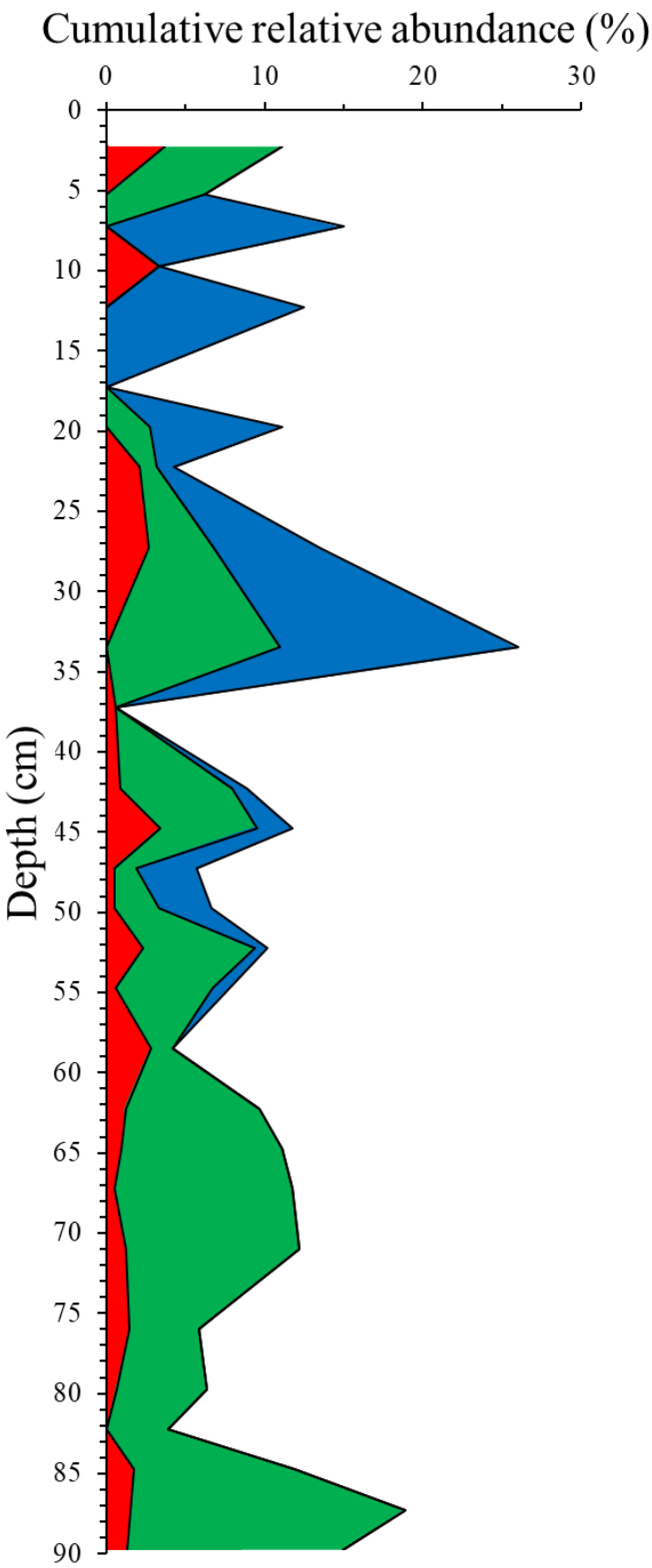

Figure 11. Cumulative relative abundances (in % of the total assemblage) of the three different *Ammonia* species *A. veneta* (red), *A. aberdoveyensis* (green) and *A. confertitesta* (blue) as a function of core depth (cm). Please keep in mind that total densities are relatively low in the top 15 cm of the core (~15-30 ind. per sample), meaning that small variations in absolute abundances induce large variations in relative abundances.

Finally, *A. confertitesta* is virtually the only *Ammonia* species found in recent living communities (~ 5 % of the 1044 individuals, total foraminiferal assemblage, Richirt et al., 2020). In view of the strong anoxic events with co-occurring sulphidic conditions in 2011 and 2012 at this site (Seitaj et al. 2015; Richirt et al. 2020), this underlines the higher resistance of *A. confertitesta*, compared to *A. veneta* and *A. aberdoveyensis*, to such adverse conditions.

Today, *A. confertitesta* is found in all (closed or open) branches of the Rhine-Meuse-Scheldt estuary (Jorissen, unpublished data). We propose two hypotheses for the arrival of *A. confertitesta* in Lake Grevelingen (i.e. Den Osse Basin), around 1986:

1) *Ammonia confertitesta* is indeed an exotic species, and its arrival in Lake Grevelingen was synchronous with its arrival on the eastern Atlantic coast.
2) *Ammonia confertitesta* was already present in the North Sea, either as an autochthonous species, or after a first anthropogenic introduction from eastern Asia, and its arrival in Lake Grevelingen reflects a secondary, local migration event.

We note that *A. confertitesta* was not observed in the assemblages of the lower part of the core (90–85 cm) when Grevelingen was open to the North Sea. This strongly suggests that this species reached this part of the North Sea between the closure of the lake in 1971 and its arrival in the basin circa 1986. This would rather argue in favour of its exotic nature, as suggested by Pawlowski & Holzmann (2008), who hypothesised an introduction of *A. confertitesta* in the North Sea in the late 19th century by means of ship ballast water. Massive imports of Japanese oysters, from 1964 to about 1980 could also represent a possible vector for *A. confertitesta*, as this has been reported for a large number of different metazoa (e.g. Polychaeta, Amphipoda, Tunicata, Cirripedia, etc., Wolff & Reise, 2002).

Unfortunately, this study does not allow us to definitely settle whether *A. confertitesta* is an exotic and/or invasive species in Europe. Even today, *A. confertitesta* is not present in all estuaries of the mid latitude East Atlantic coast. For instance, it is absent in the French Auray estuary (Fouet et al., in prep.). Therefore, the absence of *A. confertitesta* in the Grevelingen estuary before its closure in 1971 could also be due to the fact that this species was not present in this particular estuary. Finally, the transformation of the Grevelingen estuary to a marine lake with occurrence of seasonal anoxia may have facilitated the colonisation of the Den Osse Basin by *A. confertitesta*, putatively more resistant to hypoxia/anoxia than its congeneric species.

6. CONCLUSION

Our investigation of the sediment record of one of the deepest basins in Lake Grevelingen highlights the important changes undergone by the foraminiferal community over the last 50 years. These changes reflect the major anthropogenic modifications of Lake Grevelingen, which was artificially turned from an estuary into a marine lake during this period. The Mo concentrations in the sediment record mark the yearly late summer–early autumn anoxic events with co-occurring presence of free sulphides in the sediment pore water. This record provides a very useful tool to detail the more conventional age model based on ^{210}Pb, allowing us to obtain a precision of about ± 3 years.

The seaward closure of the basin in 1971 induced an important change in foraminiferal communities, from high proportions of *H. germanica* and *A. aberdoveyensis*, which are typical estuarine mudflat species, to assemblages dominated by *E. margaritaceum*, typical for marine influence, *E. oceanense*, considered as an opportunistic species, and *E. magellanicum*, which seems to be tolerant to oxygen depletion. This taxonomic change could be explained by the disappearance of tides, much weaker hydrodynamics, increased eutrophication and increased salinity immediately after the closure of the basin. The opening of the seaward sluice (in the Brouwersdam) in autumn 1978, to counterbalance the eutrophication, increased the water renewal, but did not solve the problem of seasonally occurring hypoxia/anoxia. At first, the sluice was opened only in winter and *E. selseyense* strongly dominated the foraminiferal assemblages, suggesting that this species benefited of more marine influence and development of seasonal hypoxia. Around 1986, the emergence of *A. confertitesta* was observed coupled with a progressive diminution of the proportion of *A. aberdoveyensis*, *H. depressula* and *Quinqueloculina* spp. in the assemblages. After the sluice was opened almost year-round in 1999 and a further reduction of the water residence time by doubling the exchange with the North Sea, the foraminiferal assemblages became very poor, so that the assemblage composition should be interpreted very carefully. The extreme scarcity of foraminiferal tests in the top 15 cm of the core, which strongly contrasts with the high abundance of living foraminiferal communities, is ascribed to post-mortem dissolution, resulting from the strongly diminished carbonate saturation state due to cable bacteria activity in the anoxic part of the sediment.

Our results indicate that *A. confertitesta* arrived in Lake Grevelingen around 1986 and has progressively supplanted other *Ammonia* species (*A. veneta* and especially *A. aberdoveyensis*) in the record. We hypothesise that this progressive takeover is the result of a greater tolerance

to seasonal hypoxia/anoxia. However, our results do not definitely confirm the exotic and/or invasive nature of *A. confertitesta*. The absence of this taxon in the lower part of the core could also indicate its absence along the Dutch coast in 1971 or that the human-induced transformation of Lake Grevelingen created more favourable environmental conditions for its settlement.

ACKNOWLEDGMENTS

We acknowledge the support of P. van Rijswijk, M. Hagens, A. Tramper, and the crew of the R/V Luctor (P. Coomans and M. Kristalijn) during the sampling campaigns. We want to thank Filip Meysman for providing datasets for pH values for carbonate saturation state calculation. This study benefited from funding of Rijkswaterstaat and of the CNRS-INSU programme EC2CO-DRIL (project AMTEP).

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