



HAL
open science

A historical record of benthic foraminifera in seasonally anoxic Lake Grevelingen, the Netherlands

Julien Richirt, Anaïs Guihéneuf, Aurélia Mouret, Magali Schweizer, Caroline Slomp, Frans Jorissen

► **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-03925917>

Submitted on 8 Dec 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3
4 JULIEN RICHIRT¹, ANAÏS GUIHÉNEUF¹, AURÉLIA MOURET¹, MAGALI SCHWEIZER¹, CAROLINE P.
5 SLOMP² AND FRANS J. JORISSEN¹
6
7

8 ¹UMR 6112 LPG, University of Angers, Nantes University, Le Mans University, CNRS, 2
9 Boulevard Lavoisier, 49045 Angers, France

10 ²Department of Earth Sciences (Geochemistry), Faculty of Geosciences, Utrecht University,
11 Princetonlaan 8a, 3584 CB Utrecht, the Netherlands
12
13

14 *Corresponding author: richirt.julien@gmail.com
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30

32 Lake Grevelingen is a former branch of the Rhine-Meuse-Scheldt estuary, which was
33 artificially transformed into a salt-water lake by a dam in 1971. This transformation
34 induced profound changes in the biological community of the basin, which have been
35 described as an ecodisaster, with seasonal hypoxia/anoxia occurring in the deepest parts
36 of the lake. Here, we investigate a sediment core sampled in 2012 in the Den Osse Basin
37 (34 m depth) of Lake Grevelingen, recording the last ~ 50 years and including the
38 transition from an estuary to a salt-water lake. Sediment molybdenum (Mo)
39 concentrations were used to refine an existing age model based on ^{210}Pb , giving us an
40 estimated precision of ± 3 years. The benthic foraminiferal succession reflects the
41 anthropogenic modifications in Lake Grevelingen and allows four successive stages to be
42 distinguished: 1) before 1971, when the system was estuarine; 2) from 1971 to 1978, when
43 the system rapidly changed into an enclosed brackish water lake; 3) from 1978 to 1999,
44 when a seaward sluice was opened during winter and 4) the period from 1999 to 2012,
45 with a year-round opening of the sluice and doubling of water exchanges with the North
46 Sea. The foraminiferal record, showing communities mainly dominated by *Elphidium*
47 *selseyense*, also highlights the appearance of the putatively exotic *Ammonia confertitesta*
48 in the mid-1980s, which thereafter progressively replaced the congeneric autochthonous
49 *Ammonia aberdoveyensis*. Finally, we hypothesise that the activity of cable bacteria, S-
50 oxidising prokaryotes present in the surface sediments of Den Osse Basin in winter and
51 spring, causes dissolution of foraminiferal tests by decreasing the pore water carbonate
52 saturation state in the sediments directly below the oxic zone. This explains the contrast
53 between the abundant living populations and the very low numbers of foraminiferal shells
54 preserved in the top ~ 15 cm of the sediment.

55

56

57

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

59

60

61

62

63

64

65

66

67

68

69

70

71

72

73

74

75

1. INTRODUCTION

77 Foraminifera are among the most widespread groups of marine unicellular eukaryotes and
78 constitute one of the most diverse groups of shelled organisms. They have a very rich fossil
79 record and are widely used for palaeoenvironmental reconstructions and palaeoecological
80 interpretations (Murray, 2006; Katz et al., 2010). Foraminifera are known to be relatively
81 tolerant to low oxygen concentrations, anoxia and/or presence of sulphides in their habitat, on
82 various timescales. This has been documented for many species from different types of
83 environments in laboratory culture (e.g. Moodley and Hess, 1992; Bernhard, 1993; Alve and
84 Bernhard, 1995; Moodley et al., 1998; Duijnsteet et al., 2003; Geslin et al., 2004; Pucci et al.,
85 2009) as well as in field studies (e.g. Piña-Ochoa et al., 2010; Langlet et al., 2013, 2014).
86 Unfortunately, studies on the foraminiferal response in systems affected by seasonal hypoxia–
87 anoxia with sulphidic conditions are still very sparse. To our knowledge, all earlier studies show
88 that the foraminiferal response to hypoxia–anoxia is species-specific (e.g. Bernhard and Alve,
89 1996; Ernst et al., 2005; Bouchet et al., 2007; Geslin et al., 2014; Langlet et al., 2014). However,
90 this species-specific response generally follows the same scheme (usually decrease in density,
91 reduction of growth and/or reproduction), with different response intensities. Recently, a study
92 investigated the temporal response of living foraminiferal communities to recent seasonal
93 anoxia in the Den Osse Basin of Lake Grevelingen (the Netherlands, Richirt et al. 2020). The
94 authors highlighted that the deepest part of this basin shows a severe decline in foraminiferal
95 populations in the months following late summer–early autumn seasonal anoxia. They
96 explained this by the presence of sulphides in the foraminiferal habitat, that would inhibit
97 foraminiferal reproduction and growth. In the shallower parts of the basin, where the duration
98 of anoxia is shorter, there was not such a major decline in the foraminiferal community.

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

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

109 (morphospecies not yet sequenced) and *Ammonia confertitesta* (*Ammonia* sp. T6 in Richirt et
110 al., 2020; phylotype T6 in Hayward et al., 2021). The latter species, *A. confertitesta*, is often
111 considered as an exotic and/or invasive species, originating from East Asia (e.g. Pawlowski &
112 Holzmann, 2008; Schweizer et al, 2011; Bird et al., 2020). *Ammonia confertitesta*, which is
113 almost the only representative of the genus *Ammonia* in the recent living assemblages (Richirt
114 et al., 2020), is characterised by very large pores (Richirt et al., 2019a) compared to *Ammonia*
115 *aberdoveyensis* and to a lesser extend *Ammonia veneta* (phylotypes T2 and T1, respectively,
116 Hayward et al., 2021). Interestingly, a preliminary study of a long core sampled in the Den Osse
117 Basin showed a clear shift from specimens with small pores to specimens with bigger pores in
118 recent times (Petersen et al., 2016). This indicates that in a recent past, *A. confertitesta* has
119 progressively replaced *A. aberdoveyensis* (and/or *A. veneta*) in Lake Grevelingen. Richirt et al.
120 (2019b), suggesting that an increase in overall porosity could be an adaptation to low oxygen
121 concentrations. The putative replacement of *A. aberdoveyensis* (and/or *A. veneta*) by *A.*
122 *confertitesta* could therefore be due to the larger tolerance of the latter species to hypoxia. The
123 study of the sedimentary foraminiferal record should enable us to shed more light on this
124 important species take-over.

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

- 128 1) How did the foraminiferal community change in response to the closure of Lake
129 Grevelingen in the 1970s and the subsequent management changes of the basin?
- 130 2) Has there been a substitution of the autochthonous *Ammonia* species (*A. veneta* and *A.*
131 *aberdoveyensis*) by the putative allochthonous species *A. confertitesta*, and, if so, is it the result
132 of an overall spreading of *A. confertitesta* across Europe, or rather of a better adaptation of this
133 phylotype to seasonal hypoxia/anoxia?

134 **2. STUDY AREA**

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

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

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

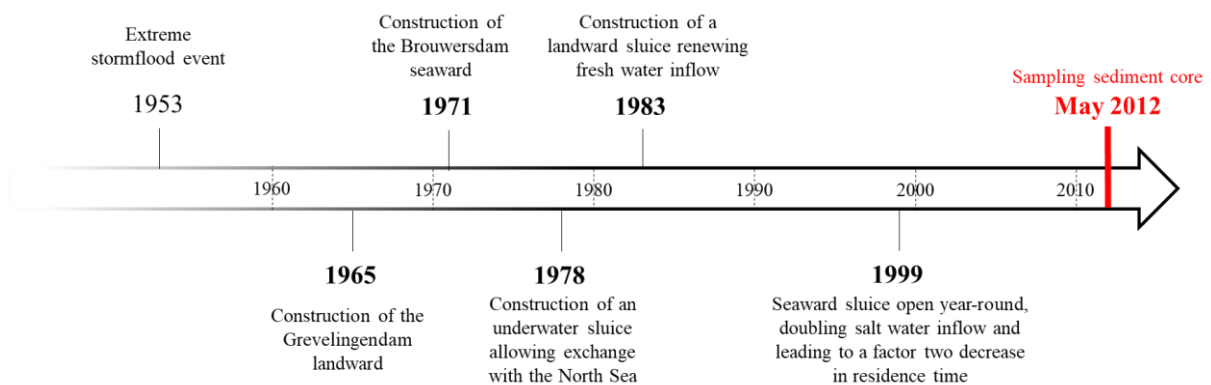
160 In 1999, the water exchanges between the Lake and the North Sea were doubled (from
161 $1245\text{--}1255 \cdot 10^6\text{ m}^3$ to $2688\text{--}2864 \cdot 10^6\text{ m}^3$ per year, Wetsteijn, 2011) by opening the
162 Brouwersdam sluice the whole year, except for a few weeks in autumn and during storm events.
163 This allowed a further decrease of the average water residence time in the Lake from 164 to 72
164 days and limited water stratification due to high temperatures in summer (Wetsteijn, 2011).
165 However, this situation was still very different compared to the estuarine situation before 1965,
166 when the water residence time was estimated to be a few days (Nienhuis, 1978; Bannink et al.,
167 1984) and average flood and ebb discharges at the location of the present Brouwersdam were
168 about $126000 \cdot 10^6$ and $135000 \cdot 10^6\text{ m}^3$ per year, respectively (calculated for 1959, Louters et al.,
169 1998), ~ 50 times higher than the current water exchanges.

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

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

178 To summarise, Lake Grevelingen, a former estuarine system, was completely closed in
179 1971. The ensuing strong increase of water residence time, bottom water stagnation and lower
180 salinity caused a major biotope shift in Lake Grevelingen and led to strong modifications of its
181 biological community (Nienhuis, 1978).

182 Today, two antagonistic groups of sulphur-oxidizing bacteria showing contrasting seasonal
183 population dynamics are present in sediments of the Den Osse Basin: cable bacteria in January-
184 May and *Beggiatoaceae* in September–December (Seitaj et al., 2015; Sulu-Gambari et al.,
185 2016a). Cable bacteria activity is known to strongly impact biogeochemical cycles (e.g. of
186 sulphur, iron or calcium) in the sediment, by promoting, for example, precipitation of iron oxide
187 in the oxic layer and dissolution of iron sulphide and calcium carbonate in the anoxic layer
188 (Risgaard-Petersen et al., 2012; Meysman et al., 2015). In the deepest part of the Den Osse
189 Basin, where the maximum oxygen penetration depth in the sediment is about 2 mm (Seitaj et
190 al., 2015), this was shown to occur seasonally, as a result of cable bacteria activity (Sulu-
191 Gambari et al., 2016a, b). This phenomenon could play a major role in foraminiferal calcium
192 carbonate test dissolution during taphonomic processes.

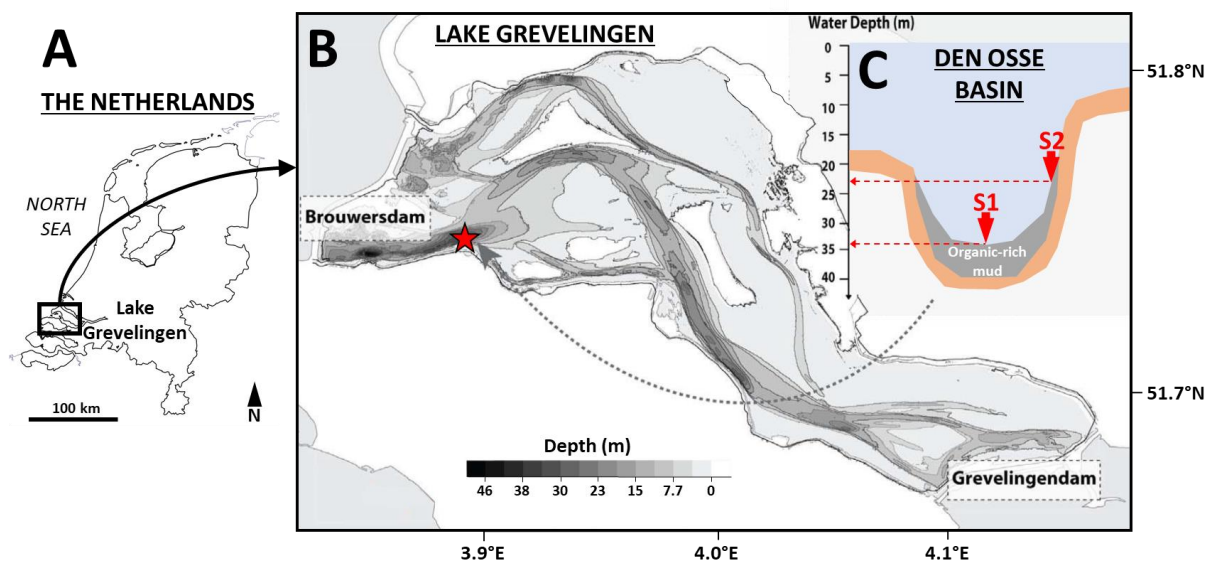


193

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

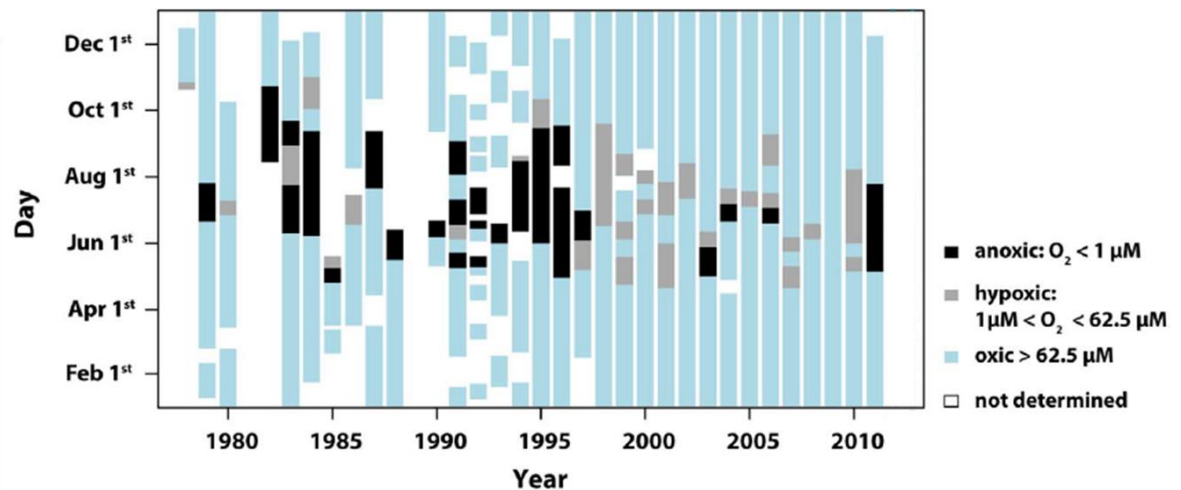
197 **3. MATERIALS AND METHODS**

198 **3.1. SAMPLING AND LABORATORY TREATMENT**



199
200 **Figure 2.** A. Map of The Netherlands (on the left) showing the location of Lake Grevelingen.
201 B. Map of Lake Grevelingen (main panel) showing the location of the sediment sampling in the
202 Den Osse Basin (red star). C. The transversal section of the Den Osse basin (top right) shows
203 the depth at which the studied sediment core was sampled at Station 1 (S1, 34 m depth). Station
204 2 (S2, 23 m depth) was investigated for living assemblages by Richirt et al. (2020), as noted in
205 the discussion. This figure was modified from Sulu-Gambari et al. (2016a).

206 The study site (station 1) is in the Den Osse Basin (51° 44.834'N, 3° 53.401'E), the main
207 former channel of the Grevelingen estuary (The Netherlands), at 34 m depth (Figure 2). Our
208 site is located at a distance of ~ 100 m from a location where water column oxygen was
209 intensively monitored since the late 1970s by the Dutch Water Agency (DWA; e.g. Wetsteijn,
210 2011). Bottom water oxygen concentrations from 1978 to 2011 from the DWA database were
211 summarised previously (Figure 3; Sulu-Gambari et al., 2017) and reveal recurring seasonal
212 hypoxia and anoxia in bottom water. These bottom water data were collected up to about 3 m
213 above the basin floor (and not at the sediment-water interface), which was at 37 m water depth
214 at this location. Consequently, bottom water anoxia measured by the water column monitoring
215 (Figure 3) is a reliable indicator of an anoxic sediment-water interface. However, oxic
216 conditions in the water column (as frequently recorded from late 1990s to 2010, Figure 3), does
217 not necessarily indicate that the basin floor was also oxic.



218

219 **Figure 3.** Periods of oxic (blue), hypoxic (grey) and anoxic (black) bottom water conditions
 220 from 1978 to 2011 at the DWA site, which is located at a distance of about 100 m from station
 221 1 in this study (figure after Sulu-Gambari et al., 2017).

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

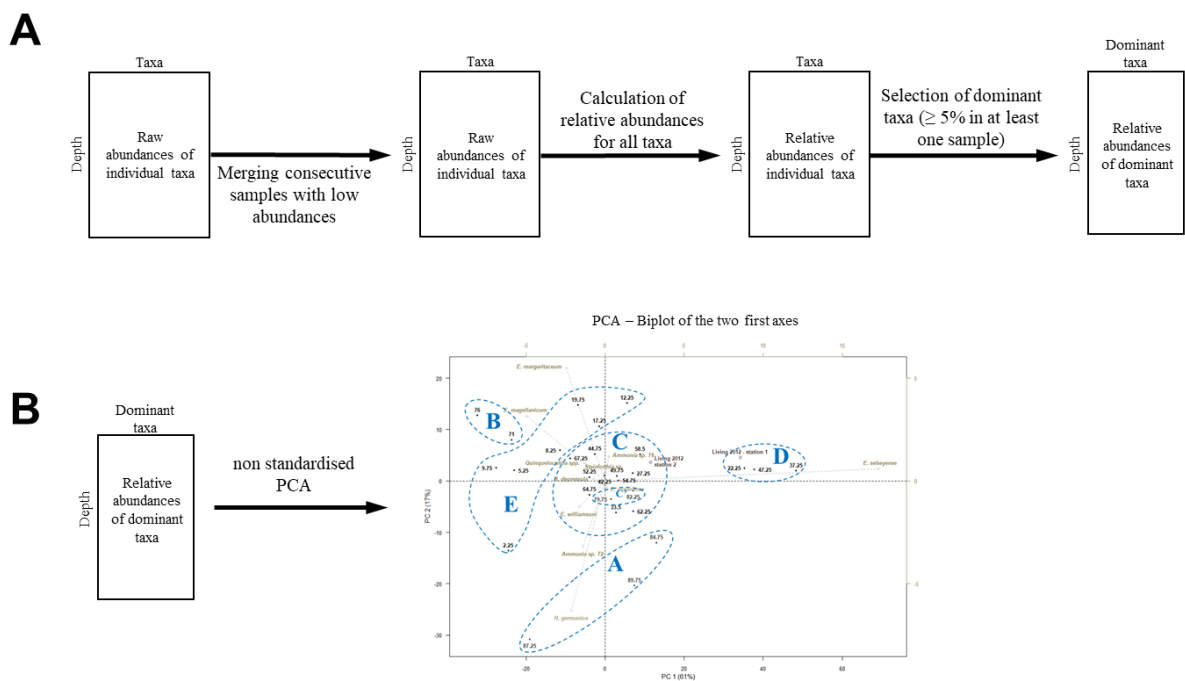
236 A major change in sediment composition was observed, from sandy deposits below 82.5
 237 cm depth, very probably representative of the strong hydrodynamics of the former estuarine
 238 system to muddy/silty sediments above 82.5 cm depth, indicative of the much lower
 239 hydrodynamics of the salt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

240 **3.2. FORAMINIFERAL ANALYSES**

241 In cases where samples had very low foraminiferal abundances, two to three adjacent
 242 samples were merged (Table 1). This concerned samples in depth intervals 4.5–6, 6.5–8, 9–
 243 10.5, 11.5–13, 32–35, 57–60, 69.5–72.5 and 74.5–77.5 cm. We compromised between (1)
 244 maximising the number of individuals (to obtain a target value of at least 50 individuals) and
 245 (2) maximising sampling resolution. The total thickness of merged samples never exceeded 3
 246 cm (Table 1).

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

251 Data on living assemblages (0–1 cm depth interval) for our station 1 and additional station
 252 2 (located at 23 m depth, impacted by a shorter seasonal oxygen depletion event; Figure 2) were
 253 taken from Richirt et al. (2020) and were computed as the sum of all seasonal samples of 2012.
 254 These samples were considered as supplementary individuals in the analysis, meaning that they
 255 did not contribute to the construction of the principal component axes. The data pre-treatment
 256 and multivariate analysis procedure are summarised graphically in Figure 4.

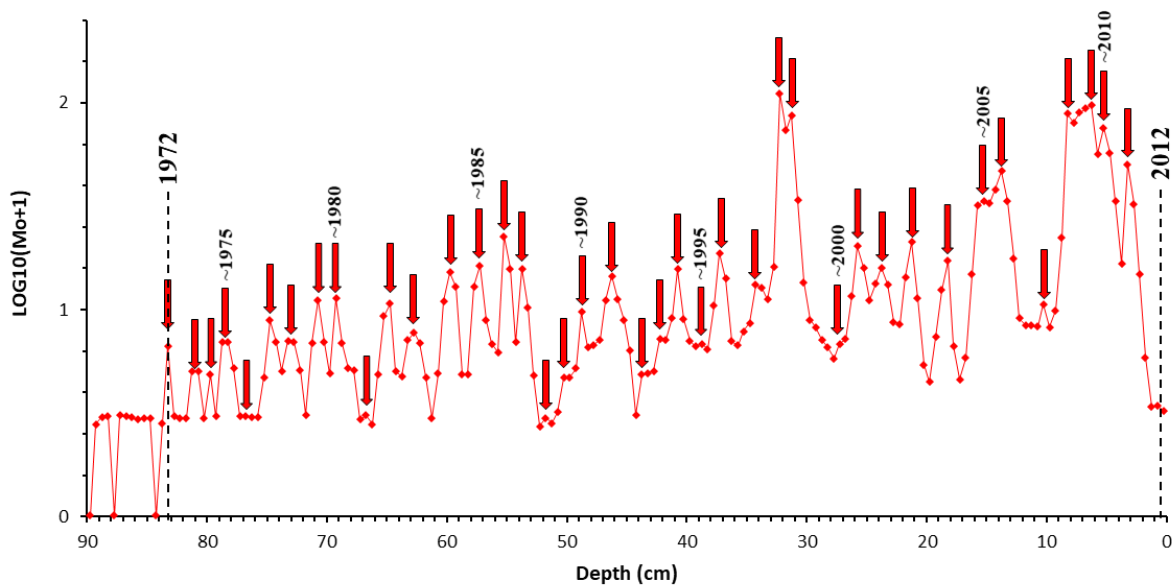


257
 258 **Figure 4.** A: Data pre-treatment procedure performed from the initial data matrix, with data
 259 matrix lines representing samples (depth) and data matrix columns representing taxa. B:
 260 Principal Component Analysis (PCA) procedure.

261 **3.3. AGE MODEL**

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

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



277 **Figure 5.** Molybdenum concentrations (ppm, detection limit = 0.06 ppm) as a function of core
278 depth (cm), modified from Sulu-Gambari et al. (2017). All values were LOG10(x+1)
279 transformed to better identify peaks. Each peak is highlighted with a red arrow and is assumed
280 to represent a yearly summer hypoxia/anoxia event. Some additional yearly hypoxia/anoxia
281 events have been added tentatively in case of broad peaks with shoulders (e.g., between 31 and
282 33 cm depth), or broad intervals without clear peaks (e.g., between 50 and 52 cm depth). Dotted
283 lines represent the two constraints of the age model: the first observed Mo peak corresponding
284

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

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

297 A further potential issue is that Mo concentrations were not measured in the same core
298 as the one used for the foraminiferal analysis. If we assume that the first Mo peak observed at
299 ~ 83 cm is characteristic of the first anoxic/sulphidic event that occurred in 1972, the year
300 following the transition from an estuary to a lake, the closure of the estuary in 1971 should have
301 taken place directly before, corresponding to a core depth of ~ 84 cm. For the same core, based
302 on a sedimentation rate of 2 cm y⁻¹ proposed in Malkin et al. (2014), the transition from an
303 estuary to a lake was estimated to have occurred at 82 cm depth by Sulu-Gambari et al. (2017;
304 2018). The same transition was found at 82.5 cm in the core used for foraminiferal analysis.
305 Consequently, when applying our Mo-based age model on the foraminiferal record, there is an
306 additional uncertainty of at most 1–2 cm, which could be the result of small differences in
307 compaction between the cores. In conclusion, we consider that our age model is reliable with a
308 precision of ± 3 years, which is sufficient for the aims of our study.

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

312 **3.4. CALCIUM CARBONATE SATURATION STATE**

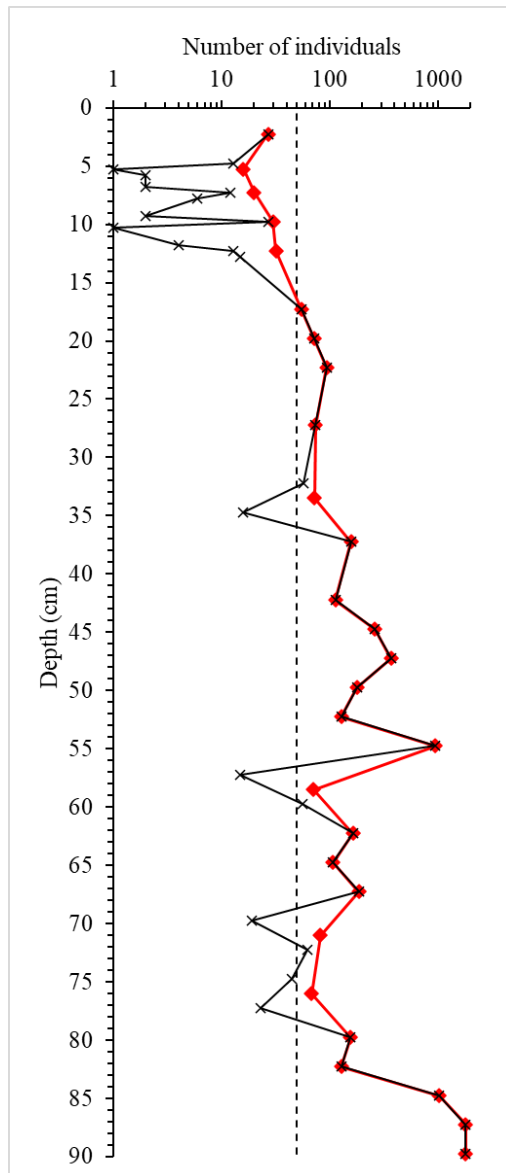
313 We used the CO2SYS software (Lewis and Wallace, 1998) to determine the variation of
314 the calcium carbonate saturation state in the sediment at our station throughout the year.
315 Monthly temperature and salinity data of 2012 are from Hagens et al. (2015) and were measured
316 in the water column at 32 m depth. Monthly values for alkalinity and PO₄³⁻ concentrations in

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

327 **4. RESULTS**

328 **4.1. FORAMINIFERAL COMMUNITIES**

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



334

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

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

341 Total foraminiferal density was relatively high between 90 and 84.5 cm depth, ranging
 342 from 1033 to 1810 individuals per sample (of 14.1 cm³; Figure 6 and Table 1). At 82.5 cm
 343 depth, the density abruptly decreased by one order of magnitude. Total densities between 82.5
 344 and 17 cm depth oscillated between 15 (57–57.5 cm depth) and 950 individuals (54.5–55 cm
 345 depth) per sample, with an average of about 175 ind. per sample.

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

348 **Table 1.** Census data for foraminifera >125 µm in the final reconstituted samples. Relative
 349 abundances of the dominant species of foraminifera (≥ 5 % of the total assemblage in at least
 350 one sample), total percentage of dominant taxa and total number of individuals in the
 351 recomposed samples (consisting of a single sample of 14.1 cm³, or 2 or 3 merged samples). We
 352 also included *A. veneta* (not considered as a dominant species), because we discuss this species
 353 later in the manuscript. For raw data of all individual samples, see Suppl. Table 1.

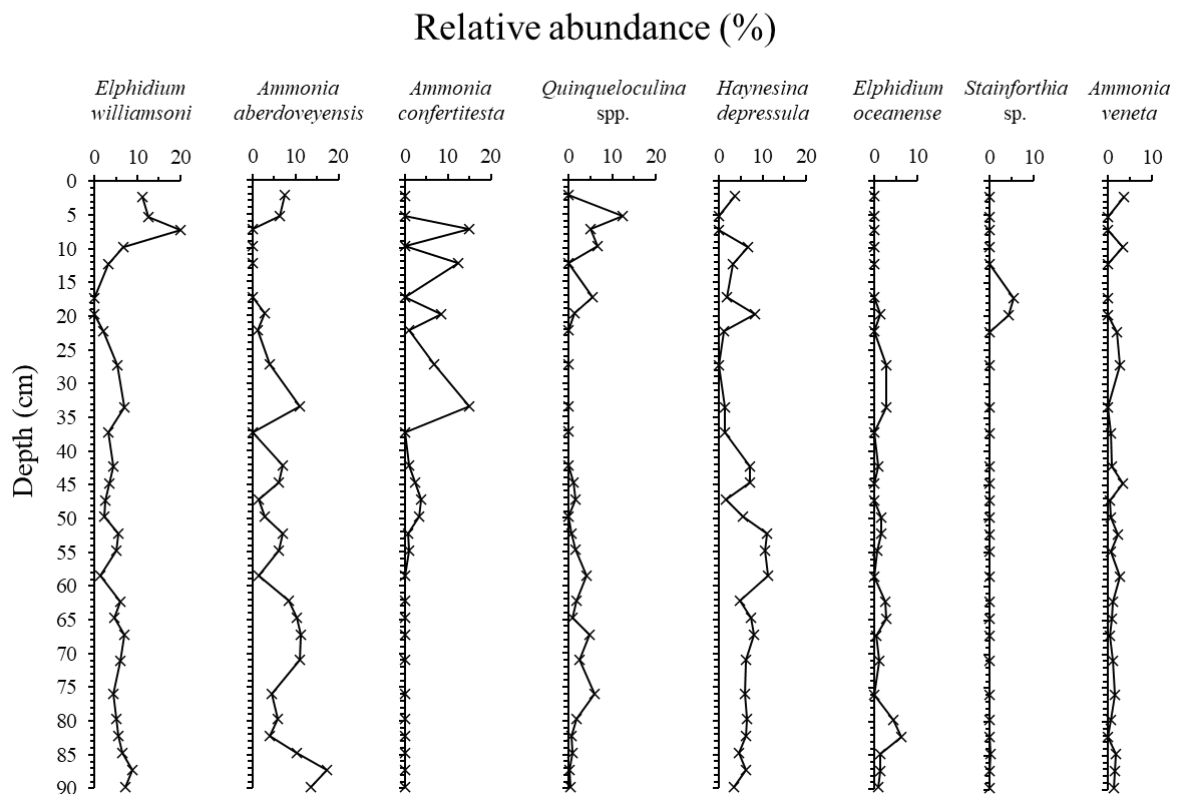
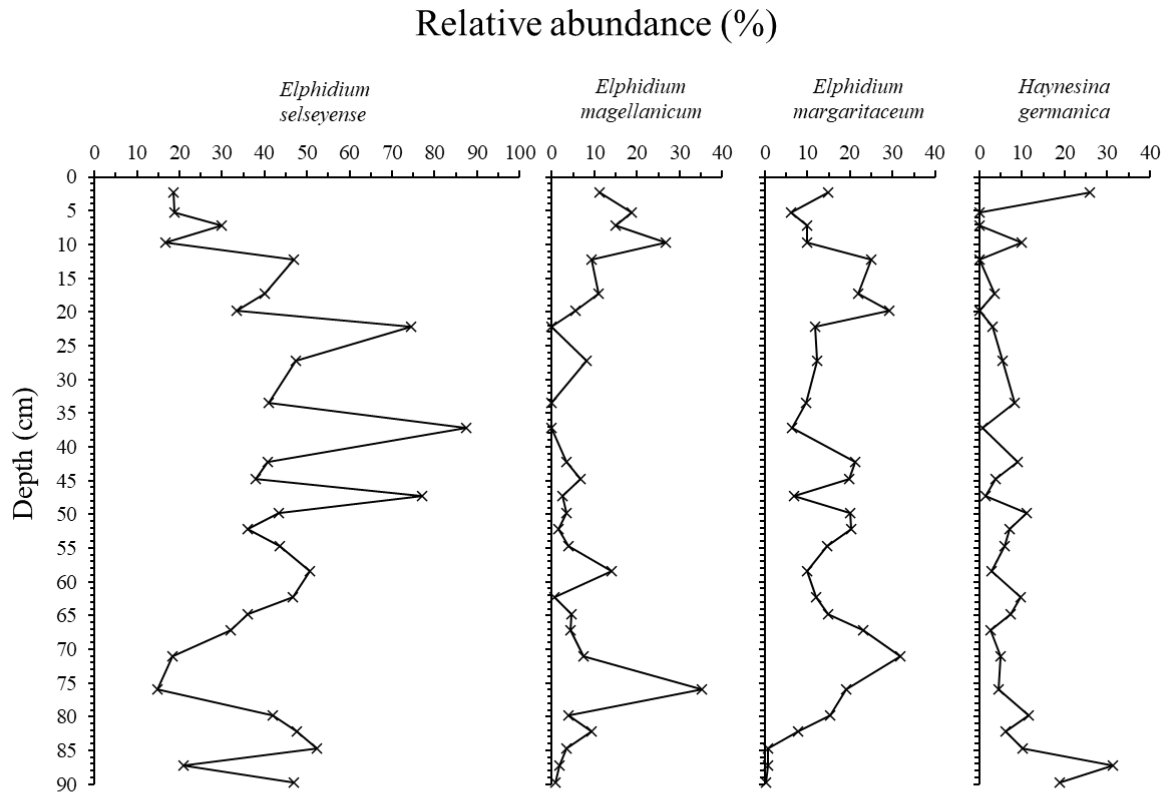
Interval depth (cm)	<i>Ammonia aberdoveyensis</i>	<i>Ammonia confertifesta</i>	<i>Ammonia veneta</i>	<i>Elphidium magellanicum</i>	<i>Elphidium margaritaceum</i>	<i>Elphidium oceanense</i>	<i>Elphidium selseyense</i>	<i>Elphidium williamsoni</i>	<i>Haynesina germanica</i>	<i>Haynesina depressula</i>	<i>Quinqueloculina spp.</i>	<i>Stainforthia sp.</i>	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

354 *Elphidium selseyense* was the dominant species in most of the samples, accounting for
355 15 to 87 % of the total assemblage (Figure 7, Table 1). The levels 47–47.5, 37–37.5 and 22–
356 22.5 cm presented peak values for this taxon (>70 %), whereas the assemblages of the top 10.5
357 cm were rather poor in *E. selseyense* (between 17 and 30 %).

358 The relative abundance of *E. magellanicum* oscillated between 0 and 35 %. A major
359 peak was present at 74.5–77.5 cm (35 %). This species showed relatively high percentages (9–
360 27 %) in the low-density samples of the topmost 17.5 cm (Figure 7, Table 1).

361 *Elphidium margaritaceum* was nearly absent between 89.5–90 and 84.5–85 cm. Above
362 these levels, relative abundances varied between 6 and 32 % with maxima around 70 cm depth,
363 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).

364 The relative proportions of *H. germanica* fluctuated generally between 1 and 10 %. This
365 species was abundant (19 and 31 %) in the first two samples (89.5–90 cm and 87–87.5 cm
366 depth), whereas it was present in low numbers, or even absent, in the 20–4.5 cm interval.
367 *Haynesina germanica* showed again an elevated percentage (26 %) in the most recent sample
368 (2–2.5 cm depth, Figure 7, Table 1).



369

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

373 All other taxa only rarely contributed more than 10 % in the total assemblage (Figure 7,
 374 Table 1). *Elphidium williamsoni* showed maximum values (11–20 %) in the top 10 cm of the
 375 core, whereas *Elphidium oceanense* always accounted for only low percentages (0–6 %),
 376 slightly decreasing upward. This taxon was absent in the top 17.5 cm. *Ammonia aberdoveyensis*
 377 showed a general decrease from about 10–17 % at the bottom of the core to a near absence at
 378 about 20 cm depth. However, it showed higher percentages again (6–7 %) in the topmost two
 379 samples (4.5–6 and 2–2.5 cm depth). *Ammonia confertitesta* was totally absent until 55 cm core
 380 depth and fluctuated between absence and 15 % thereafter. *Ammonia veneta* was always present
 381 in low percentages, never exceeding 4 %, without a clear pattern. *Quinqueloculina* spp. showed
 382 two main presence intervals, between 80 and 44.5 cm (up to 6 %) and from 20 to 4.5 cm depth
 383 (up to 13 %). *Haynesina depressula* (up to 11 %) tended to be more abundant in the lower 40
 384 cm of the core. Finally, *Stainforthia* sp. was absent in most samples, but was present at 19.5–
 385 20 and 17–17.5 cm depth (with 4 and 6 %, respectively).

386 4.2. MULTIVARIATE ANALYSIS

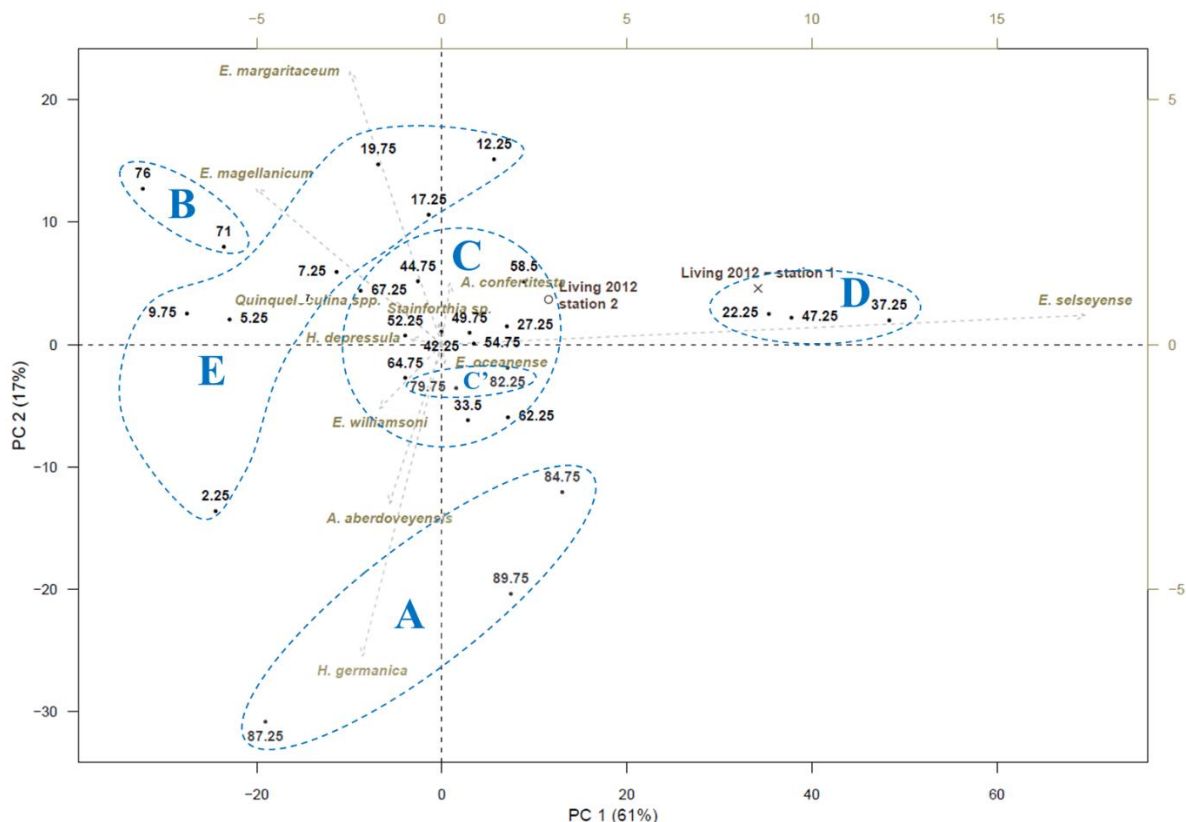
387 The first two axes of the non-standardised PCA based on relative abundance data account
 388 for 61 % and 17 % of the total variability of the dataset, respectively (Suppl. Table 2).

389 Table 2 presents the contributions of the dominant taxa to the first two PCs. *Elphidium*
 390 *selseyense* has a strong positive contribution to PC1, whereas *E. magellanicum* has a slight
 391 negative contribution to this axis. *Elphidium margaritaceum* and *E. magellanicum* have a
 392 positive contribution to PC2, whereas *H. germanica* and *A. aberdoveyensis* load negatively on
 393 this axis. Figure 8 presents a scatter plot for PC1 and PC2, in which we added the living
 394 assemblages of station 1 (same station as the long core) and of the nearby, shallower station 2
 395 (water depth 23 m) which is less severely affected by seasonal hypoxia/anoxia (Richirt et al.,
 396 2020), as supplementary individuals.

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

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

<i>Elphidium williamsoni</i>	-0.8	-1.8
<i>Elphidium oceanense</i>	0.0	-0.2
<i>Haynesina germanica</i>	-1.3	-41.8
<i>Haynesina depressula</i>	-0.2	0.0
<i>Quinqueloculina</i> spp.	-0.5	0.8
<i>Stainforthia</i> sp.	0.0	0.2



399

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

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

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

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

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

415 **Group C** is composed of samples with low absolute scores on both PCs (i.e. centred on
416 the scatter plot, Figure 8), indicative of average assemblages. These “typical” assemblages are
417 dominated by *E. selseyense*, have a high percentage of *E. margaritaceum*, a lower percentage
418 of *A. aberdoveyensis* and *H. germanica* (compared to group A), and contain *A. confertitesta*
419 from 55 cm onward. This concerns most samples from 67.5 to 27 cm depth as well as the 82–
420 82.5 and 79.5–80 cm samples (subgroup C'). The living community of station 2 (Den Osse
421 Basin, 23 m water depth) plots together with this group.

422 **Group D** is composed of three samples with very high scores on PC1, reflecting
423 uncommonly high percentages of *E. selseyense*. This concerns the 22–22.5 cm, 37–37.5 cm and
424 47–47.5 cm samples. The living assemblage of station 1 is very similar, as shown by its
425 proximity on the scatter plot (Figure 8).

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

434 **5. DISCUSSION**

435 **5.1. TEMPORAL EVOLUTION OF THE FORAMINIFERAL COMMUNITY**

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

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

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

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

459 **Group A** includes samples from 90 to 84.5 cm depth (estimated period ~ 1968 to 1971).
460 They contain a sandy sediment, and are situated immediately below the shift to a much finer
461 sediment at 82.5 cm. These samples represent the estuarine phase of the basin, before its
462 seaward closure in 1971. The foraminiferal assemblages are characterised by high density
463 (between 1000 and 2000 ind. per 14.1 cm³ sample), and by high percentages of typical
464 estuarine/mudflat species such as *H. germanica* and *A. aberdoveyensis* (e.g. Alve & Murray,
465 1994; 2001; Thibault de Chanvalon et al., 2015; Saad & Wade, 2016; 2017). In view of the
466 location of station 1, in the middle of the Den Osse Basin at 34 m depth (the main former
467 channel of the Grevelingen estuary), the sandy sediment reflects the strong hydrodynamics of
468 this site, when it was still an estuary. Currents were too strong to allow deposits of clays and
469 silts, so that the former channel floor was covered by a sandy lag deposit, with a very high
470 foraminiferal density. The strong currents undoubtedly facilitated the transport of allochthonous
471 foraminifera, such as the taxa cited above, which are typical of estuarine mudflats. However,
472 *H. depressula*, a species typical of marine influence (Murray 1983; Darling et al., 2016) is
473 present with substantial proportions as well, showing that foraminifera were not only
474 transported from the inner to the outer estuary, but also from the North Sea into the outer
475 estuary.

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

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

485 The assemblages of these two samples show a strongly increased percentage of the more
486 marine species *E. margaritaceum* and the euryhaline species *E. oceanense* (Darling et al.,
487 2016), contrasting with a strong decrease of the percentages of the more estuarine species *H.*
488 *germanica* and *A. aberdoveyensis*. This suggests that in the first years after the closure of the
489 former estuary, the basin floor was still inhabited by species typical of marine influence (high
490 salinity), whereas inner estuarine species were no longer living, or transported to the study area.
491 Salinity, measured on surface waters, was consistently high (~ 30) in the years immediately
492 following the closure of the basin (1972–1974, Bannink et al., 1984), allowing marine taxa to
493 inhabit the former main channel.

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

499 In this period, surface water salinity showed a progressive decrease, from ~ 30 in 1974
500 to a minimum of ~ 23 in 1978, due to the input of rainwater (Bannink et al., 1984). In case these
501 salinity values partly reflect conditions on the basin floor, this could suggest that *E.*
502 *magellanicum* and *E. margaritaceum* are more tolerant to lower salinities than *E. selseyense*.
503 Unfortunately, the ecology of these three species is still imperfectly known. In the literature,
504 the European representatives of *E. magellanicum* are generally considered as euryhaline (20–
505 30 in Fjords, Gustafsson & Nordberg, 1999; 2000; 10–20 in the western Baltic Sea, Schönfeld
506 et al., 2018; shallow marine at Dunkirk beach, Lévy et al., 1969). *Elphidium selseyense* appears
507 to be opportunistic and tolerant to a large range of salinity (Darling et al., 2016). Conversely,
508 *E. margaritaceum* has been reported as a more marine species which tolerates only slight
509 salinity variations (Alve & Murray, 1999; Darling et al., 2016).

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

512 strongly modified the ecosystem structure and functioning of Lake Grevelingen (Nienhuis,
513 1978; Saeijs & Stortelder, 1982). The strengthened water column stratification and the much
514 longer residence times led to a progressive increase of nutrient concentrations between 1971
515 and 1978 (Bannink et al., 1984). The opening of the Brouwersdam in late autumn 1978,
516 resulting in limited salt water inflow, induced a further strengthening of the salinity
517 stratification of the water column, which led to hypoxia/anoxia and mass mortality in the
518 deepest parts of the basin in summer 1979 (Bannink et al., 1984).

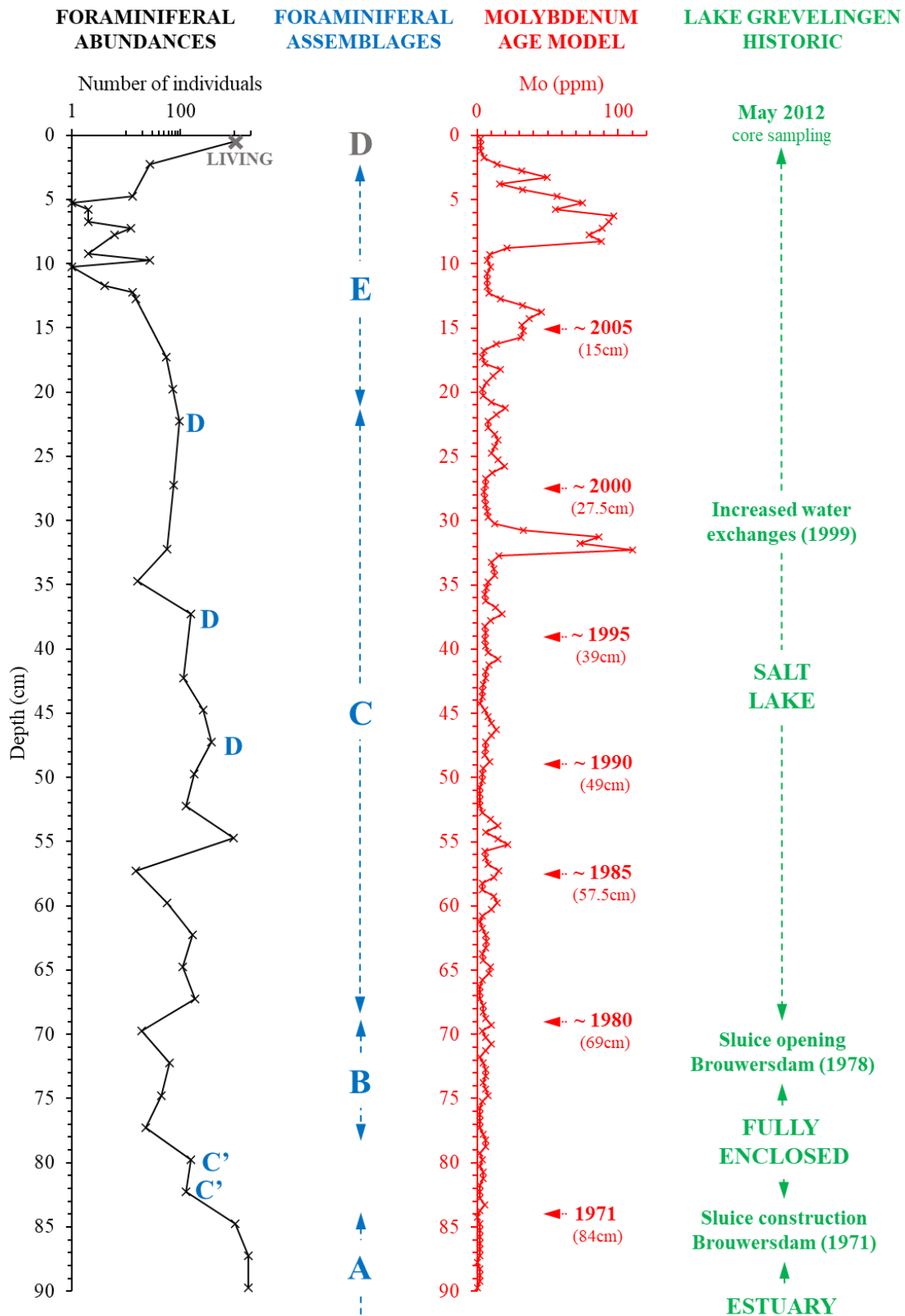
519 The three *Elphidium* species that dominated the assemblages during this period were
520 apparently more resistant to these rapidly changing conditions than other taxa. Their tolerance
521 regarding low oxygen conditions is shown by their presence in the recent assemblages of this
522 site (Richirt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

524 The remaining samples of **Group C** represent the 67.5 to 27 cm interval (estimated
525 period ~ 1980 to 2000). To remedy the increase of eutrophication phenomena observed in the
526 1970s, the basin was partly reopened by an underground sluice in 1978. This sluice was initially
527 opened only in winter. Consequently, surface water salinity almost immediately rose to ~ 30
528 and nutrient concentrations showed a major decrease (Bannink et al., 1984). However, this did
529 not solve the problem of bottom water oxygen deficiency, and in the next 20 years, an
530 intermittent succession of major later summer/early autumn hypoxic/anoxic periods was
531 observed, especially in the deepest parts of Lake Grevelingen (Figure 3). This is confirmed by
532 the results of Lindeboom & Sandee (1984), who found anoxic conditions coupled with the
533 presence of sulphide at a few mm depth in the sediment in May and June 1982, at much
534 shallower stations, with depths < 10 m. In 1999, the sluice was opened year-round, to further
535 increase water exchanges.

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

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

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



562

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

568 **Group D** contains only three samples (47–47.5, 37–37.5 and 22–22.5 cm core depth,
569 deposited in ~ 1991, ~ 1996 and ~ 2003, respectively). The foraminiferal densities in these
570 samples are comparable to densities from group C and range from 94 to 370 ind. per sample.
571 The composition of these samples stands out by exceptionally high proportions of *E. selseyense*
572 (> ~ 75 %). This is very similar to the composition of the living assemblage in 2012 at the same
573 station (Richirt et al., 2020), as shown by their proximity on the PCA scatter plot. This suggests
574 that the three samples of group D reflect similar conditions, which could be characterised by
575 rather severe anoxic conditions with the presence of sulphides in the topmost sediment, as
576 recorded in 2012 (Seitaj et al., 2015). It appears that *E. selseyense* could be particularly tolerant
577 to such low oxygen conditions; this is confirmed by its strong dominance in the living
578 community sampled at this site in 2012 (Richirt et al., 2020).

579 Finally, **Group E** comprises all samples in the top 20 cm of the core (estimated period
580 ~ 2003 to 2011). This group of samples has been deposited in the years after the decision had
581 been taken to open the seaward sluice year-round (in 1999), leading to a further decrease in
582 water residence times. The total foraminiferal densities are extremely low in this interval (rarely
583 exceeding 15 ind. per sample). Because of the low foraminiferal densities, several samples had
584 to be merged. In spite of the merging procedure, relative proportions are still based on low
585 numbers (from 16 to 72 specimens) and should be considered with caution. Even when taking
586 into account the high sedimentation accumulation rate at this location, the unexpected very low
587 densities strongly contrast with the elevated densities of living communities, which attained a
588 maximum of 634 individuals per 14.1 cm³ sample in May 2012 when the long core was sampled
589 (recalculated from Richirt et al., 2020; Figure 9).

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

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

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

604 **5.2. CABLE BACTERIA ACTIVITY RESPONSIBLE FOR FORAMINIFERAL TEST**
 605 **DISSOLUTION**

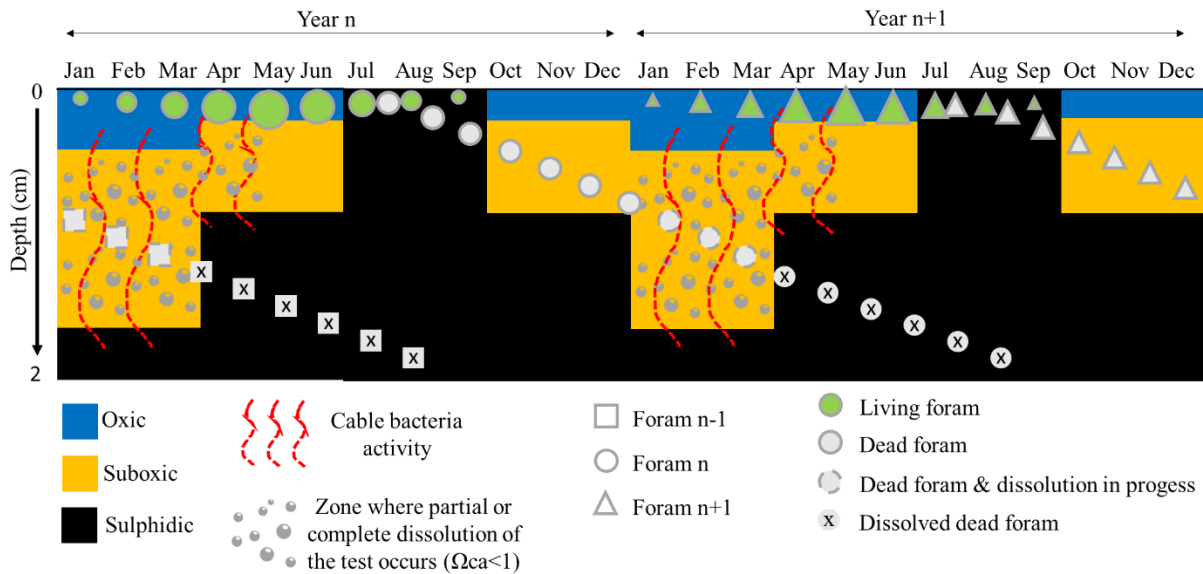
606 Cable bacteria activity promotes carbonate precipitation in the oxic zone (maximum oxygen
 607 penetration depth about 2 mm at this site, even in winter, see Seitaj et al., 2015), and carbonate
 608 dissolution immediately below, where oxygen is absent (Risgaard-Petersen et al., 2012;
 609 Meysman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

616 **Table 3.** Values of calcium carbonate saturation state at station 1 at different depths in the
 617 sediment for each month of 2012. Red: $\Omega_{Ca} < 1$, indicating increased carbonate dissolution.
 618 Blue: $\Omega_{Ca} > 1$, 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

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

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



633 **Figure 10.** Conceptual scheme showing two consecutive years to explain the low density of
 634 dead foraminifera (in grey) in the first 20 cm of the core. The seasonal succession of oxic (blue),
 635 suboxic (orange) and sulphidic (black) zones and presence of cable bacteria (red dotted curves)
 636 are from Seitaj et al. (2015). Presence and densities (size of the signs) of living foraminifera (in
 637 green) are from Richirt et al. (2020). Squares, circles and triangles represent the yearly
 638 successive foraminifera generations.
 639

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

644 The increased inflow of saline, warm and well oxygenated water induced by the opening
 645 of the Brouwersdam sluice in 1999 should have improved the oxygenation and led to a
 646 reduction of the duration of anoxic events in the bottom waters compared to the situation before
 647 1999 (Figure 3; Wetsteijn, 2011; Sulu-Gambari et al., 2017). However, the increased
 648 concentration and large peaks in the Mo record in the last ~ 30 cm of the core suggest the
 649 presence of increased sulphide concentrations in the pore waters during the same period. Sulu-
 650 Gambari et al. (2017) explained this contradiction (i.e. the better oxygenation of bottom waters

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

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

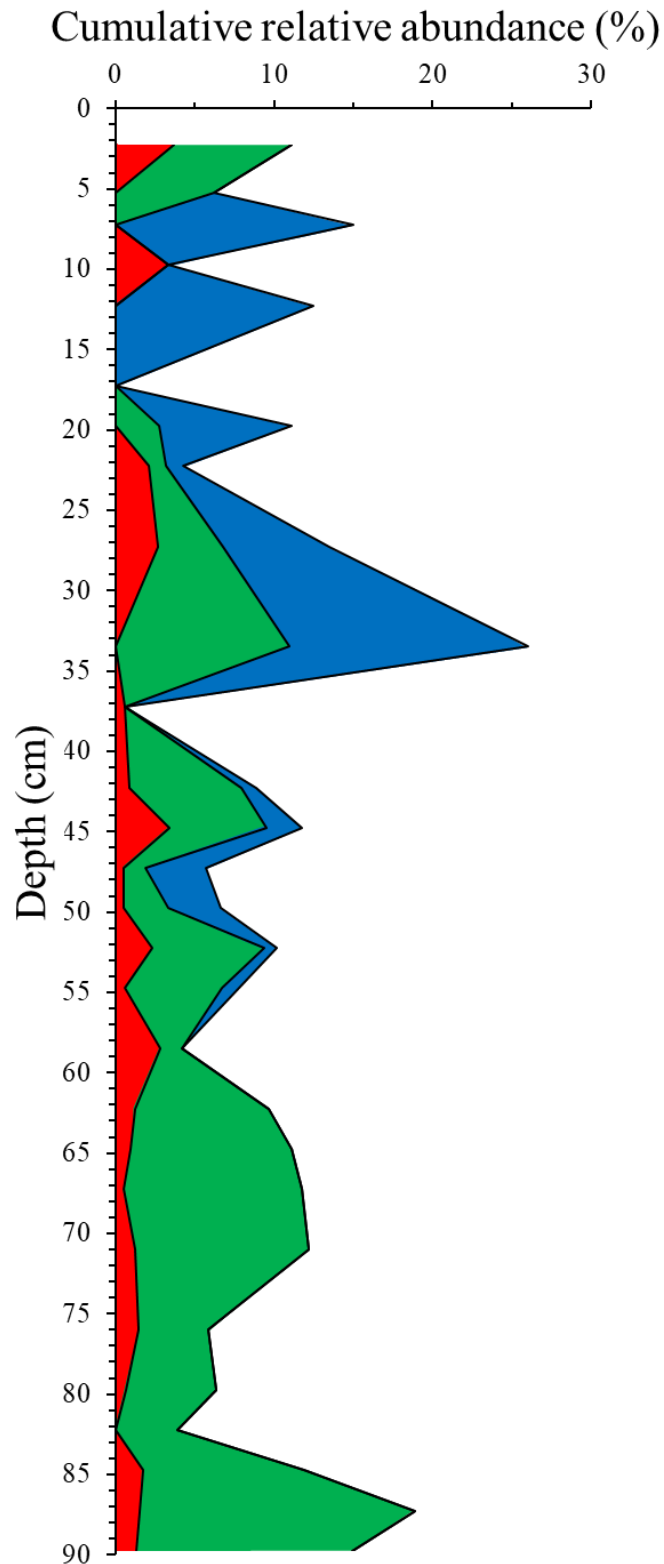
662 **5.3. TEMPORAL SUCCESSION OF AMMONIA SPECIES**

663 The historical record for Lake Grevelingen presented here shows the arrival of *A.*
664 *confertitesta* at 54.5–55 cm core depth (estimated year ~ 1986), and its subsequent progressive
665 replacement of *A. aberdoveyensis* (Figure 11). It has already been suggested that *A. confertitesta*
666 could be an exotic and/or invasive species originating from east Asia and introduced in the
667 eastern Atlantic Ocean by anthropogenic activities (Pawlowski & Holzmann, 2008; Schweizer
668 et al, 2011; Bird et al., 2020). Concerning the other two representatives of the *Ammonia* genus
669 observed in our sediment core, *A. veneta* is considered cosmopolitan (Holzmann & Pawlowski,
670 2000; Hayward et al., 2021) whereas *A. aberdoveyensis* seems to be restricted to the north
671 Atlantic (Hayward et al., 2004; Hayward et al., 2021). The latter two species are both assumed
672 autochthonous in Europe and could at present be progressively replaced by the seemingly exotic
673 *A. confertitesta* (Pawlowski & Holzmann, 2008; Schweizer et al. 2011).

674 This species replacement suggests that *A. confertitesta* is more resistant than *A.*
675 *aberdoveyensis* to the seasonal hypoxia/anoxia found in Lake Grevelingen after the closure in
676 1971. This hypothesis is corroborated by the much higher test porosity measured in *A.*
677 *confertitesta* compared to *A. aberdoveyensis* (22.45 ± 3.85 % versus 12.18 ± 3.8 %,
678 respectively, Richirt et al. 2019a), suggesting that this phylotype could resist oxygen deficiency
679 by increasing its gas exchanges with the surrounding environment. The fact that *A. confertitesta*
680 is rather poorly represented (about 5 % of the total assemblage) in the living assemblages in
681 2012 was explained by a phase offset between: 1) the time of repopulation of the site in winter

682 2011–2012 after its decimation due to anoxic and sulphidic conditions in summer 2011, and 2)
683 the availability of its preferred food sources, in spring 2012 (Richirt et al. 2020).

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



690

691 **Figure 11.** Cumulative relative abundances (in % of the total assemblage) of the three different
 692 *Ammonia* species *A. veneta* (red), *A. aberdoveyensis* (green) and *A. confertitesta* (blue) as a
 693 function of core depth (cm). Please keep in mind that total densities are relatively low in the top
 694 15 cm of the core (~15-30 ind. per sample), meaning that small variations in absolute
 695 abundances induce large variations in relative abundances.

696 Finally, *A. confertitesta* is virtually the only *Ammonia* species found in recent living
697 communities (~ 5 % of the 1044 individuals, total foraminiferal assemblage, Richirt et al.,
698 2020). In view of the strong anoxic events with co-occurring sulphidic conditions in 2011 and
699 2012 at this site (Seitaj et al. 2015; Richirt et al. 2020), this underlines the higher resistance of
700 *A. confertitesta*, compared to *A. veneta* and *A. aberdoveyensis*, to such adverse conditions.

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

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

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

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

726

6. CONCLUSION

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

735 The seaward closure of the basin in 1971 induced an important change in foraminiferal
736 communities, from high proportions of *H. germanica* and *A. aberdoveyensis*, which are typical
737 estuarine mudflat species, to assemblages dominated by *E. margaritaceum*, typical for marine
738 influence, *E. oceanense*, considered as an opportunistic species, and *E. magellanicum*, which
739 seems to be tolerant to oxygen depletion. This taxonomic change could be explained by the
740 disappearance of tides, much weaker hydrodynamics, increased eutrophication and increased
741 salinity immediately after the closure of the basin. The opening of the seaward sluice (in the
742 Brouwersdam) in autumn 1978, to counterbalance the eutrophication, increased the water
743 renewal, but did not solve the problem of seasonally occurring hypoxia/anoxia. At first, the
744 sluice was opened only in winter and *E. selseyense* strongly dominated the foraminiferal
745 assemblages, suggesting that this species benefited of more marine influence and development
746 of seasonal hypoxia. Around 1986, the emergence of *A. confertitesta* was observed coupled
747 with a progressive diminution of the proportion of *A. aberdoveyensis*, *H. depressula* and
748 *Quinqueloculina* spp. in the assemblages. After the sluice was opened almost year-round in
749 1999 and a further reduction of the water residence time by doubling the exchange with the
750 North Sea, the foraminiferal assemblages became very poor, so that the assemblage
751 composition should be interpreted very carefully. The extreme scarcity of foraminiferal tests in
752 the top 15 cm of the core, which strongly contrasts with the high abundance of living
753 foraminiferal communities, is ascribed to post-mortem dissolution, resulting from the strongly
754 diminished carbonate saturation state due to cable bacteria activity in the anoxic part of the
755 sediment.

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

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

764 **ACKNOWLEDGMENTS**

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

770 **REFERENCES**

- 771 Alve, E., Bernhard, J.M., 1995. Vertical migratory response of benthic foraminifera to controlled
772 oxygen concentrations in an experimental mesocosm. *Marine Ecology Progress Series* 116,
773 137–151.
- 774 Alve, E., Murray, J.W., 2001. Temporal variability in vertical distributions of live (stained) intertidal
775 foraminifera, southern England. *Journal of Foraminiferal Research* 31, 12–24.
776 <https://doi.org/10.2113/0310012>
- 777 Alve, E., Murray, J.W., 1999. Marginal marine environments of the Skagerrak and Kattegat: a
778 baseline study of living (stained) benthic foraminiferal ecology. *Palaeogeography,*
779 *Palaeoclimatology, Palaeoecology* 146, 171–193. <https://doi.org/10.1016/S0031->
780 [0182\(98\)00131-X](https://doi.org/10.1016/S0031-0182(98)00131-X)
- 781 Alve, E., Murray, J.W., 1994. Ecology and taphonomy of benthic foraminifera in a temperate
782 mesotidal inlet. *Journal of Foraminiferal Research* 24, 18–27.
783 <https://doi.org/10.2113/gsjfr.24.1.18>
- 784 Bannink, B.A., Van der Meulen, J.H.M., Nienhuis, P.H., 1984. Lake grevelingen: From an estuary
785 to a saline lake. An introduction. *Netherlands Journal of Sea Research* 18, 179–190.
786 [https://doi.org/10.1016/0077-7579\(84\)90001-2](https://doi.org/10.1016/0077-7579(84)90001-2)
- 787 Bernhard, J.M., 1993. Experimental and field evidence of Antarctic foraminiferal tolerance to anoxia
788 and hydrogen sulfide. *Marine Micropaleontology* 20, 203–213. <https://doi.org/10.1016/0377->
789 [8398\(93\)90033-T](https://doi.org/10.1016/0377-8398(93)90033-T)
- 790 Bernhard, J.M., Alve, E., 1996. Survival, ATP pool, and ultrastructural characterization of benthic
791 foraminifera from Drammensfjord (Norway): response to anoxia. *Marine Micropaleontology*
792 28, 5–17. [https://doi.org/10.1016/0377-8398\(95\)00036-4](https://doi.org/10.1016/0377-8398(95)00036-4)
- 793 Bird, C., Schweizer, M., Roberts, A., Austin, W.E.N., Knudsen, K.L., Evans, K.M., Filipsson, H.L.,
794 Sayer, M.D.J., Geslin, E., Darling, K.F., 2020. The genetic diversity, morphology,
795 biogeography, and taxonomic designations of *Ammonia* (Foraminifera) in the Northeast

796 Atlantic. Marine Micropaleontology 155, 101726.
797 <https://doi.org/10.1016/j.marmicro.2019.02.001>

798 Bouchet, V.M.P., Debenay, J.-P., Sauriau, P.-G., Radford-Knoery, J., Soletchnik, P., 2007. Effects
799 of short-term environmental disturbances on living benthic foraminifera during the Pacific
800 oyster summer mortality in the Marennes-Oléron Bay (France). *Marine Environmental*
801 *Research* 64, 358–383. <https://doi.org/10.1016/j.marenvres.2007.02.007>

802 Charrieau, L.M., Filipsson, H.L., Nagai, Y., Kawada, S., Ljung, K., Kritzberg, E., Toyofuku, T.,
803 2018. Decalcification and survival of benthic foraminifera under the combined impacts of
804 varying pH and salinity. *Marine Environmental Research* 138, 36–45.
805 <https://doi.org/10.1016/j.marenvres.2018.03.015>

806 Crusius, J., Calvert, S., Pedersen, T., Sage, D., 1996. Rhenium and molybdenum enrichments in
807 sediments as indicators of oxic, suboxic and sulfidic conditions of deposition. *Earth and*
808 *Planetary Science Letters* 145, 65–78. [https://doi.org/10.1016/S0012-821X\(96\)00204-X](https://doi.org/10.1016/S0012-821X(96)00204-X)

809 Darling, K.F., Schweizer, M., Knudsen, K.L., Evans, K.M., Bird, C., Roberts, A., Filipsson, H.L.,
810 Kim, J.-H., Gudmundsson, G., Wade, C.M., Sayer, M.D.J., Austin, W.E.N., 2016. The genetic
811 diversity, phylogeography and morphology of Elphidiidae (Foraminifera) in the Northeast
812 Atlantic. *Marine Micropaleontology* 129, 1–23.
813 <https://doi.org/10.1016/j.marmicro.2016.09.001>

814 de Nooijer, L.J., Toyofuku, T., Kitazato, H., 2009. Foraminifera promote calcification by elevating
815 their intracellular pH. *PNAS*, 106, 15374–15378. <https://doi.org/10.1073/pnas.0904306106>

816 Dickson, A.G., 1990. Standard potential of the reaction: $\text{AgCl(s)} + \frac{1}{2}\text{H}_2\text{(g)} = \text{Ag(s)} + \text{HCl(aq)}$, and
817 and the standard acidity constant of the ion HSO_4^- in synthetic sea water from 273.15 to 318.15
818 K. *The Journal of Chemical Thermodynamics* 22, 113–127. [https://doi.org/10.1016/0021-](https://doi.org/10.1016/0021-9614(90)90074-Z)
819 [9614\(90\)90074-Z](https://doi.org/10.1016/0021-9614(90)90074-Z)

820 Donders, T.H., Guasti, E., Bunnik, F.P.M., van Aken, H., 2012. Impact van de Brouwersdam op
821 zuurstofcondities in de Grevelingen; reconstructies uit natuurlijke sediment archieven. TNO-
822 rapport, TNO-060-UT-2011-02116. Geological Survey of the Netherlands.

823 Duijnste, I. a. P., Ernst, S.R., Zwaan, G.J. van der, 2003. Effect of anoxia on the vertical migration
824 of benthic foraminifera. *Marine Ecology Progress Series* 246, 85–94.
825 <https://doi.org/10.3354/meps246085>

826 Egger, M., Lenstra, W., Jong, D., Meysman, F.J.R., Sapart, C.J., Veen, C. van der, Röckmann, T.,
827 Gonzalez, S., Slomp, C.P., 2016. Rapid Sediment Accumulation Results in High Methane
828 Effluxes from Coastal Sediments. *PLOS ONE* 11, e0161609.
829 <https://doi.org/10.1371/journal.pone.0161609>

830 Ernst, S., Bours, R., Duijnste, I., Zwaan, B. van der, 2005. EXPERIMENTAL EFFECTS OF AN
831 ORGANIC MATTER PULSE AND OXYGEN DEPLETION ON A BENTHIC
832 FORAMINIFERAL SHELF COMMUNITY. *Journal of Foraminiferal Research* 35, 177–197.
833 <https://doi.org/10.2113/35.3.177>

834 Fouet, M., Heliot, S., Singer, D., Barras, C., and Jorissen, F. J.: How to adapt foraminiferal index to
835 estuaries? Application of the MII index, in preparation, 2021.

836 Geslin, E., Barras, C., Langlet, D., Nardelli, M.P., Kim, J.-H., Bonnin, J., Metzger, E., Jorissen, F.J.,
837 2014. Survival, Reproduction and Calcification of Three Benthic Foraminiferal Species in
838 Response to Experimentally Induced Hypoxia, in: Kitazato, H., M. Bernhard, J. (Eds.),
839 *Approaches to Study Living Foraminifera: Collection, Maintenance and Experimentation*,

- 840 Environmental Science and Engineering. Springer Japan, Tokyo, pp. 163–193.
841 https://doi.org/10.1007/978-4-431-54388-6_10
- 842 Geslin, E., Heinz, P., Jorissen, F., Hemleben, Ch., 2004. Migratory responses of deep-sea benthic
843 foraminifera to variable oxygen conditions: laboratory investigations. *Marine*
844 *Micropaleontology* 53, 227–243. <https://doi.org/10.1016/j.marmicro.2004.05.010>
- 845 Gustafsson, M., Nordberg, K., 2000. Living (Stained) Benthic Foraminifera and their Response to
846 the Seasonal Hydrographic Cycle, Periodic Hypoxia and to Primary Production in Havstens
847 Fjord on the Swedish West Coast. *Estuarine, Coastal and Shelf Science* 51, 743–761.
848 <https://doi.org/10.1006/ecss.2000.0695>
- 849 Gustafsson, M., Nordberg, K., 1999. Benthic foraminifera and their response to hydrography,
850 periodic hypoxic conditions and primary production in the Koljö fjord on the Swedish west
851 coast. *Journal of Sea Research* 41, 163–178. [https://doi.org/10.1016/S1385-1101\(99\)00002-7](https://doi.org/10.1016/S1385-1101(99)00002-7)
- 852 Hagens, M., Slomp, C.P., Meysman, F.J.R., Seitaj, D., Harlay, J., Borges, A.V., Middelburg, J.J.,
853 2015. Biogeochemical processes and buffering capacity concurrently affect acidification in a
854 seasonally hypoxic coastal marine basin. *Biogeosciences* 12, 1561–1583.
855 <https://doi.org/10.5194/bg-12-1561-2015>
- 856 Hayward, B.W., Holzmann, M., Grenfell, H.R., Pawlowski, J., Triggs, C.M., 2004. Morphological
857 distinction of molecular types in *Ammonia* – towards a taxonomic revision of the world’s most
858 commonly misidentified foraminifera. *Marine Micropaleontology* 50, 237–271.
859 [https://doi.org/10.1016/S0377-8398\(03\)00074-4](https://doi.org/10.1016/S0377-8398(03)00074-4)
- 860 Hayward, B.W., Holzmann, M., Pawlowski, J., Parker, J.H., Kaushik, T., Toyofuku, M.S., Tsuchiya,
861 M., 2021. Molecular and morphological taxonomy of living *Ammonia* and related taxa
862 (Foraminifera) and their biogeography. *Micropaleontology* 67, 109–274.
- 863 Hermans, M., Risgaard-Petersen, N., Meysman, F.J.R., Slomp, C.P., 2020. Biogeochemical impact
864 of cable bacteria on coastal Black Sea sediment. *Biogeosciences* 17, 5919–5938.
865 <https://doi.org/10.5194/bg-17-5919-2020>
- 866 Holzmann, M., Pawlowski, J., 2000. Taxonomic relationships in the genus *Ammonia* (Foraminifera)
867 based on ribosomal DNA sequences. *Journal of Micropalaeontology* 19, 85–95.
868 <https://doi.org/10.1144/jm.19.1.85>
- 869 Jørgensen, B.B., Postgate, J.R., Postgate, J.R., Kelly, D.P., 1982. Ecology of the bacteria of the
870 sulphur cycle with special reference to anoxic—oxic interface environments. *Philosophical*
871 *Transactions of the Royal Society of London. B, Biological Sciences* 298, 543–561.
872 <https://doi.org/10.1098/rstb.1982.0096>
- 873 Katz, M.E., Cramer, B.S., Franzese, A., Hönisch, B., Miller, K.G., Rosenthal, Y., Wright, J.D., 2010.
874 Traditional and emerging geochemical proxies in foraminifera. *Journal of Foraminiferal*
875 *Research* 40, 165–192. <https://doi.org/10.2113/gsjfr.40.2.165>
- 876 Langlet, D., Baal, C., Geslin, E., Metzger, E., Zuschin, M., Riedel, B., Risgaard-Petersen, N.,
877 Stachowitsch, M., Jorissen, F.J., 2014. Foraminiferal species responses to in situ,
878 experimentally induced anoxia in the Adriatic Sea. *Biogeosciences* 11, 1775–1797.
879 <https://doi.org/10.5194/bg-11-1775-2014>
- 880 Langlet, D., Geslin, E., Baal, C., Metzger, E., Lejzerowicz, F., Riedel, B., Zuschin, M., Pawlowski,
881 J., Stachowitsch, M., Jorissen, F.J., 2013. Foraminiferal survival after long-term in situ
882 experimentally induced anoxia. *Biogeosciences* 10, 7463–7480. [https://doi.org/10.5194/bg-10-](https://doi.org/10.5194/bg-10-7463-2013)
883 7463-2013

- 884 Lévy, A., Mathieu, R., Momeni, I., Poignant, A., Rosset-Moulinier, M., Rouvillois, A., Ubaldo, M.,
885 1969. Les représentants de la famille des Elphidiidae (foraminifères) dans les sables des plages
886 des environs de Dunkerque. Remarques sur les espèces de *Polystomella* signalées par O.
887 Terquem, *Revue de Micropaléontologie* 2, 92–98.
- 888 Lewis, E., Wallace, D.W., 1998. R: Program developed for CO₂ system calculations ORNL/CDIAC-
889 105. Carbon Dioxide Information Analysis Centre, Oak Ridge National Laboratory.
- 890 Lindeboom, H.J., Sandee, A.J.J., 1984. The Effect of Coastal Engineering Projects on
891 Microgradients and Mineralization Reactions in Sediments. *Water Science and Technology* 16,
892 87–94. <https://doi.org/10.2166/wst.1984.0046>
- 893 Routers, T., Berg, J.H. van den, Mulder, J.P.M., 1998. Geomorphological Changes of the
894 Oosterschelde Tidal System During and After the Implementation of the Delta Project. *Journal*
895 *of Coastal Research* 14, 1134–1151.
- 896 Eueker, T.J., Dickson, A.G., Keeling, C.D., 2000. Ocean *p*CO₂ calculated from dissolved inorganic
897 carbon, alkalinity, and equations for *K*₁ and *K*₂: validation based on laboratory measurements
898 of CO₂ in gas and seawater at equilibrium. *Marine Chemistry* 70, 105–119.
899 [https://doi.org/10.1016/S0304-4203\(00\)00022-0](https://doi.org/10.1016/S0304-4203(00)00022-0)
- 900 Meysman, F.J.R., Risgaard-Petersen, N., Malkin, S.Y., Nielsen, L.P., 2015. The geochemical
901 fingerprint of microbial long-distance electron transport in the seafloor. *Geochimica et*
902 *Cosmochimica Acta* 152, 122–142. <https://doi.org/10.1016/j.gca.2014.12.014>
- 903 Moodley, L., Hess, C., 1992. Tolerance of Infaunal Benthic Foraminifera for Low and High Oxygen
904 Concentrations. *The Biological Bulletin* 183, 94–98. <https://doi.org/10.2307/1542410>
- 905 Moodley, L., van der Zwaan, G.J., Rutten, G.M.W., Boom, R.C.E., Kempers, A.J., 1998. Subsurface
906 activity of benthic foraminifera in relation to porewater oxygen content: laboratory
907 experiments. *Marine Micropaleontology* 34, 91–106. [https://doi.org/10.1016/S0377-9088398\(97\)00044-3](https://doi.org/10.1016/S0377-9088398(97)00044-3)
- 908 Muelen, J.H.M. v d, Leentvaar, J., Rooy, N.M. de, 1984. Environmental impact statement on the
910 problem of a fresh or salt lake Grevelingen. *Water science and technology* 16, 107–120.
- 911 Murray, J.W., 2006. *Ecology and Applications of Benthic Foraminifera*. Cambridge University
912 Press, 426 p.
- 913 Murray, J.W., 1983. Population dynamics of benthic foraminifera; results from the Exe Estuary,
914 England. *Journal of Foraminiferal Research* 13, 1–12. <https://doi.org/10.2113/gsjfr.13.1.1>
- 915 Nienhuis, P.H., 1978. Lake grevelingen: A case study of ecosystem changes in a closed estuary.
916 *Hydrobiological Bulletin* 12, 246–259. <https://doi.org/10.1007/BF02259186>
- 917 Nienhuis, P.H., Veld, J.C.H. in 't, 1984. Grevelingen: From an Estuary to a Saline Lake. *Water*
918 *Science and Technology* 16, 27–50. <https://doi.org/10.2166/wst.1984.0043>
- 919 Orr, J.C., Epitalon, J.-M., Gattuso, J.-P., 2015. Comparison of ten packages that compute ocean
920 carbonate chemistry. *Biogeosciences* 12, 1483–1510. <https://doi.org/10.5194/bg-12-1483-2015>
- 921 Pawlowski, J., Holzmann, M., 2008. Diversity and geographic distribution of benthic foraminifera:
922 a molecular perspective. *Biodiversity and Conservation* 17, 317–328.
923 <https://doi.org/10.1007/s10531-007-9253-8>
- 924 Petersen, J., Riedel, B., Barras, C., Pays, O., Guihéneuf, A., Mabilieu, G., Schweizer, M., Meysman,
925 F.J.R., Jorissen, F.J., 2016. Improved methodology for measuring pore patterns in the benthic
926 foraminiferal genus *Ammonia*. *Marine Micropaleontology* 128, 1–13.
927 <https://doi.org/10.1016/j.marmicro.2016.08.001>

- 92 Piña-Ochoa, E., Høglund, S., Geslin, E., Cedhagen, T., Revsbech, N.P., Nielsen, L.P., Schweizer,
929 M., Jorissen, F., Rysgaard, S., Risgaard-Petersen, N., 2010. Widespread occurrence of nitrate
930 storage and denitrification among Foraminifera and Gromiida. PNAS 107, 1148–1153.
931 <https://doi.org/10.1073/pnas.0908440107>
- 93 Pucci, F., Geslin, E., Barras, C., Morigi, C., Sabbatini, A., Negri, A., Jorissen, F.J., 2009. Survival
933 of benthic foraminifera under hypoxic conditions: Results of an experimental study using the
934 CellTracker Green method. Marine Pollution Bulletin, Foraminifera and Marine Pollution 59,
935 336–351. <https://doi.org/10.1016/j.marpolbul.2009.08.015>
- 936 Richirt, J., Schweizer, M., Bouchet,
937 V.M.P., Mouret, A., Quinchar, S., Jorissen, F.J., 2019a. Morphological distinction of three
938 *Ammonia* phylotypes occurring along european coasts. Journal of Foraminiferal Research 49,
938 77–94.
- 93 Richirt, J., Champmartin, S., Schweizer, M., Mouret, A., Petersen, J., Ambari, A., Jorissen, F.J.,
940 2019b. Scaling laws explain foraminiferal pore patterns. Scientific Reports 9, 9149.
941 <https://doi.org/10.1038/s41598-019-45617-x>
- 94 Richirt, J., Riedel, B., Mouret, A., Schweizer, M., Langlet, D., Seitaj, D., Meysman, F.J.R., Slomp,
943 C.P., Jorissen, F.J., 2020. Foraminiferal community response to seasonal anoxia in Lake
944 Grevelingen (the Netherlands). Biogeosciences 17, 1415–1435. <https://doi.org/10.5194/bg-17-1415-2020>
- 94 Risgaard-Petersen, N., Revil, A., Meister, P., Nielsen, L.P., 2012. Sulfur, iron-, and calcium cycling
947 associated with natural electric currents running through marine sediment. Geochimica et
948 Cosmochimica Acta 92, 1–13. <https://doi.org/10.1016/j.gca.2012.05.036>
- 94 Saad, S.A., Wade, C.M., 2017. Seasonal and spatial variations of saltmarsh benthic foraminiferal
950 communities from north Norfolk, England. Microbial Ecology 73, 539–555.
951 <https://doi.org/10.1007/s00248-016-0895-5>
- 95 Saad, S.A., Wade, C.M., 2016. Biogeographic distribution and habitat association of *Ammonia*
953 genetic variants around the coastline of Great Britain. Marine Micropaleontology 124, 54–62.
954 <https://doi.org/10.1016/j.marmicro.2016.01.004>
- 95 Saeijs, H.L.F., Stortelder, P.B.M., 1982. Converting an estuary to Lake Grevelingen: Environmental
956 review of a coastal engineering project. Environmental Management 6, 377–405.
957 <https://doi.org/10.1007/BF01871888>
- 95 Schönfeld, J., 2018. Monitoring benthic foraminiferal dynamics at Bottsand coastal lagoon (western
959 Baltic Sea). Journal of Micropalaeontology 37, 383–393. <https://doi.org/10.5194/jm-37-383-960-2018>
- 96 Schweizer, M., Polovodova, I., Nikulina, A., Schönfeld, J., 2011. Molecular identification of
962 *Ammonia* and *Elphidium* species (Foraminifera, Rotaliida) from the Kiel Fjord (SW Baltic Sea)
963 with rDNA sequences. Helgoland Marine Research 65, 1–10. <https://doi.org/10.1007/s10152-964-010-0194-3>
- 96 Seitaj, D., Schauer, R., Sulu-Gambari, F., Hidalgo-Martinez, S., Malkin, S.Y., Burdorf, L.D.W.,
966 Slomp, C.P., Meysman, F.J.R., 2015. Cable bacteria generate a firewall against euxinia in
967 seasonally hypoxic basins. PNAS 112, 13278–13283.
968 <https://doi.org/10.1073/pnas.1510152112>
- 96 Seitaj, D., Sulu-Gambari, F., Burdorf, L.D.W., Romero-Ramirez, A., Maire, O., Malkin, S.Y.,
970 Slomp, C.P., Meysman, F.J.R., 2017. Sedimentary oxygen dynamics in a seasonally hypoxic
971 basin. Limnology and Oceanography 62, 452–473. <https://doi.org/10.1002/lno.10434>

- 972 Sulu-Gambari, F., Hagens, M., Behrends, T., Seitaj, D., Meysman, F.J.R., Middelburg, J., Slomp,
973 C.P., 2018. Phosphorus Cycling and Burial in Sediments of a Seasonally Hypoxic Marine
974 Basin. *Estuaries and Coasts* 41, 921–939. <https://doi.org/10.1007/s12237-017-0324-0>
- 975 Sulu-Gambari, F., Roepert, A., Jilbert, T., Hagens, M., Meysman, F.J.R., Slomp, C.P., 2017.
976 Molybdenum dynamics in sediments of a seasonally-hypoxic coastal marine basin. *Chemical*
977 *Geology* 466, 627–640. <https://doi.org/10.1016/j.chemgeo.2017.07.015>
- 978 Sulu-Gambari, F., Seitaj, D., Behrends, T., Banerjee, D., Meysman, F.J.R., Slomp, C.P., 2016a.
979 Impact of cable bacteria on sedimentary iron and manganese dynamics in a seasonally-hypoxic
980 marine basin. *Geochimica et Cosmochimica Acta* 192, 49–69.
981 <https://doi.org/10.1016/j.gca.2016.07.028>
- 982 Sulu-Gambari, F., Seitaj, D., Meysman, F.J.R., Schauer, R., Polerecky, L., Slomp, C.P., 2016b.
983 Cable Bacteria Control Iron–Phosphorus Dynamics in Sediments of a Coastal Hypoxic Basin.
984 *Environ. Sci. Technol.* 50, 1227–1233. <https://doi.org/10.1021/acs.est.5b04369> Thibault de
985 Chanvalon, A., Metzger, E., Mouret, A., Cesbron, F., Knoery, J., Rozuel, E., Launeau, P.,
986 Nardelli, M.P., Jorissen, F.J., Geslin, E., 2015. Two-dimensional distribution of living benthic
987 foraminifera in anoxic sediment layers of an estuarine mudflat (Loire estuary, France).
988 *Biogeosciences* 12, 6219–6234. <https://doi.org/10.5194/bg-12-6219-2015>
- 989 Toyofuku, T., Matsuo, M.Y., Nooijer, L.J. de, Nagai, Y., Kawada, S., Fujita, K., Reichart, G.-J.,
990 Nomaki, H., Tsuchiya, M., Sakaguchi, H., Kitazato, H., 2017. Proton pumping accompanies
991 calcification in foraminifera. *Nature Communications* 8, 1–6.
992 <https://doi.org/10.1038/ncomms14145>
- 993 Toyofuku, T., Nooijer, L.J. de, Yamamoto, H., Kitazato, H., 2008. Real-time visualization of
994 calcium ion activity in shallow benthic foraminiferal cells using the fluorescent indicator Fluo-
995 3 AM. *Geochemistry, Geophysics, Geosystems* 9. <https://doi.org/10.1029/2007GC001772>
- 996 Pppström, L.R., 1974. The boron/chlorinity ratio of deep-sea water from the Pacific Ocean. *Deep*
997 *Sea Research and Oceanographic Abstracts* 21, 161–162. <https://doi.org/10.1016/0011->
998 7471(74)90074-6
- 999 Wetsteijn, L.P.M.J., 2011. Grevelingenmeer: meer kwetsbaar? Een beschrijving van de ecologische
1000 ontwikkelingen voor de periode 1999 t/m 2008-2010 in vergelijking met de periode 1990 t/m
1001 1998., RWS Waterdienst. ed. Lelystad, Netherlands.
- 1002 Wolff, W.J., Reise, K., 2002. Oyster Imports as a Vector for the Introduction of Alien Species into
1003 Northern and Western European Coastal Waters, in: Leppäkoski, E., Gollasch, S., Olenin, S.
1004 (Eds.), *Invasive Aquatic Species of Europe. Distribution, Impacts and Management*. Springer
1005 Netherlands, Dordrecht, pp. 193–205. https://doi.org/10.1007/978-94-015-9956-6_21