Short-term response of benthic foraminifera to fine sediment depositional events simulated in microcosm

Corentin Guilhermic[1], Maria Pia Nardelli[1], Aurélia Mouret[1], Damien Le Moigne[1], Hélène Howa[1]

[1] Université Angers, Nantes Univ., Le Mans Univ, CNRS, LPG, Laboratoire de planétologie et géosciences, UMR CNRS 6112, F-49000 Angers, France

Correspondence to: Corentin Guilhermic (corentin.guilhermic@etud.univ-angers.fr)

"Maria Pia NARDELLI" <mariapia.nardelli@univ-angers.fr>

"Aurelia MOURET" <aurelia.mouret@univ-angers.fr>

"Damien LE MOIGNE" <damien.lemoigne@ univ-angers.fr>

"Helene HOWA" <helene.howa@univ-angers.fr>

Abstract

A microcosm experiment was designed to describe how benthic foraminifera react to fine sediment deposits varying in frequency and intensity, as it may occur regularly or occasionally in coastal benthic environments, caused by discharges from (e.g.) river flooding, tidewater glacier melting in polar regions or diverse anthropic activities linked to harbour or watershed management. The influence of seabed burial resulting from these events on the ecology of benthic ecosystems is often overlooked, and the resilience of benthic communities is poorly known. During a 51-day long experiment, a typical northeastern Atlantic intertidal foraminiferal community, mainly represented by *Ammonia confertitesta* and *Haynesina germanica* species, was subjected to two kinds of sedimentary disturbance: 1) one-time high volume (OHV) deposit, i.e. about 3 cm thick sediment added in one time at the beginning of the experiment; and 2) frequent low volume (FLV) deposits, i.e. about 0.5 cm added each week for 4 weeks. The geochemical environment (e.g. dissolved oxygen penetration in the sediment, salinity, temperature and nutrient content in the supernatant water) was monitored to follow the microcosm steady state before and during the experiment. In both disturbed microcosms, *H. germanica* showed a significant linear decrease in abundance during the experiment while the total abundance of foraminifera was significantly affected only by the OHV treatment, suggesting a stronger effect of a single thick deposit on standing stocks and biodiversity compared to frequent low sediment supplies. Concerning the vertical migration of foraminifera after sedimentary disturbances, the two dominant species moved upwards to the water- sediment interface with migration speeds estimated at 0.41 and 0.47 mm/h respectively for *A. confertitesta* and *H. germanica*. In the FLV treatment, the resilient state was already reached within the day following a low thickness burial while in the OHV it was achieved between 1 and 7 days after the 3 cm thick deposit. These results suggest that foraminifera can migrate rapidly after a sedimentary burial to recover their preferential life position under the new sediment-water interface, but in case of an abrupt thick burial, several days are needed to reach a resilient state.

Keywords: biotic recovery, migration, oxygen penetration depth, disturbance, deposit

1 Introduction

Coastal marine environments are subject to recurrent, erratic, or rare sedimentary depositional events that abruptly bring sediment to the seafloor. Sediment depositional events in coastal marine areas occur under the influence of various drivers such as river flooding (Extence et al., 2013; Dyer, 1988; Hir et al., 2001; Jalón-Rojas et al., 2015), glacier melting in polar regions (D'Angelo et al., 2018; Fossile et al., 2022; Hodson et al., 1998; Meslard et al., 2018), storms (Bolliet et al., 2014; Budillon et al., 2006), or anthropic activities such as dredging (Wolanski and Gibbs, 1992) or land-use along catchment basins (Bussi et al., 2016; Kuhnle et al., 1996).

These sediment deposits, when thick and abrupt, can asphyxiate biota and provoke long-lasting destabilisation of aquatic benthic ecosystems. In particular, fine-grained sediment deposition can lead to a decline in microhabitat quality and affect benthic ecosystems in several ways (e.g**.** Larson and Sundbäck, 2012; Mestdagh et al., 2018; Wood, 1997) : (1) by constituting a physical barrier that disrupts the connection to the water column, thereby impeding food supply and oxygen exchange ; (2) by altering the substrate's geochemical composition and thus substrate suitability for some taxa, (3) by providing a highly porous, water-saturated substrate which instability can prevent recolonization from refuge areas.

The question of the impact of sediment supply to benthic realms becomes urgent in the context of the ongoings climate change: among the most impressive consequences on coastal marine environments there is the disruption of water cycles, including enhanced glacier melting at high latitudes and extreme oscillation of rainfall patterns at lower latitudes, both significantly affecting the sedimentary supply to coastal areas. Excessive deposition of fine sediment is generally recognized to have deleterious effects on aquatic biodiversity, and is even considered as one of the major threats to biodiversity in freshwater environments (Dudgeon, 2019; Mathers et al., 2022, 2022; Sánchez-Bayo and Wyckhuys, 2019) and on marine benthic environments (Alve, 1999; Anschutz et al., 2002). Biota burial and changes in substrate type can delay recovery of crucial benthic ecosystem function. The recovery rate is controlled by a complex combination of ecological and physical forcings (Norkko et al., 2006; Thrush et al., 2006). Among these, the ability of organisms to quickly migrate through the sediment is crucial to recover their preferential habitat at the surface or inside the sediment column. Despite several studies focused on the response of mega and macrobenthos to physical disturbance (Bolam et al., 2011; Cottrell et al., 2016; Hendrick et al., 2016; Mestdagh et al., 2018), few is known about meio and microfauna, which represent lower steps of the trophic chain and therefore have the potential to control the ecosystem functioning through a bottom-up relationship.

Benthic foraminifera (Eukaryotes, Rhizaria) are unicellular organisms belonging to meiofauna and are highly sensitive to sedimentary and geochemical changes in their environment (e.g. Murray, 2006) and present several characteristics making them powerful bio-indicators of marine environmental characteristics (Schönfeld et al., 2012): (i) high density in marine sediments; (ii) short life cycles; (iii) occupation of specific ecological niches and microhabitats, including superficial, shallow and deep infaunal sediment layers (up to 10-20 cm depth). Because of these characteristics, foraminifera have increasingly been used as biotic tools for assessing the quality status of coastal marine environments (Alve et al., 2016; Barras et al., 2014; Belart et al., 2018; Bouchet et al., 2018a, 2012; Fontanier et al., 2020; Frontalini and Coccioni, 2008; Frontalini et al., 2009;

Jorissen et al., 2022; Laut et al., 2021; Martins et al., 2013, 2015, 2016; Murray, 2006; Nesbitt et al., 2015). Moreover, Bouchet et al. (2018b) showed that benthic foraminifera can be better bio-indicators than macrofauna as they can be present on a larger

75 spectrum of environmental gradients compared to macrofauna and generally more sensitive (and therefore absent) to highly stressed conditions. In Artic fjords, foraminiferal ecological response to environmental stress has been observed to mirror the ones of macrofauna, with decreasing diversity and a dominance of opportunistic taxa (Wlodarska-Kowalczuk et al., 2013). In natural marine environments, vertical and horizontal distribution of benthic foraminiferal faunas are controlled by several parameters, noticeably organic matter and oxygen content in their habitats (e.g., Contreras-Rosales et al., 2012; Goineau et al.,

80 2012; Gooday et al., 2000; Jorissen et al., 1995; Langezaal et al., 2006; Schumacher et al., 2007). Following the conceptual model from Jorissen et al. (1995) taken over by Van der Zwaan et al. (1999) and Koho et al. (2015), foraminiferal vertical distribution is limited, in eutrophic systems, by oxygen concentration in bottom and sediment porewaters, and by organic matter availability in oligotrophic realm. Beyond these two geochemical drivers, a third factor seems to affect the benthic environment that is the physical forcing by sediment supply to the bottom. Some recent studies of naturally stressed coastal

85 environments focused on the response of foraminiferal communities to excessive fine sediment supply due to natural processes. Various environments were prospected: turbidites in canyon channels and terraces (Bolliet et al., 2014; Dessandier et al., 2016; Duros et al., 2017; Goineau et al., 2012; Hess and Jorissen, 2009); prodelta river flooding (Goineau et al., 2012) and river-dominated shelf (Dessandier et al., 2016). Other studies concentrated on anthropic activities that directly cause massive fine sediment supply in coastal areas and the associated effects on benthic foraminifera faunas (e.g., oil drill cutting disposal,

90 Mojtahid et al., 2006; exacerbated land-use, Fontanier et al., 2018; industrial waste, Fontanier et al., 2020). Most of these studies mainly focus on massive and sudden/occasional deposits of sediment and the fact that they are performed in natural environments represents a limit for the interpretations. Indeed, in natural settings, sediment supply, organic matter input and oxygen availability often covary and synergically affect benthic communities and microhabitats distribution. Experimental studies are therefore the only way to test the effect of a single parameter in a controlled setting where environmental variability

95 can be artificially reduced. For these reasons, we designed an experiment to test, in microcosms, the effect of different patterns of fine-grained sediment deposits on benthic foraminiferal communities, without varying organic matter content and oxygen availability. Two different modes of sediment input were selected to characterise the vertical migration and survival of foraminifera under the pressure of various physical disturbances: a single thick sediment deposit and thin and recurrent sediment deposits, in order to test if the ecological response is affected by the amplitude and the frequency of the sedimentary

100 disturbance or not. The ecological responses we observed concerned density and diversity variations at different time intervals and their vertical distribution (representing their migration ability) after the two disturbance's regimes.

Our experimental design was not intended to exactly reproduce a natural environment but rather to control a single ecological driver, i.e., the fine-grained sediment supply.

2 Material and Methods

2.1 Biological model

In our experiment, we used benthic foraminifera species, that inhabit on the mudflats of the French Atlantic coast. Foraminifera samples were collected at low tide, in the upper mudflat of the bay of Bourgneuf called La Couplasse, a vast maritime bay enclosed by the island of Noirmoutier. The assemblages were largely dominated by two species, *Ammonia confertitesta* Zheng, 1978 (Hayward et al., 2021, often reported as *Ammonia tepida* in literature) and *Haynesina germanica* (Ehrenberg, 1840). These two species live in similar shallow infaunal microhabitats, i.e., near the sediment-water interface on tidal mudflat at temperate latitudes. They are often associated and dominant in such natural coastal environments and are not expected to be in exclusive competition (Alve, 2001; Morvan et al., 2006; Murray and Alve, 2000; Thibault de Chanvalon et al., 2015). The species *Ammonia confertitesta* has already been used in microcosms and cultured in investigations focusing on growth and calcification processes (Bradshaw, 1957; Denoyelle et al., 2012; Geslin et al., 2014; Nardelli et al., 2014; Stouff et al., 1999), effects of contaminants (Denoyelle et al., 2012; Le Cadre and Debenay, 2006; Suokhrie et al., 2017) or metabolical responses to stressed environments (Geslin et al., 2014; Heinz and Geslin, 2012; Jauffrais et al., 2016a; Koho et al., 2018; Nardelli et al., 2014). Therefore, this species was chosen here for its high ability to withstand experimental living conditions for long lasting periods of time (up to several months). The second species, *Haynesina germanica*, has also been studied in experimental conditions, for its ability to sequester chloroplasts and perform photosynthesis (Jauffrais et al., 2016b), or for its metabolic responses to stressed environments (Deldicq et al., 2021; Langlet, 2020; Seuront and Bouchet, 2015). However, previous experiments involving *H. germanica* only lasted several days. Although both species were never used in microcosms testing sediment input, we expected them to respond to sediment depositional events that would directly disturb the stability of their shallow infaunal microhabitat.

2.2 Experimental design

Two scenarii were implemented in two different aquaria to simulate simultaneously: 1) a "One-time High Volume" (OHV) scenario in which the microcosm received one single sedimentary load resulting in a thick deposit; and 2) a "Frequent Low Volume" (FLV) scenario with four successive (1-week period) small supplies each burying the microcosm under a thin sediment layer. In parallel, a control microcosm, in a third aquarium, received no sediment input during the experiment (Fig. 1).

The three glass aquaria (50 x 15 x 26 cm; 750 cm^2 surface area) were designed to allow 5 consecutive samplings at one-week interval without disturbing the rest of the microcosm. For this purpose, in each aquarium, five compartments (10 cm long; 150 cm^2 surface area) can be successively isolated from the rest of the microcosm by inserting Plexiglass plates into 4 pairs of

135   small gutters attached to the aquarium walls (Fig. 1c). At each consecutive sampling time, sediment samples and geochemical measurements were collected from the newly isolated compartment. To limit evaporation, the three aquaria were covered with
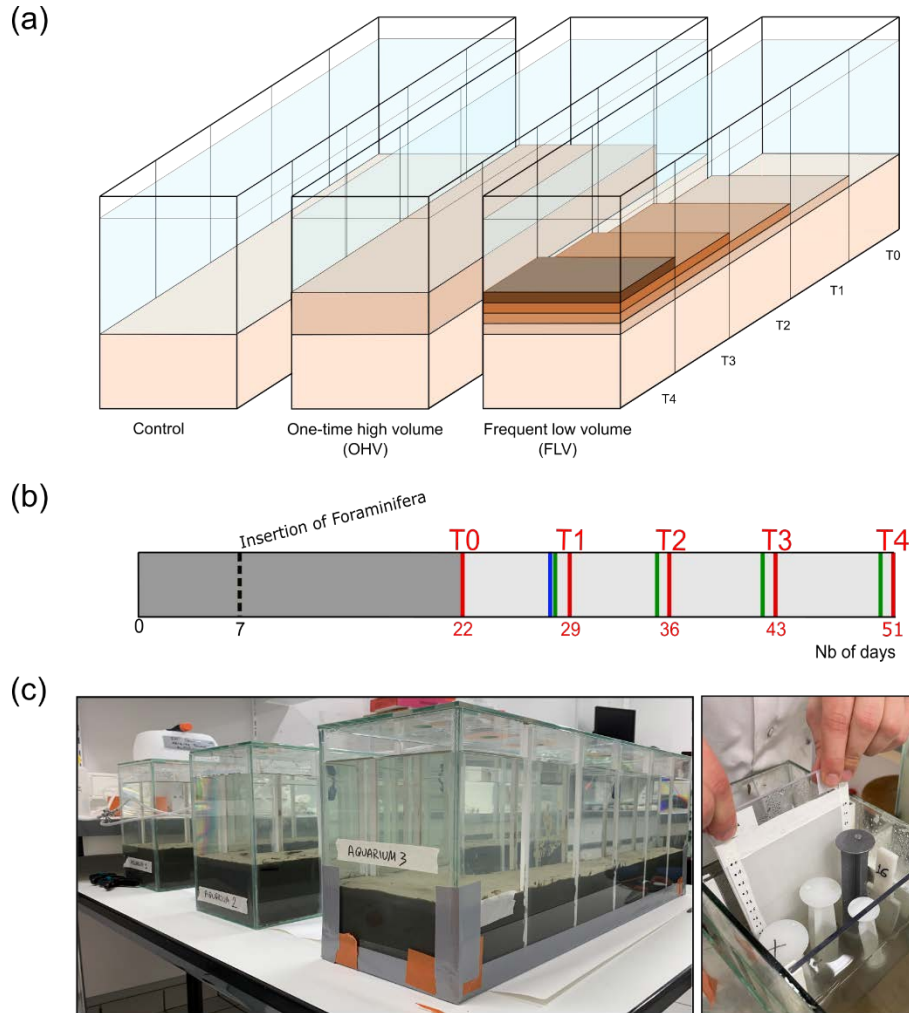
Figure 1: a) The three aquaria correspond to the control and the two sediment deposit modes. Successive deposit layers are symbolized by darker colours. The sampling times (T0 to T4) are mentioned at level of the associated compartment, which was sampled at that time, and are also linked to b) the timeline showing sediment inputs (blue bar for OHV and green bars for FLV) and core sampling times (D+2 after disturbances, red bars) as a function of the number of days of the experiment, starting from the introduction of the sediment into the aquaria (day 0). The insertion of foraminifera occurred on day 7 and the dark grey area represents the period (22 day long) for geochemical and foraminifera equilibration. c) Picture of the experimental set-up after the sediment substrate addition on day 5 and in-place sampling devices (syringes) after the section closing by Plexiglas plates (right).

a large glass plate with a hole above each compartment allowing the introduction of a continuous bubbling system to maintain good oxygenation and mixing of the water in the aquaria.

2.3 Experimental preparation

Natural coastal seawater, with a salinity of 33 and very low turbidity, was collected and microfiltered using paper filters with a mesh size of 0.45 µm before filling a 100-litre water tank. This filtration ensured the removal of organic or mineral detritus and of macro-, meso- and micro-organisms that might have interfered in the microcosms. A closed water circuit equipped with a pump was installed to initially fill the aquaria from the water tank. On day 35, after a breakdown of the pumping system, it was decided to manually renew the water in the aquaria by replacing it completely at each sampling time and at about 2/3 of the volume twice a week, with water from the tank.

The sediment used to constitute the initial sediment (Fig. 1, light beige), was collected at low tide on the Couplasse mudflat (Bourgneuf Bay, 47°0'57" N, 2°1'29" W) on January 13, 2021, and stored in sealed plastic bags at -20°C until the experiment was set up. The purpose of this freezing step was to preserve in-situ organic matter content and freshness, and to kill any biota that might be living in this sediment. In this way, we were also sure that this sediment substrate was free of the *in situ* foraminiferal community. Grain size analysis on sediment aliquots performed using a laser diffraction particle analyser Malvern Mastersizer 3000 revealed a unimodal distribution (mode 6 µm), with a D_{50} of 10 µm and a D_{90} of 47 µm. Proportion of silt and clay were 93% and 7%, respectively. The material used to simulate sedimentary disturbance was prepared as follow: the sediment collected at La Couplasse was unfrozen and diluted with the microfiltered seawater in order to obtain a highly turbid solution. This dense solution was slowly introduced into the water column of the aquaria via a small diameter plastic tube. The particles settled down on the prior sediment surface. To seed the microcosms in a controlled manner, living foraminifera were collected on February 16, 2021, at low tide, at the same location as for the sediments, i.e. the Couplasse mudflat. Surface sediment was sieved *in situ* to recover the 125-500 µm size fraction. This size fraction included foraminifera and possibly meiofauna or juveniles of macrofauna and some organic matter detritus. Samples were conditioned in 500 mL plastic bottles with 1/5 sediment and 4/5 *in situ* seawater. Then, the samples were stored in the temperature-controlled room (at 14°C) where the experiment was conducted and were air-bubbled until insertion into the microcosms.

On day 0 (February 16, 2021; Fig. 1b), a layer of approximately 9 cm thick was placed on the bottom of each aquarium, carefully avoiding the formation of internal voids, and ensuring a flat sediment surface. The required amount of sediment was thawed and homogenized just before filling the aquaria. After a few hours, the necessary time for the settling of the fine particles, filtered seawater was gently introduced to fill the aquaria with a 10 cm high water column, avoiding any disturbance at the water-sediment interface. The three aquaria, kept oxygenated by the air-bubbling system, were left to stand for seven days prior the insertion of foraminifera to allow for sediment compaction and initial equilibration of the redox fronts.

On day 7 (February 23, 2021; Fig. 1b) the sediment was seeded with living foraminifera, the major challenge was to obtain a spatial distribution of living specimens as homogeneous as possible over the entire sediment surface in each aquarium. Each

microcosm was divided in 40 rectangles (5 x 3.75 cm). For this purpose, foraminiferal samples were mixed and then split into 5 ml sub-samples. The 5 ml aliquots were carefully inserted with a small syringe into each rectangle of a grid placed just above the sediment-water interface and immediately removed after insertion of the foraminifera. Then, a 15-day rest period was observed before the first sampling (T0) to let the individuals reach their preferential microhabitats in the sediment.

2.4 Experimental procedure

The sampling period began on day 22 (Fig. 1b), after filling the aquaria with sediment and water on day 0 and inserting the foraminifera on day 7 (Fig. 1b). Five successive samplings (T0 to T4) were done every week, each in one compartment of each microcosm (Fig. 1a). On day 22, a first sample (T0) was taken from the first compartment of the three microcosms, before the application of any disturbance. After sampling, the compartment was closed using Plexiglas plates carefully inserted in gutters placed on the side of the microcosms (white vertical lines on the glass; Fig. 1c) and drained of its water. The water in the remaining part of the aquaria was renewed the next day with water from the 100L-tank. In the control microcosm (left aquarium in Fig. 1a), the next 4 samplings (T1 to T4) were done in successive compartments of the aquarium that were not subjected to any sedimentary disturbance throughout the whole experiment. In the "One-time High Volume" microcosm (middle aquarium in Fig. 1a), a 2.7 cm thick (after definitive particle settling) sediment layer was added at once, the day before sampling T1 (day 29, blue bar Fig. 1b). Afterwards, samplings T2 to T4 were done in successive compartments of the aquarium without further addition of sediment. After each sampling, the compartment was closed and emptied. In the "Frequent Low Volume" microcosm, a smaller amount of sediment was added each week (day 28, day 35, day 42, day 50; green bars Fig. 1b) to stack layers of approximatively 0.3-0.5 cm thickness each. Samplings T1 to T4 were done in successive compartments of the aquarium, on the day following each sediment addition. Therefore, T4 sampled a sedimentary column containing the four successive 0.3-0.5 cm layers in the last compartment.

2.5 Control of the stability of the microcosms

To monitor the stability of the microcosms, salinity and temperature measurements were performed daily with a WTW® Multi 3620 probe (measurement resolution of 0.1 and 0.1°C for salinity and temperature, respectively). Air-bubbling ensured a good oxygenation and mixing of water, thus preventing water stratification. A lateral view of each aquarium was photographed daily using a Nikon D3400 camera to monitor visual changes in the sediment column (e.g., colour, compaction, bioturbation). The effect of sediment disturbance as a physical cover of the sediment surface was followed by dissolved oxygen profiling in the sediment giving the oxygen penetration depth (OPD). However, no measurements were available at T3 due to experimental failure. Measurements were done the day after each sampling time (i.e., 2 days after the sedimentary disturbance), using 50 µm tip diameter Clark-type Unisense™ microelectrodes mounted on an automated micro-manipulator (Revsbech, 1989) taking

measurements with a 50 µm vertical step. Significant differences among sampling times and/or microcosms were tested by ANOVA and Tuckey post-hoc tests to investigate further and more detailed relations performed using R software.

Additionally, nutrient content (NH_4^+, NO_2^- and NO_3^-) in the water column was monitored and displayed as Total Inorganic Nitrogen (TIN). Indeed, fluxes from the sediment column resulting from the degradation of organic matter can lead to very high accumulations of inorganic N in the water column, which can result in the alteration of geochemical equilibria in the sediment (Hansen and Blackburn, 1992; Kristensen and Blackburn, 1987; Silverberg et al., 1995). 5 ml of water were collected at least every 3 days, filtered (0.2 µm, RC25, Sartorius ©) and stored at -20°C. Concentrations of all nutrients were measured using a spectrophotometric analyser (Genesys 20, Thermo-fischer ©). Ammonium (NH_4^+) concentrations were analysed using the Berthelot method adapted for small and seawater samples (Metzger et al., 2019). Nitrite concentrations were measured by a colorimetric reaction with the Griess reagent (Griess, 1879). The analysis of nitrate is the second step in the sequential determination described in García-Robledo et al. (2014) involving the use of vanadium chloride (VCl_3) to reduce nitrate into nitrite. Nitrate concentrations [NO_3^-] can therefore be calculated from the measured NO_2^- + NO_3^- using the following relation (García-Robledo et al., 2014):

$$[NO_3^-] = (Abs^V_{NOx} - Abs^V_{reagents} - S^V_{NO2^-} * [NO_2^-]) / S^V_{NO3}$$

Where: Abs^V_{NOx} is the final measured absorbance i.e., combination of [NO_2^-] and [NO_3^-], $Abs^V_{reagents}$ is the absorbance of VCl_3 without [NO_2^-] or [NO_3^-], S^V_{NO2} and S^V_{NO3} are the slope of calibration curves after VCl_3 adding, [NO_2^-] is the previously calculated concentration of nitrite in the sample.

2.6 Experimental sediment sampling procedure

At each sampling event (18h after the physical disturbance), one compartment of the aquarium was physically separated from the rest of the aquarium, the overlying water was carefully pumped out to limit sediment resuspension, and four cores (2.9 cm internal diameter, ~ 8.5 cm long) were collected using adapted syringes, acting as miniature disposable piston corers. Two cores were used for foraminiferal analyses (including one replicate), one for porosity analysis (data not shown in this paper) and one was resin-embedded for further geochemical analyses (data not shown in this paper). Foraminiferal cores were immediately sliced every 0.2 cm down to 4 cm depth, then every 0.5 cm from 4 to 7 cm depth.

For living foraminifera analyses, sediment slices were labelled with CellTracker Green (CTG). CTG is a dye which is hydrolysed during metabolization by living individuals, resulting in a fluorescent green staining of the cytoplasm (Bernhard et al., 2006; Choquel et al., 2021; Geslin et al., 2014; Nardelli et al., 2014; Pucci et al., 2009; Richirt et al., 2020; Ross and Hallock, 2018). This CTG label therefore identifies foraminifera with an active metabolism and is highly reliable to detect short temporal responses of foraminifera to disturbances. Following Bernhard et al. (2006), samples for foraminiferal analyses

were incubated at experiment temperature (14°C) in a CTG solution (CellTracker[TM] Green, 1mM final concentration) in microfiltered seawater during 24h. After incubation, the solution was fixed in 70% ethanol and sieved over 125 µm mesh
235   screens (corresponding to the minimal size of the foraminifera introduced in the experiment). The counting process of living individuals was performed under epifluorescence stereomicroscopy (i.e., 470 nm excitation; Olympus SZX13). Only specimens presenting a clear and continuous fluorescence were picked and counted at the species level. Total foraminiferal abundances (per core) were calculated taking in account the counting of all individuals living in the whole sediment column of 7 cm depth with a section of 6.60 cm^2 and expressed in number of individuals per 10 cm^2 (ind. 10 cm^{-2}), being the sum of
240   individuals counted in each core slice. Foraminiferal densities per core slice were expressed as individuals per 10 cm^3 (ind. 10 cm^{-3}).

Additionally, one core from the second sampling time of the "One-time High Volume" microcosm (OHV T1) was selected to test for an eventual correlation between vertical migration rate and foraminiferal test size. Following the procedure of Richirt et al. (2020), high-resolution pictures (6016 x 4016 pixels) of the entire assemblage picked in each core slice were taken using
245   a camera (Nikon[TM] D750) set on a stereomicroscope. Each specimen of the investigated assemblage was placed on its ventral or dorsal side to obtain a picture of the maximal test length. Images were processed using ImageJ software (Schneider, 2012) with which the maximum diameter of each isolated individual was measured, and the specimen area was calculated in $µm^2$ (Richirt et al., 2020). In our study, data are presented by species and on a vertical scale corresponding to all slices of the investigated core OHV T1. Statistical analysis was performed using R software. Univariate ANOVA tests were performed to
250   compare the size of individuals in all core slices. Tukey post-hoc test was carried out when the ANOVA was significant. Displacement speeds were estimated on the same core OHV T1. To do so, we measured the vertical distance between the initial water-sediment surface and the level within the newly deposited sediment reached by living foraminifera. This distance was therefore travelled upwards between the time of sediment addition and the sediment sampling time (i.e. 18h). The maximum speeds (mm.h^{-1}) were calculated by species, using the maximum vertical distance travelled by individuals of the
255   two species *Ammonia confertitesta* and *Haynesina germanica*. The accuracy of the distance measurement is 0.2 cm (core slice thickness). The mean speeds (mm h^{-1}) were calculated by species, based on the vertical distance travelled above the initial water-sediment interface, weighted by the number of living individuals found at this level.

3 Results

3.1 Geochemical stability of the microcosms

260 Temperature and salinity were kept constant during the whole experiment in the 3 microcosms (Salinity 32.9 ± 0.50; T 14.7 ± 0.18°C). The monitoring of TIN concentrations in the water column throughout the whole experiment, is presented in Fig. 2. From the filling of the aquaria (day 0) until day 15, a strong addition of 340 µmol L^{-1} of TIN was observed, with a concentration increasing from 60 µmol L^{-1} at the maximum of 400 µmol L^{-}. This approximately 3-day peak (day 14 to day 16) was immediately followed (day 17) by an abrupt strong decrease to a concentration of about 160 µmol L^{-1}. TIN then showed a

265 progressive decrease with oscillations of about 100 µmol L^{-1} in amplitude, with the maximum of these oscillations occurring just before water renewal. From T1 until T4, the concentration remained below 100 µmol L^{-1}, except for relative peaks of about 110-150 µmol L^{-1} observed just after each sediment disturbance. Variations in TIN concentrations were relatively synchronized in all three aquaria, except just after the sediment disturbance at T4 in the FLV microcosm.

At the first sampling time T0, OPD varied between 1.3 mm and 1.8 mm in the three aquaria (Fig. 3). This variation has a lower
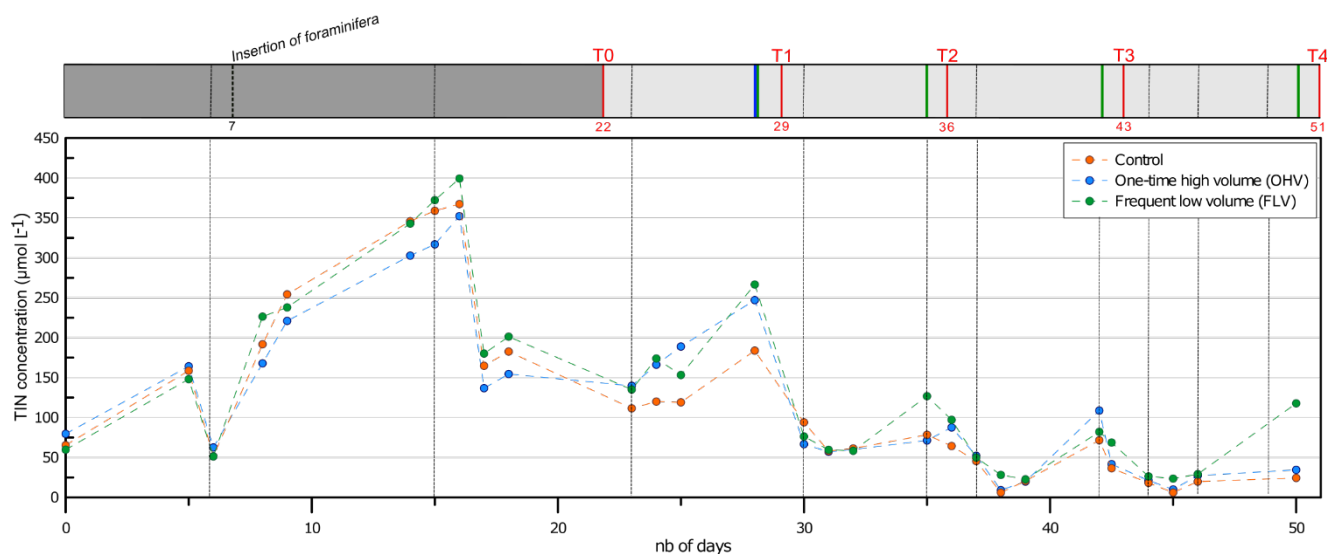
Figure 2: Total inorganic nitrogen concentration in the water column ($NH4^+$, $NO2^-$ and $NO3^-$) in the three aquaria throughout the experiment. Vertical black dotted lines indicate water renewals (after each sampling time and more frequently after the pump breakdown at day 35). The header displays the timeline explained in Figure 1b.

270 range than the 2 mm resolution (size of the upper core slices) used in our foraminifera analysis. From T0 to T1, in both control and FLV microcosms, oxygen penetration showed a significant shallowing (p-values < 0.05) to a depth of 1.2 +/- 0.2 mm and then remained stable until T4. At T1 and within the OHV microcosm, at T1, OPD deepened to 2.1 +/- 0.1 mm after the massive deposit. After T1 and until the end of the experiment, oxygen penetration presented a shallowing trend reaching the same depth as in the other two microcosms at T4 (1.3 +/- 0.3 mm for the control microcosm, 1.2 +/- 0.2 mm for the OHV microcosm and

275 1.2 +/- 0.2 mm for the FLV microcosm).

Lateral views of the OHV and FLV aquaria show the sedimentary column at 4 different moments of the experiment (Fig. 4), allowing us to track sediment compaction and colour changes during and after the sedimentary deposits. At day 14 (before any disturbance), the sediment column (i.e., the "substratum" of the experiment) was homogeneous in the three aquaria. It was

280 already compacted, and no more fine sediment was visible in suspension in the overlying water column. A few millimetric black spots, scattered within the sediment matrix, were most likely microniches of organic matter anaerobic remineralisation
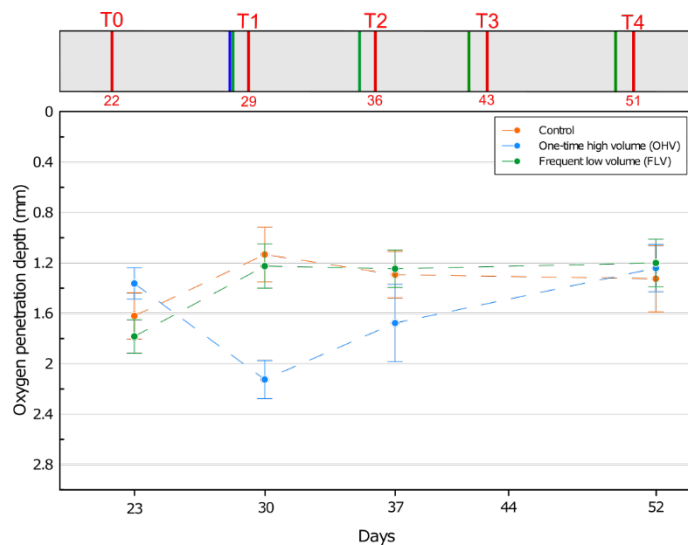
Figure 3: Mean oxygen penetration depth with associated standard deviation for each microcosm and at each sampling time. No data available for T3. On the y axis, 0 at the top represents the water-sediment interface. The header displays the timeline explained in Figure 1b.

(Jørgensen, 1977; Lehto et al., 2017; Widerlund et al., 2012). At 9 cm height in the aquaria, the initial water-sediment interface was clearly visible as a doublet of yellowish and black millimetric layers (2-3 mm), constituted of the material (foraminifera and associated particulate organic matter) introduced on day 7. The upper yellowish layer corresponded to the well oxygenated

285 layer of this material. Its thickness was consistent with measured OPD (Fig. 3). The underlying black layer corresponded to the anaerobic degradation of the introduced organic matter.

On day 28, the first sediment addition occurred in two aquaria. A thick layer (about 4.3 cm) of beige sediment in the OHV microcosm and a thin layer (about 1 cm) in the FLV one, were deposited above the former water-sediment interface that was
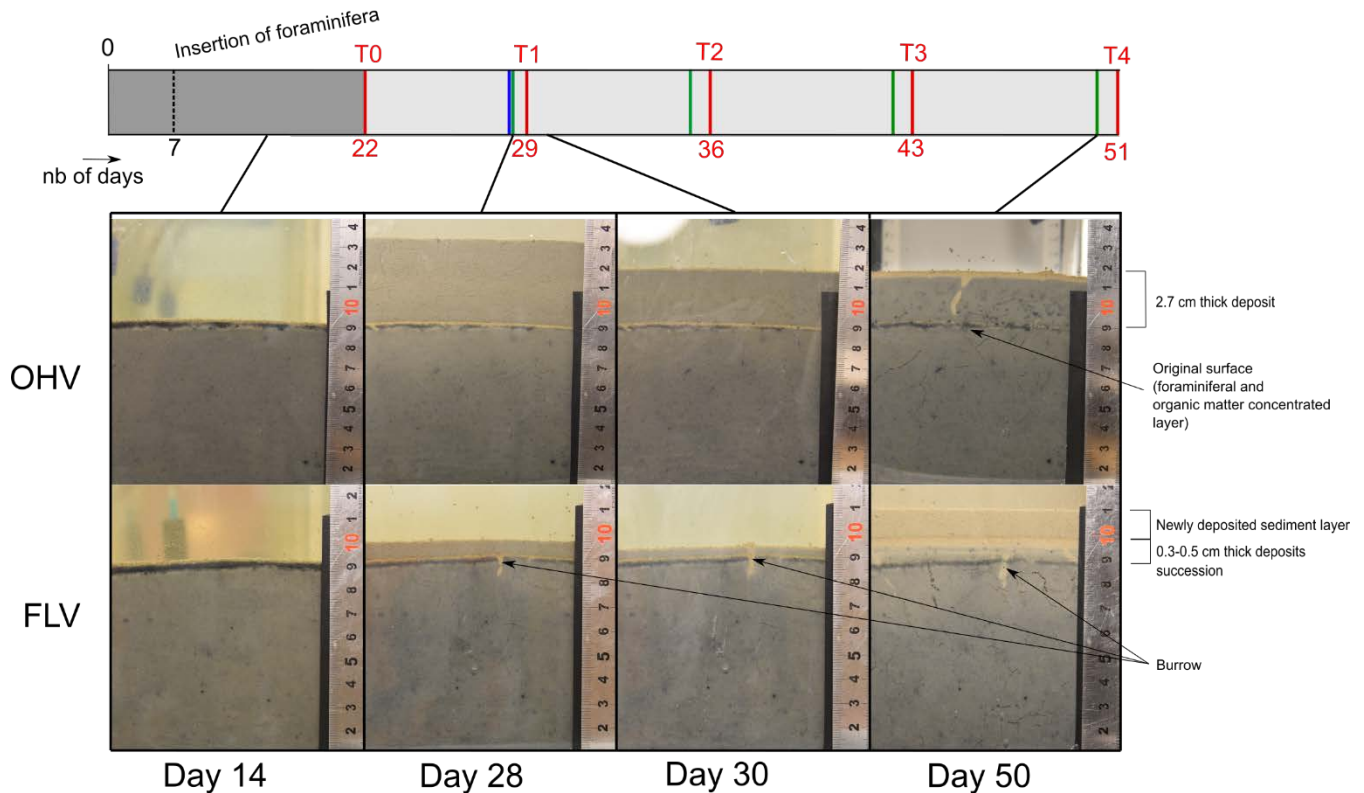
Figure 4: Lateral views of the "One-time high volume" (OHV) and "Frequent low volume" (FLV) sedimentary disturbances, at 4 different times during the experiment. The header displays the timeline explained in Figure 1b.

still very clearly visible. On day 30, the sediment layer thickness in both aquaria was already reduced to 2.7 cm in the OHV microcosm and to 0.5 cm in the FLV one. This rapid compaction of about 1/3 of the newly deposited sediment occurred within 2 days. In both aquaria, the first T1 deposit was well marked between the initial surface (yellow/black doublet) and a very thin (< 1 mm) yellowish layer at the new water-sediment interface. This light colour underlined the good oxygenation of the superficial sediment less than two days after the deposit.

On day 50, in the FLV microcosm, it was possible to detect the 4 successive supplies of sediment by observing the layering of yellow/black doublets in the final 2 cm thick layer. As a final last important observation, we noticed the rare development of small vertical burrows (Ø < 1 mm, a few cm long) in all three aquaria. In our experiment, the bioturbation was limited by the freezing of the sediment used to fill the aquaria and the initial sieving (< 500 µm) of the biological material introduced on day 7.

3.2 Effects of sedimentary disturbances on total foraminiferal abundances

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Variations in total foraminiferal abundances were analysed during the experiment for the three aquaria. At T0, before any sedimentary disturbance, the total foraminiferal abundances varied in the three aquaria between 790 and 1483 ind. 10 cm^{-2} (Fig. 5). In the OHV microcosm, a linear regression demonstrates a significant (R^2= 0.55; p-value=0.01) decreasing trend in foraminiferal abundances over time, with an average loss of about 300 ind. 10 cm^{-2} (863 ± 73 ind. 10 cm^{-2} at T0 and 582 ± 31

305 ind. 10 cm^{-2} at T4).

There is no such significant trend in foraminiferal abundances with time, neither in the control microcosm (R^2=0.15; p-value =0.29), nor in the FLV microcosm (R^2=0.23; p-value =0.22). In the case of the control microcosm, the high variability between replicates was maximum at T4, ranging from 650 to 1100 ind. 10 cm^{-2}.
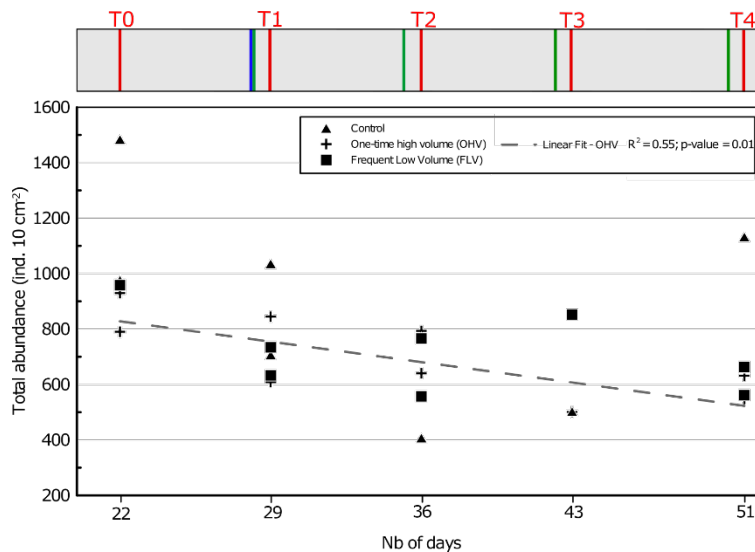
Figure 5: Total foraminiferal abundances (>125 µm) per core sampled in each microcosm at each sampling times. The displayed values are the abundances of two replicate cores (n=1 for Control T3, FLV T0 and FLV T3). The regression line is shown for OHV with R2 and associated p-value (other regression lines are not drawn because not significant). Days from the start of the experiment are indicated on the x-axis. The header displays the timeline explained in Figure 1b.

3.3 Effects of sedimentary disturbances on assemblage composition

Variations in relative species abundances per core were analysed for the three microcosms over the course of the experiment (Fig. 6). The foraminiferal assemblage used in this experiment was mainly composed by *Ammonia confertitesta* and *Haynesina germanica*. At T0, in all the aquaria, *H. germanica* was dominant, accounting for 63 to 79% of the assemblage. Thereafter, the abundances of *A. confertitesta* and *H. germanica* balanced out to become equally distributed at T3. At T4, *A. confertitesta* exceeded 50% in all aquaria, and became particularly dominant in the FLV microcosm where it accounted for 68 % of the assemblage. Relative abundances showed a clear shift from an initial domination of *H. germanica* over *A. confertitesta* to a more balanced assemblage. A few specimens of *Elphidium* spp., another species known to live in low abundances in the upper
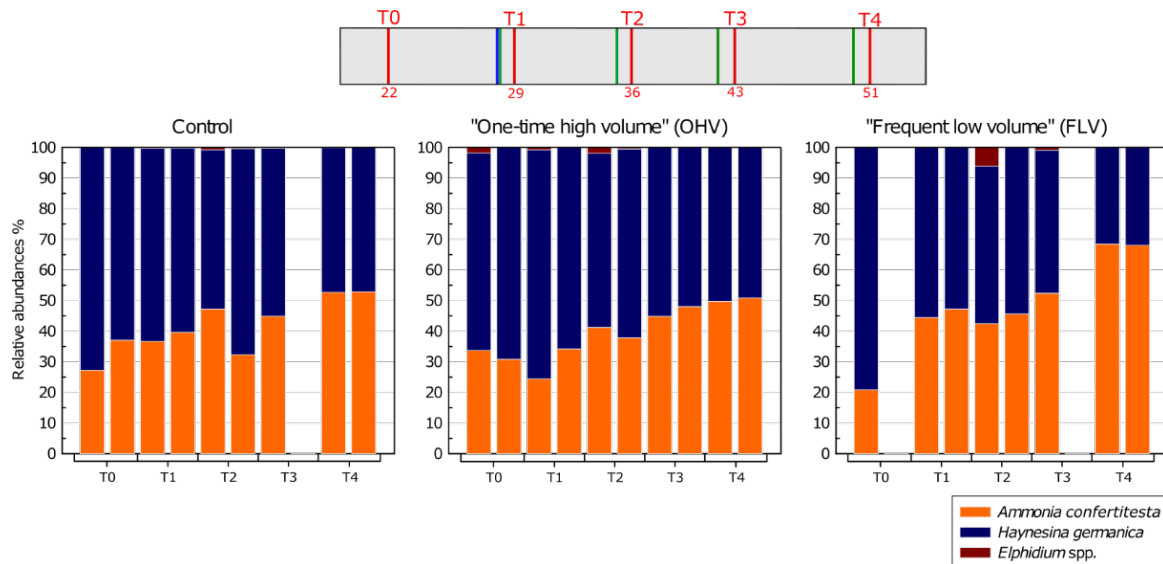
Figure 6: Relative abundances (%) of each species (>125μm) per core – with replicates – sampled in each microcosm at each sampling times. The displayed values are the relative abundances of two replicate cores (n=1 for Control T3, FLV T0 and FLV T3). The header displays the timeline explained in Figure 1b. Note the absence of a second replicate in the Control T3 and FLV T0 and T3 due to sampling failures.

mudflat of Bourgneuf Bay in winter (Choquel, 2021), were occasionally found in the sediment samples of the three aquaria. They represented at maximum 6% of the total assemblage (31 individuals counted out of 506 ind.) in only one core (FLV T2 replicate) but were mostly absent from the other cores or present at less than 2 %.

Variations in the abundances of *A. confertitesta* and *H. germanica* per core analysed for the duration of the experiment in the three aquaria were therefore examined more specifically (Fig. 7). In the control microcosm, the total abundances of *A. confertitesta* and especially *H. germanica* were very variable between replicates throughout the experiment.

325 Concerning *Ammonia confertitesta*, abundances in the OHV microcosm did not show any significant trend in time and were found in the narrow range of 220 - 300 ind. 10 cm^{-2}, except at T1 just after the thick single sedimentary disturbance, when
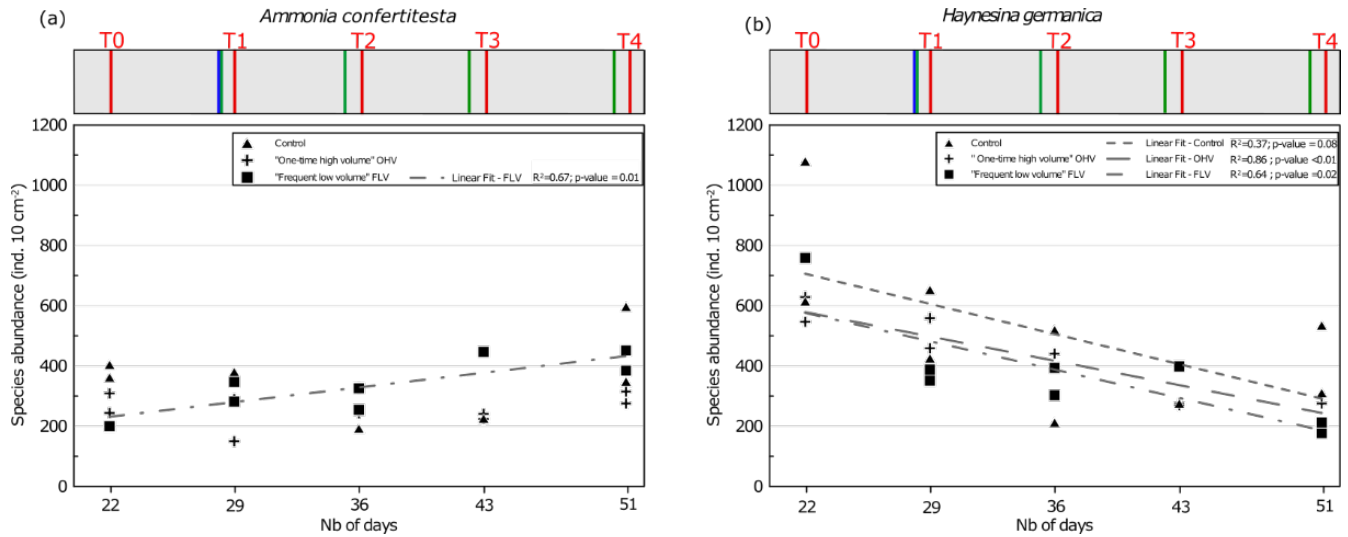
Figure 7: Foraminiferal abundances of the two main species in sampled replicates, A) *Ammonia confertitesta* **and B)** *Haynesina germanica* **at each sampling time. Replicates are missing at FLV, T0, T3; Control T3. The regression line is shown for FLV with R2 and associated p-value (other regression lines are not drawn because not significant). The header displays the timeline explained in Figure 1b.**

abundances dropped to 150 ind. 10 cm^{-2}. In the FLV microcosm, a significant increasing trend occurred (p-value < 0.05), doubling total abundances from T0 to T3, and then abundances remained stable between T3 and T4. However, the lack of a second replicate at T0 did not provide information on the initial variability. Concerning *H. germanica*, total abundances

330 significantly (p-value < 0.05) decreased throughout the experiment, from ~600 to ~300 ind. 10 cm^{-2} in the OHV and from ~750 to ~200 ind. 10 cm^{-2} in the FLV. In the control microcosm, abundances decreased from 1100 ind. 10 cm^{-2} at T0 to 300 ind. 10 cm^{-2} at T4. The high variability between replicates, particularly at T0 and T4, partially concealed the decreasing trend and resulted in a relatively bad correlation, with a R^2 of 0.37 and a p-value of 0.08.

335 **3.4 Effects of sedimentary disturbances on vertical distributions**

In the Control microcosm (Fig. 8a), vertical distributions of both species, *Ammonia confertitesta* and *Haynesina germanica,* showed the highest densities of individuals in the uppermost 0.2 cm of sediment throughout the whole experiment. The uppermost 0.2 cm layer contained between 58 and 81 % of the total assemblage found in the 7-cm sediment column. For both species, a similar exponential decrease with depth occurred down to 0.8 to 1.4 cm. Below this depth, no living individuals

340 were found. Concerning the OHV treatment, a vertical profile similar to the one of the Control microcosm occurred at T0, with maximum densities in the uppermost 0.2 cm and an exponential decreasing profile with depth, down to about 2 cm depth (Fig.

8b). At T1, 18h after the addition of about 2.9 cm of sediment (before full compaction) above the initial water-sediment interface (dotted line in Fig. 8b), the foraminiferal vertical distribution displayed unimodal profiles with modes, or maximum densities, situated 2.3 cm below the new surface, or 0.6 mm above the initial water-sediment interface. Densities then showed a quite symmetrical decreasing upwards and downwards the density peak. Approximately 71% of the fauna was found between 2 and 3 cm depth, where the specific composition of the assemblage was equally represented by *A. confertitesta* and *H. germanica*. No living foraminifera were detected above 0.2 cm depth and below 3.4-3.6 cm depth, in both replicates. The few individuals that reached the upper sediment layers (from 2.2 cm to 0.8 cm depth) and those that remained at depth below the mode, were identified as belonging to the species *H. germanica*. At T2, after full compaction giving a total sediment height of 2.7 cm above the initial water-sediment interface (Fig. 4), the assemblages had shifted toward the new surface to concentrate in the upper layers of the sediment column (0 to 1.2 cm depth maximum below the new sediment surface). Vertical profiles showed exponential decreasing with depth. Only a few specimens, belonging exclusively to *H. germanica,* were found in layers deeper than 1.2 cm (Fig. 8b). This distribution remained quite similar in the successive sampling times T3 and T4, with a slight increase (30%) of *A. confertitesta* in the topmost layer (0-0.2 cm) and a decrease in the deeper layers (below 0.4 cm depth). In Fig. 8c, assemblage profiles in the "frequent low volume" (FLV) microcosm are drawn shifted upwards from the initial water-sediment interface. The distance between the new and former interfaces illustrates the thickness of the sediment supplied before each sampling time. On the day before each sampling time (T1 to T4), successive 0.3-0.5 cm thick sediment deposits were added, and thus the ancient surface (black dotted line in Fig. 8c) was further buried. At T0, assemblages displayed a similar vertical distribution profile as the other microcosms (Fig. 8c). However, the assemblage was not balanced. *Ammonia confertitesta* was only present above 0.2 cm depth, with ~ 900 ind. 10 cm^{-3}, whereas *H. germanica* was present to 1.2 cm depth and was 75% dominant in the surface layer, with ~ 3100 ind. 10 cm^{-3}. At T1, the vertical distribution of foraminifera, in both replicates, was back to the original profile of T0, with a maximum foraminiferal density above 0.4 cm depth and no specimens below 1.2 cm depth. However, the assemblages showed a decrease in the relative density of *H. germanica* compared to T0 (70 % in the upper layer). At T2 and T3, most specimens were still concentrated in the uppermost 0.2 cm, with about 2000 ind. 10 cm^{-3}. Below the 0-0.2 cm level down to the initial water-sediment interface (0.8 cm depth at T2 and 1.1 cm depth at T3), the vertical distribution displayed persistent low densities of less than 100 ind. $10cm^{-3}$ and 100-300 ind. 10 cm^{-3} for T2 and T3 respectively. From T1 to T4, *H. germanica* densities decreased in the uppermost layer in favour of *A. confertitesta*, while it remained dominant in the deeper layers (Fig. 8c). At T4, *A. confertitesta* largely dominated the 0 to 0.4 cm depth layers, with about 1900 ind. 10 cm^{-3} versus 200 ind. 10 cm^{-3} for *H. germanica*. Below 0.4 cm depth, lower densities (~140 to 240 ind. 10 cm^{-3}) of *A. confertitesta* were observed whereas *H. germanica* appeared more abundant below 0.4 cm depth (~660 to 860 ind. 10 cm^{-3}).
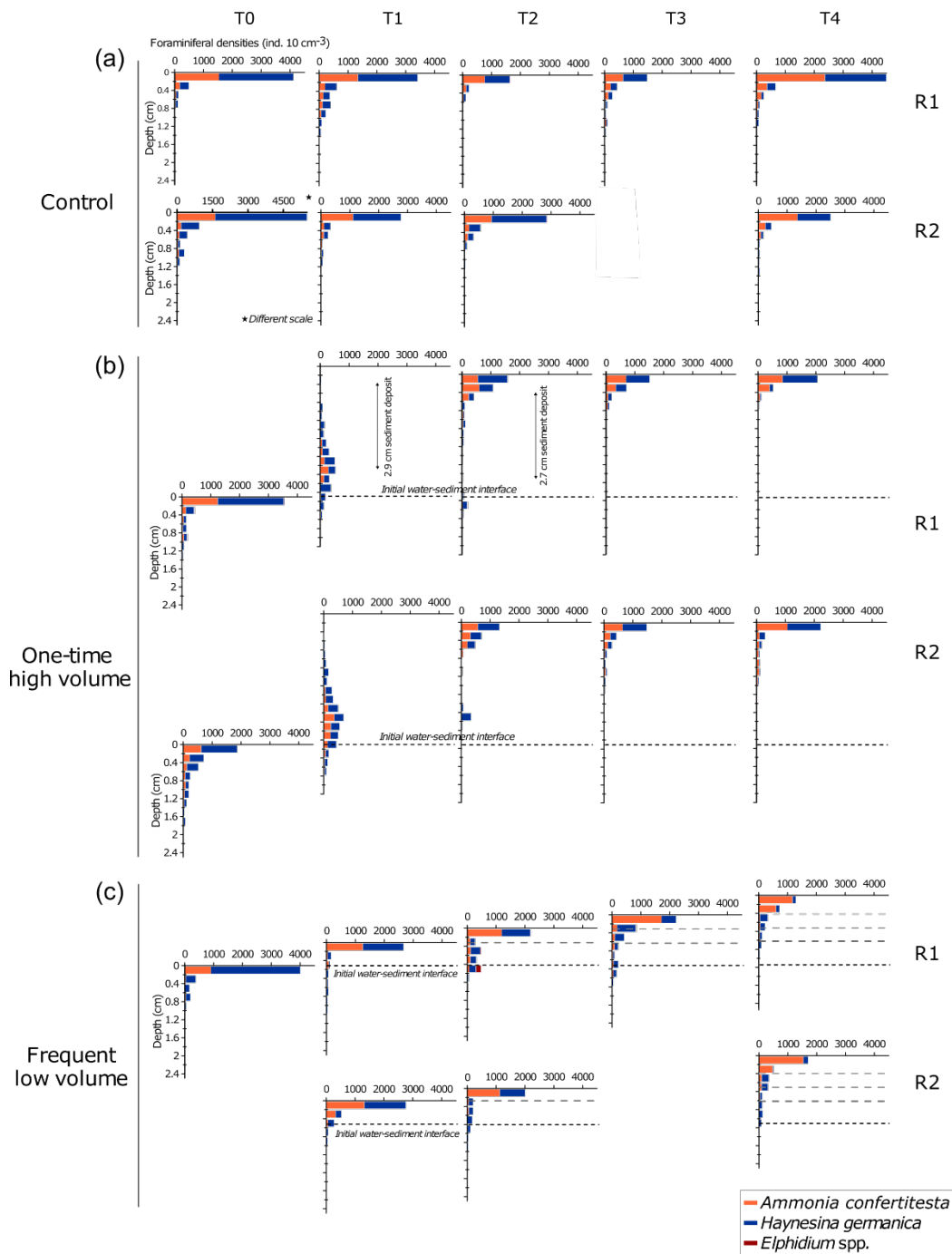
Figure 6: Vertical distribution of specific densities of living foraminifera in replicates at each sampling time displayed for each microcosm. The water-sediment interface of each plot is aligned with the previous one to illustrate the added sediment layers in the OHV and the FLV microcosms. The scale of x-axis of the Control T0 replicate 2 is different than the others. Note the absence of a second replicate in the Control T3 and FLV T0 and T3 due to sampling failures.

3.5 Foraminiferal migration: relationship with test sizes and specific speed

375   To evaluate the migration speed of each species, data from the OHV core T1 replicate 1 (T1 R1) was used. This core was collected at T1, 18 hours after the disturbance that buried the initial water-sediment interface under a thick sediment layer (2.9 cm after compaction, Fig. 4). The foraminifera spread in the added sediment layer displayed a unimodal vertical distribution, where the density peak was located in the sediment slice 2.2-2.4 cm depth below the new surface, thus at 0.5-0.7 cm above the initial interface. Compared to the distribution profile displayed before the disturbance (T0), we observed an upward migration

380   of both species *Ammonia confertitesta* and *Haynesina germanica*, with a maximum vertical distance covered of 2.6 cm at the time of sampling (Fig. 8b). Some individuals of the two species did not migrate at all as they were still present below the initial interface (6% of total *A. confertitesta* individuals versus 14% for *H. germanica*). The weighted mean speed was different between the two species (respectively 0.41 mm h^{-1} for *A. confertitesta* and 0.47 mm h^{-1} for *H. germanica*).
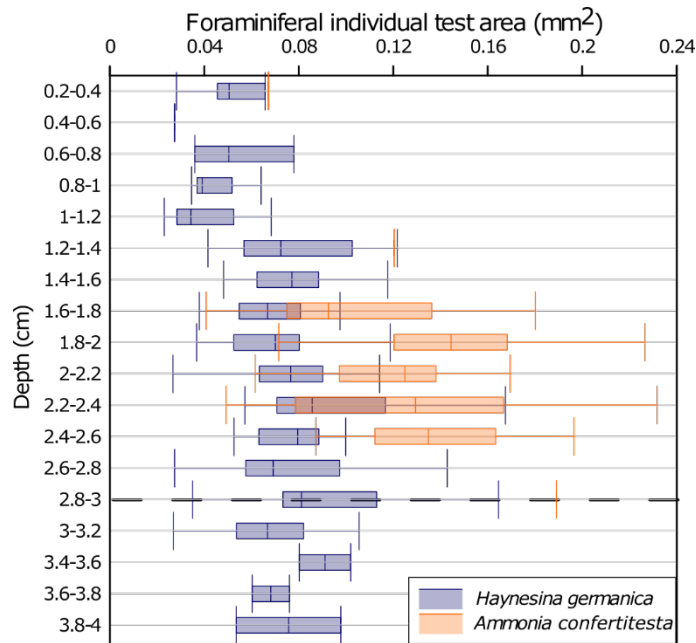
Figure 7: Vertical distribution of benthic foraminiferal test size in the "One-time high volume" microcosm, core T1 R1. Values are shown as box plots (median, 25 and 75 quartiles) The depth is expressed by sediment slices. The dotted line (at the 2.8-3 level) symbolizes the initial water-sediment interface before the sedimentary disturbance.

   Based on the results of the T1 R1 core from the OHV microcosm, we investigated the correlation between the individual's test

385   size of each species and their location in the sediment column to find an eventual relationship between size and migration speed. To do so, a morphometric analysis was performed on the test of each specimen found at each sediment layer. The vertical distribution of the individual test area (mm²), mean values and standard deviations, are shown by species in Fig. 9.

The results showed a very high heterogeneity of test areas for *Ammonia confertitesta*, with values spreading from 0.04 mm^2 to 0.2 mm^2, around median values per slice of approximately 0.1 mm^2. The statistical test did not reveal significant differences (ANOVA, p-value = 0.119) in *A. confertitesta* test size between the different sediment slices. For *H. germanica*, however, statistically significant differences were found between sediment slices (ANOVA, p-value= 6.17e^{-6}). However, the Tuckey post-hoc test highlighted significant differences between the 0.8 to 1.2 cm depth interval compared to the two similar depth intervals 2-2.6 cm and 2.8-3.0 cm. Above 0.8 cm depth, the size of *H. germanica* specimens did not show significant differences with the other levels.

4 Discussion

4.1 Geochemical and physical stability of the experimental system

Parameters like temperature, salinity, TIN in overlying water and O_2 penetration in the sediment were monitored throughout the experiment in order to control the geochemical stability of the microcosms. While water in the microcosms was often renewed, temperature and salinity remained constant, whereas TIN concentrations and OPD demonstrated that the geochemical stability of the microcosm was difficult to reach.

In the first part of the experiment (before day 14; Fig. 2), the high TIN concentrations could be attributed to the seeding of the microcosm, including, along with living foraminifera, high quantities of phytodetritus, meiofauna and fecal pellets ($< 500 \, \mu m$). This organic matter supply concentrated within a 0.3 cm layer at the sediment surface (organic matter concentrated layer; Fig. 4). The mineralisation of this organic matter is an additional source of TIN in the overlying water of the microcosms. After T0, recurrent increases of TIN underlined by sharp peaks (days 16, 28, 35 and 42), occurred from the water renewals until the following sampling (Fig. 2). This testified of continuous fluxes of TIN released from the sediment to overlying waters, causing an increase of TIN concentration in the water column interrupted by water renewals in the aquaria. The peak amplitudes gradually diminished due to the progress of organic matter mineralisation and impoverishment of the system.

Even if the geochemical state of TIN in the microcosm was not perfectly stable, the regular renewals of seawater prevented excessive accumulation of organic matter degradation products in the overlying waters and sediment, and were sufficiently effective to maintain TIN concentrations at a lower concentration range than that observed in the *in situ* sediment of the Bourgneuf Bay (Metzger et al., 2019).

The aerobic degradation of the organic matter added with the introduction of foraminifera on day 7 was probably responsible for the shallowing of the Oxygen Penetration Depth observed between T0 and T1, in the control and "Frequent Low Volume" (FLV) microcosm. From the introduction of foraminifera, the ODP stabilization in both microcosms was reached after 22-29 days (i.e., between T0 and T1). Indeed, previous experimental studies of meso-microcosms involving reworked sediment showed stabilization of oxygen fluxes and OPD after an equilibration period of 2-3 weeks (Ernst et al., 2002; Hansen and

420   Blackburn, 1991, 1992; Porter et al., 2006). In the FLV microcosm, a steady state set up from T1 until the end of the experiment, despite recurrent additions of small volumes of sediment that did not to affect OPD, whose values were similar to those of the Control microcosm. In the OHV treatment, the addition of a large volume of sediment at once was most likely the driving factor for the deepening of the OPD at T1 (Fig. 3). Indeed, the sediment added in the microcosm settled by decantation to form a deeper oxygenated and water-enriched layer (Fig. 4). It then took up to a maximum of 3 weeks for the OPD to reach a level

425   similar to that observed in Control and FLV microcosms during a steady state (T4, Fig. 3).

These results suggest that the large abrupt sediment supply could have a significant impact (p-value < 0.05) on OPD, and as such could be a driver of redox front shifts and microhabitat disturbance. In contrast, recurrent low sediment supply, resulting in the deposition of thin layers, did not show significant differences to the control and thus may be considered to have only slight or negligible impacts on benthic habitats.

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4.2 Effect of sediment disturbance on benthic foraminiferal abundances

A significant decreasing trend in total foraminiferal abundance is observed in the OHV treatment (Fig. 5). The foraminiferal living faunas are therefore more affected by the arrival of a higher amount of sediment in one time than by recurrent thinner inputs (FLV). This is in accordance with previous observations reported for marine areas subject to high sedimentary deposits,

435   e.g. turbidites deposits. In fact, Tsujimoto et al. (2020) reported lower abundances of benthic foraminifera after the deposit of about 10 cm of sediment after the 2011 Tohoku-oki earthquake, due to burial-associated foraminiferal death. This matches with other previously reported observations after turbidite events (e.g. Bolliet et al., 2014; Hess and Jorissen, 2009). In the case of the study of Tsujimoto et al. (2020) a first recolonisation of the superficial sediment by some of the species of the original assemblage (pre-turbidite) is observed within 5 months from the event, suggesting either the survival of some species

440   to the thick sediment deposit (and migration towards the surface) or the recolonisation of superficial sediment from refuge zones close to the sampling site. Since the recolonisation from refuge zones was impossible in our set-up, our results suggest that part of the assemblage could survive this kind of deposit at least during a short time interval (4 weeks). The presence of pre-event faunas on the recolonised sediment could be due to the remigration of buried faunas at the surface. The survival and reproduction of this fauna on longer time scales, however, were not assessed in our experiment. It is quite possible that

445   assemblages facing a similar event within a natural environment would receive species coming from refuge zones, as suggested by long term observations reported by (Bolliet et al., 2014; Hess and Jorissen, 2009; Tsujimoto et al., 2020).

The two other treatments of our set up (Control and FLV) did not show clear and significant trends, supporting the hypothesis that total foraminiferal abundances are not affected by frequent low volume sediment inputs. However, the trends were significantly different when we looked at the two main species of our microcosms separately. In fact, *Ammonia confertitesta*

450   did not suffer from a significant decline in abundance, neither in the control nor in the two treatments (Fig. 6 & 7a). The only significant linear regression was observed for the "Frequent Low Volume" microcosm where a slight increase of *A. confertitesta* abundance was observed through time. However, we believe that this result is untrustworthy as it was probably

due to a lack of replicates for the T0 and T3. Our observations were restricted to the > 125 µm fraction of faunas, only including adult specimens, so that we could exclude the possibility that reproductions during the experiment would be the reason for this increase.

In contrast, *Haynesina germanica* showed significant linear decreasing trends in the two disturbed microcosms (OHV and FLV) with time (Fig. 7b), suggesting that this species is more sensitive to all kinds (i.e., frequency and intensity) of burial than *A. confertitesta*. However, despite insignificant p-value (0.08) and a lower R^2 (0.37) than the two disturbed microcosms, a similar decreasing trend was also visible for the control microcosm. It is therefore difficult to completely attribute the decline of *H. germanica* to the different sediment inputs. The role of the experimental conditions on the species' response should be considered. Indeed, of the two main species used in our set up, *A. confertitesta* (often reported as *Ammonia tepida* in the existing literature) was widely used as a target species in experimental studies, and it is known to tolerate well laboratory conditions, also during longer time periods (i.e. days to months, e.g., (Bradshaw, 1957; de Nooijer et al., 2009; Denoyelle et al., 2012; Geslin et al., 2014, 2004; Le Cadre and Debenay, 2006; Nardelli et al., 2014; Koho et al., 2018; Deldicq et al., 2020; Stouff et al., 1999), which is in agreement with our observations (Fig. 7a). *Haynesina germanica* has been rarely used in previous experimental set-ups and only in short-time experiments (i.e., hours to days, e.g., Deldicq et al., 2021; Jauffrais et al., 2016b; Langlet, 2020; Seuront and Bouchet, 2015). The reason for the decreasing trend of *H. germanica* abundance in our control microcosm can be attributed to several experimental factors. It has a more restricted diet based on specific epipelic microalgae (Choquel, 2021, unpublished; Lee et al., 1989; Pillet et al., 2011), compared to the *Ammonia* group, which can alternatively feed on organic detritus, bacteria and meiofauna (Dupuy et al., 2010; Mojtahid et al., 2011; Pascal et al., 2009; Wukovits et al., 2018). Moreover, recent experimental results showed that *H. germanica*'s diet can switch from high quality (low C:N values) to lower quality organic material but that this switch often drives lowered fitness of the species (Wukovits et al., 2021). As the experiment was designed to observe the foraminiferal response to sedimentary deposits, we decided not to add extra organic matter during the experiment and limit the tested variables. The consequent decrease of organic matter quality during time could have been unfavourable to *H. germanica* in the competition with *A. confertitesta*. Moreover, it has been shown that *H. germanica* is a kleptoplastidic species that can assimilate undigested chloroplasts from specific microalgal preys (Choquel, 2021, unpublished; Jauffrais et al., 2016b; LeKieffre et al., 2018) and perform photosynthesis as an alternative metabolism (LeKieffre et al., 2018b). However, our experiments were mostly conducted in the dark (except at the sampling times), so this metabolism was unavailable to limit starvation.

4.3 Effect of sediment disturbance on benthic foraminiferal vertical distribution

4.3.1 Foraminiferal response to sedimentary deposits

According to the specific preferences, benthic foraminifera can have epifaunal to shallow infaunal (within the first 2 cm of sediment,), intermediate (1-4 cm) or deep (> 4 cm) infaunal microhabitats (Corliss, 1991). The two main species living in our

485 microcosm are mainly epifaunal or shallow infaunal (Alve, 2001; Bouchet et al., 2009; Cesbron et al., 2016; Murray and Alve, 2000; Papaspyrou et al., 2013; Thibault de Chanvalon et al., 2015). This preferential shallow life position is obvious when no bioturbation-induced modification of the sedimentary microhabitats occurs (e.g., Alve, 2001; Cesbron et al., 2016; Jorissen et al., 1992; McCorkle et al., 1997; Mojtahid et al., 2010; Murray, 2006). In accordance with the literature, most of living individuals of these two species were always located in the uppermost centimetre of the control microcosm (Fig. 8a). Similarly,

490 in both OHV and FLV microcosms, at T0 before the physical disturbance, most of foraminifera were observed in the 0-0.2 cm layer. According to Jorissen et al. (1995), this shallow habitat preference, in a not food-limited environment as the one in our microcosms, is mainly driven by oxygen availability. In our microcosms, the oxygen penetration depths varied within a range of 1.2 and 2.2 mm below the sediment surface in all the aquaria at all sampling times. This means that despite the significant OPD variations observed between T0 and T1, the oxic layers at all core tops were always thinner than the slicing resolution of

495 0.2 cm used for foraminiferal analysis. Therefore, it was impossible to determine a possible effect of OPD stabilisation on vertical distribution of the living foraminifera within the topmost 0.2 cm. Nevertheless, we can assess that the near absence of fauna below 0.2 cm depth could have been limited by oxygen availability. After the disturbances, in both the "One-time high volume" and "Frequent Low Volume" microcosms, an upward migration of the fauna was observed within a short time, i.e. 18h after each sediment addition. In the FLV treatment, the migration through the added sediment (0.2-0.5 cm) was rapid and

500 seemed to have followed the recovery of the oxic front in the uppermost layer (< 0.2 cm, Fig. 8c and Fig. 3). The same dynamic was repeatedly observed at all successive sampling times (1 day after a new disturbance event) and therefore suggests that in the FLV microcosm the resilience of the microhabitat was achieved within 18h after the sedimentary disturbance. This observation is in accordance with previous studies reporting rapid migration of epifaunal species after physical disturbance, but largely reduces the recovery time as previously reported (i.e., 22 days, Ernst et al., 2002). As we did not measure the

505 dissolved oxygen evolution between the moment of each sediment supply and subsequent sampling times, we cannot assess if this migration was performed under hypoxic conditions.

A rapid upward migration was also observed in the OHV treatment, following the addition of a thick (2.9 cm after 1 day of compaction) layer of sediment (Fig. 8b). In this microcosm, however, at T1 no living individuals were able to reach the sediment-water interface. The observed unimodal distribution centred within the added sediment layer suggests that the

510 migration started rapidly after the disturbance. At T2, the vertical distribution was comparable to the two other microcosms, with a peak at the surface and it remained the same in the following sampling periods, suggesting that the recovery was achieved within two weeks after the disturbance.

In the OHV microcosm, the foraminiferal fauna was positioned between 0.8 and 3 cm depth at T1, being in their migration phase before reaching the surface at T2 (Fig. 8b). During this period of migration, the OPD was measured at 2.1 ± 0.1 mm

515 depth (Fig. 3), meaning that all the foraminifera had been moving through anoxic sediment layers. The possibility of migration of benthic foraminifera through anoxic sediment and towards oxygenated layers was already reported by Geslin et al. (2004) for deep-sea species. The shallow-infaunal species we had in our microcosm, however, are generally reported as sensitive to oxygen depletion, in terms of motility. Despite several studies pointing out the ability of coastal foraminiferal species,

including *Ammonia* spp., to survive day to months long anoxia (e.g.., (Geslin et al., 2014; Nardelli et al., 2014), there is no consensus about their ability to actively move under anoxic conditions. In some studies, the vertical migration of *Ammonia tepida* (assimilated to *Ammonia confertitesta* here) was reported as being driven by the redox fronts. For example, Thibault de Chanvalon et al. (2015) attributed the observed bimodal distribution of this species in estuarine intertidal mudflats to the combination of downward burial by bioturbation and the ability of the specimens burrowed up to 3 cm down in the sediment to move back to the surface. These authors suggested that *A. tepida* is able to detect the oxygenated layer through geochemical gradients of other chemical species (e.g. NO_3^-, Mn^{2+} or Fe^{2+}). Other studies, however, highlighted the reduction or stop of motility of *A. tepida* in absence of oxygen and attributed this to a state of reduced metabolism or dormancy induced by the anoxia (e.g., Maire et al., 2016). In accord to this hypothesis, Koho et al. (2018) reported changes in *Ammonia confertitesta* ultrastructure as a stress response to oxygen depletion and suggested that these change could be related to dormancy (NB : In Koho et al., (2018), *Ammonia confertitesta* was mentioned as *Ammonia* sp. T6, one of the phylotypes of *Ammonia* distinguished by molecular identification (Holzmann and Pawlowski, 2000), and renamed *Ammonia confertitesta* by Hayward et al. (2021)). Additionally, in support of this theory, Le Kieffre et al. (2017) showed that *Ammonia tepida* highly reduces its metabolism and C_{org} uptake when exposed to anoxic conditions (LeKieffre et al., 2017). Our results rather support the hypothesis of Thibault de Chanvalon et al. (2015) stating that *A. tepida* would be able to follow redox fronts. The monitoring of water column concentration of nutrient (Fig. 2) and oxygen penetration depth throughout the experiment (Fig. 3) gave us evidence of stabilisation of sedimentary redox fronts 14 days after the first depositional event. Moreover, the presence of a C_{org}-enriched layer, corresponding to the original sediment surface, at 2.7 and 0.5 to 1.5 cm (respectively at T1 to T4) depth in the OHV and FLV microcosms did not seem to have influenced the upward migration, suggesting that oxygen, more than organic matter availability, was the major driving factor. Similarly, *Haynesina germanica* also showed high migration skills after the sedimentary disturbances. This species has recently been suggested to be able to move under low-oxygenated conditions and also to take advantage of the presence of existing trails to move into cohesive sediment (Deldicq et al., 2020). This agrees with our observations of rapid migration within 1 day after the FLV treatment and maximum 1 week after the OHV treatment (Fig. 8c).

4.3.2 Vertical migration speeds

Only a few studies quantified the locomotion speed of benthic foraminifera in the sediment (Bornmalm et al., 1997; Deldicq et al., 2021; Gross, 2000; Hemleben and Kitazato, 1995; Kitazato, 1988; Maire et al., 2016; Severin and Erskian, 1981). Some of them and additional studies quantified foraminiferal motion speeds in petri dishes with different substrates only focusing on horizontal movement (e.g.,.Bornmalm et al., 1997; Jauffrais et al., 2016a; Khare and Nigam, 2000; Kitazato, 1988; Maire et al., 2016; Seuront and Bouchet, 2015). In our study we estimated the average speed of vertical migration of *Ammonia confertitesta* and *Haynesina germanica* through the added sediment in the two disturbed microcosms. We calculated the speeds based on the vertical distribution at T1 in the OHV microcosm, because this was the only sampling time showing an ongoing

migration, while the definitive life position was already reached in the other microcosms at this time. Our estimation assumes that the speed was constant over time (18h from the sediment disturbance and T1) and that the locomotion started right at the moment of the sediment addition, which could have led to an underestimation of the speeds. A possible bias could also be added by the ~1 cm sediment compaction observed during the 18h (Fig. 4), which, on the opposite, could give an overestimation of the speed as a result. We calculated the specific mean speeds *A. confertitesta* (0.41 mm h^{-1}) and *H. germanica* (0.47 mm h^{-1}) (Table 1). As none of the individuals reached the water-sediment interface 18h after the disturbance, the calculated speeds were about maximum values. Recent studies from Deldicq et al. (2020) used flat aquaria to study vertical and horizontal locomotion abilities of *A. confertitesta* and *H. germanica* in the sediment in two dimension. Cameras tracked the migration pathways of specimens of both species on a short period of time, 48 to 72 h, in absence of physical disturbance. Based on the distance travelled every 10 minutes, Deldicq et al. (2020) calculated average speeds for both species and obtained values of 0.72 ± 0.25 mm h^{-1} for *A. confertitesta* and 1.1 ± 0.4 mm h^{-1} for *H. germanica* (Table 1).

In our microcosms, the mean migration speeds of both species are of the same order of magnitude, with the speed of *H. germanica* being twice lower. If we retain the speeds reported by Deldicq et al. (2020), an average time of 40 and 26 hours would have been needed for *A. confertitesta* and *H. germanica* respectively to go back to the water-sediment interface, which is consistent with our observations that no specimens had reached the sediment surface 18h after the disturbance. The differences in speed values could be explained by methodological bias and/or ecological reasons. Indeed, we weighted the migration speeds on the base of the number of specimens counted at each layer within a core, and our sampling resolution (18h) was much lower than that (10 minutes) of Deldicq et al. (2020). If the migration activity is not homogeneous through time as assumed, the low resolution of our observation could have led to an underestimation of the actual speed. Additionally, as suggested by Maire et al. (2016), the presence of both anoxic conditions and potential stress induced by sediment disturbance in our OHV microcosm can be a major factor for lowering locomotion speeds. However, Kitazato (1988) and Khare and Nigam (2000) pointed out the overestimation of speed calculated from individuals presenting crawling-like movement on a glass surface as they encounter less resistance than from sediment matrix. Both this study and Maire et al. (2016) support the capacity of our species to cover a few centimetre distance in a few hours. Differently from Maire et al. (2016), however, our results show that anoxic conditions do not induce a complete stop of the motility for *A. confertitesta*.

We compared our results to the experimental study conducted by Severin and Erskian (1981) that induced physical disturbance (from 0.5 to 4 cm of sediment suddenly added on the sediment surface containing living foraminifera) on a benthic foraminiferal species other than ours (i.e., *Quinqueloculina impressa*). The authors observed that the time of first emergence of this species after burial was a function of the deposit thickness, as follows: $T = 434.3\ D^2$; with T= time of first emergence and D = burial depth in centimetres. If we apply this relationship to the two species in the OHV microcosm, it would have taken 52.7 h, corresponding to 2.2 days, to the first individuals to reach the surface, after crossing the 2.9 cm thick deposit (Table 1), corresponding to a speed of 0.55 mm h^{-1}. Despite the methodological differences (different species, sandy sediment), our findings are in accordance with the results from Severin and Erskian (1981). In their model, the migration speeds are higher when foraminifera have to cross thinner layers. If we apply this model to the FLV treatment, for which speeds were not estimated, we would assume that the speeds would be higher for specimens crossing only a 0.5 cm thick layer of added sediment. For both studied species, based on the formula of Severin and Erskian, (1981), we calculated average speeds of 2.7 mm h^{-1}, which are almost 3-fold higher than the ones reported by Deldicq et al., (2020). The reliability of this value should be tested in further specific studies. Nevertheless, these findings further suggest that the stress induced by physical disturbances and the amplitude of the disturbance (in terms of thickness of sediment deposit) can be a controlling factor influencing foraminiferal migration speed.

Species	Velocities (mm.h-1)			Experimental conditions	Article
	Min	Mean	Max		
Ammonia tepida/confertitesta		**0.41**	1.44	Fine sediment disturbance migration speed, vertical	This study
	1.00 ± 0.30		2.99 ± 0.22	Seawater + Nitrogen and Carbon inputs, horizontal	Jauffrais et al., 2016
		2.19 ± 0.66		Sieved sediment (>100µm)	Maire et al., 2016
		0.72 ± 0.25		Sediment, vertical + horizontal	Deldicq et al., 2020
Haynesina germanica		**0.47**	1.44	Fine sediment disturbance migration speed, vertical	This study
		1.1 ± 0.4		Sediment, vertical + horizontal	Deldicq et al., 2020
Ammodiscus anguillae	0.04	**0.16**	0.41	Sediment aquaria, vertical + horizontal	Bornmalm et al., 1997
Quinqueloculina impressa		**0.41**		Sandy sediment - burying (0.5 to 4 cm), vertical	Severin and Erskian, 1981
Quinqueloculina sp.	2.04	**5.76**	8.34	Seawater, horizontal	Khare and Nigam, 2000
Mix of species	0.48		4.9	Sediment, vertical + horizontal	Kitazato, 1988
	0.018		1.32	Sediment, vertical + horizontal	Hemleben and Kitazato, 1994
	0.003		1.94	Sediment, vertical + horizontal	Gross, 2000

Table 1: Summary of published foraminiferal vertical migration speeds obtained in experimental sets.

4.4 General overview on benthic communities' response to depositional events

The existing literature about the effects of sediment deposition on benthic communities in experimental set ups mainly concentrates on macro and megafauna and is limited to relatively short-lasting experiments (from 4 to 32 days). Some interesting observations can be pointed out. Mestdagh et al. (2018), for example, simulated a sudden deposit of about 4 cm of sediment and observed a complete recovery of different species of molluscs and crustacean within 15 days after the disturbance. No decay of abundances of certain species were observed, indicating that some macrofaunal species can deal with 4 cm depth burial without problems. Only individuals with sessile behaviours showed a wide mortality. Similarly, Cottrell et al. (2016) observed a weak migration ability of *Mytilus edulis* through thin added sediment layers (<2 cm), but no migration below thicker deposits. The species mortality was also observed to be largely affected by burial duration, increased temperature, and anoxia induced by organic matter mineralisation. This was attributed to a short-term tolerance to anoxia, which was not sufficient to overcome oxygen depletion on longer time scales.

Whomersley et al. (2009) in a 9-month lasting study focusing on the effect of different frequency of depositional events on both macro and meiofauna, showed different responses of the two faunal types in terms of diversity, species abundances and turnover. Compared to Mestdagh et al. (2018), they observed a more intense impact of burial on macrofauna, with decreasing diversity under both low and high depositional intensity. Macrofauna was also generally more impacted than meiofauna (represented here by nematodes), especially on the low frequency burial. However, a shift in communities species composition was only noticed for meiofauna, while no effects were observed on abundances, suggesting a more rapid species turnover under stressful conditions. Similarly to our results, the high intensity of burial seems to further affect their communities compared to weaker deposits (Whomersley et al., 2009). However, contrary to what is reported for nematodes, in our study we observed a significant decay in foraminiferal abundances in the "One-time High Volume" microcosm (OHV, Fig. 5). This difference could be related to a lower motility and/or turnover rates of foraminifera compared to nematodes, or, also to the short duration of our experiment (51 days) compared to the one of Whomersley et al. (2009) (9 months). The fact that the vertical migration of living foraminifera through newly deposited layers in the the OHV treatment was way longer (1 to 7 days) than for the FLV (<18h), supports the hypothesis of the low motility as the main limit for survival after burial. Compared to foraminifera, nematodes are much more mobile and possibly able to faster reach favourable niches after a physical disturbance. This let conclude that the response, even for a same faunal type (i.e., meiofauna), can be variable. It is therefore crucial to study the response of different components of benthic compartments for the assessment of the effects of physical disturbance in the benthic marine environments.

The knowledge about the specific responses of different faunal types is also important when considering the trophic links between the compartments. For example, Bolam et al. (2011) suggested that trophic network disruption, caused by physical instability, can affect macrofaunal response to depositional events. The study simulated the impact of dredged sediment upon macrofaunal assemblages and showed different migration abilities for different macrofaunal taxa (e.g., polychaete less performant than gastropods) after burial. The authors suggested that the observed survival of successful migrating species can

be overestimated on short time observation, because dependant on the migration of other co-existing species including preys in a long-term dynamic. In this way, it appeared as fundamental to deepen the knowledge on the response of species from lower trophic levels to similar physical disturbances to holistically interpret the experimental observation at the scale of the whole benthic community.

630   If we consider all these observations together, we can therefore conclude that in a condition of physical instability, benthic communities respond in a species-specific way in terms of abundances, diversity and migration. Less mobile and highly specialist species are negatively affected compared to highly mobile and less trophic restricted species. The main factors influencing the community resilience seem to be turnover time, organic matter/oxygen availability, burial depth, frequency of sediment depositions and migration of co-existing species. The interaction of these parameters can complicate the prevision

635   of long-term consequences of similar physical conditions in natural settings, but a loss of more sensitive species, both from macrofauna and meiofauna can be supposed on the base of the existing experimental results.

5 Conclusions

Physical disturbances are often neglected as an important driving factor ecologically influencing biodiversity and standing stocks. The ongoing climate change is supposed to, at least regionally or locally, affect natural variability of sediment input

640   from the continent to coastal environments. The lack of information about the potential consequences on benthic faunal abundances and diversity could be a strong limit to imagine ecosystem resilience scenarii.

The results of our experimental study suggest that benthic foraminiferal assemblages respond differently to sedimentary depositional events of different intensity and thickness. On the one hand, the total foraminiferal abundances were significantly negatively affected only by the "one-time high volume" treatment, suggesting that occasional and thick sediment deposits

645   potentially have higher impact on standing stocks compared to a regular frequent lower stress (represented by the "frequent low volume" treatment). On the other hand, both type of tested sedimentary disturbances appeared to negatively influence the abundances of one of the two major species of the set-up, *Haynesina germanica*. This result suggests that the tolerance of this species to the physical disturbance, no matter its intensity and frequency, is lower than the one of *Ammonia confertitesta*. In a natural environment this could mean that a lowered biodiversity can be driven by physical disturbance.

650   At the scale of microhabitat distribution in the sediment, while the recovery of shallow microhabitat by the tested species was very quick after the "frequent low volume" deposit (< 24 h), the "one-time high volume" treatment induced longer recovery times (i.e., ≤ 7 days). This difference is also reflected in the geochemical steady state of the porewater. Indeed, the recovery of oxygen penetration depth, similar to the one at the first foraminifera sampling, was relatively quick for the FLV microcosm (< 24h after each disturbance) while a transitory deepening of the OPD was observed later (T1) in the OHV microcosm (24 h

655   after the disturbance) and a resilient steady state was not reached until 38 (T2) to 52 (T4) days after the disturbance.

The recovery of superficial microhabitat by buried specimens, however, do not seem to be strictly driven by the oxic front. In the OHV microcosm, foraminifera migrated through a thick anoxic sediment layer to reach the water-sediment interface.

Considering that the added sediment layer was not enriched in organic matter and that probably the most food-enriched area of the microcosm was the ancient interface (cf. black layer in Fig. 4), we can conclude that the upward migration was not

660 driven by food research, but most likely by oxygen depletion.

Author contributions:

CG, MPN, AM and HH designed the experiment; CG, MPN, AM and DLM performed the sampling procedures and measurements; CG analysed the data; CG and MPN wrote the original manuscript draft, MPN, AM and HH reviewed and edited the manuscript.

665 **Declaration of interests**

The authors declare that they have no conflict of interest.

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