Sediment reworking of intertidal sediments by the benthic foraminifera Haynesina germanica: the importance of motion behaviour and densities

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Sediment reworking of intertidal sediments by the benthic foraminifera *Haynesina germanica*. The importance of motion behaviour and densities.

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Abstract

This study aimed to describe for the first time the vertical motion behaviour of the intertidal foraminifera *Haynesina germanica* and its contribution to bioturbation. Its infaunal behaviour leads to the creation of one-end tube within the first centimetre of sediment. In addition, a vertical trail following behaviour was described for the first time in foraminifera, which may be linked to the sustainability of the biogenic sedimentary structures. As a consequence, *H. germanica* produces a vertical transport of both mud and fine sediment fractions similarly to the sediment reworking mode reported for gallery-diffusor benthic species. This finding allows us to refine the bioturbating mode of *H. germanica* previously classified as surficial biodiffusor. Furthermore, sediment reworking intensity appeared to be dependent on the foraminiferal density. *H. germanica* would adapt its motion behaviour to deal with the intra-specific competition for food and space that may occur when density increases. Consequently, this behavioural modification would affect both the species and the individual contribution to sediment reworking processes. *In fine*, sediment reworking in *H. germanica* may further contribute to the bioirrigation of intertidal sediments which has implications on oxygen availability in sediments and on aerobic microbial processes involved in carbon and nutrient cycling at the sediment-water interface.

Keywords

Intertidal foraminifera – *Haynesina germanica* - Motion behaviour – Tube building species - Vertical sediment reworking – Density-dependent effect

1. Introduction

Bioturbation, which is the biological transport of particles and associated dissolved elements, constitutes a major process driving the benthic ecosystem functioning of marine soft-sediment, contributing to carbon and nutrient cycling and organic matter mineralisation

(Gilbert et al., 1996; Mermillod-Blondin and Rosenberg, 2006; Volkenborn et al., 2016, 2012). The role of benthic macro-invertebrate species as bioturbators generally depends on their mode of sediment reworking that is further modulated by species-specific traits and the time allocation patterns between these traits (De Backer et al., 2011; François et al., 1997; Gérino et al., 2003; Grémare et al., 2004; Kristensen et al., 2012; Pascal et al., 2019). Conversely to macrofaunal taxa, the contribution of meiofauna to fluxes (i.e. sediment particles and dissolved elements) at the sediment-water interface has been far less studied (Bonaglia et al., 2014; Giere, 2009; Nascimento et al., 2012; Pike et al., 2001), and barely considered in an attempt to estimate community bioturbation potential based on a review of 1033 benthic invertebrate species from the northwest European continental shelf (Queirós et al., 2013).

Nevertheless, meiofaunal species display distinct biological activities (e.g. crawling, burrowing, construction and maintenance of burrows, ingestion/defecation of particles) suggesting a significant contribution to sediment reworking processes and therefore to the geochemical and microbial structuration of the sedimentary environment (Chandler and Fleeger, 1984; Nehring et al., 1990; Pike et al., 2001; Reichelt, 1991; Bonaglia et al., 2020, 2014; Middelburg and Meysman, 2007; Rysgaard et al., 2000). Until recently, studies assessing meiofaunal bioturbation in soft-bottom sediments focused on the effect of the whole meiofauna communities without considering the role of individual species (Alkemade et al., 1992; Bonaglia et al., 2020, 2014; Nascimento et al., 2012; Rysgaard et al., 2000). Moreover, most publications on the role of benthic meiofauna focused on nematodes and harpacticoid copepods while they may not be the dominant taxa in all soft-bottom communities (see Schratzberger and Ingels (2018) for a review). Amongst meiobenthic organisms, benthic foraminifera is a key group of the meiofauna in soft-bottom sediments; representing up to 50% of the eukaryotic biomass (Murray, 2006). Nevertheless, they are still relatively poorly

78 studied for their bioturbation activities despite their significant role in carbon and nitrogen
79 cycling (Moodley et al., 2002, 2000; Risgaard-Petersen et al., 2006).
80 In soft-bottom habitats, motion behaviour of intertidal foraminifera can generate horizontal
81 displacement of sediment particles (Bouchet and Seuront, 2020; Deldicq et al., 2021a, 2021b).
82 Some species may be involved in the vertical transport of sediment as they actively burrow in
83 the sediment (Kitazato, 1988; Deldicq et al. 2021b; 2020) either to reach their preferential
84 microhabitat (Geslin et al., 2004; Linke and Lutze, 1993; Moodley et al., 1998) or to escape
85 after being buried by a storm or by macro-invertebrate bioturbation (Bouchet et al., 2009;
86 Thibaut de Chanvalon et al., 2015; Maire et al., 2016). Such vertical movements may (i) have
87 major impacts on the stability and erodibility of the surficial sediment layer (Coull, 1999;
88 Nehring, 1993), (ii) produce a substantial downward transport of particles and (iii) enhance
89 fluxes of dissolved oxygen and solutes at the sediment-water interface (Aller and Aller, 1992;
90 Schratzberger and Ingels, 2018). To our knowledge, only one study estimated the sediment
91 reworking rates generated by a benthic foraminiferal community to Db = 0.19 cm^2 day^{-1} (Db :
92 bioturbative diffusion rate) in the upper 5 mm (Gross, 2002).
93 The present study aimed at filling the gap between the motion behaviour and the sediment
94 reworking induced by benthic foraminifera, a key group in intertidal sediments. To do so, we
95 considered the species *Haynesina germanica*, a key foraminiferal species in tidal mudflats. In
96 detail, it is one of the most abundant species in intertidal mudflats (Francescangeli et al.,
97 2020), and it has an intense and constant displacement in and on the sediment suggesting that
98 it contributes significantly to sediment reworking (Seuront and Bouchet, 2015; Deldicq et al.,
99 2020; 2021a). In this context, the objectives of this study were twofold. Firstly, we aimed at
100 characterizing the vertical motion behaviour of this species by experimentally describe its
101 displacements and the biogenic sedimentary structures built below the sediment-water
102 interface. Secondly, we aimed at quantifying species vertical sediment reworking induced by

H. germanica considering different densities similar to those observed in its environment. To do so, thin ant-like aquaria and particle-tracer method were used to monitor the behaviour of the species, its putative effects on both sediment matrix (i.e. production of biogenic structure) and sediment reworking rates (downward transport of particles). Such experimental approaches may provide new insights on the microhabitat choice of *H. germanica* in the sediment, which ultimately provides a better characterisation of the spatial distribution and the intensity at which sediment particles are displaced by this species.

2. Material and Methods

2.1. Vertical motion behaviour

2.1.1. Collection of living H. germanica

Surface sediment (i.e. 0-1 cm) was collected at the end of February-early March in 2019 at low tide in the Authie Bay (50°22’20’’N, 1°35’45’’E, Fig. 1). Samples were stored in plastic containers (100 ml) and transported to the Laboratory of Oceanology and Geosciences at the Marine Station of Wimereux (France), then washed through a 125 µm sieve. Individuals of *Haynesina germanica* were sorted with a brush and kept 24h-long for acclimation to the experimental condition in a controlled-temperature room at 18°C (MIR-154, Panasonic, Japan; temperature fluctuation ± 0.3 °C, light intensity 170 µmol m^{-2} s^{-1}). One day after, only active individuals (i.e. producing a displacement track on a thin layer of sediment to distinguish living from dead specimens) were selected for the experiments.

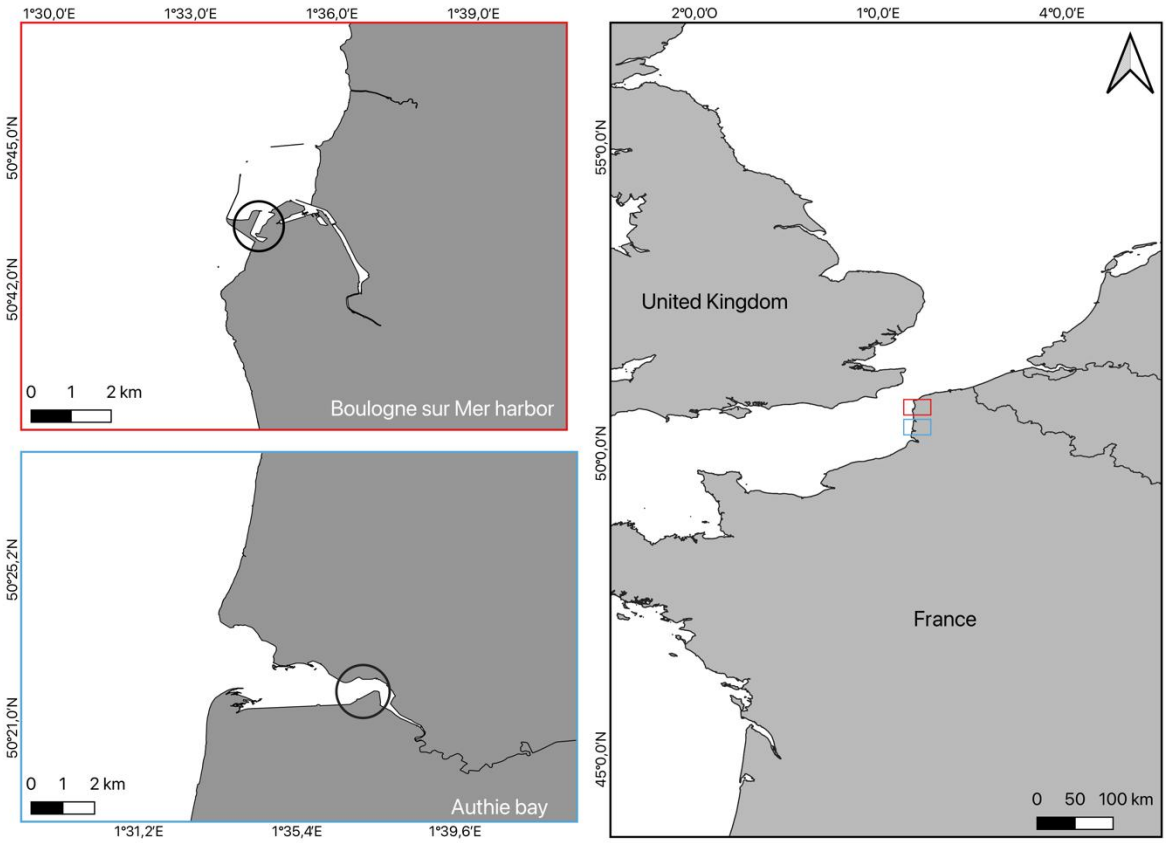

Figure 1. Map showing sampling sites in the Hauts-de-France in the eastern English Channel (France). In red: Boulogne-sur-Mer harbor and in blue: the Authie bay.

2.1.2. Experimental set-up

Experiments were conducted in thin aquaria (10 x 1 x 10 cm, n = 3) filled with thawed sediment from the Authie Bay (depth of 7-8 cm) and overlain with oxygenated natural sea water (Fig. 2). All aquaria were maintained at 18°C for 2 weeks prior to the introduction of foraminifera. For each experiment, about 150 active individuals were randomly placed at the sediment surface corresponding to a density of 15 indiv cm^{-2}. The displacement of each individual in and on the sediment was recorded using time-lapse photography (i.e. one image every 10 min; Nikon V1 with a Nikkor 10–30 mm lens). In total, 3 experiments were performed: one in February (48 h long, Experiment R1) and two in March (72 h long, Experiments R2 and R3).

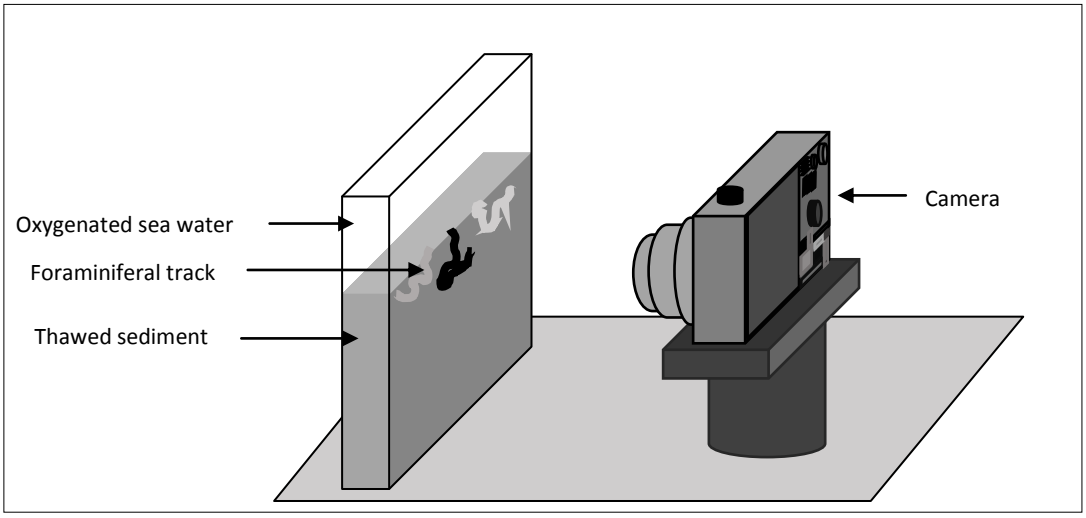

Figure 2. Experimental set-up for time-lapse assessment of foraminiferal motion-traits over a 48 and 72 h periods.

136

137 *2.1.3. Quantification of behavioural traits*

138 Images were analysed by using the software Fiji (Schindelin et al., 2012). The method
139 allowed to visually follow each individual and extract the coordinates from each image
140 combined by the computer program. The coordinates thereby gave the individual's trajectory
141 during the time of the experiment. During the experiment, it was only possible to track
142 individuals that are visible along the wall of the aquarium that face the camera. We therefore
143 only kept individuals that exhibited visible tracks throughout the whole 48 and 72 h
144 experiments. In total, we followed the trajectories of 35 individuals.

145 Three motion traits were investigated following Seuront and Bouchet (2015) and Deldicq
146 et al. (2020): the activity index, the travelled distance and the vertical position of the
147 individuals. The level of activity (i.e. time allocated to locomotion by each individual) was
148 estimated with the activity index A_i which correspond to the ratio between t_{move} and t_{active} as
149 follows:

150 $$A_i = 100 \times (t_{active} / t_{move})$$

where t_{move} includes the total time taken by an individual to move from its initial to its final position, which thereby includes the time periods when individual remains inactive. In contrast, t_{active} only considers the time periods when an individual actually moves between its initial and final position.

The distance travelled by each individual between two images (i.e. 10 min) was assessed as follows:

$$D_t = \sqrt{((x_t - x_{t+1})^2 + (y_t - y_{t+1})^2)}$$

where (x_t, y_t) and (x_{t+1}, y_{t+1}) are the coordinates between two successive images taken at times t and t + 10 min and the total distance travelled within 48 and 72 h was then calculated and normalized by the experiment duration to obtain velocity.

To assess the preferential position of *Haynesina germanica*, the vertical position of each individual in the sediment was recorded for every picture based on a 2-depth classification depending on the test position, i.e. “surface” when the test remained visible at the surface and “Burrowed” when the test was below the sediment-water interface. The number of individuals was estimated for each position and each 10-min period during the time of the experiment.

In addition, based on preliminary observations, the intensity and the occurrence of trail following behaviour in existing burrow were monitored for each individual. Thus, the time taken by an individual to perform trail following during the experiment was estimated and expressed in percentage of time.

2.1.4. Quantification of the biogenic structure built by Haynesina germanica

The maximum depth reached by *Haynesina germanica* specimens for each experiment was recorded by measuring the distance of the deepest biogenic structure from the interface. In addition, to quantify how much *H. germanica* could alter the sediment matrix, the length and

width of each visible burrow were measured every 2 hours for each experiment. The surface occupied by each burrow (*Si*) was then estimated as follow:

$$Si = \text{Length} \times \text{Width}$$

Then the surface occupied by all the burrows (hereafter *SB*) within the first centimetre of the sediment was estimated every 2 hours by summing together all the individual burrow surfaces *Si*.

2.2. Quantification of sediment reworking

2.2.1. Sediment and living fauna sampling

Sediment cores (1 x 1 x 5 cm, N = 15) and surface sediment were collected in August 2020 in Boulogne-sur-Mer harbour (50°43'6"N, 1°34'25"E, Fig. 1), an intertidal mudflat located on the French coasts of the English Channel. Please note that sediments collected from the two sampling sites i.e. Authie Bay and Boulogne sur Mer harbour and used in the present study had comparable grain size distributions (20 % and 80 % of sand and silt, respectively), TOC contents (between 1 and 2%) and salinity values (33.8 PSU). After collection, cores were stored during 48 h in a freezer (-20°C) to ensure that the sediment was free of macro- and meio-organisms that could produce sediment reworking. Frozen sediment cores were disposed in a 15 litre aquarium (35 x 20 x 25 cm) filled with natural filtered and oxygenated sea water. The aquarium was kept in temperature-controlled incubators (MIR-154, Panasonic, Japan) at 18°C with a 12h:12h light/dark cycle for few days. Surface sediment samples were stored in plastic containers (100 ml), transported to the laboratory, and washed through a 125 µm mesh-size sieve. Individuals of *Haynesina germanica* were subsequently sorted with a brush and then acclimated for 24 hours in temperature-controlled incubators at 18°C with filtered natural seawater.

2.2.2. Experimental set-up

Luminophores i.e. natural sediment particles coloured with fluorescent paint (Mahaut and Graf, 1987) were used to estimate sediment reworking rates by foraminifera. Two size fractions of luminophores were used: <63 µm pink silt (D_{50} ≈ 10-20 µm, Environmental Tracing LLC, UK) and >125 µm green sand (D_{50} ≈ 175-200 µm, Environmental Tracing LLC, UK) to fit with the *in situ* grain size distribution of the sediment. Moreover, the use of two size fractions of luminophores with only one fraction that can be ingested by foraminifera (pink luminophores with a size < 63 µm) could inform about the influence of ingestion-egestion mechanisms by foraminifera on sediment reworking.

Four experimental treatments were performed: (1) without foraminifera (Control, N= 3), (2) with a low foraminiferal density (LD = 10 indiv cm^{-2}, N = 3), (3) with a medium density (MD = 30 indiv cm^{-2}, N = 3), and (4) with a high foraminiferal density (HD = 90 indiv cm^{-2}, N = 3). Experimental densities were determined following local *in situ* densities of *Haynesina germanica* reported through a year (Bouchet, *unpubl. data*).

Before running the experiments, active individuals were extracted from previously acclimated individuals then gently deposited on the sediment surface in sediment cores corresponding to LD, MD and HD treatments. Considering that living foraminifera usually start to move within a few minutes (Bouchet and Seuront, 2020; Deldicq et al., 2020; Seuront and Bouchet, 2015), a mixture of 20 mg of pink silt and 20 mg of green sand luminophores were homogeneously and gently spread on the sediment surface of each core with a Pasteur pipette one hour after foraminifera introduction.

The experiment lasted for 14 days. At the end of the experiment, the water was immediately removed and sediment cores were frozen in order to stop all foraminiferal movements. The next day, the top 2 cm of sediment was sliced in 0.2 cm-thick layers.

225 *2.2.3. Luminophore counting*

226 Each layer was homogenized and dried at 50°C and subsequently photographed under UV
227 lights using a digital camera (Nikon V1 with a Nikkor 10−30 mm lens). Settings were
228 adjusted for adequate fluorescent detection and the photographic field (10 × 8 cm) allowing to
229 visualize luminophore particles. Images were then analysed with the image-analysis software
230 Fiji (Schindelin et al., 2012) for luminophore counting. Briefly, luminophores were selected
231 using an appropriate set of RGB threshold levels that differentiated fluorescent particles from
232 the sediment. Pixels above and below the threshold were added to a binary matrix where
233 luminophore pixels were assigned a value of 1 and sediment pixels a value of 0 and were
234 counted using the Analyze Particle tools. The number of luminophores counted in one layer
235 was converted into percentage of tracer found in this layer comparatively to the total number
236 of luminophores recovered from the whole core. Then, we obtained the vertical distribution of
237 luminophores in sediments for each core.

238

239 *2.2.4. Sediment reworking coefficients*

240 The effect of *Haynesina germanica* on particle transport was estimated using the diffusion-
241 advection-nonlocal model in non-steady state conditions (Mugnai et al., 2003). This model
242 links a nonlocal component to a diffusion–advection model (Gérino et al., 1994; Officer and
243 Lynch, 1982). Biological diffusive transport (diffusion (D), cm^2 $year^{-1}$) was defined as
244 omnidirectional transport in the sediment column and is analogous to molecular diffusion in
245 water. Biodiffusion spreads tracers in the sediment column (Guinasso and Schink, 1975) by
246 the exchange of small amounts of material with adjacent parcels of sediment. Biologically
247 mediated vertical transports account for advective transport and nonlocal transport.
248 Bioadvection (V, centimetres per year) is created by head-down deposit-feeders like worms
249 that feed in the deeper sediment and egest faecal pellets at the surface (conveyor belt

organisms). This feeding mode causes an accelerated rate of sediment burial within the feeding zone. Nonlocal transport results from largely open burrows into which surface particles may fall. This nonlocal reworking is modelled as a removal function that simulates the transport of surface material (expressed in grams of transported tracer per day) in a deposition zone.

The basic equation is:

$$\frac{\partial C_{(z,t)}}{\partial_t} = D\frac{\partial^2 C_{(z,t)}}{\partial_z^2} - V\frac{\partial C_{(z,t)}}{\partial_z} + K_{(z,t)} - R_{(z,t)} \qquad \textit{(eq. 1)}$$

where C is the normalized tracer concentration, t is time (years), z is depth (centimetres), D is the diffusive reworking rate ($cm^2\ year^{-1}$), V is the advective transport rate (centimetres per year), R is the removal function that determines the mass of tracer (grams per day) removed from the surface and K is the injection function of the nonlocal transport that simulates tracer inputs (grams per day) into the deposition zone of the sediment column; K_e is a constant parameter (per day) estimated from the model, and depths Z_{min} and Z_{max} represent the upper and lower limits of the deposition zone, respectively. The nonlocal transport is thus quantified by a flux of sediment removed from the surface. In this case, $R_{(z,t)} = 0$ for $z > 0$ and $R_{(z,t)} = K_{(z,t)}$ ($Z_{max} - Z_{min}$) for $z = 0$ and $K_{(z,t)} = Ke$ for $z \in [Z_{min},Z_{max}]$ and $K_{(z,t)} = 0$ for $z \in [Z_{min},Z_{max}]$. As luminophores were added as pulse input at the surface of the sediment at the beginning of each experiment, the model was applied under non-steady-state conditions. Thus, model eq. 1 was used with the upper boundary condition of an instantaneous source of unit strength (maximal C of tracer) at $z = 0$ at $t = 0$, a lower boundary $C \rightarrow 0$ at $z \rightarrow \infty$, and initial condition $C = 0$ at $z > 0$. The general solution was given by Officer and Lynch (1982) as:

$$C_{(z,t)} = \frac{1}{\sqrt{\pi D_t}} exp\left[\frac{-(z - V_T)^2}{4D_t}\right] - \frac{V}{2D} exp\left(\frac{V_z}{2D}\right) erfc\left(\frac{z + V_t}{4D_t}\right) - R_e t + K_e \qquad \textit{(eq. 2)}$$

with

$$R_e = K_e(Z_{max} - Z_{min})$$

and

$$erfc(x) = 1 - \frac{2}{\sqrt{\pi}} \int_0^x e^{-t^2} dt$$

where c is a normalized concentration relative to unit input. The model allows the calculation of the theoretical tracer concentration given suitable values of the parameters D, V, Z_{min}, Z_{max}, and K_e. These parameters were obtained from profiles that produced the best fit with the experimental data using the least squares method.

Sediment reworking coefficients (i.e. biodiffusion, advection and nonlocal transport) were calculated for each core. In addition, to assess the effect of density on species' vertical sediment reworking, sediment coefficients were also estimated per individual by dividing it by the density within each replicate (Duport et al., 2006).

2.3. Statistical analysis

A linear mixed model has been used to determine whether the instantaneous velocity of individuals significantly depended on their vertical position and their trail following behaviour. In the linear model, vertical position (i.e. surface, burrowed) and trail following (i.e. yes, no) were fixed factor and individual was included as repeated factor (corresponding to individual random effect estimated from several measurements made on the same individual).

Vertical distributions of luminophores were presented with the mean ± SD of the three replicate cores. The influences of luminophore grain sizes on sediment reworking coefficients (i.e. biodiffusion, nonlocal transport and advection) and maximum penetration depth (Z_{max}) were tested using repeated-measures ANOVAs (RM-ANOVAs) to consider the non-independence of measurements performed with pink and green luminophores in the same

cores. As no significant differences in sediment reworking variables were detected between luminophore sizes (see results), sediment reworking coefficients and maximum penetration depth were calculated by using the addition of the percentages of pink and green luminophores for each layer of each core. Then, these sediment reworking variables were compared among foraminifera treatments using one-way analyses of variance (ANOVA). Both sediment coefficients and maximum penetration depth values were ln(x+1) transformed to homogenize variances after the homoscedasticity of variances and the normality distribution of the residuals were tested using Bartlett's and Shapiro's tests, respectively. Bonferroni-Dunn post hoc tests were subsequently performed if significant differences were detected among foraminiferal treatments to evaluate which density treatments differed (Zar, 2009). All statistical analyses were performed using R.3.5.2. Software (R Core Team, 2019).

3. Results

3.1. Vertical motion behaviour

Individuals actively moved during the experiment, being active almost 73±7% (mean ± SD) of their time in the sediment. Noticeably, some individuals showed a permanent activity throughout the longer experiment i.e. 72h-long. The distance travelled by individuals ranged from 7 to 52 mm with a mean distance of 26 mm. In the three experiments, all the individuals that started to move exhibited a similar behaviour i.e. surface displacement for several minutes consistently followed by active burial. However, individuals showed different types of strategy: (i) staying a long period burrowed in the sediment (i.e. below the top millimetres) or (ii) rapidly get back to the top millimetres though they rarely return to the sediment surface. When some individuals reached the sediment surface, they preferentially returned just below the top millimetres of sediment after several minutes crawling at the surface. Hence, the majority of individuals spent more than 70% of their time burrowed in the sediment. The

instantaneous individual velocity of individuals burrowing in the sediment was 32% lower than those of individuals dwelling at the sediment surface ($p < 0.05$; Table 1).

Table 1. Statistical results assessing the effects of vertical position and trail following on individual instantaneous velocity (linear mixed model). (df: degree of freedom, *: p<0.05, ***: p<0.001)

Predictor	Estimate	Std. Error	df	t_{value}	p_{value}
Vertical position	0.15	0.07	17	2.1	0.04^{*}
Trail following	0.47	0.06	7.9	7.3	8×10^{-5} ***

In addition, 19 out of the 35 individuals were observed having a trail following behaviour i.e. moved through existing gallery previously built either by another congener or by itself. Noticeably, individuals typically spend ~15±19% of their time using existing tracks. Trail following behaviour increased by 15% the instantaneous individual velocity of individuals ($p < 0.05$; Table 1, Fig. 3).

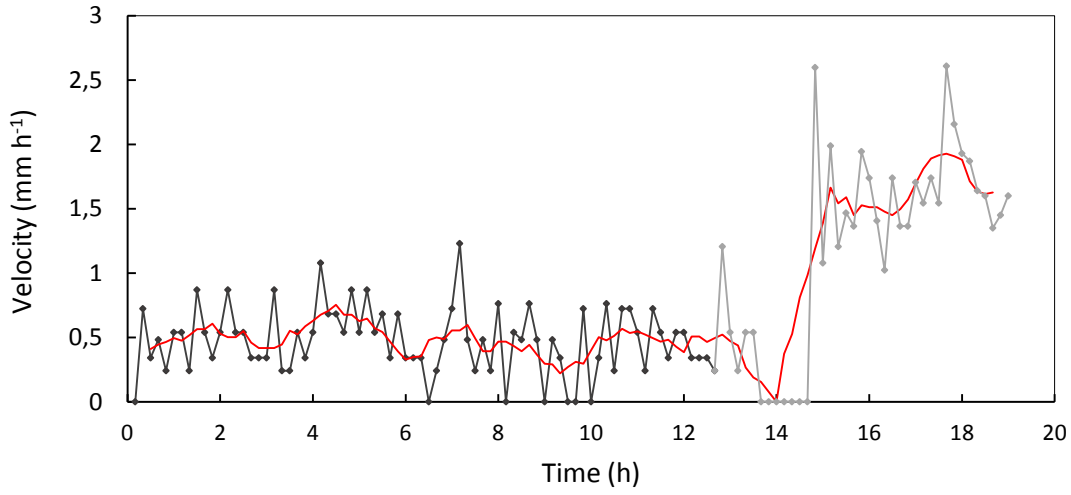

Figure 3. Example of temporal change in the instantaneous velocity of an individual of *H. germanica*. The black line corresponds to a situation when the individual is moving without trail following behaviour while the grey line corresponds to a situation when the individual is performing a trail following behaviour. The red-line is the 3-order simple moving average of the velocity.

3.2. Effect of *Haynesina germanica* on the sediment matrix

During the experiment, individuals built an intense network of burrows which persisted throughout the experiment. Precisely, visible galleries could reach a maximum depth of 1 cm and the majority of individual dwelled below ~0.5 cm depth (Fig. 4).

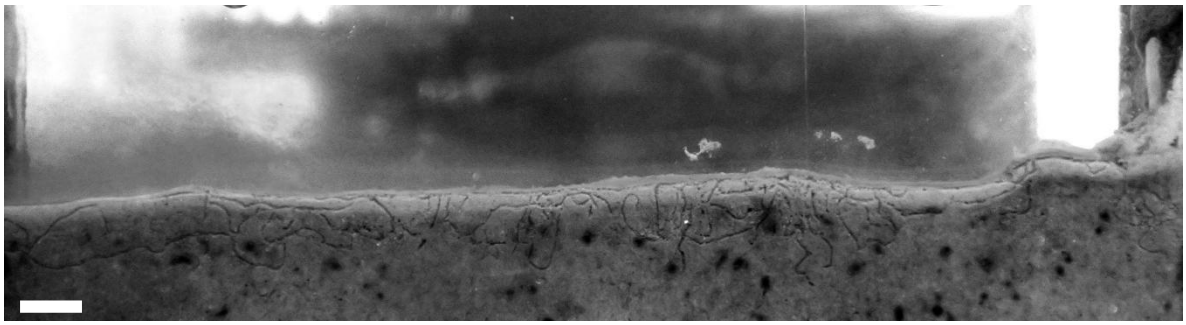

Figure 4. Archetypical structuration of the gallery network consecutive of the displacement of *H. germanica* in the sediment after 24 of the experiment R2. Scaled bar = 1 cm.

The surface occupied by burrows (S_B) rapidly increased within the first 32h of the experiments to reach a steady value of 6 and 8% for experiment R3 and experiments R1/R2 respectively (Fig. 5). Then, the increase was much slower the last 40h, to reach a S_B of 8 and 10% (experiment R3 and experiments R1/R2 respectively, Fig. 5).

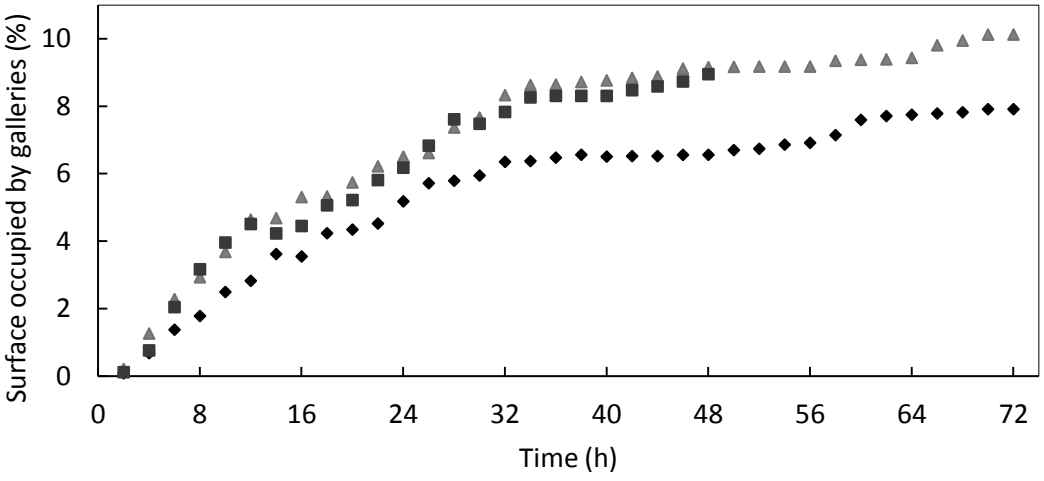

Figure 5. Temporal changes in the surface occupied by the gallery network (S_G in %) for the three experiments: R_1 (grey square). R_2 (grey triangle), R_3 (black diamonds).

3.3. Vertical sediment reworking

3.3.1. Influence of sediment grain size

The vertical profiles of the two size fractions of luminophores (i.e. green sand and pink silt) were comparable (Suppl. Mat. Fig. 1). Thus, no significant differences in sediment reworking coefficients and maximum penetration depth were found between the green sand fraction and the pink silt fraction (repeated-measures ANOVAs, $p > 0.35$ for sediment reworking coefficients and maximum penetration depth) despite the fact that only the pink silt fraction could be ingested by foraminifera. For this reason, the two size fractions were pooled together to calculate a percentage of luminophores per layer for each core.

3.3.2. Effect of density

The average percentage of luminophores recovered at the sediment surface (0–0.2 cm layer) at the end of the experiment was 92% in the control columns and decreased with foraminifera to 77, 50% and 54% in LD, MD and HD treatments, respectively (Fig. 6).

In treatments with foraminifera, luminophore vertical profiles were characterized by exponential decreases of luminophores with depth, indicating a biodiffusive reworking of sediment by foraminifera. Only 1.5 to 5 % of total luminophores added to cores were found below 1.8 cm in the sediment (Fig. 6). The maximum penetration depth (Z_{max}) of luminophores varied between 1 cm in the control treatment to 1.87 cm, 1.93 cm and 1.53 cm in the LD, MD and HD treatments, respectively (Table 2). Noticeably, the maximum penetration depth was significantly higher in the MD treatment than in the other three treatments (Bonferroni-Dunn test, $p < 0.05$).

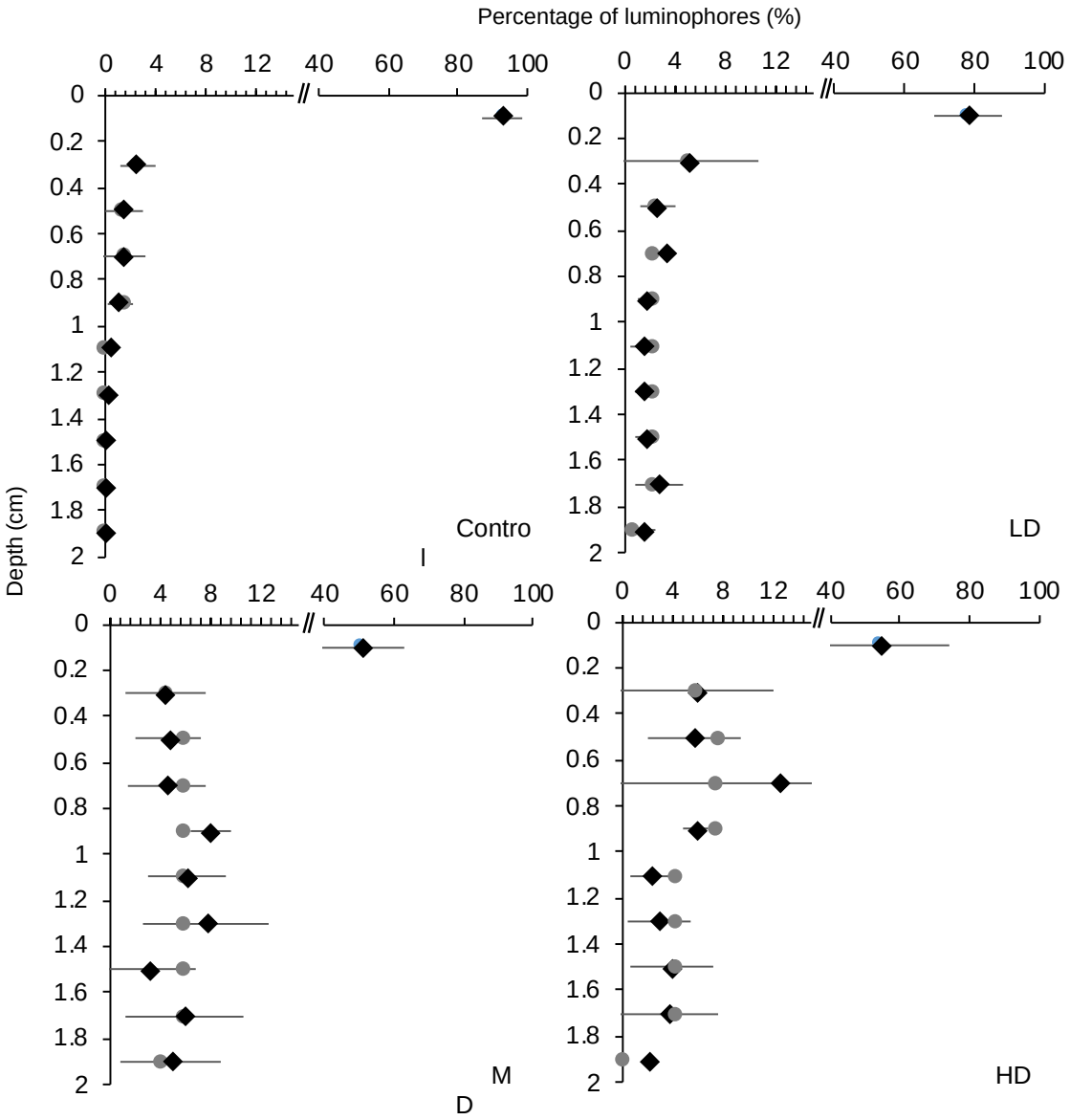

Figure 6. Depth profiles (means ± SD) of luminophores (black diamonds) in the four treatments and calculated profiles obtained with the advection–diffusion–nonlocal model (grey circles). Treatments: Control, LD (10 indiv cm^{-2}), MD (30 indiv cm^{-2}), HD (90 indiv cm^{-2}).

388

Table 2. Mixing rates of sediment estimated in the four treatments. Advective, diffusive and nonlocal transport coefficients are presented as means (SD) (N=3 for each treatment). Z_{min} and Z_{max} are the respective upper and lower limits of the sediment layer influenced by nonlocal transport.

Treatment	Advection (cm y^{-1})	Biodiffusion (cm^2 y^{-1})	Nonlocal transport (g d^{-1})	Z_{min} (cm)	Z_{max} (cm)
Control	0 (0)	0.14 (0.03)	0.02 (0.02)	0.47	1.00
LD (10 indiv cm^{-2})	0 (0)	0.19 (0.09)	0.07 (0.03)	0.27	1.87
MD (30 indiv cm^{-2})	0 (0)	0.21 (0.08)	0.29 (0.15)	0.40	1.93
HD (90 indiv cm^{-2})	0 (0)	0.23 (0.1)	0.29 (0.27)	0.40	1.53

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390

391 Modelled data were fitted adequately to experimental data (Fig. 7). Sediment reworking
392 coefficients obtained from model simulations are shown in Table 3. No bioadvection was
393 observed in the experiments. Biodiffusion and nonlocal transports coefficients varied
394 significantly among treatments (one-way ANOVA, $p < 0.05$; Tables 2, 3). Biodiffusion rate
395 was the highest in the HD treatment with 0.23 ± 0.1 cm^2 y^{-1} (Bonferroni-Dunn test, $p < 0.05$;
396 Table 3). The highest nonlocal transport rates were measured in the MD and HD treatments
397 with 0.29 ± 0.15 g d^{-1} and 0.29 ± 0.27 g d^{-1}, respectively (Bonferroni-Dunn test, $p < 0.05$;
398 Table 3).

Table 3. Effect of each density treatment on coefficient of sediment reworking (comparison with the control treatment) and maximum penetration depth (Z_{max}). Bonferroni-Dunn test with N=3 for each treatment. 0: no significant difference; +: significant increase.

Variable	Density treatment		
	LD (10 indiv cm^{-2})	MD (30 indiv cm^{-2})	HD (90 indiv cm^{-2})
Biodiffusion	0	0	+

Nonlocal transport	0	+	+
Maximum penetration depth	0	+	0

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402 The individual contribution to biodiffusion significantly decreased with the foraminiferal
403 density (Bonferroni-Dunn test, $p < 0.05$, Fig. 7A). In comparison, the individual contribution
404 to nonlocal transport was significantly higher in the MD treatment than in the HD and LD
405 treatments (Bonferroni-Dunn test, $p < 0.05$, Fig. 7B).

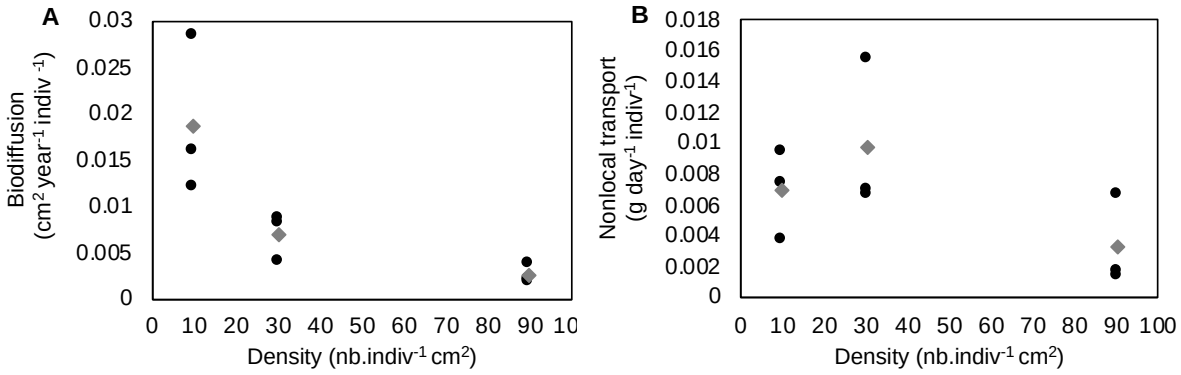

Figure 7. Biodiffusion (A) and nonlocal transport (B) per individual as a function of *H. germanica* density. Values for each replicate are presented with dark circles and mean value for the three replicates with grey diamonds.

406

407 **4. Discussion**

408 4.1. *Haynesina germanica* is an infaunal species

409 During the experiments, *Haynesina germanica* occasionally moved at the surface, but the
410 species preferentially dwelled in the first centimetre of the sediment; in accordance with its
411 previously reported positive geotaxis (i.e. moving downward; Seuront and Bouchet, 2015).

Furthermore, *H. germanica* specimens rapidly created sustainable one-end tubes that may confirm a preference of *H. germanica* for an infaunal mode (Seuront and Bouchet, 2015). Burrowing is energetically expensive as it implies displacing particles within a cohesive sediment matrix (Dorgan et al., 2006, 2005; Hunter and Elder, 1989; Trevor, 1978). As a consequence, displacement in muddy sediment requires morphological (e.g. body deformation, appendages) and behavioural (e.g. reduce activity, reuse existing track) adaptations (Dorgan et al., 2006, 2005).

In the present study, individuals preferentially reused existing tubes, a well-known strategy to reduce the cost of locomotion. For example, trail following in gastropod species reduces their mucus production which is a considerable energetic burden (Davies and Blackwell, 2007; Tankersley, 1989). Benthic foraminifera are also able to produce mucus (e.g. Langer and Gehring, 1993) of the same nature than gastropod mucus (Ng et al., 2013). Besides allowing individuals to adhere to the substrate and move faster, mucus may also stabilize the sediment as particles are bound together by extracellular polymeric substance secreted by organisms (Nehring, 1993; Nehring et al., 1990; Reichelt, 1991; Riemann and Schrage, 1978). The sustainability of the biogenic sedimentary structures built by *H. germanica* may be thus enhanced by individual mucus production which would contribute to the stabilisation of the sediment matrix. Mucus layers may also enhance bacterial and fungi development (Moens et al., 2005) which are potential food sources for benthic foraminifera (Langer and Gehring, 1993; Mojtahid et al., 2011). Therefore, the trail-following behaviour of *Haynesina germanica* reported from the present study may be an adaptive response to the physical constrain triggered by cohesive sediment but it may be also linked to feeding activities on microbial communities favoured by tube-associated mucus.

4.2. *Haynesina germanica* is a tube-building species generating a non-selective transport of sediment

The sediment reworking induced by *Haynesina germanica* was characterized by two processes: the biodiffusion of sediment particles likely occurring in the surface layer and the nonlocal transport of particles fallen in one-end tube structures produced by the species. This mode of sediment reworking is similar to the one of the two polychaete species *Hediste diversicolor* and *Allita virens* that are classified as gallery biodiffusors (Duport et al., 2006; François et al., 2002; Gilbert et al., 2007; Michaud et al., 2005). Thus, our findings suggest that *Haynesina germanica*, which was initially classified as a surficial biodiffusor species, may be redefined as a gallery biodiffusor species. Indeed, surficial biodiffusor species like the cockle *Cerastoderma edule* (Richard et al., 2021) do not display a burrow-dwelling behaviour and hence do not generate biogenic sedimentary structures such as burrows and tubes in the sediment (Kristensen et al., 2012; Mermillod-Blondin et al., 2003). Furthermore, this work further contributes to confirm the infaunal microhabitat of *H. germanica* (Seuront and Bouchet, 2015).

In turn, *H. germanica* did not produce any bioadvective transport of particles. Classically, this phenomenon is associated with the feeding behaviour of conveyor species which produce a transport of sediments through their gut from the sediment-water interface to their egestion depth (e.g. Gérino et al., 2003). For example, downward-conveyor deposit species such as *Cirriformia grandis* ingest fine particles (size range: 16-32 µm) at the sediment surface and egest them at depth in the sediment (Ruddiman et al., 1980; Shull and Yasuda, 2001; Wheatcroft, 1992; Wheatcroft and Jumars, 1987). Therefore, the fact that *H. germanica* did not produce bioadvection and reworked sediment particles irrespectively of their sizes (only pink luminophores could be ingested for foraminifera in the present experiment) showed that

sediment reworking induced by *H. germanica* was not related to particle ingestion and egestion.

In conclusion, *H. germanica* produces a vertical transport of sediment particles through their burrows, as observed in gallery-diffusor benthic species like the amphipod *Corophium volutator* (De Backer et al., 2011, 2010). The tube building activity of foraminifera has been previously reported and described for *Quinqueloculina impressa* (Severin et al., 1982; Severin and Erskian, 1981) and Rotaliidae (Langer and Gehring, 1993). Other meiobenthic taxa (e.g. nematode, copepod, ostracod) are able to disturb the sediment through their biogenic sedimentary structures (Bonaglia et al., 2014; Cullen, 1973; Kristensen et al., 2012). These biogenic sedimentary structures alter sediment properties but also water exchanges at the sediment-water interface by bioirrigation (Aller and Aller, 1992; Coull, 1999; Giere, 2009; Mermillod-Blondin et al., 2004). Thus, the present experiment suggests that the production of tubes and the sediment reworking by *H. germanica* may contribute to biogeochemical processes at the sediment-water interface.

4.3. Sediment reworking in *Haynesina germanica* is constrained by density

In the present study, the burial depth and the percentage of tracer recovered at the sediment surface at the end of the experiment significantly differed among density treatments. For example, we reported that the maximum penetration depth of luminophores was significantly higher in the MD treatment than in the LD treatment. In fact, increasing density may force *Haynesina germanica* to increase their burrowing depth in the thin aquaria. Such change in the burrowing behaviour may provide an advantage to *H. germanica* to limit intra-specific competition for food and space that occurred at the sediment-water interface when the density increases as previously evidenced for macrofauna (Michaud et al., 2010). It has been well described for macro-invertebrate organisms, like in brittle star and polychaetes that increase

their prospecting area toward deep sediment layer when density increases (Duport et al., 2006; Peterson and Andre, 1980; Rosenberg et al., 1997). However, individuals from the HD treatment (90 indiv cm^{-2}) exhibited a lower burrowing depth compared to the MD treatment, suggesting that they may be a threshold beyond which density may limit the prospection ability of *H. germanica*. Although speculative, we may hypothesize that congeners interactions or competition become too intense at higher densities. Thereby, the alternance between infaunal and epifaunal modes observed in the present study may be a behavioural response of *H. germanica* to both space and food competition. It further suggests that the species can actively modify its vertical position in response to environmental factors according to its ecological requirements.

In addition, a positive effect of *Haynesina germanica* densities was detected on biodiffusion and nonlocal transport processes. A significant increase in biodiffusion transport was measured between the MD (30 indiv cm^{-2}) and the HD (90 indiv cm^{-2}) treatments. Furthermore, the nonlocal transport of luminophores was four time higher in the MD treatment than in the LD treatment (10 indiv cm^{-2}). Previous studies dealing with biodiffusors species of macro-invertebrates also reported higher sediment reworking with increasing densities (Duport et al., 2006; Ingalls et al., 2000; Ouellette et al., 2004; Sandnes et al., 2000; Sun et al., 1999). However, most of these studies showed a density threshold beyond which the mean contribution of each individual on total sediment reworking rate decreased. The present results were consistent with these previous studies as we observed a significantly lower individual contribution to biodiffusion and nonlocal transport with a density of 90 indiv cm^{-2} than with a density of 30 indiv cm^{-2}. Thus, at the highest density, the competition for trophic resource and space might hamper the individual feeding rate and crawling behaviour (Ingalls et al., 2000; Levinton, 1985, 1979; Miron et al., 1992, 1991; Sandnes et al., 2000; Sun et al., 1999).

Conclusion

The results of the present study open new perspective on the understanding of the contribution of intertidal benthic foraminifera to sedimentary fluxes at the sediment-water interface. Specifically, it provides new insights in *Haynesina germanica* specific behavioural traits and their effect on the vertical transport of surface sediment. This species may be classified as a gallery-biodiffusor species with a non-negligible contribution to biodiffusion and nonlocal transport processes. Such gallery diffusion mode commonly enhances the exchange of water and dissolved elements (e.g. oxygen, orthophosphate, sulphates) between sediment and water and therefore is prone to affect geochemical processes and micro- and meiobenthic communities (Aller, 1994; Mermillod-Blondin and Rosenberg, 2006; Michaud et al., 2009). Therefore, the motion behaviour of organisms is intrinsically linked to their foraging activity (Pyke, 1984). Further studies are needed to understand the benefit of tube-building behaviour for *H. germanica* and its effects on dissolved fluxes. Our results also highlighted a density-dependent effect of both community and individual sediment reworking intensity and depth. To simulate the role of complex communities of foraminifera in soft-bottom sediments, it would be interesting to evaluate the relationship between foraminiferal density and sediment reworking by considering different bioturbation functional groups of foraminifera (i.e. epifaunal-, surficial- and gallery biodiffusors, Deldicq et al., 2020) occurring in natural environments.

Acknowledgements

The authors thank the Région Hauts-de-France, the Ministère de l'Enseignement Supérieur et de la Recherche and the European fund for regional economic development for their financial

support through the attribution of the CPER research project CLIMIBIO. Noémie Deldicq PhD fellowship is funded by the Ministère de l'Enseignement Supérieur et de la Recherche.

Authors' contribution

N.D., V.M.P.B. and F.M-B conceived the idea of this study and V.M.P.B. obtained financial support. N.D. and V.M.P.B. provided significant input on experimental design. N.D. performed the behavioural experiments and analysed the images. N.D. and F.M-B. analysed the data and performed the statistical analyses. N.D., F.M-B. and V.M.P.B. contributed to the interpretation of the data and the discussion of the results presented in the manuscript. N.D. wrote the draft manuscript. N.D., F.M-B. and V.M.P.B. revised the article critically for intellectual content and gave final approval of the submitted version.

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