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

3

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5

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28 **Abstract**

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

45

46 **Keywords**

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

49 **1. Introduction**

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

53 (Gilbert et al., 1996; Mermillod-Blondin and Rosenberg, 2006; Volkenborn et al., 2016,
54 2012). The role of benthic macro-invertebrate species as bioturbators generally depends on
55 their mode of sediment reworking that is further modulated by species-specific traits and the
56 time allocation patterns between these traits (De Backer et al., 2011; François et al., 1997;
57 Gérino et al., 2003; Grémare et al., 2004; Kristensen et al., 2012; Pascal et al., 2019).
58 Conversely to macrofaunal taxa, the contribution of meiofauna to fluxes (i.e. sediment
59 particles and dissolved elements) at the sediment-water interface has been far less studied
60 (Bonaglia et al., 2014; Giere, 2009; Nascimento et al., 2012; Pike et al., 2001), and barely
61 considered in an attempt to estimate community bioturbation potential based on a review of
62 1033 benthic invertebrate species from the northwest European continental shelf (Queirós et
63 al., 2013).

64 Nevertheless, meiofaunal species display distinct biological activities (e.g. crawling,
65 burrowing, construction and maintenance of burrows, ingestion/defecation of particles)
66 suggesting a significant contribution to sediment reworking processes and therefore to the
67 geochemical and microbial structuration of the sedimentary environment (Chandler and
68 Fleeger, 1984; Nehring et al., 1990; Pike et al., 2001; Reichelt, 1991; Bonaglia et al., 2020,
69 2014; Middelburg and Meysman, 2007; Rysgaard et al., 2000). Until recently, studies
70 assessing meiofaunal bioturbation in soft-bottom sediments focused on the effect of the whole
71 meiofauna communities without considering the role of individual species (Alkemade et al.,
72 1992; Bonaglia et al., 2020, 2014; Nascimento et al., 2012; Rysgaard et al., 2000). Moreover,
73 most publications on the role of benthic meiofauna focused on nematodes and harpacticoid
74 copepods while they may not be the dominant taxa in all soft-bottom communities (see
75 Schratzberger and Ingels (2018) for a review). Amongst meiobenthic organisms, benthic
76 foraminifera is a key group of the meiofauna in soft-bottom sediments; representing up to
77 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 $Db = 0.19 \text{ cm}^2 \text{ day}^{-1}$ (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

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

110

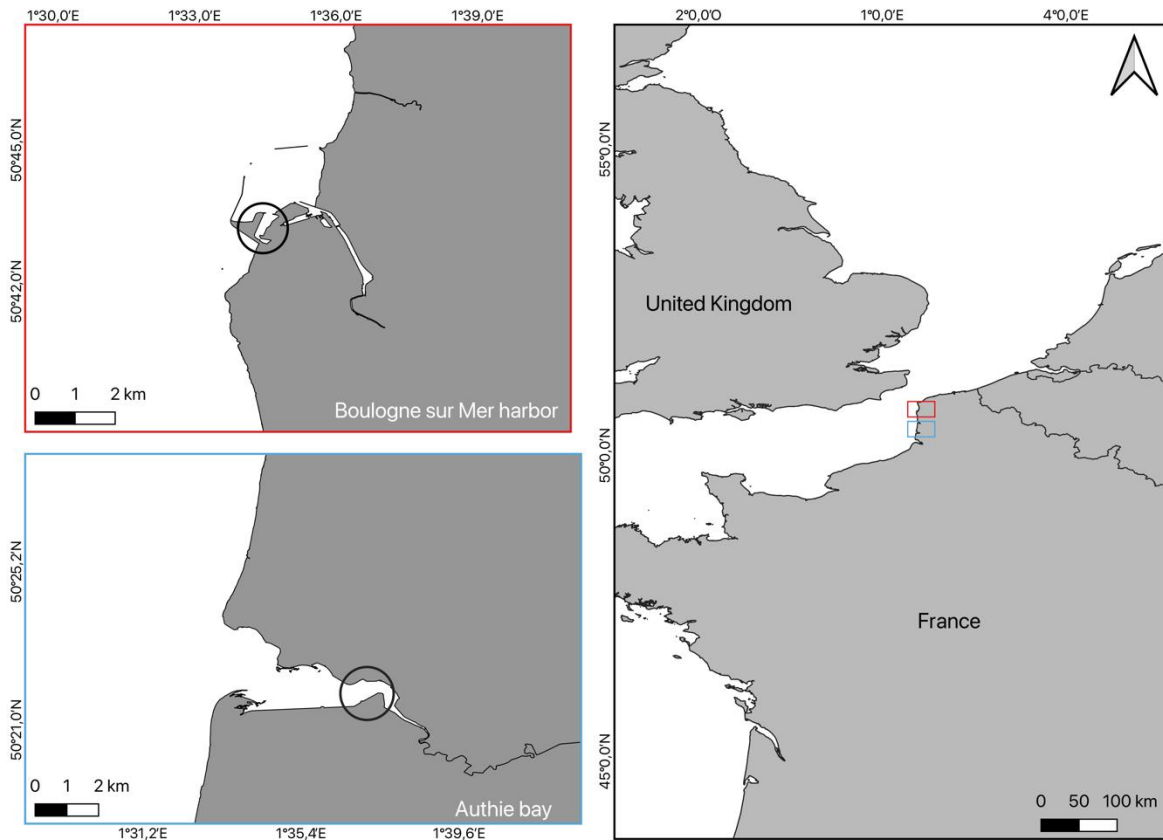
111 **2. Material and Methods**

112 2.1. Vertical motion behaviour

113 2.1.1. Collection of living *H. germanica*

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

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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.

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2.1.2. Experimental set-up

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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).

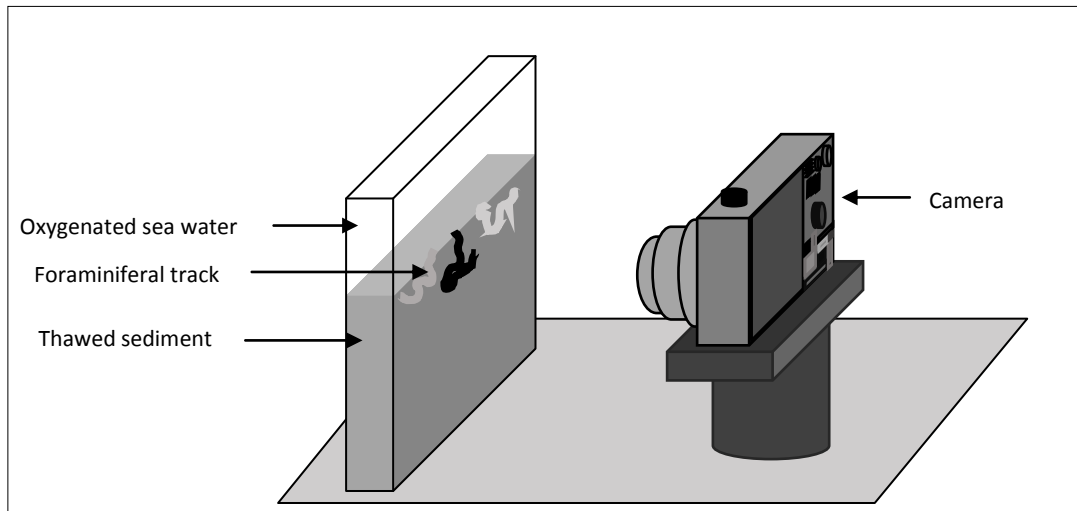


Figure 2. Experimental set-up for time-lapse assessment of foraminiferal motion-trait over a 48 and 72 h periods.

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2.1.3. Quantification of behavioural traits

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

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

150

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

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

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

$$157 \quad D_t = \sqrt{(x_t - x_{t+1})^2 + (y_t - y_{t+1})^2}$$

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

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

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

170

171 *2.1.4. Quantification of the biogenic structure built by Haynesina germanica*

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

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

$$177 \quad S_i = \text{Length} \times \text{Width}$$

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

181

182 2.2. Quantification of sediment reworking

183 2.2.1. Sediment and living fauna sampling

184 Sediment cores (1 x 1 x 5 cm, N = 15) and surface sediment were collected in August 2020
185 in Boulogne-sur-Mer harbour (50°43'6"N, 1°34'25"E, Fig. 1), an intertidal mudflat located on
186 the French coasts of the English Channel. Please note that sediments collected from the two
187 sampling sites i.e. Authie Bay and Boulogne sur Mer harbour and used in the present study
188 had comparable grain size distributions (20 % and 80 % of sand and silt, respectively), TOC
189 contents (between 1 and 2%) and salinity values (33.8 PSU). After collection, cores were
190 stored during 48 h in a freezer (-20°C) to ensure that the sediment was free of macro- and
191 meio-organisms that could produce sediment reworking. Frozen sediment cores were disposed
192 in a 15 litre aquarium (35 x 20 x 25 cm) filled with natural filtered and oxygenated sea water.
193 The aquarium was kept in temperature-controlled incubators (MIR-154, Panasonic, Japan) at
194 18°C with a 12h:12h light/dark cycle for few days. Surface sediment samples were stored in
195 plastic containers (100 ml), transported to the laboratory, and washed through a 125 µm
196 mesh-size sieve. Individuals of *Haynesina germanica* were subsequently sorted with a brush
197 and then acclimated for 24 hours in temperature-controlled incubators at 18°C with filtered
198 natural seawater.

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2.2.2. *Experimental set-up*

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

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

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

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

224

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), $\text{cm}^2 \text{ year}^{-1}$) 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

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

255 The basic equation is:

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

256 where C is the normalized tracer concentration, t is time (years), z is depth (centimetres), D
 257 is the diffusive reworking rate ($\text{cm}^2 \text{ year}^{-1}$), V is the advective transport rate (centimetres per
 258 year), R is the removal function that determines the mass of tracer (grams per day) removed
 259 from the surface and K is the injection function of the nonlocal transport that simulates tracer
 260 inputs (grams per day) into the deposition zone of the sediment column; K_e is a constant
 261 parameter (per day) estimated from the model, and depths Z_{min} and Z_{max} represent the upper
 262 and lower limits of the deposition zone, respectively. The nonlocal transport is thus quantified
 263 by a flux of sediment removed from the surface. In this case, $R_{(z,t)} = 0$ for $z > 0$ and $R_{(z,t)} = K_{(z,t)}$
 264 $(Z_{max} - Z_{min})$ for $z = 0$ and $K_{(z,t)} = K_e$ for $z \in [Z_{min}, Z_{max}]$ and $K_{(z,t)} = 0$ for $z \in [Z_{min}, Z_{max}]$. As
 265 luminophores were added as pulse input at the surface of the sediment at the beginning of
 266 each experiment, the model was applied under non-steady-state conditions. Thus, model eq. 1
 267 was used with the upper boundary condition of an instantaneous source of unit strength
 268 (maximal C of tracer) at $z = 0$ at $t = 0$, a lower boundary $C \rightarrow 0$ at $z \rightarrow \infty$, and initial condition
 269 $C = 0$ at $z > 0$. The general solution was given by Officer and Lynch (1982) as:

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

270 with

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

271 and

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

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

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

280

281 2.3. Statistical analysis

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

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

293 cores. As no significant differences in sediment reworking variables were detected between
294 luminophore sizes (see results), sediment reworking coefficients and maximum penetration
295 depth were calculated by using the addition of the percentages of pink and green
296 luminophores for each layer of each core. Then, these sediment reworking variables were
297 compared among foraminifera treatments using one-way analyses of variance (ANOVA).
298 Both sediment coefficients and maximum penetration depth values were $\ln(x+1)$ transformed
299 to homogenize variances after the homoscedasticity of variances and the normality
300 distribution of the residuals were tested using Bartlett's and Shapiro's tests, respectively.
301 Bonferroni-Dunn post hoc tests were subsequently performed if significant differences were
302 detected among foraminiferal treatments to evaluate which density treatments differed (Zar,
303 2009). All statistical analyses were performed using R.3.5.2. Software (R Core Team, 2019).

304

305 **3. Results**

306 3.1. Vertical motion behaviour

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

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

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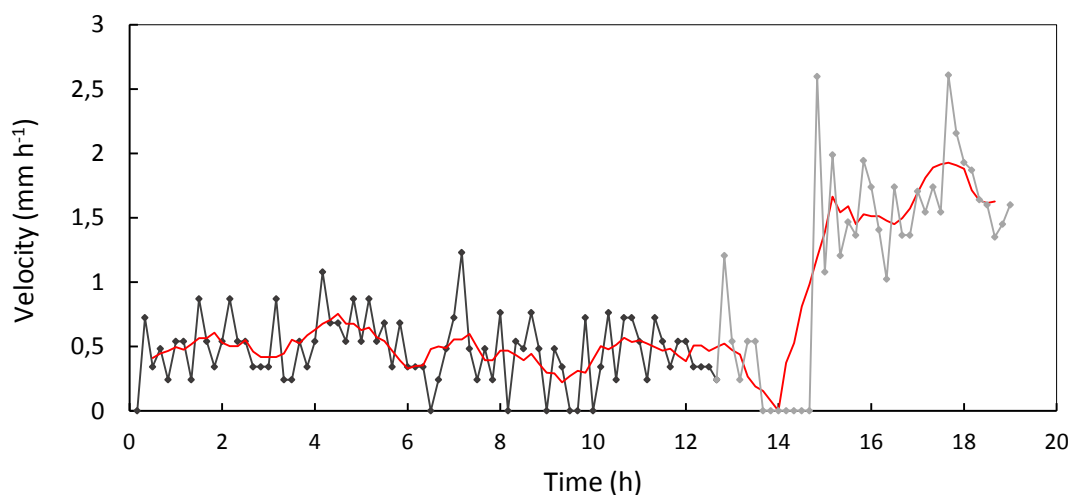
Table 1. Statistical results assessing the effects of vertical position and trail following on individual instantaneous velocity (linear mixed model). (df: degree of freedom, *: $p < 0.05$, ***: $p < 0.001$)

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} ***

321

322 In addition, 19 out of the 35 individuals were observed having a trail following behaviour
323 i.e. moved through existing gallery previously built either by another congener or by itself.
324 Noticeably, individuals typically spend $\sim 15 \pm 19\%$ of their time using existing tracks. Trail
325 following behaviour increased by 15% the instantaneous individual velocity of individuals (p
326 < 0.05 ; Table 1, Fig. 3).

327



328

329 **Figure 3.** Example of temporal change in the instantaneous velocity of an individual of *H. germanica*. The black
330 line corresponds to a situation when the individual is moving without trail following behaviour while the grey
331 line corresponds to a situation when the individual is performing a trail following behaviour. The red-line is the
332 3-order simple moving average of the velocity.

333

334 3.2. Effect of *Haynesina germanica* on the sediment matrix

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

338

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340

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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.

342

343 The surface occupied by burrows (S_B) rapidly increased within the first 32h of the
344 experiments to reach a steady value of 6 and 8% for experiment R3 and experiments R1/R2
345 respectively (Fig. 5). Then, the increase was much slower the last 40h, to reach a S_B of 8 and
346 10% (experiment R3 and experiments R1/R2 respectively, Fig. 5).

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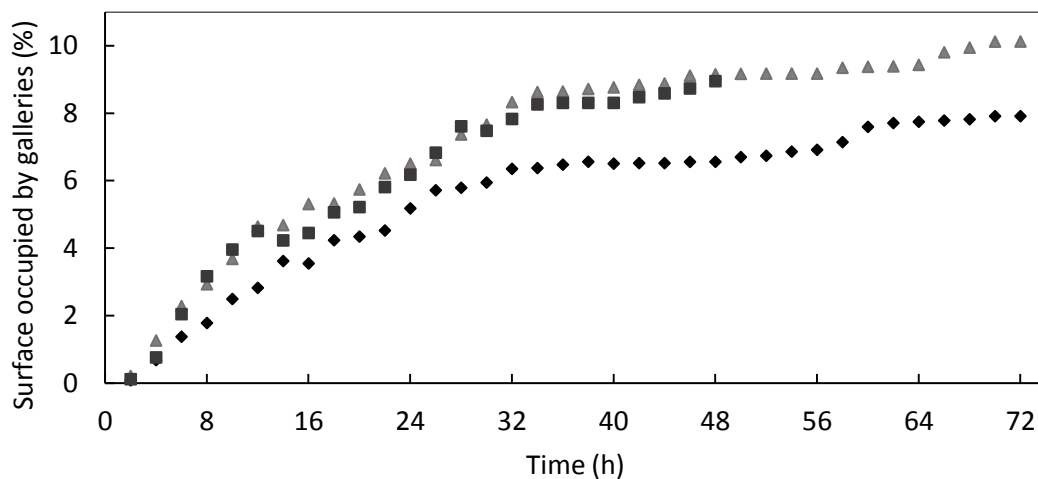


Figure 5. Temporal changes in the surface occupied by the gallery network (S_G in %) for the three experiments: R₁ (grey square), R₂ (grey triangle), R₃ (black diamonds).

356

357 3.3. Vertical sediment reworking

358 *3.3.1. Influence of sediment grain size*

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

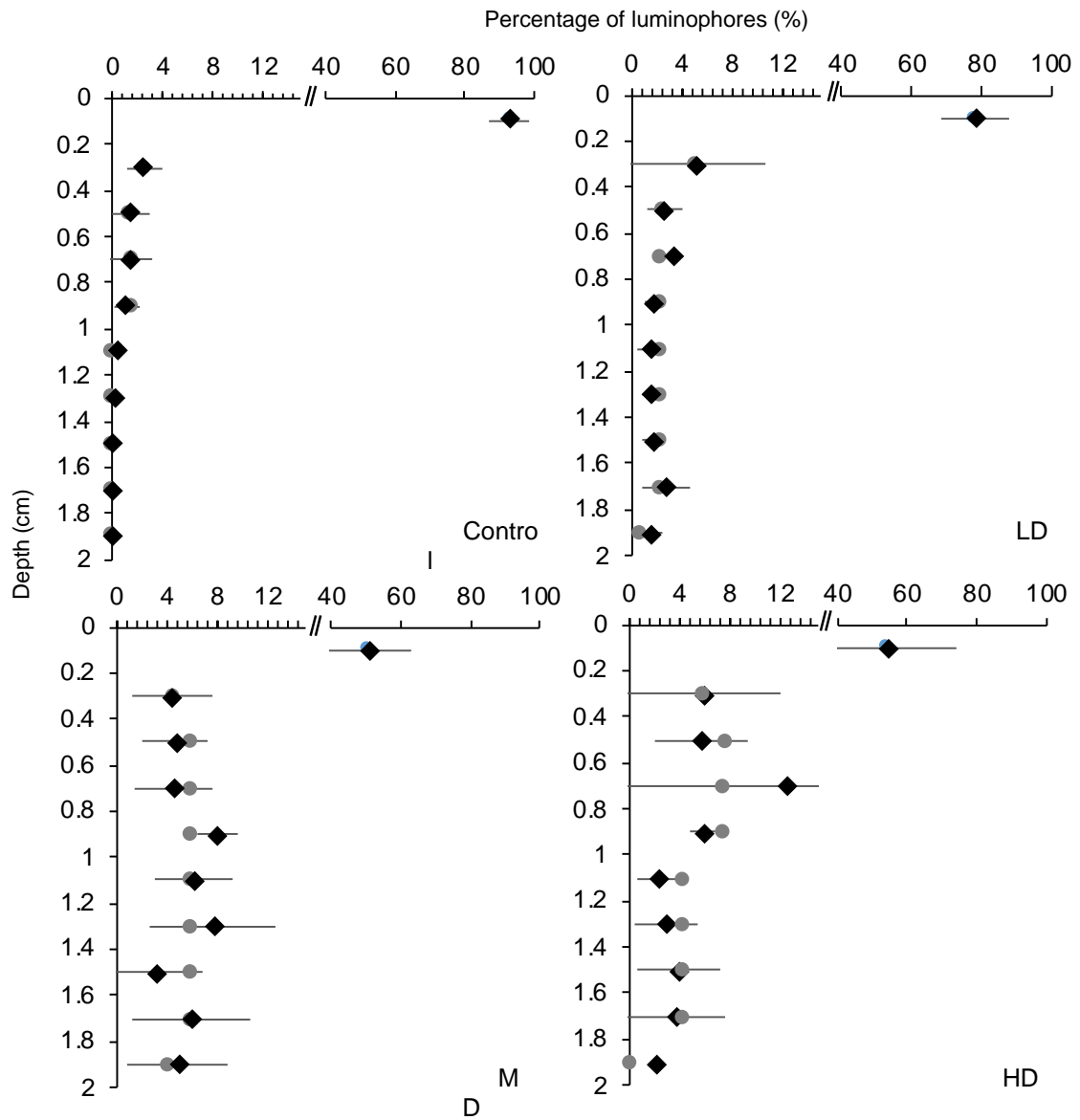
366

367 *3.3.2. Effect of density*

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

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

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Figure 6. Depth profiles (means \pm 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).

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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

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

lower limits of the sediment layer influenced by nonlocal transport.

389

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 $0.23 \pm 0.1 \text{ cm}^2 \text{ y}^{-1}$ (Bonferroni-Dunn test, $p < 0.05$;
 396 Table 3). The highest nonlocal transport rates were measured in the MD and HD treatments
 397 with $0.29 \pm 0.15 \text{ g d}^{-1}$ and $0.29 \pm 0.27 \text{ g d}^{-1}$, 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

399

400

401

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).

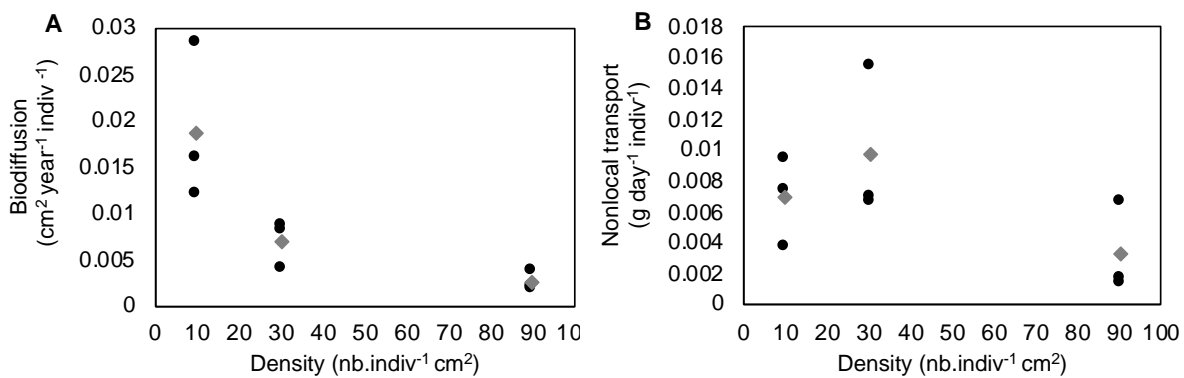


Figure 7. Biodiffusion (A) and nonlocal transport (B) per individual as a function of *H. germanica* density. Values for each replicate are presented with dark circles and mean value for the three replicates with grey diamonds.

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).

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

419 In the present study, individuals preferentially reused existing tubes, a well-known strategy
420 to reduce the cost of locomotion. For example, trail following in gastropod species reduces
421 their mucus production which is a considerable energetic burden (Davies and Blackwell,
422 2007; Tankersley, 1989). Benthic foraminifera are also able to produce mucus (e.g. Langer
423 and Gehring, 1993) of the same nature than gastropod mucus (Ng et al., 2013). Besides
424 allowing individuals to adhere to the substrate and move faster, mucus may also stabilize the
425 sediment as particles are bound together by extracellular polymeric substance secreted by
426 organisms (Nehring, 1993; Nehring et al., 1990; Reichelt, 1991; Riemann and Schrage, 1978).
427 The sustainability of the biogenic sedimentary structures built by *H. germanica* may be thus
428 enhanced by individual mucus production which would contribute to the stabilisation of the
429 sediment matrix. Mucus layers may also enhance bacterial and fungi development (Moens et
430 al., 2005) which are potential food sources for benthic foraminifera (Langer and Gehring,
431 1993; Mojtahid et al., 2011). Therefore, the trail-following behaviour of *Haynesina*
432 *germanica* reported from the present study may be an adaptive response to the physical
433 constrain triggered by cohesive sediment but it may be also linked to feeding activities on
434 microbial communities favoured by tube-associated mucus.

435

436 4.2. *Haynesina germanica* is a tube-building species generating a non-selective
437 transport of sediment

438 The sediment reworking induced by *Haynesina germanica* was characterized by two proc-
439 esses: the biodiffusion of sediment particles likely occurring in the surface layer and the
440 nonlocal transport of particles fallen in one-end tube structures produced by the species. This
441 mode of sediment reworking is similar to the one of the two polychaete species *Hediste diver-*
442 *sicolor* and *Allita virens* that are classified as gallery biodiffusors (Duport et al., 2006; Fran-
443 çois et al., 2002; Gilbert et al., 2007; Michaud et al., 2005). Thus, our findings suggest that
444 *Haynesina germanica*, which was initially classified as a surficial biodiffusor species, may be
445 redefined as a gallery biodiffusor species. Indeed, surficial biodiffusor species like the cockle
446 *Cerastoderma edule* (Richard et al., 2021) do not display a burrow-dwelling behaviour and
447 hence do not generate biogenic sedimentary structures such as burrows and tubes in the sedi-
448 ment (Kristensen et al., 2012; Mermillod-Blondin et al., 2003). Furthermore, this work further
449 contributes to confirm the infaunal microhabitat of *H. germanica* (Seuront and Bouchet,
450 2015).

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

460 sediment reworking induced by *H. germanica* was not related to particle ingestion and eges-
461 tion.

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

474

475 4.3. Sediment reworking in *Haynesina germanica* is constrained by density

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

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

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

510

511 **Conclusion**

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

530

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536

537 **Authors' contribution**

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

545

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