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1 **Assessing behavioural traits of benthic foraminifera: implications for**
2 **sediment mixing**

3 Noémie Deldicq^{1*}, Laurent Seuront^{2,3,4}, Dewi Langlet¹, Vincent M.P. Bouchet¹

4 ¹Univ. Lille, CNRS, Univ. Littoral Côte d'Opale, UMR 8187, LOG, Laboratoire d'Océanologie et de Géosciences,
5 F 62930, Wimereux, France.

6 ²CNRS, Univ. Lille, Univ. Littoral Côte d'Opale, UMR 8187, LOG, Laboratoire d'Océanologie et de Géosciences,
7 F 62930, Wimereux, France.

8 ³Department of Marine Resource and Energy, Tokyo University of Marine Science and Technology, 4-5-7 Konan,
9 Minato-ku, Tokyo 108-8477, Japan.

10 ⁴Department of Zoology and Entomology, Rhodes University, Grahamstown, 6140, South Africa.

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13 *Corresponding author:

14 E-mail: noemie.deldicq@outlook.fr

15 Tel: 03 21 99 29 42

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25 **Short title: Intertidal foraminifera behavioural traits**

26 **Abstract**

27 The assessment of behavioural traits of marine organisms is increasingly recognized as a key
28 issue to understand their role in ecosystem processes, such as bioturbation and nutrient cycling.
29 The movement ability of intertidal foraminifera suggest that they may have a role, yet to be
30 quantified, in benthic-pelagic coupling through their movement on the sediment, at the
31 sediment-water interface and within the sediment. In this context, we investigated the
32 behavioural traits of 5 benthic foraminiferal species typical of European temperate mudflats
33 under standardized trophic light and temperature conditions. Behavioural traits related to
34 motion of *Ammonia tepida*, *Haynesina germanica*, *Criboelphidium williamsoni*, *Miliammina*
35 *fusca* and *Quinqueloculina seminula* species were assessed through their travelled distance,
36 velocity, tortuosity of the path, position in the sediment and activity index. By analogy with
37 macrofauna bioturbation functional groups, we describe the studied foraminifera as
38 biodiffusers-species with 3 sub-groups defined according to their vertical position in the
39 sediment. *C. williamsoni* belongs to the epifaunal-biodiffusers group while *A. tepida* and *H.*
40 *germanica* belongs to surficial-biodiffusers. Finally, the species *Q. seminula* and *M. fusca* are
41 considered as gallery-biodiffusers species. Our results further suggest that features such as
42 velocity, activity and tortuosity may mediate sediment-mixing intensity. Therefore, *Q.*
43 *seminula*, *H. germanica* and *C. williamsoni* which are the most active species, would have
44 larger effect than the less active *A. tepida* and *M. fusca* on particles reworking rates. Taken
45 together, our results suggest that benthic foraminifera may play an underestimated role in
46 bioturbation processes.

47 **Keywords**

48 Benthic foraminifera – intertidal - motion behaviour – functional trait – bioturbators groups

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50 1. Introduction

51 Trait-based studies have largely been implemented to describe ecosystem functioning,
52 especially over the last decade (Braeckman et al. 2010, Cardinale et al. 2011, Gothland et al.
53 2014). Specifically, traits — defined as “*the morphological, physiological or phenological*
54 *features measurable at the individual level, from the cell to the whole-organism level*” (Violle
55 et al. 2007)— can either be demographical (e.g. birth, mortality), biological (e.g. size, growth),
56 ecophysiological (e.g. nutrient assimilation, resource uptake) or behavioural (e.g. locomotion,
57 species interactions). These features determine the role of a species in the ecosystem; hence
58 allow defining functional traits (Violle et al. 2007, Gagic et al. 2015). For instance, a
59 comprehensive assessment of species-specific behavioural traits associated to locomotion is
60 one way to understand the role of species in the structure and functioning of coastal ecosystems.
61 Specifically in soft sediment environment, the behavioural traits related to faunal motion are
62 intrinsically considered as functional traits involved in bioturbation processes through the
63 displacement of sediments particles and the related enhancement of fluxes of both dissolved
64 and particulate materials (Mermillod-Blondin et al. 2004, Mermillod-Blondin & Rosenberg
65 2006, Kristensen et al. 2012, 2014). For instance, surface sediment displacement intensity is
66 directly linked to the type of activity (feeding, tube building) in the terebellid polychaete
67 *Eupolyornia nebulosa* (Maire et al. 2007c). Recent methodological improvements such as high-
68 frequency image analysis and automated acquisition help to quantify behavioural traits
69 associated to bioturbation, see Maire et al. (2008) for a review. Continuous observation of *Abra*
70 *ovata* showed that this bivalve’s behavioural activity is linked to sediment-mixing intensity
71 (Maire et al. 2007a). Depending on their behavioural traits, bioturbating species can induce
72 various changes on the benthic compartment such as the microbial community structure (Banta
73 et al. 1999, Marinelli et al. 2002, Papaspyrou et al. 2006) and in the biogeochemical reactions
74 occurring in the sedimentary column (Gutierrez & Jones 2006). Trait-based approaches hence

75 allow the description of different functional groups of macrofauna species such as gallery-
76 diffusors, biodiffusors, regenerator, upward- and downward-conveyors (François et al. 1997).
77 There is still, however, a limited knowledge on the role of the meiobenthic compartment in
78 bioturbation processes (see review in Schratzberger & Ingels 2017).

79 Meiofaunal taxa activity (nematodes and copepods) increase bacterial growth, oxygen
80 fluxes, denitrification and organic matter mineralisation (Aller & Aller 1992, Bradshaw et al.
81 2006, Middelburg & Meysman 2007, Nascimento et al. 2012, Piot et al. 2013, Bonaglia et al.
82 2014). Benthic foraminifera, despite their high abundance and ecological importance in the
83 marine meiobenthos (Murray 2006, Schönfeld et al. 2012), have essentially been ignored in
84 most studies dealing with meiofaunal bioturbation. Furthermore, little is known on
85 foraminiferal traits (e.g. habitats, metabolism, feeding modes, displacements), and only a few
86 studies quantified the motion behaviour of foraminifera (e.g. Kitazato 1981, 1988, Seuront &
87 Bouchet 2015, Jauffrais et al. 2016b). Hence, all benthic foraminiferal functions may not yet be
88 identified, particularly those involved in bioturbation processes. Benthic foraminifera can move
89 over relatively long distances (Seuront & Bouchet 2015) and their movements types (rotating,
90 spinning, crawling) are driven by both their number of pseudopods (Kitazato 1994) and the
91 morphology of their tests (i.e. spiral or quinqueloculine, Wetmore 1988). Foraminiferal motion
92 varies in intensity (Severin 1987, Gross 2002) and induces sediment displacements (Kitazato
93 1988, Hemleben & Kitazato 1995) that have so far only been quantified for deep-sea
94 communities (Gross 2002). These displacements create trails at the sediment surface (e.g.
95 *Quinqueloculina impressa*, *Criboelphidium excavatum*) and galleries (e.g. *Ammotium cassis*,
96 *Criboelphidium excavatum* subsp. *clavatum*) in the sediment (Richter 1964, Severin et al.
97 1982, Linke & Lutze 1993, Hemleben & Kitazato 1995, Bornmalm et al. 1997, Gross 2002).
98 Recently, Seuront and Bouchet (2015) showed a negative geotaxis in *Ammonia tepida* and a
99 positive geotaxis in both *C. excavatum* and *Haynesina germanica* suggesting that these species

100 move on and in the sedimentary column to colonize different microhabitats depending on their
101 ecological requirements (Wetmore 1988, Linke & Lutze 1993, Murray 2006). Hence, benthic
102 foraminiferal functional traits associated to motion behaviour may exist and be involved in
103 sediment mixing. This further suggests that the assessment of behavioural traits is an absolute
104 prerequisite to a comprehensive description of foraminiferal role in particulate fluxes at the
105 sediment-water interface. Yet, behavioural traits such as activity, motion intensity and vertical
106 position are poorly described in benthic foraminifera. In this context, the objectives of this study
107 are (i) to assess the horizontal and vertical dynamic of 5 intertidal foraminiferal species at the
108 sediment-water interface, (ii) to quantify the motion behaviour of these species and (iii) to use
109 the emergent vertical position and behavioural traits as a stepping stone to objectively classify
110 these species into functional groups. In intertidal mudflats from temperate environment, oxygen
111 penetration depth rarely reached 1 cm and foraminifera are mainly distributed in the 0-1 cm
112 layer (Geslin et al. 2011, Cesbron et al. 2016). This study hence specifically focused on
113 foraminifera living in the top 1st cm of sediment.

114 **2. Material and Methods**

115 *2.1. Sediment sampling and experimental set-up*

116 Surface sediment (0-1 cm) was collected from February to June 2018 at low tide in the
117 Authie Bay (50°22'20"N, 1°35'45"E), an intertidal mudflat located on the French coasts of the
118 English Channel for living benthic foraminifera. Sampled sediment was stored in plastic
119 containers (100 ml) and transported to the laboratory, where it was washed through a 125 µm
120 mesh-size sieve. Living benthic foraminifera were subsequently individually sorted with a
121 brush, identified and their pseudopodial activities checked with an inverted phase-contrast
122 microscope. Five intertidal species were considered in this study due to their high density at the
123 study site: the planispiral species *Haynesina germanica* and *Criboelphidium williamsoni*, the
124 trochospiral species *Ammonia tepida*, the agglutinated species *Miliammina fusca* and the

125 porcelaneous species *Quinqueloculina seminula*. Recent molecular investigations showed that
126 the phylotypes *H. germanica* S16, *C. williamsoni* S1 and *A. tepida* T6 occur in the Authie Bay
127 (Schweizer, unpublished data). Individual sizes ranged from 300 to 800 μm in diameter.
128 Depending on the abundance at the time of sampling, 8 to 33 individuals per species were used
129 for the experimentation (Table 1). Before behavioural observations, individuals were kept
130 overnight 12h-long for acclimation under the experimental condition in a controlled-
131 temperature room at 18°C. Behavioural observations were performed in 300 ml aquaria filled
132 with 25-30ml defrost Authie-Bay sediment and 250 ml unfiltered eastern English-Channel
133 seawater (30 PSU). We used defrost sediment to make sure sediment was free of moving macro-
134 and meio-organisms (since nematodes, copepods and macrofaunal organisms are killed during
135 sediment freezing) and that only foraminiferal tracks could be observed at the sediment surface.
136 After the 12-h acclimation period, foraminifera were placed randomly at the surface of sediment
137 (Fig. 1). Note that the overlaying water was fully saturated in oxygen though a 10-min vigorous
138 air bubbling immediately before spreading living foraminifera on the sediment surface. At the
139 end of the 24h-experiment, dissolved-oxygen saturation was about 56% in the overlaying
140 seawater right above the sediment-water interface (HI9829 Multiparameter Meter, Hannah
141 instruments).

142 2.2. Quantification of behavioural traits

143 Individual displacements in and on the sediment were recorded by time-lapse photography
144 (1 image every 10 min for 24 hours) using a digital camera (Nikon V1 with a Nikkor 10–30
145 mm lens; Fig. 1). For each foraminifera, 144 images were combined in image-analysis software
146 Fiji to extract (x,y) coordinates using the Manual tracking plugin (Schindelin et al. 2019). The
147 behavioural traits of the above-mentioned species were investigated adapting the method
148 described in Seuront and Bouchet (2015). Five parameters were used to characterise the traits
149 of each study species.

150 First, the level of activity i.e. time allocated to motion by each individual, was estimated
151 with the activity index A_i . This index is based on the ratio between the total time taken by one
152 individual to move from its initial to its final position (t_{move}) and the time that the individual
153 spent moving between these positions (t_{active}):

$$154 \quad A_i = 100 \times (t_{\text{active}} / t_{\text{move}})$$

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

$$157 \quad D_t = \sqrt{(x_t - x_{t+10})^2 + (y_t - y_{t+10})^2}$$

158 where (x_t, y_t) and (x_{t+10}, y_{t+10}) are the coordinates between two successive images taken at times
159 t and $t+10$ min and the velocity (mm h^{-1}) of each individual was subsequently calculated
160 considering the total distance travelled in 24 h.

161 The complexity (or tortuosity) of movement paths was assessed using fractal analysis. The
162 fractal dimension measures the degree to which the trajectory fills the available space and is
163 bounded between $D = 1$ for a line (i.e. the simplest instance of a trajectory) and $D = 2$ for a
164 movement so complex that it actually fills the whole available space. The fractal dimensions of
165 foraminifera trajectories were estimated using the box dimension method (see Seuront, 2010,
166 2015 for reviews), which relies on the “ l cover” of the object, i.e. the number of boxes of length
167 l required to cover the object. A more practical alternative is to superimpose a regular grid of
168 boxes of length l on the object and count the number of boxes occupied by a subset of the object.
169 This procedure is repeated using different values of l . The surface occupied by the trajectory of
170 a foraminifera is then estimated using a series of counting boxes spanning a range of surfaces
171 down to some small fraction of the entire surface. The number of occupied boxes increases with
172 decreasing box size, leading to the following power-law relationship:

$$173 \quad N(l) \propto l^{-D_s}$$

174 where l is the box size, $N(l)$ is the number of boxes occupied by the trajectory, and D_b is the
175 box fractal dimension. The fractal dimension D_b is estimated from the slope of the linear trend
176 of the log-log plot of $N(l)$ versus l .

177 Finally, to assess the preferential position of the 5 studied species, the vertical position in
178 the sediment of each individual was determined for every picture based on a 3 depths categories
179 classification. When the test remained visible at the surface and the width of the path was
180 indistinguishable, the individual was considered to be crawling on the sediment surface (Fig.
181 2A,D). In turn, when the individual was burrowing into the sediment, its position was divided
182 in two categories: it was considered as moving at the sediment-water interface when half of the
183 test was visible (Fig. 2B,E) and to be burrowed in the sediment when a swelling at the sediment
184 surface was the only indication of the presence of the test in the sediment (Fig. 2C,F).

185 2.3. Statistical analyses

186 Because activity index, distance travelled, and velocity were non-normally distributed
187 (Kolmogorov-Smirnov test, $p < 0.05$), multiple comparisons between species were conducted
188 using the Kruskal-Wallis test, and a subsequent multiple comparison procedure based on the
189 Mann-Whitney test was eventually used to identify distinct group of measurements. The
190 presence of significant differences in fractal dimensions between species was assessed using an
191 analysis of covariance (Zar 2009). All statistical analyses were performed using © R.3.5.2.
192 software (R Core Team 2019).

193 3. Results

194 Among the 230 individuals picked for the experiment, 103 individuals were analysed as we
195 kept only those possible to track from the start to the end of the experiment (Table 1).

196 3.1. Activity index

197 *Criboelphidium williamsoni* was the most active species with a mean activity index at 89%
198 corresponding to 21/24h of displacement in the sediment (Fig. 3A, Table 1). This species

199 activity index is significantly larger ($p < 0.05$) than *Ammonia tepida*, *Haynesina germanica* and
200 *Quinqueloculina seminula*, which are not significantly different from each other ($p < 0.05$).
201 These 4 species have a significantly higher activity index than *Miliammina fusca* ($p < 0.05$)
202 which was the less active species with a mean activity index at 50% (Fig. 3A).

203 3.2. Distance and velocity

204 *Quinqueloculina seminula* moved significantly faster ($p < 0.05$, Fig. 3C) and over longer
205 distances (Fig. 3B) than the other. The four other species were discriminated in two other
206 homogeneous groups with species moving slowly over short distances (*Miliammina fusca* and
207 *Ammonia tepida*; Fig. 3B,C, Table 1) and species that moved at intermediate speed over
208 intermediate distances (*Criboelphidium williamsoni* and *Haynesina germanica*; Fig. 3B,C,
209 Table 1).

210 3.3. Tortuosity

211 Fractal dimensions D were in the range 1-1.3, indicating relatively linear trajectories. The
212 analysis of covariance identified a group of 4 species (*Miliammina fusca*, *Ammonia tepida*,
213 *Haynesina germanica* and *Quinqueloculina seminula*) moving significantly more tortuously
214 than *Criboelphidium williamsoni* (Fig. 3D).

215 3.4. Vertical position

216 *Miliammina fusca* and *Quinqueloculina seminula* individuals were essentially observed (i.e.
217 100% and 70 to 90%, respectively) burrowed in the sediment throughout the experiment (Fig.
218 4A,B). Conversely, the vast majority (90-100%) of *Criboelphidium williamsoni* individuals
219 remained on the sediment surface during the first three hours, before progressively moved to
220 the sediment-water interface (10 to 100%) and were barely observed down into the sediment
221 (Fig. 4C). *Haynesina germanica* gradually burrowed from the sediment surface down into the
222 sediment with time to be essentially (75 to 80%) located into the sediment after 15 hours of
223 observations (Fig. 4D). Finally, *Ammonia tepida* exhibited a slightly different temporal pattern.

224 First, a vast majority of them (95%) dug from the sediment surface down into the sediment in
225 less than an hour, before progressively spreading out back up towards to sediment-water
226 interface (Fig. 4E).

227 **4. Discussion**

228 This study is based on 24-h long observations assessing the behavioural traits of five species
229 of benthic foraminifera to further understand their implication in sediment mixing. For instance,
230 macrofaunal species behavioural traits affect the way they displace sediment particles (François
231 et al. 1997, Maire et al. 2006, 2007a). It allowed for their classification in functional groups i.e.
232 biodiffusors, regenerators or conveyors (François et al. 1997, Kristensen et al. 2012). The
233 intensity of species activity is further directly linked to their life-mode which drives sediment
234 mixing and bio-irrigation (Gérino et al. 2003, Gilbert et al. 2007, Maire et al. 2008, 2016,
235 Kristensen et al. 2012). Considering that foraminifera fundamentally displace sediment over
236 short distances due to their small size (Gross 2002, present work), we hereafter consider
237 foraminifera as biodiffusors since they are “*organisms with activities that usually results in a*
238 *constant and random local sediment bio-mixing over short distance*” (Kristensen et al. 2012).

239 More specifically, biodiffusors are typically divided in 3 subgroups (epifaunal-, gallery- and
240 surficial-biodiffusors) depending on their life-mode in the sediment (Kristensen et al. 2012). In
241 this context, our high-frequency image analysis of foraminiferal behaviour showed species-
242 specific preferential depths of activity, that we used hereafter to classify the studied intertidal
243 foraminiferal species in different biodiffusors functional subgroups (Fig. 5). Furthermore,
244 motion-behaviour features (activity index, travelled distance, velocity and tortuosity) drive
245 intra-functional group variability.

246 *4.1. Foraminifera as biodiffusors*

247 *4.1.1. Epifaunal-biodiffusors*

248 In our experiments, *Criboelphidium williamsoni* only moved on the sediment surface and
249 at the sediment-water interface. This observation is consistent with previous studies describing
250 this species as epifaunal (Allison et al. 2010) and reporting the highest density of the species in
251 the uppermost oxygenated sediment layers (Alve & Murray 2001, Bouchet et al. 2009). This
252 kleptoplastic species can host 10 times more active chloroplasts in its cytoplasm than other
253 temperate-water species (Lopez 1979). Kleptoplasty suggesting a preference for well-lighted
254 surface sediment, this species most likely have a surface-limited effect on the sediment mixing
255 and bio-irrigation. Consequently, *C. williamsoni* may be considered as an epifaunal-biodiffusor
256 (Fig. 5) which include “organisms that occur predominantly above the sediment–water
257 interface. Their activities are limited to near-surface sediments and generally redistribute fine
258 particles randomly over very short distances along the surface” (Kristensen et al. 2012).

259 4.1.2. Surficial-biodiffusors

260 *Haynesina germanica* and *Ammonia tepida* tended to avoid the surface sediment and both
261 preferred the sediment-water interface and burrowed position. Specifically, at the end of the
262 experiment, *A. tepida* individuals were evenly distributed between these two positions while *H.*
263 *germanica* ones preferred to be completely burrowed. These results are consistent with *in situ*
264 observations where *A. tepida* is found on and in the sediment (Goldstein et al. 1995, Bouchet et
265 al. 2009) while *H. germanica* mainly occur at the sediment surface (Alve & Murray 2001,
266 Bouchet et al. 2009). The latter can sequester photosynthetically active chloroplasts, which
267 might be used as food sources under low-light condition (Jauffrais et al. 2016a). Our results
268 suggest that both species could alternate between epifaunal and infaunal micro-habitats (Fig.
269 5). As a consequence, we classify these species in the surficial-biodiffusors group which are
270 “organisms with activities mostly restricted to the uppermost few centimetres of the sediment,
271 and these species rarely venture above the sediment–water interface” (Kristensen et al. 2012).

272 To be consistent with this definition, further assessments are needed to understand how deep
273 *H. germanica* and *A. tepida* can mix the sediment.

274 4.1.3. Gallery-biodiffusors

275 Quinqueloculine-shaped species (i.e. *Quinqueloculina seminula* and *Miliammina fusca*)
276 moved immediately from the surface down into the sediment layer and stayed buried during the
277 remaining time of experiment. These two species are hence clearly not restricted to the
278 sediment-water interface. *Quinqueloculina seminula* has, however, previously been described
279 as an epifaunal species (Di Bella et al. 2015, Martins et al. 2015) preferring oxic-zone (Moodley
280 et al. 1998), but is also known to be tolerant to low-oxygen events (Bernhard et al. 1997, Martins
281 et al. 2011, 2013, Langlet et al. 2014). Since in our 24-hours long observations specimens never
282 went back to the surface, these species may rather be considered as infaunal; with the ability to
283 create galleries in the sediment (Severin & Erskian 1981, Severin et al. 1982). As a
284 consequence, *Q. seminula* and *M. fusca* should be considered as gallery-biodiffusors (Fig. 5)
285 which are organisms “*inducing diffusive local bio-mixing of particles and vertical transport of*
286 *particles from the upper regions of the sediment to the lower limit of burrow penetration*”
287 (Kristensen et al. 2012).

288 4.2. Features explaining intra-functional group variability

289 Life traits such as individual size and foraging strategy affects role in species-specific
290 functional role in bioturbation processes (François et al. 1997, Gérino et al. 2003, Solan et al.
291 2004, Mermillod-Blondin 2011). For instance, macrofauna species displace a quantity of
292 sediment which is a direct proportion to their volumetric size (Dorgan et al. 2005). In our study,
293 quinqueloculine-shaped species (i.e. *Quinqueloculina seminula* and *Miliammina fusca*) are
294 species with the larger test volume suggesting that they would displace more sediment than the
295 other species investigated in the present work. However, effects of benthic fauna on fluxes at
296 the sediment-water interface depend on sediment reworking and bio-irrigation modes rather

297 than on the biogenic structure volume produced (Bouchet et al. 2009). Intensity of bioturbation
298 is hence a complex interplay between numerous life traits.

299 More specifically, the rate by which particles are physically moved also depends on feeding
300 strategies (Gérino et al. 2007). Tortuosity gives key information on that aspect (Pyke 1984; Bell
301 1991). In our study, the five species exhibited a relatively low tortuosity value. It implies that
302 they explored their environment extensively with close-to-linear trajectory. Such extensive
303 search strategy (or transecting e.g. Bell 1991) in the case of the 5 studied species, is optimal
304 under spatially-located food patches (Pyke 1984, Seuront & Stanley 2014, Seuront & Bouchet
305 2015). This foraging strategy is consistent with what is known of the trophic ecology of the five
306 species used in this study e.g. microphytobenthos, bacteria, metazoans (Nomaki et al. 2008,
307 Dupuy et al. 2010, Jauffrais et al. 2016b, Chronopoulou et al. 2019). For instance, *Haynesina*
308 *germanica* and *Ammonia tepida* are both herbivorous, feeding on benthic diatoms (Ward et al.
309 2003, Pascal et al. 2008). Recently, an in situ study showed that the feeding behaviour of
310 intertidal benthic foraminifera is more complex than what is observed experimentally
311 (Chronopoulou et al. 2019). Intertidal foraminifera exhibited clear varied and species-specific
312 trophic behaviour and were actually able to feed on different food sources. Specifically, *A.*
313 *tepida* may prefer to feed on algae but it is actually also able to feed on bacteria (Pascal et al.
314 2008). Since microphytobenthos, bacteria and metazoans microscale (i.e. centimetre-scale)
315 distributions are extremely patchy (Pinckney & Sandulli 1990, Danovaro et al. 2001, Spilmont
316 et al. 2011), all the studied species would benefit from the extensive search strategy to optimize
317 their likelihood to locate food patches. Such extensive displacement tends to maximize
318 sediment mixing (Seuront 2010, Viswanathan et al. 2011). However, species feeding strategy
319 has not been investigated throughout our experiment since we used homogenised defrost
320 surface-sediment therefore containing labile organic-matter, living bacteria, dead macro- and
321 meio-faunal organisms and the non-filtered overlaying contains microalgae. To further assess

a supprimé: is

a supprimé: This behavioural strategy is consistent with an optimal foraging strategy.

325 whether foraging-strategy would affect sediment-mixing rate, motion-behaviour of
326 foraminiferal species in a patchy and homogeneous controlled-food-condition needs to be
327 assess.

328 The five studied species showed significant differences between their respective activity
329 index, travelled distance and velocity. Within the functional groups above mentioned, species
330 may not have the same sediment mixing intensity and this intensity may most likely depend on
331 the detailed properties of species-specific motion behaviour. Within the gallery-biodiffusers,
332 *Quinqueloculina seminula* was the second most active species and travelled the longest
333 distances, while *Miliammina fusca* was the less active species and over lowest distances.
334 Similarly, the surficial-biodiffuser *Haynesina germanica* was more active and moved further
335 than *Ammonia tepida*. As a consequence, *Q. seminula* and *H. germanica* may rework a larger
336 volume of sediment. Furthermore, irrespective of their functional group, the most active species
337 (i.e. *Criboelphidium williamsoni*, *Q. seminula* and *H. germanica*) may contribute more to
338 sediment mixing than the less active species such as *A. tepida* and *M. fusca* (Fig. 5).

339 **Conclusion**

340 Based on the monitoring of species-specific behavioural traits this study assigned for the
341 first time intertidal benthic foraminiferal species into the biodiffusers-functional group. Hence,
342 the preferential depth of activity being fundamentally the prime feature allowing differentiating
343 between species. Secondary features like (i) size, (ii) feeding-modes, (iii) activity index, (iv)
344 travelled distance (v) velocity and (vi) tortuosity would most likely mediate the intensity of
345 bioturbation and explain the intra-functional group differences. To definitively validate our
346 classification, further work is needed on the quantification of sediment reworking rate of the
347 five studied species. Furthermore, our observations showed that foraminifera create physical
348 disturbances at the sediment surface, previously described as sediment pellets (Chandler 1989).
349 Such a pelletised surface layer created by benthic organisms activity can ease the resuspension

350 of sediments by tidal currents (Davis 1993, Willows et al. 1998, Orvain et al. 2003, 2004) and
351 affect sediment bio-irrigation. These physical and chemical changes will affect microbial
352 communities (Bertics & Ziebis 2009, Piot et al. 2013), organic matter mineralization and
353 nutrient cycle (Gilbertson et al. 2012, Aller 2014). Meiofaunal species activity e.g. copepods,
354 nematodes and foraminifera will consequently increase organic matter and NO_x fluxes which
355 strongly affect benthic-pelagic coupling and therefore ecosystem functions (Danovaro et al.
356 2008, de Goeij et al. 2013). This suggest that foraminifera might play a underestimated role on
357 sediment cohesiveness and dissolved-elements benthic fluxes (Schratzberger & Ingels 2017).
358 This study supports the fact that, in a context of biodiversity change, assessing life traits of
359 benthic foraminifera is critically needed to understand their role in ecosystem functioning.

360

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618

619 **Table captions**

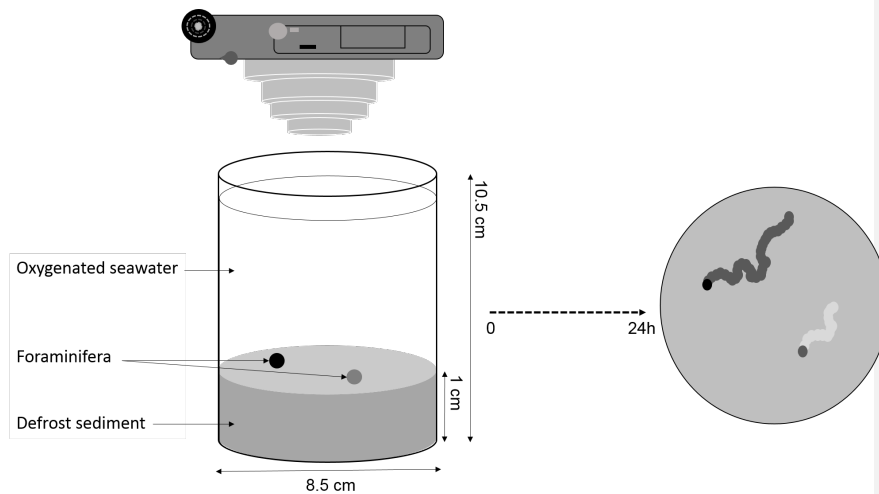
620 Table 1. Number N of individuals of each species used for experimentations and the subsequent
 621 number n of individuals for which (x,y) coordinates were extracted with mean (\bar{X}) and standard
 622 deviation (σ) for each parameters.

Species		<i>Q. seminula</i>	<i>H. germanica</i>	<i>C. williamsoni</i>	<i>A. tepida</i>	<i>M. fusca</i>
Total individual	N	30	90	30	60	20
Analysed individual	n	16	30	16	33	8
Distance (mm)	\bar{X}	88.25	51.51	44.18	17.29	14.06
	σ	32.95	19.63	13.50	5.94	4.67
Velocity (mm.h ⁻¹)	\bar{X}	3.67	2.15	1.84	0.72	0.59
	σ	1.37	0.82	0.56	0.25	0.19
Activity index (%)	\bar{X}	76.33	83.31	89.80	78.49	50.77
	σ	17.41	12.21	7.08	13.17	15.52
Tortuosity	\bar{X}	1.16	1.15	1.10	1.14	1.12
	σ	0.05	0.03	0.05	0.03	0.03

623

624 **Figures captions**

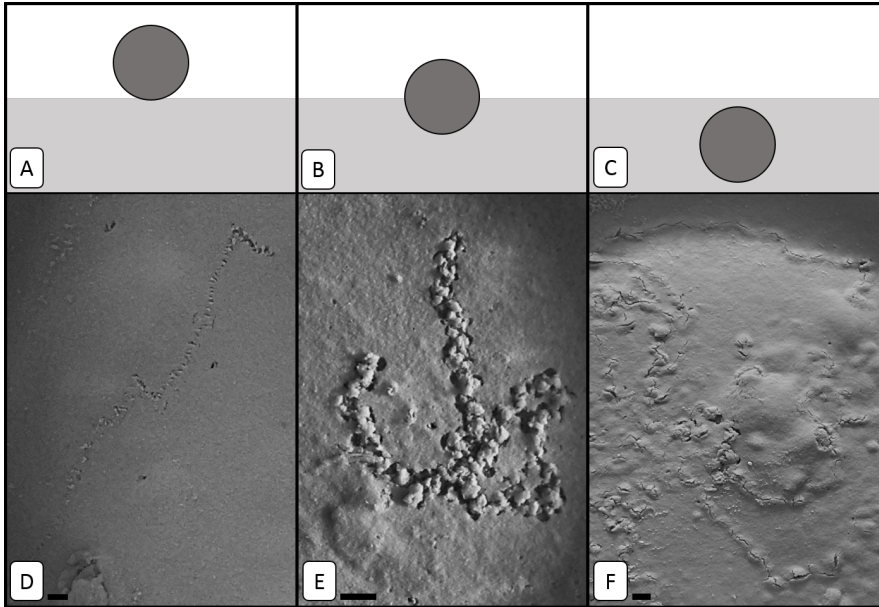
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627 Figure 1. Experimental set-up for time-lapse assessment of foraminiferal life trait

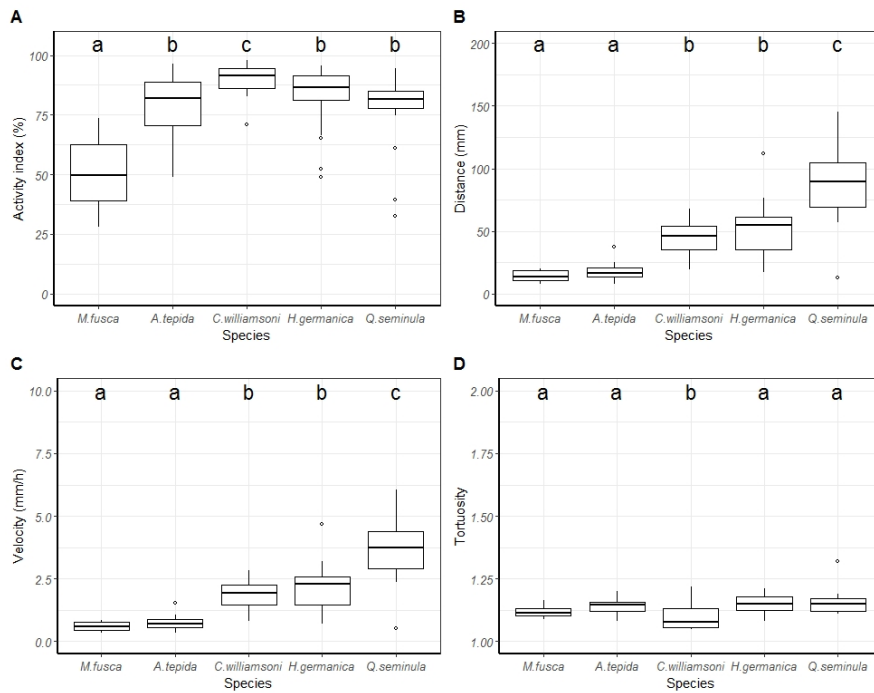
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630 Figure 2. Schematic representation (A, B and C) and images (D, E and F) of the three vertical
 631 position categories, which can be taken by a foraminifer. (A and D) Surface – (B and E)
 632 Sediment-water interface – (C and F) Burrowed. Examples from *Haynesina germanica* (D and
 633 E) and *Quinqueloculina seminula* (F). Scale bars = 0.2 mm.

634



635

636 Figure 3. Box and whiskers plots of the four calculated parameters (A) Activity index (%) – (B)

637 Distance (mm) – (C) Velocity (mm.h⁻¹) – (D) Tortuosity for all species. The letters ‘a’, ‘b’, ‘c’

638 indicate significant distinct groups of measurements (Mann-Whitney test, p < 0.05). The box

639 represents the first, second and third quartiles and the whiskers extend to 1.5 times the

640 interquartile range values outside this range are represented by open circles.

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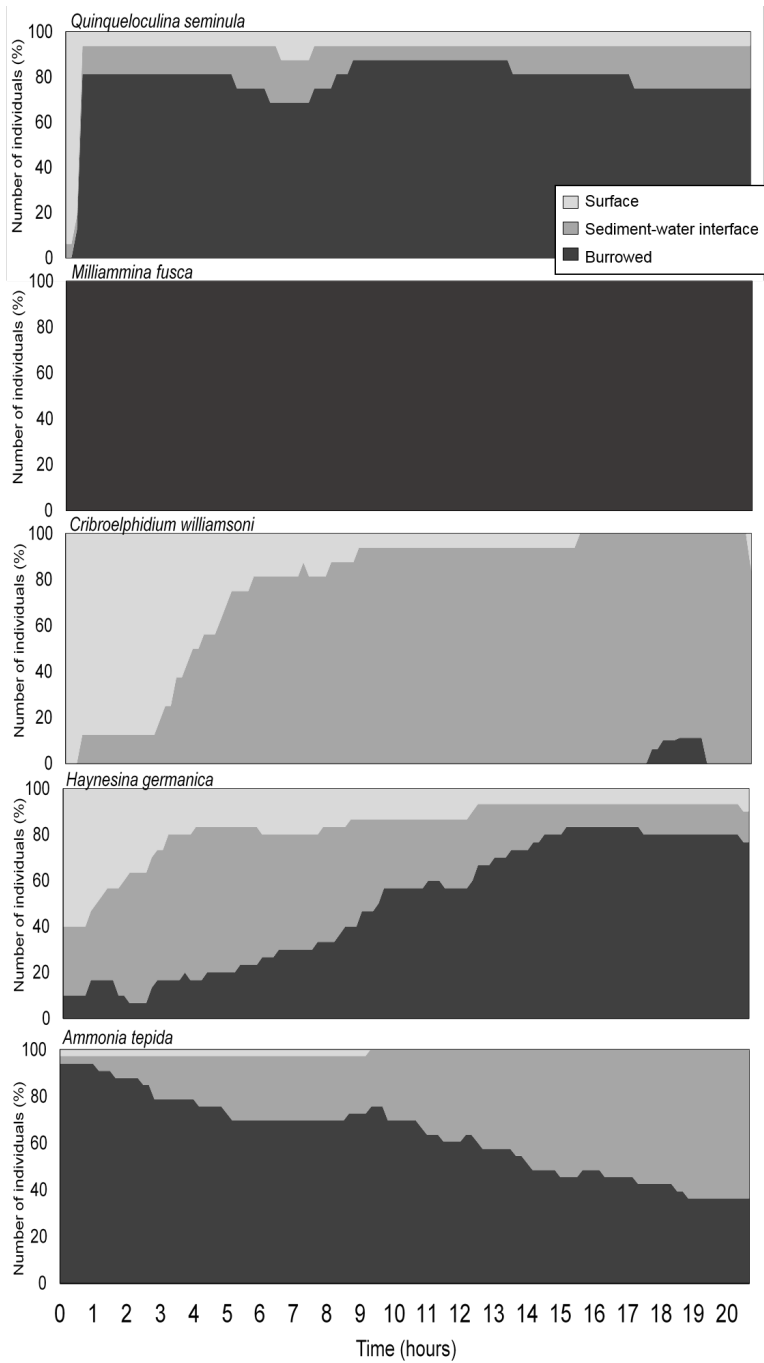
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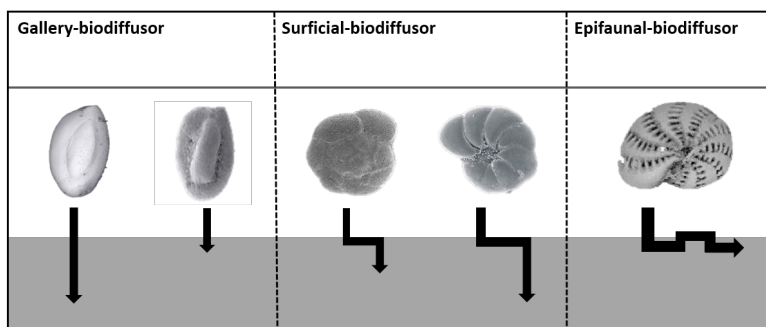
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650 Figure 4. Temporal evolution of the vertical position of each studied species

Species	Activity	Distance	Position
<i>Quinqueloculina seminula</i>	Intensive	High	Burrowed
<i>Criboelphidium williamsoni</i>		Medium	Surface
<i>Haynesina germanica</i>		Low	Surface → Burrowed
<i>Ammonia tepida</i>	Low	Low	Surface → Burrowed
<i>Milliammina fusca</i>			Burrowed



651
 652 Figure 5. Conceptual schema summarizing the difference between studied species and their
 653 classification into functional groups with *Q. seminula* and *M. fusca* in gallery-biodiffusor group,
 654 *A. tepida* and *H. germanica* in surficial-biodiffusor and *C. williamsoni* in epifaunal-
 655 biodiffusors.

656
 657