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Assessing behavioural traits of benthic foraminifera: implications for sediment mixing

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Short title: Intertidal foraminifera behavioural traits

Abstract

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

Keywords

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

1. Introduction

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

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

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

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

2. Material and Methods

2.1. Sediment sampling and experimental set-up

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

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

2.2. Quantification of behavioural traits

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

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

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

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

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

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

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

$$N(l) \propto l^{-D_b}$$

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

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

2.3. Statistical analyses

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

3. Results

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

3.1. Activity index

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

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

3.2. Distance and velocity

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

3.3. Tortuosity

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

3.4. Vertical position

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

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

4. Discussion

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

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

4.1. Foraminifera as biodiffusors

4.1.1. Epifaunal-biodiffusors

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

4.1.2. Surficial-biodiffusors

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

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

4.1.3. Gallery-biodiffusors

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

4.2. Features explaining intra-functional group variability

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

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

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

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

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

Conclusion

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

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

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Table captions

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

Species		*Q. seminula*	*H. germanica*	*C. williamsoni*	*A. tepida*	*M. fusca*
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

Figures captions

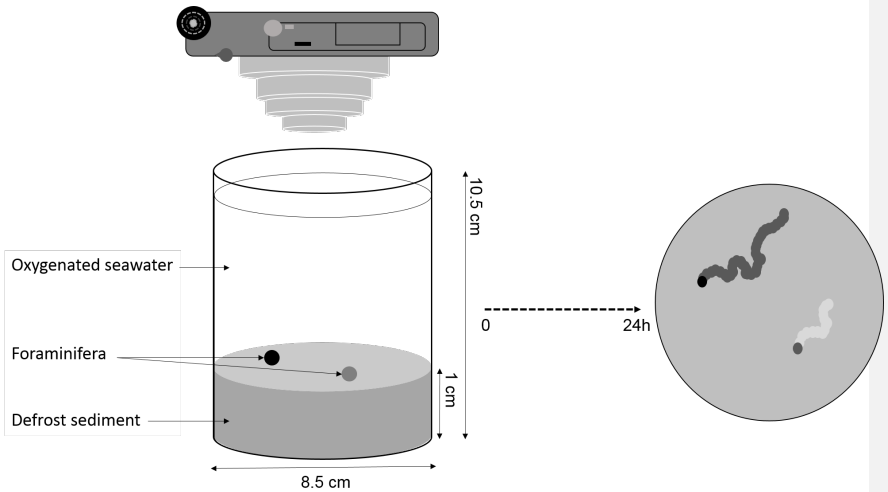


Figure 1. Experimental set-up for time-lapse assessment of foraminiferal life trait

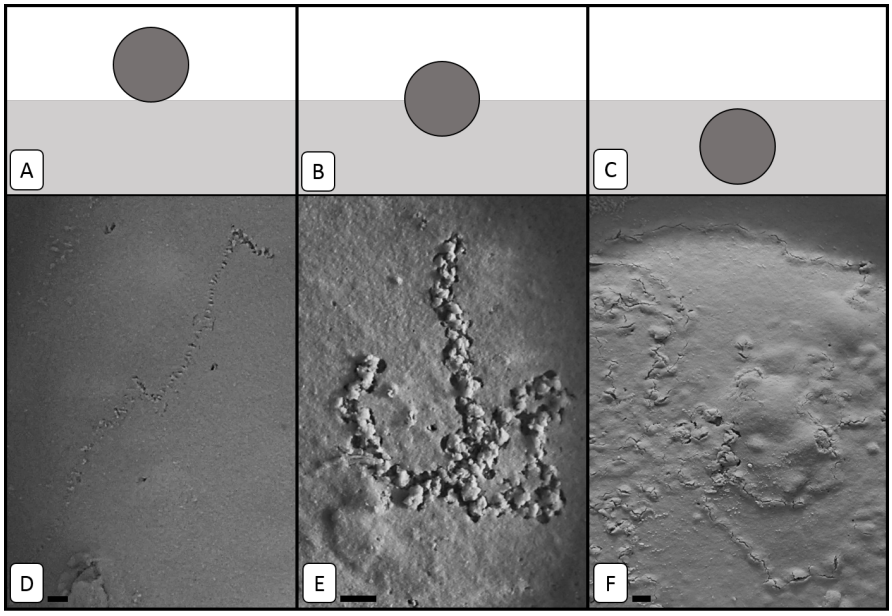


Figure 2. Schematic representation (A, B and C) and images (D, E and F) of the three vertical position categories, which can be taken by a foraminifer. (A and D) Surface – (B and E) Sediment-water interface – (C and F) Burrowed. Examples from *Haynesina germanica* (D and E) and *Quinqueloculina seminula*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

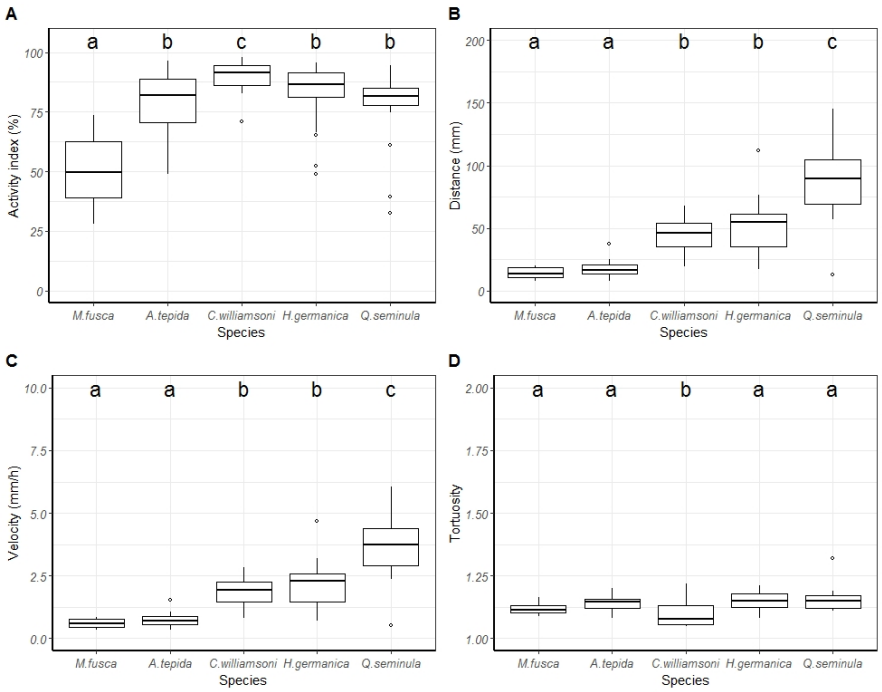
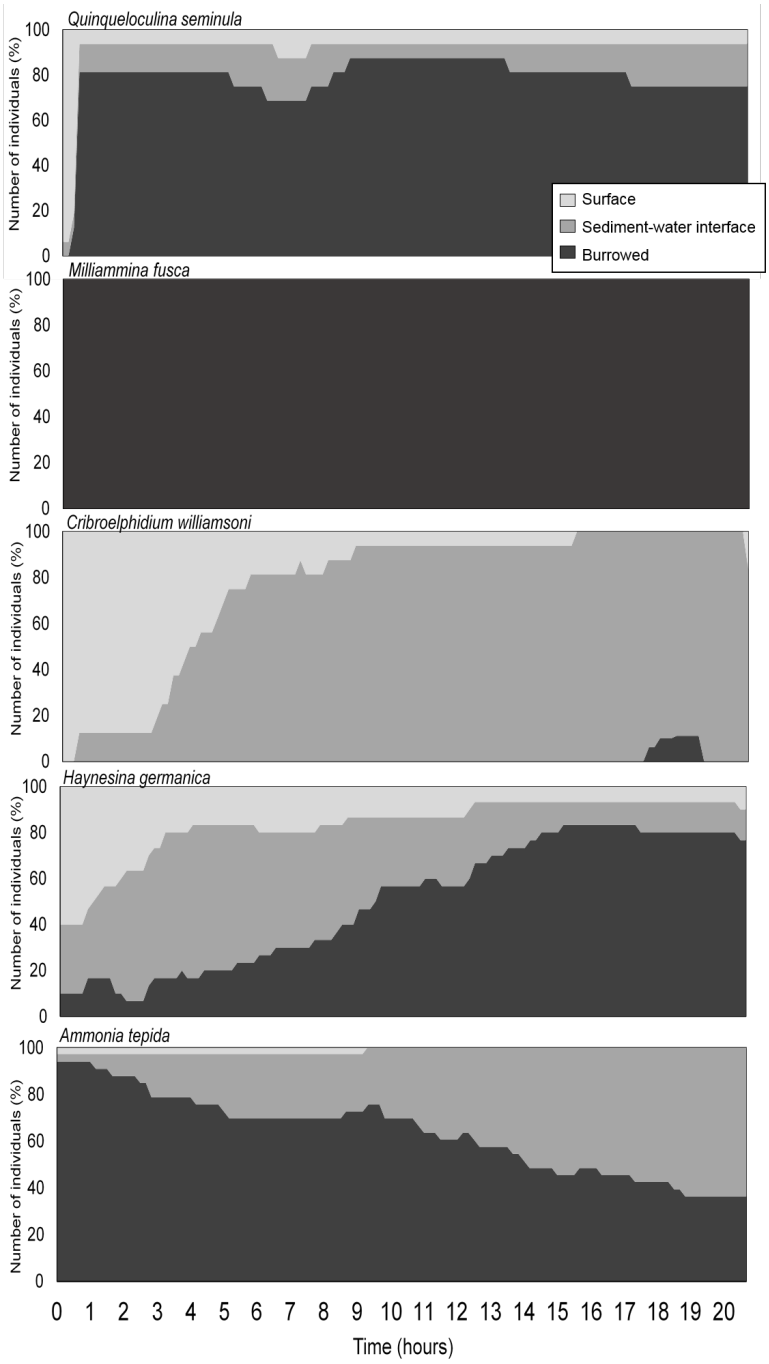


Figure 3. Box and whiskers plots of the four calculated parameters (A) Activity index (%) – (B) Distance (mm) – (C) Velocity ($mm.h^{-1}$) – (D) Tortuosity for all species. The letters 'a','b','c' indicate significant distinct groups of measurements (Mann-Whitney test, $p < 0.05$). The box represents the first, second and third quartiles and the whiskers extend to 1.5 times the interquartile range values outside this range are represented by open circles.


Quinqueloculina seminula
Milliammina fusca
Cribroelphidium williamsoni
Haynesina germanica
Ammonia tepida
Number of individuals (%)
0
20
40
60
80
100
Surface
Sediment-water interface
Burrowed
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
Time (hours)

649

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

Species	Activity	Distance	Position
Quinqueloculina seminula	Intensive	High	Burrowed
Cribroelphidium williamsoni		Medium	Surface
Haynesina germanica			Surface → Burrowed
Ammonia tepida		Low	
Milliammina fusca	Low		Burrowed

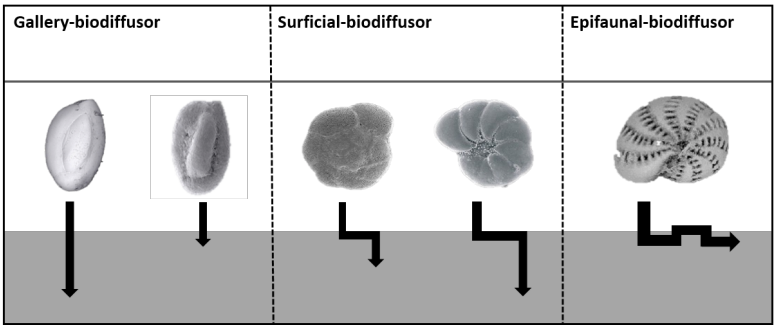


Figure 5. Conceptual schema summarizing the difference between studied species and their classification into functional groups with *Q. seminula* and *M. fusca* in gallery-biodiffusor group, *A. tepida* and *H. germanica* in surficial-biodiffusor and *C. williamsoni* in epifaunal-biodiffusors.