Inter-specific and inter-individual trait variability matter in surface sediment reworking rates of intertidal benthic foraminifera

Noémie Deldicq1 · Laurent Seuront1,2,3 · Vincent M. P. Bouchet1

Received: 13 December 2020 / Accepted: 21 May 2021 / Published online: 19 June 2021
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2021

Abstract

Although benthic foraminifera are an important component of meiofauna and contribute to carbonate production and carbon/nitrogen cycles, their role in bioturbation processes remains poorly known. Five dominant intertidal benthic foraminiferal species were recently classified into functional bioturbator groups according to their sediment reworking mode and intensity. Our study aimed at identifying potential drivers (i.e. size and/or travelled distance) of species-specific surface sediment reworking rate. The travelled distance and surface sediment reworking rate of *Haynesina germanica*, *Cribroelphidium williamsoni*, *Ammonia tepida*, *Quinqueloculina seminulum* and *Miliammina fusca* were assessed through image analysis. Our results show that the surface sediment reworking performed by these species is not size-dependent, but dependent on their motility traits through interspecific differences in the travelled distance. Smaller species (i.e. *Quinqueloculina seminulum* and *Haynesina germanica*) contributed more to surface sediment reworking than larger ones (i.e. *Ammonia tepida*, *Cribroelphidium williamsoni* and *Miliammina fusca*). These observations stress the critical role of motion behaviour in surface sediment reworking processes by intertidal foraminifera. Finally, we stress that the high inter-individual variability observed in conspecific motion behaviour may be important to decipher the role of foraminifera in sediment bioturbation. Noticeably, the species characterized by a strong inter-individual variability are also the species that have the highest surface sediment reworking rates. This last observation may inform on the species-specific phenotypic plasticity and, therefore, the potential for the functional role of these species to be maintained in their natural environment. This is particularly relevant in an era of global change where ecosystem balance is increasingly threatened by various stressors such as heat-waves, ocean acidification and pollution.

Introduction

Bioturbation activities of benthic fauna contribute to the structure and functioning of most marine soft-sediment ecosystems; see Kristensen et al. (2012) for a review. Sediment particle reworking typically drives (i) substrate physical properties such as granulometry and erodibility and (ii) bacterial communities (Orvain et al. 2003, 2004). This process affects chemical gradients and increases dissolved fluxes at the sediment–water interface (Orvain et al. 2004; Kristensen et al. 2012; Schratzberger and Ingels 2018; Bonaglia et al. 2020). Overall, bioturbation contributes to the mineralisation of organic matter; thereby enhancing carbon and nutrient cycling (Aller 1994; Mermillod-Blondin and Rosenberg 2006; Meysman et al. 2006; Kristensen et al. 2012).

Meiobenthos refers to organisms that are retained in the size fraction between 63 and 1000 µm (Mare 1942; Hulings and Gray 1971; Higgins and Thiel 1988). Their role in bioturbation processes has received an increasing amount of attention over the last decade. Beyond the fact that they may be more abundant, diverse and resilient to environmental disturbances than macro-invertebrates (Gerlach 1978; Bouchet et al. 2018, 2020), their contribution to sediment reworking and bio-irrigation is non-negligible compared to...
those of macro-invertebrates (Rysgaard et al. 2000; Gross 2002; Näslund et al. 2010; Bonaglia et al. 2014; Bouchet and Seuront 2020). Through their movement and feeding activity, meiofaunal organisms further structure and constrain microbial communities that are crucial for organic matter mineralization (De Mesel et al. 2004; Moens et al. 2005; Nascimento et al. 2012). They also affect the oxygen penetration depth, increasing solute transport (e.g. sulphides) into the sediment (Aller and Aller 1992; Rysgaard et al. 2000; Bonaglia et al. 2020). For instance, in an intertidal mudflat, nematode displacements have been shown to stimulate microphytobenthos accumulation in the surface biofilm leading to a shift in diatom community (D’Hondt et al. 2018). Taken together, these observations strongly suggest that the role of meiofauna in bioturbation processes needs to be urgently considered in studies dealing with benthic ecosystem functioning as they play an important role in soft-sediment ecosystems (Näslund et al. 2010; Nascimento et al. 2012; Bonaglia et al. 2014, 2020).

Traditionally, foraminifera have been overlooked in studies assessing total meiofaunal bioturbation, mostly because these works only considered metazoan meiofauna (Schratzberger and Ingels 2018). These abundant and diverse organisms in intertidal mudflats are able to significantly alter sediment structure through the creation of burrows and cyst building both at the interface and deeper into the sediment (Severin and Erskian 1981; Kitzato 1988, 1994; Chandler 1989; Green and Chandler 1994; Gross 2000, 2002; Bouchet and Seuront 2020; Deldicq et al. 2020), leading to sediment mixing (Gross 2002). Surface sediment reworking rates of the intertidal foraminiferal species Ammonia tepida and Quinqueloculina seminulum were recently shown as comparable to those of macrofaunal species (Bouchet and Seuront 2020). These observations highlighted the non-negligible importance of benthic foraminifera to contribute to sediment reworking processes. Furthermore, meiofauna (including foraminifera) can increase rates of solute transport and stimulate aerobic decomposition and nitrification processes in the oxic zone (Aller and Aller 1992; Aller 1994; Bonaglia et al. 2020). Recently, five dominant intertidal foraminifera have been classified in distinct functional groups (e.g. surficial-, epifaunal- and gallery-biodiffusors; see Deldicq et al. 2020) that underpinned their differences in the type and intensity of sediment reworking. Distinct species-specific behavioural patterns related to their displacement both within the sediment and at the sediment–water interface were, therefore, hypothesized to differently affect sediment reworking rates (Deldicq et al. 2020).

These preliminary results on the potential of benthic foraminifera to contribute to bioturbation processes emphasize the need to further estimate surface sediment reworking rates of foraminiferal species to better understand their role in benthic ecosystem functioning. In this context, the specific objectives of this study were (i) to estimate individual surface sediment reworking rate (hereafter referred as SSRR) of five dominant intertidal foraminifera species in temperate intertidal mudflats, (ii) to understand how morphological traits or those related to their displacements would influence SSRR, and (iii) to further link these traits and SSRR intensity to the functional groups recently introduced for benthic foraminifera (Deldicq et al. 2020).

**Materials and methods**

**Studied species**

Five intertidal species were selected considering their high abundance in the foraminiferal assemblage at the study site: (i) the prolate ellipsoid-shaped *Quinqueloculina seminulum* and *Miliammina fusca* (Fig. 1a, b), (ii) the trochospiral *Ammonia tepida* (Fig. 1c) and (iii) the planispiral *Haynesina germanica* and *Cribroelphidium williamsoni* (Fig. 1d, e). In contrast to the other species that have a calcareous shell, *Miliammina fusca* is an agglutinated species.

Note that *C. williamsoni*, *H. germanica* and *A. tepida* may co-occur with species that are morphologically identical though they are genetically distinct (Pawlowski et al. 1995; Hayward et al. 2004; Saad and Wade 2016). Despite morphological similarities, those species may have different ecological requirements (Richirt et al. 2020), hence different behavioural traits. Molecular identification is, therefore, needed to discriminate morphospecies before the assessment of their behavioural traits. In our sampling site, we find *H. germanica* S16, *C. williamsoni* S1 and *A. tepida* T6 (Schweizer M., personal communication). Depending at the abundance at the time of sampling, between 8 and 33 individuals per species were used for the experiment (Table 1).

Please note that conspecifics of each species were similar in size, i.e. with uniform length and width of the test. The size of prolate ellipsoid-shaped species (i.e. *M. fusca* and *Q. seminulum*) ranged between 500–700 µm and 450–650 µm in length and 250–350 and 200–300 µm in width, respectively. For the trochospiral species *A. tepida*, both length and width ranged between 450–650 µm. Finally, the size of planispiral species (i.e. *C. williamsoni* and *H. germanica*) ranged between 450–650 and 350–550 µm in length and 350–550 and 300–500 µm in width, respectively.

**Sediment sampling and experimental set-up**

Sampling was performed in the Authie Bay (50°22′20″N, 1°35′45″E) which is an intertidal mudflat located on the French coast of the English Channel. This estuary is a well-preserved area that is sparsely populated and slightly impacted by industrial and recreational activities (e.g. Henry...
et al. 2004). It is characterized by a semidiurnal macrotidal regime where tidal range can exceed 10 m during highest astronomical tides (McLusky and Elliott 2004). Among the intertidal zones located along the northern part of the French coast, the Authie Bay is the one displaying the highest diversity in foraminiferal species (Francescangeli et al. 2020).

Surface sediment (0–1 cm) was collected from February to June 2018 at low tide and stored in plastic containers (100-ml). Samples were then transported to the laboratory, where it was washed through a > 125-µm mesh-size sieve. During the sampling period, temperature has increased from ~7 °C (February) to ~18 °C (June), which may have induced a seasonal effect on the organism’s activity as evidenced for macrofaunal species (Pascal et al. 2019). A recent study on Haynesina germanica showed, however, that the species’ SSRR has a low thermal dependence in the range 6–24 °C (Deldicq et al. 2021). In this study, we assume that the potential seasonal effect could be negligible through the use of an acclimation period carried out before running the experiment. Hence, living benthic foraminifera were subsequently individually sorted with a brush, identified and their pseudopodial activities checked under an inverted phase-contrast microscope (Olympus IX71, Tokyo, Japan). Only active individuals were subsequently imaged to measure the shell size parameter, i.e. maximum length and width of each individual (Olympus SZX16, Tokyo, Japan, TC capture software).

Prior to behavioural observations, individuals were kept for 24-h at the experimental temperature (18 °C) in a temperature-controlled room (MIR-154, Panasonic, Japan; temperature fluctuation ± 0.3 °C, light intensity 170 µmol m−2 s−1). Behavioural observations were performed in 300-ml aquaria filled with 25–30-ml of thawed Authie Bay sediment (i.e. ~1 cm thick) (Fig. 2). We used previously frozen sediment to ensure that the sediment was free of moving macro- and meio-organisms so that the only tracks observed on the sediment surface would be those from foraminifera.

### Quantification of behavioural traits

After the acclimation period, foraminifera were randomly placed on the sediment surface (Fig. 2), under 250-ml of
natural unfiltered and air saturated seawater (salinity = 33) following 10 min of vigorous air bubbling immediately before spreading foraminifera on the sediment surface. In total 15 experiments were performed.

Individual displacements in and on the sediment were recorded by time-lapse photography (Fig. 2; 1 image every 10 min for 24-h) using a digital camera (Nikon V1 with a Nikkor 10–30 mm lens). For each foraminifera, 144 images were combined in the image-analysis software Fiji to extract \((x, y)\) coordinates using the Manual tracking plugin (Schindelin et al. 2012). A total of 230 active (i.e. moving) individuals was initially selected for the experiment. Please note that the majority of living individual initially deposited at the sediment surface moved during the experiment but the coordinates could not be extracted for all individuals. Indeed, during the experiment, it was not possible to track all individuals (i) because some burrowed into the sediment up to a depth where their paths were not visible and/or (ii) because some paths crossed and consequently individual trajectories were lost. We, therefore, only kept individuals that exhibited visible tracks throughout the whole 24-h experiment so that the information related to their behavioural traits had the same statistical weight. In total we followed the trajectories of 103 individuals. Note that at the end of each 24-h experiment, dissolved oxygen saturation was consistently ca. 56% in the overlying seawater directly above the sediment–water interface (HI9829 MULTIPARAMETER Meter, HANNAH INSTRUMENTS).

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

\[
D_t = \sqrt{\left(x_t - x_{t+10}\right)^2 + \left(y_t - y_{t+10}\right)^2}
\]

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, respectively. The total distance travelled within 24 h, \(D_{24}\), was subsequently calculated by summing individual \(D_t\).

### Quantification of surface sediment reworking rates

To estimate the surface sediment reworking rate of intertidal foraminifer we used the calculation method previously used for macrofaunal species such as sea urchins (Hollertz and Duchêne 2001; Lohrer et al. 2005; Maire et al. 2008):

\[
SR = \frac{(DT \times CS)}{\Delta t}
\]

where \(DT\) is the distance travelled during a time interval \(\Delta t\) and \(CS\) the cross section, i.e. surface reworked along the motion plane (Maire et al. 2008, see Fig. 3A, for an example). This calculation method was recently applied on two intertidal foraminiferal species, i.e. *Ammonia tepida* and *Quinqueloculina seminulum* (Bouchet and Seuront 2020). Nevertheless, in their calculations, the authors used the maximum test length rather than the cross section as the morphological component. However, test length may not
be optimal as some foraminifera such as *Q. seminulum* and *M. fusca*, have asymmetrical shapes with test length greater than test width (Fig. 1a,b). Noticeably, the length/width ratio is close to 1 for *A. tepida*, 1.2 for *H. germanica* and *C. williamsonti* and to 2 for *Q. seminulum* and *M. fusca*. The use of the surface area, therefore, appears to be more accurate for the calculation. However, measurement of the cross section involves the characterisation of the organism’s height (Fig. 3). Due to their small size, foraminifera are manipulated under binocular microscope that makes very difficult to measure their cross section as it involves a vertically positioning of the individual (Fig. 3B).

We, therefore, assume that the surface area corresponding to the larger part of the test, i.e. umbilical sides may be used for the estimation of the surface sediment reworking performed by foraminifera. Hence, using the measurements of maximum length and width (see Sect. 2.2), the surface area (mm$^2$) of each individual ($S_i$) was estimated under the assumption of an ellipse-shaped shell:

$$S_i = \pi \times \frac{\text{Length}}{2} \times \sqrt{\frac{\text{Width}}{2}}$$

Since we used conspecifics of similar size, the mean surface area $S$ for each species was then calculated and subsequently used for the calculation of the individual surface sediment reworking rate ($SSRR_i$, mm$^3$ ind$^{-1}$ 10 min$^{-1}$) as follow:

$$SSRR_i = S \times D_t$$

where $D_t$ is the distance travelled (mm ind$^{-1}$ d$^{-1}$) by each individual between two images (i.e. 10 min).

In our experiments, individuals of both species can move on the surface (Fig. 4A), at the interface (Fig. 4B) or in the sediment (Fig. 4C).

When the individual was observed crawling at the sediment surface or at the interface only $\frac{1}{3}$ and $\frac{2}{3}$ of the mean surface area $S$ was considered in the $SSRR_i$ calculation, respectively (Fig. 4A, B). Conversely, when the individual was observed burrowed in the sediment, the total of the mean surface area $S$ was used (Fig. 4C).

Finally, the individual surface sediment reworking rate ($SSRR_i$, mm$^3$ ind$^{-1}$ day$^{-1}$) were estimated as follow:

$$SSRR_i = \sum_{t=0}^{24} SSRR_{i(t)}$$

where $SSRR_{i(t)}$ is the individual surface sediment reworking rate between two images (i.e. within 10 min).

### Data analysis

Because the surface area of individual foraminifera, their travelled distances and $SSRR_i$ were non-normally distributed (Shapiro–Wilk test, $p < 0.05$), a Kruskal–Wallis test was applied to infer the presence of significant differences between species, and eventually followed by a Dunn test to identify distinct groups of measurements. All statistical analyses were performed using R 3.5.2. software (R Core Team 2019).

### Results

#### Species-specific size

In our experiment, the mean surface area of *A. tepida* is almost twice as large as those of *H. germanica* and *Q. seminulum* (Table 1). Indeed, there were significant
differences in the surface area $S_i$ between species (KW test, $p < 0.05$), and three distinct groups were identified as $S_{H. germanica} = S_{Q. seminulum} < S_{M. fusca} < S_{C. williamsoni} = S_{A. tepida}$ (Dunn test, $p < 0.01$; Table 1).

**Travelled distance**

Among the five studied species, $Q. seminulum$ display the highest mean travelled distance, i.e. 130 mm d$^{-1}$ with all individuals being in the range 12—145 mm d$^{-1}$. In contrast, $M. fusca$ and $A. tepida$ are the species that travelled the least distances, i.e. between 12 and 32 mm d$^{-1}$ and 17 and 37 mm d$^{-1}$, respectively (Fig. 5). With intermediate values, the mean travelled distance of $H. germanica$ and $C. williamsoni$ ranged between 16 and 112 mm d$^{-1}$ and 19 and 67 mm d$^{-1}$ (Fig. 5). Hence, three groups of homogeneous travelled distance were identified: $D_{M. fusca} = D_{A. tepida} < D_{C. williamsoni} = D_{H. germanica} < D_{Q. seminulum}$ (Fig. 5; Dunn test, $p < 0.01$).

Our results showed a strong intra specific variability in the distance travelled by individuals of $H. germanica$, $C. williamsoni$ and $Q. seminulum$. For instance, the travelled distance between individuals of $Q. seminulum$ may range from 12 to 142 mm d$^{-1}$ (Fig. 5).

**Surface sediment reworking rate**

Individual surface sediment reworking rates ranged from 1.15 mm$^3$ day$^{-1}$ for $M. fusca$ up to 21.6 mm$^3$ day$^{-1}$ for $Q. seminulum$, and significantly differed between species (KW test, $p < 0.05$; Fig. 6). *Quinqueloculina seminulum* showed higher $SSRR_i$ than the other species (Dunn test, $p < 0.01$).

Three groups of $SSRR_i$ were subsequently identified as $SSRR_i A. tepida = SSRR_i M. fusca < SSRR_i M. fusca < SSRR_i C. williamsoni = SSRR_i H. germanica < SSRR_i Q. seminulum$ (Fig. 6; Dunn test, $p < 0.01$). As a consequence, the most and the least efficient surface sediment reworkers are $Q. seminulum$ and $M. fusca$, respectively. As previously evidenced for the travelled distance, $SSRR_i$ values showed a strong intraspecific variability in $H. germanica$, $Q. seminulum$ and $C. williamsoni$ species. Noticeably, the difference in the $SSRR_i$ between individual of the aforementioned species may be one order of magnitude while it is restricted between 1 and 3 mm$^3$ day$^{-1}$ for $M. fusca$ (Fig. 6).

**Discussion**

A methodological note on individual surface sediment reworking calculation

In the present work, $SSRR_i$ was estimated using the surface area of the test, whereas Bouchet and Seuront (2020) considered the test length in their calculation. Hence, these authors showed $SSRR_i$ values expressed as a surface unit, i.e. in cm$^2$ ind$^{-1}$ d$^{-1}$. However, the studied foraminifera moved in and on the sediment, hence were *ipso facto* displacing a volume of particles rather than a surface. The use of the surface area of the test instead of the maximum test length, therefore, appears as more ecologically relevant allowing to express $SSRR_i$ as volume of sediment particles displaced. Furthermore, the prolate ellipsoid-shaped test of $Q. seminulum$ and $M. fusca$ are asymmetrical with the length much longer than the width. Similarly, within rotalid species, i.e. $A. tepida$, $H. germanica$ and $C. williamsoni$ test length typically is about 1.2 times larger than test width. As a consequence, the approach followed by Bouchet and Seuront (2020) most likely leads to a biased estimation of the $SSRR_i$ values by considering only the length as representative of the test size.

---

**Fig. 5** Value of the travelled distance (mm) for each experiment performed on the five tested species. The box represents the first, second and third quartiles and the whiskers extend to 1.5 times the inter-quartile range; individual values are represented by black dots. $n$ denotes the number of individuals used in the experiments. Letters on top (‘a’, ‘b’ and ‘c’) identify significantly different groups (Dunn test, $p < 0.05$) between species.
We further stress that the use of the larger surface area of the test is consistent with the surface involved in the burrowing behaviour of planispiral and trochospiral species. In our experiment, planispiral species, i.e. *H. germanica* and *C. williamsoni* burrowed in the sediment by successively orienting both their umbilical and apertural sides perpendicular to the direction of movement (Fig. 7A, B). Additionally, as previously observed (i.e. Langer et al. 1989), trochospiral species such as *A. tepida* moved with a corkscrew movement with its umbilical side oriented toward the direction of the displacement. The aforementioned species have ornamentations (e.g. pores, interlocular spaces and spikes) that have been expected to influence the displacement of foraminifera within the sediment (Langer et al. 1989). The pseudopodial network may then be extended outside the shell through ornamental features. Therefore, both shell surfaces, i.e. apertural, spiral, umbilical, are likely to be involved in the displacement of these foraminiferal species. In contrast, prolate
ellipsoid-shaped species such as *Q. seminulum* and *M. fusca* burrowed in the sediment with their mouth oriented toward the direction of displacement (Fig. 7C).

These observations indicate that the apertural side (i.e. the cross section) is likely to be the surface that is essentially involved in the displacement of *Q. seminulum* and *M. fusca*, which, therefore, may lead to an overestimation of SSRR in the present study. Such observations were, however, made during the burrowing process of these two species as they never reached the sediment surface and remained burrowed in the sediment throughout the rest of the experiment (Deldicq et al. 2020). This may not necessarily suggest that it is the only side involved in the displacement hence the sediment reworking. In addition, all studied foraminiferal species left a track in the sediment that is greatly larger than the individual width (Fig. 8). This observation is consistent with the above-mentioned potential underestimation of the SSRR of these two species.

In the present study, we consider the temporal evolution in the vertical position of each individual in our SSRR calculation. This method allows a more rigorous estimation of the surface sediment reworking intensity of each species as it considers the real portion of the surface area of the test that is actively involves in the reworking of surface particles during individual displacement (Fig. 4).

Taken together, these observations suggest that considering both the surface area of the test as a proxy of foraminiferal test size and the position of each individual in the sediment may allow a reliable assessment of species-specific surface sediment reworking rate. However, behavioural observations dealing with the functional morphology of prolate ellipsoid-shaped species are needed to further identify which surfaces areas of their test are involve in the displacement of sediment particles.

**SSRR** is not size-dependent but trait-dependent through interspecific differences in motion behaviour

Our results showed that the largest foraminiferal species (*A. tepida*) did not rework the sediment more than the smallest species such as *H. germanica* and *Q. seminulum*. In contrast, *Q. seminulum* can even rework up to three times more sediment than the larger *A. tepida* (Fig. 6) despite a test surface area nearly half that of *A. tepida* (Table 1). This result indicates that the species-specific SSRR could be inversely size-dependent as evidenced in the five species. Specifically, the higher the species-specific SSRR, the lower the species-specific SSRR. Here, the travelled distance is likely the parameter that drives the intensity in the surface sediment reworking performed by the five foraminiferal species. These results are consistent with previous works on macro-invertebrate species, where large bivalves may have lower sediment reworking rates than small polychaetes since the latter have more intensive displacements, i.e. different motion-behaviour traits (Mermillod-Blondin et al. 2004; Michaud et al. 2005; Gilbert et al. 2007).

Furthermore, differences in SSRR, between foraminiferal species have been previously hypothesised following the assumption that species with distinct bioturbing modes would exhibit different SSRR; see Deldicq et al. (2020) for further details. Noticeably, the five species considered in the present study were recently classified in the following bioturbing groups: *Q. seminulum* and *M. fusca* as gallery-biodiffusors, *H. germanica* and *A. tepida* as surficial-biodiffusors and *C. williamsoni* as an epifaunal-biodifusor (Deldicq et al. 2020). This classification implies that they would contribute differently to benthic-ecosystem functioning (Deldicq et al. 2020). For instance, *C. williamsoni* that prefers surface sediment was classified as epifaunal-biodifusor meaning that the species would rework particles at the surface. In contrast, *H. germanica* and *A. tepida* move in and on the sediment, hence they may rework particles more deeply than *C. williamsoni* (Deldicq et al. 2020). Finally, *Q. seminulum* and *M. fusca* prefer to be burrowed in the sediment that may likely induce the reworking of sediment particles below the interface. As these species do not occupy the same microhabitat, they may consequently exhibit differences in their SSRR. Therefore, to consider the functional classification of the five studied species in the estimation of their SSRR, we include the position of their test in the sediment.

Based on this study’s findings, it occurs that, although *C. williamsoni* is larger than *H. germanica* and that both species displayed similar travelled distance, the latter rework

![Fig. 8](image-url) The position of the individual at the beginning of the experiment indicated by the red circle. B Visual observation of the width of the path that is greatly larger than the individual width during the displacement of *Q. seminulum* after 24 h of experiment. Scaled bar = 0.5 cm
the surface sediment more efficiently. This is consistent with previous studies which showed that gallery-biodiffusor (i.e. burrow-dwelling organism) macro-invertebrates are more efficient bioturbators than epifaunal-biodiffusors as they displaced a larger amount of sediment particles through their burrowing activity (Mermillod-Blondin et al. 2004; Michaud et al. 2005). However, in the present study, the most and the least efficient species in reworking surface sediment (i.e. *Q. seminulum* and *M. fusca*) both belong to the gallery-biodiffusor group. As a consequence, the potential link between the intensity of surface sediment reworking and the functional group of a species is not straightforward. We may suggest that the motion behaviour of foraminifera, i.e. travelled distance and vertical position (e.g. Deldicq et al. 2020) both matter in their ability to rework surface sediment. 

In macrofauna, species-specific sediment reworking rate is intrinsically linked to abiotic and biotic factors such as food concentration, temperature and chemical properties of the sediment (Przeslawski et al. 2009, Maire et al. 2007a, b; Mestre et al. 2013; Verdelhos et al. 2015; Bernard et al. 2016; Pascal et al. 2019). In the present study, the experimental set-up do not provide all the food sources such as live prey that some species, e.g. *A. tepida* may feed (Dupuy et al. 2010; Jauffrais et al. 2016) as we used thawed sediment to eliminate macro- and meio-benthic bioturbation effects. Foraging activity is, however, intrinsically linked to organism displacement (e.g. Pyke 1984; Bell 1991; Seuront 2010, 2015). This stresses the need to further investigate the effect of food concentration and diversity on the *SSRR* of intertidal foraminifera. In addition, the effect of progressive oxygen depletion on foraminiferal activity hence sediment reworking intensity should be further investigated although we did not observed temporal changes in the activity of our five species during our experiments.

**Inter-individual variability matters in the contribution of benthic foraminifera to *SSRR*$_i$**

Beyond the interspecific variability discussed above (Sect. 4.2), *SSRR*$_i$ of the five studied species were consistently characterised by inter-individual variability (i.e. up to one order of magnitude for *Q. seminulum*; see Fig. 5,6). Note that the differences identified here cannot be related to environmental factors or size, since our experiments were performed on similar-sized individuals under controlled conditions in the absence of any cues. The above mentioned inter-individual variability is then more likely to be an intrinsic property of the species considered here. 

Behavioural plasticity has previously been reported in foraminifera (Hallock and Hansen 1979; Seuront and Bouchet 2015; Prazeres et al. 2017), but also in pelagic copepods (e.g. Seuront et al. 2004) and intertidal gastropods (e.g. Chapperon and Seuront 2011) with individuals from the same species showing both a large repertoire of behavioural traits (e.g. feeding activity, trajectory complexity, intensity of displacement) and a large variability in the values of each trait. Noticeably, in our experiments, conspecific individuals of *Q. seminulum*, *C. williamsoni* and *H. germanica* displayed a high variability in their travelled distance but also in their motion behaviour, e.g. tortuosity, vertical position (see Deldicq et al. 2020 for further details). Please note that the lowest inter-individual variability was observed for *M. fusca* and may result from the analysis of only 8 individuals.

Having a wide diversity in the behavioural repertoire between conspecific individuals may be a selective advantage for species facing long-term environmental fluctuations as previously suggested for intertidal gastropods (Chapperon and Seuront 2011). Such evolutionary adaptation to increase survival in a changing environment can, in turn, also affect individual contribution to ecosystem processes (Maltagliati et al. 2006; Bolnick et al. 2011). Noticeably, the species characterized by the highest inter-individual variability (i.e. *Q. seminulum*, *C. williamsoni* and *H. germanica*) are also the species that contribute most to *SSR*, (see Fig. 6). This last observation is particularly relevant as it may inform on the species-specific phenotypic plasticity and, therefore, the sustainability of the functional role of these species that live in a highly variable environment such as intertidal sedimentary ecosystems.

Taken together our observations may suggest that inter-individual trait variations matter in the *SSRR* of the five studied foraminiferal species. This is consistent with previous studies showing that inter-individual variations can have large ecological consequences on ecosystem processes such as primary production, nutrient cycling than interspecific variability (Crutsinger 2006; Lecerf and Chauvet 2008; Bolnick et al. 2011).

**Conclusion**

Our study revealed that bioturbation by benthic foraminifera is the result of the complex interplay between species-specific features such as motion behaviour, phenotypic plasticity and functional classification, i.e. bioturbation mode. Note that the individuals smaller than 125 µm were not considered in the present study. It would be interesting to consider smaller-sized fractions as their surface sediment reworking rate might be different from those of adult specimen. Indeed, previous experiments have shown that juveniles can contribute more or equally than adults to the functioning of benthic ecosystem (Wukovits et al. 2018). Furthermore, they represent a large part of the foraminiferal community and have high energetical needs for growth (Caralp 1989; Murray 1983; Nomaki et al. 2006; Wukovits et al. 2018). Hence, their displacements would also matter in the reworking of
surface sediment particles. Despite their relatively small size, these five benthic foraminiferal species showed non-negligible sediment mixing rates at the sediment water interface through their active displacements. Additional studies are nevertheless needed to further estimate the role of intertidal foraminifera to bioturbation processes because the species-specific traits that control their activity in and on the sediment may depend on both allogenic (e.g. temperature, food availability) and autogenic (e.g. size, age) factors.

Acknowledgements The PhD fellowship of N.D. was funded by the Ministère de l’Enseignement Supérieur et de la Recherche. We thank the Région Hauts-de-France, the Ministère de l’Enseignement Supérieur et de la Recherche and the European Fund for Regional Economic Development for their financial support through the CPER research project CLIMIBIO. The authors are grateful to Magali Schweizer for providing information on the phylotypes occurring at the sampling site (research project AMTEP, funded by the CNRS-INSU programme EC2CO) and Fabio Francescangeli for the SEM-images of foraminiferal species. The authors are grateful to Grégory Beaugrand for his comments on an earlier version of the manuscript. The editor and the four reviewers’ comments greatly contributed to improve this paper.

Author contributions ND and VMPB conceived the idea of this study and VMPB obtained financial support. ND and VMPB, provided significant input on experimental design. ND performed the behavioural experiments and analysed the images. ND performed the statistical analyses. ND, LS and VMPB contributed to the interpretation of the data and the discussion of the results presented in the manuscript. ND wrote the draft manuscript. ND, LS and VMPB revised the article critically for intellectual content and gave final approval of the submitted version.

Funding The PhD fellowship of N.D. was funded by the Ministère de l’Enseignement Supérieur et de la Recherche. This study received the financial support of the CPER research project CLIMIBIO funded by the Région Hauts-de-France, and the European Fund for Regional Economic Development. Molecular investigations of spiral-shaped foraminiferal phylotypes were done within the research project AMTEP, funded by the CNRS-INSU programme EC2CO.

Data availability All data generated or analysed during this study are included in this published article.

References

Aller RC (1994) Bioturbation and remineralization of sedimentary organic matter: effects of redox oscillation. Chem Geol 114:331–345
Aller RC, Aller JY (1992) meiofauna and solute transport in marine muds. Limnol Oceanogr 37:1018–1033. https://doi.org/10.4319/lo.1992.37.5.1018

Bell W (1991) Searching behaviour: the behavioural ecology of finding resources. Springer, Berlin
Bernard G, Duchêne J-C, Romero-Ramirez A, Lecroart P, Maire O, Ciatat A, Deflandre B, Grémaire A (2016) Experimental assessment of the effects of temperature and food availability on particle mixing by the bivalve Abra alba using new image analysis techniques. PLoS ONE 11:e0154270. https://doi.org/10.1371/journal.pone.0154270
Bolnick DI, Amarasekare P, Araujo MS, Bürger R, Levine JM, Novak M, Rudolf VH, Schreiber SJ, Urban MC, Vasseur DA (2011) Why intraspecific trait variation matters in community ecology. Trends Ecol Evol 26:183–192. https://doi.org/10.1016/j.tree.2011.01.009

Bonaglia S, Nascimento FJA, Bartoli M, Klawonn I, Brüchert V (2014) Meiofauna increases bacterial denitrification in marine sediments. Nat Commun 5:5133. https://doi.org/10.1038/ncomms6133
Bonaglia S, Hedberg J, Marzocchi U, Ibarg S, Glud RN, Nascimento FJA (2020) Meiofauna improve oxygenation and accelerate sulfide removal in the seasonally hypoxic seabed. Mar Environ Res 159:104968. https://doi.org/10.1016/j.marenvres.2020.104968

Bouchet VMP, Seuront L (2020) Strength may lie in numbers: intertidal foraminifera non-negligible contribution to surface sediment reworking. OJMS 10:131–140. https://doi.org/10.4236/ojms.2020.103010

Bouchet VMP, Telford RJ, Rygg B, Oug E, Alve E (2018) Can benthic meiofauna serve as proxies for changes in benthic macrofaunal community structure? Implications for the definition of reference conditions. Mar Environ Res 137:24–36. https://doi.org/10.1016/j.marenvres.2018.02.023
Bouchet V, Deldicq N, Baux N, Daunin JC, Pezy JP, Seuront L, Mear Y (2020) Benthic foraminifera to assess ecological quality statuses: the case of salmon fish farming. Ecological Indicators 117:106607.

Carap LH (1989) Size and morphology of the benthic foraminifer Melonis barleeanum: relationship with marine organic matter. J Foramin Res 19:235–245
Chandler GT (1989) Foraminifera may structure meiobenthic communities. Oecologia 81:354–360. https://doi.org/10.1007/BF00377083

Chappiron C, Seuront L (2011) Variability in the motion behaviour of intertidal gastropods: ecological and evolutionary perspectives. J Mar Biol Ass 91:237–244. https://doi.org/10.1017/S002531541000007X

Crutsinger GM (2006) Plant genotypic diversity predicts community structure and governs an ecosystem process. Science 313:966–968. https://doi.org/10.1126/sience.1128326

D’Hondt A-S, Stock W, Blommaert L, Moens T, Sabbé K (2018) Nematosmates stimulate biomass accumulation in a multispecies diatom biofilm. Mar Environ Res 140:78–89
De Mesel I, Derycke S, Moens T, Van der Gucht K, Vincx M, Swings J (2004) Top-down impact of bacterivorous nematodes on the bacterial community structure: a microcosm study. Environ Microbiol 6:733–744. https://doi.org/10.1111/j.1462-2920.2004.00610.x

Deldicq N, Seuront L, Langlet D, Bouchet V (2020) Assessing behavioural traits of benthic foraminifera: implications for sediment mixing. Mar Ecol Prog Ser 643:21–31. https://doi.org/10.3354/meps13334

Deldicq N, Langlet D, Delaeter C, Beaugrand G, Seuront L, Bouchet V (2021) Effects of temperature on the behaviour and metabolism of an intertidal foraminifera and consequences for benthic ecosystem functioning. Sci Rep 11:4013

Dupuy C, Rossignol L, Geslin E, Pascal P-Y (2010) Predation of mud-flat meio-macrofauna metazoans by a calcareous foraminifer, Ammonia tepida (Cushman, 1926). J Foraminiferal Res 40:305–312. https://doi.org/10.2113/gsfr40.4.305
Francescangeli F, Quijada M, Armanyot du Chateaulet E, Frontalini F, Trentesaux A, Billon G, Bouchet VMP (2020) Multidisciplinary study to monitor consequences of pollution on intertidal benthic ecosystems (Hauts de France, English Channel, France): comparison with natural areas. Marine Environmental Research 160:105034.

Gerlach S (1978) Food-chain relationships in subtidal silty sand marine sediments and the role of meiofauna in stimulating bacterial productivity. Oecologia 33:55–69

Gilbert F, Hulth S, Grossi V, Poggiale J-C, Desrosiers G, Rosenberg R, Gérino M, François-Carcaill F, Michaud E, Stora G (2007) Sediment reworking by marine benthic species from the Gullmar Fjord (Western Sweden): importance of faunal biovolume. J Exp Mar Biol Ecol 348:133–144. https://doi.org/10.1016/j.jembe.2007.04.015

Green A, Chandler GT (1994) meiofaunal bioturbation effects on the partitioning of sediment-associated cadmium. J Exp Mar Biol Ecol 180:59–70

Gross O (2000) Influence of temperature, oxygen and food availability on the migration activity of benthic foraminifera: evidence by microcosm experiments. In: Liebezeit G, Dittmann S, Kröncke I (eds) Life at Interfaces and Under Extreme Conditions. Springer, Netherlands, Dordrecht, pp 123–137

Gross O (2002) Sediment interactions of foraminifera: implications for food degradation and bioturbation processes. J Foramin Res 32:414–424. https://doi.org/10.2113/0320414

Hallcock P, Hansen HJ (1979) Depth adaptation in Amphistegina: change in lamellar thickness. Bull Geol Soc Den 27:99–104

Hayward BW, Holzmann M, Grenfell HR, Pawlowski J, Triggs CM (2005) The functional group approach to bioturbation: the effects of feeding bivalve Abra ovata during summertime and wintertime, with a comparison between two models of sediment reworking. J Exp Mar Biol Ecol 343:21–36. https://doi.org/10.1016/j.jembe.2006.10.052

Maire O, Duchène JC, Grémare A, Malyuga VS, Meysman FJR (2007a) A comparison of sediment reworking rates by the surface deposit-feeding bivalve Abra ovata during summertime and wintertime, with a comparison between two models of sediment reworking. J Exp Mar Biol Ecol 343:21–36. https://doi.org/10.1016/j.jembe.2006.10.052

Maire O, Lecroart P, Meysman F, Rosenberg R, Duchène JC, Grémare A (2008) Quantification of sediment reworking rates in bioturbation research: a review. Aquat Biol 2:219–238. https://doi.org/10.3354/am036271

Maire O, Lecroart P, Meysman F, Rosenberg R, Duchène JC, Grémare A (2008) Quantification of sediment reworking rates in bioturbation research: a review. Aquat Biol 2:219–238. https://doi.org/10.3354/am036271

Henry F, Amara R, Coixet L, Lacouture D, Bertho M-L (2004) Heavy metals in four fish species from the French coast of the Eastern English channel and Southern Bight of the North Sea. Environ Int 30:675–683

Higgins R, Thiel H (1988) Introduction to the study of meiofauna. Smithsonian Institution Press, Washington

Hollez K, Duchène J-C (2001) Burrowing behaviour and sediment reworking in the heart urchin Brissopsis lyrifera Forbes (Spionidae). Mar Biol 139:951–957. https://doi.org/10.1007/s00227-002-0602-9

Hulings N, Gray J (1971) A manual for the study of meiofauna. Smithsonian Contributions Zool 78:1–84

Jaffraus T, Jesus B, Geslin E, Briand F, Jézéquel VM (2016) Locomotion speed of the benthic foraminifer Ammonia tepida exposed to different nitrogen and carbon sources. J Sea Res 112:58–68. https://doi.org/10.1016/j.seares.2018.01.006

Kitazato H (1994) Foraminiferal microhabitats in four marine environments around Japan. Mar Micropaleontol 24:29–41. https://doi.org/10.1016/0377-8398(94)90009-4

Kristensen E, Penha-Lopes G, Delefosse M, Valdemarsen T, Quintana CO, Banta GT (2012) What is bioturbation? The need for a precise definition for fauna in aquatic sciences. Mar Ecol Prog Ser 446:285–302. https://doi.org/10.3354/meps09506

Langer M, Hottinger L, Huber B (1989) Functional morphology in low-diverse benthic foraminiferal assemblages from tidal flats of the North Sea. Senckenbergiana Maritima Frankfurtam-Main 20:81–99

Lecerf A, Chauvet E (2008) Intraspecific variability in leaf traits strongly affects alder leaf decomposition in a stream. Basic Appl Ecol 9:598–605. https://doi.org/10.1016/j.baae.2007.11.003

Lohrer AM, Thrush SF, Hunt L, Hancock N, Lundquist C (2005) Rapid reworking of subtidal sediments by burrowing spionid urchins. J Exp Mar Biol Ecol 321:155–169. https://doi.org/10.1016/j.jembe.2005.02.002

Maire O, Duchène JC, Grémare A, Malyuga VS, Meysman FJR (2007a) A comparison of sediment reworking rates by the surface deposit-feeding bivalve Abra ovata during summertime and wintertime, with a comparison between two models of sediment reworking. J Exp Mar Biol Ecol 343:21–36. https://doi.org/10.1016/j.jembe.2006.10.052

Maire O, Duchène J, Bigot L, Grémare A (2007b) Linking feeding activity and sediment reworking in the deposit-feeding bivalve Abra ovata with image analysis, laser telemetry, and luminophore tracers. Mar Ecol Prog Ser 351:139–150. https://doi.org/10.3354/meps07147

Moens T, dos Santos G, Thompson F, Swings J, Fonsêca-Genevois V, Hallock P, Hansen HJ (1999) Bioturbation: the effects of feeding bivalve Brissopsis lyrifera on microbial communities and biogeochemical processes in marine sediment. Aquat Microb Ecol 36:271–284. https://doi.org/10.3354/ame036271

Mestre NC, Brown A, Thaatje S (2013) Temperature and pressure tolerance of larvae of Crepidula fornicata suggest thermal limitation of bathymetric range. Mar Biol 160:743–750. https://doi.org/10.1007/s00227-012-2128-x

Meyman FJR, Galaktionov OS, Gribsbølt H, Middelburg JJ (2005) Bio-irrigation in permeable sediments: an assessment of model complexity. J Mar Res 64:589–627. https://doi.org/10.1357/002224006778157575

Michaud E, Desrosiers G, Mermillod-Blondin F, Sundby B, Stora G (2003) The functional group approach to bioturbation: the effects of biodepositors and gallery-depositors of the Macoma balthica community on sediment oxygen uptake. J Exp Mar Biol Ecol 326:77–88. https://doi.org/10.1016/j.jembe.2005.05.016

Moens T, dos Santos G, Thompson F, Swings J, Fonseca-Genevois V, Vinçx M, Des Mesel I (2005) Do nematode mucus secretions affect bacterial growth? Aquat Microb Ecol 40:77–83. https://doi.org/10.3354/ame040077

Murray JW (1983) Population dynamics of benthic foraminifera: results from the Exe estuary, England. J Foramin Res 13:1–12

Näslund J, Nascimento FJA, Elmgren G (2012) Meiofauna enhances organic matter mineralization in soft sediment ecosystems. Limnol Oceanogr 57:338–346. https://doi.org/10.4319/lo.2012.57.1.0338

Näslund J, Nascimento FJ, Gunnarsson JS (2010) Meiofauna reduces bacterial mineralization of naphthalene in marine sediment. ISME J 4:1421–1430. https://doi.org/10.1038/ismej.2010.63

Nomaki H, Heinz P, Nakatsuka T, Shimanaga M, Ohkouchi N, Ogawa NO, Kogure K, Ikemoto E, Kitazato H (2006) Different ingestion
patterns of $^{13}$C-labeled bacteria and algae by deep-sea benthic foraminifera. Mar Ecol Prog Ser 310:96–108

Orvain F, Hir PL, Sauriau P-G (2003) A model of fluff layer erosion and subsequent bed erosion in the presence of the bioturbator, *Hydrobia ulvae*. J Mar Res 61:823–851. https://doi.org/10.1357/00224003322981165

Orvain F, Sauriau PG, Sygut A, Joassard L, Le Hir P (2004) Interacting effects of *Hydrobia ulvae* bioturbation and microphytobenthos on the erodibility of mudflat sediments. Mar Ecol Prog Ser 278:205–223. https://doi.org/10.3354/meps278205

Pascal L, Maire O, Dellandre B, Romero-Ramirez A, Grémaire A (2019) Linking behaviours, sediment reworking, bioirrigation and oxygen dynamics in a soft-bottom ecosystem engineer: the mud shrimp *Upogebia pusilla* (Petagna 1792). J Exp Mar Biol Ecol 516:67–78. https://doi.org/10.1016/j.jembe.2019.05.007

Pawlowski J, Bolivar I, Farhni J, Zaninetti L (1995) DNA analysis of “*Ammonia beccarii*” morphotypes: one or more species? Mar Micropaleontol 26:171–178. https://doi.org/10.1016/0377-8398(95)00022-4

Prazeres M, Roberts TE, Pandolfi JM (2017) Variation in sensitivity of large benthic foraminifera to the combined effects of ocean warming and local impacts. Sci Rep 7:45227. https://doi.org/10.1038/srep45227

Przeslawski R, Zhu Q, Aller R (2009) Effects of abiotic stressors on infaunal burrowing and associated sediment characteristics. Mar Ecol Prog Ser 392:33–42. https://doi.org/10.3354/meps08221

Pyke GH (1984) Optimal foraging theory: a critical review. Annu Rev Ecol Syst 15:523–575. https://doi.org/10.1146/annurev.es.15.1.523

R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Richirt J, Riedel B, Mouret A, Schweizer M, Langlet D, Seitaj D, Meysman FJR, Slomp CP, Jorissen FJ (2020) Foraminiferal community response to seasonal anoxia in Lake Grevelingen (the Netherlands). Biogeosciences 17:1415–1435. https://doi.org/10.5194/bg-17-1415-2020

Rysgaard S, Christensen P, Sørensen M, Funch P, Berg P (2000) Marine meiofauna, carbon and nitrogen mineralization in sandy and soft sediments of Disko Bay, West Greenland. Aquat Microb Ecol 21:59–71. https://doi.org/10.3354/ame021059

Saat SA, Wade CM (2016) Biogeographic distribution and habitat association of *Ammonia* genetic variants around the coastline of Great Britain. Mar Micropaleontol 124:54–62. https://doi.org/10.1016/j.marmicro.2016.01.004

Schindelin J, Arganda-Carreras I, Frise E, Kaynig V, Longair M, Pietzsch T, Preibisch S, Rueden C, Saalfeld S, Schmid B, Tinevez J, White DJ, Hartenstein V, Eliceiri K, Tomancak P, Cardona A (2012) Fiji: an open-source platform for biological-image analysis. Nat Methods 9:676–682. https://doi.org/10.1038/nmeth.2019

Schratzeberger M, Ingels J (2018) Meiofauna matters: the roles of meiofauna in benthic ecosystems. J Exp Mar Biol Ecol 502:12–25. https://doi.org/10.1016/j.jembe.2017.01.007

Seuront L (2010) How does salinity influence the swimming speed of the estuarine calanoid copepod *Eurytemora affinis*? J Plankton Res 31:1223–1225

Seuront L (2015) When complexity rimes with sanity: loss of fractal and multifractal behavioural complexity as an indicator of sub-lethal contaminations in zooplankton. In: Springer (ed) Marine Productivity: perturbation and resilience of socio-ecosystems, In: Ceccal. New York, pp 129–137

Seuront L, Bouchet VMP (2015) The devil lies in details: new insights into the behavioural ecology of intertidal foraminifera. J Foramin Res 45:390–401. https://doi.org/10.2113/gsjfr.45.4.390

Seuront L, Hwang J, Tseng L, Schmitt F, Souissi S, Wong C (2004) Individual variability in the swimming behavior of the sub-tropical copepod *Oncaea venusta* (Copepoda: Pooiclostomatoida). Mar Ecol Prog Ser 283:199–217. https://doi.org/10.3354/meps283199

Severin KP, Erskian MG (1981) Laboratory experiments on the vertical movement of *Quinqueloculina impressa* Reuss through sand. J Foramin Res 11:133–136. https://doi.org/10.2113/gsjfr.11.2.133

Verdelhos T, Marques JC, Anastácio P (2015) Behavioral and mortality responses of the bivalves *Scrobicularia plana* and *Cerastoderma edule* to temperature, as indicator of climate change’s potential impacts. Ecol Ind 58:95–103. https://doi.org/10.1016/j.ecolind.2015.05.042

Wukovits J, Bukenberger P, Enge AJ, Gerg M, Wanek W, Watzka M, Heinz P (2018) Food supply and size class depending variations in phytodetritus intake in the benthic foraminifer *Ammonia tepida*. Biology Open 7:bio030056.

**Publisher’s Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.