

THE DEVIL LIES IN DETAILS: NEW INSIGHTS INTO THE BEHAVIOURAL ECOLOGY OF INTERTIDAL FORAMINIFERA

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ABSTRACT

The motion behaviour of three species of intertidal foraminifera, *Ammonia tepida*, *Criboelphidium excavatum* and *Haynesina germanica*, was investigated continuously in the laboratory. We first infer the presence of geotactic and phototactic responses. Significant geotactic responses were observed for all three species; *A. tepida* was found to be negatively geotactic while *C. excavatum* and *H. germanica* showed positive geotaxis. In contrast, no response to light was ever observed. The detailed nature of motility, investigated in terms of both geometric and stochastic complexity of their motion behaviour, was consistently characterised by a strong inter-specific, inter-individual and intra-individual variability. Specifically, *A. tepida* and *H. germanica* were characterised by an intensive search behaviour (they explore their environment slowly with straighter trajectories), while *C. excavatum* adopted an extensive search strategy (it moves more rapidly with more convoluted trajectories). These observations are discussed in the specific context of the ecology of these species. We see their responses as adaptive advantages in spatially and temporally complex environments prone to a range of both predictable and unpredictable rapid stressors. From a methodological point of view, we showed that previous methods used to infer foraminiferal motion behaviour are likely to have systematically underestimated their speed and distance travelled by a factor ranging from 2 to 80.

INTRODUCTION

Living benthic foraminifera are an important and abundant group of the benthic meiofauna. They play a key role in the trophic web of intertidal mudflats (Degré et al., 2006). There are about 4000 benthic species, with hundreds of living individuals being easily found in a few cubic centimetres of sediment (Schönfeld et al., 2012). They occur in all types of environments, from tropical to polar, including temperate ecosystems (Murray, 2006). Most of the species (except soft-shelled monothalamous ones) can be preserved in sediment through fossilisation processes, hence allowing the reconstruction of palaeo-environments (Hayward et al., 2004; Dolven et al., 2013). To correctly interpret the fossil record, environmental in-situ studies have focused on the ecology of living species (Alve, 1995; Murray & Alve, 2000; Mojtahid et al., 2006; Morvan et al., 2006; Bouchet et al., 2007). Despite an increasing interest in the study of living benthic foraminifera, there is still an incomplete knowledge of their biology and ecology.

To validate in-situ observations, living foraminifera have been used in the laboratory for nearly a century (e.g., Myers, 1935; Le Calvez, 1938; Jepps, 1942; Arnold, 1953). In contrast, the understanding of the behavioural ecology of foraminifera is still in its infancy, despite a fair amount of work related to their vertical and horizontal rates of movement (Arnold, 1953, 1974; Zmiri et al., 1974; Severin & Erskian, 1981; Severin et al., 1982; Severin, 1987; Kitazato, 1988; Wetmore, 1988; Weinberg, 1991; Anderson et al., 1991; Bornmalm et al., 1997; Manley & Shaw, 1997; Bernhard, 2000; Gross, 2000; Khare & Nigam, 2000).

Negative geotaxis is by far the most widely reported behavioural property among foraminifera (Murray, 1963, 1979, 1991; Richter, 1964; Lee et al., 1969; Moodley, 1990), which has been routinely used to separate them from the sediment (Lee et al., 1969; Arnold, 1974; Anderson et al., 1991; Bernhard, 2000). However, the mechanisms used by epifaunal and infaunal foraminifera to remain at the surface and within the sediment are still poorly understood and have barely been quantitatively assessed (Murray, 2006). Negative and positive geotaxes are mechanisms that epifaunal and infaunal foraminifera utilize (Moodley, 1990; Bernhard, 2000), sometimes in combination with positive (Jepps, 1942; Zmiri et al., 1974; Kitazato, 1981; Lee, 1990; Manley & Shaw, 1997) and negative (Myers, 1943) phototaxis. For instance, Manley & Shaw (1997) reported a variable geotaxis in *Elphidium crispum*, but an overwhelming positive phototaxis. This response to light allows *E. crispum* to remain epifaunal, and has been reported in species that contain endosymbionts (Lee, 1990). This response is hence likely a function of the presence of algal chloroplasts that are hosted by this species through ontogeny (Lee & Anderson, 1991; Murray, 1991).

Similarly, the amount of work published on the motion behaviour of foraminifera is still very limited (Kitazato, 1988; Weinberg, 1991; Bornmalm et al., 1997; Khare & Nigam, 2000). To our knowledge, the most extensive study conducted so far to assess the motion behaviour of foraminifera is based on 118 measurements of 1-min interval movement velocity among 22 species (Kitazato, 1988). Average velocities ranged between 8.0 and 82.3 $\mu\text{m min}^{-1}$ and significantly differed among species, with epifaunal species moving consistently faster than infaunal ones. Behavioural ecologists are using increasingly complex quantitative methods (e.g., Seuront, 2010; Viswanathan et al., 2011; Méndez et al., 2013). Most reports of foraminiferal behaviour are still essentially based, however, on qualitative statements such as “the movement of individuals [...] was quite smooth” (Kitazato, 1988, p. 346) or “they move laterally [...] in meandering patterns and [...] with predominantly straighter patterns in the vertical plane” (Bornmalm et al., 1997, p. 175), and quantitatively limited to mean speed (Kitazato, 1988; Weinberg, 1991; Bornmalm et al., 1997; Khare & Nigam,

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TABLE 1. Foraminiferal species considered, their geographic origin, and the number N of individuals considered under each experimental condition (i.e., Control and Geotaxis experiments) and the subsequent number n of successive (x,y) coordinates used to describe their motion behaviour.

Species	Origin	Control		Geotaxis	
		N	n	N	n
<i>Ammonia tepida</i>	Texel, The Netherlands	23	2760	12	1440
<i>Criboelphidium excavatum</i>	Baie of Authie, France	9	1080	11	1320
<i>Haynesina germanica</i>	Bay of Authie, France	12	1440	11	1320

2000). Note that these comments are not criticisms of the cited studies, as the aforementioned comments are ancillary to the main point of these papers.

In this context, the objectives of the present work were two-fold. First, we assess the presence and nature of the geotactic behaviour of three foraminiferal species characteristic of intertidal temperate ecosystems (Murray, 2006), that is, *Ammonia tepida*, *Criboelphidium excavatum* and *Haynesina germanica*. These species have been specifically chosen for their different ecological niches: *C. excavatum* and *H. germanica* are respectively infaunal (Thomsen & Altenbach, 1993) and epifaunal species (Bouchet et al., 2009), while *A. tepida* is known as an epifaunal/infaunal species (Goldstein et al., 1995). There are, however, some inconsistencies in the literature in the definition of the microhabitats occupied by these species. For instance, Richter (1964) reported *C. excavatum* as epifaunal and *H. germanica* as infaunal, while Murray (2006) considered *Ammonia* species as strictly infaunal. As behavioural responses are often the end product of a combination of intrinsic and extrinsic factors (Pyke, 1984; Bell, 1991), if foraminifera respond positively (or negatively) to gravity, the motion could also involve a negative (or positive) response to light. As such, the potential behavioural response of *C. excavatum*, *H. germanica* and *A. tepida* to light was also investigated.

Second, we aim to go beyond standard description of foraminiferal movement behaviour based on the presence/absence of any tactic behaviour (e.g., Zmiri et al., 1974; Manley & Shaw, 1997) and mean speed (e.g., Kitazato, 1988). As such, we specifically focus on the detailed nature of their motility, in terms of geometric and stochastic complexity of their motion behaviour, species-specific variability and specimen-specific variability. This approach is critical to understanding the ecology of motile organisms, as the adaptive value of individual variability in motion behaviour is increasingly acknowledged as a competitive advantage in temporally and spatially complex landscapes [see, e.g., Chapperton & Seuront (2011) for a discussion on this topic].

MATERIALS AND METHODS

SEDIMENT COLLECTION AND STUDY SPECIES

Sediments were collected in two intertidal muddy areas, the Baie of Authie (50°22'32"N, 1°35'43"E; Pas de Calais, France) on June 17, 2014 and Texel Island (53°08'17"N, 4°48'07"E; The Netherlands) on June 27, 2014. The sediment surface was gently scraped off to collect benthic foraminifera. The sediment was sieved in the laboratory on

the same day using a 63 μm mesh sieve. Prior to individual collection, the $> 63 \mu\text{m}$ fraction was kept in a temperature controlled room at 22°C overnight.

This study focused on 3 intertidal species, *Ammonia tepida*, *Haynesina germanica* and *Criboelphidium excavatum*, which typically occur abundantly (up to few thousands of individuals per cubic centimetre) in European mudflats (Murray, 2006). *Ammonia tepida* was found in Texel (The Netherlands), while *C. excavatum* and *H. germanica* were found in the Bay of Authie, France (Table 1).

EXPERIMENTAL SET-UP AND BEHAVIOURAL OBSERVATIONS

The motion behaviour of *A. tepida*, *C. excavatum* and *H. germanica* was investigated in Petri dishes (7.5 cm in diameter) filled with in-situ seawater ($S = 32$ PSU) to a height of 5 to 7 mm. All experiments were conducted under homogenous dim light conditions (light intensity: 450 lux; Light Probe Meter™ 403125, Extech Instruments, Nashua, USA, and irradiance: 65 $\mu\text{mol m}^{-2} \text{s}^{-1}$; Light Intensity Recorder MDS-MkV, Alec Electronics Inc., Kobe, Japan) provided by a series of fluorescent lamps in a temperature-controlled room at 22°C, a temperature representative of the conditions experienced in-situ by these species at the time of sampling. The *A. tepida* individuals were in the size range 300–400 μm , while the *C. excavatum* and *H. germanica* specimens were both in the range 150–200 μm . Between 9 and 23 distinct individuals were used in each experimental treatment (Table 1).

Control treatments were conducted with the Petri dish lying horizontally (Fig. 1A), whereas the geotactic-response treatments were conducted in Petri dishes elevated at one end to provide a slope of 12% (Fig. 1B), a condition previously identified as sufficient to elicit a geotactic response in foraminifera (Manley & Shaw, 1997) and tardigrades (Beasley, 2001). Prior to each experiment, living individuals were carefully sorted under a stereomicroscope with a brush, and immediately transferred in the middle of the experimental Petri dish (Fig. 1A–C), where they were allowed to acclimatize for 5 minutes. The motion behaviour of the specimen was subsequently recorded every 10 min using a digital camera (Nikon V1 mounted with a Nikkor 10–30 mm lens). Each individual was recorded for 20 hours, after which the resulting 120 images were assembled as QuickTime™ movies using Time Lapse Assembler (version 1.5.3). The x and y coordinates were subsequently extracted and combined into a 2D picture using Labtrack (DiMedia, Kvistgard, Denmark), and used to characterise motility. All experiments were conducted under similar tidal and diel conditions to avoid any behavioural bias that may relate to endogenous diel and/or tidal rhythms.

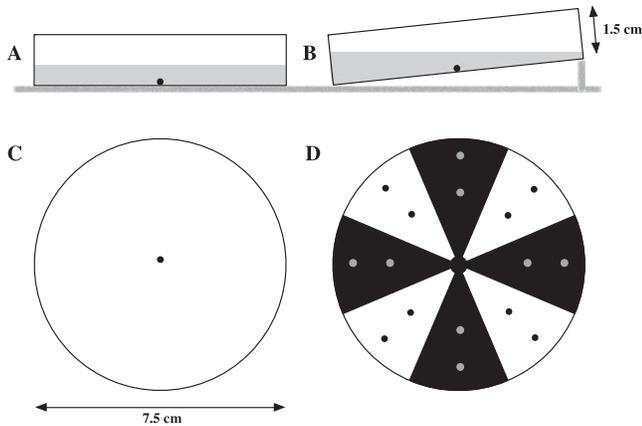


FIGURE 1. Schematic illustration of the experimental set-up used to assess the response of the foraminifera *Ammonia tepida*, *Criboelphidium excavatum* and *Haynesina germanica* to gravity and light. Control and geotaxis experiments were respectively run with a Petri dish lying horizontally (A) and tilted with a 12% slope (B). Both experiments were started with a foraminifer individual located in the middle of the experimental Petri dish (A–C). The response to light was assessed covering the experimental Petri dish with a plastic lid painted in black except for four evenly-spaced truncated conical perforated sections that allow light to reach the inner base of the dish. Light-response experiments were conducted with 16 foraminifera evenly distributed over the light (black dots) and dark (grey dots) areas, while control treatments that were set up in an identical manner, but run in total darkness.

To assess the potential response of foraminifera to light, a plastic Petri dish lid was painted black except for four evenly-spaced, truncated conical perforated sections (Fig. 1D). The truncated conical sections through which light could pass will be referred to as area A_{Light} and represented 50% of the total area; the remaining area of the petri dish, which prevented the entry of light, will be referred to as area A_{Dark} . This plastic lid was placed at 1.5 cm from the bottom surface of the base of the experimental Petri dish containing 16 foraminifera evenly placed over the areas A_{Light} and A_{Dark} . After 24 h, the relative distribution of specimen in areas A_{Light} and A_{Dark} were recorded, and compared to the results of control treatments that were set up in an identical manner, but kept in total darkness for 24 h.

BEHAVIOURAL ANALYSES

The level of activity of each specimen was estimated as the percentage of time allocated to motion. Specifically, an activity index A_i was defined as $A_i = 100(t_{path}/t_{move})$, where t_{path} and t_{move} are the time taken by a specimen to move from its start to stop location and the time a specimen was actually moving along its trajectory, respectively.

The distance D_i (mm) travelled between two successive images was computed from the (x, y) coordinates as

$$D_i = \sqrt{(x_t - x_{t+1})^2 + (y_t - y_{t+1})^2}$$
, where (x_t, y_t) and (x_{t+1}, y_{t+1}) are the position of a specimen at time t and $t + 1$, respectively. The movement speed v_i (mm h^{-1}) was subsequently estimated as $v_i = Df$, where f is the sampling rate of the camera (i.e., $f = 6$ images per hour).

The direction θ_i taken by a specimen between three successive positions (x_t, y_t) , (x_{t+1}, y_{t+1}) and (x_{t+2}, y_{t+2}) was

estimated as $\theta_i = 180 - [(180/\pi)\theta_e]$, where $\theta_e = \arccos \left[\frac{(D_{1-2})^2 + (D_{2-3})^2 - (D_{1-3})^2}{2(D_{1-2})(D_{2-3})} \right]$ and where D_{1-2} , D_{1-3} and D_{2-3} are the distances between the positions (x_t, y_t) and (x_{t+1}, y_{t+1}) ; (x_t, y_t) and (x_{t+2}, y_{t+2}) ; and (x_{t+1}, y_{t+1}) and (x_{t+2}, y_{t+2}) ; see Jerde & Visscher (2005) for more details. Average movement speeds and directions and their standard deviations were measured over the duration of each individual track.

The tortuosity of movements was estimated using the net-to-gross displacement ratio (NGDR) as $\text{NGDR} = \text{ND}/\text{GD}$. The net distance travelled by a specimen (ND) is the shortest distance between the starting and ending point of the trajectory. The gross distance (GD) travelled (i.e., the actual distance travelled by a specimen along its trajectory)

was estimated as $\text{GD} = \sum_{t=1}^{t_{track}} D_t$. The NGDR provides a measure of the relative linearity of motion; low NGDRs imply more convoluted trajectories than high NGDRs, with the limit $\text{NGDR} = 1$, corresponding to a linear motion. The NGDRs were estimated at the smallest available resolution (1/6 h) for each individual track. We also estimated the net direction taken by each specimen between the beginning and the end of its trajectory. Averaged distances (net and gross) and their standard deviations were estimated for each species for control and geotaxis experiments. The movement speed was estimated from the net distance, v_{net} , for comparison with the actual speed of the experimental specimens.

STATISTICAL ANALYSES

As the distribution of the estimated parameters (activity index, net and instantaneous distance, swimming speed and NGDR) were non-normally distributed (Kolmogorov–Smirnov test, $p < 0.01$), non-parametric statistics were used throughout this work. Specifically, the behavioural properties observed between control and geotactic experiments (distance, speed and NGDR) were compared using the Wilcoxon–Mann–Whitney U -test (Siegel & Castellan, 1988). Multiple comparisons between species were conducted using the Kruskal–Wallis test (KW test hereafter), and the Jonckheere test for ordered alternatives (J test hereafter; Siegel & Castellan, 1988) was used to identify distinct groups of measurements. The distributions of the distances (D_i) were tested for uniformity with the Kolmogorov–Smirnov test. The autocorrelation functions (ACF) and the Box–Ljung statistic were used to test for autocorrelation in the successive distances displaced for all lags up to seven moves (Turchin, 1998). The non-parametric Watson’s U^2 test was used to test for differences in the successive directions (θ_i) and the net direction between control and geotaxis experiments. The distributions of directions θ_i in control and geotaxis experiments were also compared to a normal distribution using the Kolmogorov–Smirnov test, and to a uniform distribution using both the Kolmogorov–Smirnov and the Watson’s U^2 tests (Zar, 2009). Finally, the probability of choosing the light and dark areas (A_{Light} and A_{Dark}) in the control and phototaxis experiment was assessed using a χ^2 goodness of fit (Zar, 2009). Correlation between variables was investigated using Kendall’s coefficient of rank correlation

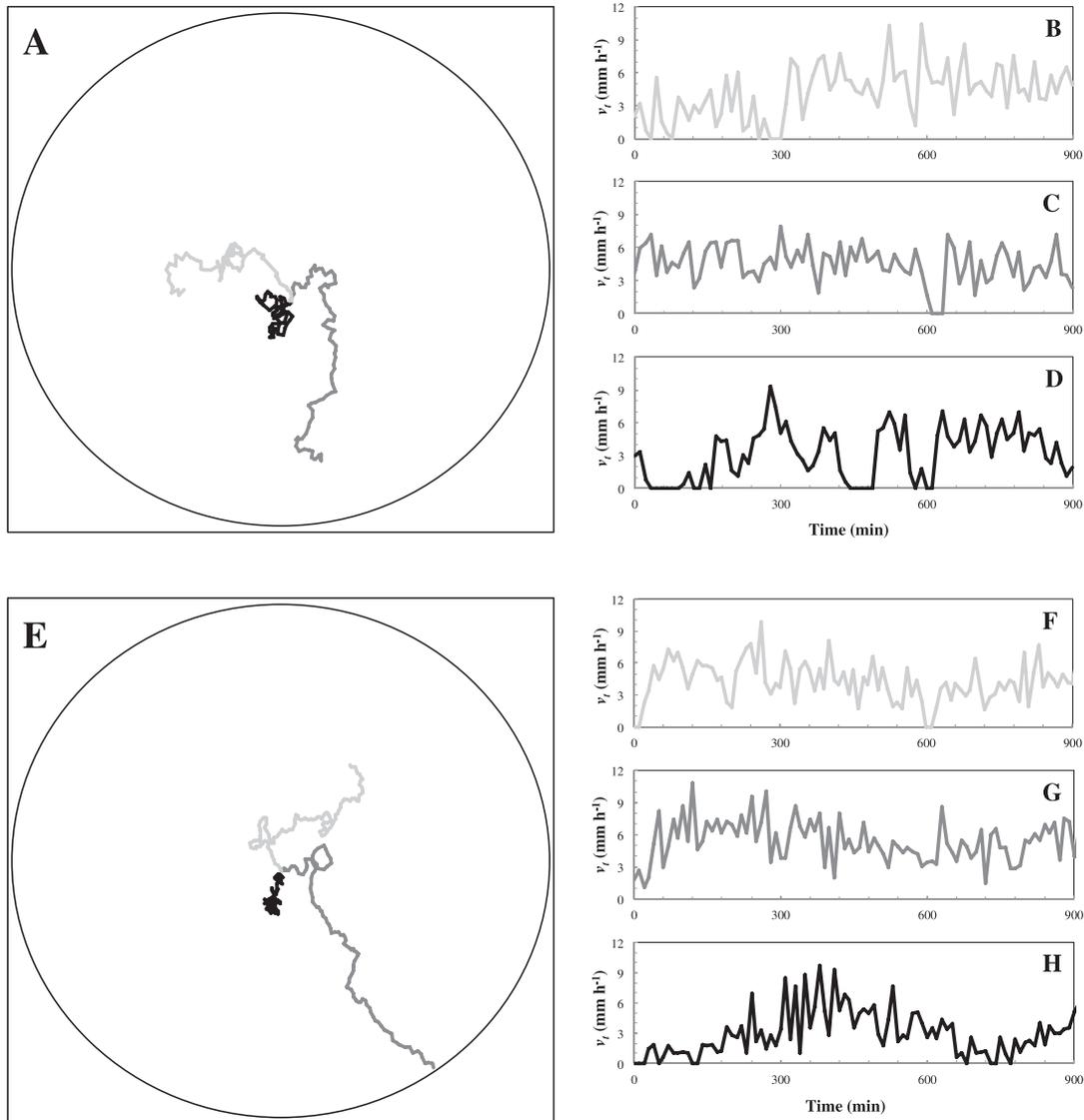


FIGURE 2. Illustration of the archetypal geometric (A, E) and stochastic (B–D, F–H) behavioural properties of three foraminiferal specimens (here *Ammonia tepida*) observed in control (A–D) and geotaxis (F–H) experiment, conducted in circular experimental arenas 7.5 cm in diameter. Distinct individuals were used in control and geotaxis experiments. Each colour code corresponds to the same *A. tepida* specimen in both (A) and (E), and the colour codes used for the three trajectories shown in (A, E) matches those used in (B–D) and (F–H).

(τ). Kendall's coefficient of correlation was used in preference to Spearman's coefficient of correlation (ρ), because Spearman's ρ gives greater weight to pairs of ranks that are further apart, while Kendall's τ weights each disagreement in rank equally (Sokal & Rolf, 1995).

RESULTS

THE BEHAVIOUR OF INTERTIDAL FORAMINIFERA: QUALITATIVE OBSERVATIONS

The motion behaviour of the three species of foraminifera considered in this work, *Ammonia tepida*, *Cibicides excavatum* and *Haynesina germanica*, was consistently characterised in both control and geotaxis experiments by a strong inter-individual variability in the complexity of the

trajectories followed by distinct individuals, and strong fluctuations in the temporal dynamics of their successive movements along the aforementioned trajectories (Fig. 2). Specifically, *A. tepida*, *C. excavatum* and *H. germanica* exhibited trajectories with highly variable levels of geometric complexity in both control and geotaxis experiments (Fig. 2A, E). Over the same period of time, the geometric complexity of foraminiferal motion behaviour hence ranges from highly meandering trajectories confined in a limited area of the experimental containers to far reaching trajectories leading to a more extensive exploration of the available space (Fig. 2A, E). In contrast, the velocity v_t of specimens along their trajectories are consistently characterised by a very high variability, independent of both the complexity of the trajectory and the treatment considered (Fig. 2B–D, F–H).

THE RESPONSE OF INTERTIDAL FORAMINIFERA TO GRAVITY

No significant differences ($p > 0.05$) were found in the net distances travelled by *A. tepida*, *C. excavatum* and *H. germanica* over the course of our 20 h experiments in both control and geotaxis experiments. Their directions were significantly uniform in control experiments ($p > 0.05$), and significantly non-uniform ($p < 0.05$) in geotaxis experiments, where they exhibited clear directionality as a response to gravity. Specifically, *A. tepida* exhibited a significant negative geotaxis (Fig. 3A). In contrast, both *C. excavatum* and *H. germanica* exhibited a significant positive geotaxis (Fig. 3B, C). The orientation angles θ_i did not significantly differ between species and experiments (U^2 test, $p > 0.05$) and were consistently best fitted by a uniform distribution.

The activity level of *A. tepida* and *C. excavatum* were significantly ($p < 0.05$) lower in the geotaxis experiment than in the control experiment, while *H. germanica* were significantly more active in the geotaxis experiment (U -test, $p < 0.05$, Fig. 4A). The activity level significantly differed between the three species in both control and geotaxis experiments (KW test, $p < 0.05$). In control and geotaxis experiments, the activity of *A. tepida* and *C. excavatum* did not significantly differ (J test, $p > 0.05$). *Ammonia tepida* and *C. excavatum* were, however, both more active than *H. germanica* in control and both less active than *H. germanica* in geotaxis experiments, respectively (J test, $p < 0.05$).

No significant differences in speed v_t were found between control and geotaxis treatments in any of the three species (U -test, $p > 0.05$, Fig. 4B), and successive distances displaced were positively autocorrelated ($p < 0.05$). Significant differences were found, however, between species in both control and geotaxis experiments (KW test, $p < 0.05$). *Ammonia tepida* and *H. germanica* did not move at significantly different rates (J test, $p > 0.05$), but were consistently slower than *C. excavatum* (J test, $p < 0.05$). The movement speed (v_t) was consistently significantly higher than v_{net} (the speed estimated from the net distance travelled by each individual foraminifera over the course of the behavioural experiments; $p < 0.05$, Fig. 5). The speed ratios v_t/v_{net} were then consistently greater than 1 for *A. tepida* (control: 1.6–16.6, geotaxis: 1.7–9.1), *C. excavatum* (control: 3.6–22.1, geotaxis: 3.4–83) and *H. germanica* (control: 1.5–52.9, geotaxis: 1.8–7.0).

The tortuosity of their trajectory was highly variable, and no significant differences were found in NGDRs between control and geotaxis experiments for all species (U -test, $p > 0.05$, Fig. 4C). Significant differences were found between the NGDRs of the three species in control and geotaxis experiments (KW test, $p < 0.05$). Specifically, the NGDRs of *A. tepida* and *H. germanica* could not be statistically distinguished from each other in both control and geotaxis treatments (J test, $p > 0.05$), and were significantly higher than in *C. excavatum*, which moved along less tortuous trajectories (J test, $p < 0.05$).

No significant correlation was found between any of the behavioural parameters ($p > 0.05$), except a significant negative correlation ($p < 0.05$) between the speed of

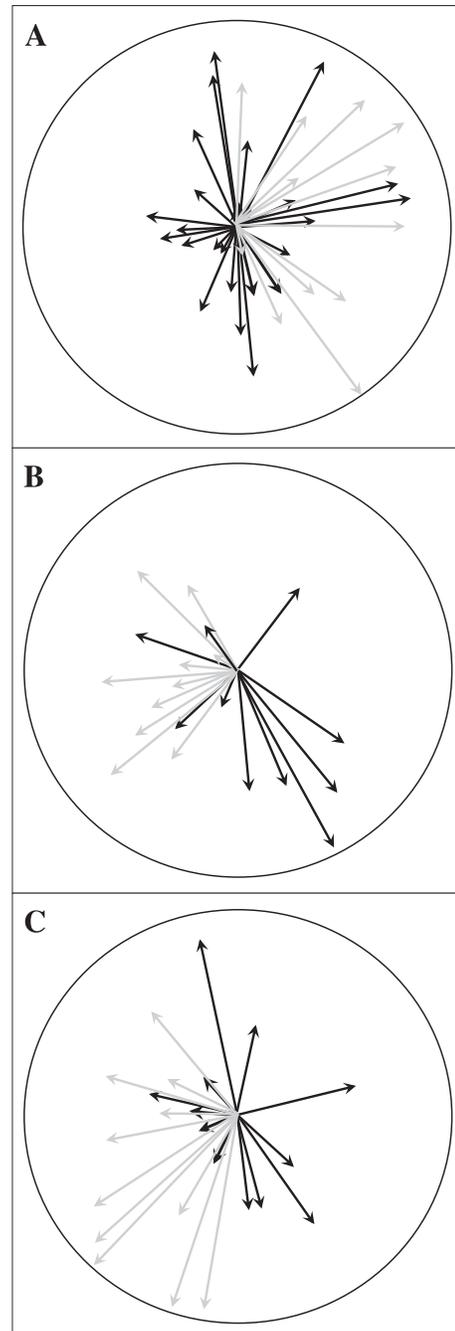


FIGURE 3. Net distance and direction travelled over 20 hours by *Ammonia tepida* (A), *Cribroelphidium excavatum* (B) and *Haynesina germanica* (C) in control (black) and geotaxis (grey) experiments in circular experimental arenas 7.5 cm in diameter. The angle of incline of the experimental arena in the geotaxis experiment has been set with a 12% slope.

movement v_t and NGDR in *C. excavatum* in the control treatment, and a significant positive correlation was found between the speeds v_t and v_{net} ($p < 0.05$) in *H. germanica* in both control and geotaxis treatments (Fig. 5E, F). In contrast, the ratio v_t/v_{net} was consistently significantly negatively correlated to NGDR ($p < 0.05$).

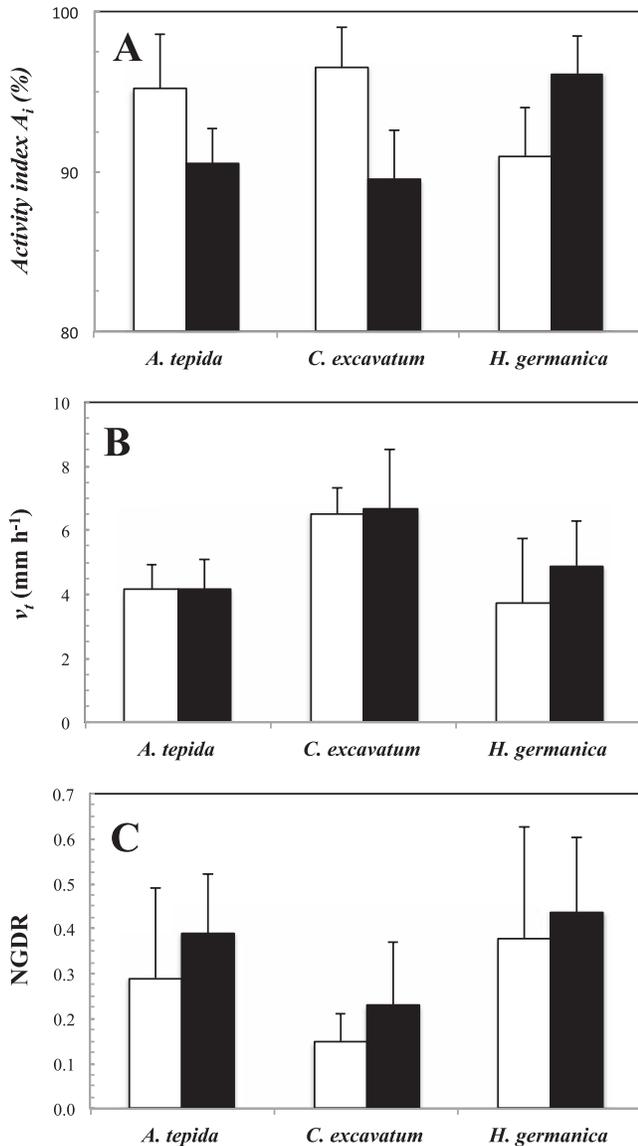


FIGURE 4. Behavioural properties [activity index, A_i (%); actual speed, v_t (mm h⁻¹) and NGDR] of *Ammonia tepida*, *Cribroelphidium excavatum* and *Haynesina germanica* estimated from 10-min resolution tracking of specimens in control (white bars) and geotaxis (black bars) experiments. The error bars are standard deviations.

THE RESPONSE OF INTERTIDAL FORAMINIFERA TO LIGHT

In both control (dark) and phototaxis experiments, no significant differences (χ^2 test, $p > 0.05$) were observed in the relative frequency of occurrence of foraminifera in light and dark areas (Table 2), suggesting the absence of any phototactic response of *A. tepida*, *C. excavatum* and *H. germanica*.

DISCUSSION

SPECIES-SPECIFIC RESPONSE TO GRAVITY

Our results unambiguously show a negative geotaxis in *A. tepida* (Fig. 3A), while *C. excavatum* and *H. germanica* were positively geotactic (Fig. 3B, C). These experimental

observations confirm some and contradict other previous conclusions essentially based on the distribution of living specimens of these species (Murray, 2006).

Specifically, our results are in agreement with previous work that identified *C. excavatum* as an infaunal species (e.g., Thomsen & Altenbach, 1993; Bouchet et al., 2007), and specifies previous work suggesting that *C. excavatum* can be considered as both an epifaunal and infaunal species (Moodley, 1990; Bouchet et al., 2009). Our results, however, do not support early work suggesting that *C. excavatum* is an epifaunal species (Richter, 1964). The positive geotactic behaviour observed in this study provides a strong support to its infaunal habitat.

Previous work suggested that *A. tepida* can be considered as both an epifaunal and infaunal species (e.g., Goldstein et al., 1995; Bouchet et al., 2009); the negative geotaxis reported here suggests *A. tepida* is epifaunal rather than infaunal, an observation consistent with the ability of *Ammonia beccarii* to crawl up through 1 cm of sediment (Lee et al., 1969). This is also consistent with our observations of *A. tepida* found on the sediment surface after spending a night at the experimental temperature. Previous observations of *A. tepida* deep into the sediment may indicate passive transport by macrofauna bioturbating activities as suggested in previous work (Moodley, 1990; Bouchet et al., 2009).

In contrast, *C. excavatum* and *H. germanica* specimens remained within the sediment layer, in accordance with their observed positive geotactic behaviour (Fig. 3B, C). Note that the increased levels of activity and lower NGDR observed in both *C. excavatum* and *A. tepida* in control treatments (Fig. 3A, C) are consistent with an increasing searching activity (i.e., more intensive search) in the absence of any stressor (here gravity). In contrast, the higher NGDRs observed during the geotaxis experiment are indicative of more extensive foraging behaviour consistent with the less complex trajectories and more extensive foraging behaviour exhibited by stressed organisms; see Seuront (2011a, b, 2015) for a detailed discussion on this topic in the context of copepod behavioural ecology. It is also possible that the observed behavioural changes are a form of expeditious adaptive response rather than a generalized stress response. It is, however, far beyond the scope of this study to delve deeply into the disentangling of adaptive behaviour to a stimulus and stress response that is generally related to parasitism, aging, disease or the presence of toxicants, for example (see Seuront, 2015 and references within).

Finally, *H. germanica*, previously reported as epifaunal (e.g., Bouchet et al., 2009), exhibited a positive geotaxis, which suggests an active avoidance of surface sediment. This result is supported by the significant increase in the level of activity exhibited by *H. germanica* in the geotaxis experiment (Fig. 4A). However, the lack of changes in the geometric complexity in the movement of *H. germanica* between control and geotaxis treatments (Fig. 4C) may indicate that the observed positive geotaxis is not stress related, hence a more *natural* behaviour than the positive and negative geotaxis respectively observed in *C. excavatum* and *A. tepida*.

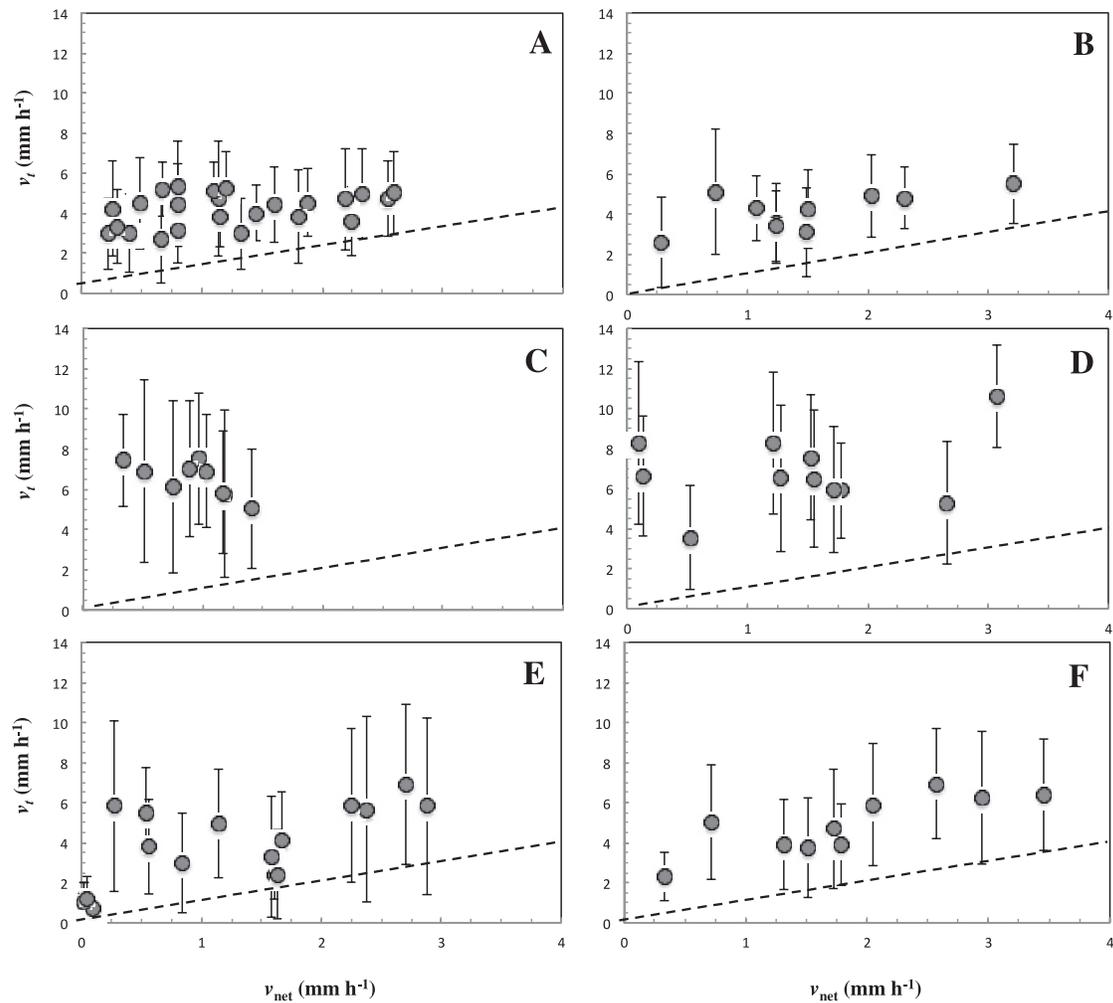


FIGURE 5. The actual speed v_i [of *Ammonia tepida* (A, B), *Cribroelphidium excavatum* (C, D) and *Haynesina germanica* (E, F)] estimated from 10-min resolution tracking of specimens as a function of the net speed v_{net} (i.e., the apparent speed estimated from the net distance travelled) under control conditions (A, C, E) and in geotaxis experiments (B, D, F). The error bars are standard deviations, and the dashed lines the first bisectrix (i.e., $v_{net} = v_i$).

The provision of a definite mechanistic explanation for the observed geotactic properties of *A. tepida*, *C. excavatum* and *H. germanica* would be, at best, highly speculative considering the current lack of knowledge on the behavioural ecology of this species. Note, however, that this study was carried out directly on the glass surface of Petri dishes. This fact warrants the need for further work to be conducted on the surface of actual sediment representative of in-situ conditions. However, our aforementioned observation on *A. tepida* specimens migrating upward through

the sedimentary column is supportive of our experimental set-up.

The geotactic behaviour observed in *H. germanica* and *C. excavatum* may be considered a behavioural adaptation related to an optimal positioning in the sediment. Vertical migration has been reported in foraminifera as a response to food, oxygen and temperature (Alve & Bernhard, 1995; Gross, 2000; Duijnsteet et al., 2003; Geslin et al., 2004; Nomaki et al., 2005). Note that *Haynesina* and *Cribroelphidium* are two of at least eight different foraminiferal

TABLE 2. Relative frequency of occurrence of foraminiferal individuals in areas of the experimental Petri dish, which allow and prevent light to pass (A_{Light} and A_{Dark} , respectively) in control experiments conducted in the dark for 24 h and in phototaxis experiments conducted for 24 h under conditions of dim light (150 lux) for 24 hours. The level of statistical significance of the χ^2 goodness of fit was fixed at $p = 0.05$; ns: non-significant.

		Control			Phototaxis		
		A_{Light}	A_{Dark}	χ^2	A_{Light}	A_{Dark}	χ^2
<i>A. tepida</i>	(n = 16)	7	9	ns	8	8	ns
<i>C. excavatum</i>	(n = 16)	11	5	ns	6	10	ns
<i>H. germanica</i>	(n = 16)	8	8	ns	9	7	ns

genera known to perform kleptoplastidy (Bernhard & Bowser, 1999); a process also referred to as chloroplast husbandry or sequestration that was first described in sacoglossa molluscs (Kawaguti & Yamasu, 1965), and subsequently found to occur in a range of protists including dinoflagellates (Lewitus et al., 1999; Eriksen et al., 2002; Takashita et al., 2002), ciliates (Dolan, 1992; Stoecker et al., 2009) and foraminifera (e.g., Lopez, 1979; Bernhard & Bowser, 1999). Specifically, kleptoplastidy has been widely reported for *H. germanica* (e.g., Lopez, 1979; Goldstein et al., 2004) and *C. excavatum* (Lopez, 1979; Pillet et al., 2011). As such, an analogy could be drawn between kleptoplastic species and the vertical migration observed in microphytobenthic cells moving upwards to the surface when the sediment is exposed at low tide and migrating downwards before it is flooded (Consalvey et al., 2004). In this context, the observed positive geotaxis may also be an indication of a downward migration triggered in our experimental setup by the immersion of the studied specimens. However, resolution of this specific issue is far beyond the scope of the present work and further work is critically needed to assess the interplay between kleptoplastidy and vertical foraminiferal behaviour.

ON THE LACK OF RESPONSE TO LIGHT OF INTERTIDAL FORAMINIFERA

The assessment of the role of phototaxis in the biology and ecology of benthic foraminifera found its root in the mid-twentieth century (Jepps, 1942; Myers, 1943). This early work reported both positive (Jepps, 1942) and negative (Myers, 1943) phototaxis. The handful of published papers that followed essentially report positive phototaxis (Zmiri et al., 1974; Kitazato, 1981; Lee, 1990; Manley & Shaw, 1997). For instance, Zmiri et al. (1974) only reported positive phototaxis in *Amphistegina radiata* under conditions of high light intensities (i.e., in the range 10^{11} – 10^{15} photons $\text{cm}^{-2} \text{s}^{-1}$), and Manley & Shaw (1997) found significant positive phototaxis in all size-classes (i.e., 250–355 μm and 500–1000 μm) but did not quantify the light intensity generated by “the fluorescent tube hung 20 cm above the specimens” (p. 962). Positive phototaxis has been claimed to be a behavioural strategy that allow species that contain endosymbionts to remain epifaunal (Lee, 1990); see also Sinutok et al. (2013) for discussion of more complex phototactic behaviour in *Marginopora vertebralis*.

Note that the absence of any phototactic response observed in the present work, even in kleptoplastic *H. germanica* and *C. excavatum*, is consistent with the insignificant light available at the surface of the sediment in tidally mixed estuarine waters (Spilmont et al., 2009), where *A. tepida*, *C. excavatum* and *H. germanica* abound and were sampled. As such, our results suggest that vertical migrations of foraminifera are unlikely to be driven by light, in contrast to microphytobenthos [i.e., microphytobenthic cells migrate upward at low tide, but only when low tides occur during the day; Consalvey et al. (2004)], hence the role of phototaxis in the biology and ecology of intertidal foraminifera may be negligible. It is finally stressed that if the intensity of ambient light used in our experiments is compatible with the values reported at the sediment surface

in shallow coastal waters (e.g., Meyercordt & Meyer-Reil, 1999), we were not able to measure the amount of light actually reaching the surface of the experimental Petri dish. Further work may hence be needed to assess the presence of light intensity thresholds that may activate/deactivate phototaxis in foraminifera.

SPECIES-SPECIFIC BEHAVIOURAL PROPERTIES

The behavioural responses revealed by continuous assessment of *A. tepida*, *C. excavatum* and *H. germanica* movements were clearly species-specific, and significantly differed even between the two species, *C. excavatum* and *H. germanica*, exhibiting similar geotactic responses (Fig. 4). This result indicates that the processes driving the observed motility pattern continue to operate in the absence of sensory cues, hence involving the presence of an innate determinant to motion behaviour (Chappon & Seuront, 2011; Seuront & Stanley, 2014). To our knowledge, this issue has yet to be investigated in foraminiferal behavioural ecology; innate sources of information are nevertheless known to be genetically determined and/or transferred through heredity, or derived from exogenous sources (Bell, 1991). As a consequence, the observed species-specific behavioural responses indicate that each species may have its own behavioural repertoire, which here specifically relates to the range of behavioural levels of activity, movement speed and trajectory complexity (Fig. 4).

The lower speed and higher NGDRs of *A. tepida* and *H. germanica*, for example, imply they explore their environment slowly and extensively with straighter trajectories. In contrast, *C. excavatum* individuals explore the environment more rapidly and intensively with more convoluted trajectories. These behavioural strategies are consistent with an optimal foraging strategy: an intensive (area restricted) search strategy (Pyke, 1984) and extensive search strategy (or transecting; Bell, 1991) are respectively optimal under conditions of high food concentration and spatially-localised food patches.

Note that the aforementioned behaviours have been recently reformulated under the popular Lévy flight foraging hypothesis, which has been used to explain the strategies of organisms searching for food, and predicts that predators should adopt Lévy search strategies (i.e., clusters of many small moves interspersed between longer moves, or relocation jumps, between them) for locating sparsely and randomly distributed prey and Brownian movement where prey is abundant (Viswanathan et al., 1999). The movement patterns we observed in the absence of cues are hence likely to be the result of natural selection of the search strategy that is best adapted to the ecological niche of each species.

The aforementioned search strategies are consistent with what is known of the trophic ecology of the three species used in this study. Specifically, *H. germanica* and *A. tepida* are both herbivorous, feeding on benthic diatoms (Ward et al., 2003; Pascal et al., 2008). In addition, *A. tepida* has recently been shown to behave as a carnivore in laboratory experiments (Dupuy et al., 2010). The ability of this species to switch feeding modes in its natural environment is still unknown. Since microphytobenthos microscale (i.e.,

centimetre-scale) distribution is extremely patchy (Seuront & Spilmont, 2002; Seuront & Leterme, 2006; Seuront, 2010; Spilmont et al., 2011), both species would benefit from the extensive search strategy to optimize their likelihood to locate food patches. In contrast, *C. excavatum* feed both on benthic diatoms (Lopez, 1979) and metazoans (Murray, 2006). The lack of clear overlap in the microscale distribution of meiofauna and microphytobenthos (Blanchard, 1990) suggests that omnivorous species such as *C. excavatum* may experience a more homogenous distribution of food items through a continuum of meiofaunal and microphytobenthos patches, which consumption would hence benefit from an intensive search strategy.

INTER-INDIVIDUAL VARIABILITY IN FORAMINIFERAL MOTION BEHAVIOUR

Besides the inter-specific variability discussed above, the motion behaviour of *A. tepida*, *C. excavatum* and *H. germanica* was consistently unambiguously characterised by a strong inter-individual variability (Figs. 2 and 5); in particular, each individual used very distinct repertoires of trajectory complexity under the same experimental conditions (Fig. 2A, E). This variability cannot be related to abiotic (i.e., temperature, salinity) or biotic (i.e., food quality and quantity, competition, predation) parameters since our experiments were conducted in the absence of any cues, and in controlled conditions of temperature and salinity. Also note that our experiments were conducted under similar tidal and diel conditions to avoid any bias that may relate to endogenous diel and/or tidal rhythms. The observed variability hence reveals the presence of innate variability in the motion behaviour that may relate to different phenotypes, and be thought of as an evolutionary adaptation to fluctuating environmental conditions to increase the chances of species persistence throughout a period of changes. Note that innate behavioural properties may be altered by the history of each individual considered, as individuals may gather distinct information directly from the same environment (e.g., Keppel & Scrosati, 2004). Limited information is available on the potential role of inter-individual behavioural variability in invertebrates in general — see Seuront et al. (2004) and Chapperon & Seuront (2011) for discussions on the ecological and evolutionary relevance of behavioural variability of copepods and intertidal gastropods — and to our knowledge this issue has yet to be introduced in foraminiferal research.

INTRA-INDIVIDUAL VARIABILITY IN FORAMINIFERAL MOTION BEHAVIOUR

All the studied *A. tepida*, *C. excavatum* and *H. germanica* specimens consistently used a diverse repertoire of movement speed and tortuosity (Figs. 2 and 5), within the species repertoire discussed above (Fig. 4). However, as previously reported for intertidal gastropods (Chapperon & Seuront, 2011), the extent to which the repertoire was used was not significantly different between individuals of the three species (Fig. 2). Note that this behavioural flexibility occurred at the smallest time scales considered in the present work (i.e., 10 min), hence suggesting an ability to

respond to short-term environmental changes. This behavioural property is likely to be adaptive in environments such as tidal flats, which are constrained both spatially and temporally by a range of rapidly changing environmental stressors, either predictable (e.g., tide, light) or unpredictable (e.g., weather conditions, predation, resource distribution and abundance). Note that a strong behavioural flexibility is also a strong competitive advantage for known omnivorous species such as *C. excavatum*, but also for species that may have the ability to switch feeding modes such as *A. tepida* (Dupuy et al., 2010).

METHODOLOGICAL CONSIDERATIONS: THE QUESTION OF SCALE

Previous assessments of foraminiferal behaviour were typically based on movement speed estimated from the net distance travelled (e.g., Kitazato, 1988). We showed, however, that estimating foraminiferal speed based on net displacements may lead to systematic and dramatic underestimations of the actual speed by a factor ranging from 1.6–17 in *A. tepida*, 3.4–83 in *C. excavatum*, and 1.5–53 in *H. germanica* (see Fig. 5). This is a serious issue as movement speed is a key input parameter in models dealing with processes such as energy budget, predator-prey and mating encounters (see e.g., Seuront & Stanley (2014) for a discussion on the effect of misestimating movement speed in mating encounter rates in pelagic copepods). In the aforementioned study, Kitazato (1988) showed that benthic foraminifera would move nearly five times faster on a glass surface compared to sediment surface since glass surface offers less resistance than sediment (see Kitazato, 1988 and Khare & Nigam, 2000 for further discussions on the topic). Still, our results show that movement speed estimated from the net distance travelled — as done in previous foraminiferal behaviour studies (e.g., Kitazato, 1988) — may be underestimated to up to a factor of 83. We thus suggest that the future of foraminiferal behavioural research may lie in a greater and more systematic focus on the detailed behavioural properties of these organisms to enhance our understanding of the processes at play in shaping foraminiferal ecology.

CONCLUSIONS

Our work shows that quantitative investigations of the geotactic and phototactic properties of foraminifera, as well as the details of the motion behaviour investigated on the basis of continuous observations, may provide valuable insights into our understanding of (i) the definition of their actual ecological niches that have been traditionally assessed through their vertical position in the sediment, (ii) their ability to respond to environmental fluctuations, and (iii) their contribution to intertidal ecosystems in terms of matter and energy fluxes that are essentially mediated by their movement behaviour. In particular, we showed that traditional approaches to the study of foraminiferal motion behaviour have systematically under-estimated their speed, which is likely to have critical consequences as it controls their energy expenditure and their ability to locate food, while avoiding predators. Beyond the biological and

ecological importance of the reported behavioural properties, our results more generally suggest that our journey to understand foraminiferal ecosystems from a bottom-up approach is still at a very early stage.

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REFERENCES

- Alve, E., 1995, Benthic foraminiferal responses to estuarine pollution: a review: *Journal of Foraminiferal Research*, v. 25, p. 190–203.
- Alve, E., and Bernhard, J. M., 1995, Vertical migratory response of benthic foraminifera to controlled oxygen concentrations in an experimental mesocosm: *Marine Ecology Progress Series*, v. 116, p. 137–151.
- Anderson, O. R., Lee, J. J., and Faber, W. W., 1991, Collection, maintenance and culture methods for the study of living foraminifera, in Lee, J. J., and Anderson, O. R. (eds.), *Biology of Foraminifera*: Academic Press, London, p. 335–357.
- Arnold, Z. M., 1953, An introduction to the study of movement and dispersal of *Allogromia laticollaris* Arnold: Contributions from the Cushman Foundation for Foraminiferal Research, v. 4, p. 15–21.
- Arnold, Z. M., 1974, Field and laboratory techniques for the study of living foraminifera, in Hedley, R. H., and Adams, C. G. (eds.), *Foraminifera*: Academic Press, London, p. 153–207.
- Beasley, C. W., 2001, Photokinesis of *Macrobotus hufelandi* (Tardigrada, Eutardigrada): *Zoologischer Anzeiger*, v. 240, p. 233–236.
- Bell, W. J., 1991, Searching behaviour: the behavioural ecology of finding resources: Springer, Berlin, 358 p.
- Bernhard, J. M., 2000, Distinguishing live from dead foraminifera: Methods review and proper applications: *Micropaleontology*, v. 46, p. 38–46.
- Bernhard, J. M., and Bowser, S. S., 1999, Benthic foraminifera of dysoxic sediments: chloroplast sequestration and functional morphology: *Earth-Science Reviews*, v. 46, p. 149–165.
- Blanchard, G. F., 1990, Overlapping microscale dispersion patterns of meiofauna and microphytobenthos: *Marine Ecology Progress Series*, v. 68, p. 101–111.
- Bornmalm, L., Corliss, B. H., and Tedesco, K., 1997, Laboratory observations of rates and patterns of movement of continental margin benthic foraminifera: *Marine Micropaleontology*, v. 29, p. 175–184.
- Bouchet, V. M. P., Debenay, J.-P., Sauriau, P.-G., Radford-Knoery, J., and Soletchnik, P., 2007, Effects of short-term environmental disturbances on living benthic foraminifera during the Pacific oyster summer mortality in the Marennes-Oléron Bay (France): *Marine Environmental Research*, v. 64, p. 358–383.
- Bouchet, V. M. P., Sauriau, P. G., Debenay, J.-P., Mermillod-Blondin, F., Schmidt, S., Amiard, J.-C., and Dupas, B., 2009, Influence of the mode of macrofauna-mediated bioturbation on the vertical distribution of living benthic foraminifera: First insight from axial tomodesitometry: *Journal of Experimental Marine Biology and Ecology*, v. 371, p. 20–33.
- Chappon, C., and Seuront, L., 2011, Variability in the motion behaviour of intertidal gastropods: ecological and evolutionary perspectives: *Journal of the Marine Biological Association of the United Kingdom*, v. 91, p. 237–244.
- Consalvey, M., Paterson, D. M., and Underwood, G. J. C., 2004, The ups and downs of life in a benthic biofilm: migration of benthic diatoms: *Diatom Research*, v. 19, p. 181–202.
- Degré, D., Leguerrier, D., du Chatelet, E. A., Rzeznik, J., Auguet, J.-C., Dupuy, C., Marquis, E., Fichet, D., Struski, C., Joyeux, E., Sauriau, P. G., and Niquil, N., 2006, Comparative analysis of the food webs of two intertidal mudflats during the two seasons using inverse modelling: Aiguillon Cove and Brouage Mudflat, France: *Estuarine, Coastal and Shelf Science*, v. 69, p. 107–124.
- Dolan, J., 1992, Mixotrophy in ciliates: A review of *Chlorella* symbiosis and chloroplast retention: *Marine Microbiological Food Webs*, v. 6, p. 115–132.
- Dolven, J. K., Alve, E., and Rygg, B., 2013, Defining past ecological status and in-situ reference conditions using benthic foraminifera: A case study from the Oslofjord, Norway: *Ecological Indicators*, v. 29, p. 219–233.
- Duijnste, I. A. P., Ernst, S. R., and van der Zwaan, G. J., 2003, Effect of anoxia on the vertical migration of benthic foraminifera: *Marine Ecology Progress Series*, v. 246, p. 85–94.
- Dupuy, C., Rossignol, L., Geslin, E., and Pascal, P.-Y., 2010, Predation of mudflat meio-macrofaunal metazoans by a calcareous foraminifer, *Ammonia tepida* (Cushman, 1926): *Journal of Foraminiferal Research*, v. 40, p. 305–312.
- Eriksen, N. T., Hayes, K. C., and Lewitus, A. J., 2002, Growth responses of the mixotrophic dinoflagellates, *Cryptoperidiniopsis* sp. and *Pfiesteria piscicida*, to light under prey-saturated conditions: *Harmful Algae*, v. 1, p. 191–203.
- Geslin, E., Heinz, P., Jorissen, F., and Hemleben, C., 2004, Migratory responses of deep-sea benthic foraminifera to variable oxygen conditions: laboratory investigations: *Marine Micropaleontology*, v. 53, p. 227–243.
- Goldstein, S. T., Watkins, G. T., and Kuhn, R. M., 1995, Microhabitats of salt marsh foraminifera: St. Catherines Island, Georgia, USA: *Marine Micropaleontology*, v. 26, p. 17–29.
- Goldstein, S. T., Bernhard, J. M., and Richardson, E. A., 2004, Chloroplast sequestration in the foraminifer *Haynesina germanica*: Application of high pressure freezing and freeze substitution: *Microscopy and Microanalysis*, v. 10, p. 1458–1459.
- Gross, O., 2000, Influence of temperature, oxygen and food availability on the migrational activity of bathyal benthic foraminifera: evidence by microcosm experiments: *Hydrobiologia*, v. 426, p. 123–137.
- Hayward, B. W., Grenfell, H. R., Nicholson, K., Parker, R., Wilmhurst, J., Horrocks, M., Swales, A., and Sabaa, A. T., 2004, Foraminiferal record of human impact on intertidal estuarine environments in New Zealand's largest city: *Marine Micropaleontology*, v. 53, p. 37–66.
- Jepps, M. W., 1942, Studies on *Polystomella* Lamarck (Foraminifera): *Journal of the Marine Biological Association of the United Kingdom*, v. 25, p. 607–666.
- Jerde, C. L., and Visscher, D. R., 2005, GPS measurement error influences on movement model parameterization: *Ecological Applications*, v. 15, p. 806–810.
- Kawaguti, S., and Yamasu, T., 1965, Electron microscopy on the symbiosis between an elysioid gastropod and chloroplasts of a green alga: *Biological Journal of Okayama University*, v. 11, p. 57–65.
- Keppel, E., and Scrosati, R., 2004, Chemically mediated avoidance of *Hemigrapsus nudus* (Crustacea) by *Littorina scutulata* (Gastropoda): effects of species coexistence and variable cues: *Animal Behaviour*, v. 68, p. 915–920.
- Khare, N., and Nigam, R., 2000, Laboratory experiment to record rate of movement of cultured benthic foraminifera: *ONGC Bulletin*, v. 37, p. 53–61.
- Kitazato, H., 1981, Observation of behaviour and mode of life of benthic foraminifera in laboratory: *Geoscience Reports of Shizuoka University*, v. 6, p. 61–71.
- Kitazato, H., 1988, Locomotion of some benthic foraminifera in and on sediments: *Journal of Foraminiferal Research*, v. 18, p. 344–349.
- Le Calvez, J., 1938, Recherches sur les foraminifères: Développement et reproduction: *Archives de Zoologie Experimentale et Générale*, v. 80, p. 163–333.
- Lee, J. J., 1990, Phylum Granuloreticulosa (Foraminifera), in Reid, P. C. et al. (eds.), *Protozoa and their role in marine processes*: Springer-Verlag, Berlin, p. 180–194.
- Lee, J. J., and Anderson, O. R., 1991, Symbiosis in Foraminifera, in Lee, J. J., and Anderson, O. R. (eds.), *Biology of Foraminifera*: Academic Press, London, p. 157–220.
- Lee, J. J., Muller, W. A., Stone, R. J., McEnery, M. E., and Zucker, W., 1969, Standing crop of foraminifera in sublittoral epiphytic

- communities of a Long Island salt marsh: *Marine Biology*, v. 4, p. 44–61.
- Lewitus, A., Glasgow, H., and Burkholder, J., 1999, Kleptoplastidy in the toxic dinoflagellate *Pfiesteria piscicida* (Dinophyceae): *Journal of Phycology*, v. 35, p. 303–312.
- Lopez, E., 1979, Algal chloroplasts in the protoplasm of three species of benthic foraminifera: taxonomy affinity, variability and persistence: *Marine Biology*, v. 53, p. 201–211.
- Manley, C. J., and Shaw, S. R., 1997, Geotaxis and phototaxis in *Elphidium crispum* (Protozoa: Foraminiferida): *Journal of the Marine Biological Association of the United Kingdom*, v. 77, p. 959–967.
- Méndez, V., Campos, D., and Bartumeus, F., 2013, Stochastic foundations in movement ecology: anomalous diffusion, front propagation and random searches: Springer, Berlin, 310 p.
- Meyercordt, J., and Meyer-Reil, L. A., 1999, Primary production of benthic microalgae in two shallow coastal lagoons of different trophic status in the southern Baltic Sea: *Marine Ecology Progress Series*, v. 178, p. 179–191.
- Mojtahid, M., Jorissen, F., Durrieu, J., Galgani, F., Howa, H., Redois, F., and Camps, R., 2006, Benthic foraminifera as bio-indicators of drill cutting disposal in tropical east Atlantic outer shelf environments: *Marine Micropaleontology*, v. 61, p. 58–75.
- Moodley, L., 1990, Southern North Sea seafloor and subsurface distribution of living benthic foraminifera: *Netherlands Journal of Sea Research*, v. 27, p. 57–71.
- Morvan, J., Debenay, J.-P., Jorissen, F., Redois, F., Bénéteau, E., Delplancke, M., and Amato, A.-S., 2006, Patchiness and life cycle of intertidal foraminifera: implication for environmental and paleoenvironmental interpretation: *Marine Micropaleontology*, v. 61, p. 131–154.
- Murray, J. W., 1963, Ecological experiments on Foraminiferida: *Journal of the Marine Biological Association of the United Kingdom*, v. 43, p. 621–642.
- Murray, J. W., 1979, Recent benthic foraminiferids of the Celtic sea: *Journal of Foraminiferal Research*, v. 9, p. 193–209.
- Murray, J. W., 1991, *Ecology and Palaeoecology of Benthic Foraminifera*: Wiley, New York, 397 p.
- Murray, J. W., 2006, *Ecology and Applications of Benthic Foraminifera*: Cambridge University Press, Cambridge, 426 p.
- Murray, J. W., and Alve, E., 2000, Major aspects of foraminiferal variability (standing crop and biomass) on a monthly scale in an intertidal zone: *Journal of Foraminiferal Research*, v. 30, p. 177–191.
- Myers, E. H., 1935, The life history of *Patellina corrugata* Williamson a foraminifer: *Scripps Institute of Oceanography Bulletin*, v. 3, p. 355–392.
- Myers, E. H., 1943, Life activities of Foraminifera in relation to marine ecology: *Proceedings of the American Philosophical Society*, v. 86, p. 439–458.
- Nomaki, H., Heinz, P., Hemleben, C., and Kitazato, H., 2005, Behavior and response of deep-sea benthic foraminifera to freshly supplied organic matter: a laboratory feeding experiment in microcosm environments: *Journal of Foraminiferal Research*, v. 35, p. 103–113.
- Pascal, P.-Y., Dupuy, C., Richard, P., and Niquil, N., 2008, Bacterivory in the common foraminifer *Ammonia tepida*: isotope tracer experiment and the controlling factors: *Journal of Experimental Marine Biology and Ecology*, v. 359, p. 55–61.
- Pillet, L., de Vargas, C., and Pawlowski, J., 2011, Molecular identification of sequestered diatom chloroplasts and kleptoplastidy in Foraminifera: *Protist*, v. 162, p. 394–404.
- Pyke, G. H., 1984, Optimal foraging theory: A critical review: *Annual Review of Ecology, Evolution, and Systematics*, v. 15, p. 523–575.
- Richter, G., 1964, Zur ökologie der Foraminiferida II: lebensraum und lebensweise von *Nonion depressulum*, *Elphidium excavatum* und *Elphidium selseyense*: *Natur und Museum*, v. 94, p. 421–430.
- Schönfeld, J., Alve, E., Geslin, E., Jorissen, F., Korsun, S., Spezzaferri, S., Abramovich, S., Almogi-Labin, A., du Chatelet, E. A., Barras, C., Bergamin, L., Bicchi, E., Bouchet, V. M. P., Cearreta, A., Di Bella, L., Dijkstra, N., Trevisan Disaro, S., Ferraro, L., Frontalini, F., Gennari, G., Golikova, E., Haynert, K., Hess, S., Husum, K., Martins, V., McGann, M., Oron, S., Romano, E., Mello Sousa, S., and Tsujimoto, A., 2012, The FOBIMO (FOraminiferal BIOMonitoring) initiative—Towards a standardised protocol for soft-bottom benthic foraminiferal monitoring studies: *Marine Micropaleontology*, v. 94, p. 1–13.
- Seuront, L., 2010, *Fractals and multifractals in ecology and aquatic science*: CRC Press, Boca Raton, FL, 344 p.
- Seuront, L., 2011a, Behavioral fractality in marine copepods: Endogenous rhythms versus exogenous stressors: *Physica A*, v. 390, p. 250–256.
- Seuront, L., 2011b, Hydrocarbon contamination decreases mating success in a marine planktonic copepod: *PLoS ONE*, v. 6, e26283, doi:10.1371/journal.pone.0026283.
- 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 Ceccaldi, H. J. et al. (eds.), *Marine Productivity: Perturbation and Resilience of Socio-Ecosystems*: Springer, New York, p. 129–137.
- Seuront, L., and Spilmont, N., 2002, Self-organized criticality in intertidal microphytobenthos patch patterns: *Physica A*, v. 313, p. 512–539.
- Seuront, L., and Leterme, C., 2006, Microscale patchiness in microphytobenthos distributions: evidence for a critical state, in Kromkamp, J. C., de Brouwer, J., and others (eds.), *Functioning of micro phyto-benthos in estuaries*: The Academy of Arts and Sciences, Amsterdam/The University of Chicago Press, Chicago, p. 165–183.
- Seuront, L., and Stanley, H. E., 2014, Anomalous diffusion and multifractality enhance mating encounters in the ocean: *Proceedings of the National Academy of Science USA*, v. 111, p. 2206–2211.
- Seuront, L., Hwang, J.-S., Tseng, L.-C., Schmitt, F. G., Souissi, S., and Wong, C.-K., 2004, Individual variability in the swimming behavior of the sub-tropical copepod *Oncaea venusta* (Copepoda: Poecilostomatoida): *Marine Ecology Progress Series*, v. 283, p. 199–217.
- Severin, K. P., 1987, Laboratory observations of the rate of subsurface movement of a small miliolid foraminifer: *Journal of Foraminiferal Research*, v. 17, p. 110–116.
- Severin, K. P., and Erskian, M. G., 1981, Laboratory experiments on the vertical movement of *Quinqueloculina impressa* Reuss through sand: *Journal of Foraminiferal Research*, v. 11, p. 133–136.
- Severin, K. P., Culver, S. J., and Blanpied, C., 1982, Burrows and trails produced by *Quinqueloculina impressa* Reuss, a benthic foraminifer, in fine-grained sediment: *Sedimentology*, v. 29, p. 897–901.
- Siegel, S., and Castellan, N. J., Jr., 1988, *Nonparametric Statistics for the Behavioral Sciences*: McGraw-Hill, New York, 399 p.
- Sinutok, S., Hill, R., Doblin, M., and Ralph, P. J., 2013, Diurnal photosynthetic response of the motile symbiotic benthic foraminiferan *Marginopora vertebralis*: *Marine Ecology Progress Series*, v. 478, p. 127–138.
- Sokal, R. R., and Rohlf, F. J., 1995, *Biometry*: W. H. Freeman, New York, 887 p.
- Spilmont, N., Denis, L., Artigas, L. F., Caloin, F., Courcot, L., Créach, A., Desroy, N., Gevaert, F., Hacquebart, P., Hubas, C., Janquin, M.-A., Lemoine, Y., Luczak, C., Migné, A., Rauch, M., and Davoult, D., 2009, Impact of the *Phaeocystis globosa* spring bloom on the intertidal benthic compartment in the eastern English Channel: a synthesis: *Marine Pollution Bulletin*, v. 58, p. 55–63.
- Spilmont, N., Seuront, L., Meziane, T., and Welsh, D. T., 2011, There's more to the picture than meets the eye: Sampling microphytobenthos in a heterogeneous environment: *Estuarine, Coastal and Shelf Science*, v. 95, p. 470–476.
- Stoecker, D., Johnson, M., de Vargas, C., and Not, F., 2009, Acquired phototrophy in aquatic protists: *Aquatic Microbial Ecology*, v. 57, p. 279–310.
- Takishita, K., Koike, K., Maruyama, T., and Ogata, T., 2002, Molecular evidence for plastid robbery (kleptoplastidy) in *Dinophysis*, a dinoflagellate causing diarrhetic shellfish poisoning: *Protist*, v. 153, p. 293–302.
- Thomsen, L., and Altenbach, A. V., 1993, Vertical and areal distribution of foraminiferal abundance and biomass in microhabitats around inhabited tubes of marine echiurids: *Marine Micropaleontology*, v. 20, p. 303–309.

- Turchin, P., 1998, Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants: Sinauer Associates Inc, Sunderland, 410 p.
- Viswanathan, G. M., Buldyrev, S. V., Havlin, S., da Luz, M. G. E., Raposo, E. P., and Stanley, H. E., 1999, Optimizing the success of random searches: *Nature*, v. 401, p. 911–914.
- Viswanathan, G. M., da Luz, M. G. E., Raposo, E. P., and Stanley, H. E., 2011, *The Physics of Foraging: An introduction to random searching and biological encounters*: Cambridge University Press, New York, 158 p.
- Ward, J. N., Pond, D. W., and Murray, J. W., 2003, Feeding of benthic foraminifera on diatoms and sewage-derived organic matter: an experimental application of lipid biomarker techniques: *Marine Environmental Research*, v. 56, p. 515–530.
- Weinberg, J. R., 1991, Rates of movement and sedimentary traces of deep-sea foraminifera and mollusca in the laboratory: *Journal of Foraminiferal Research*, v. 21, p. 213–217.
- Wetmore, K. L., 1988, Burrowing and sediment movement by benthic foraminifera, as shown by time-lapse cinematography: *Revue de Paléobiologie, Genève*, v. Vol. Spéc. n°2, Benthos'86, p. 921–927.
- Zar, J. H., 2009, *Biostatistical Analysis, Fifth Edition*: Pearson, Upper Saddle River, New Jersey, USA, 960 p.
- Zmiri, A., Kahan, D., Hochstein, S., and Reiss, Z., 1974, Phototaxis and thermotaxis in some species of *Amphistegina* (Foraminifera): *Journal of Protozoology*, v. 21, p. 133–138.

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