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How does macrofaunal bioturbation influence the vertical distribution of living benthic foraminifera?

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ABSTRACT: The vertical distribution of benthic foraminifera in coastal sediments seems tightly controlled by bioturbation processes. However, it still remains unclear whether living specimens found at depth around biogenic structures actively migrated from the sediment surface to reach oxygenated food-rich micro-environments or have been passively transported by macrobenthic organisms. The present study experimentally demonstrates that the vertical distribution of *Ammonia tepida*, one of the dominant species of foraminiferal assemblages in temperate intertidal mudflats, is tightly dependent on macrofaunal bioturbation modes and rates. The high degree of similarity between vertical profiles of foraminifera and inert particle tracers revealed that this species is not able to (1) efficiently resist biologically induced downward transport and (2) initiate rapid upward migrations to the oxic zone. The strong decrease of locomotion activity recorded in anoxic conditions suggests that encystment and inactivity are the first strategic responses to sudden oxygen depletion.

KEY WORDS: Foraminifera · *Ammonia tepida* · Bioturbation · Anoxia · Locomotion activity · Vertical distribution

INTRODUCTION

Foraminifera are heterotrophic single-celled eukaryotes that are widespread in all marine ecosystems and particularly abundant in coastal soft-bottom substrates, where they often dominate meiofaunal communities (Moodley et al. 2000, Murray 2007). Benthic foraminifera present a large variety of feeding modes, including osmotrophy and suspension feeding, although most of them are opportunistic omnivorous deposit feeders (Lipps 1983, Pascal et al. 2008, Dupuy et al. 2010). They are also probably common prey for many benthic organisms (Lipps 1983). By facilitating the transfer of energy from photosynthesis and microbial respiration to the upper trophic levels, living benthic foraminifera may play a significant role in coastal food web dynamics (Moodley et al. 2000). Benthic foraminifera also influence organic matter mineralization and nutrient cycles at the sediment–water interface, although their contribution to global aerobic respiration seems limited in coastal areas (Geslin et al. 2011, Cesbron et al. 2016). Nevertheless, recent laboratory experiments revealed that the influence of benthic foraminifera in remineralization processes could be much more important than estimated so far since numerous species are able to live under anoxia and sustain anaerobic metabolism (Risgaard-Petersen et al. 2006, Bernhard et al. 2012). Some species developed the capacity to store intracellular nitrates and to use them as electron acceptors when oxygen is lacking. All denitrifying species are nevertheless facultative anaerobes, preferentially respiring on oxygen that yields the highest energetic gain (e.g. Piña-Ochoa et al. 2010a). Denitrification may thus represent an alternative transient metabolism pathway allowing them to temporarily survive in anoxic habitats until

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they can reach the oxic zone. The life strategy of benthic foraminifera (i.e. aerobic vs. anaerobic metabolism) and their subsequent impact on global carbon and nitrogen cycling would therefore fundamentally depend on their microhabitat within the sediment column with respect to vertical profiles of oxidants.

In shallow cohesive sediments, the vertical distribution of living foraminiferal species seems tightly linked to the sediment–water interface, where the highest densities are most often observed (e.g. Alve & Murray 2001, Thibault de Chanvalon et al. 2015). However, they are not necessarily confined to the surficial oxygenated sediment layer, and significant abundances of living specimens can be observed deeper in the substratum (Goldstein et al. 1995, Bouchet et al. 2009). In benthic environments with scarce macrofauna, the vertical zonation of living foraminifera seems mainly controlled by food and oxygen availabilities, with the relative importance of these 2 factors varying according to environmental conditions (Jorissen et al. 1995). It has also been suggested that foraminifera could change their habitat depth to avoid predation and minimize competition (van der Zwaan et al. 1999). Conversely, in sediments inhabited by macrobenthic communities, the occurrence of foraminifera below the sediment surface seems largely controlled by the biogenous sediment mixing, usually called bioturbation (Kristensen et al. 2012). Bioturbation has profound physical and biogeochemical consequences. In particular, it deeply influences the structure and porosity of the sediment matrix, increases the oxygen penetration depth (OPD), alters the vertical sequence of oxidants and can induce intermittent small-scale redox oscillations (Aller 1982, 2014, Volkenborn et al. 2012). It also enhances the incorporation of freshly sedimented particulate organic matter and its transfer to deeper anoxic layers (Krantzberg 1985). Collectively, these biologically mediated processes generate a 3-dimensional (3D) mosaic of food-rich and oxygenated sedimentary microenvironments quickly colonized by bacteria and microphytobenthos that constitute favorable habitats for foraminifera (Nomaki et al. 2006). Macrobenthic deposit feeders are considered the main sediment engineers, dominating bioturbation processes in nearly all sedimentary environments (Aller 1982). However, they induce different effects on their surrounding environment depending on their size, density and nature of their specific behaviours (Maire et al. 2006, Gilbert et al. 2007, Norkko et al. 2013).

Several studies have investigated the link between macrofaunal activity and foraminiferal vertical distribution (e.g. Lipps 1983, Moodley 1990, Koller et al. 2006, Diz & Frances 2008, Bouchet et al. 2009), but no general consistent pattern is apparent. Particularly, (1) the exact mechanisms by which bioturbation influences the vertical distribution of foraminifera and (2) the behavioural responses of buried specimens still remain unclear. For instance, it has been shown that some foraminiferal species rapidly build a protection or resting cyst and remain immobile when exposed to anoxia (Linke & Lutze 1993, Heinz et al. 2005). This encystment behaviour is considered an adaptation to rapid changes in environmental conditions, as the space between the test and the sedimentary envelope represents a microhabitat temporarily protecting the cell against chemical disturbances. Conversely, there are also evidences that foraminifera could actively migrate using their pseudopods (i.e. amoeboid movement) within the sediment (Moodley et al. 1998, Gross 2000, Geslin et al. 2004) and thus be potentially capable of reaching food-rich oxygenated microenvironments at depth around biogenic structures. Field observations carried out by Bouchet et al. (2009) at different stations of an intertidal mudflat reinforced this last assumption, as living benthic foraminifera were found below the sediment surface in areas hosting sediment-dwelling organisms but were not present within anoxic layers in the absence of irrigating infauna, even though the sediment was actively reworked by downward conveyors. Assuming that foraminifera, as other slow-moving meiofaunal organisms inhabiting soft substrates, are likely to be passively transported below the sediment surface through sediment reworking processes (Lipps 1983, Langer et al. 1989), those findings would suggest that foraminifera are somehow able to resist downward transport and then to selectively decide on their life position within the sedimentary column despite intense bioturbation activities.

In this study, we experimentally examined the capacity of *Ammonia tepida,* one of the dominant foraminiferal species inhabiting intertidal muddy sediments at temperate latitudes (Alve & Murray 2001), to avoid long-term burial into deep anoxic layers through fast upward migration. In a first set of experiments, we compared the effects of large bioturbators, belonging to different functional groups, on their distribution in the sediment column. In a second set of experiments, we investigated the response of *A. tepida* to passive burial caused by a fast single-sediment reworking event. Additionally, the influence of sudden oxygen depletion on their locomotion activity was assessed using image analysis techniques.

MATERIALS AND METHODS

Fauna and sediment collection

Living specimens of *Ammonia tepida* were collected in an intertidal mudflat of the Aiguillon Bay (French Atlantic coast) (46° 15′ 13.81″ N, 1° 8′ 21.02″ W) where densities are particularly high. The surficial sediment layer (ca. 1 cm) was sieved over a 500 µm mesh to remove macrofauna and larger meiofauna. Sediment samples were immediately packed in cool boxes with natural seawater from the site and transported to the laboratory, where they were kept in a thermo-regulated room in aerated seawater at *in situ* temperature (13°C) and salinity (28). Foraminifera were fed weekly with a mixture of *Tetraselmis* spp. (green algae) until the beginning of the experiments.

Macrobenthic organisms used in the first set of experiments, the heart urchin *Echinocardium cordatum*, the mud shrimp *Upogebia pusilla* and the annelid polychaete *Hediste diversicolor*, are efficient bioturbators known to induce high sediment reworking and bioirrigation rates but over different modes because of specific behaviours (Kristensen et al. 2012). All specimens were collected in mudflats of Arcachon Bay (44° 40′ 47.22″ N, 1° 8′ 37.38″ W) using a grab sampler for the echinoderms and the worms and a manual bait piston pump for the mud shrimp. Undamaged specimens of the same length (i.e. maximal length, from the tip of the rostrum to the tip of the telson for the mud shrimp) (38.7 ± 0.6, 45.6 ± 0.6 and 56.7 ± 0.7 mm for *E. cordatum*, *U. pusilla* and *H. diversicolor*, respectively) were held separately in tanks containing natural sediment with flow-through *in situ* seawater for 2 d before being used in the experiments.

Expt 1: Effects of bioturbating macrobenthic species on the vertical distribution of *Ammonia tepida*

Experiments were conducted in plexiglass tubes (height = 50 cm, internal diameter = 9.4 cm) filled to a depth of 40 cm with natural sediment from Arcachon Bay (median grain diameter = 12 µm, organic carbon = 2.75% dry weight, nitrogen = 0.56% dry weight) and overlain with 10 cm of running *in situ* seawater. The sediment was previously sieved through a 100 µm mesh in a seawater bath to remove adult *A. tepida*, allowed to settle for 24 h to retain the finest fraction and well homogenized. All sediment cores were maintained at *in situ* temperature (13°C) for 10 d prior to the introduction of the macrofauna, to allow for the stabilization of the sediment matrix and geochemical gradients and thus keep it representative of the *in situ* sediment properties.

Three replicated (n = 3) macrofaunal treatments were run: one treatment with *E. cordatum* (1 ind. core^{-1}), one with *U. pusilla* (1 ind. core^{-1}) and one with *H. diversicolor* (4 ind. core^{-1}). Animal densities in experimental enclosures (144 ind. m^{-2} for the heart urchins and the mud shrimp and 576 ind. m^{-2} for the worms) are in the range of those usually reported in the field (e.g. Dworschak 1987, Degraer et al. 2006, Duport et al. 2006, D'Andrea & De Witt 2009). Additionally, 1 experimental enclosure was kept without macrofauna as a control treatment. Foraminiferal samples were washed on both 300 and 125 µm sieves with micro-filtrated seawater, and living individuals were picked up with a brush under a stereomicroscope (Nikon SMZ25). After an acclimation period of 5 d to allow for macrofaunal burrow establishment, exactly 1200 living adult specimens of *A. tepida* (125–300 µm range size) and 10 g of luminophores (fluorescent-dyed sediment particles, 20 µm) were evenly distributed across the sediment surface in each replicate. Such densities of *A. tepida* are commonly observed in the intertidal mudflats along the French west coast (Thibault de Chanvalon et al. 2015). Sediment cores were kept in total darkness and continuously flushed with flow-through seawater for 16 d. At the end of the experiments, sediment cores were sliced in 0.5 cm layers between 0 and 5 cm depth, in 1 cm layers between 5 and 10 cm depth, and in 2 cm layers between 10 and 40 cm depth. Each slice was sieved over a 125 µm mesh to separate foraminifera from the finer fraction (sediment + luminophores), which was immediately freeze dried, weighed and homogenized. Afterwards, a subsample of 1.5 g was carefully dispersed over a Petri dish under UV light and photographed (Nikon D100 digital camera). Images were analyzed and luminophores counted using AviExplore software (Romero-Ramirez et al. 2016). Living foraminifera were visually counted in each sediment slice under a stereomicroscope. The relative concentrations of both foraminifera and luminophores in each slice were then used to compute corresponding 1-dimensional (1D) vertical profiles.

Sediment reworking rates were quantified by fitting luminophore or foraminifera depth profiles with a 1D advection–diffusion model (Meysman et al. 2003):

$$\frac{\partial C}{\partial t} = D_b \frac{\partial^2 C}{\partial z^2} - \omega \frac{\partial C}{\partial z} \quad (1)$$

where C is the tracer concentration, t is the time period, D_b is the biodiffusion coefficient, z represents

the depth in the sediment column and ω is the bioturbation coefficient. D_b and ω values were estimated by convergent iterations and weighted least-squares regressions of observed luminophore (D_b^L, ω^L) or foraminifera (D_b^F, ω^F) profiles on predicted tracer concentrations (see Maire et al. 2008 for further details).

Expt 2: Response of *Ammonia tepida* to a passive downward transport

Experiments were conducted in 18 plexiglass tubes (height = 12 cm, internal diameter = 3.6 cm) filled with 8 cm of sieved sediment (<100 µm) and overlain with 4 cm of seawater. All sediment cores were kept in a tank with running seawater (13°C) for 10 d to allow for the physical and chemical stabilization of the sediment matrix. At the beginning of the experiments, 500 specimens of living foraminifera (125–300 µm range size) plus 2 g of luminophores were spread on the sediment surface of each core. After a few minutes, the uppermost 3 cm were mixed using a glass stick (3 mm diameter). Vertical movements were consistently repeated 300 times over the whole sediment surface. Preliminary trials revealed that this method allows for a spatially homogeneous mixing of the first 3 cm of the sediment column without damaging foraminifera. To avoid resuspension of the finest particles, the overlying water was previously removed with a syringe and slowly reintroduced afterwards. After 1 h, 3 control cores were sliced in 2 mm layers between 0 and 3 cm depth, in 5 mm layers between 3 and 5 cm depth, and in 1 cm layers between 5 and 8 cm depth to assess initial vertical profiles. The 5 other triplicates were similarly sliced after 3, 9, 16 and 32 d to assess temporal changes in both foraminifera and luminophore vertical profiles.

Assessment of porewater oxygen concentration vertical profiles

Oxygen concentrations were measured with a Clark-type microelectrode (tip 50 µm) (Unisense), which was pushed down into the sediment at 100 µm vertical increments. The electrode calibration was achieved between the oxygen concentration of the overlying water measured by Winkler titration and a zero oxygen signal in the anoxic part of the sediment column. In the first set of experiments, 4 profiles were performed in all treatments at the end of the incubation period. In the second set of experiments, 2 profiles per experimental sediment core were performed about 1 h after the mixing event and at the end of the incubation period. The OPD was determined as the depth for which the microelectrode zero signal was reached.

Expt 3: Locomotion activity monitoring

Prior to each experiment, 100 living individuals in a size range of 125 to 300 µm were carefully collected with a pipette (tip 20 µl) under a stereomicroscope and gently deposited on the bottom of 5 (i.e. 20 specimens in each) Petri dishes (diameter 9 cm) previously covered by a thin layer of fine sediment (grain size <63 µm). They were allowed to acclimatize for 15 min before the locomotion activity (i.e. successive displacements of the test) was monitored under infrared lighting using an automated image analysis system adapted from Maire et al. (2007). Given the range of locomotion speed (0.5–7.7 mm h^{-1}) usually reported in benthic foraminifera (Kitazato 1988, Wetmore 1988), measurements were carried out for 12 h. A video sensor (µEye UI-1490SE, 3840 × 2748 pixels, IDS Imaging) connected to a microcomputer was fixed right above the Petri dish. In all experiments, the frequency of image acquisition was 10 min. Time-lapse sequences were analyzed with custom-made video tracking procedures, allowing for the recording of every individual position (x–y coordinates) in the successive images. An image-to-image analysis then allowed for the computation of trajectories of each foraminifer (Video S1 in the Supplement at www.int-res.com/articles/suppl/m561p083_supp/).

The proportion of active (i.e. moving) foraminifera was estimated in each Petri dish. For each single active specimen, the following parameters were calculated: (1) the percentage of time active (i.e. allocated to locomotion) (PTA), (2) the distances travelled between 2 successive displacements (D_i, mm), (3) the total distance travelled during the 12 h of the experiments (D_t, mm), and (4) the mean locomotion speed (V_l, mm h^{-1}) estimated as the average of movement velocities between successive displacements ($V_l = \frac{1}{n}\sum_{i=1}^{n}(6D_i)$).

The locomotion activity of *A. tepida* was first investigated in oxic conditions (Treatment 1). The 5 Petri dishes were then filled with well-oxygenated

filtered seawater (13°C, salinity 28, oxygen concentration >270 µM). A second set of experiments was conducted in a hermetic microcosm with a nitrogen-saturated atmosphere to investigate the locomotion activity of *A. tepida* under anoxic conditions (Treatment 2). Five Petri dishes were then filled with filtered seawater previously flushed with nitrogen. The oxygen concentration was continuously measured with a mini-optode (OXROB10, Pyroscience) connected to a FireSting oxygen meter (Pyroscience) in another Petri dish filled with the same volumes of sediment and nitrogen-flushed seawater. The oxygen concentration remained below detection limits (oxygen <0.1 µM) during the whole duration of the experiments. After 12 h, image recordings were stopped. Foraminifera were then kept under anoxic conditions for 60 h, and their locomotion activity was monitored for a further 12 h (Treatment 3). Afterwards, the anoxic water was replaced by well-oxygenated seawater, and after 15 min of acclimation, their locomotion activity was monitored for 12 h (Treatment 4). Additionally, we examined the behaviour of specimens found in anoxic layers at the end (i.e. 32 d) of Expt 2. Individuals collected from different depth intervals below the oxic zone of each 3 replicated cores were then pooled. Sixty of them were randomly selected to run 12 h experiments in oxic conditions (Treatment 5).

Statistical analysis

Results are generally reported as the mean ± SD of n replicate measurements. Differences in (1) OPD between treatments of Expt 1 and (2) locomotion activity parameters (PTA, D_t, V_l) between Treatments 1, 3 and 5 of Expt 3 were analyzed using Kruskal-Wallis non-parametric ANOVAs. Whenever appropriate, least significant difference (LSD) tests were used to assess differences among treatments. Differences in (1) biodiffusion and biotransport coefficients calculated based on luminophores (D_b^L, ω^L) and foraminifera (D_b^F, ω^F) profiles, (2) OPD measured in each sediment core at the beginning and at the end of Expt 2 and (3) locomotion activity parameters (PTA, D_t, V_l) between Treatments 1 and 2 and Treatments 2, 3 and 4 of Expt 3 were tested using paired-sample Wilcoxon signed rank (SR) tests. Differences in penetration depth between tracers (i.e. luminophores and foraminifera) and experiment durations were assessed using a 2-way ANOVA.

RESULTS

Expt 1: Effects of bioturbating macrobenthic species on the vertical distribution of *Ammonia tepida*

In the absence of macrofauna, luminophores in control cores remained at the sediment surface throughout the 16 d experiment. Regarding foraminifera, 99 ± 0.5% were recovered after sediment core slicing, and 95 ± 2% of them were found in the uppermost 0.5 cm (Fig. 1A) where oxygen is present (Fig. 2). Luminophore and foraminifera depth profiles obtained after 16 d in enclosures colonized by the 3 macrobenthic species are presented in Fig. 1B–D. The presence of bioturbators induced intense sediment reworking as revealed by the quantity of luminophores buried at depth. On average, 82 ± 8, 84 ± 19 and 93 ± 2% of luminophores initially deposited at the sediment surface were found below 0.5 cm in the presence of *Echinocardium cordatum*, *Upogebia pusilla* and *Hediste diversicolor*, respectively.

Vertical luminophore profiles showed marked inter-specific contrasts linked to faunal identity. In enclosures inhabited by the heart urchin *E. cordatum,* the sediment surface was completely reworked after 16 d. Nevertheless, the presence of a subsurface peak of luminophores in 2 replicates indicated that small surficial patches of sediment could be buried without being disaggregated. Biodiffusion (D_b^L) and biotransport (ω^L) coefficients averaged 21.36 ± 5.70 $cm^2\ yr^{-1}$ and 3.12 ± 0.47 yr^{-1}, respectively. All luminophores initially added at the sediment–water interface were found between 0 and 5 cm, while their absence below 5 cm indicates that *E. cordatum* did not actively transport inert particles to this depth.

In the presence of the thalassinid crustacean *U. pusilla*, luminophore depth profiles were characterized by a large subsurface peak between 1 and 3 cm, corresponding to 66 ± 26% of fluorescent particles. Vertical luminophore profiles also consistently exhibited smaller subsurface peaks, illustrating the non-local transport of particles at depth. The maximum burying depth of luminophores was 12 cm after 16 d. Biodiffusion (D_b^L) and biotransport (ω^L) coefficients averaged 10.09 ± 5.20 $cm^2\ yr^{-1}$ and 26.08 ± 15.69 yr^{-1}, respectively.

In cores inhabited by the polychaete *H. diversicolor*, luminophore depth profiles typically showed a large subsurface peak between 0.5 and 1 cm, corresponding to 74 ± 18% of fluorescent particles. Although the majority of luminophores was found just below the sediment–water interface, this species is

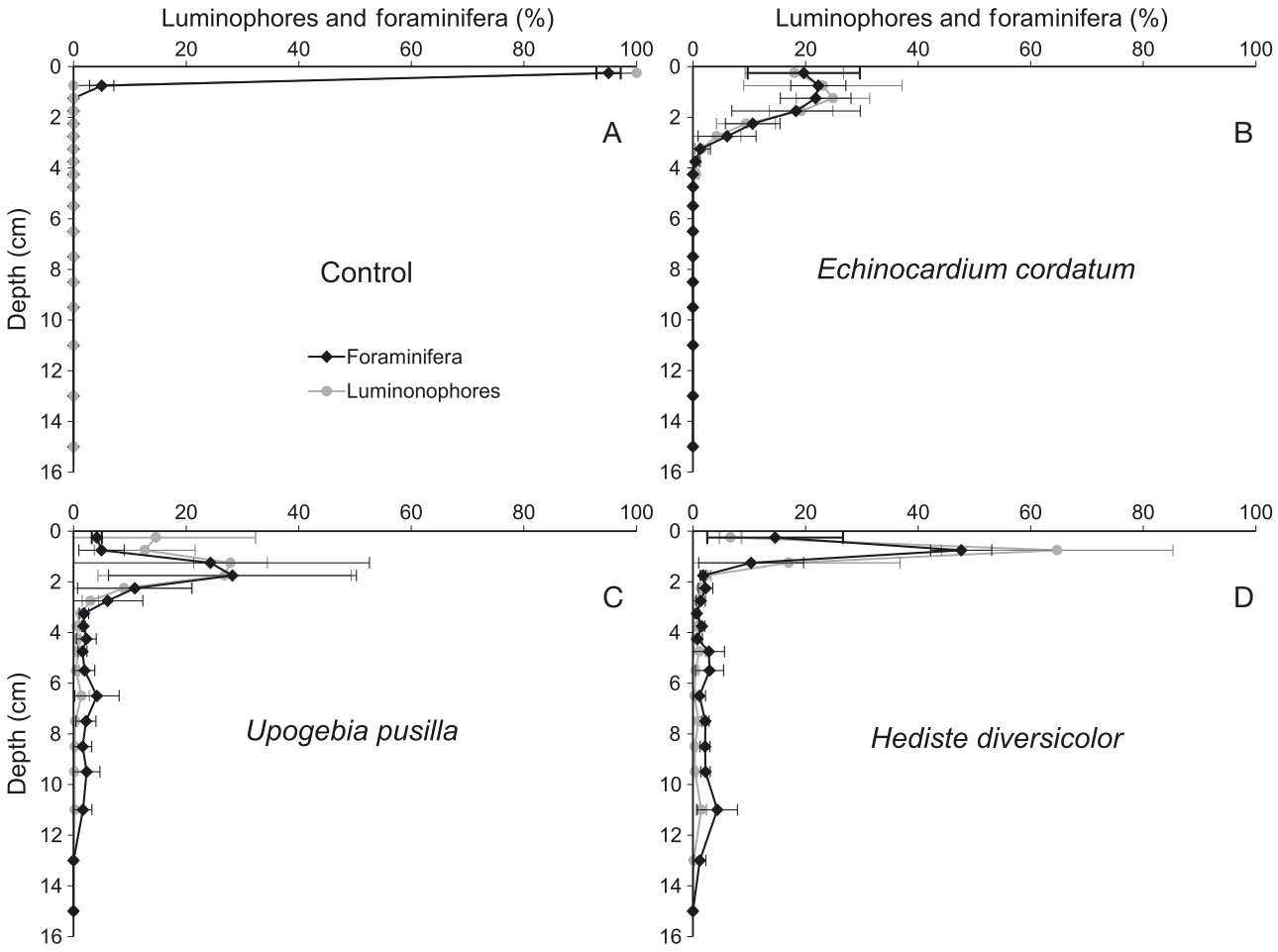

Fig. 1. Vertical profiles (mean ± SD; n = 3) of luminophores (grey circle) and foraminifera (black diamond) initially deposited at the sediment surface of experimental enclosures (A) without macrofauna and (B,C,D) colonized by the 3 studied macrobenthic species, recorded after 16 d (results of Expt 1)

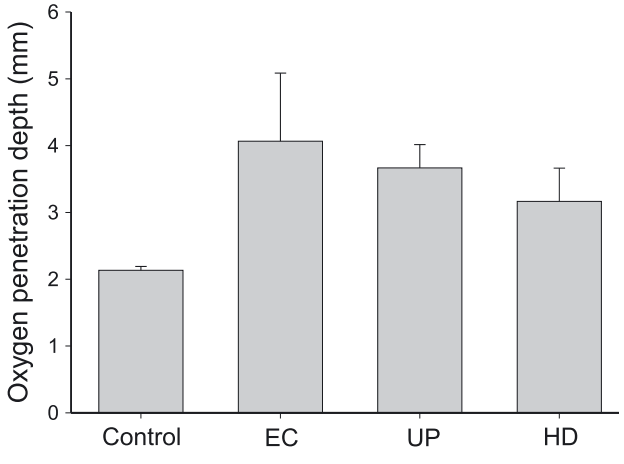

Fig. 2. Mean oxygen penetration depth (OPD) (n = 12) measured after 16 d in experimental enclosures without macrofauna (control treatment) and colonized by *Echinocardium cordatum* (EC), *Upogebia pusilla* (UP) and *Hediste diversicolor* (HD). Error bars = +SD. OPD did not vary significantly between species treatments (Kruskall-Wallis test, $p > 0.05$)

also able to translocate particles deeper, as illustrated by the presence of smaller luminophore peaks up to 14 cm. Biodiffusion (D_b^L) and biotransport (ω^L) coefficients averaged 1.23 ± 0.47 cm^2 yr^{-1} and 20.36 ± 0.43 yr^{-1}, respectively.

After 16 d of incubation, 70 ± 7, 78 ± 9 and 71 ± 5% of foraminifera were recovered in sediments inhabited by *E. cordatum*, *U. pusilla* and *H. diversicolor*, respectively. Unrecovered specimens may have been ingested by macrobenthic organisms or lost during core slicing. In addition, 80 ± 10, 96 ± 1 and 90 ± 4% of recovered foraminifera were found in anoxic sediment layers (<0.5 cm, Fig. 2) down to 5, 12 and 14 cm in the presence of the 3 macrobenthic species, respectively. The OPD did not vary significantly between species treatments (Kruskall-Wallis test, $p > 0.05$). However, in the presence of burrow-dwelling organisms such as *U. pusilla* and *H. diversicolor*, foraminifera transported at depth along the burrows

may remain in more or less intermittent oxic conditions depending on their distance from the burrow walls as well as specific ventilation activities and rhythms. Overall, patterns of foraminifera redistributions observed at the end of the experiment were very similar to those of luminophores for all treatments and replicates (Fig. 1B–D). Biodiffusion (D_b^F) and biotransport (ω^F) coefficients calculated from foraminifera vertical profiles averaged 22.54 ± 5.43 cm^2 yr^{-1} and 2.89 ± 0.69 yr^{-1}, 8.94 ± 4.65 cm^2 yr^{-1} and 37.05 ± 3.58 yr^{-1}, and 1.05 ± 0.07 cm^2 yr^{-1} and 17.50 ± 1.74 yr^{-1} in the presence of *E. cordatum*, *U. pusilla* and *H. diversicolor*, respectively. They were not significantly different than those calculated from luminophore profiles (Wilcoxon SR test, $p > 0.05$ in both cases).

Expt 2: Response of *Ammonia tepida* to a passive downward transport

After sediment core slicing, 96 ± 3% of *A. tepida* specimens were recovered. Cumulative depth profiles of both luminophores and foraminifera obtained in control cores and after 3, 9, 16 and 32 d are shown in Fig. 3A–E, respectively. The near linear appearance of the first part of the cumulative luminophore profiles (i.e. until 99% of the inventory of tracers were recovered), corresponding to a mean depth of 3 cm, attested to a consistent and homogeneous sediment reworking between replicates. The position of foraminifera in depth profiles appeared most of the time slightly below the position of luminophores, whereas their penetration depth was significantly lower (2-way ANOVA, $p < 0.05$). This slight shift between vertical profiles as well as the difference in penetration depth may be due to the difference in size of foraminifera and luminophores. Nevertheless, for all experiment durations, patterns of both luminophore and foraminifera redistributions remained very similar to each other and to those observed in control cores. Particularly, both luminophore and foraminifera penetration depths did not vary significantly between experiment durations (2-way ANOVA, $p > 0.05$). OPD values measured during the second set of experiments are presented in Fig. 4. They significantly differed between the beginning and the end of the experiments after 16 and 32 d (Wilcoxon SR test, $p < 0.05$ in both cases). This may result from a decrease in sedimentary organic matter concentration, which has been partially consumed through microbial respiration. However, all the profiles consistently showed that foraminifera buried below 4 mm remained in anoxic conditions during the whole duration of all experiments.

Expt 3: Locomotion activity monitoring

Analysis of image sequences revealed a large inter-individual variability in all treatments and for all locomotion activity parameters (i.e. PTA, D_t and V_l) as well as marked temporal fluctuations of the locomotion speed (V_l) at an individual scale (Fig. 5). In oxic conditions (Treatment 1), 100% of foraminifera were active (Fig. 6), crawling at the sediment surface without any apparent preferential direction (Video S1 in the Supplement). While moving, each individual continuously accumulated sediment particles with pseudopods around its test, thus progressively forming a sedimentary envelope (i.e. cyst) (Fig. 7), which was periodically abandoned as a new one was built. On average, individuals of *A. tepida* were active (PTA) 68 ± 18% of the experiment duration, travelling (D_t) 17.51 ± 5.33 mm in 12 h with a mean motion speed (V_l) of 2.19 ± 0.66 mm h^{-1} (Fig. 8A–C).

During the first 12 h following oxygen depletion (Treatment 2), 64% of foraminifera remained active but reduced their locomotion activity, as illustrated by the significant decreases of PTA, D_t and V_l (Figs. 6 & 8A–C) compared to Treatment 1 (Wilcoxon Mann-Whitney test, $p < 0.05$ in all cases) (Table 1). Moreover, visual observations revealed that their behaviour was different than in Treatment 1, as the cyst built around the test became rapidly bigger than in oxic conditions and was not abandoned (Video S2 in the Supplement at www.int-res.com/articles/suppl/m561p083_supp/). After 3 d in anoxia (Treatment 3), all foraminifera were encysted, and only 27% of them were still moving. D_t was significantly lower than in Treatment 1 (LSD test, $p < 0.05$) but not significantly different than in Treatment 2 (Wilcoxon SR test, $p = 0.48$). Conversely, V_l was significantly lower than in Treatments 1 (LSD test, $p < 0.05$) and 2 (Wilcoxon SR test, $p < 0.05$), suggesting that active specimens decreased their locomotion activity by reducing motion speed. As soon as the anoxic overlying water was replaced by well-oxygenated seawater (Treatment 4), 92% of *A. tepida* specimens were active. PTA, D_t and V_l were significantly higher than in Treatment 3 (Wilcoxon SR test, $p < 0.05$ in all cases). Regarding specimens that remained buried in anoxic layers for 32 d, 100% of them were still alive and became rapidly active once placed in oxic conditions (Treatment 5). Although all activity parameters were significantly lower than in Treatment 1 (LSD test, $p < 0.05$ in all cases), D_t and V_l were significantly higher than in Treatment 3 (LSD test, $p < 0.05$ in all cases).

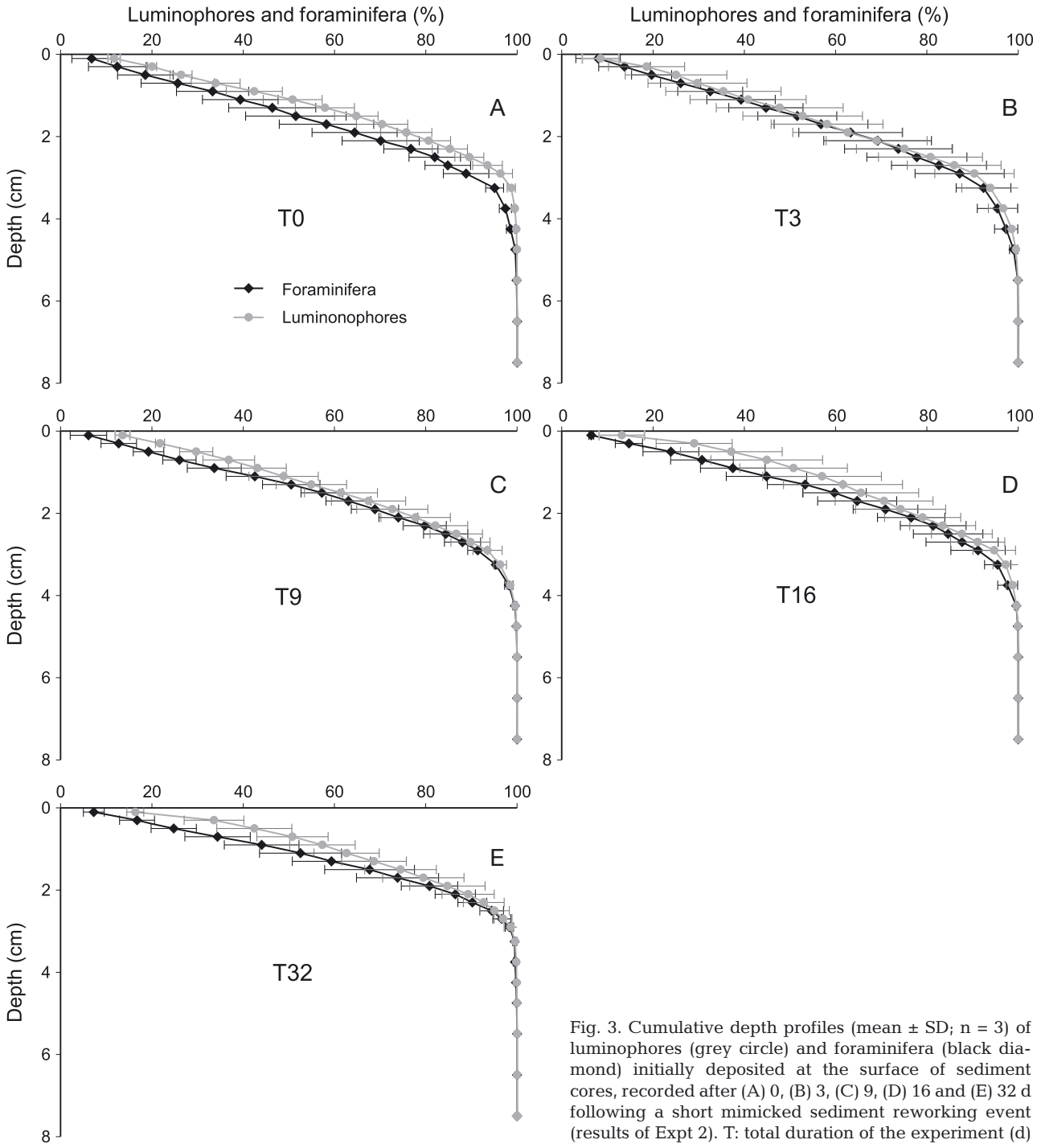

Fig. 3. Cumulative depth profiles (mean ± SD; n = 3) of luminophores (grey circle) and foraminifera (black diamond) initially deposited at the surface of sediment cores, recorded after (A) 0, (B) 3, (C) 9, (D) 16 and (E) 32 d following a short mimicked sediment reworking event (results of Expt 2). T: total duration of the experiment (d)

DISCUSSION

Effects of bioturbating macrobenthic species on the vertical distribution of *Ammonia tepida*

The presence of *A. tepida* close to the sediment surface in the absence of bioturbation is consistent with the vertical stratifications of mobile foraminiferal species (including *A. tepida*) usually reported in sedimentary environments (Moodley 1990, Alve & Murray 2001, Thibault de Chanvalon et al. 2015). They are also in good agreement with previous experimental studies proving that many common benthic species preferentially inhabit the sediment surface (Moodley et al. 1998, Langezaal et al. 2003). This general trend is usually explained by both food con-

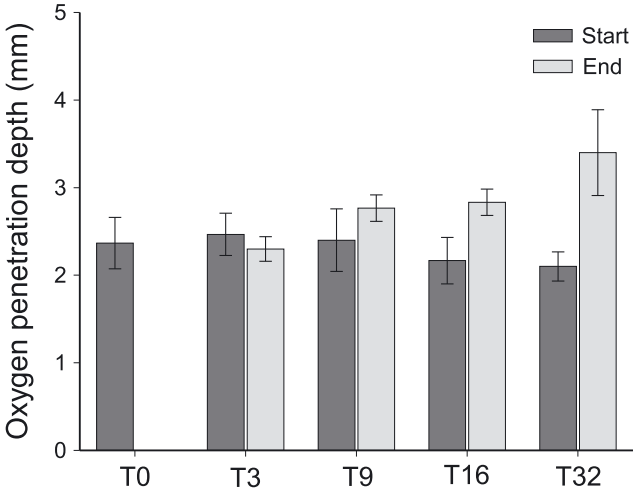

Fig. 4. Mean oxygen penetration depth (OPD) (n = 6) measured 1 h following a short mimicked sediment reworking event (dark grey) and after 3, 9, 16 and 32 d (light grey) in the same experimental enclosures of the corresponding treatment. Error bars = ±SD. Differences in OPD between the beginning and the end of the experiments were only significant after 16 and 32 d (Wilcoxon SR test, $p < 0.05$ in both cases). T: treatment

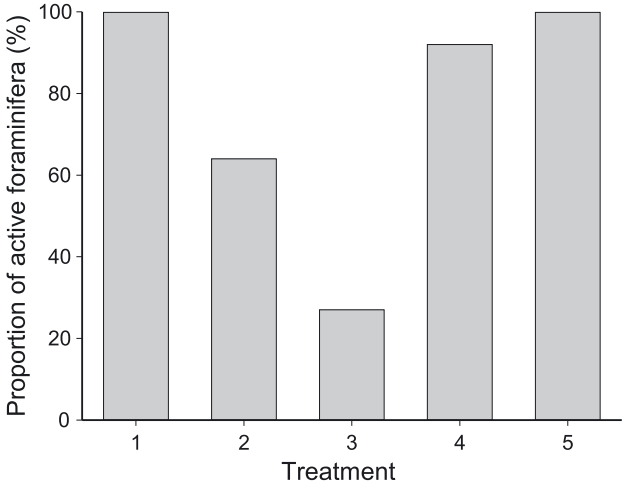

Fig. 6. Proportion of foraminifera which were active (i.e. moving) during the 12 h of the experiments carried out in oxic conditions (Treatment 1, n = 100), in anoxic conditions immediately following the oxygen depletion (Treatment 2, n = 100), after 3 d in anoxic conditions (Treatment 3, n = 100), in oxic conditions after 3 d in anoxia (Treatment 4, n = 100) and in oxic conditions after 32 d buried in anoxic sediment layers (Treatment 5, n = 60)

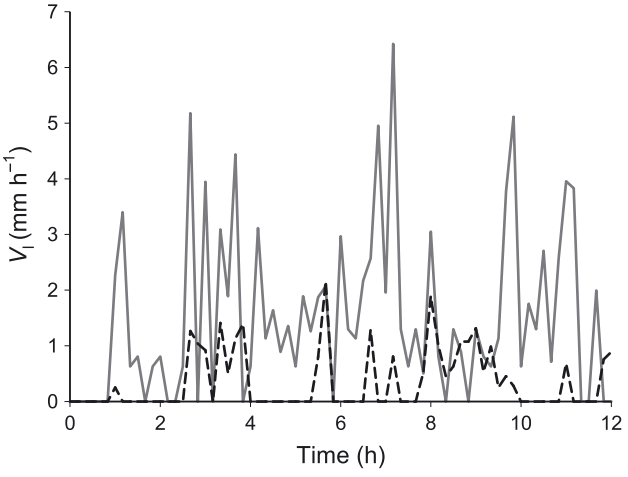

Fig. 5. Examples of temporal changes in locomotion speed (V_l) recorded in single individuals during the 12 h of the experiments under oxic conditions (solid grey line) (Treatment 1) and after 3 d under anoxic conditions (dashed black line) (Treatment 3) (see 'Materials and methods — Expt 3'). EC: *Echinocardium cordatum*; UP: *Upogebia pusilla*; HD: *Hediste diversicolor*

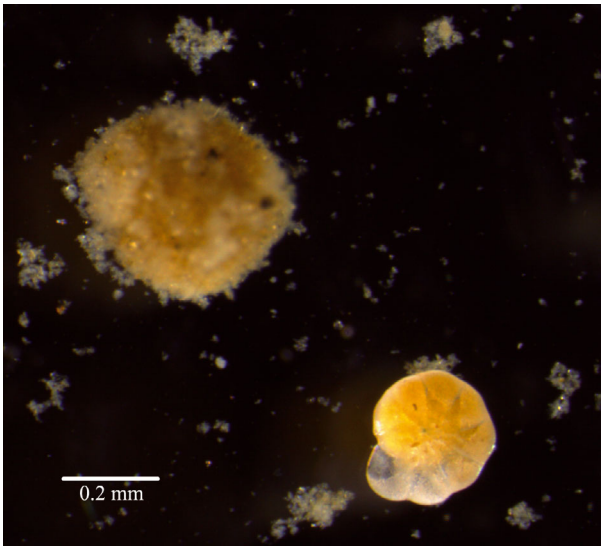

Fig. 7. Encysted (left) and free specimen (right) of *Ammonia tepida* observed at the end of locomotion activity monitoring (Expt 3) carried out in anoxic and oxic conditions, respectively

centration and oxygen availability (e.g. Jorissen et al. 1995). Indeed, in coastal weakly bioturbated cohesive sediments, labile food sources are particularly abundant at the sediment surface where (1) sedimented fresh particulate organic matter accumulates (Wollast 1998) and (2) microphytobenthos, constrained to the uppermost millimeters by critical light requirements, often develop with bacteria in dense biofilms (Cartaxana et al. 2011). Typically, OPD in such environments does not exceed a few millimeters (Glud 2008), as observed in both sets of experiments and for all treatments of the present study (Figs. 2 & 4). According to the TROX model (Jorissen et al. 1995), this shallow oxic–anoxic boundary represents

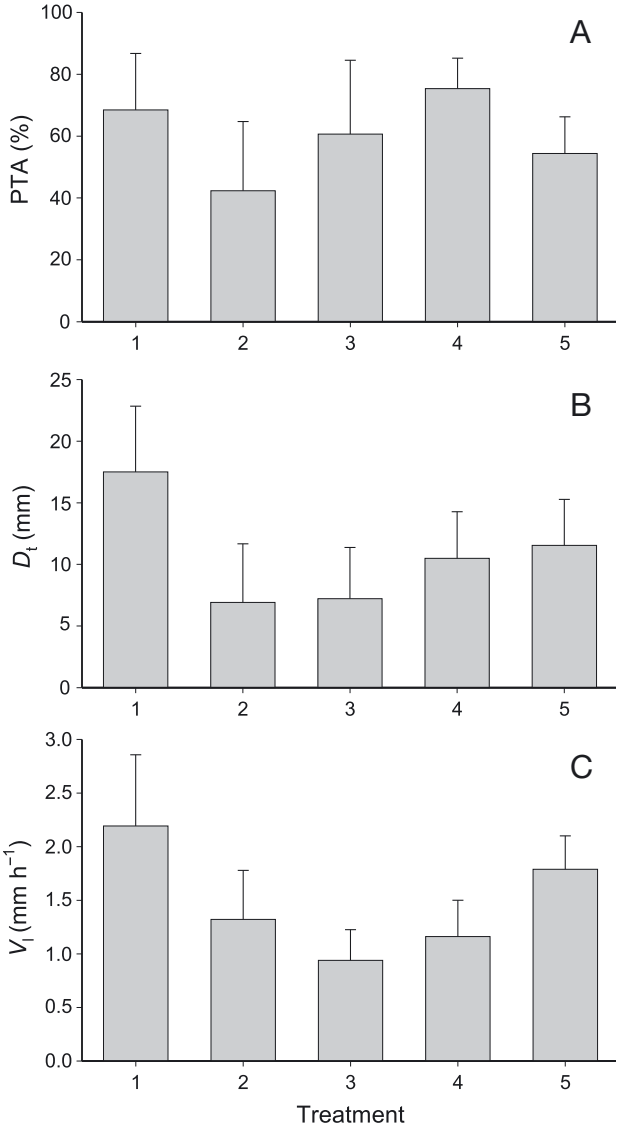

Fig. 8. Locomotion activity parameters (A) PTA, (B) D_t and (C) V_l of *Ammonia tepida* recorded during 12 h in oxic conditions (Treatment 1), in anoxic conditions immediately following the oxygen depletion (Treatment 2), after 3 d in anoxic conditions (Treatment 3), in oxic conditions after 3 d in anoxia (Treatment 4) and after 32 d buried in anoxic sediment layers (Treatment 5). PTA corresponds to the percentage of time individuals were active during the 12 h of the experiments, D_t is the total distance travelled and V_l is the mean locomotion speed. Error bars = +SD

a chemical barrier for the downward migration of many benthic foraminiferal species, although it is now well acknowledged that several of them including *A. tepida* can survive for extended periods of time without oxygen (Bernhard & Alve 1996, Langlet et al. 2014, Nardelli et al. 2014).

In contrast, in experimental enclosures colonized by macrofaunal species, foraminifera experienced intense bioturbation rates, as illustrated by the high values of both biodiffusion (D_b^L) and biotransport (ω^L) coefficients. These values are in the same range as those reported in previous studies based on similar *ex situ* incubations (François et al. 2002, Duport et al. 2006, Gilbert et al. 2007, Nogaro et al. 2008). Regarding sediment reworking, macrobenthic organisms can be separated into 4 major categories (Kristensen et al. 2012). The spatangoid urchin *Echinocardium cordatum* is a typical example of surficial biodiffusors (inducing a biodiffusive-like reworking of the top few centimeters of the sediment column), while *Upogebia pusilla* and *Hediste diversicolor* are respectively considered regenerators and gallery biodiffusors, both inducing (1) the progressive burying of the sediment surface through continuous upward transport of deep sediment and (2) the downward transport of surficial particles within burrows and galleries.

The comparison of vertical profiles of *A. tepida* between macrofaunal treatments evidences that their distribution within the sediment column is tightly governed by the functional traits of the dominant infauna and accordingly by the functional diversity of macrobenthic communities. These results are in agreement with the findings of previous studies, which investigated the stratification patterns of living benthic foraminiferal assemblages in bioturbated sedimentary environments (Goldstein et al. 1995, Saffert & Thomas 1998, Berkeley et al. 2007). It has been shown that the densities of some foraminiferal species can be particularly high in sediments surrounding tubes and burrows and very low (almost null) in deep sediment otherwise (Aller & Aller 1986, Koller et al. 2006). Bouchet et al. (2009) also revealed using 3D imaging that in intertidal mudflats predominantly inhabited by sediment-dwelling organisms, the stratification of living foraminifera correlated well with the vertical arrangement of irrigated biogenic structures. More recently, Thibault de Chanvalon et al. (2015) reported particular vertical profiles of *A. tepida* in an intertidal mudflat. Indeed, their distribution along the sediment column (0–5 cm depth) was consistently characterized by a peak of density at the sediment surface, which is the favorable microhabitat (fresh food and high oxygen concentration), followed by a strong decrease of density between 1 and 3 cm and an increase of density between 3 and 5 cm. To explain the 1 to 3 cm density minimum, the authors suggested an active migration of buried specimens towards the sediment surface before they are completely immobilized by a lack of oxygen and a strongly lowered metabolism. Comparing foramini-

Table 1. Proportion of active *Ammonia tepida* and corresponding locomotion activity parameters (mean ± SD) measured in 5 experimental treatments with different oxic and anoxic conditions. PTA corresponds to the percentage of time individuals were active, D_t is the total distance travelled and V_l is the mean locomotion speed

Treatment	Description	Proportion of active foraminifera (%)	PTA (%)	D_t (mm)	V_l (mm h^{-1})
1	Oxic conditions	100	68 ± 18	17.51 ± 5.33	2.19 ± 0.66
2	Anoxic conditions immediately following oxygen depletion	64	42 ± 22	6.91 ± 4.76	1.32 ± 0.45
3	Anoxic conditions after 3 d in anoxia	27	60 ± 24	7.21 ± 4.16	0.93 ± 0.28
4	Oxic conditions after 3 d in anoxia	92	75 ± 9	10.49 ± 3.78	1.16 ± 0.34
5	Oxic conditions after 32 d in anoxia	100	54 ± 11	11.54 ± 3.73	1.79 ± 0.31

feral profiles reported by Thibault de Chanvalon et al. (2015) and results of the present study (Expt 1 with *H. diversicolor*), similar trends can be observed: a large peak of density close to the sediment surface, very low densities below the OPD and smaller subsurface peaks deeper in the sediment. Although the densities observed at depth (below 3 cm) in the present study were lower than those reported by Thibault de Chanvalon et al. (2015), probably linked to the relatively short duration of our experimental incubations, it seems that the vertical distribution of *A. tepida* recorded *in situ* by these authors may be well explained by the specific mode of bioturbation of *H. diversicolor*, the dominant macrobenthic species at the study site.

Despite such recent investigations, the exact mechanisms by which benthic macrofauna controls the vertical distribution patterns of foraminiferal assemblages are still not completely understood. Hence, 2 different, although non-exclusive, interpretations have been drawn from *in situ* observations and microcosm experiments. On the one hand, the occurrence of significant abundances of foraminifera in deep anoxic sediment layers has been considered by some authors as primarily resulting from their advection through bioturbation processes (e.g. Lipps 1983, Langer et al. 1989, Goldstein et al. 1995, Saffert & Thomas 1998, Thibault de Chanvalon et al. 2015). On the other hand, geochemical properties of the irrigated sediment surrounding biogenic structures led some other authors to suggest that bioturbation mainly influences the vertical distribution of foraminifera indirectly, through the creation at depth of oxic and organically enriched microhabitats where competition and predation intensities are reduced (e.g. Corliss 1985, Moodley 1990, Linke & Lutze 1993, Alve & Bernhard 1995, Diz & Frances 2008, Bouchet et al. 2009). However, none of these previous studies consistently compared the vertical distributions of abundances of foraminifera with those of inert particle tracers. Therefore, it appears difficult to draw any sound ecological conclusion on the relative importance of these 2 key mechanisms (i.e. biologically mediated downward transport vs. independent migratory behaviour) on the presence of foraminifera at depth. The results of the present study clearly support the former interpretation (i.e. biogenic advection). Indeed, the high degree of similarity between luminophore and *A. tepida* vertical profiles suggests that specimens initially deposited at the sediment surface did not selectively decide on their life position through self-locomotion but were instead mixed within the sediment matrix as inert particles. The massive transport of surficial specimens far below the OPD also highlights that foraminifera were not able to rapidly develop any special mechanisms (e.g. attachment to sediment grains with pseudopodia or encystment) to efficiently resist downward transport.

Response of *Ammonia tepida* to a fast passive downward transport and to anoxic conditions

Quantification of locomotion activity indicates that all tested individuals of *A. tepida* were highly mobile under oxic conditions, moving at a mean speed of 2.19 mm h^{-1}. This value is in the range of motion speeds previously reported for species inhabiting shallow coastal embayments (Kitazato 1988, Wetmore 1988). It is, however, worth noting that these authors estimated motion velocities based on the total distance travelled by foraminifera, which may lead to significant underestimations (Seuront & Bouchet 2015). Recently, Seuront & Bouchet (2015) estimated that *A. tepida* would be able to move nearly 2 times faster. However, comparisons with the results of the present study would not be meaningful since speed measurements were then performed on a glass surface and with larger specimens (300–400 µm range size). As underlined by Kitazato (1988), loco-

motion rates in organisms using amoeboid (i.e. crawling-like) movement are likely to be higher on a glass surface than on the sediment since the former substrate offers less resistance to the traction of the test by extended pseudopodia. However, regardless of its maximum locomotion velocity, and also assuming that it is certainly easier, even for an unicellular organism, to move at the surface of the sediment than through pore spaces, both the aforementioned and the present studies support the idea that *A. tepida* owns the locomotor capacities to cover long distances (up to several millimeters) through the sedimentary matrix in a few hours.

To explicitly infer the response of *A. tepida* to a passive downward transport, the vertical distribution of individuals buried at depth by a short reworking event was followed over time. Here again, luminophore and foraminifera vertical profiles remained very similar to each other for all experimental durations and to those observed in control cores. Our results clearly indicate that *A. tepida* did not initiate any discernible (>2 mm) upward migrations toward the sediment surface and thus suggest that reduction of motion activity is obviously the first strategic response to a severe oxygen depletion. This was confirmed by the reduction of the locomotion speed and the formation of a protection cyst observed under anoxic conditions during Expt 3. Such an encystment behaviour has already been reported in several foraminiferal species (Heinz et al. 2005) and particularly in *Elphidium incertum* when exposed to anoxia (Linke & Lutze 1993).

The results of the second set of experiments are somehow in opposition with those of some previous studies, which experimentally demonstrated that numerous foraminiferal species (but not including *A. tepida*) could actively move through the anoxic sediment (Alve & Bernhard 1995, Gross 2000, Duijnstee et al. 2003, Ernst & van der Zwaan 2004, Ernst et al. 2005). Upward migrations undertaken to avoid long-term burial into anoxic layers have been observed in deep-sea and shallow-water assemblages (Moodley et al. 1998, Gross 2000, Langezaal et al. 2003, Geslin et al. 2004). A strong decline of porewater oxygen content seems to be the main factor inducing those migrations (Moodley et al. 1998, Geslin et al. 2004). However, it also clearly appeared from these previous studies that all foraminifera do not respond similarly to sediment disturbances. Therefore, a number of species dealt with a prolonged oxygen depletion by remaining inactive (i.e. encystment and dormant forms) for extended periods of time (Linke & Lutze 1993, Bernhard & Alve 1996, Moodley et al. 1998, Gross 2000). Thibault de Chanvalon et al. (2015) have suggested that a reduction of the metabolic activity is the most probable mechanism explaining the high abundances of living *A. tepida* occurring in the deep sediment layer (3–5 cm). These 2 different strategies (i.e. active upward migration vs. inactivity through encystment or dormancy) in response to a sudden emergence of unfavorable conditions certainly result from specific tolerance levels to hypoxia or anoxia (Geslin et al. 2014, Nardelli et al. 2014) but would also illustrate specific adaptive behaviours to contrasted sedimentary environments. Indeed, one could easily imagine that foraminifera living in weakly bioturbated sediments can rapidly reach the sediment surface after being buried. Conversely, as any long-term displacements would be steadily opposed to intense sediment reworking, encystment and lowering cell metabolism by entering transient dormant states may then represent the best way to deal with very frequent vertical retranslocations and subsequent periodic exposures to anoxic conditions.

In coastal mudflats, *A. tepida* consistently exhibits maximum densities at the sediment–water interface but is also commonly found in subsurface layers. Such a vertical distribution pattern has usually been explained by the opportunistic behaviour of this species and its ability to colonize deep organic-rich areas (Moodley & Hess 1992, Goldstein et al. 1995, Bouchet et al. 2009). Conversely, our results suggest that the presence of *A. tepida* at depth in bioturbated environments could largely result from its incapacity to (1) efficiently resist downward transport by macrofauna and (2) rapidly migrate towards the sediment surface upon burial. Therefore, specimens of *A. tepida* found in deep anoxic sediment layers would be considered as dormant forms waiting for a return of more favorable environmental conditions. The fate of dormant forms in the field would thus tightly depend on sediment reworking and bioirrigation processes allowing for their transport back to the sediment–water interface and an intermittent supply of oxygen at depth, respectively.

CONCLUSIONS

Our results showed that *Ammonia tepida*, probably like many other foraminiferal species inhabiting soft-bottom cohesive substrates, is not able to resist biologically induced vertical mixing and therefore to steadily remain in its optimal vertical position within the sediment column. Instead, its depth position may strongly vary over short temporal scales, directly

dependent on temporal changes in sediment reworking modes and rates. The deep influence of bioturbation processes on the vertical distribution of living benthic foraminifera may explain that depth stratification patterns may be totally different from one area to another (see review by Alve & Murray 2001) as they are profoundly linked to functional diversity of macrobenthic communities. Inactivity, suggesting a reduction of the metabolic activity, seems to be the first response of such foraminiferal species to their transport into deep sediment layers, allowing them to survive frequent exposure to unfavorable anoxic conditions. Recently, it has been proved that many benthic foraminifera are able to store intracellular nitrate and to achieve a complete denitrification (Risgaard-Petersen et al. 2006, Piña-Ochoa et al. 2010a). This alternative metabolism pathway may partly explain how several species can survive for unexpected periods of time in complete anoxia (Piña-Ochoa et al. 2010b, Koho et al. 2011, Langlet et al. 2014). All denitrifying foraminifera nevertheless preferentially respire on oxygen, only switching to anaerobic metabolism in cases of prolonged exposition to anoxia (Piña-Ochoa et al. 2010a). Therefore, by passively transporting a significant part of the surficial standing crop of foraminifera into deep anoxic sediment layers, macrofauna could indirectly, and in an unexpected way, influence sedimentary carbon and nitrogen cycling and the overall functioning of soft-bottom marine benthic ecosystems.

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