Linking feeding activity and sediment reworking in the deposit-feeding bivalve *Abra ovata* with image analysis, laser telemetry, and luminophore tracers

Olivier Maire[1,*], Jean-Claude Duchêne[1], Lionel Bigot[2], Antoine Grémare[1]

[1]**Université Pierre et Marie Curie-Paris 6 and CNRS, UMR7621, 66650 Banyuls-sur-Mer, France**
[2]**Laboratoire d'Ecologie Marine, ECOMAR, Université de La Réunion, Avenue René Cassin-BP 7151, 97715 Saint Denis Cedex, France**

ABSTRACT: The quantitative relationship between activity (as detected by the comparison of grey levels in successive images using automated software) and sediment reworking in the deposit-feeding bivalve *Abra ovata* was investigated based on simultaneous and continuous measurements using laser telemetry, luminophore tracers, and image analysis. Total activity included both feeding (siphoning) and shell and/or foot activity. Sediment reworking was assessed through the measurements of surface sediment handling and vertical sediment mixing during 2 separate experiments. Surface sediment handling correlated positively with surface feeding activity. Shell and/or foot activity induced oscillatory movements of the superficial sediment layer but did not account for true vertical sediment mixing. Conversely, feeding activity induced intense vertical sediment mixing. Quantitative changes in feeding activity and vertical sediment mixing based on a biodiffusion model were positively correlated. These results underscore the importance of considering both the nature and intensity of infaunal activity when parameterizing models of sediment reworking.

KEY WORDS: *Abra ovata* · Sediment reworking · Activity · Micro-topography · Laser telemetry · Luminophores · Biodiffusion · Image analysis

INTRODUCTION

The water–sediment interface is a key zone for marine biogeochemical cycles, since its functioning largely controls the fate (i.e. resuspension, remineralization, burial) of sedimented organic matter. Sedimentary systems are characterized by a suite of tight and complex associations between physical, chemical, and biological processes operating at different spatial and temporal scales (Waldbusser & Marinelli 2006), and the biological processes of major interest in this context are locomotion, burrowing, feeding, and bioirrigation. Through these ecological processes, the infauna has an impact on oxygen uptake (Andersen & Kristensen 1988, Glud et al. 2003), porewater fluxes (Marinelli 1992, 1994), and sediment reworking (Rhoads 1974, Aller 1982). The resulting effects are clearly dependent on the nature and the intensity of infaunal activity (Boudreau & Marinelli 1994, Gérino et al. 1998, Maire et al. 2006).

Field and laboratory studies have been conducted to link infaunal activity with both porewater transport and sediment reworking (Bianchi 1988, Marinelli 1992, 1994, Lindsay & Woodin 1996). To our knowledge, these studies were all based on indirect (Bianchi 1988), independent (Lindsay & Woodin 1995, 1996), or discontinuous (Marinelli 1992, 1994) activity measurements. It is difficult to assess infaunal activity over the same temporal and spatial scales as biogeochemical processes within the sediment column. For example, the assessment of vertical sediment mixing is an indirect measurement arrived at by fitting a model to the vertical profile of a tracer (Boudreau 1986a,b, Boudreau & Imboden 1987, Meysman et al. 2003). The methodological constraints (e.g. the minimal thickness of an analyzed sediment layer), and the decay kinetics

of commonly used tracers estimate mixing rates for processes occurring over relatively long periods of time (several weeks) and at relatively large spatial scales (the scales of vertical sectioning of cores, typically ≥0.5 cm) (Rice 1986, Sharma et al. 1987, Gérino et al. 1998). Infaunal activity per se is also difficult to quantify. It often affects restricted areas and may change over short time scales (typically a few minutes; Grémare et al. 2004). Moreover, a given organism may have different kinds of activity (Grémare et al. 2004) inducing different sediment mixing modes (François et al. 1997, 2001). The occurrence of multiple infaunal activities, each causing different types of sediment mixing with different intensities, combined with marked temporal changes in the intensity of a given activity (Fuller et al. 1988) further complicates the establishment of a quantitative relationship between infaunal activity and sediment mixing rates.

New experimental techniques in sediment profile imaging have recently been introduced to assess vertical sediment mixing (Gilbert et al. 2003, Solan et al. 2004, Maire et al. 2006). These approaches combine luminophore pulses and high resolution image analysis to estimate vertical sediment mixing over short time scales (i.e. a few minutes, Solan et al. 2004, Maire et al. 2006). Similar image analysis techniques also allow continuous quantification of infaunal activity at a high spatial resolution (Duchêne & Rosenberg 2001, Hollertz & Duchêne 2001).

Using these techniques, the surface feeding activity of the deposit-feeding bivalve *Abra ovata* was recently quantified (Grémare et al. 2004). The results showed that the addition of low concentrations of organic matter significantly enhanced the feeding activity of this bivalve. In sediment column experiments using thin aquaria, and the same techniques with *Abra ovata*, a low organic input also induced a significant increase of vertical sediment mixing (Maire et al. 2006), suggesting a positive relationship between the intensity of feeding activity and vertical sediment mixing. However, these measurements were not made simultaneously, since activity was measured at the sediment surface whereas sediment mixing was measured within the sediment column. *A. ovata* processes large quantities of surface sediment (A. Grémare pers. obs.), the amounts of which can be quantified by comparing successive micro-topographic mappings based on the projection of a laser line onto the sediment surface (Roy et al. 2002, 2005). This approach, using consecutive micro-topographic maps, could allow a quick assessment of surface sediment handling by *A. ovata*, thereby facilitating the assessment of the relationship with the surface feeding activity of *A. ovata*.

The objectives of this study were to assess the quantitative relationship between feeding activity and sediment reworking for *Abra ovata* employing simultaneous and continuous measurements. Sediment reworking (i.e. surface or volume of sediment that has been mixed through bivalve activity) was estimated with separate measurements of both surface sediment handling (sediment volume per time, $mm^3\ h^{-1}$) and vertical sediment mixing (sediment surface per time, $cm^2\ yr^{-1}$). Surface sediment handling was quantified using laser telemetry. Feeding activity and sediment mixing were assessed using recently developed image analyzing techniques (Grémare et al. 2004, Maire et al. 2006).

MATERIALS AND METHODS

Bivalve collection and maintenance. *Abra ovata* is a deposit-feeding bivalve that lives buried a few centimeters below the sediment surface and feeds at the water–sediment interface using its inhalant siphon (Grémare et al. 2004, Maire et al. 2006). It is generally found in sandy mud in northwest Mediterranean lagoons, where up to several thousand individuals per m^2 can be observed (Guelorget & Mayère 1981). *A. ovata* specimens were hand-collected in June 2005 at a water depth of <1 m on the north side of the Lapalme Lagoon (France). The water temperature was 20°C and salinity 30.5 psu. Bivalve specimens were kept in lagoon sediment and well-aerated lagoon seawater at the Observatoire Océanologique de Banyuls-sur-Mer (France). Salinity was progressively increased to 37 psu (i.e. the salinity of running seawater in the laboratory, which is within the range of weekly variations in the lagoon during summertime), within 7 d. Bivalves were then kept in flow-through tanks with circulating surface seawater (20°C, 37 psu) and lagoon sediment for 2 wk before being used for experiments. They were fed every other day with crushed Tetramin® brand fish food and were starved 48 h before the beginning of each experiment. The shell length of each specimen used during the study was 13 mm (corresponding to a mean width of 10 mm and a mean thickness of 4 mm). Two experiments were carried out sequentially. The first experiment determined the relationship between bivalve surface feeding activity and surface sediment handling, and the second assessed the relationship between bivalve feeding activity and vertical sediment mixing.

Surface sediment experiment. Four experimental boxes (L = 17.5 cm, W = 11.5 cm, D = 7.5 cm) were filled with 5 cm of natural lagoon sediment (median grain diameter: 103 µm, organic carbon: 4.55% dry wt, nitrogen: 0.56% dry wt) previously sieved through a 1 mm mesh to remove macrofauna, and then stored in a flow-through tank with surface seawater. After 48 h, these boxes were placed in a larger aquarium with temperature-controlled circulating seawater (20°C, 37 psu) and

a single bivalve was gently deposited at the sediment surface (Fig. 1A). All bivalves used during the study buried within a few minutes.

After a 24 h acclimation period, bivalve activity and surface sediment handling were recorded for 27 h under infrared lights. Surface sediment handling rates were measured over a 64 cm^2 (8 × 8 cm) surface area, since preliminary experiments showed that the surface area of sediment prospected by the inhalant siphon of 13 mm long bivalves never exceeded 60 cm^2 (O. Maire pers. obs.). The micro-topography of the studied sediment area was assessed using a laser telemeter (Sick OD 80-15 N152, frequency = 21.7 measures s^{-1}, with each measure being the average of 64 data points) fixed on 2 Parker 600 mm step motor tables, and placed 9 cm above the sediment surface (Fig. 1A). The horizontal resolution was 200 µm (resulting in a matrix of 16×10^4 measurement points covering the observed sediment surface), and the vertical resolution was 15 µm. Voltages generated by the laser telemeter were converted to distances using a calibration curve established with a series of 20 objects of known sizes standing on a horizontal surface, which resulted in a suitable range of distances between the laser source and the top of each object. An entire scan lasted 67 min. This duration was determined by the characteristics of the laser telemeter (see above) and the size of the surface studied. There

was no time interval between 2 consecutive scans. The bivalve's siphon occasionally interfered with telemetry measurements. These events were easily detected and were discarded and replaced by interpolated values using the 8 neighboring points. Surface sediment handling rates (sediment volume per time) were assessed by summing the absolute values of the differences in micro-topography between 2 consecutive scans divided by the time duration of an entire scan.

Surface feeding activity (i.e. siphon motion) was monitored using an automated image acquisition system composed of a video sensor (VC51, fitted with a 25 mm objective) connected to a microcomputer and driven by the CVAB software (Grémare et al. 2004). The sensor was fixed 30 cm above the sediment at an angle of 45° to avoid interference with the laser telemeter (Fig. 1A). Preliminary trials showed that: (1) the entire studied sediment surface could be in focus using this set up, and (2) perspective distortion resulted in only a slight (<10%) underestimation of activity. The frequency of image acquisition was 15 s, which has proven adequate for assessing surface-feeding activity in *Abra ovata* (Grémare et al. 2004). Images were saved in JPEG format (736 × 568 pixels) and were afterwards assembled into an AVI film. Image processing was performed using this film with the CVAB software. Surface feeding activity was evaluated using a pixel-by-pixel comparison of grey levels between 2 consecutive images. Modified objects were defined as the sets of adjacent pixels for which the difference between the 2 images was higher than the noise of the captor (i.e. 25 units on a 0 to 255 scale). Differences were then attributed to feeding if the grey levels of modified pixels in the first of the 2 images were between 100 and 170 (on a 0 to 255 scale). Surface feeding activity was then expressed as cm^2 of siphon h^{-1}. This procedure accounts for all siphon movements occurring at the water–sediment interface (e.g. even those occurring at the same location multiple times). It was validated by superposing the time series of areas affected by siphon activity and actual video recordings.

The relationships between temporal changes in surface feeding activity and surface sediment handling rates were assessed using simple linear regression models (with surface feeding activity as the independent variable and surface sediment handling rate as the dependent variable).
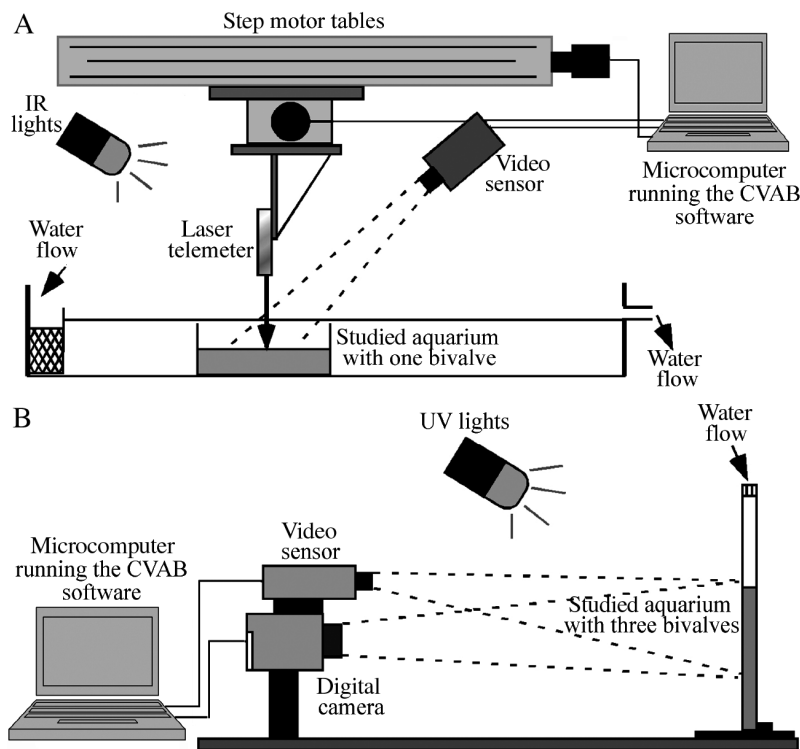

Fig. 1. Experimental setup used during (A) the sediment surface and (B) the sediment column experiments

Sediment column experiment. Five thin aquaria (L = 17 cm, W = 1.2 cm, D = 33 cm) were filled with 15 cm of lagoon sediment collected at the same time as the bivalves and pre-sieved through a 1 mm mesh to remove any macrofauna. These aquaria were kept in a thermoregulated room under circulating seawater (20°C, 37 psu, 1 wk). Vertical sediment mixing was quantified using luminophores (Mahaut & Graf 1987) as described by Maire et al. (2006) (Fig. 1B). Three bivalves were gently deposited on the sediment surface. After 24 h of acclimation, 3 g of luminophores (100 to 160 µm particle size) were evenly sprinkled across the sediment surface of each aquarium. Aquaria were then kept in darkness with circulating seawater (20°C, 37 psu) during the entire experiment (48 h). The side showing the highest number of feeding cones (Maire et al. 2006) after the acclimation period was photographed under UV lights every 10 min using a digital camera (Nikon D100). Settings were adjusted for adequate fluorescent detection, and the photographic field (17 × 12 cm) had a resolution superior to that of the size of luminophores (1 pixel = 75 × 75 µm).

Images were saved in JPEG format (RGB color, 2240 × 1680 pixels) and then assembled into an AVI film and processed using CVAB software (Maire et al. 2006). The water–sediment interface was first visually discriminated and manually traced with the segmented line tool in CVAB. Luminophores were then selected using an appropriate set of RGB threshold levels that differentiated target particles from the background sediment. Pixels above the threshold were added to a binary matrix where luminophore pixels were assigned a value of 1 and sediment pixels a value of 0. Each column of pixels was then translated vertically so that the y-coordinate of the water–sediment interface was 0. This flattened the water–sediment interface. After this operation, the pixel y-position in the image directly corresponded to its depth within the sediment (Solan et al. 2004, Maire et al. 2006). Using exactly the same set up and procedures, Maire et al. (2006) showed that the vertical profiles of luminophore concentrations recorded along the walls were similar to those classically obtained by slicing the sediment in whole aquaria. Wall effects could thus be considered limited.

Sediment mixing was first estimated by measuring luminophore particle displacement between 2 consecutive images. This surface was standardized relative to the total surface of luminophore particles to compensate for temporal changes in the amount of visible luminophore. For each image, luminophore pixels were also summed for each pixel line (i.e. depth) and vertical profiles of luminophore concentrations were generated. Vertical sediment mixing rates were then assessed using a simple biodiffusive model (Crank 1975) fitted to those vertical profiles,

which resulted in the computation of biodiffusion coefficients (Db).

Temporal changes in bivalve activity were recorded simultaneously with sediment mixing for the same sides of the 5 aquaria studied. Activity was assessed using the automated image acquisition system used during the surface sediment experiment, except that the axis of the captor lens was perpendicular to the vertical side of each studied aquarium (Fig. 1B). The photographic field (17 × 12 cm) had a resolution of 230 × 211 µm. Both feeding (i.e. siphon) activity and periodic oscillatory movements of the water–sediment interface were detected. Conversely to the surface sediment experiment, it was not possible to distinguish between these 2 types of activity. Total activity was therefore defined as the sum of the image areas affected by these 2 types of activity per unit of time.

Both luminophore displacements and total activities were summed and divided by the time duration since the beginning of the experiment. The so-called average cumulative luminophore displacements and average cumulative total activities were plotted together with Dbs over time, and the relationships between these variables were assessed using simple linear regression models. This procedure was carried out both on the whole aquaria and on restricted areas where only feeding activity occurred.

RESULTS

Sediment surface experiment

The position of the shell of *Abra ovata* did not change within the sediment after the acclimation period. During feeding periods, they extended their inhalant siphon and collected surface sediment within well-defined sub-areas. Bivalves periodically retracted their inhalant siphon, after which the siphon re-emerged and began to collect sediment in a new sub-area. This resulted in a series of consecutively prospected sub-areas (Fig. 2). The first prospected sub-area was always located in the immediate vicinity of the buried bivalve. Conversely, there was no clear temporal pattern in terms of: (1) distance of the sub-area centers from the bivalve or (2) angular sectors of the sub-areas. Bivalves never explored the same sub-area twice before the prospecting of the total area delimited by the extension of their inhalant siphon was accomplished. Surface feeding activity was between 0.04 (Bivalve 3) and 7.89 cm^2 h^{-1} (Bivalve 4). For all 4 studied bivalves, there were significant temporal changes in surface feeding activity, and the greatest values were measured during the first 6 h of the experiments (Fig. 3). Besides surface feeding activity,
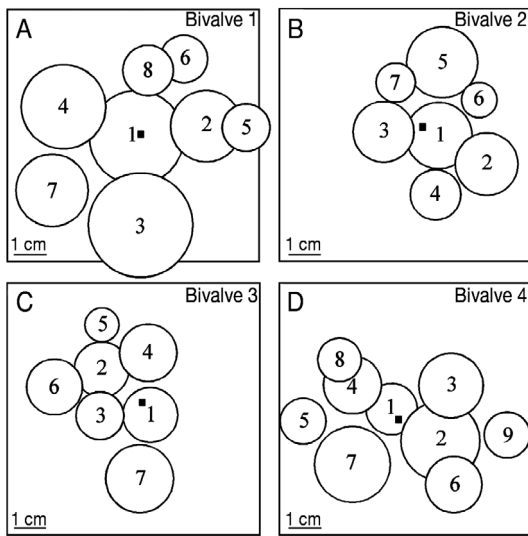
Fig. 2. *Abra ovata.* Sediment surface experiment. (A–D) Spatial repartitions of the sub-areas successively affected by the surface feeding activity of *A. ovata*. The center of each circle corresponds to the barycenter of each sub-area. The size of each circle is proportional to the surface of each sub-area. The number within each sub-area refers to the prospecting time sequence (i.e. Area 1 was prospected first, then Area 2, and so on). Squares indicate the positions of the bivalves within the sediment

intermittent oscillatory movements of the superficial sediment layer were also detected. They were due to foot and shell movements as later observed during sediment column experiments (see 'Results: Sediment column experiment').

For all 4 bivalves, there was only 1 area characterized by major sediment accumulation, which was located close to the buried bivalves and corresponded to 1 ejection mound, and surface feeding activity mostly created a large number of small pits in the sediment (Fig. 4). There were also some limited areas of sediment accumulation resulting from the production of fecal pellets or from surface feeding activity, and a close correspondence between the areas affected by surface feeding activity and the appearance of disturbed surface sediment. When computed over the total area studied and for the duration of the experiment, the surface sediment handling resulted either in a low net sediment accumulation (i.e. 4 and 12% of total sediment handled after 24 h for Bivalves 2 and 4, respectively) or in a low net sediment excavation (i.e. 8 and 7% of total sediment handled after 24 h for Bivalves 1 and 3, respectively). Surface sediment handling rates were between 2.0 (Bivalve 2) and 907.7 mm^3 h^{-1} (Bivalve 4), and correlated significantly with surface feeding activity because of the peak synchronicity for these 2 parameters (Table 1).
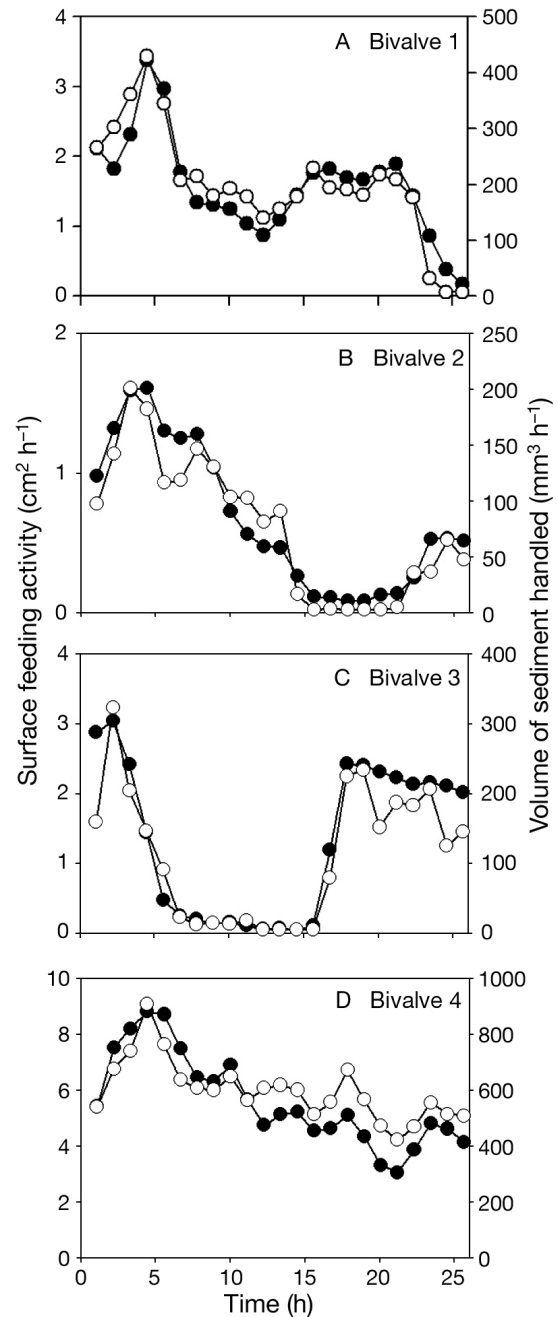

Fig. 3. *Abra ovata.* Sediment surface experiment. Temporal changes in surface feeding activity (●) and volume of sediment handled (○) by the 4 tested bivalves

Sediment column experiment

There were 2 types of activity corresponding to: (1) feeding (i.e. siphoning) activity, or (2) shell and/or foot movements. Feeding activity occurred in restricted (i.e. conical) areas and resulted in significant vertical sediment displacements, whereas shell and/or foot
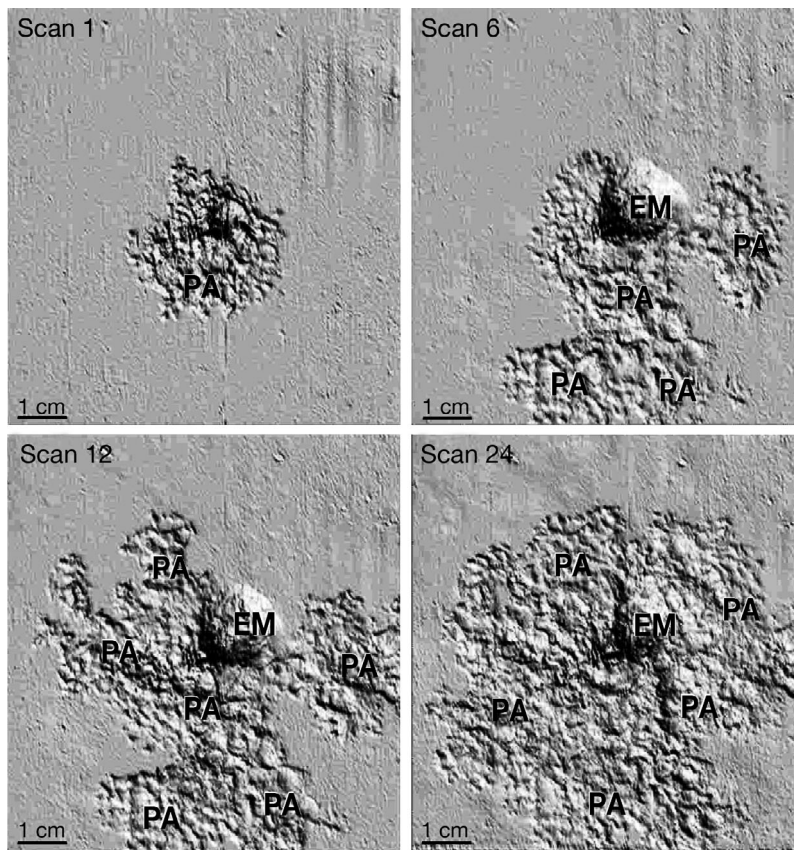
Fig. 4. *Abra ovata*. Sediment surface experiment. Bivalve 1. Shaded relief maps of differences in micro-topography between Scans 1, 6, 12, and 24, and Scan 0. PA: prospected area, EM: ejection mound

Table 1. Surface sediment experiment. Determination coefficients and associated probabilities of the simple linear regression models linking surface feeding activity and the volume of sediment handled

Bivalve	Surface feeding activity vs. volume of sediment handled		
	n	r^2	p
1	23	0.871	< 0.001
2	23	0.906	< 0.001
3	23	0.890	< 0.001
4	23	0.799	< 0.001

movements provoked short-term (less than 1 min), transient uplifts of the superficial sediment layer. As indicated by the disappearance of the luminophores from the water–sediment interface, the proportion of the sediment surface affected by feeding activity was close to 100% for all 5 aquaria after 24 h, and during that same period shell and/or foot movements affected between 14 and 25% of this surface (Table 2). Feeding activity and shell and/or foot movements occurred dur-

ing between 61 and 99, and 41 and 81% of the duration of the experiment, respectively (Table 2). These 2 types of activities occurred simultaneously during 27 to 72% of the experiment duration (Table 2).

When considering the whole aquaria and experiment durations, total activities covered between 294×10^{-5} and 15 cm^2 h^{-1} and luminophore displacements between 234×10^{-5} and 9.78 cm^2 h^{-1}. There was no significant positive correlation between total activity and luminophore displacement for 4 of 5 aquaria (Table 3). Moreover, the proportion of the variance of luminophore displacement explained by changes in total activity remained very limited (<7.5%). Average cumulative total activities tended to increase during the first part of the experiments and then stabilized in all 5 aquaria (see Fig. 5 for Aquarium D). Average cumulative luminophore displacements showed the same temporal changes in 4 of 5 aquaria (see Fig. 5 for Aquarium D). The only exception was Aquarium A, where average cumulative luminophore displacements tended to decrease with experiment duration after only 7 h (data not shown). As both average total activities and average cumulative luminophore displacements were standardized relative to the experiment duration, decreases in these 2 indices indicated intervals of lower intensity for total activity and luminophore displacements. Dbs were between 1.74 and 112.35 cm^2 yr^{-1}. Aquaria A and B showed sharp increases in Dbs at around 16 h. Analysis of the biodiffusive model fits to vertical luminophore profiles showed that these differences corresponded to slight changes in luminophore profiles, but were amplified by the inability of the biodiffusive model to account for the presence of both surface and sub-surface peaks of luminophore concentrations (Fig. 6). Average cumulative total activities and average cumulative luminophore displacements correlated positively for 4 of 5 aquaria, and the determination coefficients of the corresponding simple linear models were higher than 0.640 for 3 of them (Table 3). Average cumulative total activities also correlated significantly with Dbs in 4 of 5 bivalves, but with lower determination coefficients. Average cumulative lumi- nophore displacements correlated positively with Dbs in only 3 of 5 bivalves, and their determination coefficients were all low (i.e.

Table 2. *Abra ovata.* Within-sediment column experiment. Proportions of time (% of entire experiment duration) devoted to feeding activity, foot and/or shell movements, and time during which both feeding activity and foot and/or shell movements co-occurred; and proportions (%) of the sediment surface affected by foot and/or shell movements

Bivalve	Time (% of experiment duration)			Sediment surface affected by movements (% of surface)
	Feeding	Foot/shell movement	Feeding/movement co-occurrence	
1	86	58	44	21
2	73	77	56	25
3	73	69	61	22
4	99	81	72	17
5	61	41	27	14

Table 3. Determination coefficients and associated probabilities of the simple linear regression models linking total activity (TA) and luminophore displacements (LD), cumulative total activity (CTA) and cumulative luminophore displacements (CLD), biodiffusion coefficients (Db) and CTA, and Db and CLD. Significant positive correlations are in **bold**

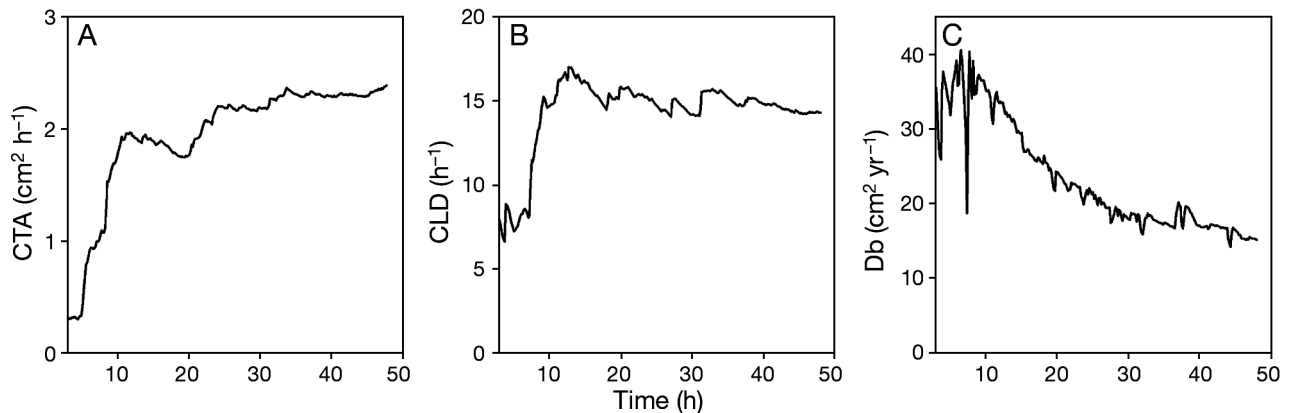| Bivalve	LD vs. TA			CLD vs. CTA			Db vs. CTA			Db vs. CLD		
	n	r^2	p	n	r^2	p	n	r^2	p	n	r^2	p
1	**198**	**0.075**	**0.001**	271	0.344	< 0.001	**240**	**0.639**	**< 0.001**	240	0.191	< 0.001
2	191	0.005	0.349	**270**	**0.640**	**< 0.001**	214	0.166	< 0.001	214	0.006	0.252
3	235	0.002	0.460	**268**	**0.196**	**< 0.001**	250	0.075	< 0.001	**250**	**0.098**	**< 0.001**
4	240	0.009	0.137	**270**	**0.749**	**< 0.001**	255	0.336	< 0.001	**255**	**0.244**	**< 0.001**
5	212	0.004	0.3570	**269**	**0.671**	**< 0.001**	245	0.583	< 0.001	**245**	**0.156**	**< 0.001**

Fig. 5. *Abra ovata*. Sediment column experiment, Aquarium D. Temporal changes in (A) average cumulative total activity (CTA), (B) average cumulative luminophore displacement (CLD), and (C) biological diffusion coefficient (Db)

<0.244). Overall, Dbs correlated better with average cumulative total activities than with average cumulative luminophore displacements, even though Dbs were computed based on the vertical distributions of the luminophores.

Fig. 7 shows an example of the observed and estimated temporal changes within a restricted area (25 cm^2) corresponding to the conical zone where only feeding activity by an individual bivalve occurred. Feeding activity was between 594×10^{-5} and 5.22 cm^2 h^{-1}, luminophore displacement between 168×10^{-5} and 2.76 cm^2 h^{-1}, and Db between 5.10 and 206.86

cm^2 yr^{-1}. Feeding activity and luminophore displacement correlated positively (n = 212, r^2 = 0.432, p < 0.001). Average cumulative feeding activity, average cumulative luminophore displacements, and Dbs all had similar temporal changes and correlated positively with one another (Fig. 8). The determination coefficients of the corresponding regression models were much higher than those obtained when considering total activity in the whole Aquarium A (Table 3). Similar results were obtained for other bivalves and other restricted areas featuring only feeding activity (data not shown).
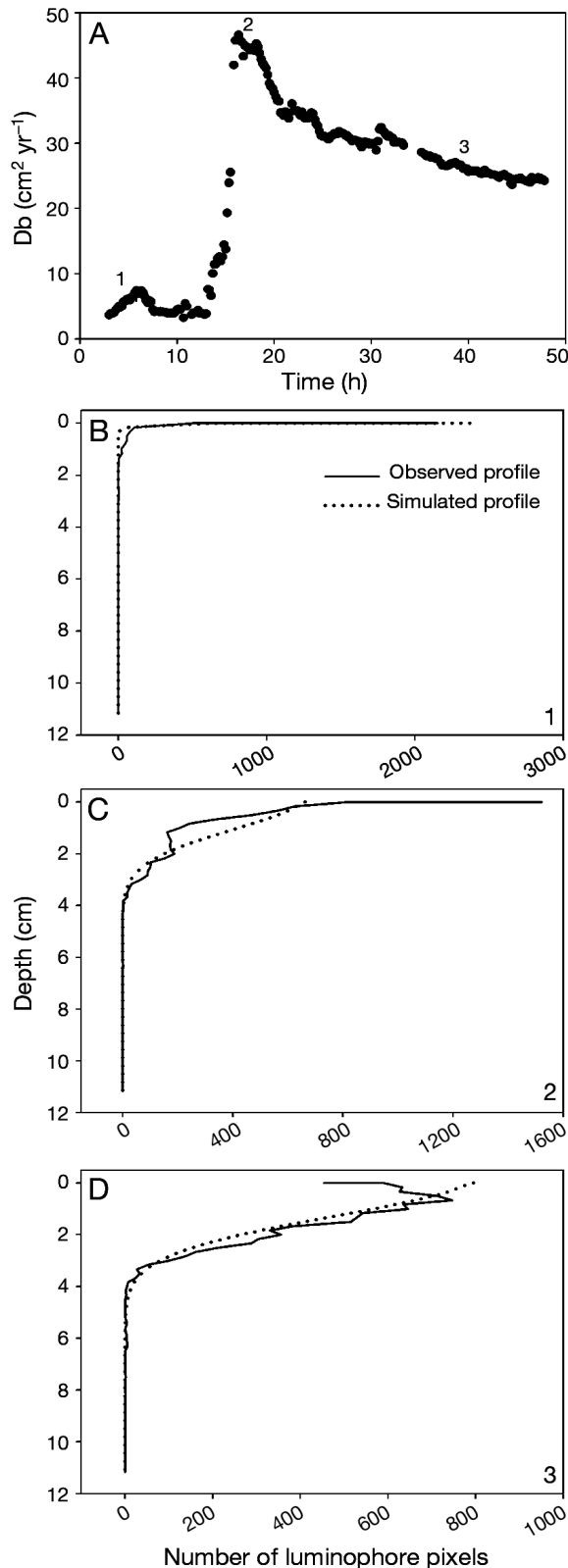
Fig. 6. *Abra ovata.* Sediment column experiment, Aquarium A. (A) Temporal changes in biological diffusion coefficients (Dbs) with (B–D) 3 profiles corresponding to very distinct values of this coefficient (1, 2, 3, respectively)

DISCUSSION

Bivalve activity

The image analysis techniques used during this study allowed the assessment of surface feeding activity during the sediment–surface experiment, while the monitoring carried out during the within-sediment column experiment described total activity (i.e. the sum of both the feeding activity and the movements of the shell and/or foot). Surface feeding activity corresponded to strong movements of the inhalant siphon outside the sediment, including scooping superficial sediment during feeding periods and, to a lesser extent, to movements of the exhalant siphon when expulsing fecal pellets and clouds of loose sediment. Similar activities of the 2 siphons have been reported for *Yoldia limatula* (Bender & Davis 1984). We also saw transitory uplift of surface sediment overlying the bivalve. This pulse-like motion mainly corresponded to shell displacements induced by the extension of the foot (O. Maire pers. obs.).

Grémare et al. (2004) observed no marked change in the surface feeding activity of *Abra ovata* during 24 h experiments. In contrast, our experiments estimated higher surface feeding activities during the first 6 h. *A. ovata* exploited the sediment in a series of distinct sub-areas with little overlap. The surface of the entire area prospected was limited by the reach of the inhalant siphon. One suggested hypothesis for this pattern is that it is less advantageous to forage in previously explored areas because the sediment presumably has a lower food value relative to the overlying fluffy layer (Jesus et al. 2005). This hypothesis could now be tested by comparing surface sediment biochemical characteristics in prospected and non-prospected areas, and by running complementary experiments under significant sediment transport, which could compensate changes in surface sediment characteristics (Rosenberg 1995). In addition, it would also be interesting to assess the possible potential role of pellet accumulation as a cue to depress deposit-feeding in *A. ovata,* as already reported for spionids (Miller & Jumars 1986).

Relationship between surface feeding activity and surface sediment handling

Techniques of sediment micro-topography mapping have been used to account for spatial micro-heterogeneity in meiofauna distribution (Sun et al. 1993) and oxygen fluxes (Jørgensen & Des Marais 1990, Roy et al. 2002, 2005). These techniques were mostly based on image analysis of photographs of the sediment surface (Sun et al. 1993), and the analysis of the projection of a

laser line onto the sediment surface (Roy et al. 2002, 2005). In this last case, micro-topography was determined by calculating the position of the laser line within successive images of the studied sediment area. The laser telemetry technique used in our experiments had a better vertical resolution (15 versus ~50 μm) than that used by Roy et al. (2002, 2005), and moreover, it is independent of sediment configuration. In contrast, for the approach used by Roy et al. (2002, 2005) micro-topography could not be directly assessed behind relatively high sediment mounds. This is particularly important when studying sediment reworking by *Abra ovata* since this bivalve creates an important ejection mound (i.e. up to 1 cm in height). The main drawback of our technique is the time needed to scan the whole studied area (67 min). This time period nevertheless proved appropriate for assessing surface sediment handling by *A. ovata*.

The individual bivalves were responsible for intense surface sediment handling. Moreover, the synchronicity between surface feeding activity and sediment handling clearly showed that the latter resulted from the former. Successive micro-topographic mappings showed several important changes in sediment microtopography: (1) a large set of small and shallow depressions over the areas prospected by the inhalant siphon, (2) 1 main ejection mound of loose sediment ejected by the exhalant siphon, and (3) a few piles of fecal pellets. Sediment excavation and accumulation were generally on the order of 5 mm but never exceeded 1 cm. This is nevertheless sufficient to affect the structure of the diffusive boundary layer and thus impact biogeochemical fluxes at the water–sediment interface (Roy et al. 2002). For all studied bivalves, there was almost no change in the average level of the sediment surface during the course of the experiment. Sediment handling by *Abra ovata* thus did not cause a detectable change in sediment compaction.

The activities of *Abra ovata* are likely to affect the physical properties of the sediment in different ways. As described for many soft-bodied benthic invertebrates (Murray et al. 2002), foot activity tends to compact the sediment. Conversely, feeding activity results in the physical disruption of the superficial sediment layer due to the creation of siphon channels and to the collection of patches of superficial sediment, which later induce the ejection of loose sediment at the water–sediment interface. The production of fecal pellets by *A. ovata* may also contribute to the expansion of the sediment because even if the pellets have a higher density, they are also coarser than the surrounding sediment (Krantzberg 1985). The lack of temporal trend in the average level of superficial sediment thus probably reflected the balance between opposite processes resulting from the overall activity of *A. ovata*.
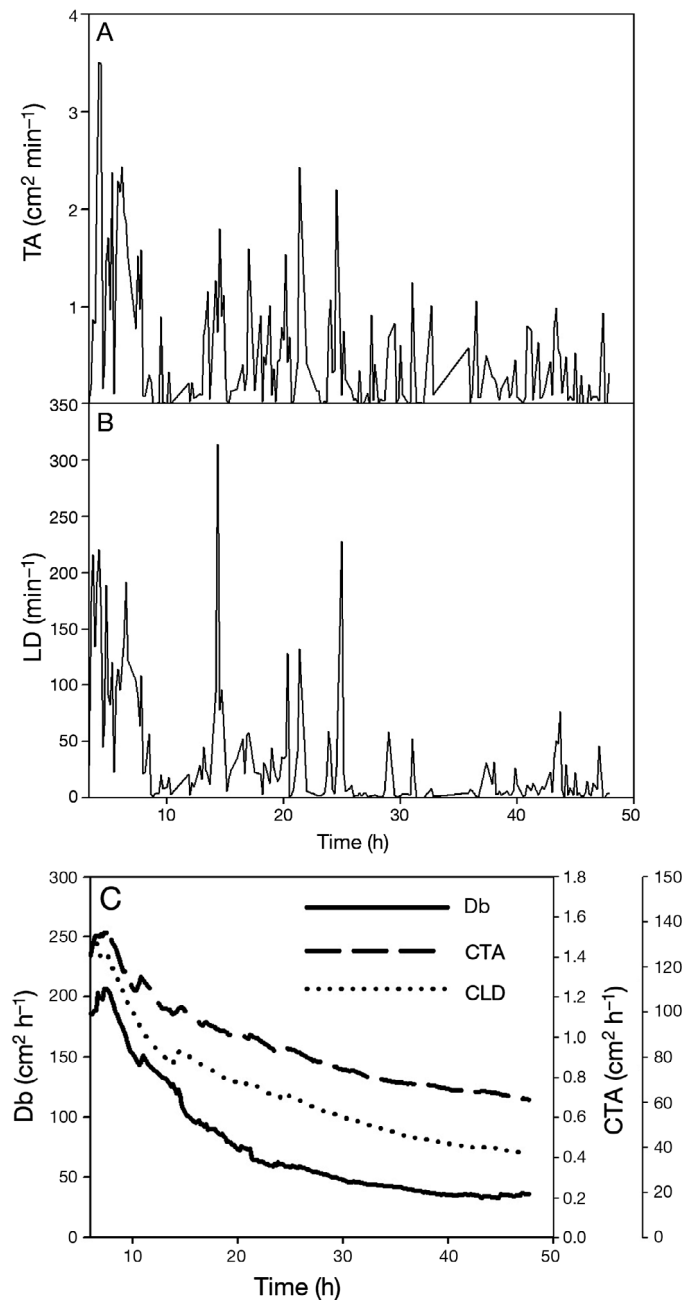

Fig. 7. *Abra ovata*. Sediment column experiment, Aquarium A. Temporal changes in (A) total activity (TA), (B) luminophore displacement (LD) and (C) average cumulative total activity (CTA), average cumulative luminophore displacement (CLD), and biological diffusion coefficient (Db) in an area only affected by feeding activity

Relationship between bivalve activity and vertical sediment mixing

Vertical sediment mixing is most often assessed indirectly by fitting mathematical models to vertical profiles of natural (radionuclides, chlorophyll *a*) or
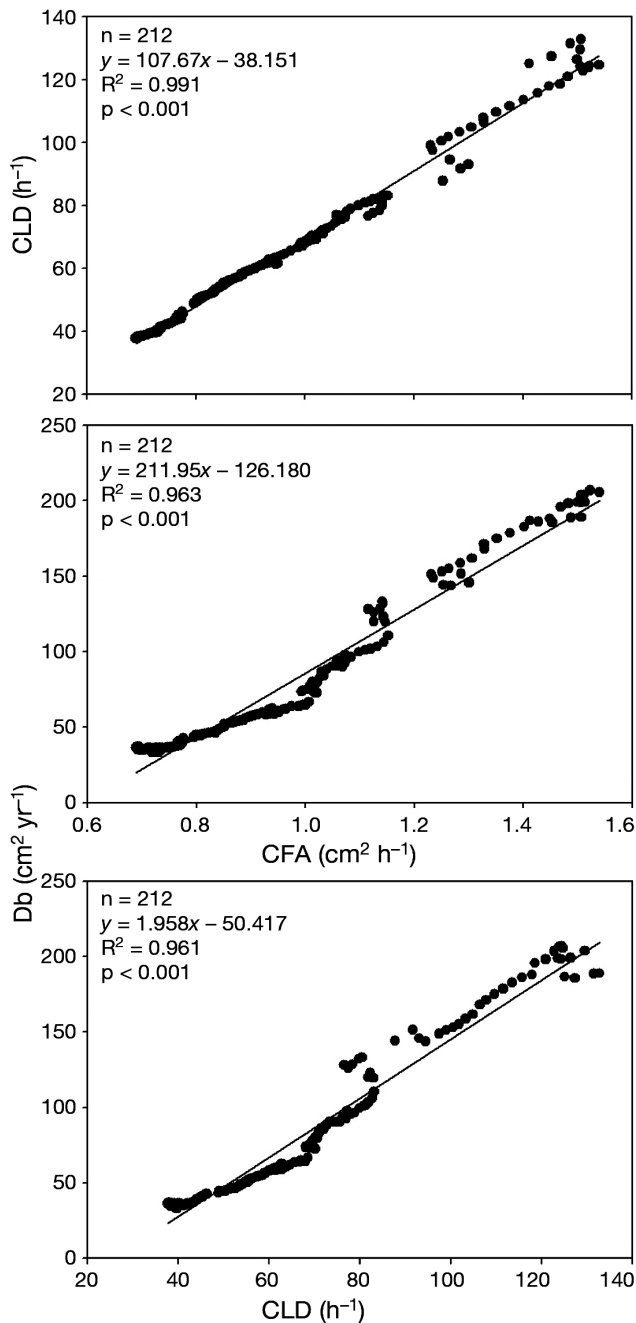
Fig. 8. *Abra ovata*. Sediment column experiment, Aquarium A. Relationships between (A) average cumulative feeding activity (CFA) and average cumulative luminophore displacements (CLD), (B) CFA and biological diffusion coefficients (Db), and (C) CLD and Db. All parameters were computed in a restricted area where only feeding activity occurred. All Db computed for this restricted area were incorporated

artificial (glass beads, metal-doped sediment, luminophores) tracers (Sharma et al. 1987, Wheatcroft 1992, Gérino et al. 1998). The most commonly used model is the biodiffusive model, which assumes that sediment particle displacements occur in a random manner over

short distances (Boudreau 1986a, François et al. 1997, Meysman et al. 2003). Although the theoretical constraints (i.e. symmetry and length criteria) of this model are most often not met (Meysman et al. 2003), it has proven efficient in assessing vertical sediment mixing rates by natural communities and individual organisms and is therefore commonly used as a tool of comparison between communities and/or species (Tromp et al. 1995, Mermillod-Blondin et al. 2005). Wheatcroft et al. (1990) showed that Db can be decomposed in $L^2/2t$, where L is a particle step length and t is a rest interval between steps. A single value of Db can correspond to very different combinations of L and t, and Db is only an imperfect description of sediment mixing. Using a non-local transport model on another data set, Maire et al. (2007) showed that: (1) in *Abra ovata* feeding on natural sediment, L and t are close to 0.2 cm and 7.6 h, respectively, and (2) temporal changes in organic matter availability had little effect on L but did significantly affect t (which was also postulated for the positive effect of temperature on sediment mixing by Wheatcroft et al. 1990). The goal of the present study was not to further refine the computation of L and t in *A. ovata* but to link short-term temporal changes in feeding activity and vertical sediment mixing rates. As stated by Wheatcroft et al. (1990), changes in Db can reflect changes in environmental parameters and in community structure. The present within-sediment column experiment was monospecific, short-term, and carried out under constant conditions. We therefore considered that the use of Db was suitable to describe the relationship between feeding activity and vertical sediment mixing.

The high frequency acquisition of images of a vertical sediment section under UV light and the computation of corresponding luminophore profiles allow a dynamic view of vertical sediment mixing based on the amount of luminophores displaced (Gilbert et al. 2003). We used image analysis techniques to quantify luminophore displacements, which were then transformed in average cumulative luminophore displacements to facilitate the comparison with Dbs. When considering the whole sediment surface over the entire duration of the within-sediment column experiment, there were only weak correlations between these 2 parameters. This was partly due to the inability of the biodiffusive model to account for the occurrence of both surface and subsurface peaks of luminophores. However, these correlations became stronger when considering restricted sediment areas only affected by feeding activity, which contributed to document the quantitative relationship between feeding activity and vertical sediment mixing. This discrepancy resulted from the co-occurrence of the 2 types of activities mentioned above. Feeding activity induced 'true' vertical sedi-

ment mixing over periods of time greater than 10 min (i.e. the time interval between 2 consecutive images taken under UV light). Conversely, foot and/or shell movements induced oscillatory uplifting movements of the superficial sediment layer resulting in intermittent displacements of large amounts of luminophore particles over short periods of time with no significant vertical sediment mixing over time periods longer than 10 min. In *Abra ovata*, high frequency measurements of luminophore displacements coupled with optical measurements of sediment mixing may therefore result in significant overestimations. Our results thus underscore the necessity of an explicit link between organism activities and sediment mixing processes even when sediment mixing rates are directly computed based on measurements of luminophore displacements (Gilbert et al. 2003). Finally, it should be underscored that foot and/or shell movements can be of high importance for processes other than sediment mixing, such as porewater fluxes.

Future applications of our methodological approach

The development of a new methodological approach coupling state of the art image analysis techniques, laser telemetry, and the use of luminophores clearly constitutes a major originality of this study. This approach can now be used for a large variety of purposes. First it must be stressed that the results of our study are based on a limited number of bivalves. Complementary experiments should now be undertaken to better quantify the relationship between feeding activity, sediment handling, and vertical sediment mixing in *Abra ovata*. Second, the effect of food availability on feeding activity and on vertical sediment mixing by *A. ovata* have already been studied independently (Grémare et al. 2004, Maire et al. 2006) and it would now be possible to do sediment column experiments under different regimes of food availability to assess the effect of food availability on the relationships between feeding activity and sediment mixing. Third, sediment mixing can be better parameterized by using step length (*L*) and resting time (*t*) than Db (Wheatcroft et al. 1990). During our study, the time interval between 2 consecutive images taken under UV light was 10 min, which was not sufficient to allow for the detection of individual luminophore displacements, but this time interval could be decreased to attempt to assess *L* and *t* directly. Fourth, it would also be interesting to use our methodological approach on other organisms featuring different sediment handling and mixing types. Results could prove helpful in parameterizing both traditional (François et al. 1997, 2001) and individual-based models of sediment reworking (Boudreau et al. 2001, Choi et al. 2002).

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