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Quantification of sediment reworking by the Asiatic clam *Corbicula fluminea* Müller, 1774

Nabil Majdi · Léa Bardon · Franck Gilbert

Abstract Active organisms modify the substratum in which they dwell. This process, called “bioturbation”, affects the way that biogeochemical fluxes are mediated at the substratum–water interface. In the frame of this work, the bioturbation potential of the Asiatic clam *Corbicula fluminea* was characterized and quantified. We measured the displacement of fluorescent particles by *C. fluminea* burying in a size-based experimental design in order to explore the effects of body-size on sediment reworking. Our results stress that *C. fluminea* belongs to the functional group of biodiffusors, and that *C. fluminea* can be considered as an intermediate sediment reworker. We suggest that bioturbation was mainly induced by the pedal-feeding activity of the clams. Results also showed that, though large clams induced displacement of particles deeper into the sediment, small clams

showed the highest net sediment reworking activity. This result was in contrast to the initial hypothesis of biovolume as the main driver for particle displacement by bioturbating organisms. Life-history traits and specific features of pedal-feeding could explain the observed pattern.

Keywords *Corbicula fluminea* · Invasive species · Bioturbation · Sediment reworking · Body-size

Introduction

Bioturbation is the process by which faunal activity affects the distribution of particles (by sediment reworking) and solutes (by burrow ventilation) within the substratum and at the substratum–water interface (Kristensen et al., 2012). Bioturbation is a typical case of “ecological engineering” effect, since bioturbating organisms can critically affect geochemical gradients and resource distributions in ecosystems (Meysman et al., 2006). The impact of bioturbation on ecosystem processes is contingent upon the potential of organisms to rework and ventilate the substratum, owing to species-specific traits such as body-size, population dynamics, metabolism, or feeding strategy (Solan et al., 2004). The bioturbation potential of several marine organisms has been characterized and measured, which has allowed: (1) quantification of bioturbation effects on marine ecosystems (Aller, 1982), and

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(2) experimental classification of bioturbating organisms into functional groups: biodiffusers, upward conveyors, downward conveyors, regenerators, blind-ended ventilators, and open-ended ventilators (Kristensen et al., 2012). Although most bioturbation studies have used marine species (Mermillod-Blondin et al., 2004; Michaud et al., 2005; Hedman et al., 2011), some work on freshwater benthos has explored the effects of bioturbation on sediment mixing and biogeochemistry (Fisher et al., 1980; Matisoff & Xiaosong, 1998; Ciutat et al., 2005; Lagauzère et al., 2009; Mermillod-Blondin et al., 2013).

Bivalves can affect freshwater ecosystems, through suspension and deposit-feeding, valve movements, burrowing behavior, and excretion (Sousa et al., 2009). The notorious Asiatic clam *Corbicula fluminea* Müller 1774 has invaded numerous North American and European continental waters, favoured by competitive traits such as hermaphroditism, high fecundity, early maturation and habitat generalism, and by its association with human activities (Sousa et al., 2008). Invasive *C. fluminea* populations show high densities (frequently more than 1,000 ind. m⁻²; McMahon, 2000); thereby they can affect other native bivalves by monopolizing and/or modifying available habitats and by hampering the recruitment of juveniles through extensive suspension and deposit-feeding (Yeager et al., 1994; Hakenkamp & Palmer, 1999; Strayer, 1999; Vaughn & Hakenkamp, 2001). In fact, filtration rates of *C. fluminea* populations are known to reduce phytoplankton biomass, while simultaneously enrich the benthic habitat with large amounts of excretion products (Cohen et al., 1984; Lauritsen, 1986). Furthermore, *C. fluminea* may affect benthic communities while pedal-feeding (Dame, 1996; Hakenkamp et al., 2001). Hard-substrate colonizers are also able to interact with complex and persistent habitats provided by *C. fluminea* shells (Gutiérrez et al., 2003; Werner & Rothhaupt, 2007; Sousa et al., 2009). The life-span of *C. fluminea* ranges between 1 and 5 years in various ecosystems, usually with a bivoltine pattern of juveniles' release (McMahon, 2000; Lucy et al., 2012). As a result, body-size distribution of *C. fluminea* varies among populations. Accurate estimations of sediment reworking by *C. fluminea* populations therefore need to include constraints associated with body-size.

Despite mounting evidence that *C. fluminea* significantly affects benthic communities (Hakenkamp

et al., 2001; Vaughn & Hakenkamp, 2001), so far, its impact on sediment reworking has been neither experimentally characterized nor included in the quantification of *C. fluminea*-induced disturbances. The purpose of the present study is to provide the first experimental quantification of *C. fluminea* bioturbation activity. Such information is necessary to evaluate biogeochemical effects and ecological importance of invasive species in benthic ecosystems.

Methods

Sampling of sediment and fauna

Sediments and adult *C. fluminea* clams were sampled in May 2012 in the Louge River (south-western France; 43.396457°N, 1.255635°W; elevation: 198 m a.s.l.). Water temperature during sampling was 12°C. Clams were collected on a sandy river bed with a shovel at 1-m water depth. The top 10 cm of the surface sediment was sampled by cores. Sediments and clams were returned to the laboratory and processed within 2 h.

The sediment was sieved (2-mm mesh size) to remove coarse particles and large macrofauna. Following mixing, the sediment was defaunated by freezing at -80°C for 5 days. Sediment grain-size characteristics were measured with a diffraction laser granulometer (Mastersizer 2000, Malvern Instruments, Orsay, France), which indicated that 86% of sediment particles were between 121 and 450 µm, or between 224 and 257 µm according to either a mode or a median value, respectively. Sediments comprised 1.9% total organic carbon, based on the loss-on-ignition method (400°C overnight after Schumacher, 2002).

Clams were acclimatized in containers with collected sediments and aerated river water at 15°C for 7 days until the start of the experiment. To assess the influence of body-size on sediment reworking activity, individual adult clams were separated into three size classes based on shell length, fresh tissue biomass (B_m), and biovolume (B_v) (Table 1). B_m of clams was determined after weighing individuals without their shell at the end of the experiment. B_v of clams was determined from volume displaced when individuals were immersed in a known volume of water in a graduated cylinder (Persoone, 1971).

Table 1 Characteristics of the living clams used in size-based treatments

Adult <i>Corbicula fluminea</i>	Shell length (cm)	Individual B_m (g)	Individual B_v (cm ³)	Individuals per column	Total B_m per column (g)
Small ($N = 40$)	1.29 ± 0.1	0.6 ± 0.1	0.69 ± 0.1	10	6.1
Medium ($N = 20$)	1.74 ± 0.1	1.28 ± 0.2	1.75 ± 0.1	5	6.4
Large ($N = 12$)	2.18 ± 0.1	2.33 ± 0.3	2.76 ± 0.2	3	7.0

Means are displayed with ±1 SD. B_m is the fresh tissue (shell-free) biomass. B_v is the biovolume

Microcosm set-up and experimental procedures

Sixteen experimental molds made from PVC tubes (height = 10 cm; internal diameter = 9.3 cm) were filled with defaunated sediments to obtain a sediment column of 9-cm height. Then, 3 g of fluorescent inert particles (particle diameter = 125–355 µm; Partrac Ltd., Glasgow, UK) were homogeneously deposited at the surface of each sediment column following Hedman et al. (2011). Four treatments of four sediment columns each were incubated in experimental containers with O₂ saturation >85%, at 15°C and under a 12:12 light:dark cycle. The four treatments consisted in 0, ten small (1,472 ind. m⁻²), five medium (736 ind. m⁻²), and three large (442 ind. m⁻²) living clams placed on surface sediment (Table 1). These experimental densities were chosen in order to establish similar clam biomass in treatments and were consistent with the range of *C. fluminea* densities observed in rivers: 315–3,206 ind. m⁻² and in sandy habitats: 54–1,215 ind. m⁻² (Lucy et al., 2012)

After 10 days of incubation, the sediment columns were gently retrieved from the experimental containers. The overlying water was removed, and the sediment was pushed up in the tubes and sectioned horizontally with a large blade into 0.2 cm layers to a depth of 1 cm, 0.5 cm layers to a depth of 3 cm, 1 cm layers to a depth of 5 cm and 2 cm layers to the bottom of the tubes. While sectioning, encountered clams were removed from the sediment and checked for mortality, and their biomass and biovolume were measured individually. The position of each individual within the sediment was inferred from the exact location of their uppermost point at collection and from their body dimensions. Then, sediment from each layer was homogenized, and subsamples were deposited in a 24-well microplate (BD Falcon™, Franklin Lakes, NJ, USA). Lumino-phore distributions were quantified by fluorescence (bottom reading fluorescence; λ excitation =

405 nm; λ emission = 502 nm; area scan: 9 × 9) using a microplate reader (Synergy Mx, Biotek, Winooski, VT, USA) following a protocol slightly modified from Lagauzère et al. (2011).

Quantification of sediment reworking activity and data analysis

Sediment reworking activities by *C. fluminea* were quantified by a one-dimensional diffusion model (Eq. 1)

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

where C is the relative concentration of luminophores, D_b is the biodiffusion coefficient, t is time (days), and z is depth (cm). In the model, the downward transport of luminophores is described by diffusion, while effects from sedimentation, advection, and reaction are neglected (Guinasso & Schink, 1975).

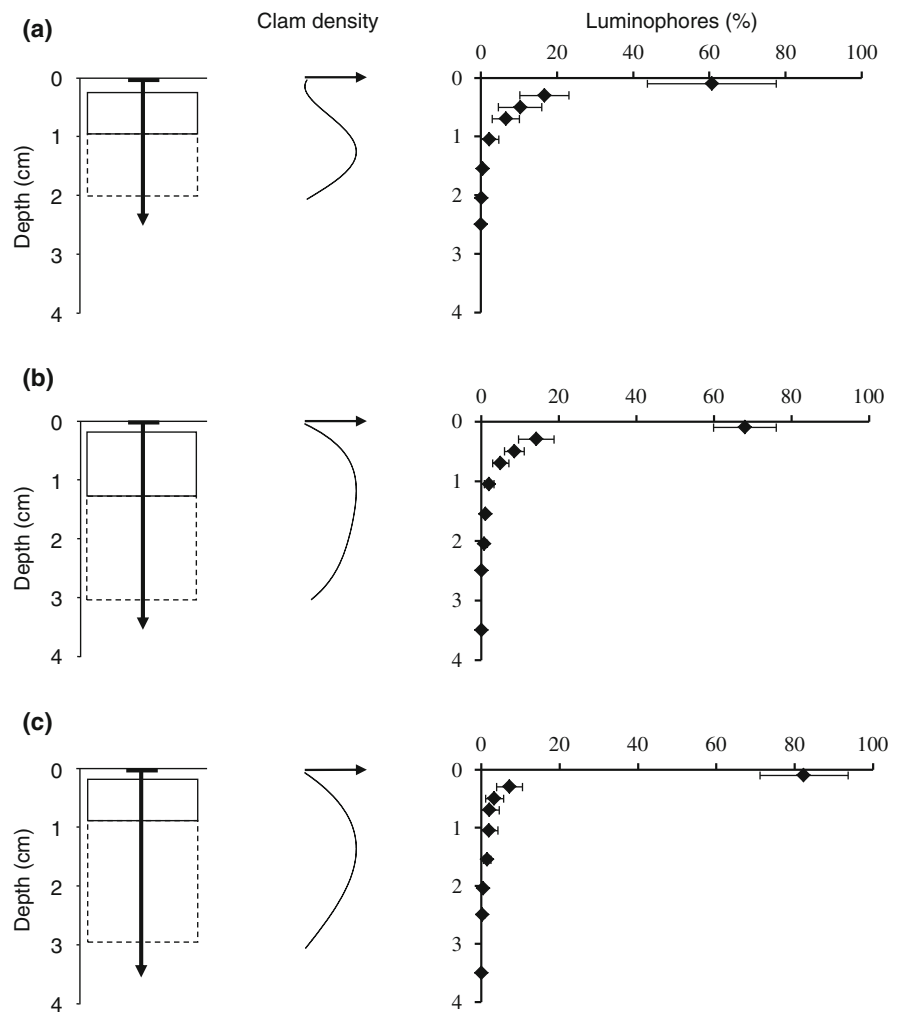
Differences between biodiffusion coefficients (D_b) were each analyzed by one-way ANOVA with treatments as factors, after assessing homogeneity of variance and normally distributed residuals using Barlett's and Shapiro–Wilk's tests, respectively. In order to standardize D_b for the effects of body mass and body volume, we also compared D_b/B_m and D_b/B_v among treatments. Tukey's HSD test was performed for a posteriori pairwise comparison of treatments. All statistical analyses were performed with R (version 2.15.12; R Development Core Team, 2012).

Results

Vertical distribution of clams and tracers

At the end of the experiment, all the clams were alive and could be recovered from the sediment at various

Fig. 1 Final repartition of clams and tracers in treatments with small (a), medium (b), and large (c) *Corbicula fluminea* individuals. *Left panel* Sediment zone where *Corbicula fluminea* individuals were found at the end of the experiment (plain rectangle shells' top, dotted rectangle shell's bottom). *Horizontal lines* are the starting point for luminophores. *Arrows* are the total range of luminophore displacement from surface. *Middle panel* Vertical repartition of clams after smoothing of relative density profiles. *Right panel* Relative vertical repartition (mean \pm 1 SD; $N = 4$) of the luminophores initially deposited at the sediment surface



depths. Clams were found to dwell down in the first few centimeters of the sediment: The highest density of small clams was found between 0.7 and 1.7-cm depth (Fig. 1), while medium and large clams were more homogeneously distributed between 0.5 and 2.6-cm depth (Fig. 1).

No downward transport of fluorescent tracers occurred in the control treatment, since we recovered >98% of luminophores in the first 0.2-cm sediment layer (data not shown). On the other hand, a mean burying of 39.4, 32.1, and 18.6% of luminophores was recorded in treatments with small, medium, and large-sized clams, respectively (Fig. 1). The difference in removal between size-based groups was significant (one-way ANOVA; $F_{2,9} = 4.1$, $P = 0.049$): small clams seemed to remove a larger fraction of particles

from the surface sediment compared to medium- and large-sized clams. In contrast, large clams transported particles deeper into the sediment than small clams: luminophores were observed down to 2.5 cm in the small-sized clam treatment, while luminophores were found down to 3.5 cm in the treatment with large-sized clams.

Sediment reworking activity of *Corbicula fluminea*

In the experimental set-up of the present study, ten small, five medium, and three large clams showed average biodiffusion coefficients (D_b) of 2.3, 1.7, and 1.1 $\text{cm}^2 \text{year}^{-1}$, respectively (Table 2). The difference in D_b between size-based groups was significant

Table 2 Biodiffusion coefficients (D_b), and D_b related to biomass (D_b/B_m) and to biovolume (D_b/B_v) calculated for the three experimental size-based treatments

<i>Corbicula fluminea</i>	D_b (cm ² year ⁻¹)			D_b/B_m (cm ² year ⁻¹ g ⁻¹)			D_b/B_v (cm ² year ⁻¹ cm ⁻³)		
	Mean	SD	Post hoc	Mean	SD	Post hoc	Mean	SD	Post hoc
Small	2.27	0.26	a	0.37	0.04	a	0.33	0.04	a
Medium	1.73	0.24	a,b	0.27	0.04	a,b	0.20	0.03	b
Large	1.13	0.34	b	0.16	0.05	b	0.14	0.04	b

Values are mean \pm 1 SD ($N = 4$). Different letters (a,b) show significant differences between treatments and result of Tukey's post hoc grouping test

(one-way ANOVA; $F_{2,9} = 8.04$, $P = 0.02$; Table 2) and indicated a progressively decreasing D_b with increasing size. This pattern of highest D_b for the smallest clams was maintained also after standardizing D_b by biomass (D_b/B_m) and biovolume (D_b/B_v). When D_b was standardized by the biomass and biovolume of clams, the highest net reworking activity could still be observed for the smallest clams (one-way ANOVA; D_b/B_m : $F_{2,9} = 11.3$, $P = 0.009$; D_b/B_v : $F_{2,9} = 16.4$, $P = 0.004$; Table 2).

Discussion

In North America and Europe, populations of the invasive species *C. fluminea* commonly exceed 1,000 ind. m⁻² (Stites et al., 1995; Cataldo & Boltovskoy, 1998; McMahon, 2000; Werner & Rothhaupt, 2007), altering ecosystem processes, community stability, and resource partitioning (Lauritsen & Mozley, 1989; Strayer, 1999; Hakenkamp & Palmer, 1999; Vaughn & Hakenkamp, 2001; Sousa et al., 2008). This study provides the first experimental quantification of sediment reworking (D_b) by *C. fluminea*. Our objective was to provide a basis to assess the ecological impact of this invasive species in soft-bottom sediments. Extrapolating the meaning of the D_b in terms of impacts of *C. fluminea* on sediment distribution is a tricky task, because D_b is not explicitly linked to specific causes of sediment particles mixing (Wheatcroft et al., 1990). We evaluated the rate of sediment reworking by *C. fluminea* populations by comparison of obtained D_b with D_b of other common biodiffusor clams in marine and freshwater environments (Table 3). We adjusted D_b to population size of 1,000 ind. m⁻². Values considered were extracted from laboratory studies all conducted at 15°C, because temperature is a keystone driver of

sediment reworking rates (Ouellette et al., 2004; Maire et al., 2007). At comparable individual size and population densities, *C. fluminea* appears to have an intermediate capacity for sediment reworking (Table 3). Although densities of native bivalves rarely exceed 1,000 ind. m⁻² in rivers (e.g., Strayer & Malcom, 2007), up to 3,206 ind. m⁻² of *C. fluminea* have been reported in rivers (Lucy et al., 2012). Furthermore, since large *C. fluminea* were shown in our study to be relatively less efficient reworkers than smaller size classes (Table 3), the net reworking effects of *C. fluminea* populations may be even larger than those of other species. Finally, specific traits, such as particle ejection several centimeters above the sediment–water interface (Rhoads, 1963) could have partly overestimated the D_b reported for *Yoldia limatula*. The body of evidence leads us to conclude that populations of *C. fluminea* may have significant effects on sediment distribution dynamics in invaded soft-bottomed reaches.

Following incubations with *C. fluminea*, the distribution of fluorescent tracers, initially deposited as a discrete layer on the sediment surface, decreased exponentially with depth. Such patterns indicated diffusive transport mechanisms and suggest that *C. fluminea* belongs to the group of biodiffusors (sensu Kristensen et al. 2012), like other freshwater and marine clams (McCall et al., 1995; François et al., 1999; Maire et al., 2006). This result also validates the use of a one-dimensional diffusion model to quantify the sediment reworking activity of *C. fluminea*. Furthermore, the functional group approach to bioturbation provides a potentially important tool to predict effects from bioturbators on benthic fluxes and the coupling between benthic macrofauna and transport of solutes across the sediment–water interface. For instance, sediment uptake of oxygen has been suggested to be less stimulated by biodiffusors than by

Table 3 Comparison of biodiffusion coefficients (D_b) adjusted to population sizes of 1,000 ind. m^{-2} , from freshwater (Fw) or marine (M) clam species used in laboratory studies

Species	Length (cm)	D_b (cm^2 year $^{-1}$)	Tracer used	Work
<i>Yoldia limatula</i> (Say 1831) (Fw)	2–3	8.03	^{137}Cs -labeled clay	McCall & Robbins (unpubl.)
<i>Venerupis aurea</i> (Gmelin 1791) (M)	2.3	7.02	Fluorescent sand	François et al. (1999)
<i>Ruditapes decussatus</i> (L. 1758) (M)	2.3	3.13	Fluorescent sand	François et al. (1999)
'Large' <i>Corbicula fluminea</i> (Fw)	2.2	2.56	Fluorescent sand	This work
<i>Anodonta grandis</i> (Say 1829) (Fw)	2–3	0.57–1.48	^{137}Cs -labeled clay	McCall et al. (1995)

For better comparison confidence, we only used data from experiments carried out at 15°C, and with bivalves with a shell size between 2 and 3 cm. When available, data are means ($N = 3$ for *V. aurea* and *R. decussatus* and $N = 4$ for *C. fluminea*). Adapted from McCall et al. (1995)

gallery-diffusors (Michaud et al., 2005). The functional group of biodiffusors gathers together sediment reworking species that generate random particle transport over short distances. Such transport is deemed similar to a constant diffusive transport of sediment particles (Boudreau, 1986; François et al., 2001). In natural environments, patterns of particle transport by *C. fluminea* are expected to be contingent upon constraints such as predation risk and oxygen availability (Saloom & Scot Duncan, 2005). Overlying water oxygen and probability for predation were either kept constant (oxygen concentration) or excluded (predation) under the experimental conditions applied here.

To provide for their food needs, adult *C. fluminea* can burrow and pedal-feed copiously on interstitial particulate organic matter and microorganisms (Reid et al., 1992; Hakenkamp et al., 2001), especially when planktonic food is scarce (Hakenkamp & Palmer, 1999). In this experiment, no additional food was supplied to the experimental containers during the incubation period. The availability of suspended material to clams was intentionally reduced in order to maximize their pedal-feeding activity and hence their impact on sediment reworking. Nevertheless, pedal-feeding seems an important feeding strategy used by clams (see Boltovskoy et al., 1995; Raikow & Hamilton, 2001), as also supported by preliminary experiments conducted at 10°C (Gilbert, unpublished data), which showed no difference in rates of sediment reworking under high versus low planktonic food availability. Therefore, we assumed that, in the present study, the sediment reworking activity of *C. fluminea* clams was mostly driven by their pedal-feeding activity. In fact, the reworking activity measured here should be considered in relation to the experimental conditions applied as a

“standard” impact of *C. fluminea* on surface sediment dynamics. In natural environments, abiotic (e.g., temperature) and/or biotic constraints (e.g., food availability, predation risk) may regulate the sediment reworking activity of *C. fluminea*. The importance of these factors should be included in future studies of bioturbation activities by *C. fluminea*. There is also abundant room for further progress which will take into account the consequences that this “non-native bioturbation” may have on affected benthic communities and processes.

During burial, benthic animals primarily displace the particles that surround their body in proportion to their volumetric size (Dorgan et al., 2005). This intuitive concept implies that body volume and morphological characters should be considered as critical drivers of sediment displacement by burying animals. In this context, the intensity of sediment reworking would positively correlate with body volume. Inter-species comparisons support this pattern in marine benthos (Gilbert et al., 2007). A positive correlation between rates of particle transport (D_b) and biovolume was not observed for *C. fluminea* in this study. In contrast, although large clams reworked particles deeper into the sediment than small clams, the net sediment reworking activity of large clams was lower than that of small clams. Possible reasons for such a counterintuitive result are threefold: (1) Small clams may spend more energy into pedal-feeding activity in order to sustain relatively higher growth rates than larger clams (Welch & Joy, 1984). (2) Small clams may experience lower friction constraints while moving within sediments, reducing the costs of burrowing frequency. (3) As an “interstitial” mode of nutrition, pedal-feeding may not scale exponentially with body-size as is the case for filtration (Riisgård, 1988; Filgeira et al., 2008); presumably because filtration efficiency is contingent upon

gill-area, whereas pedal-feeding relies on foot extension ability and burrowing efficiency.

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