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Sediment reworking by marine benthic species from the Gullmar Fjord (Western Sweden): Importance of faunal biovolume

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Abstract

In order to compare and quantify sediment reworking activities by different species/functional groups of macrofauna, a laboratory experiment was carried out with species from the Gullmarsfjord (Western Sweden). Monospecific communities of *Amphiura filiformis*, *Echinocardium cordatum*, *Scalibregma inflatum* and *Abra nitida* were introduced in experimental mesocosms, with identical densities (795 ind. m^{-2}), for 10 days. Sediment reworking was studied by quantifying downward and upward movements of fluorescent inert tracers (luminophores). Luminophores with different colour were initially deposited both at the sediment surface and within the sediments. Population biomass and biovolume were also determined. Surface tracers reworking coefficients ranged from 0.6 to 2.2 $cm^2\ y^{-1}$ and 0.9 to 4.1 y^{-1}, respectively for the biodiffusive-like and non-local transports. Calculated biodiffusive-like coefficient was between 1.0 and 2.3 $cm^2\ y^{-1}$ for the deep tracers. For both tracers, the *E. cordatum* population presented the highest reworking coefficients. Among the morphological and/or ethological parameters that could determine overall patterns of reworking and differences between species, results have shown a direct relationship between the apparent biodiffusive mixing and the biovolume of the individuals ($D_b = 0.35$ * Biovolume). This suggests that the biovolume of macrofauna may allow a rough estimate of the biodiffusive-like reworking intensity of particles deposited on the sediment surface.

Keywords: Biomass; Bioturbation; Biovolume; Functional Groups; Macrofauna; Sediment reworking

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1. Introduction

Bioturbation, i.e. particle reworking and pore water irrigation activities by benthic fauna, is recognized as one of the major processes that influence the structure and function of sediment environments (Lohrer et al., 2004). Through bioturbation, the uni-omnidirectional displacement of organic and inorganic particles and periodic irrigation of faunal constructions introduce temporal and spatial heterogeneity in the sediment system (Rhoads, 1974; Aller, 1982; Berkenbusch and Ashley, 1999; François et al., 2001). Furthermore, transport of reactants across redox boundaries may considerably affect rates and pathways of organic matter mineralization (Aller, 1994; Gilbert et al., 1996; Hulthe et al., 1998; Sun et al., 1999; Grossi et al., 2003). Thus, quantification of particle transport by fauna is of vital importance for accurate diagenetic models (Soetaert et al., 1996; Boudreau, 1997) and for a qualitative and quantitative understanding of organic matter mineralization in bioturbated deposits.

Bioturbating macrofauna can be classified on the basis of the mode of sediment mixing and overall function of the benthic community. Accordingly, five types of functional groups which aggregate species sharing analogue particle mixing modes have been defined: biodiffusors, upward conveyors, downward conveyors, regenerators and gallery-diffusors (Gardner et al., 1987; François et al., 1997; Gérino et al., 2004). Although it is anticipated that patterns and overall intensity of sediment reworking are different for the various functional groups of macrofauna, variability is also evident between species within the same functional group (François et al., 1999). Additionally, there are difficulties associated with comparing sediment reworking activities of different species and functional groups. For example, quantification of sediment reworking is normally based on models specifically defined according to the different functional groups including advection and diffusion and/or non-local transport (e.g. Berner, 1980; Boudreau, 1986; Gérino et al. 1994; François et al., 1997). Due to a range of experimental conditions and general design of experiments, it is often complicated to directly compare experimental and field observations on sediment reworking. Recent experiments have demonstrated that parameters related to the benthic community such as density of individuals (Sun et al., 1999; Ingalls et al., 2000; Sandnes et al., 2000; Mermillod-Blondin et al., 2001; Duport et al. 2006), to environmental/experimental conditions such as temperature (Ouelette et al., 2004), or to the type and size of tracers added to the experimental cores (Wheatcroft, 1992; Gérino et al., 1998; Caradec et al., 2004), often govern observed the reworking intensity observed for the benthic organisms.

In the present work, the same experimental conditions (i.e. organism density, temperature, type and size of tracers) were applied to four species (*Amphiura filiformis*, *Echinocardium cordatum*, *Scalibregma inflatum* and *Abra nitida*) of macrofauna in experimental microcosms. As the main goal was to compare and quantify sediment reworking activities by different species/functional groups of macrofauna, and to determine the morphological and/or ethological parameters that determine overall patterns of reworking, species were selected from different functional groups of fauna. Comparing reworking activities by single-species macrofaunal communities constitutes one of the first steps to understand and quantify a natural benthic macrofauna community that also include intra-species feedbacks.

2. Materials and methods

2.1. Sediment sampling and preparation of tracers

In July 2001, sediment from the deep trench of the Gullmar Fjord station (Alsbäck; N58° 19′.4, longitude E11° 32′.8; depth: 118 m) was sampled with an Olausson box corer (0.5 m × 0.5 m). Two layers (surface, 0–9 cm; deep, 9–40 cm) of sediment were removed from the box corer and sieved (0.1 and 0.3 cm, respectively) separately. Back in the laboratory, a 6-cm layer of the sieved surface sediment was deposited on top of an 18-cm layer of the sieved deep sediment in a large (0.8 m × 0.8 m) plastic container. Deep water from the Gullmar Fjord (salinity 32 ppt) filled the remainder of the container. The sediment and seawater system was connected to a continuous flow of deep water from the Fjord and allowed to acclimatize in the container for a month.

Sediment reworking activities by benthic macrofauna was quantified using the displacement of fluorescent inert particles (luminophores; e.g., Gérino et al., 1998) added to the sediment surface and to a discrete layer ~3 cm in the sediment. Cakes of luminophores were made according to the following procedure: (1) moulds were made from PVC rings (height: 3.5 cm; I.D.: 9.7 cm) fixed on a PVC plate; (2) 0.5 cm of the sieved surface sediment was added to the moulds; (3) luminophores (1.8 g; 100–160 μm diameter; green colour, λexc: 400 nm; λem: 502 nm; Partrac Ltd, UK) were homogeneously deposited on the sediment surface; (4) the moulds were filled with the sieved surface sediment; (5) luminophores (1.8 g; 100–160 μm diameter; red colour, λexc: 300 nm; λem: 597 nm; Partrac Ltd, UK) were homogeneously deposited on the sediment surface. This allowed the red ("surface tracers") and the green

("deep tracers") luminophores to be located at the sediment surface and at a layer ~3 cm in the sediment. Cakes of sediment and luminophores were stored frozen until the beginning of the bioturbation experiment.

2.2. Incubation of benthic macrofauna

Following the removal of the overlying seawater, 15 PVC cores (height: 20 cm; I.D.: 9.8 cm) were inserted into the sediment of the large plastic container. Each core was sealed with a rubber plug at the bottom and removed from the container. A frozen cake of luminophores was carefully deposited on the surface of each core. Deep water from the Gullmar Fjord was added to each core through a flow-through system, and the cores were stored in a temperature controlled room (10 °C) for 2 days until start of experiments.

The same day, a Van Veen grab was used to sample benthic macro fauna from the Alsbäck site. Animals were sorted and back at the laboratory, selected species (*A. nitida*, *S. inflatum*, *A. filiformis* and *E. cordatum*) were placed in meshed cages and allowed to acclimatize for 2 days in a running water system (Deep water from the Gullmar Fjord; temperature controlled room: 10 °C). The overlying water was removed from the experimental cores and monospecific communities were mimicked by the addition, for each species, of 6 individuals at the surface of sediment cores. Triplicates were done for each species, giving a total of 12 inhabited and 3 control (without added macrofauna) sediment cores. The experimental cores were connected to the water flow-through system and incubated for macrofaunal reworking study.

After 10 days of incubation, the overlying seawater was removed and the experimental cores were vertically sectioned in 0.5-cm thick layers from the surface down to 4 cm depth, and in 1-cm thick layers down to 18 cm. The sediment from each layer was removed separately, freeze-dried and homogenised. Sediment subsamples were taken for counting of luminophore under UV-light (digital camera Olympus C-2500L; image analysis software Image-Pro Plus).

During sectioning of the sediment layers, observed animals, which were found all alive, were removed from the sediment layers. Organism biomass was determined as alcohol-preserved wet-weight (analytical balance; 0.001 g) by blotted-drying individuals on filter paper for 2 min. The biovolume of the organisms was calculated by measuring linear dimensions of each species and fitting nearest geometric models (Hillebrand et al., 1999). Measurements were done with the whole animals (e.g. including the shell).

2.3. Benthic macrofauna used in this study

Within the muddy assemblage of the Gullmarsfjord (Josefson et al., 2002), the species *A. filiformis*, *E. cordatum*, *S. inflatum* and *A. nitida*, were chosen for their potential (or demonstrated) reworking activity.

The echinoderm *A. filiformis* is known to stretch its arms above the sediment for feeding (Buchanan, 1964) and to rapidly transport sediment down along the arms to the disc at 3–4 cm below the surface (Persson and Rosenberg, 2003). In the Gullmar Fjord, Josefson et al. (2002) showed a rapid burial down to 5 cm depth of phytodetritus by *A. filiformis* already 9 h after a simulated planktonic bloom. Overall, *A. filiformis* is considered as an efficient sediment reworker (Rosenberg et al., 1997; Solan and Kennedy, 2002; Gilbert et al., 2003).

The surface deposit feeder *E. cordatum* may rapidly transport particles from the sediment surface deeper (~6.5 cm) into the sediment (Osinga et al., 1997). *E. cordatum* creates a circular spot on the sediment around the opening of its burrow. When feeding immediately adjacent to the burrow is terminated, *E. cordatum* moves to another spot (Cramer et al., 1991).

Scaligbregmidae are active burrowers usually found in soft bottoms where they construct galleries down to depths of ~60 cm (Rouse and Pleijel, 2001), the maximum depth depending on the composition of the sediment (Fauchald and Jumars 1979). Blair et al. (1996) showed that in continental slope sediments dominated by the surface/sub-surface deposit feeder *S. inflatum*, fresh algal material was rapidly transported from the surface down to 4–5 cm depth. The polychaetes created galleries downward from the surface, and were moving up and down in the surface sediment.

The surface deposit feeder *A. nitida* is able to rework the surface sediment (Bellas et al., 2006) by selecting food at the sediment-water interface with their inhalant siphon (Persson and Rosenberg, 2003). *A. nitida* has an overall activity that varies depending of food availability, from only small lateral oscillations of the siphon and no sediment uptake, to very intense events corresponding to shell displacement (Grémare et al., 2004).

The respective number of added individuals, density, biomass and biovolume in the sediments for the different studied species are presented in Table 1.

2.4. Data modelling and statistical analysis

The reaction–diffusion model used in this study to describe luminophore redistribution following macrofaunal

Table 1
Number of added individuals, density, biomass and biovolume in the sediments for the different studied species

Species	Number	Density (ind. m^{-2})	Biomass (g)	Biovolume (cm^3)
Amphiura filiformis	6	795	0.25	2.25
Echinocardium cordatum	6	795	2.22	6.61
Scalibregma inflatum	6	795	1.66	1.06
Abra nitida	6	795	1.41	2.02

reworking is based on the general diagenetic equation (Berner, 1980):

$$\frac{\partial Q}{\partial t} = \frac{\partial}{\partial z}\left(D_b \frac{\partial Q}{\partial z}\right) + R(Q) \quad (1)$$

where Q is the quantity of the tracer, t time from additions of the tracer, z depth in the sediment (z=0 at the water-sediment interface), D_b the apparent biodiffusion coefficient, and $R(Q)$ the non-continuous displacement of tracer. The displacement is defined as follows:

$$R(Q(z,t)) = \begin{cases} \dfrac{r}{z_2 - z_1}\displaystyle\int_0^{z_1} Q(x,t)dx \text{ if } z \in [z_1; z_2] \text{(a)} \\ -rQ(z,t) \text{if } z \in [0; z_1] \text{(b)} \\ 0 \text{ if } z > z_2 \text{(c)} \end{cases} \quad (2)$$

where z_1 and z_2 define the upper and lower limits of the tracer redistribution, x and z are depth variables, and r (the biotransport coefficient) the percentage of tracer that left the [0, x_1] deposit and was redistributed in the [z_1, z_2] layer. The redistribution of tracer between z_1 and z_2, and the disappearance of tracer from the 0–z_1 layer, are described by Eq. 2a and b, respectively. Eq. 2c denotes that no tracer movement occurs below the sediment depth z_2.

Non-local displacement of tracers was originally exemplified in a model describing gallery-diffusion of macrofaunal reworking (François et al., 2002).

This biological reworking process describes the diffusive-like mixing of particles in the region of intense burrowing activity, and the rapid transport of organic and inorganic material from the upper sediment layers to the lower regions of reworking (i.e. 'biotransport').

According to the experimental conditions, the following initial conditions were used:

$$Q(z,0) = \begin{cases} Q_0 \text{ if } z \in [x_1; x_2] \\ 0 \text{ else} \end{cases} \quad (3)$$

where [x_1; x_2] is the tracer deposit layer.

Finally, a zero-flux Neuman boundary condition was considered:

$$\frac{\partial Q}{\partial z}(0,t) = \lim_{z \to +\infty} \frac{\partial Q}{\partial z}(z,t) = 0 \quad (4)$$

This bioturbation model applied to tracer redistributions allowed us to quantify two particle mixing coefficients: an apparent biodiffusion coefficient D_b and a non-local biotransport coefficient r. The parameters' estimation has been performed by the least square method. The biodiffusion coefficient D_b takes into account the diffusion-like transport due to the activity of the organisms. We assume that the actual concentration dependent diffusion of tracers is negligible. The biotransport coefficient (r) represents a non-local mixing pattern associated with a biologically induced transfer of

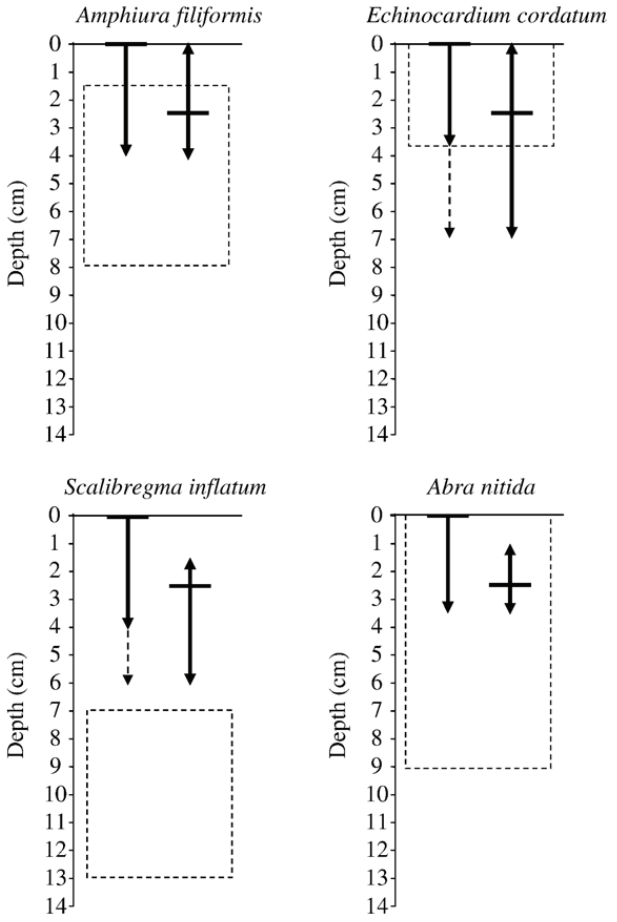

Fig. 1. Sediment zone (dotted rectangle) where individuals were found at the end of the experiment and range of luminophore movements (solid arrows) from surface (surface tracers) and 2.5 cm deep in the sediments (deep tracers) due to the four studied macrobenthic species (*A. filiformis*, *E. cordatum*, *S. inflatum* and *A. nitida*). Horizontal lines are the starting points for luminophores. Dotted arrows represent potentialities of tracer burying (i.e. potential deeper displacement of surface tracers according to the downward transport of deep tracers).

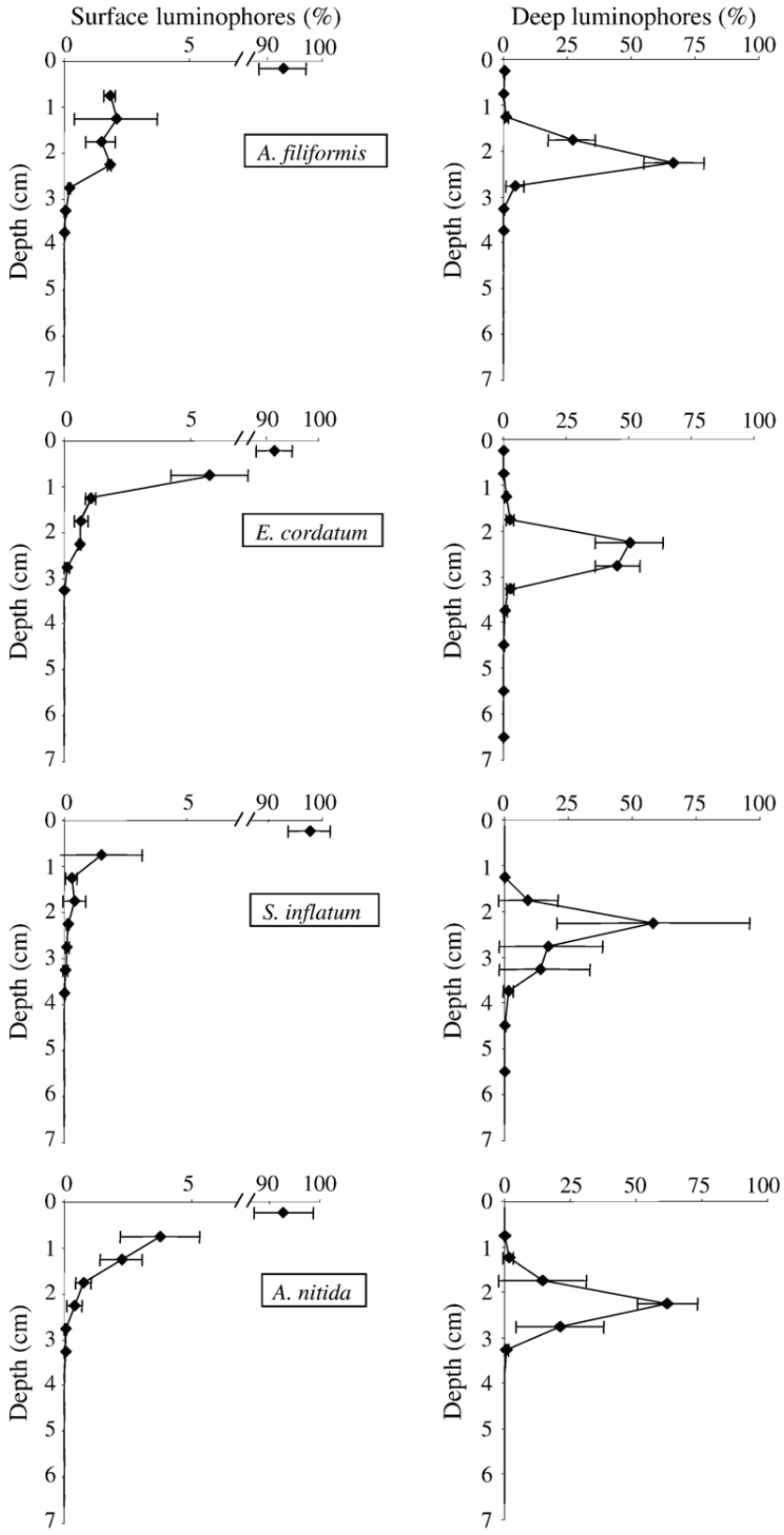

Fig. 2. Repartition profiles (Mean ± SD; $n = 3$) of the luminophores initially deposited at the sediment surface (surface tracers; left) and 2.5 cm deep in the sediment (deep tracers; right), for the four studied macrobenthic species.

particles from one place to another in a discontinuous pattern (i.e. a non-continuous transport; Boudreau, 1986; Meysman et al., 2003).

Differences between species were studied using a one-way analysis of variance (ANOVA). Bartlett's test

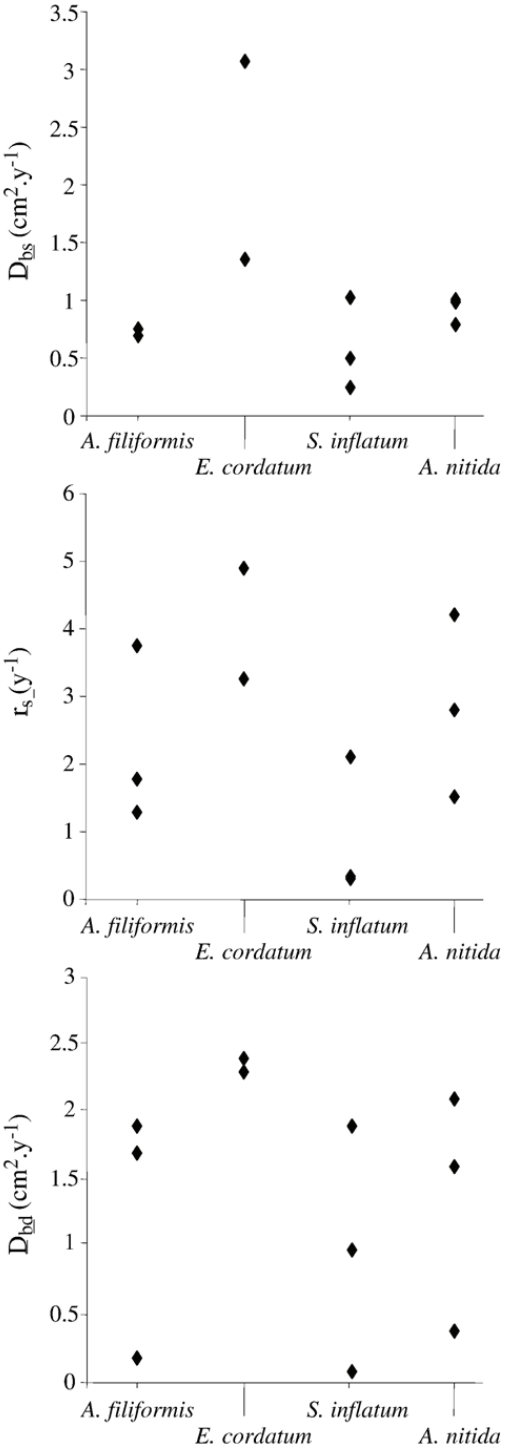

Fig. 3. Biodiffusion (D_{bs} and D_{bd}) and biotransport (r_s) coefficients calculated for the four studied macrobenthic species. D_{bs} and r_s: coefficients for the surface tracers; D_{bd}: coefficient for the deep tracers. Values are individual points for triplicate observations.

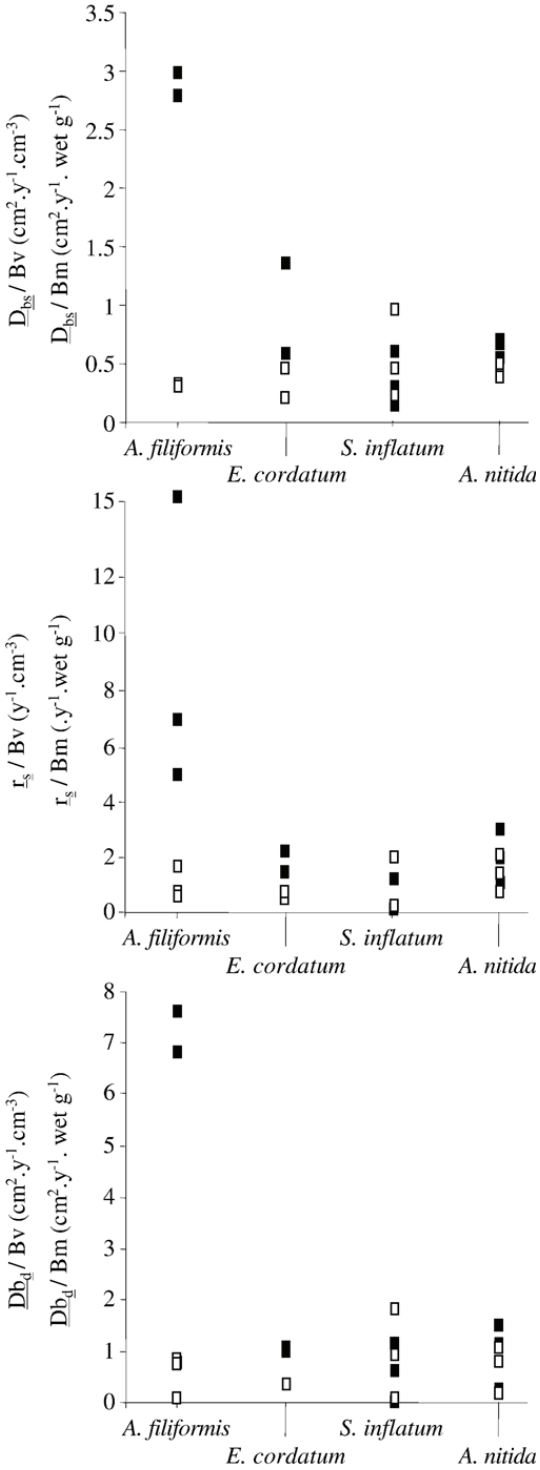

Fig. 4. Biodiffusion (D_{bs} and D_{bd}) and biotransport (r_s) coefficients per wet biomass (solid symbol) and per biovolume (open symbol) calculated for the four studied macrobenthic species. D_{bs} and r_s: coefficients for the surface tracers; D_{bd}: coefficient for the deep tracers. Values are individual points for triplicate observations.

was employed to test for homogeneity of variance. Heteroscedastic data were transformed and then evaluated using ANOVA.

3. Results

3.1. Spatial distribution of organisms and luminophores

At the end of the experiment, the four species were recovered at different depths in the sediment (Fig. 1). Individuals of *A. filiformis* and *S. inflatum* were found from 1.5 to 8 cm and 7 to 13 cm in the sediment, respectively. Occasionally, however, individuals of both *E. cordatum* and *A. nitida* were observed just at the sediment-water interface (0–0.5 cm), or down to 3.5 cm and 9 cm in the sediment, respectively.

In the control cores without macrofauna, luminophores initially deposited on the sediment surface or deposited at a layer ~3 cm in the sediment were only found at discrete sediment layers (data not shown). This demonstrated that sediment reworking was below the level of quantification in cores without macrofauna. However, due to freezing, thawing and compaction of the sediment cakes during the experimental procedure, luminophores initially deposited at ~3 cm were recovered at ~2.5 cm in the sediment (Fig. 2). In sediments with macrofauna, tracers initially added on the sediment surface were found down to 3.5 (*E. cordatum* and *A. nitida*) or 4 cm (*A. filiformis* and *S.*

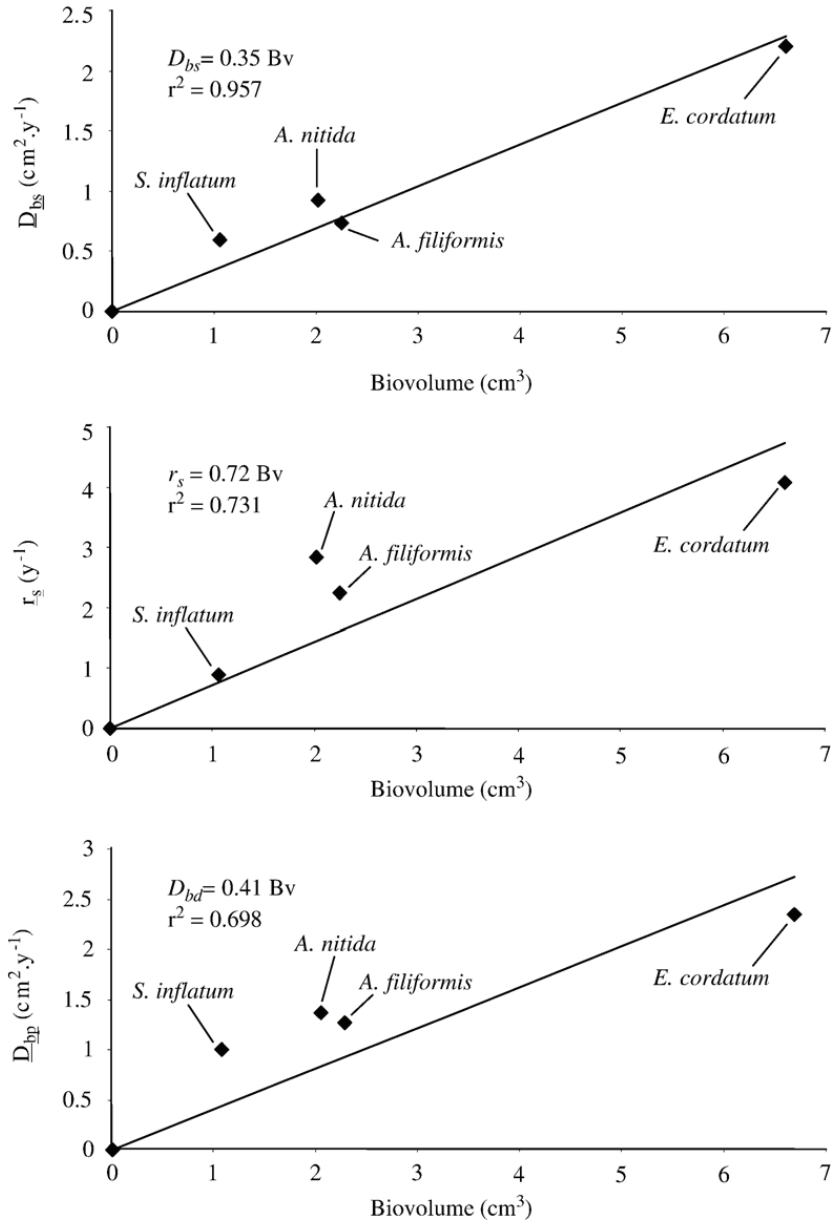

Fig. 5. Biodiffusion (D_{bs} and D_{bd}) and biotransport (r_s) coefficients as a function of the biovolume for the four studied macrobenthic species. D_{bs} and r_s: coefficients for the surface tracers; D_{bd}: coefficient for the deep tracers. Values are means for triplicate observations.

inflatum) in the sediment (Fig. 2). In addition to observations of surface luminophores deeper in the sediment (i.e. a downward transport of particles), luminophores deposited at a discrete layer within the sediment were observed both closer to the sediment surface (upward transport) and deeper than 2.5 cm (downward transport). Patterns by which the luminophores were repartitioned were different between species (Fig. 2). For example, most pronounced downward transport of luminophores deposited at ~3 cm within the sediment was observed for the surface deposit feeder *E. cordatum* and the surface/sub-surface deposit feeder *S. inflatum*. These species were able to translocate particles down to 7 and 6 cm in the sediment, respectively. In sediments with *A. filiformis* and *A. nitida*, luminophores were found closer the deposition layer, i.e. not below 3–4 cm depth. In sediments with *A. filiformis* and *E. cordatum*, luminophores deposited within the sediment were after the incubation period observed at the sediment surface, i.e. there was a significant upward transport of sediment particles. For the *S. inflatum* and *A. nitida* species, tracers were also moved upwards, but their range of displacement was reduced to 1 and 1.5 cm up, respectively.

3.2. Quantification of sediment reworking

In our experimental system, quantification of sediment reworking activities showed that the transport of luminophores deposited on the sediment surface could be explained by a continuous (D_{bs}) and a non-continuous transport of tracer (r_s). On the other hand, luminophores deposited within the sediment were only influenced by a continuous transport (D_{bd}) (Fig. 2).

Overall, lowest rates of sediment mixing were calculated for *S .inflatum* while highest rates of sediment transport were found in sediments inhabited by *E. cordatum* (Fig. 3). The apparent diffusion coefficient induced by macrofaunal reworking (D_b), estimated either from the distributions of luminophores deposited on the sediment surface (D_{bs}) or luminophores within the sediment (D_{bd}), were 0.59±0.33 $cm^2\ y^{-1}$ (D_{bs}) and 1.00±0.73 $cm^2\ y^{-1}$ (D_{bd}), and 2.20±0.85 $cm^2\ y^{-1}$ (D_{bs}) and 2.35±0.05 $cm^2\ y^{-1}$ (D_{bd}) (mean±SD; $n=3$) for *S. inflatum* and *E. cordatum*, respectively. The non-continuous transport of tracer (r_s) was 0.88±0.86 and 4.08±0.83 y^{-1} for cores with *S. inflatum* and *E. cordatum*, respectively (Fig. 3).

There were significant differences in the calculated D_{bs} between species (ANOVA, $p=0.04$) while r_s (ANOVA, $p=0.09$) and D_{bd} (ANOVA, $p=0.52$) were not significantly different.

During incubations, there were 6 individuals of the same species of macrofauna in each core. In order to compare sediment reworking activities in the various inhabited sediments, the mixing coefficients were normalized to faunal biomass and biovolume of individuals (Fig. 4). Normalized to biomass, biodiffusive and non-local sediment transport rates were highest for the echinoderm *A. filiformis*, and progressively decreasing rates for *E. cordatum*, *A. nitida* and *S. inflatum*. Mixing surface rates normalized to biomass were significantly different (ANOVA) between species (D_{bs}/Bm, ***$p=0.0002$; r_s/Bm, ***$p=0.0042$). There was, however, no significant difference for the normalized biodiffusive mixing estimated from luminophores deposited within the sediment (D_{bd}/Bm, $p=0.12$). Normalizing sediment reworking to macrofaunal biovolume (D_{bs}/Bv, r_s/Bv and D_{bd}/Bv) erased the difference (ANOVA, $p>0.5$) in sediment mixing between species (Fig. 4).

4. Discussion

4.1. Macrofaunal reworking activities

From a bioturbation functional point of view, and according to their respective general behaviour, *A. filiformis*, *E. cordatum* and *A. nitida* could be classified as biodiffusors, and *S. inflatum* as a gallery-diffusor.

Results clearly shown that particulate tracers were not only transported downwards from the sediment surface, but that all four species also induced an upward transport of particles. The echinoderms *A. filiformis*, *E. cordatum* were able to translocate luminophores initially deposited ~3-cm deep in the sediment to the sediment surface. Unlike conveyor-belt feeders (e.g. oligochaetes) that transport particles from sub-surface to the sediment surface by burrowing into sediments to feed, while defecating on the sediment surface (Rhoads, 1974; Robbins et al., 1979), the investigated species could not be related to functional groups with such patterns of reworking.

When comparing the distribution of luminophores following sediment reworking by macrofauna and the vertical location of the organisms, the efficient reworking zones for *A. filiformis* and *A. nitida* appeared above their bodies and limited by the size of the arms and siphons, respectively (Fig. 1). Individuals of *E. cordatum* were found in the main mixing zone (~0–3 cm) suggesting a mode of particle reworking essentially governed by its surface/sub-surface locomotion behaviour. In contrast, individuals of *S. inflatum* were recovered significantly below the depth where luminophores were observed.

By constructing U-shaped galleries deep in the sedimentary column, the polychaete allowed surface material to enter the burrow and likely accumulate at the first vertical bend.

4.2. Quantification of sediment reworking

The quantification of sediment reworking was realized using the broad gallery-diffusion model developed by François et al. (2002). This model is compatible with different reworking modes since it can describe both a diffusive-like mixing of particles in the upper sediment layers and a rapid transport of material below, a pattern that was observed with the four different species studied. Quantification of particle mixing demonstrated that *E. cordatum* was the most efficient sediment reworker in our study. This was especially significant for biodiffusive transport of surface tracers with a mean D_{bs} of 2.20 $cm^2\ y^{-1}$. *A. filiformis* and *A. nitida* presented similar reworking intensities roughly corresponding to half of those measured for *E. cordatum*. The less efficient mixing was realized by the polychaete *S. inflatum*. Despite the lack of significance, both the non-local transport of surface tracers (r_s) and the biodiffusive transport of deep tracers transport (D_{bd}) also showed the same tendency.

In previous investigations, Sandnes et al. (2000) and Gilbert et al. (2003) experimentally determined reworking intensities of natural benthic communities dominated by *E. cordatum* and *A. filiformis*. These species were observed to mix the sediment with an intensity of 1 to 5 $cm^2\ y^{-1}$ and 35 $cm^2\ y^{-1}$, respectively. In contradiction with the present study, these results could present *A. filiformis* as a powerful reworker compared to *E. cordatum*. However, macrofaunal densities utilized in Sandnes et al. (2000) and Gilbert et al. (2003) were significantly different (*E. cordatum*: 4 to 40 ind. m^{-2}; *A. filiformis*: ~2500 ind. m^{-2}) than the constant one used in this study (795 ind. m^{-2}). A direct comparison of previously and present measured reworking intensities is therefore difficult, although we may consider that, in this case, the observed differences are rather reflecting variation in organism density than of their reworking capacity.

It appears difficult to conclude in a general particle reworking intensity based on the concept of macrofaunal functionality, and functional traits associated with the different species seem to commonly overrule the general functional characteristics. In this study, there were pronounced variability in measured reworking intensities also between different species within the same functional group. In François et al. (1999) morphological parameters (e.g. size of the siphons) could not explain observed differences in reworking activities between the biodiffusor bivalves *Ruditapes decussatus* and *Venerupis aurea*.

It is likely that population characteristics (e.g. density; Sun et al., 1999; Ingalls et al., 2000; Sandnes et al., 2000) alone or in combination with environmental parameters (e.g. temperature; Ouellette et al., 2004) influence the apparent mixing coefficients in a non-linear way. Aiming to compare reworking characteristics between species and/or functional groups, the present study was performed at a constant temperature (10 °C) and a fixed density of organisms (795 ind. m^{-2}). Macrofaunal biomass, however, varied between populations. Patterns of sediment mixing rates for macrofauna still remained following normalization of sediment reworking to biomass of individuals in each core (Fig. 4), although the normalized rate was highest for the *A. filiformis* cores compared to the other species. Thus, variations in biomass between populations (e.g., Duplisea et al., 2001; Emmerson et al., 2001; Nizzoli et al., 2002) could not explain the observed variations in sediment mixing rate. In contrast, continuous and non-local mixing coefficients normalized to the biovolume of individuals demonstrated no difference between species and within each functional group of fauna (Fig. 4). The importance of macrofaunal biovolume rather than biomass for sediment reworking activities, suggest a direct coupling between sediment transport and the space occupied by the organisms. Experiments demonstrated that D_{bs}, one of the most commonly used parameter to quantify sediment reworking, is a linear function of the biovolume: $D_{bs}=0.35$ * Biovolume ($r^2=0.957$; Fig. 5), suggesting that the simple knowledge of organisms' biovolume may allow to easily estimate the biodiffusive-like reworking intensity of surface deposited particles. During movement, benthic organisms potentially displace (e.g. by pushing directly into the frontal and surrounding sediment; Dorgan et al. 2005) a quantity of sediment in proportion to its volumetric size. Our results suggest that the species investigated (*A. filiformis*, *A. nitida*, *E. cordatum*, *S. inflatum*), although belonging to different functional groups of macrofauna, have a similar reworking intensity when displacing sediment particles.

We did not test, however, species for which sediment reworking is essentially related to their feeding ethology (e.g. upward or downward conveyor) rather than their body displacement. In our work, the observed relationships between biovolume and sediment mixing only concerns biodiffusive-like transport but not non-local transport as realized by conveyors. Nevertheless, we could assume that bigger are conveyor organisms higher is the quantity of particles ingested and transported,

suggesting that such relationships between biovolume and sediment reworking might also specifically exist for non-local transport. Further experiments are requested to investigate this point.

Recently, studies by Michaud et al. (2005, 2006) showed that, in bioturbated sediments inhabited by *Macoma baltica*, *Mya arenaria* and *Nereis virens* populations with identical biovolumes, sediment oxygen uptake and nutrients fluxes were significantly different. This was explained by the differences in solute penetration inside the burrows and in the behaviour of the species belonging to different functional groups: periodic ventilation by the gallery-diffuser (*N. virens*) *vs* steady activity of biodiffusers (*M. baltica*, *M. arenaria*). Contrary to sediment reworking, changes in fluxes are not solely directly induced by the activities of bioturbating organisms (sediment mixing and bio-irrigation). Indeed, fluxes also depend on the rapid responses of bacterial activities to changes driven by bioturbation (Aller, 2001). Contrary to sediment reworking, this may explain the lack of relationships between organism biovolume and sediment fluxes.

In the present study, we observed a direct coupling between the biovolume of macrofauna and rates of particle reworking by fauna. The relation was most pronounced for the diffusive-like transport of particles deposited on the sediment surface (Fig. 5). Indeed, the non-continuous (non-local) particle transport is not only related to activities (and particularly movements) of macrofauna, but also to animal-independent events such as particle fall down the burrows. Similarly, transport of deep located tracers within the sediment seemed to be rather affected by the initial construction of biogenic structures (e.g. burrows) build by the organisms such as gallery-diffusors than their further displacements.

5. Conclusion

Experiments demonstrated a direct relation between sediment reworking intensity (D_{bs}) and the biovolume of individuals: $D_{bs} = 0.35 * \text{Biovolume}$. This suggests that the biovolume of macrofauna allows a rough estimate of the biodiffusive-like reworking intensity of particles deposited on the sediment surface.

Nevertheless, this relationship between biodiffusive-like transport and biovolume must be confirmed for the other functional groups and/or populations presenting variable biovolumes. Also it would be interesting to study the biovolume-sediment reworking relationships with communities where interactions between species/functional groups can occur.

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