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The functional significance of bioturbation and biodeposition on biogeochemical processes at the water–sediment interface in freshwater and marine ecosystems

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Abstract. Benthic invertebrates have important ecosystem engineering functions (bioturbation and biodeposition) in freshwater and marine benthic systems. Bioturbation and biodeposition affect the metabolism of the water–sediment interface through modification of water–sediment fluxes or organic-matter enrichment of sediments by biodeposits. The functional significance of these processes depends strongly on the type of invertebrate activities (the functional traits of the invertebrates) and on the modulation of this activity by environmental conditions. The aim of my article is to propose a common framework for the role of bioturbation/biodeposition in benthic habitats of both marine and freshwater environments. In these ecosystems, hydrological exchanges between the water and sediments (interstitial flow rates) control the microbial activity inside sediments. The ability of ecosystem engineers to influence benthic microbial processes differs strongly between diffusion-dominated (low interstitial flow rates) and advection-dominated (high interstitial flow rates) habitats. Bioturbation/biodeposition may play a role in diffusion-dominated habitats where invertebrates can significantly modify water and particle fluxes at the water–sediment interface, whereas a slight influence of ecosystem engineers is expected in advection-dominated habitats where fluxes are predominantly controlled by hydrological processes. A future challenge will be to test this general framework in marine and freshwater habitats by quantifying the interactions between the functional traits of species and the water–sediment exchanges.

Key words: ecosystem engineers, benthic habitats, microbial activity, hydrological exchanges.

General Context

Water–sediment interfaces are dynamic zones that regulate the fluxes of organic matter, nutrients, and contaminants between the water column and sediments in marine and freshwater ecosystems (Palmer et al. 1997, Covich et al. 2004). At these interfaces, ecological processes are mediated through complex interactions between the abiotic characteristics of sedimentary habitats and the activities of resident organisms (Giller et al. 2004). Microorganisms are the key actors of biogeochemical processes in sedimentary habitats (Sundbäck et al. 2004, Battin et al. 2008), but the feeding and bioturbation actions of meio- and macroorganisms can have a marked effect on microbial activities in sediments (Kristensen et al. 1985, Aller 1994, Rosenberg 2001). Many examples have highlighted the key ecological role played by ecosystem engineers (Jones et al. 1994) in marine, lake, estuarine, and stream habitats (Rhoads 1974, Krantzberg 1985, Statzner et al. 2000, Meysman et al. 2006). As ecosystem engineers, organisms that redistribute particles and modify water fluxes at the water–sediment interface affect the availability of electron acceptors (e.g., dissolved O_2), organic matter, and nutrients to sedimentary microorganisms (Kristensen 2000, Mermillod-Blondin and Rosenberg 2006). Bioturbation and biodeposition are 2 major engineering processes occurring at the water–sediment interface of freshwater and marine ecosystems.

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Bioturbation and Biodeposition Processes

Bioturbation is related to several activities of benthic organisms, including sediment reworking caused by burrowing activities, construction of tubes and burrows, and irrigation of these biogenic structures (Gerino et al. 2003). Biodeposition is the settling of feces and pseudofeces produced by suspension-feeding animals (Haven and Morales-Alamo 1966) and by organisms that convert coarse particulate organic matter into fecal pellets (Joyce and Wotton 2008). My paper is focused on the implications of these 2 processes for understanding particle transport (sediment reworking, feces and pseudofeces deposition) and water exchanges (permeability change, bioirrigation) at the water–sediment interface. These 2 physical changes are major modulators of microbial activities and biogeochemical processes in marine and freshwater benthic habitats.

The potential for bioturbation/biodeposition to be critical processes in terrestrial and aquatic environments has been recognized since Darwin and his seminal work on earthworms and soil formation (Darwin 1881 in Meysman et al. 2006). In aquatic ecosystems, scientific research on these processes really began in the middle of the 20th century and was focused on lake (reviewed by Krantzberg 1985) and marine sediments (reviewed by Rhoads 1974). The role of bioturbation/biodeposition in stream and river sediments was studied later (e.g., Chatarpaul et al. 1979) and has received less attention than in lake and marine benthic systems (Boulton et al. 2010). Consequently, the coupling between bioturbation/biodeposition processes and biogeochemical processes has been quantified unequally among aquatic ecosystems. My goal was to use the literature to: 1) review the main effects of bioturbation/biodeposition on benthic microbial activities, 2) describe how these effects are linked to the functional traits (mode of bioturbation/biodeposition) of invertebrates, and 3) propose a conceptual framework linking the functional significance of bioturbation/biodeposition on biogeochemical processes with the physical structure of the benthic habitats.

General Influences of Bioturbation and Biodeposition Processes on Biogeochemical Processes at the Water–Sediment Interface

In marine, lake, and wetland habitats, bioturbation by invertebrates that build and irrigate biogenic structures (tubes, burrows) increases the area available for solute exchange and oxic/anoxic boundaries (Aller 1983, Forster and Graf 1995, Vopel et al. 2003, Lewandowski et al. 2007, D'Andrea and DeWitt 2009). Consequently, bioturbation may increase the aerobic respiration of sedimentary microorganisms by up to 250% (Kristensen 2000, Mermillod-Blondin et al. 2004, Karlson et al. 2005, Quintana et al. 2007) and can significantly influence the fluxes of nutrients (NO_3^-, NH_4^+, PO_4^{3-}, SO_4^{2-}, Fe) and dissolved organic matter at the water–sediment interface (Caliman et al. 2007, Lewandowski et al. 2007). Bioturbation processes also significantly influence the fate of pollutants (metals, organic pollutants) and emission of greenhouse gases (N_2O, CH_4) at the water–sediment interface (Ciutat et al. 2005, Granberg et al. 2005, 2008, Lagauzère et al. 2009, Stief and Schramm 2010). The influence of biodeposition on sedimentary biogeochemical processes has been reported from environmental studies designed to determine the effect of mussel and oyster cultures on marine benthic habitats (e.g., Chamberlain et al. 2001, Callier et al. 2006). Most of these studies showed that organically rich feces and pseudofeces accumulate at the water–sediment interface and create reducing conditions in the sediment (Nizzoli et al. 2005, Lindqvist et al. 2009). This organic-matter enrichment stimulates O_2 uptake by microorganisms at the sediment surface (Heilskov and Holmer 2001) and often increases the flux of nutrients at the water–sediment interface (Christensen et al. 2003, Gibbs et al. 2005, Giles and Pilditch 2006). However, the effect of biodeposition on benthic fauna is dependent on suspension-feeder densities. At high densities, high rates of biodeposition affect macrofaunal diversity by reducing O_2 availability at the water–sediment interface (Commito and Boncavage 1989). At low densities, the organic-matter enrichment by biodeposits has a positive influence on macrofaunal diversity by providing an important resource for benthic species without producing unfavorable anaerobic conditions (Norkko et al. 2001). The benthic–pelagic coupling induced by biodeposition also influences pollutant dynamics because contaminated particles in free water are accumulated in fecal pellets and pseudofeces and deposited at the sediment surface (Cho et al. 2004, Schaller et al. 2010).

These patterns of the influences of bioturbation and biodeposition on biogeochemical functioning at the water–sediment interface mainly arose from studies performed in benthic habitats with fine sediment texture and low physical exchange of water between free and interstitial water like standing-water areas of lakes, ponds, and marine offshore areas where hydrological exchanges between free water and interstitial water are dominated by water diffusion. In contrast, the influence of bioturbation and biodeposition on biogeochemistry has been poorly studied in advection-dominated benthic habitats like areas of streams, rivers, and shallow estuaries, which are characterized by important hydrological exchanges between free water and interstitial water (Boulton et al. 2002). Despite the scarcity of studies performed in advection-dominated systems, Mermillod-Blondin and Rosenberg (2006) stressed that the physical features (advection-dominated vs diffusion-dominated systems) of the water–sediment interfaces interact with the species' bioturbation mode to drive microbial processes (O_2 uptake, N cycling) in sediments. Thus, research on the engineering functions of benthic animals and their modulation by environmental factors must be integrated to understand the influence of bioturbation/biodeposition processes on the metabolism of benthic ecosystems (Bulling et al. 2008).

Ecosystem Engineering Functions: the Functional Group Approach

The bioturbation/biodeposition functions of benthic invertebrates vary strongly according to their biological traits (mode of feeding, mode of locomotion, ingestion–digestion mechanisms, ecophysiology; Pearson 2001, Hughes et al. 2005). Functional groups (functional group = a group of species having similar effects on major ecosystem processes; Chapin et al. 1992) have been widely developed (e.g., Pearson 2001) and used to simplify the description of community roles in ecosystems. For instance, benthic species in river ecosystems often are classified into functional feeding groups according to their roles in organic-matter processing (Cummins 1974, Cummins and Klug 1979). With respect to bioturbation processes, invertebrates belong to distinct functional groups according to their mechanical activities that modify sediment properties and influence biogeochemical processes (Gerino et al. 2003). Five functional groups of bioturbators have been defined in soft-bottom sediments (François et al. 1997, 2002): 1) biodiffusors are organisms whose activities on the surface result in random sediment mixing; 2) upward conveyors and 3) downward conveyors are organisms whose feeding activities (ingestion and egestion) move sediment vertically upward or downward, respectively; 4) regenerators are digging organisms that relocate sediment and generate open burrows that fill with surface particles when abandoned; and 5) gallery-diffusors are organisms that build extensive galleries of burrows that are irrigated by biotic activities. This functional group approach considers 4 functional traits (sediment mixing rate, burrowing depth, biogenic structure produced, and bioirrigation rate of tubes and burrows) that are the most relevant to assess the influence of bioturbators on biogeochemical processes (aerobic microbial activity, nutrient fluxes) in marine and freshwater diffusion-dominated sediments (Banta et al. 1999, Michaud et al. 2005, Caliman et al. 2007). For instance, animals that produce and irrigate deep burrows and galleries (gallery-diffusers), such as the polychaete *Nereis* sp. in marine sediments or the oligochaete *Tubifex tubifex* in wetland sediments, stimulate aerobic microbial activities and N fluxes at the water–sediment interface (Svensson et al. 2001, Michaud et al. 2005, Mermillod-Blondin and Lemoine 2010). In contrast, animals, such as bivalves, that mix sediments without creating biogenic structures have a lower influence on fluxes and microbial activities occurring in sediments (Pelegri and Blackburn 1995a, Michaud et al. 2006). Mermillod-Blondin et al. (2002) demonstrated that the bioturbation modes of freshwater invertebrates determine their influence on biogeochemical processes in advection-dominated sediments. Gallery-diffusers (tubificid worms) stimulated microbial activities in sediments, whereas biodiffusors (*Asellus aquaticus*) did not (Mermillod-Blondin et al. 2002). Therefore, a common classification of bioturbation groups based on quantification of functional traits can be developed in diffusion-dominated and advection-dominated habitats of marine and freshwater environments.

To my knowledge, no functional-group classification has been developed to characterize the role of different suspension-feeders on benthic biogeochemical processes through feces and pseudofeces production. The mode of biodeposition is comparable for all suspension-feeder species, but the biodeposition rate (quantity of feces and pseudofeces produced) may differ strongly among species and groups of species (Rhoads 1974, Zhou et al. 2006). Moreover, the effects of biodeposition on benthic processes are related to the quality of organic matter and the quantity of biodeposits, which are influenced by the rate of fecal pellet production and the quality of the ingested particles (Hughes et al. 2005, Gergs et al. 2009). By considering suspension-feeding efficiency and biodeposition rate of benthic species, one could develop a functional-group classification for the biodeposition process similar to the classification developed for bioturbation. Thus, the effect of benthic invertebrates on microbial processes at the water–sediment interface could be associated with 5 major functional traits that summarize the intensity of bioturbation/biodeposition process exhibited by a species at the water–sediment interface (see functional traits indicated in Fig. 1). However, such a functional approach cannot be used without considering the variability of environmental factors, such as hydrodynamics (Chamberlain et al. 2001, Biles et al. 2003), food resources (Hansen and Kristensen 1998, Spooner and Vaughn 2006, Lauringson et al. 2007), temperature (Ouellette et al. 2004, Przeslawski et al. 2009), and contaminants (Mulsow et al. 2002, Lagauzère et al. 2009). All

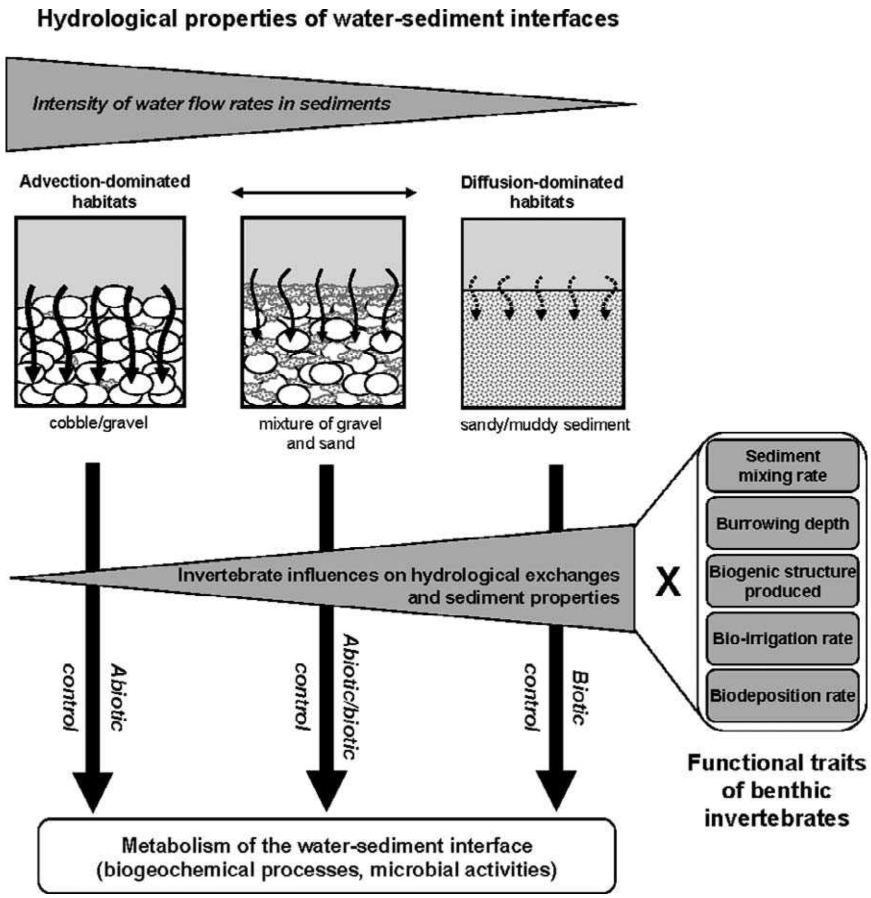

FIG. 1. The interactions between hydrological properties of the habitats and the engineering activities (bioturbation and biodeposition) of invertebrates dictate the biogeochemical processes at the water–sediment interface. X indicates that the influences of benthic invertebrates on hydrological exchanges and sediment properties are highly linked with the functional traits of the organisms.

modulate bioturbation/biodeposition processes in aquatic ecosystems. The degree of hydrological exchanges occurring at the water–sediment interface appears to be the main factor influencing the potential contribution of bioturbation/biodeposition on biogeochemical processes in marine and freshwater benthic habitats (Boulton et al. 2002, Mermillod-Blondin and Rosenberg 2006). I propose to develop a qualitative scheme of the role of bioturbation/biodeposition on microbial processes in benthic environments based on the hydrological characterization of the habitats rather than on their membership in marine or freshwater ecosystems.

Patterns of Hydrological Exchanges Modulate the Significance of Bioturbation/Biodeposition Processes in Benthic Habitats

The biogeochemical processes occurring at the water–sediment interface in standing- and running-water ecosystems are driven mainly by hydrological exchanges between surface and interstitial layers (Forster et al. 1999, Fellows et al. 2001, Boulton et al. 2010). The magnitude of hydrological exchanges dictates the availability of dissolved O_2, nutrients, and organic C for microorganisms (reviewed by Brunke and Gonser 1997). In a comparison between advection-dominated and diffusion-dominated systems, Mermillod-Blondin and Rosenberg (2006) showed that microbial respiration at the water–sediment interface in microcosms was 2× higher in a hyporheic system with a permanent water infiltration than in a system characterized by diffusion-dominated conditions. Benthic systems range from low to high hydrological exchanges in relation to hydrodynamics and sedimentary structure (Palmer et al. 1997), so the ability of ecosystem engineers to influence microbial processes will depend on the benthic habitat studied. Boulton et al. (2002) hypothesized that invertebrates can act as "direct vectors" of water and materials in lentic systems (diffusion-dominated habitats), whereas they act only as "modulators" of water fluxes in lotic systems (advection-dominated habitats). This conceptual view suggests a greater influence of bioturbation in diffusion-dominated than in advection-dominated systems (Hakenkamp and Palmer 2000). This prediction was confirmed by bioturbation studies reported from both marine and freshwater benthic habitats. In high hydrological exchange zones like the hyporheic zone of streams, the modification of microbial respiration by invertebrate bioturbation ranges between −20 and +50% (Pusch and Schwoerbel 1994, Marshall and Hall 2004, Mermillod-Blondin and Rosenberg 2006). The degree of respiration change depends on the bioturbation traits of the species tested (sediment mixing rate, burrowing depth, production of U-shaped tubes or galleries of burrows; Mermillod-Blondin et al. 2002). These results were linked to the low ability of bioturbators to influence sediment permeability and interstitial flow rates (Boulton et al. 2002). In contrast, bioturbation by U-shaped tube burrower and gallery-diffusor invertebrates may increase microbial respiration at the water–sediment interface of diffusion-dominated systems by up to 250% (Pelegri and Blackburn 1995b, Svensson and Leonardson 1996, Karlson et al. 2005, Mermillod-Blondin et al. 2008). In these systems, production and irrigation of deep burrows (gallery-diffusion) may increase the flux of water in sediments by up to 2000% (Rasmussen et al. 1998). These results illustrate clearly that the potential contribution of bioturbation to benthic microbial processes varies across the spectrum of hydrological conditions. Therefore, I propose a conceptual model that takes into account the hydrological properties of benthic habitats and the functional traits of invertebrates to allow a better prediction of bioturbation/biodeposition effects on sediment biogeochemistry (Fig. 1). In advection-dominated habitats, hydrological exchanges between surface and interstitial water are little affected by invertebrate bioturbation, and the contribution of bioturbators to microbial processes is reduced. In diffusion-dominated habitats, the opposite is observed because the physical hydrological exchanges are low and can be dramatically affected by bioturbators, depending on their bioturbation functional traits (Fig. 1; Mermillod-Blondin and Rosenberg 2006).

In the scheme presented in Fig. 1, use of the hydraulic exchanges at the water–sediment interface to evaluate the significance of bioturbation can be applied to the different habitats of a river (riffles, pools, erosion zones, sedimentation zones). For example, when hydrological exchanges at the water–sediment interface are impaired by fine sediment deposition (Schälchli 1992, Wood and Armitage 1997), hydrological exchanges in sediments will be low and deep burrowing by the tubificid worm *Tubifex tubifex* could efficiently restore hydrological exchanges and aerobic biogeochemical processes in sediments (Nogaro and Mermillod-Blondin 2009). Thus, the significance of bioturbation on sedimentary microbial processes is dependent on the hydrological-exchange context.

This modulation of engineering function by hydrological exchanges at the water–sediment interface has been poorly studied in the process of biodeposition. Nevertheless, the effects of biodeposition are strongly influenced by hydraulic conditions that determine the zones of biodeposition in aquatic ecosystems. For example, the fecal pellets produced by suspension-feeding invertebrates living in high-flow conditions (e.g., blackflies in streams) are flushed away from the site of production and deposited in zones of low flow (Malmqvist et al. 2001, Wotton and Malmqvist 2001, Wharton et al. 2006). Similarly, the influence of shellfish farming on marine sediments is influenced by hydrodynamics that modulate the sedimentation rate of biodeposited material (Callier et al. 2006). Therefore, the significance of biodeposition intensity, as with bioturbation traits (Fig. 1), is likely to be highest in zones of low-energy hydrological conditions associated with diffusion-dominated microhabitats (where deposition occurs).

Conclusions

My paper presents a general qualitative framework linking the significance of bioturbation/biodeposition processes to the hydrological characteristics of the water–sediment interfaces. This approach focuses on the local characteristics of the water–sediment interfaces and the functional traits of benthic invertebrates. My hope is that the approach will be used in both marine and freshwater sciences. However, this marine–freshwater bridge must be tested on a wide range of habitats ranging from deep-sea bottom to stream riffles. If characterization of hydrological exchanges occurring at the water–sediment interface can be done easily through tracer experiments, one major challenge in future studies will be to quantify the functional traits of the benthic species (right panel of Fig. 1) and their influences on ecological processes. Moreover, these functional traits may be modulated by environmental conditions. For example, Nogaro et al. (2009) and Michaud et al. (2010) clearly showed that the biogenic structures produced by benthic animals and their contributions to water fluxes at the water–sediment interface can be strongly influenced by the organic-matter content of the sediment. Thus, assessing the role of benthic ecosystem engineers in marine and freshwater ecosystems will require determining the complex relationships between the physical habitat, the microbial compartment, and the activities of the benthic fauna. A combination of experimental and modeling work is probably the most promising method to quantify the importance of ecosystem engineers on the biogeochemical functioning of aquatic ecosystems.

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