



REVIEW

What is bioturbation? The need for a precise definition for fauna in aquatic sciences

Erik Kristensen^{1,*}, Gil Penha-Lopes², Matthieu Delefosse¹, Thomas Valdemarsen¹,
Cintia O. Quintana^{1,3}, Gary T. Banta⁴

¹Institute of Biology, University of Southern Denmark, Campusvej 55, 5230 Odense M, Denmark

²Centro de Oceanografia, Laboratório Marítimo da Guia, Faculdade de Ciências da Universidade de Lisboa, Avenida Na Senhora do Cabo 939, 2750-374 Cascais, Portugal

³Oceanographic Institute of University of São Paulo, Praça do Oceanográfico 191, Cidade Universitária, 05508-120 São Paulo, Brazil

⁴Department of Environmental, Social and Spatial Change, Roskilde University, Universitetsvej 1, 4000 Roskilde, Denmark

ABSTRACT: The term 'bioturbation' is frequently used to describe how living organisms affect the substratum in which they live. A closer look at the aquatic science literature reveals, however, an inconsistent usage of the term with increasing perplexity in recent years. Faunal disturbance has often been referred to as particle reworking, while water movement (if considered) is referred to as bioirrigation in many cases. For consistency, we therefore propose that, for contemporary aquatic scientific disciplines, faunal bioturbation in aquatic environments includes *all transport processes carried out by animals that directly or indirectly affect sediment matrices. These processes include both particle reworking and burrow ventilation.* With this definition, bioturbation acts as an 'umbrella' term that covers all transport processes and their physical effects on the substratum. Particle reworking occurs through burrow construction and maintenance, as well as ingestion and defecation, and causes biomixing of the substratum. Organic matter and microorganisms are thus displaced vertically and laterally within the sediment matrix. Particle reworking animals can be categorized as biodiffusers, upward conveyors, downward conveyors and regenerators depending on their behaviour, life style and feeding type. Burrow ventilation occurs when animals flush their open- or blind-ended burrows with overlying water for respiratory and feeding purposes, and it causes advective or diffusive bioirrigation exchange of solutes between the sediment pore water and the overlying water body. Many bioturbating species perform reworking and ventilation simultaneously. We also propose that the effects of bioturbation on other organisms and associated processes (e.g. microbial driven biogeochemical transformations) are considered within the conceptual framework of ecosystem engineering.

KEY WORDS: Particle reworking · Biomixing · Burrow ventilation · Bioirrigation · Ecosystem engineering · Sediment

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INTRODUCTION

The term bioturbation is frequently used in scientific literature to describe how living organisms affect the substratum in (or on) which they live. A search on Web of Science gave >2650 bioturbation hits in late

2011. The term originates from ichnology, to describe traces of life in fossil and modern sediments, and has subsequently been adopted in soil and aquatic sciences (e.g. Meysman et al. 2006a, Huhta 2007, Wilkinson et al. 2009). So, why then ask what bioturbation means? A closer look at the aquatic science lit-

*Email: ebk@biology.sdu.dk

erature reveals a diverse usage of the term, particularly with respect to animal activities. In many cases, the original meaning from ichnology is strictly followed, and the term refers solely to the redistribution of particles and the formation of biogenic structures by burrowing animals. In other cases, it is used in the context of all physical disturbances caused by animals on the substratum, including particle (reworking) and water (ventilation) movements. To underline the ambiguity, bioturbation has, in some cases, even been used directly to describe altered microbial processes associated with animal disturbances.

We have therefore decided to assess the term bioturbation and its applications for fauna in aquatic sciences. We start with the historical background of how the term originated in different scientific disciplines and how its usage has evolved through time. In this context, we cover bioturbation broadly from the first studies on reworking mechanisms in ichnology and pedology to its recent usage in describing active displacement of particles and water by fauna in aquatic sediments. Considering this overview and our own experience, we propose a precise and useful definition of faunal bioturbation that is applicable to contemporary aquatic science disciplines—without compromising past studies. We propose that bioturbation acts as an ‘umbrella’ term to cover all possible transport processes and associated physical modifications by which aquatic animals affect the substratum in (or on) which they live. It is our hope that this effort will prevent future mystification in the aquatic science literature and among scientists working with animal–sediment relations. Although we initially consider ichnology and pedology in our overview, we will only focus on identifying types of particle reworking and burrow ventilation activities that can be classified as bioturbation in contemporary aquatic sediments, where it occurs and by which types of animal. It is here that we feel the need for a rigorous definition is most pressing.

HISTORICAL BACKGROUND

While the definition of the term bioturbation is equivocal in aquatic sciences, the origin of the term is quite clear. Charles Darwin was the first to describe the effects of animals on the structure of the substratum in which they live (Darwin 1881). He conducted life-long and detailed studies on how earthworms in Staffordshire, UK, brought soil particles from deep layers to the surface and by doing so buried chalk and cinders placed at the surface years before. This

central topic of his last book (Darwin 1881) is the foundation of what we now consider as bioturbation, yet he did not specifically use the term. In the years to come, a number of researchers were encouraged by Darwin’s new research, which resulted in several publications on how fauna and flora affect soil and sediment textures (see review by Johnson 2002). Some of these late 19th century scientists described their fascination of the large-scale consequences of the relatively modest action of small animals. Although the presence of masses of coiled excrements from lugworms *Arenicola marina* (Fig. 1) was noted as early as the 16th century (Belon 1555), the first aquatic example that quantified the physical disturbance was by Davison (1891). He described in detail the amazing amount of sand brought to the surface by ‘lobworms’ (i.e. *A. marina*) and estimated that populations of this worm on the coast of Northumberland, UK, could annually produce up to 3000 tons of faecal casts per acre.

After a gap of about 30 yr, Rudolf Richter’s pioneering efforts in the 1920s improved the understanding of traces left by benthic fauna in North Sea tidal flats (e.g. Richter 1927). Together with Othenio Abel (Abel 1935), he provided rudiments of modern descriptive bioturbation by introducing the term ‘Lebensspuren’ to denote the visual traces of burrowing animals. However, it was 2 decades later that Richter (1952) introduced the term bioturbation to describe fossil biogenic structures found in sedimentary rocks. He defined ‘Bioturbaten Textur’ as ‘alle Texturen umfasst, die einem Sediment oder Boden nachträglich durch

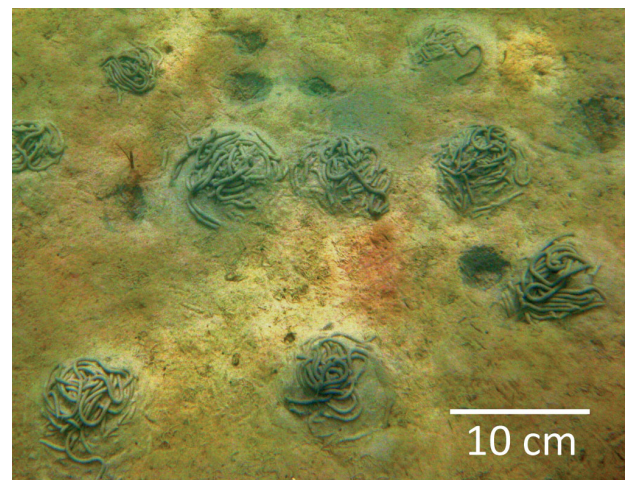


Fig. 1. Intertidal sandflat dominated by the polychaete *Arenicola marina* at Løgstør Broad, Limfjorden, Denmark. The dramatic effect of *A. marina* bioturbation (i.e. particle reworking) on sediment topography by subsurface feeding and surface defecation is evident (photo: E. Kristensen)

Organismen verursacht worden sind' (Richter 1952, p. 68), i.e. that bioturbated textures include all structures in a sediment or soil that have been caused by activities of living organisms. Richter (1952) also separated the term bioturbation into phytoturbation (traces in soil caused by growing plants) and zooturbation (traces of burrowing animals in sediment). This subdivision of bioturbation has, however, never gained much support in the literature. The same year, bioturbation appeared for the first time in the title of an ichnology paper by Schäfer (1952) where he described faunal traces in intertidal marine sediment.

The term bioturbation was soon adopted from ichnology by other scientific disciplines (e.g. pedology and aquatic sciences), and its usage escalated rapidly during the 1960s and 1970s. It was used in pedology to describe biological processes by animals and plants that physically disrupt soil horizons and alter soil properties (e.g. Blum & Ganssen 1972, see also review by Johnson 2002). Thus, terrestrial plants can affect soils in a manner analogous to animal burrow construction by establishing root structures that can disrupt soil horizons and break up bedrock. In aquatic sciences, it was primarily applied to describe effects of animal particle reworking and biogenic structures on biological, ecological and biogeochemical properties of modern sediments (e.g. Rhoads 1967, Winston & Anderson 1971). Water transport induced by fauna (i.e. burrow ventilation, irrigation, or bioirrigation) was not at this early stage fully considered an integrated part of bioturbation.

The word ventilation as a term to describe how sediment-dwelling aquatic animals flush their burrows originates from the physiological literature and refers to the respiratory need for pumping oxic water. This terminology was adopted by the first physiologists studying the respiratory movements by the polychaetes *Arenicola marina* (van Dam 1937) and *Nereis virens* (Lindroth 1938). A divergence arose a few years later when G. P. Wells published a series of excellent papers on the nervous and respiratory system of *A. marina* (e.g. Wells 1945, 1949). For unknown reasons he denoted the respiratory pumping by this polychaete as irrigation—which otherwise describes watering of agricultural areas or medical washing of wounds. Subsequently, both terms were used frequently in aquatic physiological and ecological literature (e.g. Mettaw 1969, Gamble 1970, Hoffmann & Mangum 1972, Foster-Smith & Shillaker 1977)—and some authors even switched between ventilation and irrigation (Dales 1961, Dales et al. 1970). No consensus for a common usage and distinction between them has ever been reached. Instead,

the term irrigation gradually changed to bioirrigation in the aquatic science literature of the early 1990s (e.g. Sweerts et al. 1991, Marinelli 1992), while some authors also changed the meaning to describe the impact of burrow ventilation on sediment pore water chemistry (e.g. Hüttel 1990).

HOW SOILS AND SEDIMENTS DIFFER

Recently, a number of excellent reviews on the present state of bioturbation research in soils and sediments have been published (e.g. Meysman et al. 2006a, Huhta 2007, Wilkinson et al. 2009). They all acknowledge Darwin for his pioneering work and provide new insights from the modern ecological theory where bioturbation is now recognized as an archetypical example of 'ecosystem engineering' by modifying, for example, geochemical gradients and redistributing food resources. They also emphasize that the use of bioturbation in soils and sediments is related to enhanced dispersal of particles by animal and plant activities, but do not fully embrace the unique biogenic water transport by faunal burrow ventilation in aquatic environments.

While bioturbation in terrestrial soils and aquatic sediments have many traits in common regarding particle reworking, they differ when it comes to water transport and gas exchange. Soils are exposed to air most of the time and are usually well-aerated to decimetre or metre depths (Bachmann & van der Ploeg 2002, Reynolds et al. 2009). They contain water as moisture and are rarely water saturated, which allows oxygen penetration to deep horizons through air-filled pores (Feng et al. 2002). Animal burrows and plant roots act as large pores that augment water infiltration during heavy precipitation periods and improve direct gas exchange with the atmosphere (Ernst et al. 2009). Thus, bioturbation-enhanced transport of water and exchange of gases in soils are primarily driven by passive physical processes, such as gravity and diffusion, and as such cannot be considered active ventilation.

Aquatic sediments, on the other hand, are fully water saturated and, except for intertidal areas, permanently covered with water. Since air-saturated water contains roughly 30 times less oxygen that diffuses about 10 000 times slower than in air, aerobic organisms buried into sediments face severe challenges. Near-coastal sediments are usually anoxic except for the upper few millimetres where oxygen is supplied by diffusion (Glud 2008). Buried organisms must therefore develop special strategies to over-

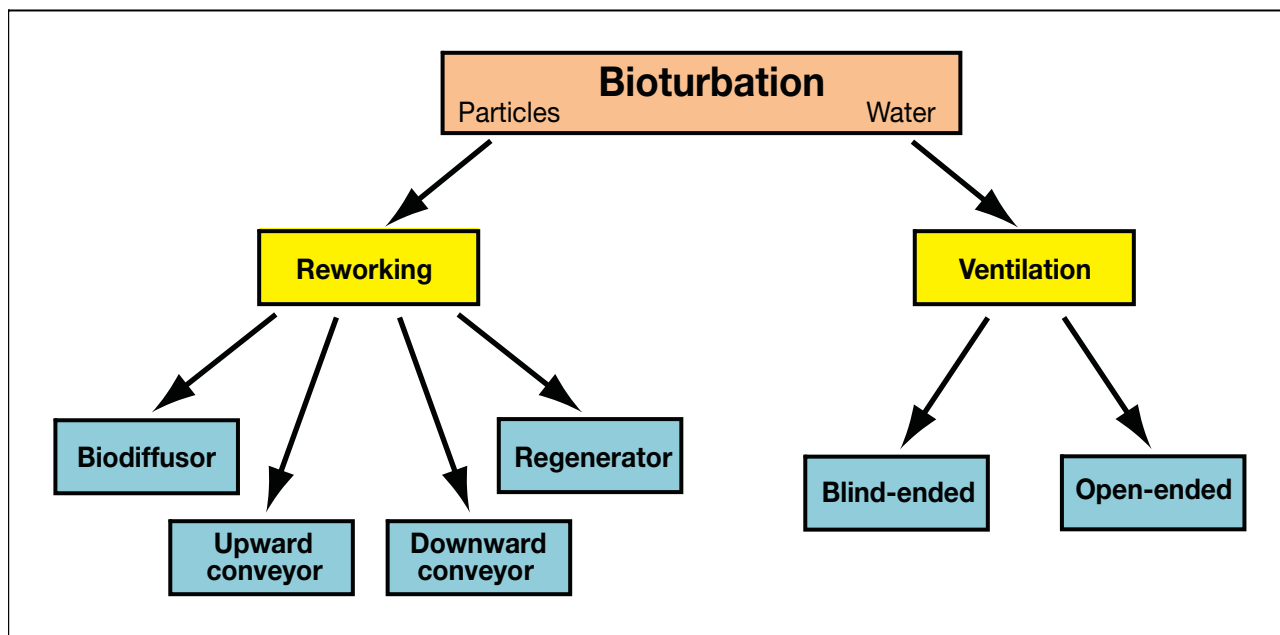


Fig. 2. The proposed definition of bioturbation and its function as an 'umbrella' term. Bioturbation is divided into 2 main categories; particle 'reworking' (i.e. movement of particles) and burrow 'ventilation' (i.e. movement of water). Reworking and ventilation are subsequently divided into several relevant subcategories of animals and burrows (see section 'Our definition' for a detailed description)

come anoxic (and even sulfidic) conditions. Most animals have evolved mechanisms by which they actively ventilate their burrows with oxygenated overlying water, but the mechanism and magnitude are only known for a select number of conspicuous species (Kristensen & Kostka 2005). Aquatic plants do not perform active ventilation, but have instead developed air-filled tissues (aerenchyma) where oxygen can diffuse rapidly to roots deep in anoxic sediments (Colmer 2003, Purnobasuki & Suzuki 2005).

OUR DEFINITION

Bioturbation is today a widely applied standard term in aquatic sciences, yet no consensus on its definition for fauna has been reached, and most studies use it implicitly for their own purpose. Although the term should describe all physical disturbances caused by animals on and in the substratum, it often refers to particle reworking only. Water transport by burrow ventilation is instead commonly denoted separately as bioirrigation. It is not appropriate to have several imprecise definitions for physical disturbances by animals within the same framework but without a common denominator.

In the present context, bioturbation is such a denominator and acts as an 'umbrella' term that covers

all faunal transport activities physically disturbing the substratum (Fig. 2). It is separated into activities by animals that directly move and mix particles by the process of reworking (Solan & Wigham 2005, Maire et al. 2008) and/or directly move water through burrows by the process of ventilation (Kristensen & Kostka 2005, Meysman et al. 2006b). Thus, for a proper consensus, we propose that faunal bioturbation in aquatic environments is defined as *all transport processes carried out by animals that directly or indirectly affect sediment matrices. These processes include both particle reworking and burrow ventilation* (Fig. 2). Active particle reworking involves faunal displacement and biomixing of particles and includes burrowing, construction and maintenance of galleries, as well as ingestion and defecation of particles. Not all of these processes result in homogeneous biomixing because mechanisms such as particle sorting during feeding, confined faecal deposition sites and tube formation can create sediment zones with different granulometry, porosity and organic content. Furthermore, collapse and infilling of abandoned dwellings can be considered indirect (passive) bioturbation. Biomixing can be either of a local nature, where frequent displacement of individual particles occurs randomly over very short distances (Boudreau 1986a), or of a non-local nature, with particles moving over longer distances in dis-

Table 1. Overview of bioturbation modes and their effect on the sediment matrix, transport (trans) process, sediment type and transport type. Particle reworking causes biomixing, which can be local by burrowing with frequent and random displacements over short distances or non-local by deposit feeding with discrete particle movement over longer distances. The local displacement occurs as diffusive-like transport, while the non-local causes long-distance upward or downward particle motion. Burrow ventilation causes bioirrigation, where the long-distance flushing of solutes within burrows occurs non-locally. The associated local pore water solute transport in sediment surrounding burrows can occur as radial molecular diffusion (diff) or pressure-induced advective pore water flow depending on the sediment type and its permeability

Bioturbation mode	Effect	Transport process	Sediment type	Transport type
Particle reworking	Biomixing	Burrowing	Sand, mud	Diffusion
		Deposit-feeding	Sand, mud	Non-local
Burrow ventilation	Bioirrigation	Burrow flushing	Sand, mud	Non-local
		Pore water trans	Sand	Advection/diff
			Mud	Diffusion

crete steps (Boudreau & Imboden 1987, Meysman et al. 2003) (Table 1). Depending on their mode of reworking, animals can be categorized as biodiffusers, upward conveyors, downward conveyors and regenerators (Boudreau 1986a,b, Gardner et al. 1987, François et al. 1997, 2002). Because of reworking, organic matter and microorganisms are displaced (biomixed) within the sediment matrix. Ventilation occurs when animals flush their open- (2 or more openings at the surface) or blind-ended (only 1 opening) burrows with overlying water for respiratory and feeding purposes, and it causes non-local bioirrigation with rapid transport of solutes out of burrows to the overlying water body (Kristensen 2001, Shull et al. 2009) (Table 1). The local solute transport around burrows is also driven by ventilation, and is either of an advective nature via generated pressure or a diffusive nature via increased concentration gradients. Advective pore water bioirrigation occurs primarily in permeable sandy sediments, while diffusive bioirrigation usually predominates in less permeable cohesive sediments as radial diffusion between the burrow lumen and the surrounding sediment.

For simplicity and clarity, particle reworking and burrow ventilation are treated separately here, because the driving mechanisms and their consequences for the sediment matrix are quite different. However, it is evident that many species modify their environment through both processes simultaneously by displacing particles and, at the same time, ventilating their burrows (Vopel et al. 2003, 2007).

We do not include biodeposition as a bioturbation activity per se, but consider it a parallel concept with its own definition (Graf & Rosenberg 1997). Thus, bio-

turbation is an active physical modification of the substratum by animals, while biodeposition enhances particle accretion at the sediment–water interface, which in many cases is driven passively by gravity. Biodeposition typically occurs when, for example, mussel and oyster beds act as biological filters that concentrate suspended particulate matter from the water column as faeces and pseudofaeces. These aggregated ‘biodeposits’ are heavier than their constituent particles and settle rapidly on the seafloor beneath the bed (Mitchell 2006, Forrest et al. 2009). Conversely, active surface and subsurface defecation by burrow-dwelling organisms and associated non-local mixing of ingested

sediment and detritus must be considered an integrated part of our definition of bioturbation. These activities are in many cases the main drivers of sediment particle reworking. The importance of both biodeposition and bioturbation as ecosystem engineering functions was stressed recently by Mermillod-Blondin (2011). He also considered these 2 concepts as separate processes, but argued that they are both major modulators of microbial activities and biogeochemical processes in aquatic environments.

PARTICLE REWORKING AND BIOMIXING

As defined above, particle reworking includes all activities by animals that directly move and mix particles horizontally or vertically in the sediment. The 4 major categories of reworking organisms, as modified from François et al. (1997) and Solan & Wigham (2005), will be briefly described in the following sections and illustrated by representative examples.

Biodiffusers

Biodiffusers (Fig. 3A) include organisms with activities that usually result in a constant and random local sediment biomixing over short distances resulting in transport of particles analogous to molecular or eddy diffusion. This mode of reworking can be divided into 3 subgroups depending on the life habits of the involved organisms: (1) Epifaunal biodiffusers (Fig. 4A) include organisms that occur predominantly above the sediment–water interface. Their activities are lim-

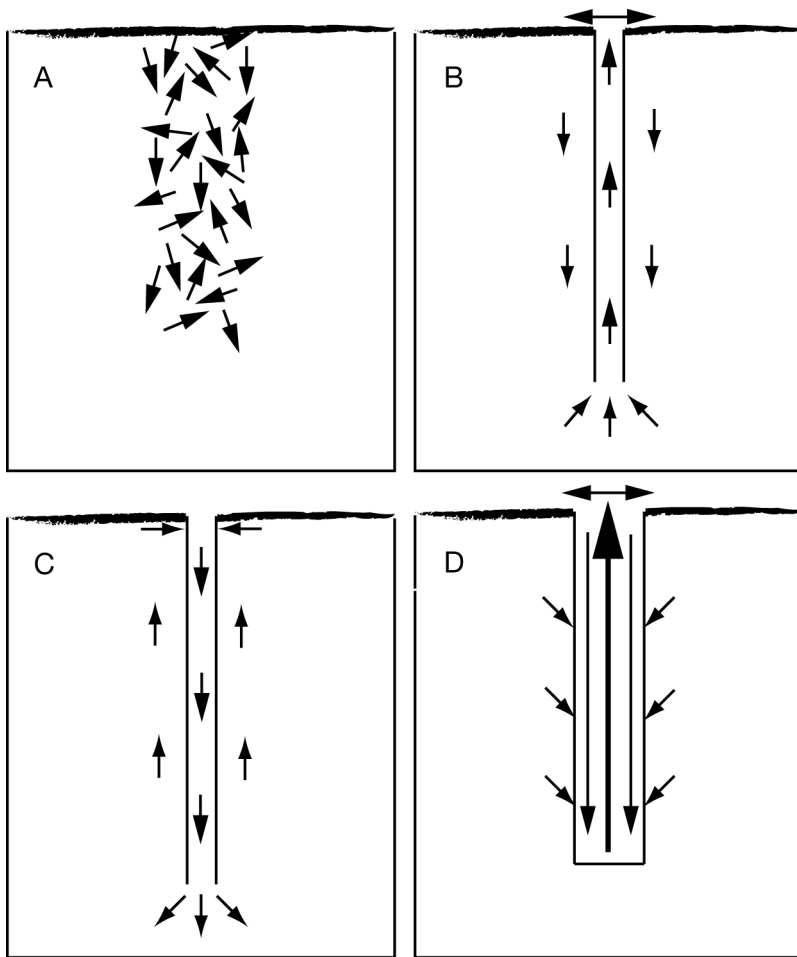
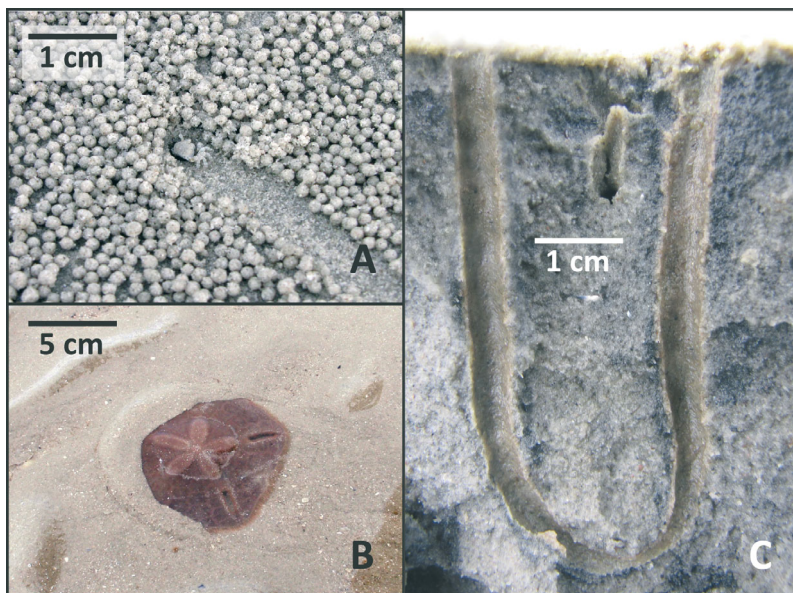


Fig. 3. The 4 major types of particle reworking conducted by benthic infauna in aquatic environments: (A) biodiffusors, (B) upward conveyors, (C) downward conveyors, (D) regenerators (modified from François et al. 1997)



ited to near-surface sediments and generally redistribute fine particles randomly over very short distances along the surface. This mode of particle transport is evident for surface-grazing fiddler crabs *Uca* spp. and sand bubbler crabs *Scopimera* spp. that forage on microorganisms only within the upper few millimetres of the sediment. The total amount of mixed sediment can be considerable as grazing fiddler crabs, for example, can handle up to 20 g sediment g^{-1} wet body weight d^{-1} (Penha-Lopes et al. 2009). Large epifaunal biodiffusors, such as benthic fish may rework sediment down to 10–15 cm depth. Dasyatid rays, for example, form large pits that can cover 1 to 3 % of the surface area and account for 12 to 22 % of spatially averaged advective particle transport on intertidal sandflats (D'Andrea et al. 2004). (2) Surficial biodiffusors (Fig. 4B) are organisms with activities mostly restricted to the uppermost few centimetres of the sediment, and these species rarely venture above the sediment–water interface. Typical examples are spatangoid urchins and sand dollars that move through the upper ~5 cm of the sediment, displacing and mixing particles with their bodies and specialized spines. The volume of sediment displaced by populations (40 ind. m^{-2}) of the spatangoid *Echinocardium* spp. can reach $20\,000 \text{ cm}^3 \text{ m}^{-2} \text{ d}^{-1}$, which is 150 times more than the volume they ingest (Lohrer et al. 2005). Furthermore, Gilbert et al. (2007) showed that populations of the brittle star *Amphiura filiformis*, the spatangoid *Echinocardium cordatum*, the polychaete *Scalibregma inflatum* and the bivalve *Abra nitida* (total for all

Fig. 4. Examples of biodiffusors: (A) the epifaunal biodiffusor *Scopimera* sp. (sand bubbler crab) from Thailand (photo: E. Kristensen); (B) the surficial biodiffusor *Echinodiscus truncatus* (keyhole sand dollar) ploughing through sandy sediment in Thailand (photo: M. Ø. Pedersen); (C) the gallery biodiffusor *Nereis diversicolor* from Denmark (photo: E. Kristensen)

species 795 ind. m^{-2}) mix sediment down to 3–4 cm depth with biodiffusion coefficients ranging from 1 to $2 \text{ cm}^2 \text{ yr}^{-1}$. (3) Gallery biodiffusers (Fig. 4C) are burrow-dwelling organisms that conduct diffusive local biomixing of particles primarily due to burrowing activity within the upper 10 to 30 cm of the sediment. They may ultimately account for vertical transport of particles from the upper regions of the sediment to the lower limit of burrow penetration. Typical gallery biodiffusers, such as many polychaetes, are responsible for extensive burrow networks that connect to the surface. *Nereis (Hediste) diversicolor* and *Marenzelleria viridis*, for example, displace particles downward at an exponentially decreasing rate with depth in the sediment. The biodiffusion coefficient for populations ($\sim 1000 \text{ ind. m}^{-2}$) of these surface deposit-feeding species is also typically 1 to $2 \text{ cm}^2 \text{ yr}^{-1}$ (François et al. 2002, Duport et al. 2006, Quintana et al. 2007).

Upward conveyors

Upward conveyors (Fig. 3B) are vertically oriented species that typically feed head-down at depth in the sediment. They transport particles from deep horizons to the sediment surface. The particles are actively moved non-locally upwards either when passing through the gut or when subsided material is ejected by water bursts during clearance of the ingestion cavity. Subsequently, the particles are returned to depth by gravity (a local advective process) as subsurface feeding voids are filled with sediment from above. Examples of head-down species are the lugworm *Arenicola marina* (Cadée 1976), the bamboo worm *Clymenella torquata* (Dobbs & Whitlatch 1982) and thalassinid shrimps (Pillay & Branch 2011). *A. marina* is one of the most conspicuous upward conveyors in shallow and intertidal sandy sediments along north-western European coasts (Beukema & De Vlas 1979, Riisgård & Banta 1998, Valdemarsen et al. 2011). It lives in deep J-shaped burrows where it ingests considerable amounts of nutrient-poor sediment from the feeding pocket in the blind end of the burrow. As a result sediment sinks downward in front of the head forming a funnel at the sediment surface. Periodically, the worm moves backward in the burrow and defecates characteristic castings at the sediment surface (Fig. 1). The amount of sediment displaced by *A. marina* is impressive (Fig. 5) and populations ($\sim 50 \text{ ind. m}^{-2}$) have been estimated to completely mix the sediment to a depth of 20 to 40 cm every year (Riisgård & Banta 1998, Valdemarsen et al. 2011). Due to its inability to ingest particles larger than $\sim 1 \text{ mm}$, gravel

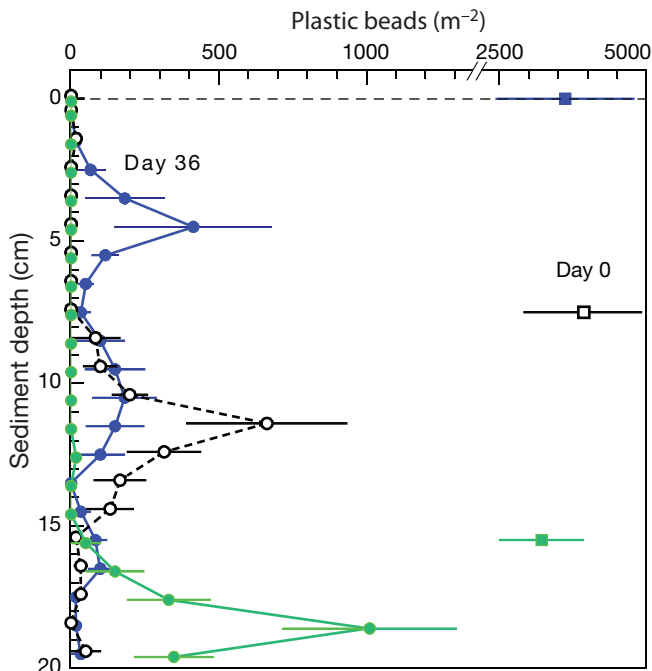


Fig. 5. Vertical transport of plastic beads ($1.5 \times 3 \text{ mm}$) in sediment inhabited by the upward conveyor *Arenicola marina* (60 m^{-2}). Beads of different colour (purple, white and green) were initially placed at 0, 7.5 and 15 cm depth in the sediment (points shown to the right represent these Day 0 positions). The beads that were too large for *A. marina* ingestion peaked after 36 d at: 4.5 cm depth (purple, drawn with blue), 11.5 cm depth (white, drawn with black), 18.5 cm depth (green). Accordingly, the burial rate was 3 to 4 cm mo^{-1} . Values are given as means ($\pm \text{SD}$). The dashed horizontal line indicates the sediment surface (Valdemarsen et al. 2011)

and shells gradually sink below the mixing depth forming a distinct layer (i.e. graded bedding) underlying well sorted sand (Jones & Jago 1993). The amount of deep sediment moved to the surface by callianassid shrimps is even more impressive than that of *A. marina*. For example, the rate of sediment turnover by a population of *Callichirus kraussi* is $\sim 12 \text{ kg m}^{-2} \text{ d}^{-1}$ (Branch & Pringle 1987). As a consequence, large mounds are formed that can be up to 5 cm tall and 15 cm wide at the base (Pillay & Branch 2011).

Downward conveyors

Some downward conveyors (Fig. 3C) exhibit a feeding strategy opposite to that of upward conveyors. Vertically oriented head-up feeders actively select and ingest particles at the surface and egest these non-locally as faeces in deeper sediment strata. Non-selective upward particle movements through continuous burrow construction and maintenance

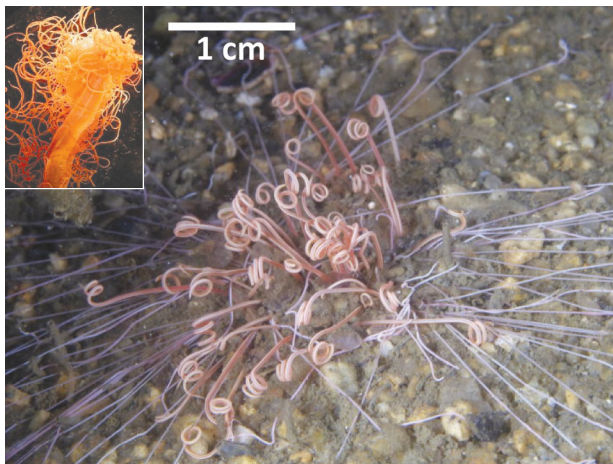


Fig. 6. *Cirriformia grandis*. Tentacles of the cirratulid polychaete *C. grandis* extended over the sediment surface. Inset shows excavated individual (photo: D. Shull)

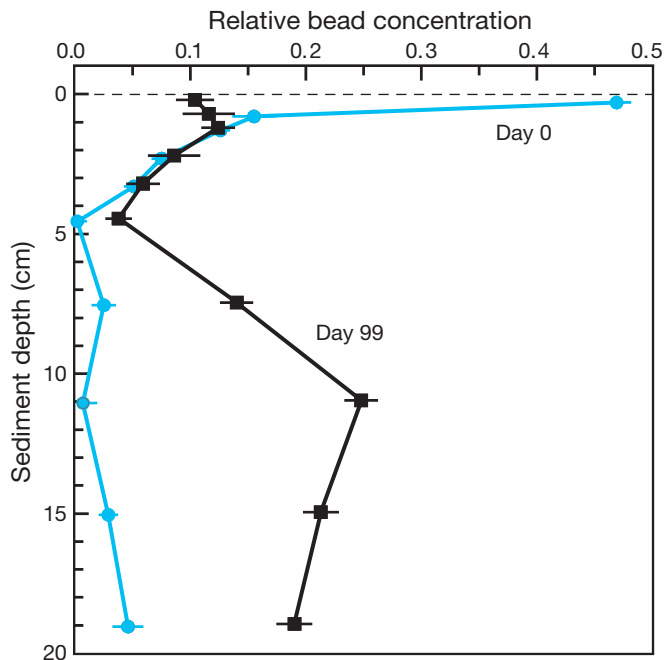


Fig. 7. Vertical transport of glass beads (16 to 32 μm) in sediment inhabited by the downward conveyor *Cirriformia grandis* (1400 ind. m^{-2}). Glass beads were initially placed at the sediment surface. Blue line: initial profile of beads 1 h after deployment; black line: the profile 99 d after deployment. Values are given as means ($\pm\text{SD}$). The dashed line indicates the sediment surface (modified from Shull & Yasuda 2001)

create space to accommodate the deposited faecal material (Shull 2001). For example, the cirratulid polychaete *Cirriformia grandis* (Fig. 6) feeds on surface deposits using its tentacles and defecates at several centimetres in depth within its burrow (Shull & Yasuda 2001). However, many upward conveyors



Fig. 8. *Ocypode* spp. Ghost crab, a typical 'regenerator' from Thailand, excavating its burrow (photo: E. Kristensen)

such as the previously mentioned malanid bamboo worms may also drag fresh surface material down their tube (Dobbs & Whitlatch 1982). Sediment ingestion by these subsurface deposit-feeders creates space at the bottom of their tubes, which is subsequently filled with surficial sediment by hoeing. This behaviour explains the presence of viable diatoms to depths of 14 cm in sediment inhabited by the malanid *Praxillella* sp. (Levin et al. 1997). Non-local downward transport may thus be responsible for otherwise unexplained subsurface peaks in sediment organic matter and tracer profiles (Fig. 7).

Regenerators

Regenerators (Fig. 3D) are excavators that dig and continuously maintain burrows in the sediment, and by doing so transfer sediment from depth to the surface. The excavated sediment is replaced either by surface sediment through current-driven infilling or by collapse of burrow walls. Ghost crabs *Ocypode* spp. and fiddler crabs *Uca* spp. are typical examples of regenerators (Fig. 8). Their burrows function as a refuge from predation and adverse environmental conditions. Fiddler crab burrows, for example, may easily reach >10 cm depth (volume of >40 cm^3). The turnover time of an average burrow is roughly 8 d when assuming a daily amount of 10 g excavated sediment (Penha-Lopes et al. 2009). Fiddler crab reworking has been simulated elegantly by Huang et al. (2007) using the lattice-automaton bioturbation simulator (LABS) within a computer environment. They identified 3 modes of fiddler crab reworking: (1) removal-and-infill, where material is excavated to

the sediment surface, and when abandoned, burrows are filled by surface material; (2) removal-and-collapse, where the infilling occurs by collapse of the burrow walls; and (3) partial-compaction-and-collapse, where part of the excavated sediment is packed into the burrow wall and abandoned burrows subsequently collapse.

Reworking and biomixing consequences

The rate by which particles are physically moved by individual species within each type of reworking mode is a function of the relative capacity, i.e. abundance, size, mode and activity, of the species to disturb the sediment matrix. By compiling the contribution of these attributes for all species involved, the total reworking by an assemblage can be readily determined (Solan et al. 2004). The various modes of reworking have nevertheless different effects on the vertical distribution of organic matter, particle sorting and grain size distribution in the sediment column. While most biodiffusors and regenerators simply move organic particles around through burrowing activities, the upward and downward conveyors in most cases ingest organic particles and move them through their guts (Table 1). Particle selectivity and gut passage may alter the chemical and physical properties of the receiving environment (Neira & Hopner 1993, Stamhuis et al. 1998, Wild et al. 2005). Labile organic particles from surface sediments delivered as biodeposits in subsurface sediments and vice versa may therefore modify the overall biogeochemical reactivity of the sediment and thus its biological functioning. The transfer of labile organic matter from oxic surface to anoxic subsurface sediment may enhance the subsurface degradation activity, while the volume-specific activity of the displaced organic matter is diminished. Conversely, degradation of subsurface organic matter is enhanced up to 10-fold when lifted to the oxic sediment surface (Kristensen & Holmer 2001). Consequently, these different reworking modes create a dynamic and heterogeneous chemical, physical and biological sediment environment that varies over a range of temporal and spatial scales, depending on the species composition and abundance of the benthic community.

BURROW VENTILATION AND BIOIRRIGATION

Ventilation by burrow-dwelling animals creates rapid exchange of water between the overlying

water and subsurface sediment. The water exchange is subsequently the driving force for bioirrigation, i.e. enhanced transport of pore water and associated solutes in the sediment surrounding the burrow. Transport of solutes, such as O_2 , HCO_3^- , NH_4^+ , SO_4^{2-} and H_2S , within sediments and across the sediment-water interface is mediated by molecular diffusion without fauna. This is a relatively slow process over millimetre to centimetre scales that is driven solely by vertical concentration gradients. Ventilation by burrowing macrofauna disrupts the diffusional gradients and strongly affects transport conditions within sediments. The associated bioirrigation or enhancement of solute transport can exceed the transport by molecular diffusion by as much as an order of magnitude. The actual extent of the enhancement depends on factors such as infaunal community composition and sediment type (Aller 2001, Kristensen 2001, Meysman et al. 2006b, Shull et al. 2009).

The mechanism and rate by which infauna ventilate burrows vary considerably within and among taxonomic groups. Many polychaetes and insect larvae use muscular sinusoid undulations or peristaltic movements of the body to move water head- or tailwards in the burrow (Barrow & Wells 1982, Riisgård & Larsen 2005, Morad et al. 2010). Bivalves, heart urchins and some polychaetes are dependent on ciliary action (Specht & Lee 1989, Riisgård & Larsen 2005, Quintana et al. 2011), while many crustaceans use forceful beating of pleopods to create the water currents (Forster & Graf 1995, Stamhuis & Videler 1998). The rate of burrow ventilation by each species depends on the purpose, such as respiratory gas exchange, food filtration, gamete transport, transport of environmental stimuli and removal of metabolic wastes (Aller 1982, Kristensen 2001). Suspension-feeders, for example, need to process large amounts of water to satisfy their demand for food, while deposit-feeders ventilate considerably less and in many cases only to satisfy their respiratory need (Christensen et al. 2000). The associated effect of bioirrigation on pore water solutes is, however, not only dependent on the ventilation rate, but also on the morphology of the burrow, i.e. if it is open- or blind-ended (Fig. 9). It is obvious that open-ended, U-shaped burrows can be flushed easily from one end to the other with a minimum of energy expenditure in all types of sediment. Blind-ended, I-shaped burrows are flushed uni- or bidirectionally depending on the permeability of the sediment. The following examples focus on well-known representatives of the 2 major types of burrow ventilation, with emphasis on the associated pore water bioirrigation.

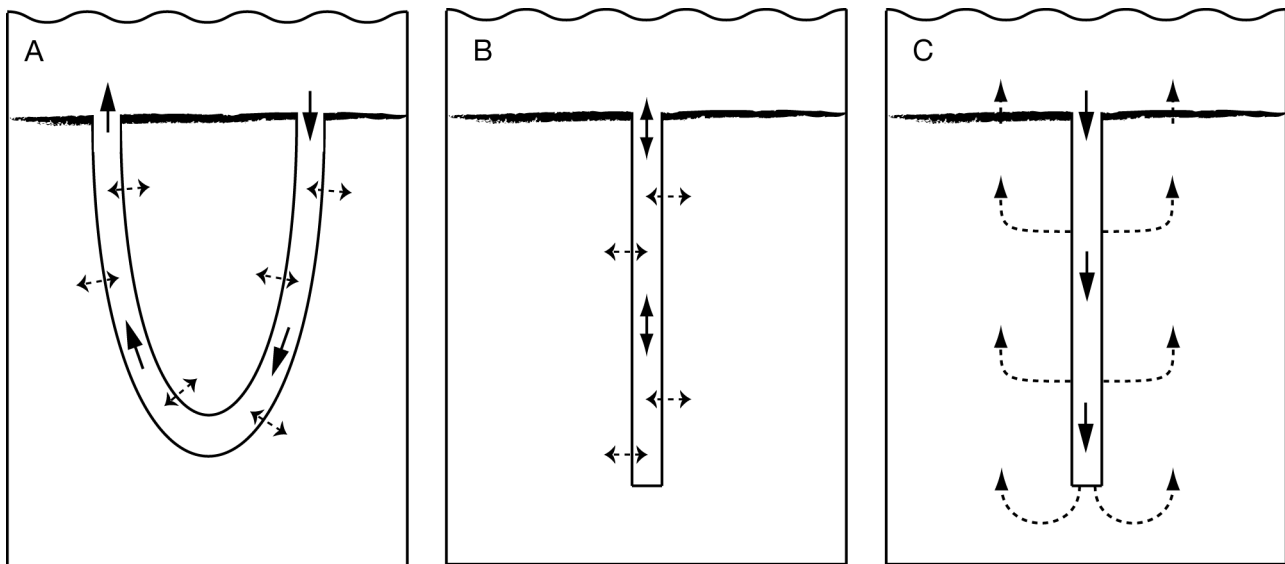


Fig. 9. The 3 major types of burrow with ventilation patterns and associated pore water bioirrigation indicated. (A) Open-ended, where water is ventilated through a burrow with at least 2 openings at the surface. Bioirrigation occurs either by radial diffusion across the wall–water interface or through advective forcing through eddy diffusion across the wall–water interface. (B) Blind-ended in impermeable sediment, where water is ventilated bidirectionally and bioirrigation occurs by radial diffusion across the wall–water interface. (C) Blind-ended in permeable sediment, where water is ventilated unidirectionally and bioirrigation occurs when the water exits the burrow by advective percolation of pore water towards the sediment–water interface

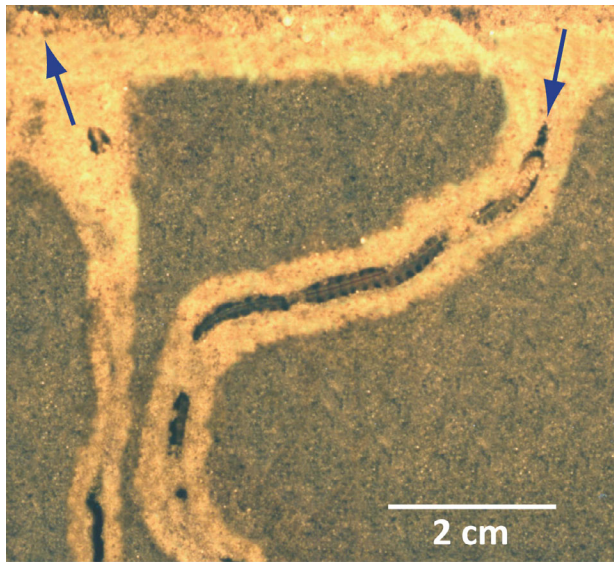


Fig. 10. Ventilated *Nereis diversicolor* burrow. Arrows indicate direction of ventilation. The worm is visible inside the burrow. The bioirrigation effect is evident from the light brown oxidized zone around the burrow (photo: E. Kristensen)

Open-ended burrows (Fig. 9A) are common for burrow-dwelling polychaetes, chironomid larvae and thalassinid shrimps that construct U- or Y-shaped galleries with 2 or more openings. These are

typically ventilated from head to tail by sinusoidal body undulations or by beating pleopods (Riisgård & Larsen 2005, Morad et al. 2010). Ventilation by species belonging to the genus *Nereis* (Fig. 10), for example, is intermittent, with active and quiescent periods in a rhythmic fashion (Kristensen 2001). The exact ventilation cycles, however, differ between species. The deposit-feeding *N. virens* is active for about 20% of the time with 5 to 10 min ventilation periods followed by 20 to 30 min inactivity (Scott et al. 1976, Kristensen 1989). Its cousin, the suspension-feeding *N. diversicolor* is considerably more active. It remains active for at least 50% of the time, only interrupted by very short periods of inactivity in a very regular pattern. A 400 mg wet wt individual of *N. diversicolor* ventilates its burrow during suspension feeding at a time-averaged rate of 3.1 ml min^{-1} , which is about 10 times faster than a similar-sized individual of *N. virens* (Christensen et al. 2000). Suspension-feeding larvae of the freshwater insect *Chironomus plumosus* exhibit even higher weight-specific ventilation than *N. diversicolor*. Thus, individual larvae (up to 50 mg wet wt) can ventilate their burrows intermittently at a rate of $\sim 3 \text{ ml min}^{-1}$ (Morad et al. 2010).

Ventilation patterns of thalassinid shrimps within the families Upogebiidae and Callianassidae tend to be different, with the former actively pumping up to

50% of the time in association with its filter-feeding behaviour (Dworschak 1981), whereas the latter is far less active, spending roughly 8% of the time ventilating for mainly respiratory purposes (Stamhuis et al. 1996). Ventilation rates of 30 to 50 ml min⁻¹ have been reported for adult individuals (~5 g wet wt) of the upogebiids *Upogebia pusilla* and *U. major* (Dworschak 1981, Koike & Mukai 1983), whereas rates of 0.6 to 5.5 ml min⁻¹ are typical for similar-sized individuals of the callianassid *Nihonotrypaea japonica* (Mukai & Koike 1984).

The presence of ventilated burrows transforms the otherwise vertical 1-dimensional diffusive transport in sediments into a spatially 3-dimensional vertical and radial bioirrigation transport (Aller 1980, Shull et al. 2009). Solute transport within the sediment matrix occurs by molecular diffusion, and solutes enter or leave the sediment both at the sediment–water interface and across burrow walls (Meysman et al. 2010). The role of ventilated burrows is therefore to increase the effective surface area available for exchange (diffusive bioirrigation) and to rapidly flush solutes into or out of the sediment through the burrow lumen. This mechanism applies particularly to water-impermeable cohesive sediments where eddy diffusion (or pore water advection) is negligible. In sandy sediments, however, vigorous ventilation by burrow-dwelling invertebrates may cause pore water advection (advective bioirrigation) to override molecular diffusion along burrow walls and thus enhance solute transport considerably (Meysman et al. 2006b). Accordingly, Kristensen & Hansen (1999) showed that advective bioirrigation dominates in the bioturbated zone and molecular diffusion below this depth in permeable sandy sediment inhabited by *Nereis diversicolor*, while diffusive bioirrigation is the dominating transport in the bioturbated zone of impermeable muddy sediment inhabited by the same species.

Blind-ended burrows (Fig. 9B,C) are the most common burrow type for conveyor-feeding and tentacular- or crown-bearing suspension-feeding polychaetes. They typically embed their body in vertical I- or J-shaped burrows. Such blind-ended burrows can be problematic when their inhabitants need to ventilate for respiratory purposes. Many species have the capacity to propel water into the burrow by locomotory peristalsis of the body (Mangum 1964, Mettaw 1969, Giangrande 1991). It is not fully clear how the exchange of water occurs for many maldanid and terebellid species occupying impermeable cohesive sediments, but it probably occurs through relatively slow internal circulation or bidirectional

water flow within the burrow (Fig. 9B). Under these circumstances solute exchange across the burrow wall must be driven by diffusive bioirrigation (Shull et al. 2009). For species with blind-ended burrows in permeable sediments, on the other hand, the ventilation is often sufficiently forceful to allow unidirectional percolation (advective bioirrigation; Fig. 9C) through sediment interstices and back to the surface (Wetthey et al. 2008). These species are often adapted to life in permeable sandy sediments as they usually avoid or even die in cohesive sediments of low permeability (Meysman et al. 2005). The sedentary and upward-conveyor *Arenicola marina* is a classic example of a species that induces advective bioirrigation (Fig. 11). Burrow ventilation at a rate of 2 to 4 ml min⁻¹ for adult individuals (2 to 4 g wet wt) is driven from tail to head by peristaltic movements of the body wall (Krüger 1971). Water that enters the burrow through the tail opening at the surface is forced into the sediment in front of the head and percolates up through the feeding funnel (Timmermann et al. 2002, Meysman et al. 2005). The ventilation activity of *A. marina* occurs in steady cycles of 40 to 60 min duration. Recently, Volkenborn et al. (2010) showed that the cyclic positive and negative pressure changes and hydraulic pulses created by *A. marina* may result in bidirectional pore water flow and highly dynamic redox oscillations within the sediment on the time scale of minutes.

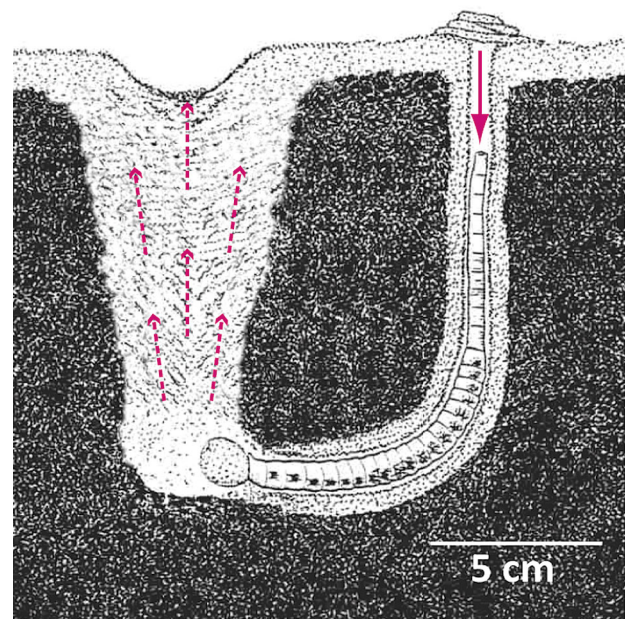


Fig. 11. *Arenicola marina*. Burrow with ventilation and bioirrigation indicated by arrows. Arrows represent direction of ventilation (right) and bioirrigation (left)

Advective bioirrigation of pore water has a more dramatic and deeper influence on solute transport than diffusive bioirrigation (Kristensen et al. 2011). Most studied cases show vertical solute profiles with a much lower build-up of reduced metabolites than is possible if molecular diffusion or diffusive bioirrigation were the only transport mechanisms. An excellent example is the spionid polychaete *Marenzelleria viridis* that lives in blind-ended burrows in sandy sediment. This species performs 2 types of ventilation: (1) headward muscular pumping of water out of the burrow and (2) tailward ciliary pumping of water into the burrow. The ciliary ventilation occurs at about 0.16 ml min^{-1} , and the muscular pumping, at 0.15 ml min^{-1} , providing advective pore water bioirrigation (Fig. 12) at a net rate of only 0.01 ml min^{-1} for 250 mg wet wt individuals (Quintana et al. 2011). On a population scale (1200 ind. m^{-2}), the slowly upward percolating pore water nevertheless enables an efficient advective bioirrigation of reduced solutes out of the sediment. The removal of solutes is much faster than by diffusive bioirrigation in the presence of a similar-sized *Nereis diversicolor* population ventilating open-ended burrows at a 2 orders of magnitude faster rate (Kristensen et al. 2011). The resulting pore

water concentrations of, for example, HCO_3^- in *M. viridis* sediment are barely higher than the overlying water level down to almost 20 cm depth (Fig. 13).

Both open- and blind-ended burrows may experience passive ventilation driven by currents or tides when at least one of the openings is raised above the surface, usually as a mound (Stieglitz et al. 2000, Munksby et al. 2002, Meysman et al. 2007). Water passing the mound creates a pressure difference between burrow openings and, thus, induces water flow through the burrow. Passive ventilation can be comparable to or higher than active ventilation by animals in areas with strong currents and large topographic features such as mounds and tidal creeks (Ray & Aller 1985, Ridd 1996).

BIOMIXING BY BURROW VENTILATION AND BIOIRRIGATION BY PARTICLE REWORKING

Substantial amounts of particles may be transferred from the overlying water and mixed deep into the sediment when burrow-dwelling suspension-feeders and other species ventilate turbid water into burrows (Riisgård 1991, Nickell & Atkinson 1995,

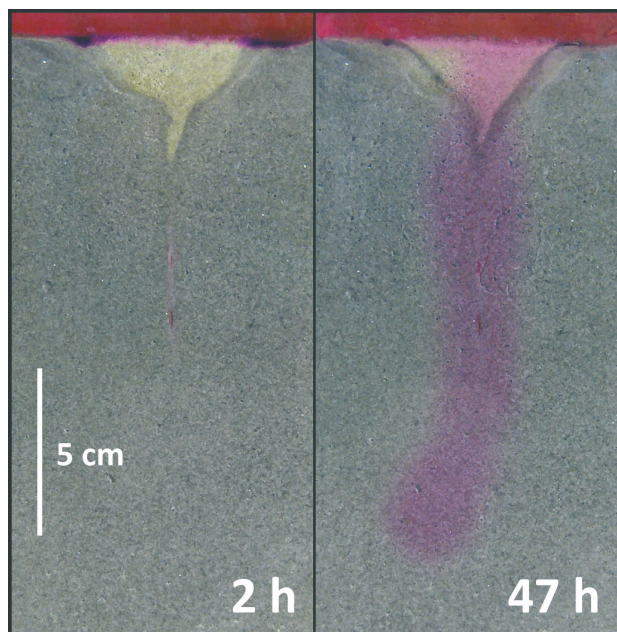


Fig. 12. Bioirrigation by *Marenzelleria viridis*. One worm was allowed to construct its burrow in a 25 cm deep and 0.5 cm wide aquarium filled with sandy sediment. At time 0, the overlying water was dyed with Rhodamine. Left panel: dye penetration after 2 h; right panel: after 47 h. The red sediment indicates pore water bioirrigation by percolation (photo: T. Hansen)

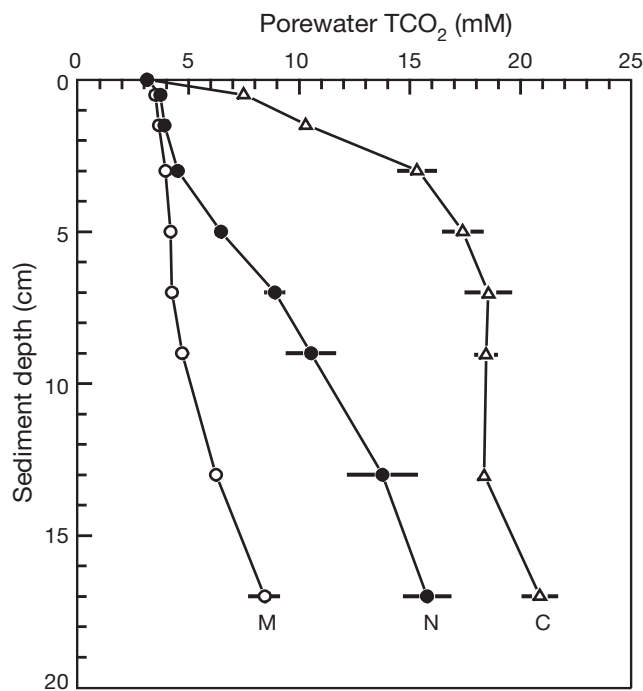


Fig. 13. Vertical pore water profiles of CO_2 in sandy sediment without fauna (C), with $1200 \text{ Nereis diversicolor m}^{-2}$ (N) and $1200 \text{ Marenzelleria viridis m}^{-2}$ (M). The sediment was sieved and homogenized initially. The profiles were obtained 16 d after introducing worms to the sediment. Values are given as means ($\pm \text{SD}$) (modified from Kristensen et al. 2011)

Griffen et al. 2004). For example, a suspension-feeding population of *Nereis diversicolor* (800 ind. m⁻²) ventilating ~2500 l m⁻² d⁻¹, has the capacity to retain phytoplankton at a rate of 134 mmol C m⁻² d⁻¹ in its burrow (Christensen et al. 2000). Much of the retained organic carbon is captured by secreted mucus nets that are later ingested by the worms (Riisgård 1991). Without suspension feeding, an unknown fraction of suspended particulate matter (SPM) entering open-ended burrows is probably also captured by the sticky mucus walls (Griffen et al. 2004), while 100% SPM must be retained in blind-ended burrows. At a concentration of, for example, 10 mg SPM l⁻¹, which is realistic for shallow coastal areas (Canal-Vergés et al. 2010), the above-mentioned *N. diversicolor* population can, with a 50% retention efficiency, move up to 13 g SPM m⁻² d⁻¹ from the overlying water and deep into the sediment. This is a remarkable amount since its particle reworking through burrowing activities has been estimated at ~38 g m⁻² d⁻¹ (Kristensen 2001). An *Arenicola marina* population (50 ind. m⁻²) in the same area ventilating at a rate of 160 l m⁻² d⁻¹ (Kristensen 2001), on the other hand, only traps 1.6 g SPM m⁻² d⁻¹ inside its blind-ended burrow, which is much less than the several kilograms of sediment reworked by populations of this species per day (Riisgård & Banta 1998, Valdemarsen et al. 2011). Nevertheless, active ventilating infauna are capable of substantial downward particle transport, which in some cases must be considered significant particle reworking.

Conversely, when organisms move particles by reworking activities, they also move the pore water associated with the particles. The volume of water processed in this way depends on sediment porosity, which typically ranges from 30 to 60%. Thus, about half the volume of reworked sediment can potentially consist of pore water. Pore water advection associated with particle mixing can be directed upwards, downwards and laterally depending on the type of organism involved. The quantity of sediment (and thus pore water) moved by reworking is, however, orders of magnitude less than the volume of water ventilated by most burrow inhabitants (Aller 1982, Kristensen 2001, Quintana et al. 2007). The chemical effect of such pore water advection may be important, however, as it, in many cases, is of non-local nature and, therefore, can move oxidized compounds rapidly over long distances to deep and reduced sediment layers and vice versa. Not much quantitative information is available on this process, but it is a possible type of bioirrigation in bioturbated sediments.

BIOTURBATION AND ECOSYSTEM ENGINEERING

From an ecological perspective, bioturbation is coupled to physical processes and associated chemical changes related to movement of particles or water. The important biological and biogeochemical consequences of bioturbation must be considered in a larger context, such as within the framework of ecosystem engineering as pointed out by Meysman et al. (2006a).

Ecosystem engineering was introduced as a concept more than a decade ago by Jones et al. (1994). They stated that organisms can be considered as ecosystem engineers when they 'directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials. In so doing they modify, maintain and/or create habitats' (Jones et al. 1994, p. 374). Thus, a critical characteristic of ecosystem engineers is that they must change the quality, quantity and distribution of resources used by other species.

This is exactly what happens when bioturbating organisms act as agents that modify microbially driven biogeochemical activity in sediment environments. Bioturbation can affect biogeochemical reactions by changing the availability of resources for microbes (e.g. carbon and nutrients) or by changing abiotic conditions affecting microbial reaction rates (e.g. redox and temperature) (Gutierrez & Jones 2006). Accordingly, D'Andrea & DeWitt (2009) and Pillay & Branch (2011) have shown that bioturbating thalassinid shrimps are important ecosystem engineers that exert major influences over ecosystem processes and community structure. Their burrowing and ventilation activities substantially affect sedimentary and biogeochemical properties and processes, translating into both positive and negative effects on co-occurring organisms spanning bacteria, microalgae, meiofauna, macrofauna and seagrasses and possibly up the food chain to fish and birds.

The heterogeneity and activity of microbial and biogeochemical reactions in any patch are therefore controlled by processes that change transport conditions (particle reworking and burrow ventilation) as indicated by the conceptual model shown in Fig. 14. The activity of bioturbating organisms alters the microbial communities of patches by affecting the availability or chemical state of substances by active transport of particles or water. The state change of particle transport is driven by reworking processes by the bioturbator (Fig. 14, Process 1). When particles are redistributed by biomixing (Fig. 14, Process 3),

their state can be modified chemically by, for example, redox changes and become available for other organisms. The state change caused by ventilation occurs when the bioturbator actively pumps water in and out of the sediment through burrows (Fig. 14, Process 2). The associated bioirrigation (Fig. 14, Process 4) may modify the chemical state of pore water solutes and thus affect microbial processes within the sediment. Bioturbation effects on sediment biogeo-

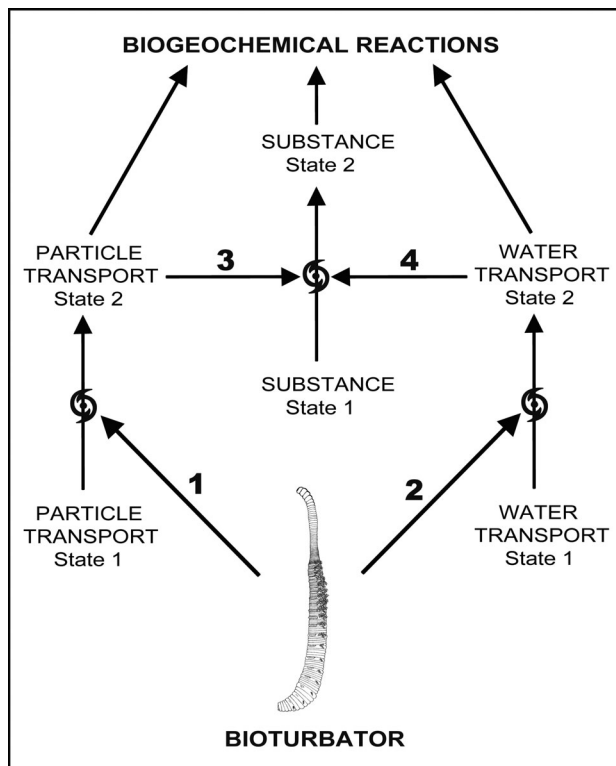


Fig. 14. Flow diagram showing the features by which bioturbating infauna act as ecosystem engineers and affect biogeochemical activity in sediment environments. The first feature includes particle transport (i.e. reworking). The state change (i.e. change of particle location) is driven by processes such as burrowing and deposit feeding by the bioturbator (Process 1). When particles (substances) are biomixed their state can be modified chemically regarding, for example, degradability and redox conditions (Process 3). The modified substance (e.g. faeces) may become available for other organisms, e.g. detritivores and decomposers. The second feature is related to water transport (i.e. ventilation). The state change means that active burrow ventilation by the bioturbator moves water in and out of burrows (Process 2). Bioirrigation may modify the chemical (e.g. redox) state of pore water (substance) surrounding burrows by removal of toxic metabolites and introduction of oxygen (Process 4), and thus provide new interfaces with enhanced microbial activity within the sediment. Part of the bioturbation effect on sediment biogeochemistry may also occur directly by transport processes, i.e. redistribution of particles and water, without associated chemical changes

chemistry also occur simply by the redistribution of particles and water, without associated chemical state changes. As all these state processes are active simultaneously for many bioturbating species, the resulting interactions cause dramatic and complex changes in the location and magnitude of early diagenetic reactions and modify the resident microbial community structure (e.g. Banta et al. 1999, Marinelli et al. 2002, Papaspyrou et al. 2006). As a consequence, the cycling of redox sensitive elements, notably nitrogen, sulphur and iron, may be intensified (Mayer et al. 1995, Gilbert et al. 2003, Gribsholt et al. 2003, Nielsen et al. 2004, Valdemarsen et al. 2010).

Instead of ecosystem engineering, the above-mentioned effects have often in the past been associated directly with the term bioturbation. However, in its strict sense as we propose, bioturbation refers only to the physical displacement of particles and water caused by macrofaunal reworking and ventilation activities in sediments, and not to the associated effect on the microbial drivers of biogeochemistry. The conceptual framework of ecosystem engineering, on the other hand, elegantly emphasizes the coupling between bioturbation as defined here and ecological processes. We hope that both terms now will be used together in their more stringent forms, thus eliminating any future uncertainty in the scientific literature.

Acknowledgements. We thank the participants of the 2nd and 3rd Nereis-Park conferences for inspiring and constructive discussions on how to define bioturbation. We owe particular gratitude to Franck Gilbert and Stefan Hulth for their initial engagement in this project. We also thank Robert C. Aller and 4 reviewers for their critical but constructive comments and feedback on our conceptual framework. This research was supported by the Danish Research Agency (Contracts 272-08-0577, 09-071369 and 09-063190/DSF). G.P.L. was supported by Fundação para a Ciência e Tecnologia (SFRH/BPD/65977/2009).

LITERATURE CITED

- Abel O (1935) Vorzeitliche Lebensspuren. Gustav Fischer, Jena
- Aller RC (1980) Quantifying solute distributions in the bioturbated zone of marine sediment by defining an average micro-environment. *Geochim Cosmochim Acta* 44: 1955–1965
- Aller RC (1982) The effects of macrobenthos on chemical properties of marine sediment and overlying water. In: McCall PL, Tevesz MJS (eds) *Animal-sediment relations*. Plenum Press, New York, NY, p 53–102
- Aller RC (2001) Transport and reactions in the bioirrigated zone. In: Boudreau BP, Jørgensen BB (eds) *The benthic boundary layer*. Oxford University Press, Oxford, p 269–301

- Bachmann J, van der Ploeg RR (2002) A review on recent developments in soil water retention theory: interfacial tension and temperature effects. *J Plant Nutr Soil Sci* 165:468–478
- Banta GT, Holmer M, Jensen MH, Kristensen E (1999) Effects of two polychaete worms, *Nereis diversicolor* and *Arenicola marina*, on aerobic and anaerobic decomposition in a sandy marine sediment. *Aquat Microb Ecol* 19: 189–204
- Barrow MJ, Wells RMG (1982) Ventilation and oxygen extraction in an arenicolid polychaete. *Comp Biochem Physiol A* 73:491–495
- Belon P (1555) La nature et diuersité des poissons avec leurs pourtraicts, representez au plus pres du naturel. Charles Estienne, Paris
- Beukema JJ, De Vlas J (1979) Population parameters of the lugworm, *Arenicola marina*, living on tidal flats in the Dutch Wadden Sea. *Neth J Sea Res* 13:331–353
- Blum WE, Ganssen R (1972) Bodenbildende Prozesse der Erde, ihre Erscheinungsformen und diagnostischen Merkmale in tabellarischer Darstellung. *Erde* 103:7–20
- Boudreau BP (1986a) Mathematics of tracer mixing in sediments. I. Spatially-dependent, diffusive mixing. *Am J Sci* 286:161–198
- Boudreau BP (1986b) Mathematics of tracer mixing in sediments. II. Nonlocal mixing and biological conveyor-belt phenomena. *Am J Sci* 286:199–238
- Boudreau BP, Imboden DM (1987) Mathematics of tracer mixing in sediments. III. The theory of nonlocal mixing within sediments. *Am J Sci* 287:693–719
- Branch GM, Pringle A (1987) The impact of the sand prawn *Callianassa kraussi* Stebbing on sediment turnover and on bacteria, meiofauna, and benthic microflora. *J Exp Mar Biol Ecol* 107:219–235
- Cadée GC (1976) Sediment reworking by *Arenicola marina* on tidal flats in the Dutch Wadden Sea. *Neth J Sea Res* 10:440–460
- Canal-Vergés P, Vedel M, Valdemarsen T, Kristensen E, Flindt MR (2010) Resuspension created by bedload transport of macroalgae: implications for ecosystem functioning. *Hydrobiologia* 649:69–76
- Christensen B, Vedel A, Kristensen E (2000) Carbon and nitrogen fluxes in sediment inhabited by suspension-feeding (*Nereis diversicolor*) and non-suspension-feeding (*N. virens*) polychaetes. *Mar Ecol Prog Ser* 192: 203–217
- Colmer TD (2003) Long-distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots. *Plant Cell Environ* 26:17–36
- D'Andrea AF, DeWitt TH (2009) Geochemical ecosystem engineering by the mud shrimp *Upogebia pugettensis* (Crustacea: Thalassinidae) in Yaquina Bay, Oregon: density-dependent effects on organic matter remineralization and nutrient cycling. *Limnol Oceanogr* 54: 1911–1932
- D'Andrea AF, Lopez GR, Aller RC (2004) Rapid physical and biological particle mixing on an intertidal sandflat. *J Mar Res* 62:67–92
- Dales RP (1961) Oxygen uptake and irrigation of the burrow by three terebellid polychaetes: *Eupolyornia*, *Thelepus* and *Neomphitrite*. *Physiol Zool* 34:306–311
- Dales RP, Mangum CP, Tichy JC (1970) Effects of changes in oxygen and carbon dioxide concentration on ventilation rhythms in onuphid polychaetes. *J Mar Biol Assoc UK* 50: 365–380
- Darwin C (1881) The formation of vegetable mould through the action of worms with observation on their habits. John Murray, London
- Davison C (1891) On the amount of sand brought up by lobworms to the surface. *Geol Mag* 8:489–493
- Dobbs FC, Whitlatch RB (1982) Aspects of deposit-feeding by the polychaete *Clymenella torquata*. *Ophelia* 21: 159–166
- Duport E, Stora G, Tremblay P, Gilbert F (2006) Effects of population density on the sediment mixing induced by the gallery-diffuser *Hediste (Nereis) diversicolor* O.F. Muller, 1776. *J Exp Mar Biol Ecol* 336:33–41
- Dworschak PC (1981) The pumping rates of the burrowing shrimp *Upogebia pusilla* (Petagna) (Decapoda: Thalassinidea). *J Exp Mar Biol Ecol* 52:25–35
- Ernst G, Felten D, Vohland M, Emmerling C (2009) Impact of ecologically different earthworm species on soil water characteristics. *Eur J Soil Biol* 45:207–213
- Feng G, Wu L, Letey J (2002) Evaluating aeration criteria by simultaneous measurement of oxygen diffusion rate and soil-water regime. *Soil Sci* 167:495–503
- Forrest BM, Keeley NB, Hopkins GA, Webb SC, Clement DM (2009) Bivalve aquaculture in estuaries: review and synthesis of oyster cultivation effects. *Aquaculture* 298: 1–15
- Forster S, Graf G (1995) Impact of irrigation on oxygen flux into the sediment: intermittent pumping by *Callianassa subterranea* and 'piston-pumping' by *Lanice conchilega*. *Mar Biol* 123:335–346
- Foster-Smith RL, Shillaker RO (1977) Tube irrigation by *Lembo websteri* Bate and *Corophium bonnelli* Milne Edwards (Crustacea: Amphipoda). *J Exp Mar Biol Ecol* 26:289–296
- François F, Poggiale JC, Durbec JP, Stora G (1997) A new approach for the modelling of sediment reworking induced by a macrobenthic community. *Acta Biotheor* 45: 295–319
- François F, Gerino M, Stora G, Durbec JP, Poggiale JC (2002) Functional approach to sediment reworking by gallery-forming macrobenthic organisms: modeling and application with the polychaete *Nereis diversicolor*. *Mar Ecol Prog Ser* 229:127–136
- Gamble JC (1970) Effect of low dissolved oxygen concentration on the ventilation rhythm of three tubicolous crustaceans, with special reference to the phenomenon of intermittent ventilation. *Mar Biol* 6:121–127
- Gardner LR, Sharma P, Moore WS (1987) A regeneration model for the effect of bioturbation by fiddler crabs on ²¹⁰Pb profiles in salt marsh sediments. *J Environ Radioact* 5:25–36
- Giangrande A (1991) Behaviour, irrigation and respiration in *Eudistylia vancouveri* (Polychaeta: Sabellidae). *J Mar Biol Assoc UK* 71:27–35
- Gilbert F, Aller RC, Hulth S (2003) The influence of macrofaunal burrow spacing and diffusive scaling on sedimentary nitrification and denitrification: an experimental simulation and model approach. *J Mar Res* 61:101–125
- Gilbert F, Hulth S, Grossi V, Poggiale JC and others (2007) Sediment reworking by marine benthic species from the Gullmar Fjord (western Sweden): importance of faunal biovolume. *J Exp Mar Biol Ecol* 348:133–144
- Glud RN (2008) Oxygen dynamics of marine sediments. *Mar Biol Res* 4:243–289
- Graf G, Rosenberg R (1997) Bioresuspension and biodeposition: a review. *J Mar Syst* 11:269–278

- Gribsholt B, Kostka JE, Kristensen E (2003) Impact of fiddler crabs and plant roots on sediment biogeochemistry in a Georgia salt marsh. *Mar Ecol Prog Ser* 259:237–251
- Griffen BD, DeWitt TH, Langdon C (2004) Particle removal rates by the mud shrimp *Upogebia pugettensis*, its burrow, and a commensal clam: effects on estuarine phytoplankton abundance. *Mar Ecol Prog Ser* 269:223–236
- Gutierrez JL, Jones CG (2006) Physical ecosystem engineers as agents of biogeochemical heterogeneity. *BioScience* 56:227–236
- Hoffmann RJ, Mangum CP (1972) Passive ventilation in benthic annelids. *Science* 176:1356–1357
- Huang K, Boudreau BP, Reed DC (2007) Simulated fiddler-crab sediment mixing. *J Mar Res* 65:491–522
- Hüttel M (1990) Influence of the lugworm *Arenicola marina* on porewater nutrient profiles of sand flat sediments. *Mar Ecol Prog Ser* 62:241–248
- Huhta V (2007) The role of soil fauna in ecosystems: a historical review. *Pedobiologia (Jena)* 50:489–495
- Johnson DL (2002) Darwin would be proud: bioturbation, dynamic denudation, and the power of theory in science. *Geoarchaeology* 17:7–40
- Jones SE, Jago CF (1993) *In situ* assessment of modification of sediment properties by burrowing invertebrates. *Mar Biol* 115:133–142
- Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69:373–386
- Koike I, Mukai H (1983) Oxygen and inorganic nitrogen contents and fluxes in burrows of the shrimps *Callinassa japonica* and *Upogebia major*. *Mar Ecol Prog Ser* 12:185–190
- Kristensen E (1989) Oxygen and carbon dioxide exchange in the polychaete *Nereis virens*: influence of ventilation activity and starvation. *Mar Biol* 101:381–388
- Kristensen E (2001) Impact of polychaetes (*Nereis* spp. and *Arenicola marina*) on carbon biogeochemistry in coastal marine sediments. *Geochem Trans* 2:92–103
- Kristensen E, Hansen K (1999) Transport of carbon dioxide and ammonium in bioturbated (*Nereis diversicolor*) coastal, marine sediments. *Biogeochemistry* 45:147–168
- Kristensen E, Holmer M (2001) Decomposition of plant materials in marine sediment exposed to different electron acceptors (O_2 , NO_3^- and SO_4^{2-}), with emphasis on substrate origin, degradation kinetics and the role of bioturbation. *Geochim Cosmochim Acta* 65:419–434
- Kristensen E, Kostka JE (2005) Macrofaunal burrows and irrigation in marine sediment: microbiological and biogeochemical interactions. In: Kristensen E, Haese RR, Kostka JE (eds) *Interactions between macro- and micro-organisms in marine sediments*. American Geophysical Union, Washington, DC, p 125–157
- Kristensen E, Hansen T, Delefosse M, Banta GT, Quintana CO (2011) Contrasting effects of the polychaetes *Marenzelleria viridis* and *Nereis diversicolor* on benthic metabolism and solute transport in sandy coastal sediment. *Mar Ecol Prog Ser* 425:125–139
- Krüger F (1971) Morphology and life of lugworm *Arenicola marina*. *Helgol Wiss Meeresunters* 22:149–200
- Levin L, Blair N, DeMaster D, Plaia G, Fornes W, Martin C, Thomas C (1997) Rapid subduction of organic matter by maldanid polychaetes on the North Carolina slope. *J Mar Res* 55:595–611
- Lindroth A (1938) Studien über die respiratorischen Mechanismen von *Nereis virens* Sars. *Zoologiska Bidrag från Uppsala* 17:367–497
- Lohrer AM, Thrush SF, Hunt L, Hancock N, Lundquist C (2005) Rapid reworking of subtidal sediments by burrowing spatangoid urchins. *J Exp Mar Biol Ecol* 321:155–169
- Maire O, Lecroart P, Meysman F, Rosenberg R, Duchene JC, Gremare A (2008) Quantification of sediment reworking rates in bioturbation research: a review. *Aquat Biol* 2: 219–238
- Mangum CP (1964) Activity patterns in metabolism and ecology of polychaetes. *Comp Biochem Physiol* 11: 239–256
- Marinelli RL (1992) Effects of polychaetes on silicate dynamics and fluxes in sediments: importance of species, animal activity and polychaete effects on benthic diatoms. *J Mar Res* 50:745–779
- Marinelli RL, Lovell CR, Wakeham SG, Ringelberg DB, White DC (2002) Experimental investigation of the control of bacterial community composition in macrofaunal burrows. *Mar Ecol Prog Ser* 235:1–13
- Mayer MS, Schaffner L, Kemp WM (1995) Nitrification potentials of benthic macrofaunal tubes and burrow walls: effects of sediment NH_4^+ and animal irrigation behavior. *Mar Ecol Prog Ser* 121:157–169
- Mermillod-Blondin F (2011) The functional significance of bioturbation and biodeposition on biogeochemical processes at the water–sediment interface in freshwater and marine ecosystems. *J N Am Benthol Soc* 30:770–778
- Mettaw C (1969) Peristaltic waves of tubicolous worms and the problem of irrigation in *Sabella pavonina*. *J Zool* 158: 341–356
- Meysman FJR, Boudreau BP, Middelburg JJ (2003) Relations between local, nonlocal, discrete and continuous models of bioturbation. *J Mar Res* 61:391–410
- Meysman FJR, Galaktionov OS, Middelburg JJ (2005) Irrigation patterns in permeable sediments induced by burrow ventilation: a case study of *Arenicola marina*. *Mar Ecol Prog Ser* 303:195–212
- Meysman FJR, Middelburg JJ, Heip CHR (2006a) Bioturbation: a fresh look at Darwin's last idea. *Trends Ecol Evol* 21:688–695
- Meysman FJR, Galaktionov OS, Gribsholt B, Middelburg JJ (2006b) Bio-irrigation in permeable sediments: an assessment of model complexity. *J Mar Res* 64:589–627
- Meysman FJR, Galaktionov OS, Cook PLM, Janssen F, Hüttel M, Middelburg JJ (2007) Quantifying biologically and physically induced flow and tracer dynamics in permeable sediments. *Biogeosciences* 4:627–646
- Meysman FJR, Galaktionov OS, Glud RN, Middelburg JJ (2010) Oxygen penetration around burrows and roots in aquatic sediments. *J Mar Res* 68:309–336
- Mitchell IM (2006) *In situ* biodeposition rates of Pacific oysters (*Crassostrea gigas*) on a marine farm in southern Tasmania (Australia). *Aquaculture* 257:194–203
- Morad MR, Khalil A, Roskosch A, Lewandowski J (2010) Quantification of pumping rate of *Chironomus plumosus* larvae in natural burrows. *Aquat Ecol* 44:143–153
- Mukai H, Koike I (1984) Pumping rates of the mud shrimp *Callinassa japonica*. *J Oceanogr Soc Jpn* 40:243–246
- Munksby N, Benthien M, Glud RN (2002) Flow-induced flushing of relict tube structures in the central Skagerrak (Norway). *Mar Biol* 141:939–945
- Neira C, Hopner T (1993) Fecal pellet production and sediment reworking potential of the polychaete *Heteromastus filiformis* show a tide dependent periodicity. *Ophelia* 37:175–185
- Nickell LA, Atkinson RJA (1995) Functional morphology of

- burrows and trophic modes of three thalassinidean shrimp species, and a new approach to the classification of thalassinidean burrow morphology. *Mar Ecol Prog Ser* 128:181–197
- Nielsen OI, Gribsholt B, Kristensen E, Revsbech NP (2004) Microscale distribution of oxygen and nitrate in sediment inhabited by *Nereis diversicolor*: spatial patterns and estimated reaction rates. *Aquat Microb Ecol* 34:23–32
- Papasprou S, Gregersen T, Kristensen E, Christensen B, Cox RP (2006) Microbial reaction rates and bacterial communities in sediment surrounding burrows of two nereidid polychaetes (*Nereis diversicolor* and *N. virens*). *Mar Biol* 148:541–550
- Penha-Lopes G, Bartolini F, Limbu S, Cannicci S, Kristensen E, Paula J (2009) Are fiddler crabs potentially useful ecosystem engineers in mangrove wastewater wetlands? *Mar Pollut Bull* 58:1694–1703
- Pillay D, Branch GM (2011) Bioengineering effects of burrowing thalassinidean shrimps on marine soft-bottom ecosystems. *Oceanogr Mar Biol Annu Rev* 49:137–192
- Purnobasuki H, Suzuki M (2005) Aerenchyma tissue development and gas-pathway structure in root of *Avicennia marina* (Forsk.). *J Plant Res* 118:285–294
- Quintana CO, Tang M, Kristensen E (2007) Simultaneous study of particle reworking, irrigation transport and reaction rates in sediment bioturbated by the polychaetes *Heteromastus* and *Marenzelleria*. *J Exp Mar Biol Ecol* 352:392–406
- Quintana CO, Hansen T, Delefosse M, Banta GT, Kristensen E (2011) Burrow ventilation and associated porewater irrigation by the polychaete *Marenzelleria viridis*. *J Exp Mar Biol Ecol* 397:179–187
- Ray AJ, Aller RC (1985) Physical irrigation of relict burrows: implications for sediment chemistry. *Mar Geol* 62:371–379
- Reynolds WD, Drury CF, Tan CS, Fox CA, Yang XM (2009) Use of indicators and pore volume-function characteristics to quantify soil physical quality. *Geoderma* 152:252–263
- Rhoads DC (1967) Biogenic reworking of intertidal and subtidal sediments in Barnstable Harbor and Buzzards Bay, Massachusetts. *J Geol* 75:461–476
- Richter R (1927) Die fossilen Fährten und Bauten der Würmer, ein Überblick über ihre biologischen Grundformen und deren geologische Bedeutung. *Paläontol Z* 9:193–240
- Richter R (1952) Fluidal-Textur in Sediment-Gesteinen und über Sedifluktion überhaupt. *Notizbl Hess Landesamtes Bodenforsch Wiesb* 6:67–81
- Ridd PV (1996) Flow through animal burrows in Mangrove creeks. *Estuar Coast Shelf Sci* 43:617–625
- Riisgård HU (1991) Suspension feeding in the polychaete *Nereis diversicolor*. *Mar Ecol Prog Ser* 70:29–37
- Riisgård HU, Banta GT (1998) Irrigation and deposit feeding by the lugworm *Arenicola marina*, characteristics and secondary effects on the environment. A review of current knowledge. *Vie Milieu* 48:243–257
- Riisgård HU, Larsen PS (2005) Water pumping and analysis of flow in burrowing zoobenthos: an overview. *Aquat Ecol* 39:237–258
- Schäfer W (1952) Biogene Sedimentation im Gefolge von Bioturbation. *Senckenbergiana* 33:1–12
- Scott DM, Mazurkiewicz M, Leeman P (1976) The long term monitoring of ventilation rhythms of the polychaetous annelid *Nereis virens* Sars. *Comp Biochem Physiol A Physiol* 53:65–68
- Shull DH (2001) Transition-matrix model of bioturbation and radionuclide diagenesis. *Limnol Oceanogr* 46:905–916
- Shull DH, Yasuda M (2001) Size-selective downward particle transport by cirratulid polychaetes. *J Mar Res* 59:453–473
- Shull DH, Benoit JM, Wojcik C, Senning JR (2009) Infaunal burrow ventilation and pore-water transport in muddy sediments. *Estuar Coast Shelf Sci* 83:277–286
- Solan M, Wigham BD (2005) Biogenic particle reworking and bacterial-invertebrate interactions in marine sediments. In: Kristensen E, Haese RR, Kostka JE (eds) Interactions between macro- and microorganisms in marine sediments. American Geophysical Union, Washington, DC, p 105–124
- Solan M, Cardinale BJ, Downing AL, Engelhardt KAM, Ruesink JL, Srivastava DS (2004) Extinction and ecosystem function in the marine benthos. *Science* 306:1177–1180
- Specht DT, Lee H (1989) Direct measurement technique for determining ventilation rate in the deposit feeding clam *Macoma nasuta* (Bivalvia, Tellinaceae). *Mar Biol* 101:211–218
- Stamhuis EJ, Videler JJ (1998) Burrow ventilation in the tube-dwelling shrimp *Callinassa subterranea* (Decapoda: Thalassinidea). III. Hydrodynamic modelling and the energetics of pleopod pumping. *J Exp Biol* 201:2171–2181
- Stamhuis EJ, Reede-Dekker T, van Etten Y, de Wiljes JJ, Videler JJ (1996) Behaviour and time allocation of the burrowing shrimp *Callinassa subterranea* (Decapoda, Thalassinidea). *J Exp Mar Biol Ecol* 204:225–239
- Stamhuis EJ, Videler JJ, de Wilde PAWJ (1998) Optimal foraging in the thalassinidean shrimp *Callinassa subterranea*—improving food quality by grain size selection. *J Exp Mar Biol Ecol* 228:197–208
- Stieglitz T, Ridd P, Müller P (2000) Passive irrigation and functional morphology of crustacean burrows in a tropical mangrove swamp. *Hydrobiologia* 421:69–76
- Sweerts JPRA, Kelly CA, Rudd JWM, Hesslein R, Cappenberg TE (1991) Similarity of whole-sediment molecular diffusion coefficients in freshwater sediments of low and high porosity. *Limnol Oceanogr* 36:335–342
- Timmermann K, Christensen JH, Banta GT (2002) Modeling of advective solute transport in sandy sediments inhabited by the lugworm *Arenicola marina*. *J Mar Res* 60:151–169
- Valdemarsen T, Kristensen E, Holmer M (2010) Sulfur, carbon, and nitrogen cycling in faunated marine sediments impacted by repeated organic enrichment. *Mar Ecol Prog Ser* 400:37–53
- Valdemarsen T, Wendelboe K, Egelund JT, Kristensen E, Flindt MR (2011) Exclusion of seagrass by benthic invertebrates; burial of eelgrass seeds and seedlings by the lugworm (*Arenicola marina*). *J Exp Mar Biol Ecol* 410:45–52
- van Dam L (1937) Über die Atembewegungen und das Atemvolumen von *Phryganea*-Larven, *Arenicola marina*, und *Nereis virens*, sowie über die Sauerstoffausnutzung bei *Anodonta cygnea*, *Arenicola marina*, und *Nereis virens*. *Zool Anz* 118:122–128
- Volkenborn N, Polerecky L, Wetthey DS, Woodin SA (2010) Oscillatory porewater bioadvection in marine sediments induced by hydraulic activities of *Arenicola marina*. *Limnol Oceanogr* 55:1231–1247

- Vopel K, Thistle D, Rosenberg R (2003) Effect of the brittle star *Amphiura filiformis* (Amphiuridae, Echinodermata) on oxygen flux into the sediment. *Limnol Oceanogr* 48: 2034–2045
- Vopel K, Vopel A, Thistle D, Hancock N (2007) Effects of spatangoid heart urchins on O₂ supply into coastal sediment. *Mar Ecol Prog Ser* 333:161–171
- Wells GP (1945) The mode of life of *Arenicola marina* L. *J Mar Biol Assoc UK* 26:170–207
- Wells GP (1949) Respiratory movements of *Arenicola marina* L.—intermittent irrigation of the tube, and intermittent aerial respiration. *J Mar Biol Assoc UK* 28:447–464
- Wetthey DS, Woodin SA, Volkenborn N, Reise K (2008) Pore-water advection by hydraulic activities of lugworms, *Arenicola marina*: a field, laboratory and modeling study. *J Mar Res* 66:255–273
- Wild C, Røy H, Huettel M (2005) Role of pelletization in mineralization of fine-grained coastal sediments. *Mar Ecol Prog Ser* 291:23–33
- Wilkinson MT, Richards PJ, Humphreys GS (2009) Breaking ground: pedology, geological, and ecological implications of soil bioturbation. *Earth Sci Rev* 97:257–272
- Winston JE, Anderson FE (1971) Bioturbation of sediments in a northern temperate estuary. *Mar Geol* 10:39–49

Editorial responsibility: Hans-Heinrich Janssen, Oldendorf/Luhe, Germany

*Submitted: July 25, 2011; Accepted: November 16, 2011
Proofs received from author(s): January 23, 2012*