Bioirrigation in Marine Sediments

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Introduction

Marine sediments cover almost 70% of planet Earth. Since the Cambrian Substrate Revolution more than 450 million years ago, the uppermost sediment layer of most of the seafloor is perfused by the burrows of bottom-dwelling animals. These organisms engage in a range of activities including burrowing, burrow excavation, feeding, feces and pseudofeces expulsions, and burrow ventilation. In concert these activities result in the displacement of sediment particles and interstitial water. These animal-induced perturbations of the sediment matrix are referred to as bioturbation. Estimates of the bioturbated layer thickness average around 10 cm on the global scale, but it can be tens of centimeters thick in coastal and continental shelf sediments.

Animal-induced exchange of solutes between the interstitial and overlying waters — a process referred to as bioirrigation — occurs simultaneously with the reworking of sediment particles as well as without particle reworking. However, the rates of mixing, directionality, and the depth of sediment that is mostly affected vary greatly. Importantly, the volume of water that is moved over a given time by a given organism is typically orders of magnitude larger than the volume of sediment particles. Particle turnover in the bioturbated layer typically occurs on time scales of months to years while pore water turnover occurs on time scales of hours to days.

Given the fundamental differences in water chemistry between the oxygenated overlying water and the nutrient-rich anoxic pore water that surrounds the organisms in the sediment, bioirrigation has profound implications for biogeochemical processes in the sediment. Bioirrigation increases the exchange of solutes across the sediment-water interface (SWI) and the supply of electron acceptors — most notably oxygen — required for microbially mediated mineralization of organic matter. Since any organic material that reaches the seafloor has to pass the bioturbated layer before it can be buried, bioirrigation is a globally important process that ultimately controls the efficiency of carbon burial as well as ocean and atmosphere chemistry on geologic time scales.

Benthic Infaunal Organisms

The seafloor is inhabited by diverse organisms (Videos 1, 2, 3). These so called "benthic infaunal organisms," or "benthic infauna," use the sediment as shelter from predation and hydrodynamic disturbances and, in many cases, as a source of food. In terms of abundance, biomass, and species richness invertebrates are the dominant group of benthic infauna, with polychaetes, crustaceans, bivalves, and echinoderms being some of the dominant taxa. The majority of benthic infauna feed either on organic material associated with sediment particles (deposit feeders) or by filtering organic particles from the water column (suspension feeders). Some organisms continuously move through the sediment (eg, burrowing echinoderms and some polychaetes), while others mostly stay at the same place (many bivalves) or establish and maintain burrows or tubes (eg, many polychaetes and crustaceans). The shape and size of burrows is very diverse: from simple, blind-ending vertical shafts, or J-shaped burrows over U-shaped and Y-shaped burrows with two burrow openings at the SWI, all the way to complex burrow networks with multiple openings. In some

cases most of the burrow volume is occupied by the animal (eg, arenicolid polychaetes) while other species maintain burrows that exceed their body size by orders of magnitude (eg, thalassinid crustaceans).

Burrow Ventilation

One fundamental challenge that all infaunal organisms face is the limited availability of oxygen, which in organic-rich cohesive sediments penetrates typically no more than a few millimeters from the SWI. Thus, to be able to live within the predominantly anoxic sediment, benthic infauna must stay connected with the oxygenated overlying water. To achieve this, some use tube-like body structures that protrude the sediment surface (eg, inhalant siphons in bivalves, Video 3), while others establish an oxic halo around their bodies (eg, many echinoderms) or maintain burrows through which they pump oxygenated water (eg, many polychaetes and crustaceans (Videos 1, 2, 4, and 5). While respiratory water currents within organisms or over their body surfaces are produced by ciliary tracts of the gill filaments (most bivalves, Video 6) or epithelial cilia (many echinoderms), respectively, burrow ventilation is achieved by whole-body contractions (eg, peristalsis in polychaetes) or moving appendages (eg, pleopod beating in crustaceans) in narrow parts of the burrows (Videos 4 and 5). Deposit feeders ventilate their burrows to access oxygen for respiration and in some cases to facilitate feeding and burrowing, while many suspension feeders acquire food from the overlying water via their respiratory currents. Consequently, time-averaged pumping rates of deposit feeders (typically less than 100 mL h⁻¹) are much smaller than those of many suspension feeders (1000 mL h⁻¹ and more). It should be noted that even the lower volumes of fluids moved per unit time by deposit feeders are still at least 1–2 orders of magnitude greater than the volumes of particles that are moved over the same time interval by some of the strongest sediment reworkers, such as arenicolid polychaetes or thalassinid crustaceans.

Bioirrigation in Cohesive Versus Permeable Sediments

Although the main purpose of burrow ventilation is the delivery of dissolved oxygen from the overlying water to the pumping organism within the sediment, some of this oxygen escapes to the surrounding anoxic sediment. The scale of impact and the dominant mode of solute transport varies among functional groups of benthic infauna and is also strongly dependent on the permeability of the sediment (Fig. 1).

In cohesive (eg, muddy) sediments, the permeability of the sediment is so low that solute transport is dominated by diffusion, which is driven by the concentration gradients between the burrow lumen and the surrounding sediment. Water transport is limited to the burrow itself, and its mixing with the interstitial water is further minimized if burrows have multiple openings (eg, in U-shaped burrows). The radial solute gradients around ventilated burrows resemble the vertical gradients at the SWI (eg, oxygen typically penetrates radially no more than a few millimeters from the burrow wall into the surrounding sediment, Video 7). Thus, the ventilated burrows can be viewed effectively as a subsurface extension of the SWI. It has been estimated that burrows often add $>1 \text{ m}^2$ surface area to each square meter of the seafloor. The diffusive exchange between the burrow and the surrounding



Fig. 1 There are multiple ways by how bioirrigation manifests itself and affects solute exchange in marine sediments. Pits and mounds due to sediment reworking activities increase the sediment surface area and interact with water currents above the sediment surface to cause advection through the sediment. Animals with oxic halos surrounding them and ventilated burrows increase the surface area over which solutes diffuse along concentration gradients. Burrow ventilation may also induce bioadvection if burrow walls are permeable or incomplete. Water injections through siphons and bio-hydraulic activities create gradients in pore water pressure that induce pore water bioadvection. Bioadvecction leads to greater oxic sediment volumes and hence also to increased rates of diffusional transport. In a strict sense burrow ventilation and water injection through siphons are hydraulic activities are well. Hydraulic activities are depicted separately to emphasize that many of these activities are not directly related to water pumping for animal respiration. The relative contribution of solute transport by diffusion and advection not only depends on the functional group of an organism but also the permeability of the burrow wall (if present) and the permeability of the sediment.

sediment is controlled by the diffusivity of the burrow wall. Many benthic organisms line their burrows with small particles and mucus, which significantly reduces the rate of diffusion across the burrow wall. This reduced diffusivity not only prevents oxygen from diffusing away from the organism, but also minimizes the diffusive flux of noxious solutes (eg, hydrogen sulfide or ammonia) from the surrounding sediment into the burrow.

In permeable (eg, sandy) sediments, solutes are additionally transported by advection, that is, transport of interstitial water, driven by pore water pressure gradients. Burrow ventilation and other bio-hydraulic activities (see below) generate pressure gradients in the pore water along which the interstitial water moves through the sediment. This "bioadvective" transport of solutes is typically orders of magnitude faster than the diffusive transport driven by solute concentration gradients. Thus, the sediment volume that is affected by bioirrigation in permeable sediments is much larger than in cohesive sediments. For example, oxygen can penetrate several centimeters from the burrow into the surrounding sediment (Videos 7 and 8). Bioadvection is typically associated with organisms with blind-ending, J-shaped burrows or organisms with below-ground exhalent siphons that inject water directly into the sediment. However, bioadvection can be important also around burrow systems with multiple openings provided that burrow wall is permeable or the lining is incomplete and the surrounding sediment is permeable.

Passive Bioirrigation

Another way in which organisms affect the exchange of solutes across the SWI is through their impact on sediment topography. The geomorphological products of deposit-feeding activity, such as defecation and excavation mounds and feeding funnels, can dominate the seafloor landscape (Fig. 2). The interaction between the uneven sediment surface and the overlying water leads to pressure variation along the SWI, which will result in advective transport of water through the sediment if the sediment is permeable. For example, undirectional flow above the SWI creates zones of increased pressure in front of a (biologically created) sediment mound and low pressure zones behind the sediment mound. Consequently, overlying water enters the sediment in front of the mound and pore water moves out of the sediment behind the mound (Video 8). It is important to note that although the topography-induced advection and bioadvection both cause increased rates of pore water transport, the effect of the former is typically limited to the uppermost few centimeters while the latter affects the entire sediment volume above the ventilated burrow, which can be tens of centimeters below the SWI and the corresponding changes in pore water pressures are orders of magnitude larger with bioadvection.

Biohydraulic Activities

Traditionally, bioirrigation has been attributed to behaviors that are directly related to water pumping that supplies the organism with oxygen for respiration. However, pore water pressure measurements indicate that many other behaviors induce changes in pore water pressure as well (Fig. 3). For example, lugworms defecate sediment onto the sediment surface, and burrowing thalassinids expel sediment when excavating their burrows. This rapid displacement of a few milliliters of sediment from depth



Fig. 2 Bioturbated intertidal sediments reworked by deposit feeding organisms. Left: Excavation mounds created by the burrowing thalassinid crustacean *N. californiensis* (Oregon, USA). Burrows can be >50 cm deep. Center: Defecation mounds and feeding funnels created by the arenicolid polychaete *A. marina* (Wadden Sea, Germany). Note the oxidized *brownish sediment* surrounding the worm at 30 cm depth in the center bottom image. *Dark clusters* on the worm are its gills. Right: Feeding traces created by the tellinid bivalve *M. nasuta* (WA, USA). Note the long inhalant and the short exhalant siphons in the right bottom image.



Fig. 3 Pore water pressure dynamics measured over 12 h in the presence of three infaunal species. Pore water pressure was measured on isolated individuals in the laboratory. Simultaneous time-lapse photography was used to assign pressure waveforms to behaviors. Pore water is pressurized during respiratory pumping while other behaviors cause short and mostly negative (ie, below the hydrostatic baseline) pressure pulses.

creates short (few seconds) but large negative pore water pressure pulses within the sediment. Injection of water through siphons allows bivalves to move their siphons through the subsurface, creating positive pressure pulses. Valve claps of bivalves (eg, during feces or pseudofeces expulsions) create large negative pulses, while burrowing through the sediment performed by muscular or hydraulic contractions causes alternating large positive and negative pressure pulses.

Pore water pressurization induced by these "bio-hydraulic activities" can be detected at tens of centimeters away from the organism. The duration and magnitude of the pressure pulses vary strongly depending on the type of activity (Fig. 3). Importantly, with tens to hundreds of hydraulically active organisms per square meter, the spheres of hydraulic influence for nearest neighbors overlap. As a result, the inhabited sediment is pressurized in a complex and highly dynamic three-dimensional fashion and the entire pore water within the permeable bioturbated layer is in continuous motion (Videos 8 and 9).

Effects of Bioirrigation on Sediment Biogeochemistry

In marine sediments, electron acceptors for organic mineralization are used sequentially based on the yield in free energy of the reduction-oxidation (redox) process, typically in the order of O_2 , NO_3^- , Mn-oxides, Fe-oxides, SO_4^{2-} , and CO_2 . In the absence of bioirrigation this results in a vertically stratified dominance of specific organic mineralization pathways controlled by diffusive transport. Burrow ventilation and bioirrigation transform this relatively simple biogeochemical zonation into a more complex three-dimensional pattern. In diffusion-dominated systems, the consequences can be well understood by approximating the bioirrigated sediment as a set of evenly distributed hollow cylinders filled with the overlying water from which the solutes radially diffuse into the surrounding sediment. This simplified model shows a remarkably good agreement between the modeled and measured depth profiles of pore water solute concentrations for a wide range of burrow size and burrow spacing settings. In systems where solute transport is driven by bioadvection, a pocket injection model is more appropriate to understand the spatial patterns of solute concentrations and fluxes. Irrespective of the sediment type and the dominant mode of solute transport, bioirrigation in general leads to enhanced rates of solute exchange across the SWI with multiple implications for biogeochemical processes.

Carbon Cycling

One of the most significant impacts of bioirrigation is the increased supply of oxygen to the predominantly anoxic subsurface sediments. Because oxygen is energetically the most favorable electron acceptor, increased oxygen supply enhances carbon remineralization by aerobic processes while inhibiting organic mineralization by anaerobic processes. Additionally, oxygen serves as an oxidant of the reduced inorganic metabolites produced during anaerobic mineralization of organic material (most notably hydrogen sulfide, produced by sulfate-reducing bacteria), thus lowering their pore water concentrations and making the conditions for anaerobic metabolism more favorable. Overall, bioirrigation increases rates of organic carbon mineralization and thus ultimately lowers the efficiency of carbon burial.



Fig. 4 Bioirrigation and the nitrogen cycling in marine sediments. Nitrogen occurs in a wide range of oxidation states (bottom row). *White squares* are the most important nitrogen species in marine sediments. Main metabolic pathways in anoxic (*dark gray*) and oxic (*light gray*) sediment are given in italics. Irrigation by infaunal organisms affects the nitrogen cycle in multiple ways (shown in *circles*): directly through increased supply of nitrogen by water pumping (nitrate) and excretions (ammonia) and indirectly through the supply of other oxidants such as oxygen. Given the sensitivity of most nitrogen pathways to the presence and absence of oxygen, bioirrigation is a key determinant of which reaction can occur when and where.

Nitrogen Cycling

Infaunal organisms affect the availability of nitrogen in multiple ways (Fig. 4). Increased rates of organic mineralization together with direct infaunal excretion increase concentrations of ammonium. Increased availability of oxygen around burrows increases the rate of nitrification leading to increased concentrations of nitrate in the sediment. If present in the overlying water, nitrate can also be supplied to the sediment directly by burrow ventilation. In anoxic sediments, nitrate then serves as an electron acceptor for organic mineralization (denitrification) leading to the production of gaseous N_2 and thus a net loss of bioavailable nitrogen from the system. Such loss can also occur via anaerobic ammonia oxidation with nitrite. Nitrate may also be recycled to ammonia via dissimilatory nitrate reduction.to ammonia. Since most of these processes are highly dependent on the presence or absence of oxygen and on the concentrations of nitrogen reactants and products, bioirrigation is a critical component of nitrogen cycling in sediments. In general bioirrigation increases rates of coupled nitrification-denitrification and is therefore extremely important for regulating the nitrogen loading of the seabed and the eventual loss of bioavailable nitrogen to the overlying water. More recently, sediments surrounding ventilated burrows, which are characterized by low ammonium concentrations (due to nitrification and pore water flushing) but high N_2 concentrations (due to denitrification), have been suggested as suitable sites for N_2 -fixation in sediments by sulfate-reducing bacteria.

Effects of Bioirrigation on Metals, Nutrients, and Pollutants

Many metals in marine sediments, such as iron and manganese, change between dissolved and particulate forms when undergoing oxidation-reduction reactions. By enhancing the supply of oxygen to sediments, bioirrigation therefore drives a complex reaction network that involves metal dissolution, precipitation, mobilization, and transport. For example, particulate iron oxides, which are exported from terrestrial systems and reach the seafloor via sedimentation, become dissolved upon their reduction by iron-reducing bacteria that utilize them as an electron acceptor for organic mineralization in anoxic sediments. This dissolved iron pool can, in turn, react with sulfides produced by anaerobic organic matter degradation by sulfate-reducing bacteria, leading to the formation of particulate iron sulfides, which give sediments their characteristic black (iron monosulfides) and gray (iron disulfides, ie, pyrite) colors (Fig. 2). Additionally, dissolved iron can be oxidized and precipitated back to iron oxides when in contact with oxygen, which is enhanced via bioirrigation and clearly visible around ventilated burrows as rust-colored sediment. Importantly, the highly reactive surfaces of iron oxides efficiently adsorb negatively charged nutrients such as phosphate. Therefore, bioirrigation leads to an increased retention of such nutrients in sediments, which has important implications for the processes in the overlying water columns such as primary productivity or eutrophication. Bioirrigation can also strongly impact the formation, distribution, and mobilization of (organo-)metallic pollutants. For example, by decreasing the zone of sulfide accumulation, bioirrigation increases the sediment volume that supports mercury methylation and, through coupling with the biologically induced pore water transport, can lead to increased fluxes of methylmercury from sediments to the overlying water.

Geochemical Dynamics

Traditionally, ventilated infaunal burrows have been viewed mainly as a subsurface extension of the sediment surface across which diffusive or advective exchange of solutes occurs. However, there is one critical difference: due to the intermittency of the hydraulic activities of benthic infauna and the constrained volume of water within the burrow, sediments surrounding ventilated burrows experience much more dynamic geochemical conditions than the surficial sediments (Videos 7, 8, 10, and 11). In diffusion-dominated systems, discontinuous pumping and the dynamic changes of burrow water chemistry results in time-dependent diffusive fluxes across the burrow wall. In permeable sediments relatively large volumes of sediment surrounding the animals are periodically flushed with oxic water. The typical time-scale at which sediment switches between oxic and anoxic conditions is in the range of minutes to hours and the durations of oxic and anoxic conditions are on the scales of minutes (Fig. 5). Since the bio-hydraulic activities of infauna and the microbial activity in sediments depend on temperature (Fig. 6), the time scales of the geochemical oscillations are expected to strongly vary seasonally.

The time scales at which the availability of electron acceptors and the presence of inhibitory solutes change in bioirrigated sediments are in the same range as many processes that are related to microbial activity. For example, the synthesis of pathway-specific enzymes in response to the availability of specific substrates happens on the scale of minutes to hours. How exactly



Fig. 5 Compilation of oxygen dynamics induced by bioirrigation of infaunal organisms in permeable sediments. Data derived from planar optode imaging of oxygen over 10 h. *Upper panel* gives two-dimensional distribution of probabilities of sediment oxygenation (ie, 50% means that oxygen at concentrations >5% air saturation was present 50% of the time). *Lower panel* gives the 2D distribution of the average numbers of oscillations between oxic and anoxic conditions per hour over the 10 h period.



Fig. 6 Oxygen dynamics in burrows ventilated by the polychaete *Nereis diversicolor* at different temperatures. *Upper panels* are time-series of oxygen concentrations (in % air saturation) within the burrow. *Bottom row* are 2-D images of oxygen concentrations, oxygen probabilities, and frequencies of oscillations between oxic and anoxic conditions over a 10 h period at both temperatures. *White dots* in oxygen concentration images are the approximate locations for which oxygen concentration time-series are shown in the *upper panels*. Oxygen concentrations and probabilities are comparable at both temperatures while oxic and anoxic oscillations occur much more frequently at summer temperatures due to changes in irrigation activity and faster sedimentary oxygen consumption.

microbial communities deal with rapidly changing geochemical conditions, particularly how they optimize enzyme synthesis and regulate metabolic activity, is largely unknown.

The Role of Bioirrigation in Benthic Ecology

Bioirrigation has manifold implications for the ecology of benthic systems. Burrows and adjacent sediment are often hotspots of benthic biodiversity as micro-, meio-, and even other macrofaunal organisms benefit from the oxygen supply and decreased concentrations of noxious solutes in and around infaunal burrows. In permeable sediment, the entire sediment above the point of injection is often characterized by much lower concentrations of pore water solutes, including hydrogen sulfide, due to the efficient flushing of the sediment by hydraulically active organisms (Fig. 7). Pore water pressurization results in a net upward transport of pore water (Video 9) which leads to increased fluxes of nutrients (eg, ammonia and silicate) towards much of the sediment surface. In shallow waters these nutrients become available to photosynthetic microalgae in the uppermost layer of the sediment, leading to increased benthic primary productivity (Fig. 7) that benefits not only the hydraulically active deposit-feeding infauna but also other benthic grazers. The bioadvection-driven leakage of anoxic and potentially ammonium- and sulfide-rich pore water through the SWI also affects recruitment because these solutes act as negative cues for many benthic species.

As any porous medium, sediments impose some resistance to the flow of water, and the pressure necessary to move water through the sediment matrix is governed by the permeability of the sediment. In permeable sandy sediments, little pressure is necessary to force water flow through the sediment, whereas more cohesive sediments are more resistant to water flow and hence the pressure necessary to move water through the cohesive sediment is larger. Since the pore water pressures that organisms can generate is finite, sediment permeability is an important factor controlling the distribution of benthic infauna. For example, organisms that reside in blind-ending burrows are typically restricted to permeable sediments. However, pressure pulses associated



Fig. 7 Exclusion experiments are one way to investigate the role of bioirrigating organisms. In the German Wadden Sea, lugworms (*A. marina*) were excluded from intertidal sand by inserting a 1 mm mesh at 8–10 cm depth (A-C). The distinct border between lugworm inhabited and non-inhabited sediments (D) coincides with dramatic changes in pore water nutrient concentrations (E), indicating an efficient flushing of nutrients by bioadvection. The *white dotted line* indicates the approximate depth of the mesh that was used to exclude the lugworms. (F) Hyperspectral imaging uncovers the extremely heterogeneous distribution of microphytobenthic biomass at the surface of bioturbated sediments. *Blue colors* represent freshly defecated sediment with low chlorophyll *a* concentrations due to digestion by the lugworms, while *red colors* show areas of enhanced primary productivity induced by bioadvective supply of nutrients from deeper sediment layers. The latter effect is also illustrated in panel G, which shows surficial chlorophyll *a* concentrations in an artificially irrigated sediment (water injected 14 cm deep in the sediment at a rate 1.5 mL min⁻¹) in comparison to non-irrigated sediment.

with some hydraulic behaviors can cause sediment fracture and the formation of macropores, that is, channels of locally increased permeability, which not only channel the pore water flow but also benefit the organisms themselves by reducing the pressures and thus energy required to force water into and through the sediment.

Methods to Study Burrow Ventilation and Bioirrigation

Burrow ventilation and the associated bioirrigation have been studied in multiple ways. Pumping rates of organisms are estimated by transferring organisms into glass tubes and measuring water displacement against controlled pressure heads. One disadvantage of this approach is that organisms often show altered pumping behavior in these slippery and unreactive artificial tubes. If burrow geometries are known, flow velocities can be used to estimate the pumping rates of animals within the sediment. Flow velocities above burrow openings can be estimated by particle image velocimetry or acoustic Doppler techniques.

To study the impact of bioirrigation and quantify how much water is forced through the sediment (bioadvection), how burrow ventilation affects the distribution of solutes around the burrows, and to what extent bioirrigation affects fluxes across the SWI, a wide range of approaches is used. Time-averaged bioirrigation rates are quantified in-situ by measuring the concentration profiles of pore water nutrients (eg, silicate or ammonium) or naturally occurring but chemically unreactive radioisotopes (eg, ²²²Ra) in the sediment. An alternative approach involves monitoring concentration changes of artificially added inert tracers (eg, bromide) or fluorescent tracers (eg, fluorescein) in the overlying or interstitial water in benthic chambers. Similarly, benthic chambers are used to quantify the effects of bioirrigation on the fluxes of relevant solutes (eg, oxygen, nutrients, CO_2) across the SWI. Microsensors are used to measure concentration profiles across burrow walls or solute concentration dynamics within and around ventilated burrows with microscale resolution. The use of optical chemical sensors that employ a target-specific fluorescent moiety immobilized on a transparent substrate (planar optodes) makes it possible to measure the geochemical dynamics in sediments in two dimensions with high temporal (seconds) and spatial (mm) resolution over extended time intervals (days and more). For example, oxygen planar optodes attached to the inside of thin aquaria reveal extremely dynamic and spatially complex redox conditions in the sediment surrounding infaunal organisms and their burrows (Fig. 5; Videos 6–9). Pressure sensors are used to measure pore water pressure

dynamics, which not only inform about the frequencies and durations of hydraulic behaviors (Fig. 3) but in concert with planar optode imaging, also document the tight link between pore water pressure gradients generated by the different behaviors of infauna, advection of solutes, and the geochemical dynamics in the sediment (Video 12). Given the spatial heterogeneity of bioturbated sediments, imaging techniques are also extremely powerful tools to measure some of the impacts of bioirrigation. For example, hyperspectral cameras have been used to generate images of the 2-D distribution of chlorophyll *a* in surficial sediments with millimeter resolution (Fig. 7). Such images allow quantitative visualization of the interplay between the effects of grazing and stimulation of microphytobenthic growth by bioadvective transport of nutrients from depth to the sediment surface.

Perspectives

Given the importance of bioirrigation for the function of marine sediments and benthic-pelagic coupling, it is critical to understand how environmental change will affect the distribution and irrigation behavior of benthic organisms. Changes in the distribution, abundance, and activity of bioirrigating species will have significant consequences for the biogeochemical cycling and the productivity of the seafloor. In a warming climate the biogeographic limits of cold-water species are moving poleward. The impact on ecosystem functions will be disproportionally large if ecosystems are invaded by so called "ecosystem engineering" species (eg, lugworms or thalassinid crustaceans), or if such species disappear and are not replaced by their functional equivalents. For example, the spionid polychaete *Marenzelleria* ssp. is currently invading the Baltic sediments, irrigating much deeper than any of the native infauna and fundamentally changing nutrient dynamics across the SWI.

Many infaunal organisms are sensitive to physical (eg, bottom-trawling) and chemical (eg, hypoxia) disturbances. Increased rates of these disturbances will negatively impact benthic communities, especially the large organisms. A shift from deep burrowing bioirrigators to smaller opportunistic species will have large effects on the function of benthic systems. Ecosystem functions will likely be affected also by more subtle changes, including behavioral responses of the infauna to non-lethal stress such as injury, increased magnitudes of diel-cycling hypoxia, or fine particle deposition due to increased erosion on land.

New technologies now enable us to address the heterogeneity and variability of the geochemical conditions of bioirrigated sediments at appropriate spatial and temporal scales. In order to more accurately predict the impact of environmental changes on the function of benthic systems and benthic-pelagic coupling it will be critical to incorporate this complexity into global scale ecosystem models.

Online Resources

Concept map "How do burrowing organisms affect the functioning of benthic ecosystems" developed for the Center for Ocean Sciences Education excellence (COSEE): cosee.umaine.edu/climb/cmv/index.cfm#/?id=7810&timer=992

Movie "The Sound of the Seafloor" streamed at the 2016 Beneath the Waves Film Festival: https://www.dropbox.com/s/u57sqypgi70r28f/The%20sound%20of%20the%20seafloor.mp4?dl=0.

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Videos

<u>Video 1: Sediment reworking by the lugworm Arenicola marina.</u> The lugworm was placed in a thin aquarium (dimensions $40 \times 30 \times 1.2$ cm) equipped with an oxygen-sensitive planar optode (pink foil on the backside of the aquarium) and a porewater pressure sensor deployed through the front plate. The surface sediment on the left is being subducted due to ingestion by the lugworm at depth and defecation on the sediment surface on the right side. Video is shown at 10.000-fold speed (66 hours in 24 seconds).

<u>Video 2: Sediment reworking by the thalassinid crustacean Neotrypaea californiensis</u>. The thalassinid was placed in a thin aquarium with dimensions $50 \times 57 \times 5$ cm. As burrow establishment progresses, the thalassinid creates new openings at the sediment surface. Note the color change of the sediment surrounding the burrow due to the oxidation of iron mono-sulfides (black) and di-sulfides (pyrite, gray) with oxygen delivered to the burrow and the surrounding sediment by the hydraulic activities of the thalassinid. Video is shown at 10.000-fold speed (91 hours in 33 seconds).

<u>Video 3: Sediment reworking by the tellinid bivalve Macoma nasuta.</u> Shown is a top-down view of an aquarium with dimensions $10 \times 10 \times 20$ cm. The inhalant siphon protrudes the sediment surface to ingest oxygenated water and food particles. The exhalant siphon is subsurface and its approximate location is several cm below the area of conspicuous particle movement on the left side. Brownish color of the sediment surface relates to high abundance of microphytobenthos. Video is shown at 10.000-fold speed (86 hours in 31 seconds).

<u>Video 4: Peristalsis by juvenile lugworms.</u> The lugworms were placed outside the sediment. When within the sediment, each peristaltic wave transports water between the burrow wall and the lugworm body in the tail-to-head direction. Adult lugworms perform 6-10 peristaltic waves per minute, each transporting approximately 0.2 mL of water. Video is shown in real-time and at 10-fold speed.

<u>Video 5: Burrow ventilation by the burrowing thalassinid crustacean Neotrypaea californiensis</u>. Burrow ventilation is achieved by pleopod beating with the abdomen located in the narrow part of the burrow. Typical adult individuals perform 15-30 beats per minute, each transporting about 0.3 mL of water. Video is shown in real time and at 10-fold speed.

<u>Video 6: Irrigation by the tellinid bivalve Macoma nasuta</u>. The exhalent siphon is located close to the transparent wall, while the inhalant siphon can be seen occasionally in the background. While feeding, water is pumped out through the exhalent siphon as can be seen from the movement of sediment particles. After 17 seconds the animal expels sediment through its inhalant siphon (pseudofeces expulsion). The last sequence is a defecation event causing sediment failure and creating a new sedimentary channel. Sediment spherules are fecal pellets that have accumulated over time. Video is shown in real time and 50-fold speed.

<u>Video 7: Oxygen dynamics associated with hydraulic activities of the thalassinid crustacean Neotrypaea californiensis.</u> Shown are effects of burrowing and burrow ventilation in muddy and sandy sediments. In the low permeability muddy sediment oxygen penetration is limited by diffusion and oxygen is only detected where the burrow is in direct contact with the oxygen-sensitive foil. In the permeable sandy sediment burrow ventilation results in advective transport of oxygen through the sediment surrounding the burrow and oxygen penetrates several centimeters from the burrow into the surrounding sediment. Video is shown at 2500-fold speed (24 hours in 34 seconds).

<u>Video 8: Oxygen dynamics in permeable sediment inhabited by lugworms.</u> Experiments were conducted in a flume tank (tank dimensions 140×26×24 cm, with a 50×24 oxygen sensitive foil). White line depicts the sediment surface, which is structured by defecation mounds and feeding funnels of the lugworms. Sixteen adult lugworms were allowed to establish burrows in the tank. Oxygen dynamics at depth are driven bioadvection induced two lugworms that ventilated and burrowed close to the oxygen sensitive foil. Increased current velocities above the sediment induced deeper oxygen penetration into the surficial sediment driven by passive bioirrigation, i.e., due to the interaction between the undirectional flow of overlying water and animal-induced sediment topography. In concert passive and active bioirrigation result in very dynamic oxygen distributions within the permeable sediment. Video is shown at 100-fold speed (2.5 hours in 90 seconds).

Video 9: Effects of hydraulic activities by a small community of benthic infauna on porewater transport in permeable sediments. The community comprised a razor clam, a nereid polychaete and eight maldanid polychaetes. Porewater flow patterns were visualized by following the pathway of an inert tracer (fluorescein, green color) injected into the sediment at 9 locations. Porewater pressure dynamics were recorded simultaneously at 2 different locations (indicated by white and blue dots) through the side wall of the aquarium. Increased porewater pressure coincides with upward movement of the tracer. Video is shown at 1000-fold speed (6 hours in 22 seconds).

Video 10: Compilation of oxygen dynamics in permeable sediments induced by biohydraulically active organisms. Video is shown at 1000-fold speed.

Video 11: Oxygen dynamics associated with hydraulic activities of the thalassinid crustacean *Neotrypaea californiensis*. Shown is an overlay of time-lapse photographs and oxygen images taken from opposite sides of a thin aquarium. The hydraulic activities of the thalassinid at different locations within the burrow cause distinct oxygen dynamics around the burrow as well as movements of the oxic-anoxic boundary at the sides of the aquarium. The latter movements were possible due to a leaking sealing gasket and water surrounding the sediment. Video is shown at 1000-fold speed (10 hours in 36 seconds).

Video 12: Synchronous dynamics of porewater pressure and oxygen concentrations in permeable sediment associated with hydraulic activities of the lugworm *Arenicola marina*. Red vertical line in the pressure record shows the time point of images, while black horizontal line is the hydrostatic baseline pressure. Increased pressure corresponds to pumping of oxic water into the sediment and forcing anoxic water out through the sediment-water interface. Intervals of negative pressure correspond to flow reversals, which draw oxic overlying water through the sediment-water interface into the sediment. Large and short negative pressure pulses are associated with defecations, as seen in time-lapse photographs by sediment deposition onto the sediment surface. Video is shown at 500-fold speed (7.5 hours in 54 seconds).