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MAKING TRACKS

Are Animal Burrows a Major Sedimentary Sink for Metals?

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As every ichnologist knows, animals play an important role in the recycling of carbon in marine sediment through burrowing and mixing of fresh sediment with older sediment, grazing and mining of intact organic remains, and the ingestion of refractory organic carbon that may lead to the excretion of more labile faecal pellets. Bioturbation also influences the solid-phase and pore-water properties of sediment by increasing the transport of diagenetic reactants and products across the sediment-water interface, which then affects the oxidation state of redox-active elements. These processes become particularly relevant when one considers that in tidal flats, the inner shelf, and in many bays and estuaries, the number of burrows present in an average sediment may range from $\sim 100/\text{m}^2$ with such larger animals as shrimp and lugworms to more than $50,000/\text{m}^2$ with such smaller animals as with threadworms or amphipods (Gingras et al., 1999).

One aspect, though, that seems to be somewhat off the radar is that those burrows are lined with organic materials, usually mucopolysaccharides and proteins, that are characterized by surface functional groups that become anionic over the pH range of marine pore-waters. This makes burrow linings and backfills highly reactive towards dissolved metal cations (e.g., Over, 1990; McIlroy et al., 2003). Similar polysaccharides associated with bacteria, the so-called extracellular polymeric substances (EPS), are extremely well studied in terms of their surface reactivity and ability to adsorb metal cations (e.g., Wei et al., 2011). Indeed, a multimillion dollar industry is devoted to utilizing EPS in the bioremediation of metal contaminants from fresh- and waste-waters (e.g., Macek and Mackova, 2011). Surprisingly, similar studies are limited with regards to the linings of marine worm burrows. In fact, as far as we are aware, only three studies have explicitly attempted to characterize the metal-binding capacity of animal-burrow mucus. Over (1990) showed that Cu, Fe, Mn, Ni, and Zn in the burrow walls of *Callianassa major* were concentrated by factors between

2 and 4 relative to the surrounding sedimentary media and that analogous Pleistocene burrow structures (i.e., *Ophiomorpha nodosa*) from environmentally similar strata were also enriched in metals, albeit in attenuated concentrations. More recently, Lalonde et al. (2010) analyzed the mucopolysaccharide linings of terrebelid worm burrows (*Thelepus crispus*) that commonly inhabit estuarine sediment on the Pacific Coast. They demonstrated that mucous material possesses unusually high surface reactivities (also referred to as total ligand density) on the order of 11 mmol/g summed over pH 4 to 10; compare this to 5.70 mmol/g for humic acids (Milne et al., 2001) or 3.2 mmol/g for bacterial surfaces (Borrok et al., 2005). This high availability of adsorptive ligands was directly translated into the quantity of metal potentially bound (e.g., using cadmium) over the pH range typical of estuarine and near-shore marine settings, indicating that on a per gram basis worm mucus is more reactive than other organic compounds associated with marine sediment. That study was followed up with an assessment of the chemical properties of commercially available purified analogue to mucopolysaccharide, mucin; the latter was used due to the inherent difficulty in isolating animal mucus from marine sediments (Petrasch et al., 2011). Once again, the mucin proved an effective biosorbent for Cd, with the concentration of available organic ligands in mucin exceeding (by up to 5 times) that of a variety of other metal-reactive organic compounds comprising the organic fraction of marine sediments.

Given the widespread utilization of mucus in burrow linings and backfills, their continuous production independent of sedimentation rates, and the recognized chemical reactivity of the constituent mucopolysaccharides, it then becomes interesting to speculate on the overall metal-binding capacity of natural bioturbated sediment and compare those findings with other sediment sorbents, such as microbial biomass and iron oxides. However, in order to make such a comparison, one first needs to have an idea about the surface area of the burrows within a given depth of marine sediment. Previous estimates have suggested that the surface area representing burrow walls can exceed that of the overlying sediment surface by a factor up to 5 (Davey, 1994). To put this into perspective, a 1 m^2 surface area

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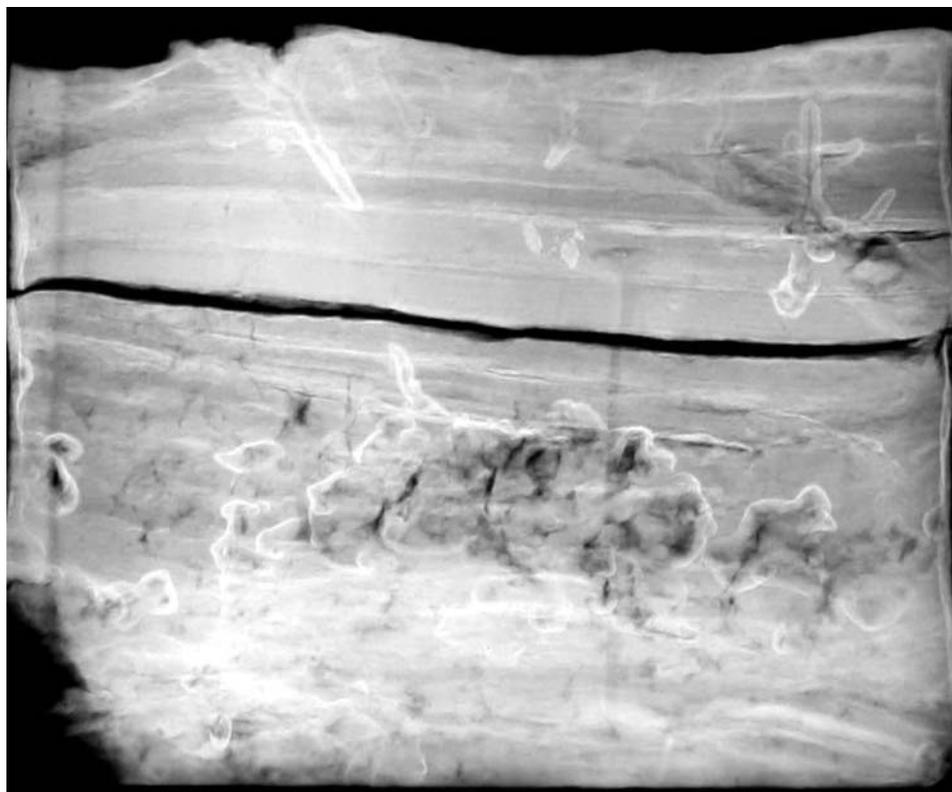


FIG. 1. X-ray of intertidal flat sediment showing amorphous Fe "clouds" forming around burrows and overprinting the burrow fabric. Location: Willapa Bay, Washington. Field of view approximately 10 cm.

of burrowed sediment would have mucus linings beneath the sediment-water interface on the order of 5 m^2 . With a burrow lining thickness of only $10 \mu\text{m}$ (Zorn et al., 2006), a mucus specific gravity of $\sim 1450 \text{ kg/m}^3$ (Celli et al., 2005), and a mucus ligand density of 11 mmol/g (Lalonde et al., 2010), those thin burrow linings could sequester up to 100 mg of Cd. These back-of-the-envelope calculations correlate well with previous experimental incubation studies that showed bioturbating organisms approximately doubling the rate of Cd removal and enabling Cd to become distributed in depth throughout the feeding range of the bioturbating organisms (in this case, to a depth of $\sim 20 \text{ cm}$ for the lugworm *Arenicola marina*) where its accumulation is otherwise restricted to surface sediments in the absence of bioturbation (Rasmussen et al., 1998). Moreover, previous incubation experiments indicated that bioturbating animals acted to prevent the remobilization of sediment-bound Cd that usually would have freely diffused out of pore-waters in the absence of bioturbation (Cuitat et al., 2005).

The impact of irrigation compounds the ability of burrow linings to sequester metals from seawater. It has been estimated that deposit-feeding animal populations (e.g., *Nereis virens*) are capable of irrigating their burrows at a rate of $100 \text{ L m}^{-2} \text{ d}^{-1}$, while suspension-feeders (e.g., *Nereis diversicolor*) are more active and can irrigate at rates of $1000 \text{ L m}^{-2} \text{ d}^{-1}$ (Kristensen and Kostka, 2005). This means that populations of burrowing animals have the capacity to cycle a water column 1–10 meters deep through their burrows each day. This ability to cycle large

volumes of water through their narrow burrows means that there exists a significant exchange of solutes between the overlying seawater and the sediment. Taking a conservative irrigation rate of $100 \text{ L m}^{-2} \text{ d}^{-1}$ and at seawater Cd concentrations of $0.05 \mu\text{g/L}$ (Drever, 1988), 0.005 mg of Cd could be stripped from seawater over the course of 24 hours. Given that fresh mucus can be continuously added to the burrow wall at a rate of 24 cm/day (Aller and Yingst, 1978), it is clear that burrow mucus can effectively scavenge all available Cd dissolved in seawater.

The story, however, does not end here. Despite the clear importance of mucus secretions as a sediment metal sink, it is likely that the calculations above underestimate the overall reactivity of burrows for three important reasons. First, the steep chemical gradients associated with the burrow-water interface and the substrate-rich mucus secretions provide an attractive environment for colonization by bacteria. In this regard, there is a much higher production of aerobic bacteria within oxygenated burrows, which in turn leads to higher aerobic mineralization rates of particulate organic materials (Kristensen et al., 1985). Similarly, in the anoxic zones of the burrow wall and proximal sediment, anaerobic rates of degradation are also high, as shown by increased rates of denitrification, Fe(III)-reduction, and sulphate reduction as compared to the bulk sediment (see Kristensen and Kostka, 2005, for review). Importantly, these respiration reactions will translocate metals originally associated with particulate organic matter into the burrow environment.

Second, the wall linings are enriched in fine particles (e.g., Fig. 1), such as metal oxides and sulphides, which form when metals such as iron, for example, are brought into the burrow via irrigation, and its concentration is then increased to a state of supersaturation with respect to ferric hydroxide, $\text{Fe}(\text{OH})_3$ as a consequence of the diffusive impermeability brought on by the mucus linings (Aller, 1983). When a newer inner burrow layer is formed the initial one moves outward and is eventually reduced so that the metals released are then fixed as sulphides (e.g., mackinawite, greigite) via bacterial sulphate reduction (Aller and Yingst, 1978). Both metal oxides and sulphides are known scavengers of trace metals and anions. As demonstrated by Aller and Yingst (1978), increased accumulation of trace metals into sediments can be driven in part by adsorption onto authigenic oxide and sulphide phases. In a similar manner, sulphate reduction also causes increased alkalinity, which facilitates the precipitation of carbonate minerals on the outer edges of the burrows (Bromley, 1996).

Third, bioturbation continually distributes the mucus throughout the sediment, and estimates suggest that the upper 10 cm of sediment can be completely mixed within just 14 days (e.g., Hines, 2006). Indeed, such sediment can be recycled through the feeding zone many times before ultimate burial below the bioturbation zone. Furthermore, many burrowing animals deposit mucus-rich faecal material at the sediment surface through bioadvection, and in the case of the soldier crab the entire exposed intertidal area can be covered with faecal pellets (Dittmann, 1993). It has even been suggested that a considerable fraction of the surface sediment, up to one-third, may be affected by bioturbation (e.g., Kostka et al., 2002). Taken together, one could certainly expect that a significant proportion of sediment particles would have a mucus coating.

So, where do we go from here? One obvious direction is to compare the metal content associated with *in situ* burrow linings with ambient sediment to validate whether in fact burrowing activity is an effective way of getting metals into the sediment column. Another is to consider what role those bound metals might have on mineral nucleation. Perhaps it is no coincidence that authigenic minerals are often associated with ancient burrows, such as the Ordovician Tyndall limestone, where the burrows form the locus for dolomite formation (Gingras et al., 2004). With burrow-associated dolomitization, it may be that Mg enriched by EPS drives the otherwise kinetically limited calcite to dolomite (i.e., dolomitization) reaction by increasing the Mg/Ca ratio. Similar diagenetic reactions may occur with Fe-cemented and siderite cemented burrows.

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