Macrofaunal Burrows and Irrigation in Marine Sediment: Microbiological and Biogeochemical Interactions

E. Kristensen and J. E. Kostka

Abstract

Construction and maintenance of burrows by macrofauna have large implications for the microbiology and biogeochemistry of marine sediments. Although a wealth of new information has become available during the last few decades, there are still significant gaps in our knowledge. In this chapter, we review the current understanding of how the structure and function of irrigated burrows affect the composition of microbial communities and associated biogeochemical processes. Although a general relationship is observed between burrow depth and diameter (inhabitant width), it is difficult to classify burrow architecture in relation to the function and trophic mode of macrofaunal inhabitants. Trophic mode (suspension-feeding versus deposit-feeding) appears to control burrow wall structure and irrigation rate and thus the exchange of solutes between sediment porewaters and the overlying water. The associated translocation of electron acceptors into and inhibitory metabolites out of the sediment in turn affects diagenetic reactions. It is well established that irrigated burrows enhance total microbial metabolism by stimulating oxic (e.g. respiration) and suboxic (e.g. nitrification–denitrification and iron reduction) reactions in the surrounding sediment. In contrast, the impacts of burrow-generated changes to diffusion scales on anoxic processes like sulfate reduction are less clear. Sediments surrounding burrow structures likely support unique microbial communities that differ from those in surficial sediments due to large differences in environmental conditions. Biogeochemical evidence clearly indicates that the activity and abundance of microorganisms are elevated around burrows. However, the mechanisms controlling microbially mediated geochemical reactions in the burrow zone remain understudied, and very little information is available to assess the impacts of burrow environments on the community structure or diversity of microorganisms. Therefore, we cannot yet generalize about direct relationships between burrows, irrigation and the distribution of microorganisms. However, much progress is already being made through the use of new and exciting experimental tools, such as microsensors and cultivation-independent molecular techniques.
Introduction

Near-surface marine sediments are perforated by burrow structures in various stages of excavation, construction, maintenance, and disrepair. They are constructed and inhabited for discrete but discernable time periods and subsequently modified, abandoned for more favorable locations, or otherwise emptied by forcible removal of the inhabitant [Diaz and Cutter, 2001]. The morphology and function of infaunal burrows vary considerably among benthic invertebrates, from simple unbranched vertical supporting shafts or tubes with one opening at the surface to complex and highly branched networks of funnels and chambers inhabited by several generations of inhabitants. Burrows function as a refuge protecting the usually soft-bodied invertebrates from predation and environmental extremes. The burrow structures also provide physical support for the digging and feeding activities of the burrow inhabitants, while the harsh chemical environment deep in burrows must be counteracted by active or passive irrigation of burrow water. Many burrow-dwellers have partly solved the latter problem by coating the burrow walls with a secreted lining of various types, ranging from thin mucus layers to thick tube walls impermeable to both advection and diffusion. The burrow linings, on the other hand, provide an attractive environment for abundant meiofaunal and microbial communities adapted to life in steep chemical gradients.

Most macrofauna actively rework the sediment and irrigate their burrow structures. Although reworking may affect substantial amounts of sediment and visually affect the seabed topography, the less apparent irrigation of burrows with overlying water is usually volumetrically orders of magnitude greater [Aller, 1982]. The renewal of burrow water associated with irrigation serves several essential purposes for the animals, such as gaseous exchange, food transport, gamete transport, transport of environmental stimuli, and removal of metabolites. However, irrigation is also an important factor controlling microbial processes within sediments. By enhancing the exchange of solutes between the sediment and overlying water, infaunal irrigation supplies dissolved electron acceptors, alters the spatial and temporal distribution of microbial reactions, and lowers the buildup of potentially inhibitory metabolic products in sediments.

The majority of organic matter decomposition is mediated by microorganisms in marine sediments, and microbial activities are intimately coupled to physical and biogenic changes in the diagenetic transport regime [Aller, 2001]. In general, benthic macrofauna enhance microbial metabolism and the capacity for organic matter decomposition in sediments through their effects on solute and particle transport. Redox oscillations mediated by macrobenthos are also believed to result in faster and more complete decomposition relative to deposits without these organisms [Sun et al., 1999]. Through the above mentioned effects on diagenetic reactions, the coupling of macrofaunal burrowing to microbial activities could have large impacts on the preservation of organic matter and the removal of nitrogen via coupled nitrification–denitrification in marine ecosystems.

In this chapter, we will briefly review the current state of knowledge on macrofaunal burrow structures, irrigation and its biogeochemical consequences, and the microbiology of the burrow wall interface. Whereas much progress has been made on the ecological and biogeochemical consequences of burrow structures, few studies have in recent years examined the diversity in burrow characteristics and faunal irrigation patterns. Furthermore, there is an obvious need to conduct more biogeochemical surveys using in situ approaches to avoid artifacts caused by the traditional laboratory experiments. It is also of concern that the abundance and community composition of microorganisms catalyzing important reactions in the burrow zone remain largely unexplored. In future studies, macrofaunal activities such as irrigation should be quantified by using high-resolution techniques in conjunction with
characterization of the microbial community with cultivation-independent molecular approaches. Other chapters of this book emphasize a modeling approach; we will instead focus on experimental evidence for macro–microorganism interactions.

**Burrow Structures**

A complete understanding of burrow microbiology and biogeochemistry can only be attained through a detailed characterization of these biogenic structures. Thus far, studies have been limited to larger burrowers, while smaller species approaching meiofaunal size have largely been ignored. Although the morphology of large burrows is easily examined by traditional approaches such as resin casts, many new photo- and microsensor techniques may be employed in future studies of small burrow structures. Even for larger macrofauna, relatively few species have been studied in sufficient detail. Environmental conditions, seasonal variations, and sediment conditions may force individuals of the same species and within the same geographical region to form widely different burrow structures. Conversely, geographically separated populations of the same species may through time evolve different burrowing behaviour, which adds to the complexity of biogeochemistry in bioturbated sediments. Despite these obvious knowledge gaps, we will draw generalizations based on the available information about burrow morphologies of common macrobenthic species and attempt to classify major burrow types. We will also provide insight into the characteristics of burrow walls and describe how these boundaries might affect chemical interactions between the burrow environment and the surrounding sediment.

**Morphology and Functional Types of Burrows**

Burrow morphology is dictated by the feeding mode, activity level, body form, and size of the macrofaunal inhabitant as well as the environmental conditions and sediment composition. Many invertebrate phyla living in marine environments have independently evolved classes, orders, genera, or species with a burrow-dwelling habit, including coelenterata (e.g. sea anemones and corals), nemertinea, nematoda, annelida (e.g. polychaetes and oligochaetes), mollusca (e.g. cockles and clams), arthropoda (e.g. insect larvae and crustaceans), pogonophora, sipuncula, echiura, priapulida, phoronida, echinodermata (e.g. brittle stars and sea urchins), and hemichordata. The three most successful burrowing classes in marine sediments are polychaeta, bivalvia, and crustacea.

The physical dimensions of macrofaunal burrows vary considerably, depending on the species and the environment (Table 1). The depth distribution of burrows in sediments varies from a few centimeters for small species and juveniles to several decimeters for many adult polychaetes and more than 3 m for large crustaceans (e.g. mud lobsters) [Pemberton et al., 1976; Rhoads and Boyer, 1982]. On the basis of the database on published mixed layer depths, Boudreau [1998] estimated that the activities and consequently the bioturbation depth of burrow-dwelling organisms have a worldwide environmentally invariant mean of 9.8 cm. This value covers a large range and reflects the high abundance of shallow burrowers (e.g. small species and juveniles) and the more scattered occurrence of deep burrowers. Despite the large variation in burrow depths, the relationships between burrow depth (cm) and diameter (cm) for the selected species given in Table 1 show a highly significant linear pattern (Figure 1A). The intercept at 8.6 cm suggests that the linearity of the relationship obtained here for adult individuals of relatively large species is probably not valid for small and juvenile organisms; a different relationship is possible for
TABLE 1. Burrow characteristics of selected benthic invertebrates. The data are given for average-sized adult individuals.

<table>
<thead>
<tr>
<th>Species</th>
<th>Length of inhabitant (cm)</th>
<th>Density of inhabitant (m⁻²)</th>
<th>Burrow diameter (cm)</th>
<th>Burrow depth (cm)</th>
<th>Burrow shape</th>
<th>No. of branches</th>
<th>No. of openings</th>
<th>Burrow wall structure</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>ANTHOZOA</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ceriantheopsis americanus</td>
<td>4–6</td>
<td>30–40</td>
<td>1.0–1.5</td>
<td>30–35</td>
<td>I</td>
<td>1–2</td>
<td>1–2</td>
<td>Tube</td>
<td>Cerianthin 1, 2</td>
</tr>
<tr>
<td><strong>POLYCHAETA</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nereis virens</td>
<td>10–20</td>
<td>~200</td>
<td>0.8–1.0</td>
<td>30–50</td>
<td>U</td>
<td>2–4</td>
<td>2–4</td>
<td>Mucus</td>
<td>3</td>
</tr>
<tr>
<td>Nereis diversicolor</td>
<td>5–10</td>
<td>500–1000</td>
<td>0.3–0.6</td>
<td>15–20</td>
<td>U–Y</td>
<td>Numerous</td>
<td>2–6</td>
<td>Mucus</td>
<td>4, 5</td>
</tr>
<tr>
<td>Ranzanides saggittaria</td>
<td>2–3</td>
<td>&gt;1000</td>
<td>0.06–0.1</td>
<td>8–10</td>
<td>I</td>
<td>0</td>
<td>1</td>
<td>Tube</td>
<td>6</td>
</tr>
<tr>
<td>Arenicola marina</td>
<td>10–20</td>
<td>~50</td>
<td>0.8–1.2</td>
<td>20–40</td>
<td>J</td>
<td>0</td>
<td>1</td>
<td>Mucus</td>
<td>7, 5</td>
</tr>
<tr>
<td>Amphitrite ornate</td>
<td>8–20</td>
<td>10–20</td>
<td>0.5–1.0</td>
<td>25–35</td>
<td>U</td>
<td>0</td>
<td>2</td>
<td>Mucus</td>
<td>8</td>
</tr>
<tr>
<td>Lanice conchilega</td>
<td>6–10</td>
<td>380</td>
<td>0.2–0.3</td>
<td>5–10</td>
<td>I</td>
<td>0</td>
<td>1</td>
<td>Mucus</td>
<td>9</td>
</tr>
<tr>
<td><strong>CRUSTACEA</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Neotrypaea californiensis</td>
<td>~1</td>
<td>~300</td>
<td>~1</td>
<td>15–20</td>
<td>Y</td>
<td>2</td>
<td>2</td>
<td>Mucus/silt</td>
<td>10</td>
</tr>
<tr>
<td>Callianassa gigas</td>
<td>~1</td>
<td>~300</td>
<td>~1</td>
<td>25–35</td>
<td>U</td>
<td>Numerous</td>
<td>3</td>
<td>Mucus/silt</td>
<td>10</td>
</tr>
<tr>
<td>Callianassa bouveri</td>
<td>1.2–2.5</td>
<td>~300</td>
<td>0.1–0.6</td>
<td>15–20</td>
<td>U–Y</td>
<td>Numerous</td>
<td>2–4</td>
<td>Mucus/silt</td>
<td>11</td>
</tr>
<tr>
<td>Callianassa subterranea</td>
<td>1–9</td>
<td>21</td>
<td>0.6–1.2</td>
<td>30–50</td>
<td>Complex</td>
<td>Numerous</td>
<td>3–5</td>
<td>Mucus/silt</td>
<td>9</td>
</tr>
<tr>
<td>Species</td>
<td>Length</td>
<td>Width</td>
<td>Density</td>
<td>Mortality</td>
<td>Age</td>
<td>Layer</td>
<td>Notes</td>
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<tr>
<td><em>Callianassa truncata</em></td>
<td>~2</td>
<td>~120</td>
<td>0.4–0.5</td>
<td>60–70</td>
<td>3–5</td>
<td>3</td>
<td>Mucus/silt</td>
<td></td>
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<tr>
<td><em>Callianassa tyrrhena</em></td>
<td>1.0–1.5</td>
<td>~150</td>
<td>~1</td>
<td>15–62</td>
<td>3–5</td>
<td>2</td>
<td>Mucus/silt</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Upogebia omissa</em></td>
<td>2.0–3.5</td>
<td>~200</td>
<td>0.4–1.3</td>
<td>8–30</td>
<td>Y</td>
<td>1–2</td>
<td>Mucus/silt</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Jaxea nocturna</em></td>
<td>5–6</td>
<td>0.1–0.2</td>
<td>2–3</td>
<td>50–90</td>
<td>U–Y</td>
<td>2–4</td>
<td>2 Mucus/silt</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Uca pugnax</em></td>
<td>1–2</td>
<td>20–130</td>
<td>1.1–1.6</td>
<td>20–40</td>
<td>I–J</td>
<td>1</td>
<td>Unlined</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Neoepisesarma versicolor</em></td>
<td>3–5</td>
<td>~0.2</td>
<td>1.8–5.2</td>
<td>55–110</td>
<td>Complex Numerous</td>
<td>2–5</td>
<td>Unlined</td>
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**MOLLUSCA**

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<th>Mortality</th>
<th>Age</th>
<th>Layer</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Solecurtis</em> sp.</td>
<td>5–8</td>
<td>~0.5</td>
<td>2–4</td>
<td>50–90</td>
<td>V–J</td>
<td>2</td>
<td>2 Mucus</td>
</tr>
</tbody>
</table>

**SIPUNCULA**

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<th>Length</th>
<th>Width</th>
<th>Density</th>
<th>Mortality</th>
<th>Age</th>
<th>Layer</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Golfingia</em> sp.</td>
<td>1–2</td>
<td>~300</td>
<td>~0.05</td>
<td>&gt;50</td>
<td>I</td>
<td>0</td>
<td>1 Unlined</td>
</tr>
</tbody>
</table>

*a* Vertical shaft with only one opening to the surface; *b* vertical but horizontally bending shaft with only one opening to the surface; *U* two connected openings to the surface; *Y* two connected openings to the surface and a vertical shaft extending deeper down; complex – no generalization possible.

smaller burrows. This outcome is likely due to biases (intentional or otherwise) of macrofauna ecologists for visible burrows or organisms that are easy to manipulate. Nevertheless, it is surprising that burrows of different larger species from widely different environments exhibit such a highly correlated relationship between depth and diameter. Obviously, the relationship also reflects the size dependence of the organisms involved, since burrow diameters usually are closely related to the inhabitant’s width [Nickell and Atkinson, 1995]. However, no relationship is apparent between burrow depth and the length of the inhabitant(s) in light of great variations in allometric dimensions among taxonomic groups, i.e. slender vermiform polychaetes versus more plump and compact crabs (Figure 1B). But within the same species, there is usually a close relationship between body length and burrowing depth, as shown for *Nereis diversicolor* by Esselink and Zwarts [1989] and *Upogebia omissa* by Coelho et al. [2000]. However, some variation may also occur within the same species, as Esselink and Zwarts [1989] found that *N. diversicolor* tends to dig deeper into sandy sediments than muddy ones. The significant interspecies depth–diameter relationship may instead point to the fact that only larger organisms with a good body condition (i.e. sufficient muscular ability) can construct and efficiently irrigate deep burrows as well as move sufficiently quickly within the burrow to obtain food. Larger organisms may also be physiologically better adapted to withstand extended periods of oxygen deficiency and harsh chemical conditions, which are more likely to occur in the water contained by deep burrows.

Some organisms construct simple unbranched vertical shafts with only one opening to the surface (Figure 2, panel 1; Table 1). These are inhabited primarily by above-sediment filter-feeders, surface deposit-feeders, and subsurface deposit-feeders (head-down conveyor-belt feeders). Vertical burrow structures appear impractical, as they usually are difficult to irrigate and thus to provide a sufficient supply of oxygen. Many of the filter-feeders and surface deposit-feeders line their burrows with diffusively impermeable leathery or parchment-like tubes [Defretin, 1971; Aller, 1983]. Some of these species solve the oxygen problem by pumping water in and out of the tube like a water lung, while others transport oxygen to the deeper parts of their bodies via their internal vascular system, supplied with oxygen from the filter or detritus-collecting organs placed in oxic water above the sediment surface.
Many subsurface deposit-feeders, such as the sedentary polychaete Arenicola marina, have solved the oxygen problem by avoiding fine-grained and water-impermeable sediments (Figure 2, panel 4). This polychaete prefers sandy sediments, where the irrigated water can percolate from the burrow and into the surrounding pore spaces between sand grains [Riisgård and Banta, 1998]. However, some species have evolved a form of mutualistic interaction, where individuals in dense populations support each other as a group and can both prevent buildup of noxious substances and supply sufficient oxygen for all individuals. For example, dense beds of the conveyor-belt-feeding maldanid polychaete Clymenella torquata often produce a second oxidized layer at their
feeding depth within sandy sediment columns, owing to both the depletion of organic mat-
ter by selective feeding and the irrigation of the resulting coarse, highly permeable sediment
layer [Rhoads, 1974; Aller, 1982, 2001]. Intertidal organisms, such as fiddler crabs (Uca
sp.), use their vertical or J-shaped unbranched burrows only as refuge when disturbed or
during high tide. Otherwise, they move around on the sediment surface, foraging on
microorganisms. These air-breathing crabs solve the oxygen problem during high tide by
plugging their burrows and so maintaining within the burrow a pocket of air that contains
sufficient oxygen until the tide recedes again [de la Iglesia et al., 1994].

The most common type of burrows is U- or Y-shaped with two or more openings to the
surface (Figure 2; Table 1). These are often inhabited by deposit-feeders or within-burrow
filter-feeders and are actively irrigated. The multiple openings to the surface allow easy pas-
sage of water through the burrows and thus are a simple solution to the oxygen problem.
Burrows of this type are typical for many errant polychaetes, such as Nereis spp. (Figure 2,
panel 2), that actively move around searching for food at the surface and occasionally form
new branches to the burrow [Davey, 1994]. Expanded forms of Y-shaped burrows are found
in many thalassinidean shrimp species [Griffis and Chavez, 1988; Dworschak, 2001]. They
first construct a U-shaped burrow with inhalant and exhalant openings. Subsequently they
dig vertically down from the bend of the U, creating a Y-shaped burrow with galleries and
blind side-branches (Figure 2, panel 3). These burrows are some of the deepest burrows
found for any organism. It is obvious that they easily can irrigate the upper part of the bur-
row and thus solve the oxygen problem here, but the deeper branches must remain mostly
anoxic. The animal has to "hold its breath" during excursion to these parts of the burrow or
alternatively switch to anaerobic metabolism. Many burrowing organisms are capable of
surviving for some time on energetically demanding anaerobic metabolism, but they must
return to the oxic environments in the upper burrow or the sediment surface at frequent
intervals to pay off the oxygen debt generated in the form of accumulated metabolites
(organic acids) [McMahon, 1988; Toulmond, 1991]. Burrow-dwellers may also endure
toxic levels of sulfide during excursions to deep galleries of their burrows. Several species
of polychaetes and thalassinid crustaceans, for example, have evolved physiological adapta-
tions or symbiotic relationships with microbial sulfide oxidizers to protect enzymes such as
cytochrome c oxidase from sulfide poisoning [Vismann, 1991; Johns et al., 1997]. A spe-
cial version of the U- or Y-shaped burrow with blind branches is constructed by grapsid
crabs [Thongtham and Kristensen, 2003]. These air-breathing intertidal animals spend most
of their time during low tide foraging for litter and other forms of detritus. They only return
to their impressive burrows to seek protection from predation and environmental extremes.
Their burrows are large and consist of a very complex disorganized network of branches
(Figure 2, panel 5). One single burrow can extend to more than 1 m into the sediment
and cover an area of more than 1 m². Only one adult crab usually inhabits one burrow, but
numerous juveniles and small thalassinidean shrimps construct narrow extensions of
the main shafts. Burrows of grapsid crabs are irrigated passively by the tidal currents and
gravity at low tide and are rarely anoxic.

Several attempts have been made to classify or model the architecture of particularly
thalassinidean burrows in relation to the function of the burrow and the trophic mode of
the inhabitant [deVaugelas and Buscail, 1990; Griffis and Suchanek, 1991; Nickell and
Atkinson, 1995]. However, most of the models have difficulties placing all species within a
fixed framework due to e.g. plasticity of feeding behavior [e.g. Miller, 2001]. Furthermore,
intraspecific differences in burrow morphology may be as great or greater than interspecific
differences under varying environmental conditions. To avoid these problems, Nickell and
Atkinson [1995] classified thalassinidean burrow morphologies on the basis of 12 burrow
features believed to be indicative of certain trophic requirements or modes (Table 2).
Although Nickell and Atkinson mostly used a particular trophic mode in relation to each feature, burrows may morphologically be related to more than one feature. The individual features of a burrow must be considered together with local environmental factors and animal anatomy, as well as activities other than feeding (e.g. irrigation). Although the specific features given in Table 2 are based on observations from thalassinidean shrimps, they are also largely valid for and can be applied to burrow-dwelling animals of other taxonomic origin (e.g. polychaetes).

All infaunal burrows alter sediment environments and affect microbial and geochemical processes by increasing the area of contact zones between sediment and the overlying water. Based on measurements of burrow dimensions with consideration of the density of individuals and the age structure of the population, a number of studies have estimated that the presence of various infaunal burrows increases the sediment–water contact zone by 50% to 400% (Table 3). Burrows of actively irrigating species are usually oxic, the oxygen penetrating only a few millimeters into the surrounding sediment. However, the oxygen penetration depth into burrows dominated by radial diffusion geometry is always less than at the oxic sediment surface. From morphometric considerations, Fenchel [1996] estimated that the surface area representing burrow walls of a population of *N. diversicolor* (burrow diameter 4 mm) exceeds that of the overlying sediment surface by a factor of

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**TABLE 2. Burrow features indicative of certain trophic requirements of the inhabitant.** Adapted from Nickel and Atkinson [1995].

<table>
<thead>
<tr>
<th>Feature no.</th>
<th>Description of feature</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Surface mounds are indicative of sediment deposition at the surface via a deposit-feeding mode.</td>
</tr>
<tr>
<td>2</td>
<td>A tightly layered lattice suggests reworking by a subsurface deposit-feeder.</td>
</tr>
<tr>
<td>3</td>
<td>Burrow depth can be indicative of the relative importance of surface detritus in the food. Surface deposit-feeding dominates in shallow burrows and subsurface deposit-feeding dominates in deep burrows.</td>
</tr>
<tr>
<td>4</td>
<td>Subcircular tunnels develop as a result of animal movements in established, but not maintained, burrows. Suspension-feeding and subsurface deposit-feeding is not likely.</td>
</tr>
<tr>
<td>5</td>
<td>Chambered burrows indicate deposit-feeding, and chambers are used as storage of surface or subsurface material.</td>
</tr>
<tr>
<td>6</td>
<td>The presence of large pieces of detritus may result from scavenging on the surface.</td>
</tr>
<tr>
<td>7</td>
<td>Oblique tunnels allow access to the sediment surface for movement of detritus or sediment and suggest a deposit-feeding trophic mode.</td>
</tr>
<tr>
<td>8</td>
<td>Numerous burrow openings to the surface suggests intimate contact with the surface and suggest a surface deposit-feeding mode.</td>
</tr>
<tr>
<td>9</td>
<td>Funnel-shaped openings enhance particle capture and suggest surface deposit-feeding mode.</td>
</tr>
<tr>
<td>10</td>
<td>A narrow exhalant shaft indicates a necessity for current generation to remove particles or capture particles and suggests a deposit-feeding or suspension-feeding mode.</td>
</tr>
<tr>
<td>11</td>
<td>U- or Y-shaped burrows allow rapid water movement and indicate a suspension-feeding mode.</td>
</tr>
<tr>
<td>12</td>
<td>Circular tunnel cross-sections facilitate efficient flow and allow close fit for filter mechanisms and indicate suspension-feeding mode.</td>
</tr>
</tbody>
</table>
up to 5. If the oxygen penetration depth at the sediment surface is 2 mm and that of the burrow wall is 1.5 mm, the ratio of oxic sediment volume associated with burrows is then up to 5.2 times the volume of oxic surface sediment.

**Structure of Burrow Walls**

The wall lining of most infaunal tubes and burrows consists of mucoid, membranous, or parchment-like secretions, which may be crusted with sand or shell debris. In some cases (e.g., burrowing crabs), the wall remains unlined and has a composition similar to the surrounding sediment or is enriched in fine particles [Dobbs and Guckert, 1988; Phillips and Lovell, 1999; Bird et al., 2000]. The lining is in most cases highly enriched in organic matter originating from the animal secretions as well as from plastered particles and detritus pulled into the burrows by the inhabitants feeding activities (Table 4). In a classic contribution, Aller and Yingst [1978] described in detail the burrow wall of the polychaete *Amphitrite ornata*. They found that the burrow wall consists of several thin-walled concentric cylinders, each 1.5–2 mm thick. The wall is lined on its inner side with a mucus layer ~5 µm thick composed of protein-rich mucopolysaccharide. Wall layers beyond the lining are often formed from a higher percentage of small particles than is found in the surrounding sediment, suggesting that particle selection occurs when animals construct and maintain tubes and burrows [Krasnow and Taghon, 1997]. The biodegradability of organic-rich wall linings is highly dependent on the chemical composition and structure of the secreted and plastered material. For example, the mucopolysaccharide secretions produced by many burrow-dwelling polychaetes (e.g., *Nereis* spp.) are readily degradable by microbial communities [Aller and Aller, 1986; Reichardt, 1988]. Structures like the fibrous, leathery cerianthin tubes of the infaunal sea anemone *Ceriantheopsis americanus*, on the other hand, are degraded at rates of less than 1% of fresh planktonic debris [Kristensen et al., 1991].

---

**TABLE 3.** Estimates of burrow wall surface area per unit sediment surface area for the listed population densities of several species of burrowing invertebrates.

<table>
<thead>
<tr>
<th>Species</th>
<th>Population density (m⁻²)</th>
<th>Burrow wall surface area (m² m⁻²)</th>
<th>Referencea</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Nereis virens</em></td>
<td>2000</td>
<td>1.25</td>
<td>1</td>
</tr>
<tr>
<td><em>Nereis virens</em></td>
<td>700</td>
<td>1.50</td>
<td>2</td>
</tr>
<tr>
<td><em>Nereis diversicolor</em></td>
<td>3500</td>
<td>3.00</td>
<td>3</td>
</tr>
<tr>
<td><em>Nereis diversicolor</em></td>
<td>15000 (juveniles)</td>
<td>1.50–4.00</td>
<td>4</td>
</tr>
<tr>
<td><em>Callianassa bouleri</em></td>
<td>450</td>
<td>2.60</td>
<td>5</td>
</tr>
<tr>
<td><em>Neotrypaea californiensis</em></td>
<td>50–100</td>
<td>0.70–1.40</td>
<td>6</td>
</tr>
<tr>
<td><em>Callianassa gigas</em></td>
<td>50–100</td>
<td>1.60–3.10</td>
<td>6</td>
</tr>
<tr>
<td><em>Callianassa subterranea</em></td>
<td>50</td>
<td>1.00–2.00</td>
<td>7</td>
</tr>
<tr>
<td><em>Upogebia pusilla</em></td>
<td>30–80</td>
<td>1.00–3.00</td>
<td>8</td>
</tr>
<tr>
<td><em>Upogebia omissa</em></td>
<td>≈200</td>
<td>2.90</td>
<td>9</td>
</tr>
<tr>
<td><em>Uca</em> sp.</td>
<td>50–100</td>
<td>0.60</td>
<td>10</td>
</tr>
<tr>
<td><em>Neoepisesarma versicolor</em></td>
<td>0.2</td>
<td>0.34</td>
<td>11</td>
</tr>
</tbody>
</table>

The permeability of tube and burrow linings to solute diffusion can be an important determinant of the chemical and biological composition of the tube or burrow habitat as well as the surrounding sediment. Linings are variously semipermeable to solute diffusion and often are impermeable to advection under natural pressure conditions. Thus, Aller [1983] found that the diffusive permeability of linings from eight infaunal species of marine invertebrates is 10-40% of that in free solution. The diffusion of anions is hindered somewhat compared with cations, indicating that linings are negatively charged at sedimentary pH levels. The permeability of linings can, therefore, affect sedimentary solute distribution differently depending on the sediment type, solute of interest, and types of controlling reactions.

The radial diffusion geometry within and around irrigated burrows and tube structures lined with semipermeable mucus creates a unique chemical microenvironment deep in sediments. The exact temporal and spatial patterns are highly dependent on the burrow type and activity pattern of the infaunal species in question [Marinelli and Boudreau, 1996; Furukawa, 2001]. Frequent irrigation of burrows causes an exchange of water and associated solutes between the burrow environment and surface water and thus drives a transport of reduced metabolites out of the sediment and oxidized electron acceptors into it. This changes both the relative dominance of oxidation–reduction reactions and distribution of oxidized and reduced solutes as well as solids. The chemical gradients in the immediate surroundings of actively irrigated burrows and tubes are usually steeper (Figure 3) and more oscillating than near the sediment surface. The radial diffusion geometry does not allow oxidized solutes to penetrate deep into the wall, whereas reduced metabolites from the surrounding anoxic sediment are maintained at high concentrations close to the burrow [Meyers et al., 1987; Gribsholt et al., 2003]. Fenchel [1996], for example, found that the diffusive thickness of the oxic zone around burrows of N. diversicolor corresponds to between 40% and 70% of the diffusive thickness of the oxic layer at the sediment surface. The presence of oxygen and associated acid produced by aerobic processes may promote localized carbonate dissolution near burrow walls [Aller et al., 1983; Furukawa, 2001]. In contrast, anoxic regions a short distance away from burrow walls may be supersaturated.
with respect to carbonate minerals, causing precipitation in a zone immediately adjacent to the zone of dissolution [Bromley, 1996].

**Burrow Irrigation**

Most burrow-dwelling animals irrigate their burrows, but the mechanisms and speed with which they create water currents are only known for a select number of conspicuous species. The magnitude and pattern of irrigation under various environmental conditions has been quantified directly for even fewer species. Biogeochemical studies have traditionally quantified irrigation and its consequences indirectly from porewater profiles by applying various modeling approaches. The results obtained provide an excellent description of the averaged impact of irrigation on the sediment environment. However, short-term changes in irrigation and associated local impacts on burrow inhabitants, represented by the macrofauna itself and microorganisms along the burrow wall, can be evaluated only by close examination at the individual burrow level. Here we provide an overview of irrigation mechanisms from representative examples. The volume of water driven by macrofaunal pumps is closely linked to the purpose of irrigation, such as respiration and filter-feeding. The rate of irrigation, in turn, exerts strict control on microbial processes as well as the exchange of solutes across burrow walls and the sediment–water interface.

**Irrigation Mechanisms**

The mechanism by which benthic animals propel the water current through their burrows varies considerably within and among taxonomic groups. Because most described mechanisms are represented within the two important burrowing classes, polychaeta and crustacea, the following examples will focus on these classes (Figure 4).
Figure 4. Irrigation patterns of various burrowing marine macrofauna: *Nereis diversicolor* [Kristensen, 2001]; *Arenicola marina* [Kristensen 2001]; *Sabella pavonina* [Wells, 1951]; *Amphitrite ornate* [Aller and Yingst, 1978]; *Callianassa subterranea* [Forster and Graf, 1995].

Many errant polychaetes irrigate their burrows from head to tail by undulations of the body in a dorso-ventral plane. The irrigation of species belonging to the genus *Nereis* is intermittent with active and quiescent periods in a more or less rhythmic fashion [Kristensen, 2001]. The exact irrigation cycles, however, differ between species. *Nereis*
virens is active for about 20% of the time with 5–10-min irrigation periods followed by 20–30 min of inactivity [Scott et al., 1976; Kristensen, 1989], whereas N. diversicolor is considerably more active, particularly when it suspension-feeds. It also has active irrigation periods of 5–10 min duration, but these are interrupted by only very short periods of inactivity in a very regular pattern, and it remains active for at least 50% of the time [Christensen et al., 2000].

Burrow irrigation by the sedentary and head-down conveyor-belt–feeding polychaete Arenicola marina is driven from tail to head by contraction and relaxation of the circular muscles of the body wall in a peristaltic fashion. Water is drawn into the burrow through the tail opening at the surface and forced into the sediment in front of the head, where it percolates up through the feeding funnel [Toulmond and Dejours, 1994]. The irrigation activity of A. marina proceeds in 40–60-min cycles. These very regular cycles are probably under the control of a pacemaker situated in the nervous system [Wells, 1949] and are linked to the feeding and defecation cycles.

Filter-feeding sabellid polychaetes live permanently in a vertical tube in the sediment with only one opening at the surface. They are equipped with a tentacular crown stretching into the overlying water with both feeding and respiratory functions. Most sabellids can actively irrigate their tubes by waves of muscular contraction of the body wall in either direction [Giangrande, 1991]. Burrow irrigation is almost continuous and water exits the tube by percolating into the surrounding deep sediment and forced by advection back to the overlying water. The extent of tube irrigation depends on how important the crown is for the total respiration of the worm. Species in which the crown is unimportant for respiratory purposes, tube irrigation is regular and continuous, and there are large spaces for water movement through the tube. For those species where the crown supplies most of the total respiration, the worm body fills the tube completely and rarely performs any irrigation movements [Giangrande, 1991].

Sedentary, surface deposit-feeding polychaetes of the family Terebellidae irrigate their burrows in a forward direction driven by piston-like or peristaltic body waves while extending the numerous feeding tentacles at the sediment surface [Dales, 1961]. The species Amphitrite ornata exhibits several irrigation patterns [Aller and Yingst, 1978]. In general, the patterns at the head end differ greatly from those at the tail end, and patterns observed during feeding differ from those when the animal is retracted into the tube. When the animals are retracted into the burrow, irrigation is detected only at the head end, as regular pulses moving in and out of the burrow. Irrigation bursts are repeated ~3 times a minute with wave generation occurring for about 15–20 s. The entire burrow is usually irrigated during feeding, typically showing large, single-velocity maxima with lower-velocity regions and periods of quiescence in between.

Thalassinidean shrimps irrigate their burrows for respiratory purposes, as in most Callianassidae, or mainly for filter-feeding purposes, as in most Upogebiae [Atkinson and Taylor, 1988]. The irrigation flow is generated by rhythmic metachronal beating of three or four pairs of abdominal appendages, the pleopods [Stamhuis and Videler, 1998]. The intermittent pumping by the deposit-feeding Callianassa subterranea is more or less regular, with about 2.5-min irrigation periods followed by about 40 min of rest [Forster and Graf, 1995]. Irrigation bouts tend to be longer in Upogebiae than in Callianassidae due to the difference in feeding strategy [Dworschak, 1981; Stamhuis and Videler, 1998].

Unlike most other burrowing macrofauna, intertidal deposit-feeding crabs (e.g. fiddler crabs, Uca spp.) do not permanently inhabit or actively irrigate their burrows. Many of these species actually plug their burrow entrances to prevent flooding during tidal inundation [Koretsky et al., 2002]. However, abandoned and unplugged burrows may instead be passively irrigated by tidal currents. Passive irrigation is particularly important in burrows
with more than one opening to the surface where at least one of the openings is raised above the surface, usually as a mound [Stieglitz et al., 2000; Munksby et al., 2002]. A water current passing over the mound creates a pressure difference between burrow openings and thus induces water flow through the burrow. Passive irrigation can be substantial in areas with strong currents and in large topographic features such as mounds and tidal creeks; in some cases the results are comparable to or higher than active irrigation by animals [Ray and Aller, 1985; Ridd, 1996].

Magnitude of Irrigation

The rate by which burrowing infauna irrigate burrows depends on several factors, including oxygen demand by the animal and the surrounding sediment, removal of toxic metabolites and demand for food transported by the water current. The latter is particularly important for suspension feeders with their need to process large amounts of water for extracting sufficient food particles (e.g. phytoplankton) from dilute suspensions [Riisgård and Larsen, 2000]. These animals rarely have problems with access to oxygen, and metabolites do not accumulate in their well-flushed burrows. Most deposit-feeders, on the other hand, irrigate their burrows discontinuously and at a relatively low rate. They have no respiratory need to irrigate continuously and vigorously; they instead devote much of their time to ingesting sediment particles of low nutritious value. Species that are not capable of performing simultaneous irrigation and feeding must therefore adapt a strategy to maximize feeding time and minimize irrigation time while still satisfying the respiratory need for oxygen. Many deposit-feeders may occasionally act as oxyregulators when oxygen levels in the overlying water are low and then spend considerably more time irrigating for respiratory purposes [Toulmond and Tchernigovtzeff, 1984; Wohlgemuth et al., 2000]. Although no more than 5% of their total metabolic energy expenditure is devoted to the movement of water during irrigation [Riisgård and Larsen, 1995], some suspension-feeders may save energy by reducing irrigation when no or only limited food is available in the overlying water. A few species, e.g. *N. diversicolor*, may under such conditions even switch to a deposit-feeding mode of life and then irrigate only for respiratory purposes [Riisgård, 1994].

The impact of feeding mode on irrigation at both the individual and the population level is clearly evident from the examples given in Table 5. No deposit-feeding population, irrespective of taxonomic group, appears capable of irrigating more than 200 L m^{-2} d^{-1}, and most species maintain an irrigation level one order of magnitude less than that. Suspension-feeders are more active and population irrigation for most species exceeds 1000 L m^{-2} d^{-1}, occasionally reaching levels an order of magnitude higher. This means that populations of suspension-feeders have the capacity to cycle a water column 1 to 10 m deep through their burrows each day. Such intense cycling of large water masses through narrow channels (i.e. burrows) has significant implications for the exchange of matter between the overlying water and the sediment environment. Thus, reduced solutes are flushed from the sediment porewaters to the overlying water, while oxidized solutes are transported the opposite way. Deposition of particulate organic matter, such as phytoplankton, within the sediment can be substantial in the presence of suspension-feeders, either by sloppy feeding of the captured particles or secondarily by organic-rich mucus secretions and faecal material deposited within the sediment.

The importance of suspension-feeding is clearly emphasized from the study of Christensen et al. [2000] on the polychaetes *N. diversicolor* and *N. virens*. Suspension-feeding individuals of *N. diversicolor* irrigate their burrows >3 times faster than their
TABLE 5.  Irrigation rates of selected burrow-dwelling macrofauna. Rates are time-integrated and presented for both an average-sized individual and for the entire population abundances given at the specified locations. The feeding mode of the macrofauna is indicated as well as the method used to quantify irrigation.

<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
<th>Abundance (m⁻²)</th>
<th>Feeding mode</th>
<th>Irrigation rate</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Individual (mL min⁻¹)</td>
<td>Population (L m⁻² d⁻¹)</td>
</tr>
<tr>
<td>Nereis virens</td>
<td>Kertinge Nor, Denmark</td>
<td>600</td>
<td>deposit</td>
<td>0.3</td>
<td>179</td>
</tr>
<tr>
<td>Nereis diversicolor</td>
<td>Kertinge Nor, Denmark</td>
<td>600</td>
<td>deposit</td>
<td>1.3</td>
<td>750</td>
</tr>
<tr>
<td>Nereis diversicolor</td>
<td>Kertinge Nor, Denmark</td>
<td>600</td>
<td>suspension</td>
<td>3.1</td>
<td>2700</td>
</tr>
<tr>
<td>Arenicola marina</td>
<td>Wadden Sea, North Sea</td>
<td>50</td>
<td>deposit</td>
<td>1.7–2.2</td>
<td>120–160</td>
</tr>
<tr>
<td>Amphitrite ornata</td>
<td>Cape Cod, USA</td>
<td>10</td>
<td>deposit</td>
<td>1.2–1.5</td>
<td>18–22</td>
</tr>
<tr>
<td>Diopatra cuprea</td>
<td>East Coast, USA</td>
<td>10–100</td>
<td>deposit</td>
<td>1.1</td>
<td>16–160</td>
</tr>
<tr>
<td>Clymenella torquata</td>
<td>Beaufort Harbor, USA</td>
<td>100–1000</td>
<td>deposit</td>
<td>0.04</td>
<td>6–60</td>
</tr>
<tr>
<td>Chaetopterus variopedatus</td>
<td>Gullmarsfjord, Sweden</td>
<td>30–100</td>
<td>suspension</td>
<td>15</td>
<td>650–2160</td>
</tr>
<tr>
<td>Callianassa subterranea</td>
<td>North Sea</td>
<td>21</td>
<td>deposit</td>
<td>0.2</td>
<td>6</td>
</tr>
<tr>
<td>Callianassa japonica</td>
<td>Yamada Bay, Japan</td>
<td>20</td>
<td>deposit</td>
<td>0.5–1.1</td>
<td>14–30</td>
</tr>
<tr>
<td>Alpheus mackayi</td>
<td>Hawaii</td>
<td>3</td>
<td>deposit</td>
<td>5.8</td>
<td>25</td>
</tr>
<tr>
<td>Upogebia pusilla</td>
<td>Grado Lagoon, Italy</td>
<td>87</td>
<td>suspension</td>
<td>25</td>
<td>880</td>
</tr>
<tr>
<td>Urechis caupo</td>
<td>Pillar Point, USA</td>
<td>61</td>
<td>suspension</td>
<td>260</td>
<td>23000</td>
</tr>
</tbody>
</table>

non–suspension-feeding conspecifics and >10 times faster than deposit-feeding individuals of \( N. \ virens \) (Table 5). Consequently, high phytoplankton concentrations in the overlying water result in a 30-fold higher deposition of particulate organic carbon to \( N. \ diversicolor \) than to \( N. \ virens \) sediment. Concurrently, the release of metabolites (\( \text{CO}_2 \) and \( \text{NH}_4^+ \)) out of the sediment is increased severalfold in sediment with \( N. \ diversicolor \) compared with that containing \( N. \ virens \) due to higher macrofaunal and microbial metabolism.

**Burrow Irrigation and Solute Transport**

Transport of solutes within sediments and across the sediment–water interface is basically mediated by molecular diffusion, a relatively slow process driven solely by concentration gradients. The presence of burrowing macrofauna with active irrigation disrupts the diffusional gradients and strongly affects the transport conditions within sediments. Macrofauna facilitate the exchange of solutes between sediment porewaters and the overlying water and influence the distribution of dissolved reactants (e.g. \( \text{O}_2 \), \( \text{NO}_3^- \), and \( \text{SO}_4^{2-} \)) and products of early diagenetic reactions (e.g. \( \text{CO}_2 \), \( \text{NH}_4^+ \), and \( \text{H}_2\text{S} \)) [Aller, 2001; Meile and Van Cappellen, 2003]. The biological enhancement of solute transport can exceed the transport via molecular diffusion by as much as an order of magnitude (Figure 5). The actual extent of the enhancement depends on such factors as reactivity of solutes, sediment composition, and infaunal community structure [Kristensen, 2000, 2001; Aller, 2001].

![Figure 5](image_url)  
**Figure 5.** Diffusive benthic oxygen uptake derived from microprofiles versus total oxygen uptake across the sediment–water interface measured with benthic chambers. The data are from a variety of continental shelf, continental slope, and deep-sea locations. The line labeled 1:1 represents the situation where diffusive and total flux are similar, whereas the 5:1 line represents the situation where the total flux is 5 times higher than the diffusive flux [modified from Meile and Van Cappellen, 2003].
The presence of irrigated burrows transforms the otherwise vertical one-dimensional diffusive transport in sediments into a spatially three-dimensional vertical and radial transport. Solute transport within the sediment matrix occurs via molecular diffusion, and solutes enter or leave the sediment both at the sediment–water interface and along burrow walls. The role of irrigation is therefore to increase the effective surface area available for exchange. This concept has usually been applied to relatively water-impermeable sediments, where eddy diffusion (or porewater advection) is negligible. In recent years, however, studies have demonstrated that advective porewater movements can occur in water-permeable, sandy sediments when exposed to pressure gradients from water currents [Glud et al., 1996; Ziebis et al., 1996]. Advective porewater flows may affect biogeochemical reaction zones deep in these sediments, leading to complex redox patterns. When water currents are deflected by protruding sediment structures at the surface, oxygenated water is forced into the sediment, generating distinct oxidized zones [Huettel et al., 1998]. This inflow must be balanced by porewater ascending from deeper sediment layers, thereby creating anoxic channels whereby reduced solutes reach the surface. Since many burrow-dwelling invertebrates living in sandy sediments irrigate vigorously [Vedel and Riisgård, 1993], porewater advection in excess of molecular diffusion may also occur along burrow walls and thus enhance solute transport. Accordingly, Kristensen and Hansen [1999] showed that porewater advection dominates in the bioturbated zone and molecular diffusion dominates below this depth in permeable sandy sediment inhabited by *N. diversicolor*; in impermeable muddy sediment inhabited by the same species, molecular diffusion is the dominating transport throughout.

**Biogeochemical Consequences of Burrow Irrigation**

Our knowledge of biogeochemical processes in marine sediments has improved considerably within the last couple of decades. At the same time we have gained some insight into the role of benthic fauna in carbon, sulfur, iron, and nutrient cycles. Most of the information provided in our review below has been obtained from small-scale laboratory assays; only a few studies have used in situ approaches. Accordingly, small enclosures on centimeter scales, either in situ (benthic chambers) or in the laboratory (core incubations), are well suited to examine the small-scale dynamics of microbial activity and fluxes across sediment–water interfaces. However, larger, mesoscale systems (flumes or sea-carousels) provide an effective linkage between small-scale manipulative systems and the natural environment. Mesoscale approaches allow researchers to evaluate the biological and chemical interactions within entire benthic communities as well as the influence of waves and currents for benthic coupling and sediment biogeochemistry [Amos et al., 1992]. Both small and mesoscale enclosures can be applied successfully for studies of sediment biogeochemistry, the actual choice depending on the purpose of the investigation [Asmus et al., 1998].

**Microbial Reactions in Time and Space**

Diagenetic reactions drive biogeochemical cycles, and conversely, the microbiology of marine sediments is largely defined by reactions associated with diagenesis [Jørgensen, 2000]. Organic matter is degraded and remineralized via a complex web of microbially catalyzed reactions that can be considered in three major classes: depolymerization or hydrolysis, fermentation, and respiration [Capone and Kiene, 1988]. Depolymerization of macromolecules is believed to occur extracellularly and is carried out by a wide range of
heterotrophic bacteria. Fermentation of monomers is carried out intracellularly under anoxic conditions. Little information is available concerning the rates and pathways of these first two steps in situ, and therefore the impact of burrow structures on these processes is not well known. The terminal metabolism of organic matter through respiration is generally considered to be the rate-controlling step, and therefore respiration reactions have been the ones best studied. Organic matter is terminally metabolized through a sequence of respiration reactions or terminal-electron-accepting processes according to the amount of free energy the bacteria glean from each electron acceptor. Only bacteria that respire oxygen are able to mediate the complete oxidation of hydrolysis products to carbon dioxide; anaerobic bacteria depend on consortia with coexisting fermentative organisms that transform hydrolysis products to intermediates such as acetate and hydrogen [Canfield et al., 2005].

Rates of organic matter degradation depend on a variety of factors, including sedimentation rate, organic matter quality (i.e., protein, cellulose, lignin content), temperature, and other physicochemical parameters at the sediment–water interface. A vertical sequence of terminal respiration processes is often observed in marine sediments whereby oxidants are depleted in the order $O_2 > NO_3^- > Fe^{III}, Mn^{IV} > SO_4^{2-} > HCO_3^-$ (Figure 6) [Froelich et al., 1979; Canfield et al., 2005]. However, respiration pathways are not determined by thermodynamics alone. Kinetics and the availability of various electron acceptors are also of critical importance, leading to the spatial overlap of respiration processes. In fact, the current paradigm is that respiration pathways often coexist in marine sedimentary environments because of non–steady-state conditions [Postma and Jakobsen, 1996] that may be forced by macrofaunal activities [Kristensen, 2001; Kostka et al., 2002a, b].

Concurrent to carbon oxidation, a large portion of electron acceptor utilization is coupled to the reoxidation of reduced inorganic metabolites produced during remineralization [Canfield et al., 1993]; typically, 90% or more of reduced species such as sulfide, iron, and manganese are recycled [Thamdrup and Canfield, 1996]. Thus, the recycling or reoxidation of respiration products often limits the supply of electron acceptors. Reoxidation may occur via abiotic chemical reactions, but it is often mediated by chemoautotrophic microorganisms [Jørgensen, 1989]. Of particular importance is the dissolved metabolite sulfide, produced from sulfate reduction. Sulfide is toxic to benthic organisms and can in extreme cases lead to defaunation of the sediment.

Of the many factors influenced by macrofauna, alteration of the diagenetic transport regime during burrow construction and irrigation is believed to have the largest impact on microbially mediated geochemical cycles (Figure 6) [Aller, 2001]. Ultimately, through respiration and reoxidation processes, diagenetic reactions are limited by the transport of solutes, and this is where burrows and irrigation can have a major impact on microbial communities and the biogeochemical processes they catalyze. Infauna affect diagenetic transport passively by increasing the sediment–water contact zone and by actively pumping water through irrigation or feeding activities (see above discussion and Kristensen [2001]). Analogous to conditions at the sediment surface, enhanced solute transport across burrow walls stimulates microbial reactions around burrows. Fluid transport near the burrow wall thereby influences the rates, pathways, and extent of organic matter remineralization and nutrient cycles [Aller, 2001]. Burrow irrigation increases the supply of soluble reactants, such as electron acceptors and carbon substrates deep in sediments, while stimulating the removal of toxic metabolites such as dissolved sulfide. Increased reoxidation and redox oscillation through intermittent irrigation apparently leads to more efficient degradation of organic matter and the emergence of suboxic pathways [Aller, 1994; Kristensen, 2001].

Translocation of $O_2$ to subsurface sediment and removal of metabolites are therefore considered the two most important mechanisms for the stimulation of carbon oxidation by burrowing fauna. When $O_2$ is introduced to otherwise anoxic sediment of low microbial
activity, the decay of anaerobically refractory organic matter will be stimulated by up to a factor of 10 [Kristensen and Holmer, 2001] and thus will enhance the total sedimentary carbon oxidation. In addition, it has been suggested that the reduced diffusion scale created by a high abundance of irrigated burrows in sediment may enhance anaerobic degradation by (e.g.) removal of inhibitory metabolites [Aller and Aller, 1998]. However, experimental evidence for the latter mechanism is still limited [Valdemarsen and Kristensen, 2005].

**Respiration Pathways and Nutrient Cycling**

Benthic-pelagic coupling is of critical importance to primary production in coastal waters, and the majority of biogeochemical studies examining interactions between
benthic macrofauna and microorganisms have been conducted in shallow, marine ecosystems. Therefore, here we will primarily focus on marine sediments from shallow continental shelves to intertidal zones.

In coastal marine sediments rich in organic matter, oxygen is rapidly utilized and anaerobic respiration is considered as important or frequently more important to carbon oxidation. Aerobic respiration has been estimated to account for roughly 50% of carbon oxidation in most coastal sediments [Thamdrup and Canfield, 2000]. Sulfate reduction on average contributes the remaining 50% of carbon oxidation on continental shelves [Jørgensen, 1983], but tends to be more important in many fine-grained intertidal environments [Kristensen et al., 2000b; Kostka et al., 2002a,b]. However, in areas inhabited by large infaunal communities, microbial Fe(III) reduction can comprise up to 100% of carbon oxidation [Kristensen et al., 2000a; Kostka et al., 2002a; Gribsholt et al., 2003]. Other respiration pathways such as nitrate reduction generally play a minor role in carbon oxidation, but denitrification may represent an important sink in the marine nitrogen cycle.

Present estimates indicate that only a small fraction of benthic oxygen consumption in shallow marine sediments is due to respiration by infauna; the fauna, in contrast, primarily impact oxygen consumption through irrigation. Oxygen uptake in sediments has been shown to increase severalfold in the presence of abundant macrofauna (Figure 5) [e.g. Christensen et al., 2000, Meile and Van Cappellen, 2003]. Faunal-mediated O2 uptake measured in situ correlates well with faunal abundance in many open ocean areas, where bottom water chemistry is relatively constant [Glud et al., 1994]. However, in shallower coastal sediments, where temperature and bottom water oxygen vary seasonally and diurnally, in situ measurements usually show no clear relationship between faunal biomass and O2 flux [Glud et al., 2003]. However, under constant conditions in the laboratory, there is a clear relationship between infaunal abundance and O2 uptake, even for intertidal sediments [Tahey et al., 1994; Papaspyrou et al., submitted].

Because O2 may be consumed by a variety of processes, including respiration by aerobic bacteria and chemical reoxidation of reduced metabolites, it has been difficult to relate any specific O2-consuming process to macrofaunal activity. Rates of biotic vs. abiotic O2 consumption have been estimated from extensive measurements in conjunction with geochemical profiling [Canfield et al., 1993; Thamdrup and Canfield, 1996], but detailed characterization of infaunal community composition or activity has rarely been included. To relate aerobic respiration directly to burrow structures or irrigation, it will be necessary to conduct careful experimentation with benthic fauna coupled with comprehensive biogeochemical assays.

Since sulfate reduction is exclusively catalyzed by anaerobic bacteria and sulfate reduction rates are easily measured with a radiotracer method, the relationship between macrofauna and anaerobic carbon oxidation in sediments has been more evident. A large number of studies have related the presence or abundance of macrofauna to sulfate reduction rates [Hansen et al., 1996; Banta et al., 1999; Kostka et al., 2002a,b; Gribsholt et al., 2003]. However, the results thus far have been equivocal. Sulfate reduction rates in the sediment zones immediately surrounding burrows are in some cases enhanced [Hines and Jones, 1985] and have been attributed to the introduction of organic substrates by transport/excretion. Hansen et al. [1996] found that sulfate reduction rates were 2 times higher in the burrow wall of bivalves than in the surrounding subsurface sediments, and the rates correlated with viable counts of sulfate-reducing bacteria. When artificial burrows were introduced into the same sediments, on the other hand, a suppression of sulfate reduction activity was observed. Kostka et al. [2002a] similarly observed a nearly complete suppression of sulfate reduction rates and a predominance of microbial iron reduction in salt-marsh sediments where fiddler crab burrows were abundant, while sulfate reduction dominated
carbon oxidation in adjacent sediments where crab burrows were absent. From high-resolution radial profiles in fiddler crab burrow walls in the same salt marsh, Gribsholt et al. [2003] showed low sulfate reduction rates in parallel with high iron reduction rates within a few centimeters of the burrow wall. The conclusion of these salt marsh studies was that a rapid iron cycle facilitated by reoxidation in the burrow wall allowed iron-reducing bacteria to outcompete sulfate-reducers for carbon substrates. At present, it appears that sulfate reduction may be stimulated or inhibited by macrofaunal burrows depending on a host of environmental parameters, including sediment geochemistry, porosity, and the ecology of burrow-dwelling organisms. The exact mechanisms by which burrows impact sulfate reduction and other anaerobic carbon oxidation pathways remain to be elucidated.

The steep chemical gradients and potential overlap between electron acceptors (e.g. oxygen) and reduced metabolites (e.g. sulfide, ammonium and reduced iron) around macrofaunal burrows and tubes provide an ideal environment for the growth of chemolithoautotrophs. This is confirmed by a higher potential dark CO2 fixation along polychaete burrow walls than in surface sediment (Table 5; Reichardt [1986, 1988]). Evidence from the literature for enhanced chemolithoautotrophic activities in infaunal burrows and tubes is mainly related to nitrification, although it has been argued that certain sulfur-oxidizing thiobacilli and *Beggiatoa* often are responsible for most of the chemoheterotrophic activity [Reichardt, 1988]. Mayer et al. [1995] concluded from their own studies and a review of the existing literature that most macrofaunal burrows exhibit nitrification potentials exceeding those from adjacent and surface sediment. Of 11 species examined, burrows or tubes of 9 species had nitrification potentials exceeding surface sediment by factors of 1.5 to 61. Nitrification potentials in burrow walls appear to be regulated by the diffusive access of ammonium from the ambient sediment and supplies of oxygen via irrigation by the burrow inhabitant. Thus, Mayer et al. [1995] found that nitrification potentials correlated positively with both the bulk sediment ammonium concentration and the macrofaunal irrigation behaviour. Furthermore, it has been argued that high nitrification potentials in macrofaunal burrows are related to an association of nitrifying bacteria with the fine-particulate and organic-rich wall linings [Henriksen et al., 1983; Kristensen et al., 1985]. The strong association to fine particles is linked to the pH-buffering capacity of clay and silt particles, which is likely to help retain an optimal pH for nitrifiers, and to the high availability of ammonium derived from microbial nitrogen mineralization of the organic particles [Canfield et al., 2005]. This information is discussed below.

The role of macrofauna in nitrification is a key linkage between the mineralization of organic nitrogen and the removal of nitrogen via denitrification. Indeed, denitrification is enhanced in the presence of burrowing macrofauna [Nielsen et al., 2004]. Macrofauna burrows may also be linked to the nitrogen cycle indirectly via their impact on anaerobic respiration pathways. Dissolved sulfide was shown to inhibit both nitrification and denitrification in laboratory cultures and in marine sediments [Joye and Hollibaugh, 1995; Joye, 2002]. As outlined above, a change in the partitioning of respiration pathways from sulfate to iron reduction has been observed in the burrow wall of fiddler crabs, and the shift in carbon oxidation pathways was accompanied by a large decrease in the accumulation of sulfide [Kostka et al., 2002b; Gribsholt et al., 2003]. In a subsequent study of the same salt-marsh sediments by Dollhopf et al. [2005b], nitrification and denitrification potential rates were strongly correlated with one another and with macrofaunal burrow abundance, indicating that coupled nitrification–denitrification was enhanced by macrofaunal burrowing activity (Figure 7). The distribution of nitrifying bacteria, as determined by quantitative PCR, was further shown to have a high positive correlation to Fe(III) and a negative correlation to dissolved sulfide. Laboratory slurry incubations supported field data, confirming that increased amounts of Fe(III) relieved sulfide inhibition of nitrification.
Thus, it was proposed that burrow structures are an important driving factor in the C, N, Fe, and S cycles of the salt marsh, facilitating solute transport and continually recycling electron acceptors critical to both the oxidation of organic matter and coupled nitrification–denitrification. Enhanced iron cycling in the burrow zone may amplify the positive effects of solute transport on coupled nitrification–denitrification by reacting with sulfides, thereby stimulating nitrogen removal in coastal ecosystems.

Figure 7. Influence of burrow abundance on (A) nitrification potential, (B) denitrification potential, and (C) the distribution of nitrifying bacteria as determined by gene copy number of ammonia monooxygenase A in sediments of a Georgia salt marsh. TS, Tall Spartina habitat (314–352 burrows m⁻²); CB, Creek bank (58–184 burrows m⁻²); SS, Short Spartina (53–99 burrows m⁻²). Winter samples have a W prefix, summer samples have no prefix. Error bars represent the standard error of the rate calculated from linear regression of duplicate assays. g wet, grams (wet weight). From Dollhopf et al. [2004, in press].
Impact of Irrigated Burrows on Sedimentary Microorganisms

The presence of burrows lined with organic coatings of various composition combined with the steep chemical gradients in their immediately surrounding sediment create microenvironments with distinctive and species-specific microbial communities and reaction properties. Furthermore, the fairly stable physico-chemical environment in burrows/tubes compared to the more frequently disturbed surface sediment allows for the development of complex microbial biofilms [Steward et al., 1996; Phillips and Lovell, 1999]. This can lead to the formation of microbial communities fundamentally different from the nearby surface and subsurface sediments, with substantial bacterial diversity, density and activity [Marinelli et al., 2002; Kinoshita et al., 2003; Lucas et al., 2003].

Though the biogeochemical consequences of burrow structures and irrigation have been well documented, the detailed interactions and mechanisms by which burrows affect microbial community composition and activity remain relatively unknown. Knowledge gaps may be at least partly blamed on the complexity of the burrow zone. Microbial communities in the burrow wall will respond to sediment characteristics, physicochemical conditions of the surrounding environment, and the species-specific ecology of the infauna over a range of spatial and temporal scales. The response of the microbial community to changes in solute transport, for example, is likely to occur rapidly (seconds to hours) and very close (micrometers to millimeters) to the burrow wall. Simply due to their small size and large phylogenetic diversity, detecting microbial community response to even large geochemical gradients remains challenging.

Knowledge Gaps: Microbiology of Burrow Structures

Especially regarding the abundance and community composition of microorganisms inhabiting the burrow wall–sediment interface, relatively few studies have been performed and the field has currently generated more questions than answers. We review existing knowledge below. However, prior to summarizing the field, it may be helpful to discuss current gaps in our knowledge.

Microbiological studies of the burrow wall environment have been diverse and thus far relatively simple, involving mostly biomass or established activity determinations. Large variations in the definition of the burrow interface make definitive or quantitative comparisons difficult. The water, tube, lining, and walls of macrofaunal burrows have all been sampled at varying spatial scales. The majority of studies have compared microbial communities in macrofaunal tubes or burrow walls with those of surface sediments or ambient sediments. Ambient sediment is usually defined as anoxic sediment at least 1 to 5 cm in radial distance from any burrow, but many past studies have considered the “surface” as 0 to 2 cm deep, while the “subsurface” is usually at >5 cm deep. Although the burrows of major irrigating infauna (polychaetes, crustaceans, and bivalves) have been represented in past work, systematic comparisons between the burrows of different organisms are, as shown earlier, diffuse and not always consistent.

The majority of studies to date have been limited geographically to shallow, coastal sediments, most studies focusing on intertidal environments and relatively few on the subtidal areas from the continental shelf to the deep sea. Considering the huge diversity of microorganisms likely to be present in marine sediments [Keller and Zengler, 2004] and in burrows in particular, most studies have investigated general bacterial populations; only a few functional groups (aerobes, sulfate-reducers, iron-reducers) have been characterized in the burrow wall.

The microbiology of burrows must also be considered in the context of broader limitations in our knowledge of the microbial ecology of marine sediments. Clearly, more information...
is available on abundance/biomass and diversity of functional groups in marine sediments than has been studied in relation to infaunal burrows. However, the general knowledge of microbial community composition in marine sediments remains limited and consensus has not been reached with regard to the variation in community structure with environmental parameters [Keller and Zengler, 2004]. For example, studies of burrow interfaces have been carried out under a range of different sediment characteristics (porosity, density, grain size distribution, organic matter content). Such characteristics are well known to drastically impact biogeochemical processes in marine sediments, and yet no information has been compiled on the influence of sediment characteristics on microbial community structure. Therefore, differences in the activity and community composition of microbial communities due to macrofaunal burrows cannot be effectively separated from those differences attributed to sediment characteristics at this time.

**Abundance and Biomass**

The majority of microbial studies carried out in burrow environments have employed simple measurements of abundance or biomass, and the perception has been that the standing stock of microorganisms is much larger in or near (within 1 cm) the burrow wall than in the surroundings. When considered from a microbiological standpoint, an analysis of the literature to date reveals relatively mild effects of burrow structures on the overall abundance of microorganisms (Table 6). The largest enhancement of abundance as direct counts in the burrow wall relative to that in surrounding sediments was by a factor of 3

<table>
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<tr>
<th>Species</th>
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<th>Biomass</th>
<th>Activity</th>
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<tr>
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<td>10.0</td>
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<td>sand</td>
<td>3.4</td>
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</table>

[Lucas et al., 2003], and half of the studies employing direct counting procedures observed no enhancement of abundance in the burrow wall [Reichardt, 1988; Bird et al., 2000]. The lack of strong bacterial enrichment in the burrow wall can be explained by extensive meiofaunal grazing along the wall [Wetzel et al., 1995]. Another explanation could be that although overall cell numbers are not enhanced in the burrow wall, the growth and activity of certain functional groups may be stimulated.

Measurements of microbial biomass as phospholipid fatty acids (PLFA) or ATP (adenosine triphosphate) have revealed an enhanced “active” bacterial biomass in the burrow wall (Table 6). Nearly all previous investigations have observed 2 to 10 times higher PLFA or ATP biomass in the burrow wall relative to that in ambient sediments [Aller and Yingst, 1978; Steward et al., 1996]. Because both PLFA and ATP are rapidly turned over in marine sediments, these cellular components should represent a sensitive measure of “viable” microbial biomass, whereas direct counts will include both live and dead cells. Microorganisms grow on an exponential scale and thus a factor of 2 to 10 difference in number is generally not considered large. However, the database remains small and the results clearly indicate a substantial enhancement of viable microbial biomass in the burrow wall zone. Viable counts of specific functional groups of organisms support this conclusion. Hansen et al. [1996] observed an order of magnitude higher counts of sulfate-reducers while Reichardt [1988] found $10^6$ times higher counts of cultivatable aerobes in the burrow wall than in the surrounding sediments.

**Microbial Community Structure**

Few studies have related microbial community composition to the unique biogeochemistry of burrows, but early evidence suggests that microbial communities are uniquely adapted to environmental conditions in the burrow wall. Several studies have compared the microbial communities of burrow structures to those of surrounding sediments by profiling of PLFA extracted from bacterial membranes. Steward et al. [1996] used quantitative comparisons supported by multivariate statistical analysis to show that the microbial communities of polychaete burrows in an intertidal sand flat were markedly different from those of surrounding surface and subsurface sediment. The authors concluded that microorganisms were responding to the physicochemical properties of the burrows. Significant differences in the PLFA profiles of prokaryotes associated with the burrow between wall and surrounding sediment were also observed in a sandy tidal flat inhabited by Thalassinidean crustaceans on the Gulf Coast of Florida. Functional groups of bacteria were also shown to differ as the PLFA biomass attributed to the sulfate-reducing bacteria was elevated in the burrow wall [Dobbs and Guckert, 1988]. In a study by Marinelli et al. [2002], artificial burrows or mimics were devised to examine the influence of irrigation, tube composition, and tube residence time on microbial communities. Burrow mimics supported the development of microbial assemblages that were similar to those observed in natural burrows in terms of the relative abundance and community composition [Steward et al., 1996]. Dominant fatty acids, including those attributed to sulfate-reducing bacteria, accumulated in response to longer mimic residence times and were negatively impacted by treatment with a bacterial exopolymer, which suggests that burrow residence time and tube composition influence colonization by prokaryotes. Irrigation frequency was not shown to be an important factor in the structuring of microbial biofilms on burrow mimics. However, the relatively short duration and colder temperatures of the experiment were cited as potential reasons why irrigation frequency did not affect microbial community structure. Not all studies of PLFAs have found the burrow environment to contain a unique
microbial community. Bird et al. [2000] observed no significant difference in microbial community structure between the burrow wall of Thalassinidean shrimp and surrounding sand-flat sediments. Limitations in the PLFA profiling method might explain the contradictory results.

While PLFA profiling is sensitive and quantitative, and the biomarker analysis can be carried out using automated instrumentation, a drawback of this technology is that PLFA signatures provide a relatively low-resolution fingerprint of microbial functional groups. Prokaryotic PLFAs must be separated from those of eukaryotes, and the phylogenetic identification of bacterial groups is limited to the family level or above. Only certain groups of bacteria can be identified with confidence such as Gram positives, Gram negatives, aerobes, anaerobes, and sulfate-reducers.

Nucleic acid–based (DNA, RNA) methods for profiling microbial communities remain tedious and suffer from some additional drawbacks of their own. However, DNA or RNA sequences provide a much higher resolution for the identification of microbial groups to the genus or species level. In addition, a plethora of new techniques within this field promise to revolutionize microbial community characterization in sediments. Not only have methods become more reproducible and quantitative, but it is now possible to relate the physiology or activity of certain microbial groups to their in situ identity. These cultivation-independent molecular techniques are still in their infancy for the analysis of burrow microbial communities. To our knowledge, only a few research groups have examined the community fingerprint or diversity of burrow wall microbial communities using nucleic acid–based technologies. Lucas et al. [2003] investigated the microbial assemblages of muddy sediments in a salt marsh by examining the community fingerprint of 5S rRNA. They used the relative intensity and number of 5S rRNA bands as operational taxonomic units to estimate microbial diversity with the Shannon index. Microbial diversity was found to differ between sediment heavily colonized by polychaetes and uncolonized sediments. However, the authors could not obtain enough sample size to specifically examine communities of the burrow wall. In addition, the method did not allow for the identification of specific microbial groups.

More recent studies have used the 16S rRNA gene as a biomarker for determination of microbial community composition associated with burrow structures. Matsui et al. [2004] utilized clone libraries, denaturing gradient gel electrophoresis (DGGE), and DNA–DNA hybridization methods to provide a thorough analysis of community composition in the tubes constructed by the polychaete genus Diopatra. Although large variations were observed in community composition between the tubes and the surrounding sediment, a principal components analysis of DGGE banding patterns showed some distinct trends. Bacterial communities in tubes from sandy sediment differed substantially from those in muddy sediment. The difference in community structure was observed for both general bacterial communities and specifically for the sulfate-reducers. In a similar study, Papaspyrou et al. [submitted] showed that molecular fingerprints of bacteria within and around burrows of nereidid polychaetes (Nereis spp.) and a Callianassid mud shrimp (Pestarella tyrrena) provided large differences between surface, burrow wall, and ambient sediment. Furthermore, the bacterial communities along burrow walls were more similar to those in the ambient anoxic sediment and showed less seasonal change than those in the surface sediment. Accordingly, it was concluded that burrow walls contain distinct microbial communities and should not be considered simple extensions of the sediment surface.

Only a single study has targeted the “active” bacteria associated with burrow structures by using quantitative RNA-based profiling. Dollhopf et al. [2005a] used reverse transcription real-time PCR to quantify the 16S rRNA of anaerobes in a radial profile through the burrow wall of a fiddler crab in muddy salt-marsh sediment. RNA extracts from pooled sediment
sections of the radial profile were examined with primer sets specific for predominant genera of sulfate- and iron-reducing bacteria. Since RNA is degraded more rapidly than DNA in sediments, RNA-based profiling should detect the “active” microbial community members. The 16S rRNA of all anaerobic groups was at a maximum within 1 cm of the burrow wall, indicating the communities were most active or stimulated there (Figure 8). Vertical depth profiles further revealed that the rRNA of known iron-reducing bacteria was more abundant in Fe(III)-rich sediments where fiddler crab burrows are abundant and microbial Fe(III) reduction has been shown to be a predominant carbon oxidation pathway.

Conclusions and Recommendations for Future Research

Ecological and sedimentological work conducted during the last few decades has provided solid evidence for how infauna construct and maintain burrows. Although individual species generally inhabit specific burrow types, the geographical variation in sediment characteristics often results in intraspecific differences in burrow morphology that are as great or greater than interspecific differences. Accordingly, most models that attempt to classify all burrowing species based on burrow characteristics (such as morphology, function, and trophic mode) have difficulties and are generally of little practical use.

The diffusivity of burrow and tube linings combined with irrigation creates a unique chemical microenvironment deep in sediments. The exact temporal and spatial patterns of chemical gradients are highly dependent on the burrow type and activity patterns of the infaunal species present. Microbial communities in the more oxidized zones surrounding infaunal burrows are often considered equivalent to communities present in surficial sediments. However, environmental conditions in the burrow wall fundamentally differ from
those at the sediment surface. The sediment surface is physically unstable over the short term due to advective forces (tides, currents) and chemically stable over longer time scales due to exchange with overlying waters [Kristensen, 2001]. In contrast, burrows are more physically stable over their lifetimes (days to weeks) but are chemically unstable over shorter time scales (minutes) due to intermittent irrigation. Burrow walls are therefore likely to support the growth of unique microbial communities that differ considerably from those in both the oxic surface and the surrounding anoxic sediment.

Overall, the microbiology associated with irrigated burrow structures is in its infancy. Biogeochemical evidence and rate measurements have clearly shown that microbial activity is elevated in the burrow zone. Viable cell counts and biomass determinations support biogeochemical evidence to indicate that microorganisms exhibit an elevated metabolic potential in or near the burrow wall. However, the mechanisms and the parameters controlling microbiobally mediated geochemical reactions in the burrow zone remain understudied, and very little information is available to assess the impacts of burrow environments on the community structure or diversity of microorganisms. The “active” microbial communities that catalyze important geochemical reactions in the burrow zone remain therefore largely unknown.

Consequently, it is too early to generalize about direct relationships between burrow structures, irrigation activity, and the distribution of sedimentary microorganisms. However, new and exciting experimental tools in biogeochemistry and microbiology are available with which these questions may be addressed. High-resolution geochemical techniques such as microsensors and other in situ approaches should be employed and tightly coupled to sampling for microbial parameters. For both the abundance and diversity of microorganisms, future research should employ more robust, cultivation-independent molecular techniques and statistical comparisons. Manipulative studies remain valuable but need to be carried out in a close collaboration between multidisciplinary groups (benthic ecologists, geochemists, and microbiologists). Macrofaunal activities such as burrowing or irrigation and geochemical reaction rates should be quantified and directly related to microbial parameters quantified in the same sediment. Such collaborative experiments have been attempted in mesocosms with artificial burrows but not with real organisms and under in situ conditions. Burrow–microorganism interactions have the potential to largely impact global biogeochemical cycles and yet this potential has not been realized.

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References


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