

Microscale oxygen distribution in various invertebrate burrow walls

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ABSTRACT

Profiles of dissolved oxygen were measured in pore waters of unburrowed sediment and the burrow walls of seven invertebrate dwellings. Burrows studied include those of *Corophium volutator*, *Heteromastus filiformis*, *Arenicola marina*, *Saccoglossus bromophenolosus*, *Clymenella* sp., *Hemigrapsus oregonensis* and *Cirriformia luxuriosa* all from mudflats in Willapa Bay, Washington. These animals comprise a range of burrow architectures ranging from simple, unlined burrows to more complex, mucous lined burrows. Oxygen penetrated unburrowed sediment between depths of 0.4–2.6 mm, whereas oxygen penetrated the burrow walls from 0.3 mm to 2.3 mm. Three groups of burrows are recognized based on the oxygen diffusive properties relative to the unburrowed sediment including those that: (1) slightly impeded oxygen penetration, (2) clearly inhibited oxygen penetration, and (3) enhanced oxygen penetration. Differences in the diffusive properties of the burrow wall are related to the burrow microstructure and presumably the microbial communities living within the burrow microenvironment. The results of this study suggest that burrow shape and burrow-wall architecture may play an important role in controlling the diffusion of oxygen, and possibly of other dissolved gases (i.e. CO₂, H₂S). The results further demonstrate that simplified assumptions (i.e. that bioturbation uniformly enhances oxygen diffusion into suboxic and anoxic sediments), while requisite for numerical modelling, are not necessarily representative of field data.

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INTRODUCTION

Sediments have distinct biogeochemical zones that develop in response to the amount of labile organic carbon buried, sedimentation rates, the availability of different terminal electron acceptors, grain size and permeability. However, the idealized vertical zonation initially described by Froelich *et al.* (1979) can be disrupted by the burrowing activity of invertebrates (Aller & Yingst, 1978; Aller, 1982; Needham *et al.*, 2004). This process, known as bioturbation, causes millimetre- to centimetre-scale biogeochemical heterogeneities that form as a result of particle remobilization, redox oscillation, excretion, irrigation and grazing of microbes by macroinvertebrates (Aller, 1994). Importantly, by exposing new substrata for microbial colonization and by introducing labile organic matter to the substrate, invertebrate activity dramatically effects the distribution and metabolic rates of different types of chemoheterotrophic populations. In addition, burrowing leads to changes in permeability (Gingras *et al.*, 1999b), porosity (Gingras *et al.*, 2002), fabric (Pedley, 1992), texture (Jaramillo, 1985; McIlroy *et al.*, 2003) and diagenetic processes not predicted from bulk sediment analyses (Gingras *et al.*, 2004).

For general modelling purposes, burrow structures are typically viewed as direct biogeochemical extensions of the sediment–water interface (Aller, 1988). In unburrowed sediment, solute and gas gradients in pore waters are coupled to chemoheterotrophic activity of subsurface bacteria. The presence of open burrows within the sediment alters the solute and gas distribution profiles because they expose the previously insulated pore waters to oxygenated waters (Aller, 1988; Aller & Aller, 1998) (Fig. 1). In addition, the impact of burrowing on diffusive solute and gas exchange is magnified by increases in the effective surface area of the sediment–water interface (i.e. tube diameter and burrow spacing). This change in surface area, up to 500% (Riedel *et al.*, 1987; Davey, 1994), is especially significant for oxygen distribution in coastal sediments characterized by a shallow (1–2 mm thick), oxic layer (Fenchel, 1996).

Given the importance of invertebrates in surficial sediment, the aim of this study is to examine the effects of burrow architectures on dissolved oxygen diffusion rates in comparison with unburrowed sediment, and thereby to evaluate the idealized assumptions used for modelling solute distribution in the burrow system using field samples. Employing microsensors, oxygen profiles were measured on a micrometer scale around the

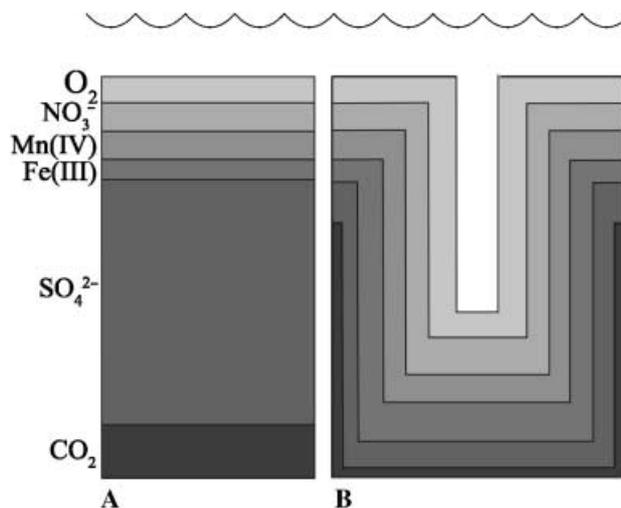


Fig. 1 (A) Idealized cross section of solute and reaction gradients in unburrowed sediment. (B) Idealized cross section of modified solute and reaction contours in burrowed substrate. (Modified from Aller, 1982).

burrows of the marine invertebrates *Corophium volutator*, *Heteromastus* sp., *Arenicola marina*, *Hemigrapsus oregonensis*, *Saccoglossus bromophenolosus*, *Chlymenella* sp., and *Cirriformia luxuriosa*.

SAMPLING AND METHODOLOGY

Willapa Bay is located in south-west Washington. The bay is a mesotidal estuary (2–3 m tidal range) and is separated from the Pacific Ocean by a 27-km-long spit derived from sand transported from the mouth of the Columbia River (Anima *et al.*, 1989). The bay measures 38 km in length and 8 km in width. Five river systems discharge into Willapa Bay from the south, east and north margins. As a result, Willapa Bay is characterized by mesohaline salinities. Sediment accumulations are dominated by siliciclastic sediments that have been transported into the bay by both fluvial (dominantly silt) and tidal (primarily sand) processes (Gingras *et al.*, 1999b; 2000).

Collection of the animal burrows occurred between August and September, 2004. All of the samples were collected during low tide from south of the Nemah River and north of Bone River (Fig. 2). Both sampling locations are within the upper estuary in close proximity to one of the fluvial discharge points and are characteristically muddy (80% finer than 6ϕ (0.0156 mm)) (Gingras *et al.*, 1999b).

Burrows and substrate were extracted using a 10.16 cm diameter by 64-cm-long PVC pipe, which was inserted into the sediment around the burrow. The sediment-filled tubes were recovered and transported to a temporary laboratory site for microsensor analysis or reserved for later sedimentological analyses at the University of Alberta. The sediment cores selected for microsensor analysis were removed from the pipe, and the inner burrow wall and surrounding suboxic sediment

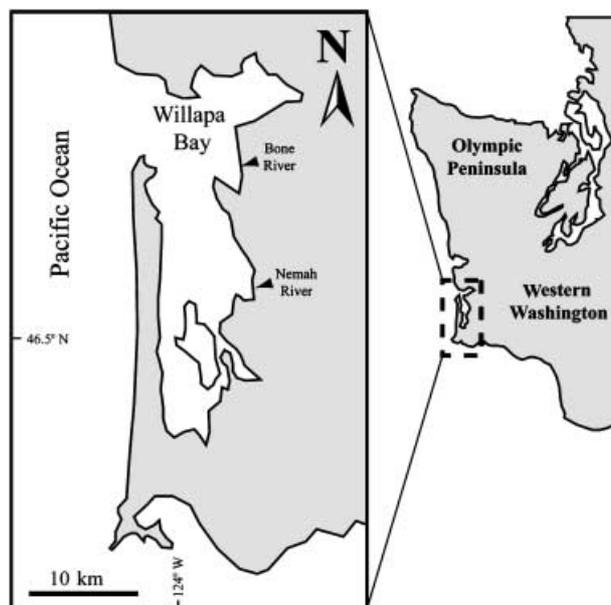


Fig. 2 Map of Willapa Bay, Washington showing sampling locations.

were exposed to atmospheric oxygen levels by splitting the core along the preferential plane of weakness created by the burrow. With the exception of *C. volutator* whose burrow generally does not penetrate suboxic sediments, all oxygen profiles of burrow walls were collected from portions of the burrow that were naturally constructed in suboxic sediments.

Oxygen profiles were taken in undisturbed (unburrowed) sediment and from burrow walls using the Unisense OX50 oxygen microsensor (Unisense, Denmark) (Fig. 3) with a 50- μ m tip. The microsensor was held by a Unisense MM33-2 micromanipulator and connected to the Unisense PA2000 picoammeter coupled with a PC data acquisition system. The electrode was calibrated by a 2-point calibration, using a 0.1 M ascorbic acid solution and atmospheric oxygen prior to analysis. The concentration of oxygen within a sample was measured by introducing the Clark-type microelectrode into the sediment or burrow wall in steps of 100 μ m intervals, the smallest reliable interval when using a 50- μ m tip. Oxygen profiles were taken from the sediment surface to a depth where the sample became anoxic or the microsensors encountered another burrow unrelated to the current analysis. Analyses were completed within 30 min following exposure of the sample to atmospheric oxygen. The oxygen profiles of several exposed samples were remeasured 3 and 24 h after initial exposure (i.e. splitting of core) to confirm measurement consistency over time.

Sediment cores returned to the University of Alberta were removed from the tubes and separated into burrowed and unburrowed sections. These samples were analysed for grain-size distribution and total organic content (TOC). Grain size was examined by drying samples overnight in a 105 °C oven and determined by X-ray absorption of a Micromeritics Sedi-

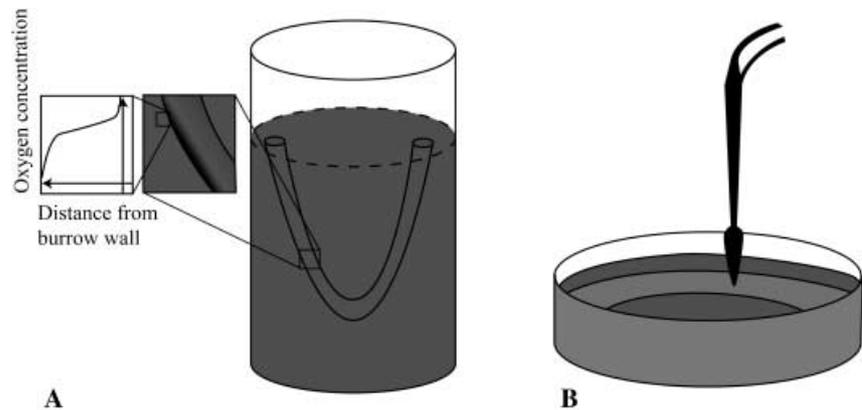


Fig. 3 Diagrams of burrow sampling procedure. (A) PVC core showing burrow and close-up of burrow wall; inset shows typical distribution of oxygen radial from burrow outward into sediment. (B) Exposure burrow with oxygen microsensors inserted perpendicular to burrow wall (modified from Nielsen *et al.* 2004).

graph 5100 (Norcross, GA, USA). Total organic content was determined using a standard combustion procedure (loss on ignition) where samples were dried overnight in a 105 °C oven, weighed after drying and then transferred to a 550 °C oven for 4 h to remove all organic carbon from the sample and then weighed again.

RESULTS

Burrow profiles – limited effects

Corophium volutator

The amphipod, *C. volutator*, commonly occurs in densities exceeding 5000 individuals per square metre in Willapa Bay. *C. volutator* ranges from 5 m to 8 mm in length and produces a U-shaped tube with a diameter of 1–2 mm (Table 1, Fig. 4A). In oxic sediment, oxygen was recorded decreasing below detection limit (1% atmospheric O₂) around 2.6 mm in depth, whereas oxygen disappeared 0.6 mm into the suboxic sediment (below the burrowing depth of *Corophium*). Oxygen was observed penetrating the burrow wall and underlying sediments to a distance of 2.2 mm in one profile (Fig. 5A). Two additional sediment profiles and four burrow wall profiles display increases in the pore water oxygen concentration at distances of 0.8–1.5 mm from the sediment/burrow surface that resulted from the introduction of oxygen from an unmeasured, adjacent burrow.

Heteromastus filiformis

Heteromastus filiformis extends 10–20 cm in length (Table 1, Fig. 4B). Burrows of *Heteromastus* are correspondingly penetrative within sediments. The burrow shape of *H. filiformis*, which branches and spirals at depth, reflects the head-down deposit feeding behaviour of this capitellid polychaete. These invertebrates appear on the mudflats of Willapa Bay in densities of 1200–1500 individuals per square metre. Three profiles were collected from the suboxic sediment located near the burrows of *H. filiformis*. The unburrowed, suboxic sediment profiles showed oxygen being consumed rapidly and falling below detection limits 0.4–0.55 mm into the sediment (Fig. 5B).

The measured portion of the burrow wall lay within suboxic sediment. Within the burrow walls, oxygen was measured in two profiles penetrating to distances of 0.5–0.65 mm.

Arenicola marina

The lugworm, *A. marina*, constructs a U-shaped burrow, with a tube diameter of 5–8 mm, which is recognized surficially by the faecal string accumulation surrounding one of the burrow openings (Table 1, Fig. 4D). This head-down deposit feeder grows to lengths of 6–12 cm. Population densities reach 40–110 individuals per square metre. The profile of unburrowed, suboxic sediment near *A. marina* shows that oxygen was completely consumed 1.1 mm across the sediment–water interface (Fig. 5C). Three oxygen profiles were measured for portions of the burrow walls formed in the suboxic sediment. In these profiles, oxygen penetrated the burrow wall and underlying sediment to a distance of 0.95 mm.

Burrow profiles – decreased O₂ penetration

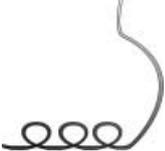
Saccoglossus bromophenolosus

The tongue worm, *S. bromophenolosus*, occurs in densities of 250–380 individuals per square metre in Willapa Bay (Fig. 4C). This hemichordate ranges in length from 15 cm to 20 cm and employs a head-down deposit feeding behaviour (Table 1). *S. bromophenolosus* lives in a vertical burrow that spirals at depth. The concentration of oxygen within unburrowed, suboxic sediment surrounding the burrow of *S. bromophenolosus* fell below detectable limits 0.8 mm into the substrata (Fig. 6A). The burrow wall profile of *S. bromophenolosus* was measured in suboxic sediments and shows a steeper gradient of oxygen consumption than the surrounding unburrowed sediment, with oxygen being consumed within 0.6 mm from the surface.

Clymenella sp.

The maldanid, *Clymenella* sp., forms a rigid, sandy U-shaped tube in muddy sands (Table 1, Fig. 4E). These tubes have diameters of 4–5 mm and extend up to 30 cm into the sediment. The bamboo worms can be found in Willapa Bay at densities up to

Table 1 Taxonomic and morphological differences of the seven sampled invertebrates from Willapa Bay, Washington

Scientific name	Common name	Lifestyle	Average animal length (cm)	Construction materials	Average burrow diameter (mm)	Figure
<i>Corophium volutator</i>	Amphipod	Filter feeder/ detritivores	>1	– Mud, silt, sometimes sand – Thin mucous lining	2–3	
<i>Heteromastus filiformis</i>	Thread worm	Head-down deposit feeder	10–20	– Mud, silt, sand – Thin to no mucous lining	1–2	
<i>Arenicola marina</i>	Lugworm	Head-down deposit feeder	10–15	– Silt, sand – No mucous lining	5–8	
<i>Hemigrapsus oregonensis</i>	Shore crab	Herbivore/ Scavenger	>4	– Mud, silt – No mucous lining	20–30	
<i>Saccoglossus bromophenolosus</i>	Tongue worm	Head-down deposit feeder	15–20	– Mud, silt – Thin mucous lining	3–4	
<i>Clymenella</i> sp.	Bamboo worm	Head-down deposit feeder	15–18	– Silt, sand – Fibrous mucous lining	4–5	
<i>Cirriformia luxuriosa</i>	Terebellid worm	Surface deposit feeder	7–15	– Mud, silt, some sand – Thick mucous lining	7–10	

570 individuals per square metre. Two profiles were recorded from the unburrowed, suboxic sediment close to the *Clymenella* sp. burrows. These profiles show that oxygen was exhausted 0.7–0.8 mm into the sediment (Fig. 6B). By contrast, the two profiles of the burrow wall in suboxic sediments show that oxygen was completely removed at distances of 0.3 mm.

Burrow profiles – enhanced O₂ penetration

Hemigrapsus oregonensis

Hemigrapsus oregonensis, also known as the green shore crab, grows up to 5 cm across the carapace (Table 1, Fig. 4F). The burrow produced by the green shore crab is J- to Y-shaped, with a tube diameter of 20–30 mm. *H. oregonensis* employs herbivory and scavenging for its nutritional requirements. These crabs are found in Willapa Bay ranging from one to 12 individuals

per square metre. The oxygen profile recorded within the unburrowed, suboxic sediment near the *H. oregonensis* burrow shows oxygen penetrating 0.8 mm into the substrata (Fig. 7A). Three oxygen profiles were collected from portions of the burrow wall that were naturally constructed within the suboxic sediments. These burrow-wall profiles show oxygen extending more deeply into the sediments, to distances of 1.5–2.0 mm.

Cirriformia luxuriosa

Cirriformia luxuriosa is a terebellid polychaete which is easily recognized by its vivid red gills and multitude of orange-red feeding tentacles (Fig. 4G). These terebellid worms range in length from 7 cm to 15 cm (Table 1). *C. luxuriosa* produces a U-shaped burrow and deposits feeds from the burrow opening at the sediment surface. A large population of *C. luxuriosa* are located in Willapa Bay where they occur in densities up to

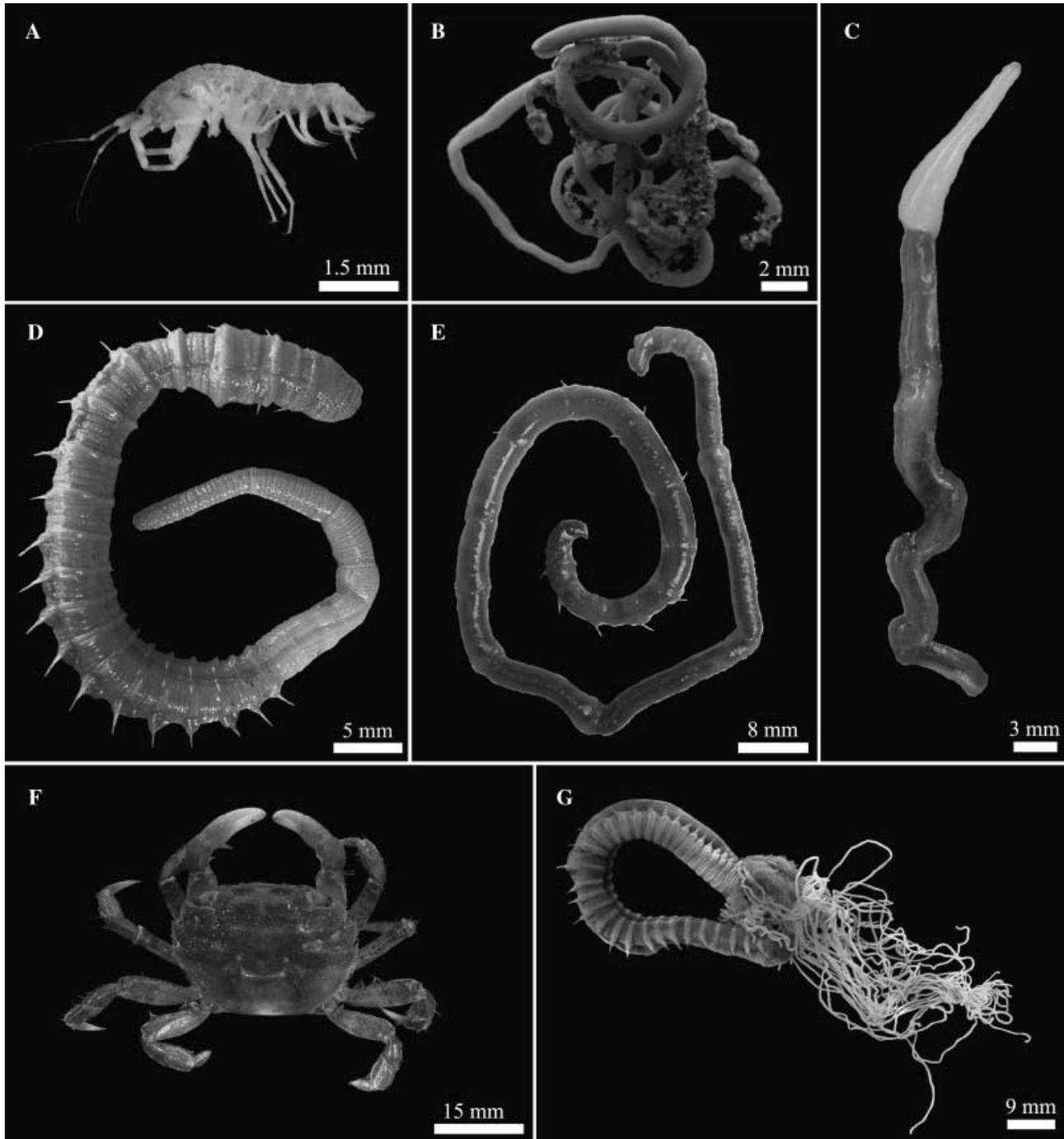


Fig. 4 Photographs of (A) *Corophium volutator*, (B) *Heteromastus filiformis*, (C) *Saccoglossus bromophenolosus*, (D) *Arenicola marina*, (E) *Clymenella* sp., (F) *Hemigrapsus oregonensis*, and (G) *Cirriformia luxuriosa*.

6 individuals per square metre. Three profiles of the suboxic sediment surrounding the burrow of *C. luxuriosa* were taken. Within these profiles, oxygen was recorded falling below measurable concentrations within 0.7 mm of the surface (Fig. 7B). By contrast, oxygen penetrated through the *Cirriformia* burrow walls between 1.7 mm and 2.1 mm.

Repeated measurements

To ensure that the recorded measurements were taken at steady-state conditions, repeat measurements were taken 3 and 24 h after initial sampling (data not shown). Profiles of oxic and suboxic sediments showed no notable changes during

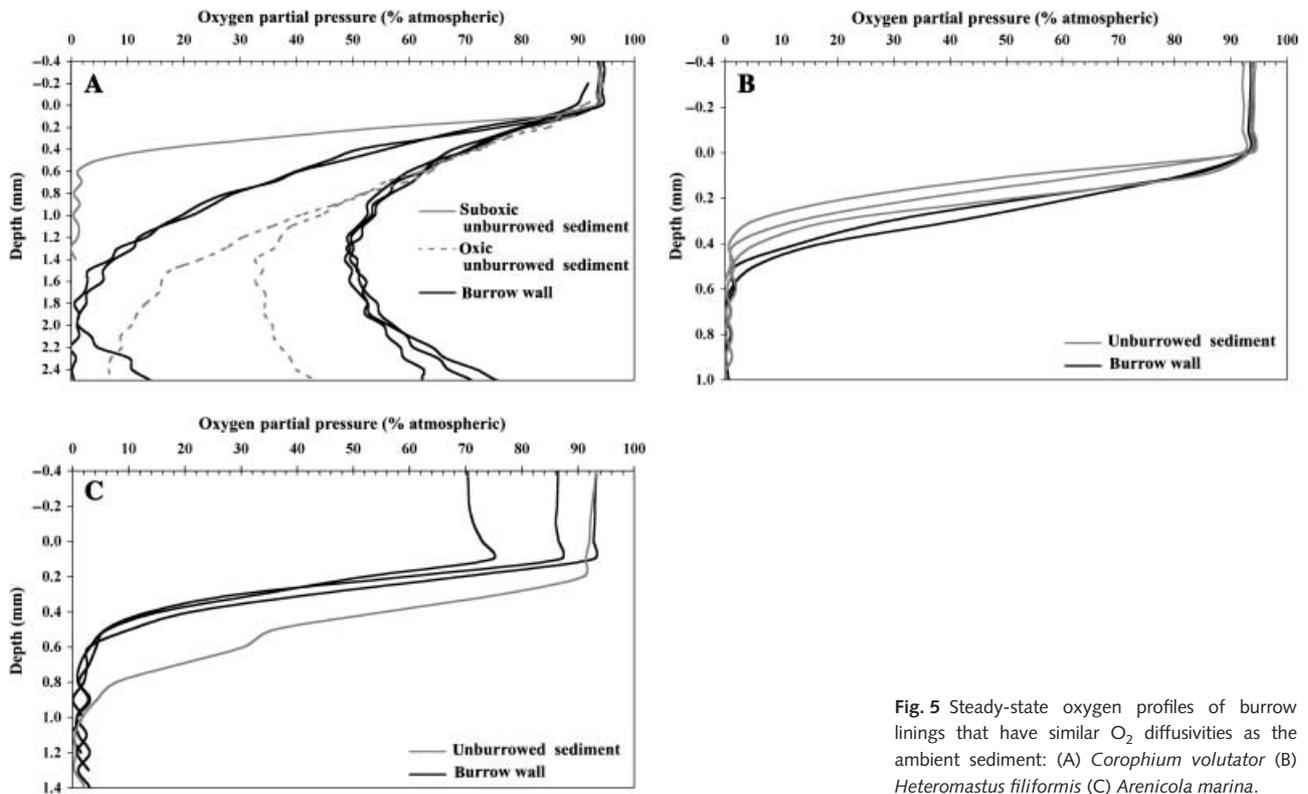


Fig. 5 Steady-state oxygen profiles of burrow linings that have similar O₂ diffusivities as the ambient sediment: (A) *Corophium volutator* (B) *Heteromastus filiformis* (C) *Arenicola marina*.

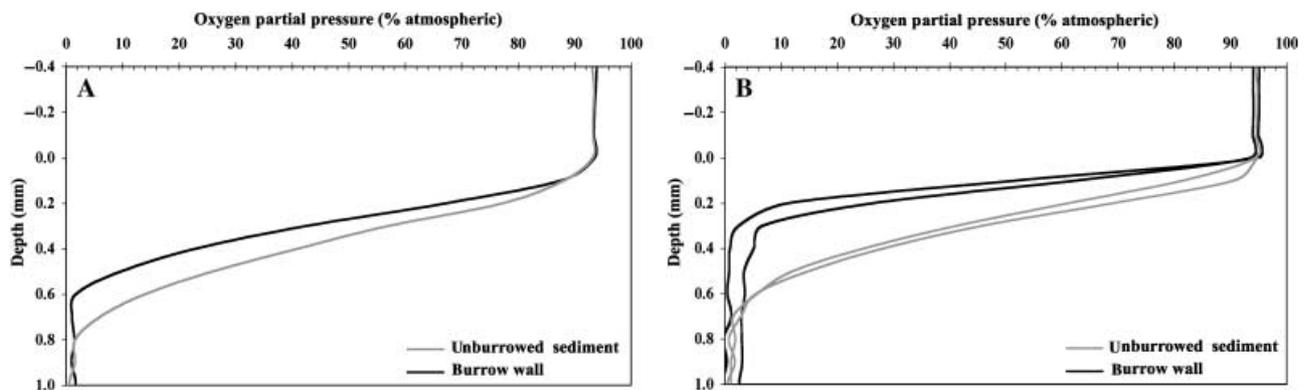


Fig. 6 Steady-state oxygen profiles of burrow linings that have clearly inhibited O₂ diffusivities compared to the ambient sediment: (A) *Saccoglossus bromophenolosus* (B) *Clymenella* sp.

that time frame. Oxygen penetration also was remeasured in the burrow walls of *Clymenella* sp., *Heteromastus* and *Saccoglossus*. These later profiles displayed no significant differences in oxygen diffusion compared to the initial results. From these data, it is inferred that the profiles represent steady-state conditions.

Sedimentological analyses

Sedigraph analysis of burrows and unburrowed sediments shows that the modal grain size ranges from lower to upper coarse clay, 2–4 μm (9–8φ). Unburrowed sediment and most burrows

displayed modal grain sizes of lower coarse clay. However, two notable exceptions are *Clymenella* sp. (3.12 μm) and *C. luxuriosa* (3.92 μm).

TOC results indicate that the organic carbon content of unburrowed and burrowed samples ranges from 3% to 6%. Unlike the grain size distribution, differences in TOC are related to the sampling location rather than burrow construction. Samples collected near Needle Point possess TOCs near the upper range of the observed results, whereas those burrows and sediment samples collected near Bone River show TOCs closer to the lower range.

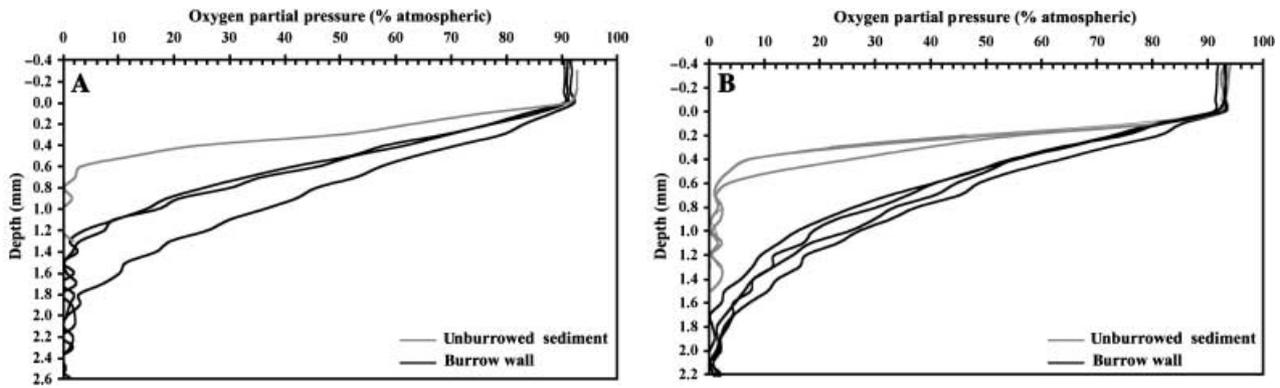


Fig. 7 Steady-state oxygen profiles of burrow linings that have enhanced O_2 diffusivities compared to the ambient sediment: (A) *Hemigrapsus oregonesis* (B) *Cirriformia luxuriosa*.

Table 2 Calculated relative oxygen diffusion gradients for burrow walls of seven invertebrates from Willapa Bay, Washington

Burrow type	Average O_2 penetration distance (mm)		Relative (burrow:sediment) O_2 Concentration Gradient
	Into burrow wall	Into sediment	
<i>Corophium volatator</i>	2.20	2.6 (estimated)	0.85
<i>Heteromastus filiformis</i>	0.50	0.6	0.83
<i>Arenicola marina</i>	0.95	1.10	0.86
<i>Saccoglossus bromophenolosus</i>	0.60	0.80	0.75
<i>Clymenella</i> sp.	0.30	0.75	0.4
<i>Hemigrapsus oregonesis</i>	1.75	0.80	2.19
<i>Cirriformia luxuriosa</i>	1.90	0.70	2.71

DISCUSSION

Oxygen penetration trends

Microsensor analysis of the seven burrow types from Willapa Bay, WA shows a significant range of diffusive properties relative to the unburrowed sediment (Table 2). Depending on the nature of the burrow margin, burrows locally impede or enhance oxygen penetration *relative* to the normal sediment–water interface. These variations in oxygen diffusion can be associated with the composition of the burrow wall, nature of the mucous lining, and the microbial communities colonizing the distinct burrow microenvironments. It should be stated that burrows always enhance the total flux of oxygen diffusing into the substrate because burrows increase the surface area of sediment in contact with oxygenated water.

Burrows that display a small relative difference in oxygen diffusion compared to the sediment – *Corophium volatator*, *H. filiformis*, *A. marina* – best conform to the simplified assumption that burrow walls are biogeochemically equivalent to the sediment–water interface. Despite that similarity, the burrows within this group nonetheless display diminished oxygen penetration relative to unburrowed sediments. *Corophium*, *Heteromastus* and *Arenicola* burrows are stabilized primarily by very thin (2–8 μm thick) mucous linings, display no grain-size selected burrow margins, and show minimal modification

of the surrounding substrate. Aller (1983) previously suggested that thin mucous linings, at least 10 μm thick, could impede diffusion by factors of 1.7–6.7. However, other parameters, such as porosity and reaction rate differences, seem to have a minimal effect on these burrows. The lack of grain-size variation between unburrowed sediment and burrows indicates there is no significant porosity difference. Furthermore, by using grain size to estimate reaction rates, results suggest that the surface area available for micro-organisms is comparable between the burrowed and unburrowed sediments. This is supported by small variation in total organic carbon values recorded for these three burrow types and the surrounding unburrowed sediment. Thus, it appears that although the burrow linings for *Corophium*, *Heteromastus*, and *Arenicola* are below Aller's (1983) suggested minimum mucous thickness, it is likely that mucous linings represent the dominant control on diffusion across the burrow–water boundary.

Oxygen profiles recorded from the burrow walls of *S. bromophenolosus* and *Clymenella* sp. show that the burrow linings impede oxygen diffusion into the surrounding sediment. *Saccoglossus* lines the inner burrow surface with a 5- μm -thick mucous lining that is constructed of several sheets of mucous. The burrow wall extends 40–50 μm into the sediment and is lightly sheathed by lower coarse clays. Although SEM data document the change in grain size towards the outer burrow wall margin, sedigraph and TOC data of the burrows are not

appreciably different from that of the surrounding sediments. Thus, we infer that the mucous lining also is the dominant control for diffusion in *S. bromophenolosus* burrows. By comparison, the burrow walls of *Clymenella* sp. represent the lower limit of oxygen diffusion compared to unburrowed sediments. *Clymenella* sp. produces a 10 µm thick burrow lining from woven strands of mucous that covers the interior burrow wall. Coarse clays, 0.5–1 µm larger than the ambient sediment, are radially packed around the burrow wall and extend up to 1.5 mm into the sediment. In the case of *Clymenella* sp., the decrease in oxygen penetration distances is likely due to a combination of factors including the presence of a mucous lining, a decrease in porosity due to preferential grain orientation and possibly lower reaction rates due to the increased grain size within the burrow.

In contrast to the above, *H. oregonensis* and *C. luxuriosa* enhance the amount of oxygen diffusion relative to the surrounding sediment. The burrow of *H. oregonensis* is unlined and displays no obvious grain manipulation or organization. As well, there are no significant differences in the relative grain size or total organic carbon between the burrow and surrounding sediment. For these reasons, the cause of the enhanced oxygen penetration in the *H. oregonensis* burrow walls is not obvious. One possibility is that the increased oxygen penetration may be related to increased porosity within the burrow wall associated with the animal's chelae penetrating the burrow wall and aerating the sediment. Like many other terebellid polychaetes, *Cirriformia* produces a burrow by collecting and coating particles from the surface with mucous and packing the sediment into the burrow wall (Aller & Yingst, 1978; Fauchald & Jumars, 1979; Jumars *et al.*, 1982). Repeated packing episodes produce concentric layers within the burrow wall. Mucous linings vary in thickness from 20 µm in outer laminae to 100 µm along the inner burrow wall. Based on SEM and sedigraph data, laminae display an increase in grain size relative to the surrounding matrix, 4 µm compared to 2 µm, respectively. TOC analysis once again shows that there is little to no difference in organic carbon between the burrow and the unburrowed sediment. It is interesting that a burrow so heavily coated in mucous enhances oxygen penetration rather than restricting diffusion. Unlike *Clymenella* sp., the sorting done by *Cirriformia* during burrow construction does not result in a preferential grain organization or associated porosity reduction. However, the increased relative grain size may represent the controlling factor of diffusion into *Cirriformia* burrows as this change would increase porosity and reduce microbial reaction rates.

Burrow spacing and irrigation

An important consideration for generalized modelling of diffusion is the effect of burrow spacing on oxygen penetration, and the assumption that solute concentrations are at a minimum or maximum halfway between the two burrows (Aller, 1982). Despite the fact that animals were densely packed in both

sampling areas (e.g. *Heteromastus* at 1500 individuals per square metre or *Clymenella* at 570 individuals per square metre), burrow spacing was not a significant factor in determining the distribution of oxygen within sediments, with the exception of *Corophium*. Oxygen penetration distances in *Corophium* burrows were the only examples of a minimum halfway between two adjacent burrows. The remaining six burrows architectures displayed no change in oxygen diffusion patterns related to burrow spacing (because oxygen penetration distances were so small). The impact of burrow spacing suggested by these models is strongly linked to the porosity (and grain size) and organic content of the burrowed sedimentary media. In sand-rich, organic-poor sediments, the assumption that solute concentrations reach a minimum or maximum at equal distances between two burrows is reasonable. However in this study, burrows were collected from very fine-grained, organic-rich sediments. In the presented examples, burrows would typically need to be within 5 mm of each other for their oxygenated zones to meet.

The fine-grained nature of the sediments examined in the present study would certainly impact the importance of irrigation on oxygen diffusion. Most of the animals studied produce a mucous lining to stabilize their burrows: the lining acts to delay oxygen diffusion across the burrow-water boundary. Furthermore, most polysaccharide membranes are impermeable to advective flow, such as that associated with burrow irrigation (Foster-Smith, 1978). Even those burrows where linings are thin or absent are unlikely to show significant change in the pattern of oxygen diffusion, as muddy sediments are also impermeable to advective flow (Aller, 1982). Thus, in this situation irrigation is a minor consideration for the distribution of oxygen within burrows.

Notwithstanding the differences in oxygen penetration related to grain size, the burrows in this study all expand the surface area of the sediment–water interface. Based on density counts done at Needle Point and Bone River, the presence of burrows increases the surface area of the sediment–water interface by up to 300%. The increased surface area associated with these burrows has a significant impact on the metabolism of aerobic microbes and the oscillation of reduced metabolites within the sediment, by providing oxygenated waters to previously insulated pore waters (Aller, 1988). However, as this study shows, the magnitude of this impact is highly dependent on the burrow architecture as the difference in oxygen penetration distance between burrows can be up to a sevenfold change.

CONCLUSIONS

Assumptions employed for generalized modelling of solute transport in bioturbated sediments (i.e. biogeochemical similarities between burrow and substrate and influence of animal behaviours) were evaluated in relation to field data. Microsensors were used to examine the distances of oxygen penetration into undisturbed sediments and through the

burrows of seven common invertebrates from Willapa Bay, Washington. Unlike the uniformity predicted by burrowing models, a wide range of oxygen diffusive profiles has been observed and three generalized groupings, with regard to oxygen diffusion, have been identified: (1) slight impedence in burrow compared to substrate, (2) significant impedence in burrow and substrate, and (3) enhanced penetration in burrow compared to substrate. Most differences in the oxygen penetration distance can be explained with physical observations of the burrow architecture (i.e. mucous linings, porosity) although some diffusion profiles also relate to the speculated microbial community.

The importance of burrow spacing and irrigation was also examined. As samples were collected from fine-grained sediments (8–9 ϕ), neither burrow spacing nor irrigation proved to be key factors in controlling oxygen distribution in the study sediments. Most importantly, despite the burrows increasing the surface area of the sediment–water interface by up to 300%, the degree to which the burrows impacted microbial metabolism or re-oxidation of reduced metabolites is highly dependent on the burrow architecture and can result in up to 7 times variation in oxygen penetration. Though O₂ was the only gas measured, it is very likely that the burrow microenvironment is also an important control on the diffusion of other dissolved gases, such as H₂S and CO₂.

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