

Oxygen measurements in the burrows of freshwater insects

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SUMMARY

1. Thin-tipped micro-electrodes were used to measure oxygen concentrations in the burrows of two common aquatic insects, the mayfly *Hexagenia limbata* and the alderfly *Sialis velata*. Both species maintain their surroundings oxygenated by drawing water from above the sediment surface into their tubes.

2. The temporal pattern of oxygen in the burrows differed between the species. The constant high oxygen concentration (>75% of air saturation) measured in the tubes of the mayfly suggest that this animal pumps water almost continuously, which is consistent with its high oxygen requirements. In contrast, oxygen concentration in burrows of the alderfly fluctuated widely over time, suggesting that this animal irrigates only irregularly, probably because it can tolerate short periods of low oxygen concentration in its burrow.

3. The interval between pumping episodes by the alderfly decreased with increasing temperature, a result of increased oxygen consumption by the animal and by sediment at high temperature.

4. Based on the tube dimensions, oxygen penetration depth and animal density in lakes, we estimate that *Hexagenia* could create an oxic micro-environment equivalent to 3–35% of the volume of the surface oxidized sediment layer created by molecular diffusion. The mosaic of oxic micro-environments created by the burrowing and irrigation of freshwater animals could influence chemical and biological processes in sediments, the fluxes of materials between the sediment and the overlying water column, and the exposure of benthic animals to sedimentary contaminants.

Keywords: benthos, bioturbation, burrowing, irrigation, oxygen

Introduction

Most burrowing animals cannot live in anoxic conditions; they require oxygen for respiration and are unable to withstand prolonged exposure to the toxic sulphide and ammonia that are often present in anoxic interstitial water (Oseid & Smith, 1975; Miron

& Kristensen, 1993). Because the oxic zone at the surface of sediments is usually very thin (Jorgensen & Revsbech, 1985), and because most burrowing animals live well below this zone, they must irrigate their burrows with oxygenated water from above the sediment–water interface. Burrow irrigation also serves other important purposes such as the procurement of food particles and the evacuation of waste products (Kristensen, 1988; Riisgard, 1991; Scott, Mazurkiewicz & Leeman, 1976).

Animals pumping oxygenated overlying water deep into sediments can have a profound influence on their diagenesis (Fisher, 1982; Kristensen, 1985; Matisoff, 1995). Penetration of oxygenated water into the sediment surrounding a burrow creates oxidized

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layers of sediment that can be seen as colour changes (Aller & Aller, 1986; Fenchel, 1996; Matisoff, 1995) and as gradients of solid-phase iron and manganese around burrows (Aller & Aller, 1986; Aller & Yingst, 1978). Modification of the redox zone in burrow walls leads to their colonization by aerobic bacteria and meiofauna (Aller & Aller, 1986; Aller & Yingst, 1978; Kristensen, 1988; Meyers, Fossing & Powell, 1987). These micro-organisms can be expected, in turn, to influence chemical reactions and their kinetics in these zones of varied redox potential.

Bioirrigation has also been invoked to explain the higher fluxes of solutes to and from sediments (measured with benthic chambers) than can be accounted for by diffusion alone (van der Loeff *et al.*, 1984; Archer & Devol, 1992; Glud *et al.*, 1994). Matisoff (1995), has shown that larvae of *Chironomus* can greatly influence nutrient fluxes and the porewater concentration of silica, ammonia, iron and manganese in the laboratory. Irrigation by animals also has the potential to influence the distribution of pollutants; for example, irrigation by marine polychaetes is reported to mobilize zinc from anoxic sediment and concentrate this trace metal in their burrow walls (Aller & Yingst, 1978).

Despite the potential importance of animals in oxygenating sediments, there are only limited data available on irrigation behaviour of marine animals (Fenchel, 1996; Forster & Graf, 1995; Jorgensen & Revsbech, 1985) and no comparable data for freshwater invertebrates. Yet freshwater sediments are inhabited by a variety of macro-benthic animals, including insects, crustaceans and bivalve molluscs, all of which can irrigate the substratum.

We measured oxygen concentration within and around the U-shaped burrows of two freshwater insects, the mayfly *Hexagenia limbata* (Serville) (Ephemeroptera) and the alderfly *Sialis velata* Ross (Megaloptera). We chose these genera because they are widespread in North America (Edmunds & Waltz, 1996; Evans & Neunzig, 1996; Roy & Hare, 1998) and play important roles in many freshwater ecosystems. The sediment-feeding mayfly converts organic detritus and its associated micro-organisms into a readily usable food source for fish (Edmunds & Waltz, 1996). Because of its large size and active burrowing, this mayfly could be a major contributor to bioturbation in freshwater sediments (Charbonneau, Hare & Carignan, 1997). The alderfly is a

major invertebrate predator, feeding non-selectively on insects, annelids, crustaceans and molluscs (Evans & Neunzig, 1996). We also measured temporal fluctuations in burrow oxygen concentrations over the range of temperatures likely to be encountered by these animals in nature. On the basis of our oxygen measurements, we estimate the importance that these insects are likely to have in extending the oxic zone below the sediment surface as well as the potential influence of their irrigation activity on their exposure to sedimentary contaminants.

Methods

Water, sediment and insect larvae were collected in March 1998 from Lake St Joseph (46°55'N, 71°07'W) which is located on the Precambrian Shield near Quebec City, Quebec, Canada. We used an Ekman grab to collect insects and sediment through a hole cut in the lake ice and transported insect larvae (separated from the sediment by sieving) in coolers to the laboratory. We sieved sediment through a 1-mm mesh aperture net to remove resident animals and coarse materials that could break the fragile tip of an oxygen micro-electrode. Larvae of the mayfly *H. limbata* and the alderfly *S. velata* were held for at least 2 days at 10 °C in unsieved lake sediment to acclimate to experimental conditions. *Sialis velata* larvae were fed one chironomid larva prior to our oxygen measurements, but not during the subsequent 10-day experimental period.

Animals were maintained, either in the dark or under red light for measurements of burrow form or oxygen profiles. Individual insects were held in a thin (0.6-cm width) Plexiglas aquarium (13 × 15 cm), filled with sieved lake sediment that permitted us to see the animal's burrow from one side. By this means, we were able to determine when the electrode tip entered the burrow as well as to estimate by eye the burrow's diameter by comparison with the electrode. Insects placed in this aquarium burrowed into sediment within seconds. We positioned this small aquarium inside a larger (12 × 28 × 20 cm) glass aquarium filled with aerated lake water. This nested design (Fig. 1) served to maintain oxygen concentration in the water near saturation, without disturbing the sediment surface or the burrowing animal, as well as to allow the entry of the micro-electrode into the sediment from a variety of angles. Two *H. limbata* (length

2.2 and 2.4 cm, wet weight 130 and 140 mg) and three *S. velata* (length 1.5–1.9 cm, wet weight 32–40 mg) larvae were arbitrarily selected for use in our experiments. Oxygen measurements were made at 10 °C for both insect species and at 4 and 20 °C for *S. velata*.

Oxygen concentration in the sediment and across burrows was measured with Clark-style, thin-tipped, oxygen micro-electrodes (737GC Diamond General Development Corp., Ann Arbor, MI, USA) having a built-in reference electrode and a silver guard cathode (Revsbech, 1989). These electrodes have a sensing tip 8–10 µm in diameter, a linear response over a range of 0–100% of air saturation, a stirring effect of <1%, a 90% response time of <1 s, and a signal drift of <1% h⁻¹. A two-point calibration was made for each oxygen profile between air-saturated water (100% air saturation in oxygen) and anoxic sediment (0% air saturation in oxygen) with the assumption of linearity. Electrode position was controlled in three dimensions by a micro-manipulator (Narishige, Japan; Fig. 1). Sensor currents were converted to voltages by a picoampere-millivolt converter and recorded on a computer with a Work Bench PC™ Data Acquisition and Control System (Strawberry Tree Inc., CA, USA; Fig. 1).

A minimum of four vertical oxygen profiles were measured for each insect taxon, in steps of 25 µm, by moving the electrode downwards from the overlying water to below the insect's burrow. Recording depths were multiplied by the cosine of the angle of the tube (relative to the vertical) to obtain the oxygen gradient

perpendicular to the burrow. The sediment–water interface was determined by visual observation. To monitor fluctuations in oxygen concentrations within burrows, we positioned the electrode near the bottom of a burrow inhabited by an animal, that is, at a depth of 2.5–3 cm below the sediment surface. Oxygen concentration in the burrow was recorded at 10-s intervals for up to 3 days.

Results

Vertical profiles of oxygen

Oxygen was evenly distributed in the air-saturated overlying water at a concentration of 360 µM at 10 °C (Fig. 2). As the electrode entered the diffusive boundary layer (DBL) above the sediment surface, oxygen concentration began to decline (Fig. 2). The mean DBL value of 0.6 ± 0.1 mm (± 1 SD, $n = 4$) that we measured at the sediment surface in our study falls within the range observed in other studies (0.2 to > 1 mm; Jorgensen & Revsbech, 1985). Penetration of the electrode into sediment was associated with a continued decrease in oxygen and its eventual drop to below detectable levels at a sediment depth of 2.5-mm (Fig. 2).

Where the electrode tip contacted a burrow wall of either *H. limbata* (Fig. 3) or *S. velata* (Fig. 4) the oxygen concentration increased sharply. A close-up of an oxygen profile across a burrow of *H. limbata* reveals that oxygen extended for up to 2 mm into the burrow wall (Fig. 5). A comparison of Figs 2 and 5 reveals

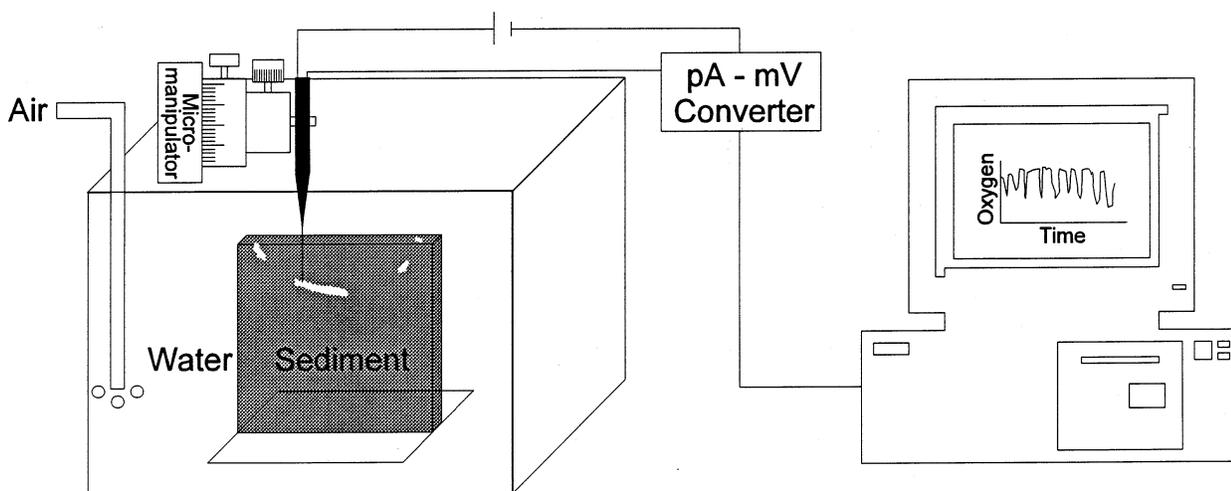


Fig. 1 Experimental apparatus for recording oxygen measurements in animal burrows.

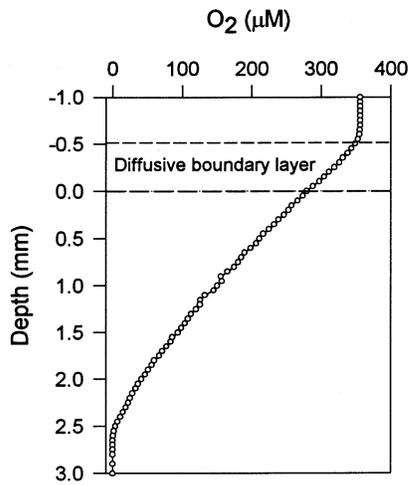


Fig. 2 Typical oxygen concentration micro-profile across the sediment-water interface for Lake St Joseph sediment in an aquarium at 10 °C. The horizontal dashed lines indicate the sediment-water interface and the upper limit of the diffusive boundary layer.

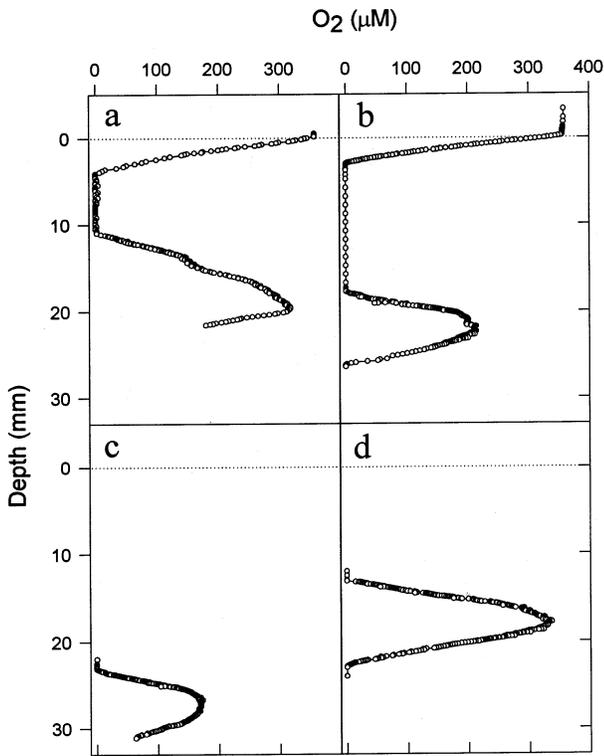


Fig. 3 Vertical oxygen micro-profiles from the overlying water into the sediment and across an inhabited burrow of *H. limbata* (10 °C) on four occasions (a-d). The animal was held in a small aquarium as shown in Fig. 1. The micro-profiles correspond to a plane perpendicular to the burrow. The horizontal dashed line indicates the sediment-water interface.

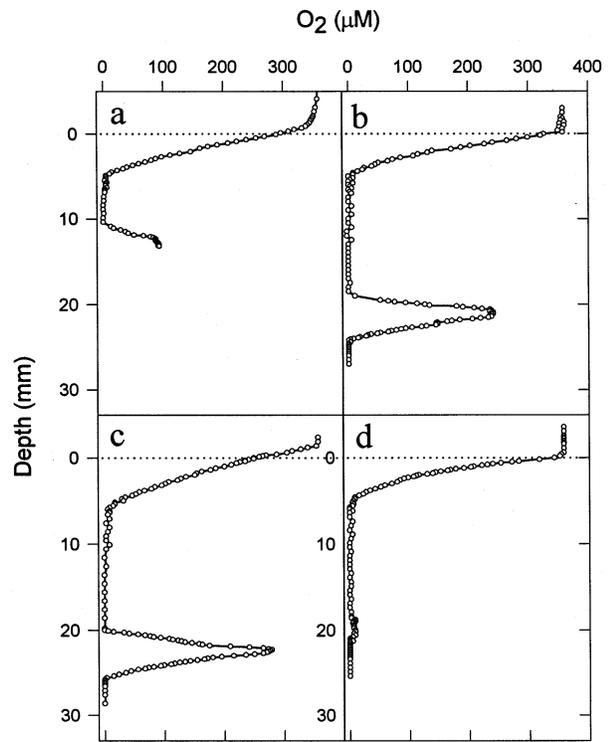


Fig. 4 Vertical oxygen concentration micro-profiles from the overlying water into the sediment and across an inhabited burrow of *S. velata* (10 °C) on four occasions (a-d). The animal was held in a small aquarium as shown in Fig. 1. The micro-profiles correspond to a plane perpendicular to the burrow. The horizontal dashed line indicates the sediment-water interface.

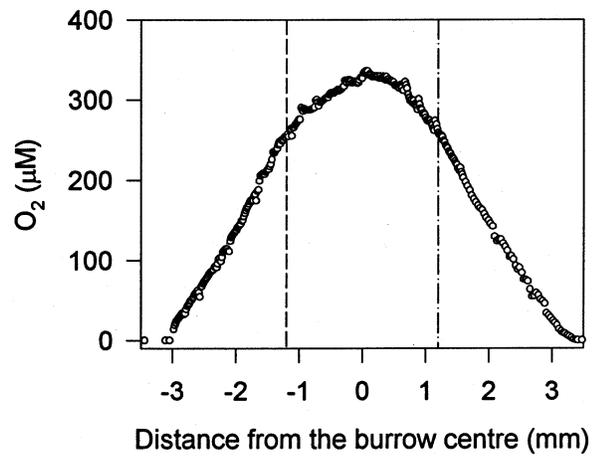


Fig. 5 Detail of oxygen concentration micro-profiles within the burrow of *H. limbata* and in sediment surrounding the burrow (10 °C). The micro-profiles correspond to a plane perpendicular to the burrow. The vertical dashed lines indicate the burrow wall.

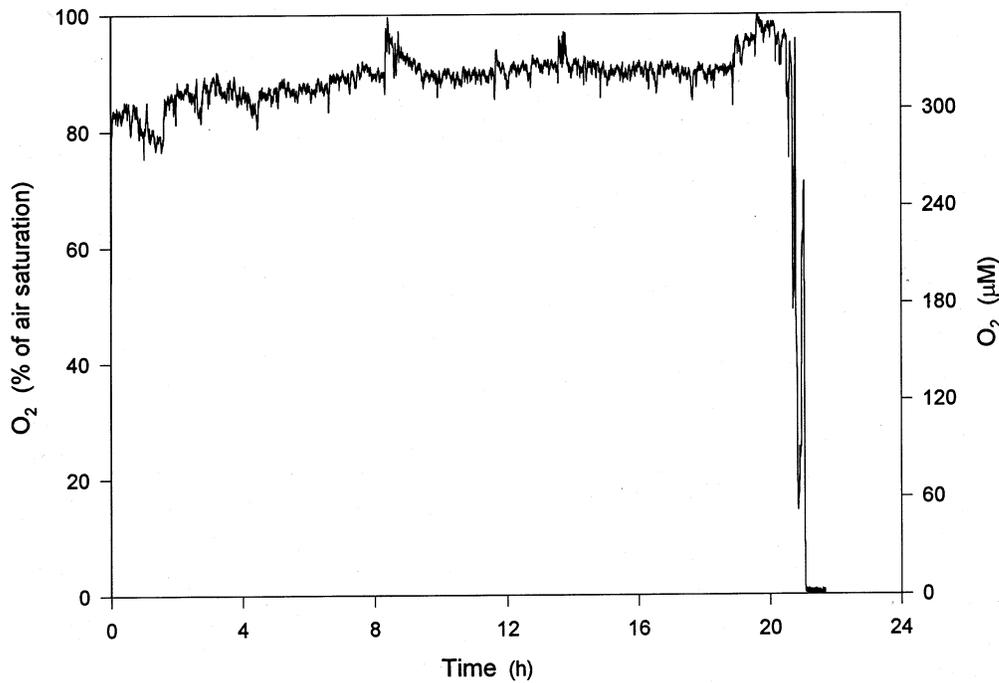


Fig. 6 Temporal fluctuations at 10 °C in oxygen concentrations in a burrow inhabited by *H. limbata*.

that the depth of penetration of oxygen into the sediment surrounding the burrow (2 mm) is slightly less than that across the sediment–water interface (2.5 mm). Peaks of oxygen tension measured in burrows were up to 96% of air saturation in the burrows of *H. limbata* (Figs 3a & d) and 82% of air saturation in those of *S. velata* (Fig. 4c). These high concentrations of oxygen in otherwise anoxic sediment indicate that animals must draw overlying water into their burrows. Lower concentrations probably represent periods of reduced (Figs 3b & c and 4a & b) or negligible (Fig. 4d) activity.

Temporal fluctuations in burrow oxygen

Over a 21-h period, oxygen concentration in the burrow of *H. limbata* remained high at 75–100% of air saturation (Fig. 6). Longer-term measurements were made difficult by the fact that this insect frequently adds a new arm to its burrow and, in doing so, blocks off an arm of the old burrow (Charbonneau & Hare, 1998). The constant, high oxygen-tension in the burrows of *H. limbata* suggest that this insect irrigates its burrow with overlying water almost continuously.

A lengthy (3-day) series of temporal oxygen measurements in the burrow of *S. velata* was simplified by

the fact that this insect changes burrow infrequently, probably because it is a sit-and-wait predator (Charbonneau & Hare, 1998). In contrast to the pattern observed for *H. limbata*, oxygen concentration in the tube of *S. velata* showed rhythmic fluctuations (Fig. 7), suggesting that alderfly movements are episodic. Periods of rising and high oxygen concentration probably coincide with activity by the insect, whereas falling and low oxygen concentration probably indicates periods of reduced or no activity.

Because the rate of most biological processes is temperature dependent, we varied the ambient temperature to determine if the burrow oxygen concentrations of *S. velata* at 10 °C would follow suit. Lowering the ambient temperature to values that would occur in winter (4 °C, Fig. 7) was accompanied by an increase in the interval between oxygen peaks. At this low temperature, the amplitude of the peaks was less than that at the higher temperature (Fig. 7). We also observed flat-bottomed valleys between peaks at a level of $\approx 50\%$ of air saturation, as a result of the lower oxygen demand by the animal and the sediment at 4 °C than at 10 °C. At an ambient temperature typical of those in summer (20 °C), the interval between oxygen peaks decreases (Fig. 7) signifying an increase in animal activity at the higher temperature.

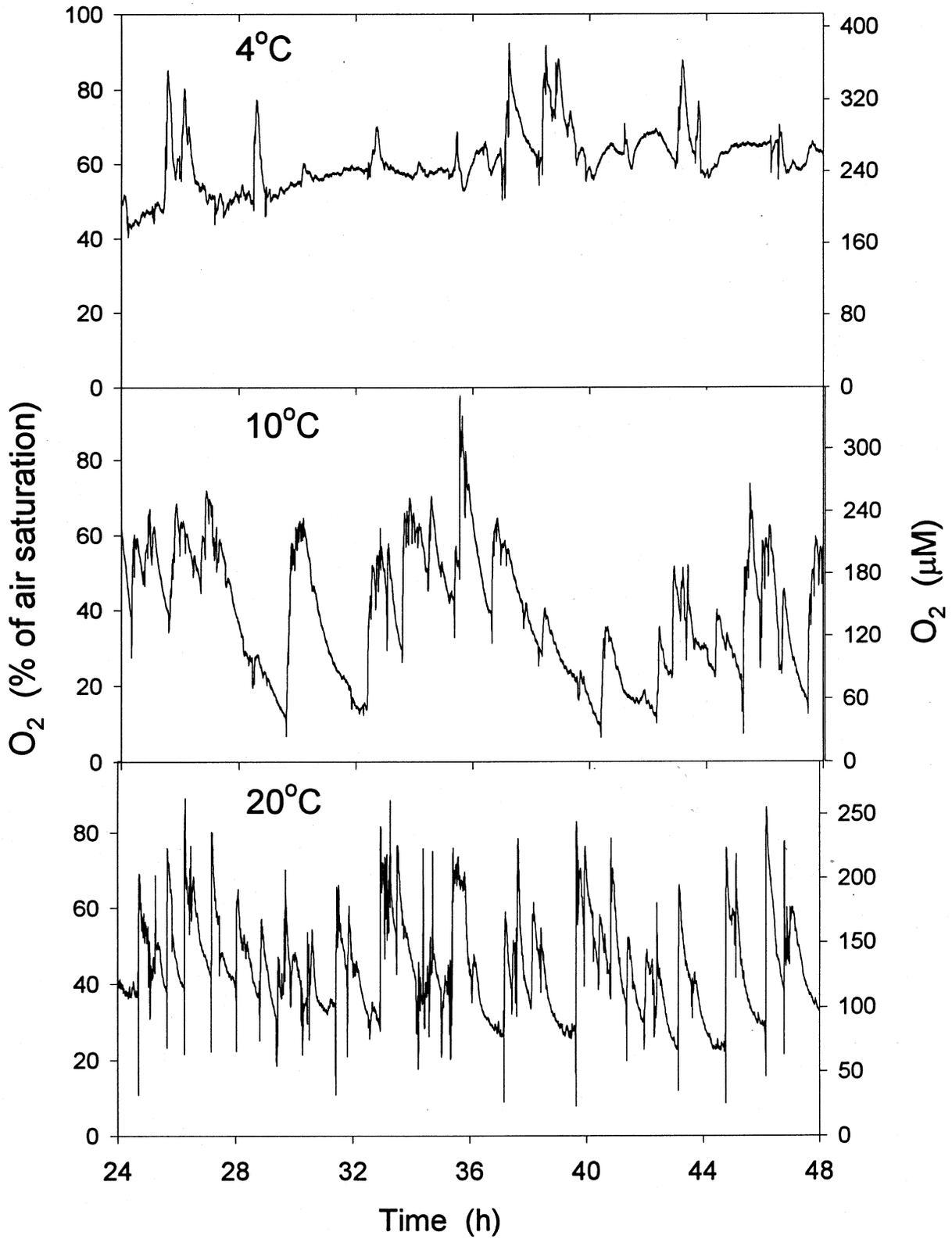


Fig. 7 Temporal fluctuations in oxygen concentrations in a burrow inhabited by *S. velata* at either 4 °C (upper panel), 10 °C (middle panel), or 20 °C (lower panel). Shown are oxygen measurements made over 24–48 h from a 72-h recording period.

Discussion

Behaviour of Hexagenia and Sialis

At 10 °C, oxygen concentration in burrows of *S. velata* resembles a series of asymmetrical peaks and valleys (Fig. 7). Although we did not observe animal movements (to avoid disturbing their behaviour), we can speculate that our oxygen recordings are correlated with their behaviour as follows. There is a rapid rise in oxygen when an animal's movements cause oxygenated water to be drawn into its burrow, followed by a brief peak during which values remain high as the animal moves nearly continuously. This peak is followed by a period of decline as oxygen in the burrow is taken up by both the animal and the surrounding sediment after animal movement has ceased. Valley bottoms are V-shaped at 10 °C, suggesting that once a critical low oxygen concentration is reached animals immediately reinitiated pumping movements. The minimum oxygen level at which activity began was at $\approx 20\%$ of air saturation ($\approx 70 \mu\text{M}$), suggesting that this is the minimum level of oxygen that the animal can tolerate at this temperature. Overall, a decrease in interval of animal activity was directly related to an increase in ambient temperature (Fig. 7). The oxygen demands of most invertebrates are known to increase with increasing temperature, within the temperature range tolerated by the animal (Sweeney, 1984).

We often observed that *H. limbata* and *S. velata* undulate the abdomen in waves from anterior to posterior, presumably creating a current of water from an opening of the burrow, over the body and out of the other opening of their U-shaped burrow (Charbonneau & Hare, 1998). The two species differ in that *H. limbata* possesses six pairs of large feathery abdominal gills that probably increase the efficiency of irrigation. The negative pressure created by this behaviour draws water from above the sediment-water interface into the insect's burrow (Eriksen, 1968). Walking movements of insects within their burrows also probably contribute to the mixing and displacement of burrow water. Insect movements serve to draw water from above the sediment-water interface into burrows to compensate for the oxygen consumed by insect respiration, as well as that lost by diffusion into the burrow walls.

Differences in the pattern of temporal change in oxygen in the burrows of the two insect species are

consistent with known differences between these genera in their sensitivity to low oxygen concentration. Mayflies are scarce or absent from organically polluted sites where decomposition leads to a reduction in oxygen concentration (Pennak, 1989; Reynoldson, Schloesser & Manny, 1989). For example, *Hexagenia* was eliminated from large parts of the western region of Lake Erie due to seasonally low oxygen concentration caused by eutrophication (Winter, Ciborowski & Reynoldson, 1996). *Hexagenia* larvae are also sensitive to sulphide (Oseid & Smith, 1975; Wang & Chapman, 1999), that can be present in anoxic sediment. This sensitivity to low oxygen and high sulphide probably requires the animal to irrigate its burrow actively and results in the constantly high oxygen concentration measured. The prominent gills of *H. limbata* attest to its high oxygen demand. Burrow irrigation by *Hexagenia* is also likely to play a part in feeding, by creating a current of particles that are trapped in setae on the legs and mouthparts (Zimmerman & Wissing, 1980; Keltner & McCafferty, 1986). Because *Sialis* larvae do not feed on suspended particles but are predators, burrow irrigation by *S. velata* must be largely for the purpose of obtaining oxygenated water. *Sialis* larvae tolerate moderate cultural eutrophication (Wiederholm, 1984) and the reduced oxygen concentration occurring under such conditions. The responses of these two insect genera to eutrophication is consistent with the occasionally low oxygen concentration that we measured in the burrows of *S. velata* compared with the constantly high values measured in those of *H. limbata*.

Scale of the oxic micro-environment created by the insects

The cylinder of oxygenated sediment that an animal creates around its burrow will increase the total volume of oxic sediment, as well as the surface available for exchange of solutes between the sediment and the overlying water column. From our observations and from measurements of burrows on radiographic images (Charbonneau & Hare, 1998 and unpublished data), we can estimate the volume of sub-surface oxic sediment and water associated with the burrows of *H. limbata* and *S. velata*. Given the mean (± 1 SD, $n = 23$) burrow length of 10 (± 3) cm and burrow radius of 2.2 (± 0.3) mm for *H. limbata* (body length 19–32 mm) and an oxygen penetration depth in the

surrounding sediment of 2 mm (Fig. 5), we estimate that a single *H. limbata* burrow represents 5.5 cm³ of oxic water and sediment. Given a density of 13 individuals m⁻² in Lake St Joseph (Charbonneau & Hare, 1998), *H. limbata* could create an oxic micro-environment of 72 cm³ m⁻², which is ≈ 3% of the superficial layer of oxygenated sediment created by molecular diffusion (assuming an oxygen penetration depth of 2.5 mm; Fig. 2). The difference in oxygen penetration depth between burrow and surficial sediment is consistent with a radial diffusion model (Aller, 1988) which predicts that for a given oxygen concentration its penetration in the sediment would be less for radial diffusion (as in a burrow) than for diffusion across a plane (as at the sediment surface). At the higher density found in many other lakes (mean of 160 larvae m⁻² in 20 lakes; Charbonneau & Hare, 1998), the volume of the oxic micro-zone created by this species at a given moment in time could represent ≈ 35% of the volume of the surface oxic layer. The volume of oxic sediment around burrows (4 cm³ burrow⁻¹ times 160 nymphs m⁻² = 640 cm³) would represent 25% of that in the surface oxic layer. In terms of surface area, daily production of burrow walls by this mayfly would represent from 1.7% (in Lake St Joseph) to 22% (in lakes with a larger population of the insect) of the surface area of the surficial sediment in the littoral zone inhabited by this insect.

Corresponding calculations were made for the alderfly. A mean (± 1 SD) burrow radius of 2.2 (± 0.9) mm and a mean individual burrow length of 4 (± 2) cm were measured for 18 *S. velata* larvae (7–18 mm in length; Charbonneau & Hare, 1998 and unpublished data). The mean depth of oxygen penetration in sediment around the burrow of this animal was 1.5 mm (data not shown). Thus, a single *S. velata* burrow represents 1.7 cm³ of oxic water and sediment. Given a density of 9 m⁻² in the study lake, *S. velata* could create an oxic microenvironment equivalent to 0.6% of the volume of the surficial oxic zone created by molecular diffusion.

The calculations above are based on the length of an individual burrow, but individual insects can dig more than one burrow a day. *Hexagenia limbata* nymphs are reported to burrow a mean (± 1 SD) distance of 24 (± 16) cm over 24 h, or ≈ 2.5 times the length of an individual burrow (Charbonneau & Hare, 1998). A comparable figure for *S. velata* is 6.6 (± 5.4) cm over 24 h or 1.7 times the length of an

individual burrow (Charbonneau & Hare, 1998). The burrows abandoned by both species are likely rapidly to become anoxic, judging from the rate at which oxygen declines in *S. velata* burrows when the animal is inactive (Fig. 7). If burrows of these insects remain intact over time then the sediment will come to resemble a labyrinth of burrows, which has been observed in the field for clay-rich sediments supporting large populations of *H. limbata* (Hare, unpublished data).

Because of its large body size, extensive burrowing, active burrow irrigation behaviour and widespread distribution, *Hexagenia* may be the predominant contributor to bioirrigation and bioturbation in the littoral sediments where it is found. The burrowing and irrigation activities of these animals are likely to influence vertical profiles of redox-sensitive chemical species such as Fe²⁺/Fe³⁺, Mn²⁺/Mn⁴⁺, HS⁻/SO₄²⁻, NH₄⁺ and sulphide-precipitated metals (Aller, 1988), as well as the fluxes of all chemical species. Given the presence of oxygen-rich zones in and near insect burrows, most freshwater sediments are likely to comprise a vertical mosaic of micro-environments similar to those reported to occur in marine sediments (Jorgensen & Revsbech, 1985; Fenchel, 1996).

Consequences of burrow irrigation for exposure to contaminants

The pioneering work by Aller and his colleagues (Aller & Yingst, 1978; Aller, 1980; Aller, Yingst & Ullman, 1983; Aller & Aller, 1986; Aller, 1988) showed that the properties of the burrow water of several large marine polychaetes and crustaceans are intermediate between those of the interstitial and overlying waters. The relative importance of the two depends on the irrigation intensity of the animals. Our results confirm that water in the burrows of two freshwater insects is not anoxic, as is the surrounding interstitial water, but that these animals draw oxygenated water from above the sediment surface. Consequently, such insects are more likely to be exposed to contaminants dissolved in the overlying water than to those in interstitial water (measurements of pollutants in the burrows of freshwater animals are not yet available due to their small size). This hypothesis is supported by the results of a field experiment in which the insects that we studied are reported to accumulate most of their trace metal cadmium, not

from the sediment and porewater in which the animals burrow, but from water and/or particles drawn into their burrows from above the sediment surface (Warren, Tessier & Hare, 1998). For *S. velata* larvae, the route of cadmium uptake from the water column is probably an indirect one via their prey (Roy & Hare 1999). Models designed to predict the toxic effects of contaminants such as trace metals from their concentrations in anoxic bulk porewater (for example, the Acid Volatile Sulphide model; Ankley *et al.*, 1996) are probably not applicable to animals that irrigate their burrows.

Our results should act as a caveat for the design of laboratory sediment toxicity tests. In laboratory tests conducted in a closed or semi-static system with a limited volume of overlying water, there is likely to be a flux of pollutants and nutrients (N and P) from the sediment to the overlying water (especially if mixing has perturbed the natural redox stratification of sediments). As a consequence, burrowing animals could take up pollutants because they irrigate their tubes with the now-contaminated overlying water and adverse biological effects could erroneously be ascribed to pollutants in sediment or interstitial water.

To conclude, observations on burrow irrigation have been made on a few larvae of two benthic insects. Given the biogeochemical importance of bioirrigation in nature, in particular for assessing the impact of sedimentary contaminants, it is important to extend these observations to a larger number of individuals and to other species. Additional useful information would also be obtained by using other microsensors and by coupling physical or chemical measurements with visual observation of the animals' behaviour. Biologists could contribute to these efforts by increasing the limited pool of information that is available on the burrowing and feeding behaviour of freshwater benthic animals.

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