Impact of irrigation on oxygen flux into the sediment: intermittent pumping by *Callianassa subterranea* and “piston-pumping” by *Lanice conchilega*

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Abstract O$_2$-flux into sediments attributed to the pumping behaviour of two macrofauna species, *Callianassa subterranea* (Decapoda) and *Lanice conchilega* (Polychaeta) was investigated. Samples were obtained from the North Sea near Helgoland in 1989 and 1990. The two species were found to transport roughly similar amounts (3 mmol m$^{-2}$ d$^{-1}$) of oxygen into the sediment although they displayed markedly different pumping behaviours. Irrigation by *C. subterranea* was intermittent and characterized by regularly recurring breathing currents which lasted 2.6 min and were separated by 40-min pauses. In addition to this regular intermittent irrigation, an irregular mode was observed. *C. subterranea* constructed a complex burrow system. At least half of the burrow wall was not in contact with oxygenated water, however, and thus not effective as additional interface for O$_2$-exchange. Sediment expelled from the burrow increased the total oxygen uptake (TOU) relative to the surrounding sediment surface.

*L. conchilega* moved water more frequently (every 4 min) than *C. subterranea*. We suggest that *L. conchilega* acted as a piston when moving in its tube, exchanging burrow water with the overlying water. This mechanism, termed ‘piston-pumping’, is also potentially important in other smaller tube dwelling organisms. At a shallow water station in the southern North Sea 21 ind of *C. subterranea* constructed 1.6 m$^2$ burrow surface per m$^2$. *L. conchilega* (300 ind m$^{-2}$) created only 0.37 m$^2$ m$^{-2}$ tube surface. On the basis of the abundance and oxygen transport associated with pumping activity, it is calculated that the two species increase TOU by 85% compared to O$_2$-flux across the sediment–water interface.

Introduction

Comparison of O$_2$-flux calculated from high-resolution microprofiles with flux measurements in sediment cores or bell-jar systems generally reveals higher total oxygen uptake (TOU) than can be attributed to molecular transport alone (Lindeboom et al. 1985; Archer and Devol 1992; Glud et al. 1994). The activity of benthic invertebrates has been recognized as one major factor enhancing the transport of solutes across the sediment–water interface. In addition, studies focusing on nutrient regeneration (Rutgers van der Loeff et al. 1984; Balzer et al. 1987) document an increase of overall fluxes in the presence of sediment-dwelling infauna. Through bioturbation and mining activity, particles are moved and interstitial water mixing is concomitantly forced (Berner 1980). Burrows are ventilated by their inhabitants in order to supply oxygen for respiration and/or to reduce potentially harmful concentrations of ammonia or sulphide. Filter-feeders also irrigate, flushing their burrows and filter apparatus with the volume of water needed to meet their nutritional requirements (Rüsgard 1991).

Halos of oxidized sediment along burrow walls of sediment-dwelling macrofaunal organisms indicate the penetration of oxygen from the interior of the burrow into the surrounding sediment (Anderson et al. 1978; Reise 1985). A distinct redox zonation arises from irrigation of burrows with overlying water (Aller 1982). Meiobrana and microorganisms also increase solute exchange rates through their movement in the interstices, though without visible effects on the colour of the sediment (Östlund et al. 1990; Aller 1992). Depending on the scale of the process, the increased flux may be viewed as a quasi random walk process or a local input by radial diffusion from burrows at different sediment.
Irrigation, the flushing of burrows and interstices, is caused by the pumping behaviour of benthic organisms. Generally, filter-feeders, with their need to process large amounts of water, pump more water than conveyor-belt feeders or surface-deposit feeders (Jørgensen 1975). However, benthic invertebrates may change their feeding mode, and different rates of irrigation are thus reported for a single species. Studying *Nereis diversicolor*, Riisgård (1991) found that pumping rates in suspension feeding animals were three times higher than those reported by Kristensen (1983a, b) for the same species and attributed these differences to the availability of sediment food versus water column food sources.

It may be anticipated that the amount of oxic water brought into contact with otherwise anoxic sediments differs substantially between benthic invertebrates featuring different pumping behaviours. All pumping activity potentially transports oxygen to depths beyond the normal oxygen penetration of a few millimeters (Revsbech et al. 1980).

In this contribution, we present evidence that the O$_2$-flux across the interface between burrow water and adjacent sediment walls is increased in a species-specific fashion by macrofaunal construction of tubes and burrows. Two invertebrate species with distinctly different behaviours were chosen to investigate the mechanisms by which this advection of O$_2$ takes place. *Callianassa subterranea* (Montagui) was chosen as an example of thalassinidian shrimps which are known to construct burrows of large surface area (Dworschak 1983; for a review see Griffis and Suchanek 1991) and may show extreme sediment-reworking activity (Dworschak 1981; Suchanek 1985). In contrast, the tube-building polychaete *Lanice conchilega* is not known to pump water into its tube (Seilacher 1951; Buhr 1976), since food acquisition occurs through surface-deposit or suspension feeding (Buhr 1976; Buhr and Winter 1977) and respiration takes place via gills located at its anterior end, which is located outside the tube when *Lanice conchilega* is in its feeding position.

In the present paper, we report measurements of the generated water flow and oxygen concentrations and subsequently present an estimate of O$_2$-flux into the sediment based on abundance, burrow size, and pumping frequency as these are affected by the two species.

**Methods**

**Samples**

Samples were obtained at 54°01'N, 07°49'E in the North Sea southwest of the island of Helgoland. The sediment consists of well sorted silty fine sand (20% by weight ≤ 63 μm) and bears abundant macrofauna (Stripp 1969; Salzwedel et al. 1985). Sediment cores were taken using a box corer (50 x 50 cm) modified to carry four acrylic core liners of 20 cm diameter to the sea floor (Forster 1991). Upon retrieval, cores were stoppered and transported in a refrigerated incubator kept at in situ temperature. Box cores without core liners were dissected on board to investigate the size, location, and depth of burrows of *Callianassa subterranea*. Individuals of both invertebrate species were transported inside the incubator in plastic vials containing sediment and water. Total length of the individual specimens was measured to the nearest 0.5 mm.

**Individuals**

*Callianassa subterranea* individuals were kept in their undisturbed burrows within sediment cores stored in a tempered water bath in the dark. Flat aquaria (50 x 45 x 5 cm) were used to observe the construction of burrows by *C. subterranea* more closely. These aquaria were filled with sediment on board and individuals were allowed to colonize the sediment. Aquaria with *C. subterranea* were kept under recirculating sea water for up to 14 mo in the laboratory without external food supply except for a water change every 3 mo.

Seven *Lanice conchilega* individuals were placed into the sediment in flat aquaria after cutting their tube to a length of 6 cm (Buhr 1976). Six rebuilt their tubes to form a "U". Water flow and oxygen measurements were conducted exclusively on these individuals' tubes.

**Burrows**

To follow the development of the visible burrow structures constructed by *Callianassa subterranea*, consecutive weekly drawings of the burrow visible through the outside of the sediment core acrylic wall were produced. After 3 mo, cores were extruded and sectioned at 1-cm intervals. Documentation of the location of openings in each section made it possible to reconstruct the three-dimensional structure of the burrow. The burrow surface area was calculated assuming an equivalent size construction from simple geometric bodies (spheres and rods). In flat aquaria, enough burrow lumina could be seen through the glass to reconstruct the geometry without cutting the sediment.

Tubes constructed by *Lanice conchilega* have a simple geometry (constant diameter) and are very sturdy. After the experiments they were simply removed from the sediment and measured.

**Oxygen**

Oxygen was measured both in sediments and in the water above burrow openings using Clark-type O$_2$-sensors (Revsbech and Ward 1983). A two-point calibration was conducted before and after each profile was measured or at least once a day during a 4-d measuring period. Electrode drift during this time was negligible (≤ 1%). Exhalent currents were indicated by intermittent oxygen concentration decreases when suboxic or anoxic water emerged from the opening. Fick's First Law was used to calculate the molecular diffusive flux from profiles of oxygen concentration. The whole sediment diffusion coefficient, $D_w$, was calculated from the temperature-corrected diffusion coefficient, $D_0$ (Li and Gregory 1974; Broeckel and Peng 1974), using the relation for sandy sediments

$$D_w = \phi^3 D_0$$  

(Berner 1980).

Porosity, $\phi$, was calculated from water content of the sediment measured as loss of weight after drying for 24 h at 65°C and assuming a dry sediment density of 2.6 g cm$^{-3}$. 

$D_w$