Marine Biology (1995) 123: 335–346

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

Received: 3 March 1995/Accepted: 19 April 1995

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 much 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 concomittently 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 sulfide. Filter-feeders also irrigate, flushing their burrows and filter apparatus with the volume of water needed to meet their nutritional requirements (Riisgård 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). Meiofauna 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

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Communicated by O. Kinne, Oldendorf/Luhe

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depths (Aller 1982; Boudreau 1984; Christensen et al. 1984).

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 × 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 temperated water bath in the dark. Flat aquaria (50 × 45 × 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 ($\leq 1\%$). 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_s, was calculated from the temperature-corrected diffusion coefficient, D_0 (Li and Gregory 1974; Broecker and Peng 1974), using the relation for sandy sediments

$$D_s = \phi^2 D_0 \tag{1}$$

(Berner 1980).

Porosity, ϕ, 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}.

Flow at burrow opening

Flow was monitored using two thermistor probes (LaBarbera and Vogel 1976). A heated thermistor's rate of cooling, dependant on the heat dissipation through flow around it, serves as a signal for current speed (anemometric principle). A second thermistor compensates for temperature changes in the ambient water. Calibration followed the procedure of Vogel (1981) and yielded a detection limit of $0.001\ \mathrm{cm\,s^{-1}}$. The sensor tip (diameter: 0.8 mm) was placed in the center of the burrow opening to measure the maximum velocity, U_{max}, and the diameter of the opening was measured to the nearest 0.5 mm. Average velocity across the cross-sectional area ($U_{av} = 0.5 \times U_{max}$) was calculated by assuming fully developed laminar flow in the tube. Mass flow of water from/to the burrow opening was calculated as the product of average flow velocity, and cross-sectional area of the opening.

Results

Burrow surface (*Callianassa subterranea*)

Twelve box cores with a total surface of 3 m^2 were dissected on three cruises (February, May and August 1989). Maximum penetration of these box cores was 40 cm. This was deep enough to reach burrows of most adult *Callianassa subterranea*. Some open burrows at the bottom of box cores indicated that burrows extended to an unknown depth below 40 cm, and a few adult individuals may thus have escaped sampling. There were 21 ($SD = 8$, $n = 5$) adult individuals of *C. subterranea* measuring 1.0 to 9.5 cm total length per m^2. Our sampling procedure recorded only some of the juveniles present, a problem also mentioned by Witbaard and Duineveld (1989). Juveniles (≤ 1 cm total length) are therefore excluded from the following considerations.

Callianassa subterranea constructs complex burrows with turning chambers interlinked by tunnels described by Witbaard and Duineveld (1989). We observed several shafts which extended to the sediment surface vertically from a main gallery with elliptical shape. Shafts are funnel- or mound-shaped at the surface and are thought to function as inhalent and exhalent openings, respectively (Suchanek 1985). There are also tunnels extending from the main gallery sideways and to strata below. Half of the length of the burrows constucted by invertebrates in the laboratory, as well as those excavated on board, was constructed a continuous tube with connections to the sediment surface or other tubes through branchings on either side. The other half of the burrows length consisted of tubes with dead ends.

In one box core examined in detail (Fig. 1a) burrows were present below 690 cm^2 of 2500 cm^2, equivalent to one quarter of the sediment surface. Main galleries were found between 5 and 32 cm sediment depth, with large individuals generally constructing burrows at greater depths than small individuals.

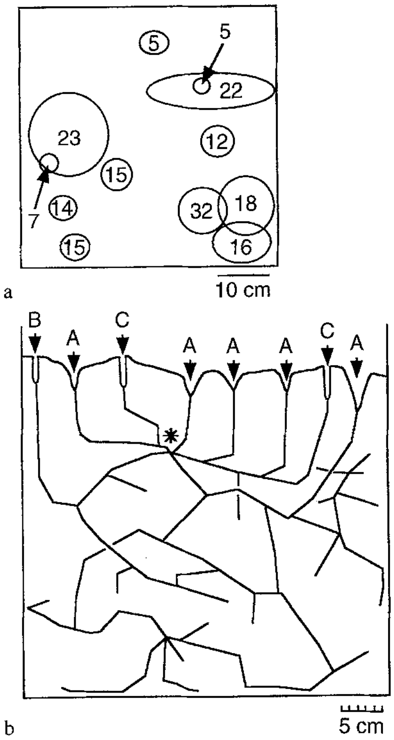


Fig. 1 *Callianassa subterranea*. **a** Aerial view of position of *C. subterranea* burrows within a box core. Burrows consist of main dwelling galleries (outline indicated by lines, sediment depth by numbers in cm) concentrated in a horizontally flattened elipsoid. From this area tunnels extend to the surface mounds and funnels as well as to deeper sediment strata. **b** Burrow in a flat aquarium (50 × 45 × 5 cm) after 1 yr. All tunnel sections of the burrow are projected onto one plane. Turning chambers are omitted in this projection. (*A* funnel; *B* hole without funnel shaped opening; *C* mound formed by expelled sediment; * intersection to neighbouring funnels)

Our observations in the laboratory showed that *Callianassa subterranea* continuously expands its burrow. When left in an initially undisturbed sediment core for 2 to 3 mo, three individuals constructed new burrows of 150 to 250 cm length. Two individuals left in flat aquaria for more than a year constructed burrows of 320 and 400 cm length (Fig. 1b). During intense mining activity, the invertebrates expelled up to five fountains of sediment from a single mound within 2 h. The individuals could be observed redistributing sediment within the burrow system by padding it to the walls some distance from the origin of the material. Nevertheless, burrows excavated from box cores always had the character of complete structures. There were roughly 20 chambers of 1.2 cm diameter per meter burrow length in the aquaria, increasing the surface of a burrow constructed by a medium size adult (4 cm length, 6 mm tunnel diameter) by 30%. The burrow surface area constructed by adult individuals therefore measures $1.6 \pm 0.6\ \mathrm{m^2\,m^{-2}}$. Burrow surface area and volume calculations are compiled in Table 1.

We could not detect any reinforcement to the burrow wall of *Callianassa subterranea* and scanning electron microscopy did not reveal any organic coating on the sediment grains.

Table 1 *Callianassa subterranea* and *Lanice conchilega*. Surface area and volume of the burrows of *C. subterranea* and *L. conchilega* below 1 m^2 of sediment surface. Calculations are based on burrow length and volume as well as species abundance (data on abundance of *L. conchilega* from Kitlar 1991)

	Calianassa subterranea	SD	*Lanice conchilega*	SD
Abundance (ind m^{-2})	21	± 8	300	± 122
Burrow length (cm)	300	–	16	± 3
Average diameter of burrow (mm)	8[a]	–	2.5	–
Burrow surface area of population ($m^2\,m^{-2}$)	1.6	± 0.6	0.37	± 0.07
Burrow volume of population ($dm^3\,m^{-2}$)	3.15	± 1.2	0.24	± 0.04

[a] The number used for average diameter is larger than 6 mm, which is normal for an adult *C. subterranea* cylindrical tunnel section within a burrow. The larger diameter accounts for 30% more burrow surface area due to turning chambers within the burrow system

Tube surface (*Lanice conchilega*)

Lanice conchilega glues sediment grains together to form a tube extending vertically into the sediment (Buhr and Winter 1977), and 1 or 2 cm into the water. We found mostly U-shaped tubes of *L. conchilega* at our station. In one sediment core thoroughly investigated (abundance: 380 ind m^{-2}), 10 of 12 tubes had this shape. These tubes were between 12 and 20 cm long (16 ± 3, $n = 10$) and reached 5 to 10 cm into the sediment (7.6 ± 1.6, $n = 10$). The tubes examined in detail had an average inner diameter of 2.5 mm (± 0.3, $n = 8$). Using the information on abundance by Kitlar (1991), the 300 ind found would create a tube surface of 0.37 ± 0.07 $m^2\,m^{-2}$.

Flow and oxygen transport

Laboratory observations revealed that before pumping, *Callianassa subterranea* positioned itself about 9 cm below the sediment surface of a funnel. The "breathing current", a type of pumping defined by the flow sensor output depicted in Fig. 2, was generated by a sequence of 21 to 23 triplet pleopod beatings resulting in peaks in the flow signal (21 peaks in Fig. 2). The pleopod movement, and coinciding flow signal signature, were confirmed by observation of an individual shrimp in its burrow within a flat aquarium. *C. subterranea* is thought to generate this pumping sequence to supply its gills with oxygen.

In a protocol covering 68 h a highly regular sequence of such breathing current signatures and pauses was recorded. There were 40-min periods (SD = 11, $n = 34$) without flow when the individal was observed processing sediment in the lower parts of its burrow. These periods alternated with breathing current signatures lasting 150 s (± 29, $n = 34$). Up to 52 consecutive breathing current signatures were generated beneath the same opening. This regular sequence of breathing current signatures and pauses is referred to as "regular irrigation". It is part of the intermittent pumping by *Callianassa subterranea* (compare Table 2 and Fig. 8).

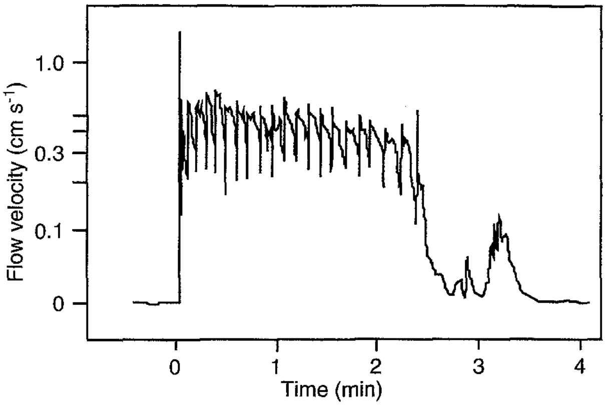


Fig. 2 *Callianassa subterranea*. Flow sensor signature of a breathing current generated by *C. subterranea* under a funnel opening (compare Fig. 1b, A). 21 discrete sequences of pleopod movement (range: 16 to 22, $n = 34$) result in a water flow of 4.5 cm^3 into the burrow lumen. Breathing current signatures like the one shown last 2.5 min and occur regularly every 40 min over many days during regular intermittent irrigation

The mean velocity of the generated inflow was 0.31 cm s^{-1} (SD = 0.11; $n = 72$). This amounted to 4.5 cm^3 water pumped in every breathing current event or 3% (21 ind m^{-2} × 4.5 cm^3 / 3150 $cm^3\,m^{-2}$) of burrow volume present below 1 m^2. Thus, little flushing of the burrow with oxygenated water actually occurs during these events.

In contrast to the regular irrigation, we also observed periods of intense arhythmic currents and relatively few breathing current signatures in another 114-h protocol (Table 2). This second distinctly different sensor output pattern, "irregular irrigation", made up 18% of the total time of protocol (Table 2). The individual rushed back and forth between different areas of the upper burrow, as observed in the aquaria and evident from the flow signals measured at different burrow openings. Current signals similar to those of the breathing current signatures occurred but lasted less than one minute. Maximum velocity of flow was 2 cm s^{-1}. Two flow events of 60 cm^3 water, or an equivalent of 40% burrow volume, were registered during the 114 h. The

Table 2 *Callianassa subterranea.* Characteristics of two flow patterns recorded during intermittent irrigation above the openings of a burrow of *C. subterranea* (114 h continuous measurement). For both patterns the number of sensor output signatures characteristic for "breathing currents" and other, non-defined flow events, are shown. A highly regular pumping pattern occurs during "regular intermittent irrigation". It contrasts with highly irregular and more frequent flow signals during "irregular irrigation". The volume of water pumped has been corrected for the percentage time that the corresponding pumping takes place

Pattern	Number of breathing currents	Number of other signals	Breathing currents h^{-1}	Other signals h^{-1}	Percentage total time (114 h)	Volume of water pumped ($dm^3 m^{-2} d^{-1}$)
Regular	121	3	1.3	0	82	2.8
Irregular	13	141	0.6	6.9	18	2.5

individual frequently changed its location during this irregular irrigation.

On several occasions, oxygen was measured at a depth of 16 mm in the burrow walls while water flow was monitored continuously using two flow sensors and one O_2-sensor at all three openings of a burrow of *Callianassa subterranea.* There was an abrupt increase of O_2-concentration in the wall 16 mm below the sediment surface when *C. subterranea* pumped overlying water into its burrow (Fig. 3). While the breathing current signature was recorded, oxygen concentrations remained high or increased slightly. When the water flow ceased, oxygen concentration started to decrease immediately at a rate of 0.42 nmol $O_2 cm^{-3} s^{-1}$ (SD = 0.02; $n = 6$). Similar measurements were done with the O_2-sensor positioned at a depth of 170 mm. During regular irrigation there was no detectable O_2 in the burrow or the wall. Oxygen was, however, present in the burrow water during irregular irrigation, increasing to 64 $\mu mol\, dm^{-3}$ (22% air saturation) at 170 mm sediment depth. O_2 was found to drop to 0 $\mu mol\, dm^{-3}$ within 0.25 mm of the inner sediment–water interface when measured during irregular irrigation. We could not measure the oxygen gradient during this transient event. A calculation of the gradient based on the above values shows that it might have been 2.56 $\mu mol\, cm^{-3} cm^{-1}$ or steeper.

Callianassa subterranea was observed to frequently move between a mound and the connecting tunnels by crossing an intersection leading to neighbouring funnels (indicated by asterisk in Fig. 1b). Oxygen was below detection limits in the funnel while the shrimp moved across the connecting intersection, indicating that oxygenated water was not drawn into the burrow system as a result of the shrimp's movement. There was also no oxygen detectable in one funnel when the individual was generating a breathing current below the other funnel, indicating an absence of significant mixing of oxygenated water at burrow intersections. The same result was obtained for a dead end tunnel nearby. It was therefore concluded that advection of oxygenated water into the burrow as a consequence of the shrimp's movement occurs only along the path it is taking. Oxygen intrusion into adjacent tunnels is neglectable.

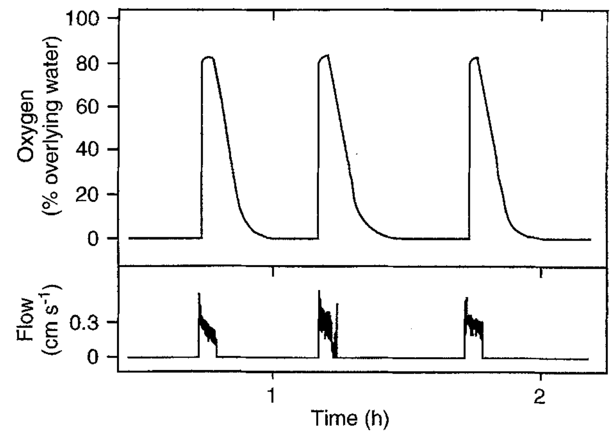


Fig. 3 *Callianassa subterranea.* Changes in O_2-concentration registered with simultaneous measurements of flow above the "inhalent" funnel opening and oxygen sensor 1 mm from burrow wall within sediment. Breathing current signatures (Fig. 2) in the lower part of figure indicate flow of oxygenated water into burrow. O_2-concentration increases indicate pulses of oxygen within sediment

Water flow by pumping *Lanice conchilega,* monitored by a flow sensor placed at the anterior tube opening, was correlated with simultaneous decreases in oxygen concentration from air saturation to 20% of air saturation (Fig. 4). The average recorded velocity of the water flowing out of the tube was 0.028 $cm\, s^{-1}$ resulting in a volume transport of 0.12 cm^3 (equivalent to 2.4 cm tube length). Flow events lasting 92 s (SD = 48; $n = 35$) and occurring every 4 min, could move a water volume of 1.7 $cm^3 h^{-1}$, twice the volume of an average individual's tube. No decrease in O_2-concentration was ever monitored at the posterior end of the tube. O_2-measurements were not obtained normal to the tube of *L. conchilega* since its structure of embedded sand grains would have caused microelectrode tips to break on first contact. Oxygen penetration depth in the ambient sediment was 2 mm, whereas oxygen profiles closer to the tube showed the oxic layer extending into the sediment (Fig. 5). Further measurements demonstrated the occurrence of oxygen within 0.5 mm distance from the tube wall. O_2-concentrations reached 20% of air saturation all the way to the very tip of the U-shaped tube at 55 mm sediment depth.

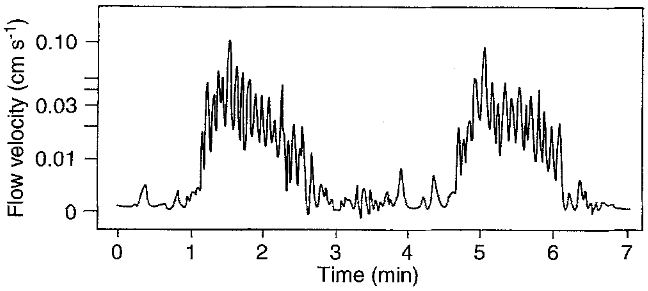


Fig. 4 *Lanice conchilega.* Flow signal recorded above opening (anterior end) of a U-shaped tube built by *L. conchilega.* Two elevated flow sensor signatures indicate a volume flow of water of 0.12 cm^3 each

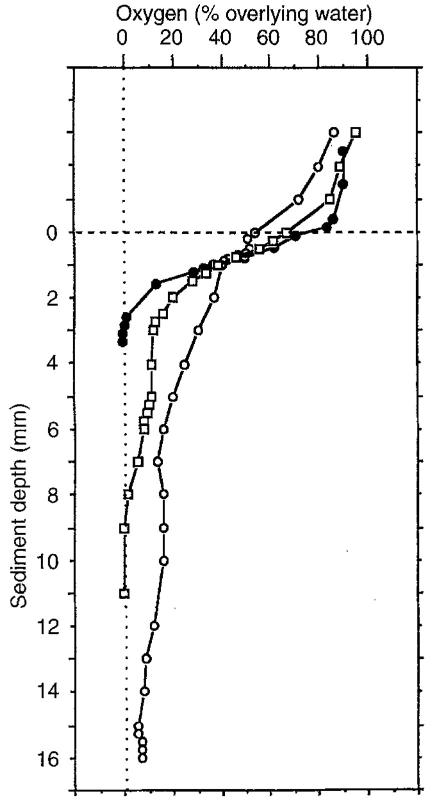


Fig. 5 *Lanice conchilega.* O_2-concentrations in sediment near a tube of *L. conchilega.* Two profiles (open symbols) within 0.5 to 1 mm of tube wall, and one profile away from tubes in the uninhabited sediment surface (filled symbols) are shown

O_2-concentration always varied with time. An extreme example is given in Fig. 6. Here, individual pulses of oxygen merge due to their high frequency of occurrence. Periods with no O_2 present were usually as long as periods with O_2-concentration above zero.

The measurements reported above are supported by the observation that *Lanice conchilega* periodically withdraws from the surface into its tube for a few seconds. On the basis of these observations we suggest that *L. conchilega* acts like a piston when moving in its tube, exchanging burrow water with the overlying water, and we propose the term "piston-pumping" for this mechanism of irrigation.

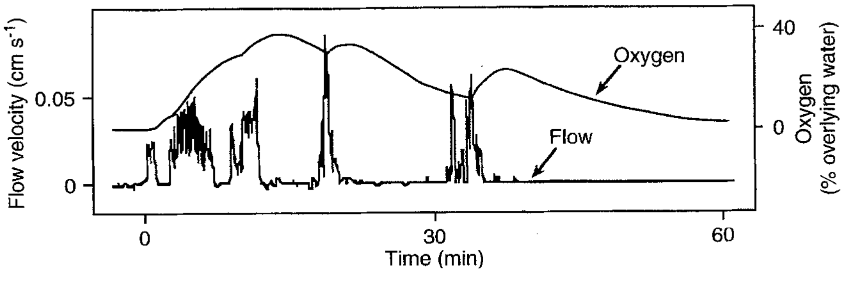
Sediment surface effects of burrow openings (*Callianassa subterranea*)

Oxygen microprofiles measured along a transect of a mound built by *Callianassa subterranea* in the laboratory are depicted in Fig. 7. Gradients and fluxes calculated from these profiles are also listed. Generally, there is more than a four-fold increase in gradient from the plain sediment surface to the tip of the mound. Gradients measured in fresh cores on board the research vessel were generally steeper than the ones from sediments that were kept in the laboratory for several months. Flux calculated from profiles measured in cores on board the R.V. "Poseidon" 3 h after retrieval were 275 mmol $m^{-2} h^{-1}$ ($n = 6$; 9 °C; $D_s = 0.75 \times 10^{-5}$ cm s^{-1}).

O_2-flux estimates

The oxygen measurements and observations reported above can be used for an O_2-flux estimate. Measurements were obtained at four different localities of the sediment: (1) the sediment surface proper, which is devoid of biological structures; (2) sediment surface on

Fig. 6 *Lanice conchilega.* Changes of O_2-concentration occurring at a depth of 5 mm sediment adjacent to a tube of *L. conchilega.* Flow signals were measured above posterior end of the individual and indicate water movement within the tube ("piston-pumping"). Increases in O_2-concentration can be seen which coincide with onset of each flow signal



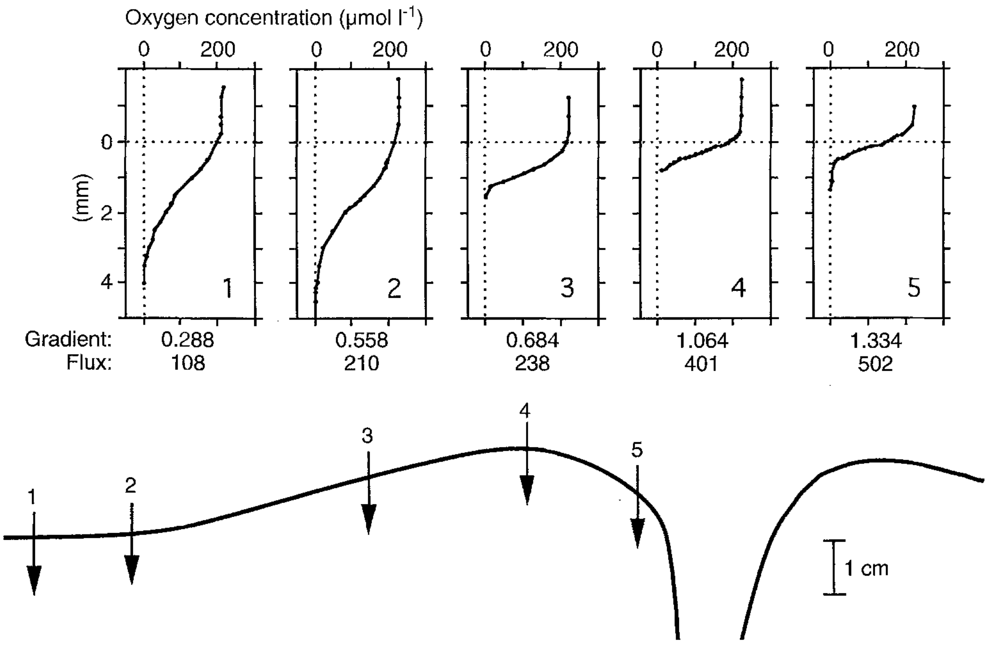


Fig. 7 *Callianassa subterranea.* O_2-profiles measured on a transect across a mound of *C. subterranea* 20 h after reduced sediment was expelled. Concentration gradients (µmol cm^{-3} cm^{-1}) and corresponding fluxes (µmol m^{-2} h^{-1}) are given below the profiles (10 °C, $\phi = 0.8$, $D_s = 1.0 \times 10^{-5}$ cm s^{-1}, where ϕ = porosity and D_s = sediment diffusion coefficient) Positions 1 to 5 on the transect refer to O_2-profiles 1–5, respectively

mounds of *Callianassa subterranea*; (3) burrow walls of *C. subterranea*; and (4) tube walls of *Lanice conchilega*. The flux of oxygen into the sediment is estimated for each of these four localities. All numbers refer to 10 °C, 1 m^2 sediment surface, and the population size below it. Assumptions made are listed along with the results of these calculations.

(1) Profiles measured in May 1989 on board after retrieval of cores (Fig. 5) result in a molecular diffusive flux of 275 µmol O_2 m^{-2} h^{-1} across the interface. In the discussion below a 30% increased O_2-flux (360 µmol O_2 m^{-2} h^{-1} or 8.64 mmol m^{-2} d^{-1}) is considered the O_2-flux at the sediment surface proper and will be used for comparison with macrofaunal effects. This is to account for topographical effects (Jørgensen and Des Marais 1990) and meiofaunal mixing of the sediment (Aller and Aller 1992) which increase solute exchange at the sediment–water interface (Kitlar 1991).

(2) Reduced sediment expelled from the mounds will be oxidized resulting in a O_2-flux greater than at the ordinary surface (Fig. 7). On average, each adult individual produces two mounds (Witbaard and Duineveld 1989) measuring 4 to 6 cm in diameter (our measurements). Calculating a minimum of 12 cm^2 per mound there are 500 cm^2 m^{-2} with O_2-flux inceased four-fold (compare Fig. 7) to 1440 µmol m^{-2} h^{-1}. 5% of the total sediment surface thus contribute 21% [(1440 × 0.05 × 100)/(1440 × 0.05 + 275 × 0.95)] of the total O_2-flux or 1.73 mmol m^{-2} d^{-1}.

(3) O_2-flux across the burrow walls is estimated separately for the two pumping rhythms observed (regular and irregular intermittent irrigation). During breathing current signatures characterizing regular irrigation, a finite volume of oxygenated water (6 cm^3 h^{-1}) is advected into the burrow. At an O_2-concentration of 292 µ*M* this equals 1.75 µmol O_2 h^{-1}. Oxygen diffuses through the burrow walls or is used for metabolism by *Callianassa subterranea.* The amount of oxygen used for the individual's metabolism is not subtracted in this calculation since its contribution seems minor (see "Discussion").

During the irregular irrigation, O_2-concentration rose from 0 to 22% saturation within the continuous burrow parts (0.8 m^2). Steady-state flux is assumed along a gradient with the slope of 1.12 µmol cm^{-3} cm^{-1} measured in the burrow wall of an artificial burrow experiment (Forster and Graf 1992). This gradient is as steep as those found at the sediment surface.

Multiplication by a time factor that takes into account the lengths of the associated irrigation rhythm yields 1.026 and 1.035 mmol m^{-2} d^{-1} for regular and irregular irrigation, respectively. Thus the two irrigation modes take equal shares in the total sum of 2.06 mmol O_2 m^{-2} d^{-1}.

(4) *Lanice conchilega* pumps water every 4 min. Assuming [in analogy to *Callianassa subterranea*, compare with (3)] that all the oxygen advected with the water (0.12 cm^3; 0.035 µmol O_2) is used by the tube wall sediment, a flux of 3.53 mmol O_2 m^{-2} d^{-1} is calculated. Since a "pulsating" oxic zone exists around the tubes (Fig. 6) all the oxygen has to be consumed in the oxic halo within 4 min. With about 1 cm^3 oxic halo volume a minimum volume-specific uptake rate of 0.15 nmol O_2 cm^{-3} s^{-1} is calculated.

The sum of O_2-consumption estimates for the four different localities above results in 15.95 mmol O_2 m^{-2} d^{-1} (Table 3). The sediment surface consumes

Table 3 *Callianassa subterranea* and *Lanice conchilega*. Oxygen flux at four locations of the sediment community: sediment–water interface, *C. subterranea* burrow wall, *C. subterranea* mound, *L. conchilega* tube wall. Absolute numbers and percentage of total sum are given

Interface	Flux (mmol $m^{-2} d^{-1}$)	Percentage
Sediment surface (1.3 times diff. flux)	8.64	54
Mounds of *C. subterranea*	1.73	11
Burrow walls of *C. subterranea*	2.06	13
Tube walls of *L. conchilega*	3.53	22
Totals	15.96	100

8.6 mmol $m^{-2} d^{-1}$, whereas 7.3 mmol $m^{-2} d^{-1}$ are accounted for by the biogenic structures and macrofaunal activities of only two species which were investigated.

Discussion

Total oxygen uptake of sediments is of interest as a measure of one key parameter in early diagenesis and community metabolism. It may be measured by following O_2-concentration change in an in situ inclosure of the sediment surface area in question (Rutgers van der Loeff et al. 1984; Balzer et al. 1987; Glud et al. 1994). Laboratory measurements of TOU are cheaper and usually performed on much smaller samples (Pamatmat 1971).

Even though measurements of TOU are adventageous for their holistic approach, problems in obtaining the measurements are numerous. Sediment cores may be too small to include sizable burrows; in situ deployments are difficult in high-tidal-current shallow seas and will have to ensure that all the openings of one burrow are located below one chamber. The high TOU values measured in situ at Oyster Ground (deWilde et al. 1986) are in doubt since Cramer (1989) described the artefacts in measurement with metal chambers. In other studies tidal currents effectively washed away bell-jar experiments (Hickel et al. 1989; Bauerfeind personal comunication) in the southern North Sea. The approach adopted here was not to measure directly, but to calculate TOU from measured pumping rates and frequencies of two invertebrate species plus the diffusive O_2-flux into the sediment. At present no TOU measurements have been published for the North Sea without serious methodological drawbacks for comparison with the sum of O_2-flux estimates presented here. Although our approach for estimating total O_2-flux seems appropriate, it includes several sources of error. The sensitivity of the calculation to different inherent and explicit assumptions will be considered below.

In the calculation of burrow wall flux respiration by *Callianassa subterranea* has not been separated from O_2-consumption by heterotrophic processes in the burrow walls. Macrofaunal respiration reduces the amount of oxygen diffusing through the burrow walls as a result of breathing currents. This diminution cannot be large, however. Respiration rates reported by Witbaard and Duineveld (1989) are on the order of 1 µmol $O_2 h^{-1} ind^{-1}$. Corrected for the invertebrate's residence time in oxygenated areas of the burrow (2.5 of 45 min), this respiration rate would result in a consumption of 0.05 µmol h^{-1} or 3% of oxygen advected into the burrow lumen.

The calculated flux for the irregular irrigation period would be larger if the gradient in the burrow wall were steeper than the sediment surface value adopted here (1.2 µmol $cm^{-3} cm^{-1}$). For a deep-sea sediment, Glud et al. (1994) gave an example of oxygen gradients around a burrow implying a flux at least six times higher than at the sediment surface. Deep-sea sediments with low carbon content may show relatively steep O_2-gradients at burrow walls. In the laboratory we measured a slope of 2.56 µmol $cm^{-3} cm^{-1}$ in deeper parts of the tunnel system with the burrow water at 22% oxygen saturation. Using this value instead of 1.2 µmol $cm^{-3} cm^{-1}$ would more than double the flux at the burrow wall interface and increase its share in the sum of O_2-consumption from 14 to 21%.

An important factor in the calculation is the wall surface in *Callianassa subterranea* burrows. The average burrow surface found in experiments by Witbaard and Duineveld (1989) was $< 100 \, cm^2 ind^{-1}$ (maximum: 680 cm^2). The value adopted in the present paper (760 cm^2) was obtained after allowing for a substantially longer time to excavate sediment. Burrow wall surfaces up to 1000 cm^2 in 400 cm long burrow systems were thus found. A flux estimate based on the previously published burrow sizes is therefore considered too low.

Measurements of O_2-gradients along a transect over a mound were done in an aquarium containing several month old sediment. The assumption that the difference in gradients between the mound and plain surfaces found in this sediment (four times higher in the mound) is the same as the difference in fresh sediments needs to be tested. The effect of mounds on sediment surface oxygen profiles may or may not be less pronounced in the field. In natural habitats, however, some of the sediment material expelled will be carried in suspension for an unknown distance (Roberts et al. 1981), leading to oxygen consumption in places other than the sediment surface or the mounds. This also renders a less pronounced topography to the mounds. Underwater video observations at the station in 1989 did show flatter mounds than the rather steep ones produced in the laboratory. The impact of up to 200 juveniles m^{-2} pumping and expelling sediment has not been assessed here.

The estimated O_2-flux across the tubes constructed by *Lanice conchilega* depends heavily on the rate of oxygen utilization within the adjacent sediment. If oxygen utilization rates exceed 0.15 nmol $O_2\,cm^{-3}\,s^{-1}$ (the rate needed to make the O_2-concentration in the tube decline to zero between two irrigation events) all the oxygen advected (3.53 $mmol\,m^{-2}\,d^{-1}$) could be utilized in the sediment, and the pulses of O_2 and periods of anoxia in between could be explained (Forster 1991). The rate of oxygen decline in a *Callianassa* burrow was 0.42 nmol $O_2\,cm^{-3}\,s^{-1}$. Prip-Olsen (personal communication) measured rates of 0.88 nmol $O_2\,cm^{-3}\,s^{-1}$ in burrows of *Nereis diversicolor*. The pulse character of O_2-flux and uptake of all advected oxygen by the sediment are not contradictory.

We conclude that the value of 15.96 mmol $O_2\,m^{-2}\,d^{-1}$ is a conservative estimate of the total oxygen uptake even if we neglect the fact that only two of many invertebrate species were considered.

Our estimate of 15.96 mmol $O_2\,m^{-2}\,d^{-1}$ used is higher than those reported from similar sediments in the North Sea. Hickel et al. (1989) measured a range of 7.5 to 13.4 mmol $O_2\,m^{-2}\,d^{-1}$ in laboratory incubations of fine sandy sediments from the southern German Bight. DeWilde et al. (1984) found an uptake of 8.7 mmol $O_2\,m^{-2}\,d^{-1}$ at Oyster Ground, a sediment also inhabited by *Callianassa subterranea*.

In the flux calculation for the sediment surface (8.7 mmol $O_2\,m^{-2}\,d^{-1}$) we accounted for increased flux due to surface microtopography and mixing by meiofauna on the order of 30%. This is supported by findings from experiments using bromide ions as tracers for solute exchange performed in parallel investigations at the same station by Kitlar (1991). She showed that movement of the overlying water by light air bubbling increased exchange rates 30% above diffusive transport levels at the sediment surface which was devoid of biological structures. Our value for oxygen uptake of the sediment surface agrees with the data given by Hickel et al. (1989) and deWilde et al. (1984) at the same temperature. From this comparison it seems that the authors did not measure oxygen uptake of the sediment due to invertebrate pumping activity.

At Oyster Ground, 17% of the TOU, equivalent to 1.5 mmol $O_2\,m^{-2}\,d^{-1}$, was attributed to the *Callianassa subterranea* population (deWilde et al. 1984; Witbaard and Duineveld 1989). This flux was attributed to burrows and macrofauna in a *C. subterranea* population of 52 $ind\,m^{-2}$, more than twice the population density reported in the present paper. The difference in TOU increase is likely due to an underestimate of oxygen uptake by burrows associated with the short-lived and therefore incomplete burrows that were investigated by Witbaard and Duineveld (1989).

Of the data reported by Hickel et al. (1989), 15.95 mmol $O_2\,m^{-2}\,d^{-1}$ is a maximum value. Still, several species that could increase TOU by respiring and advecting O_2 are excluded from our O_2-flux estimate. High biomass values have been reported previously from our station even though *Callianassa subterranea* had not been included in these reports (Gerlach et al. 1985; Salzwedel et al. 1985; Duineveld et al. 1991). Frequent and extreme variations in abundance of individual species that do occur throughout the southern North Sea (Salzwedel et al. 1985) may change the magnitude of the flux of oxygenated water into the sediment. Macrofaunal abundances reported by Kitlar (1991) include *Chaetopterus variopedatus* (10 $ind\,m^{-2}$), *Owenia fusiformis* (maximum 5750 $ind\,m^{-2}$), numerous bivalves and polychaetes and sediment-foraging species like *Echinocardium cordatum* (25 $ind\,m^{-2}$) in addition to *Lanice conchilega* and *Callianassa subterranea*. Therefore, burrow wall surface in situ could easily exceed 2.5 $m^2\,m^{-2}$ · We could expect a total uptake of ≥ 20 mmol $O_2\,m^{-2}\,d^{-1}$, if all other species were included.

Irrigation by *Lanice conchilega* and *Callianassa subterranea* almost doubled the TOU estimate (185%) compared to the calculated O_2-flux at the sediment surface. It increased total oxygen uptake to 240% of the calculated diffusive O_2-flux at the sediment surface (6.6 mmol $O_2\,m^{-2}\,d^{-1}$).

Biological aspects of flux estimate

Using a box corer at the location investigated we sampled a species, *Callianassa subterranea*, previously reported as rare (Salzwedel et al. 1985) and not included in recent ICES (International Council on Exploraion of the Sea) studies (Duineveld et al. 1991). *C. subterranea* had been found earlier in high numbers by Lutze (1938). Witbaard and Duineveldt (1989) and Adema et al. (1982) report its distribution in sandy sediments containing a minimum of 10% silt throughout the southern North Sea. It was obvious from observation of burrows penetrating the box core's bottom (45 cm depth) that our data do not include all individuals present. In situ rasin casts by Atkinson and Nash (1990) on the Scotish West Coast show a maximum depth of 81 cm for burrows constructed by this species. This is not the first case in which gear used in investigations of benthic fauna proved inadequate for sampling large invertebrate species which are the predominant bioturbators. A similar problem was reported in the Santa Catalina Basin (Smith et al. 1986; Wheatcroft et al. 1990).

Data presented in the present paper indicate that a period of approximately one year is needed for a complete burrow to be established under laboratory conditions. Witbaard and Duineveld (1989) estimated a burrow surface area of 150 $cm^2\,ind^{-1}$ (10 mm thoracal length) from 3-m-old burrows. They left one individual of the same size for 7 mo, and it created 680 cm^2 burrow surface. Burrows of 4.2 m length, as produced in our aquaria over a period of one year, may not endure in situ due to bed load sediment clogging parts of the burrow system. However, comparing burrows freshly retrived in box corers, we believe that 3 m burrow length (750 cm^2) is close to average under in situ conditions.

Lanice conchilega constructs vertical tubes in intertidal areas with abundances of up to 10 000 ind m^{-2} (Buhr 1976; Buhr and Winter 1977). The biofacies of subtidal sediments in the German Bight (Seilacher 1951) show that tubes in the shape of a "U" and "double-U" are the dominant relict form in *L. conchilega*-tubes. Abundance of *L. conchilega* varies from 0 and 900 ind m^{-2} between years and throughout the southern German Bight (Hickel et al. 1989).

O_2-flux at a burrow wall occurs if a gradient exists across the wall surface. A burrow wall is not effective for O_2-exchange where the burrow water remains anoxic. The case of *Callianassa subterranea* illustrates that oxygenated water is not in contact with the burrow walls everywhere. *C. subterranea* is effectively adapted to hypoxic conditions (Pritchard and Eddy 1979; Powilleit 1991) and does not pump much water during each breathing current signature. Since the oxygenated water volume (6 ml) is much less than the burrow volume and the burrow is branched, some areas of the burrow walls will not contact oxygen during any part of the irrigation pattern. As a consequence, burrow wall surface area is only partially available for O_2-flux in intermittent irrigation. More intense irregular irrigation periods exist which take 18% of the time budget and supply oxic water to a sediment depth of 17 cm. But at least 50% of the wall in *C. subterranea* burrows stays permanently anoxic. A relatively larger portion of the total burrow wall surface is available for O_2-flux in *Lanice conchilega.* Oxygen was found at all depths in the adjacent sediment along the tube.

Those parts of the burrow walls which do come into contact with oxygen during irrigation do so only periodically. The two types of irrigation represented here differ considerably in this respect. In Fig. 8 the time of active pumping and pauses in between are shown for a 2 h interval. In the regular intermittent pumping rhythm generated by *Callianassa subterranea* long pauses occur. The walls that have become oxic during irrigation turn anoxic within approximately 18 min (Fig. 3). Piston-pumping by *Lanice conchilega* produces a faster sequence of irrigation and pauses. Therefore tube walls of this species are more frequently available for O_2-flux into the sediment (Fig. 6).

Most sediment-reworking thalassinid decapods irrigate their burrows (Dworschak 1981; Gust and Harrison 1981). Filter-feeding decapod shrimps in Y-shaped burrows may effectively oxygenate the total burrow surface 24 h d^{-1} (Griffis and Suchanek 1991), even though this pumping activity may also be interupted by resting periods. The volume of water pumped by the two species investigated here is much smaller in comparison. For instance Riisgård (1991) calculated a volume of 8.4 $m^3 m^{-2} d^{-1}$ for filter-feeding *Nereis diversicolor*. In such a case the upper limit of potential O_2-flux is reached, because a constant maximum O_2-flux at the wall interface is retained at all times. If, however, individual species in a macrofauna community pump oxic water at rates below this upper limit, then in each event a combination of burrow geometry, irrigation pattern, and water volume pumped result in the actual O_2-flux.

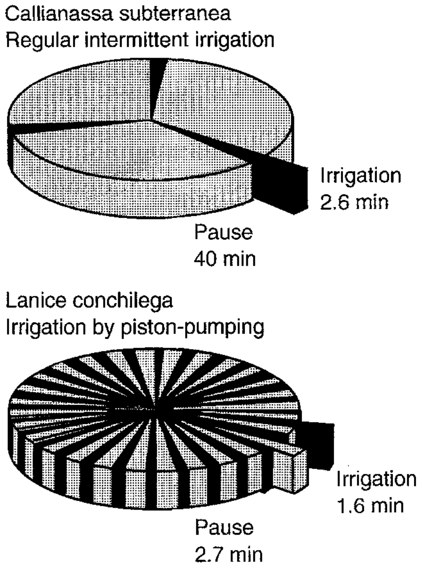


Fig. 8 *Callianassa subterranea* and *Lanice conchilega*. Comparison of irrigation rhythms in a 2-h period. In the "piston-pumping" polychaete *L. conchilega* irrigation lasts 1.5 min (on average) with 2.5-min pauses between irrigation pulses. The intermittently pumping *C. subterranea* irrigates for 2.5 min on average followed by 40-min periods without pumping

Comparison of the species investigated reveals that even though the oxygenated burrow walls of *Callianassa subterranea* are twice as large (0.8 m^2/0.37 m^2) as the tube walls of *Lanice conchilega*, the latter are more effective in stimulating O_2-flux (Table 3). This is due to a relatively larger burrow wall area exposed to oxygen in *L. conchilega* and more frequent influx of oxic water into the tubes during piston-pumping. This points to the potential importance of a mechanism like piston-pumping in solute exchange.

We present here evidence for an irrigation mechanism which we term "piston-pumping" in *Lanice conchilega*, an organism for which irrigation activity has not been previously reported. This term is related to the definition given by Lee and Swartz (1980), in which they state that the body diameter of individuals inhabiting tubes tends to be close to the inner diameter of their tube, whereas in a burrow the inhabitant is considerably thinner than the diameter of the burrow. With the close fit of body to the tube diameter the individual acts as a "piston-pump", drawing water into the tube and pushing it out the other end whenever it moves within the tube. *L. conchilega* is a suspension/deposit feeding invertebrate with gills located at its anterior end. This polychaete's modes of food supply and respiration do not support the idea of "deliberate" pumping of water through the U-shaped tube. Mixing of oxic surface water with burrow water results in changing O_2-concentrations along the entire tube wall, as shown in Fig. 6. These observations support the idea of irrigation by piston-pumping.

Piston-pumping may be a mechanism by which many polychaete species advect oxygenated water into sediments. The smaller the volume within the tube relative to the corresponding wall interface, the faster the O_2-concentration in the tube should approach zero. Since surface to volume ratio for a given length of tube increases inversely with radius, O_2 advected by piston-pumping at high frequency will be more effectively transported into the ambient sediment in small tube diameters than in large ones. If widespread, this phenomenon would contribute considerably to irrigation by small tube-building polychaetes occurring in high abundances.

Acknowledgements This work was supported by grant 03F0548 of the German Federal Ministry of Research and Technology, BMFT. We acknowledge the help of W. Queisser, M. Teucher, J. Kitlar and W. Ziebis who were all involved in discussions that lead to new technical details or implimentations of ideas. We thank B. Bebout who, with his comments, considerably helped to improve the manuscript.

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