Impact of biogenic sediment topography on oxygen fluxes in permeable seabeds

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ABSTRACT. Boundary layer flows, interacting with roughness elements at the sediment surface, alter the small-scale flow regime. Consequently, pressure differences are generated that are the driving forces for advective pore-water flow. We investigated topography-induced transport of oxygen in a permeable coastal sediment from the Mediterranean Sea (Isola del Giglio, Italy). The sediment surface was characterized by a high abundance (120 m^-2) of sediment mounds (average height: 4 cm) built by the mud shrimp Callianassa truncata (Decapoda, Thalassinidea). Boundary layer flow velocities recorded in situ ranged between 2 and 16 cm s^-1. Detailed experiments were performed in a recirculating laboratory flow channel. A natural sediment core, 20 cm deep with a surface area of 0.3 m^2, was exposed to a unidirectional flow of varying current velocity (3, 6, 10 cm s^-1). The alteration of the small-scale flow regime at a sediment mound was documented by vertical velocity profiles measured in 1 mm resolution with temperature-compensated thermistor probes. Oxygen distribution in the sediment was investigated with Clark-type microelectrodes. At a smooth surface, oxygen penetration depth in the permeable sediment did not exceed 4 mm, independent of flow velocity. In contrast, the topography-induced advective oxygen transport increased significantly with current speed. Oxygen reached down to almost 40 mm at the upstream foot of a 1 cm high sediment mound at a flow velocity of 10 cm s^-1. Thus, the oxic sediment volume increased locally by a factor of 4.8 compared to the oxic zone underneath a smooth surface. At a natural abundance of 120 mounds m^-2 the oxic sediment volume per m^2 seabed was calculated to be 3.3-fold higher than in a seabed with a smooth surface. In a parallel experiment, advective solute transport was also demonstrated in a less permeable sediment (k = 5 x 10^-12 m^2) from the North Sea intertidal flat. Due to the lower permeability the effect on O_2 transport was less than in the Mediterranean sand, but oxygen penetration depth increased locally 2-fold at a sediment mound under a flow velocity of 10 cm s^-1. The experiments showed the high spatial and temporal variability of oxygen distribution in a coastal seabed depending on sediment surface topography, boundary layer flow velocities and sediment permeability.

KEY WORDS: Oxygen - Advective transport - Boundary layer flow - Permeable sediment - Callianassa truncata - Sediment-water exchange

INTRODUCTION

Among the chemical species being transferred between the water column and the sediment, oxygen plays a key role in biological and geochemical processes. The supply of oxygen to the seabed is essential for aerobic life within the sediment. Among the electron acceptors in marine sediments, oxygen is energetically the most valuable for the mineralisation of organic compounds and the chemical or bacterial oxidation of reduced products from anaerobic mineralisation. It also affects the availability of respiratory electron acceptors within the sediment column used in anaerobic microbial processes. Nitrate and sulphate for example are regenerated from ammonia and sulphide through oxidation by O_2. The extent of the oxic (containing oxygen) and oxidised zone (having positive redox potential) regulates the distribution of bacterial and protozoan communities (Fenchel 1969, Blackburn 1987, Giere 1993, Berninger & Epstein 1995, Fenchel & Finlay 1995). In turn, the zonation of microbial activity has a strong influence on organic matter degradation, mineral cycling and nutrient...

In situ investigations revealed that in coastal environments oxygen penetrates by diffusion from the overlying water usually not deeper than 2 to 5 mm into the sediment (Revsbech et al. 1980, Andersen & Helder 1987). Burrowing macrofauna transport supernatant water to deeper sediment layers by irrigating their tubes and burrows. Dissolved substances, like oxygen, diffuse through the burrow walls (Aller 1983, Forster & Graf 1992) into the ambient sediment. The enlargement of the sediment-water interface can considerably increase the solute exchange between the seabed and the overlying water (Hylleberg & Henriksen 1980, Aller 1982, Kristensen 1985, Huettel 1990) depending on the density of organisms and their bioturbation and bioirrigation behaviour (Forster & Graf 1995).

In areas exposed to tidal waves and strong bottom currents, hydrodynamic forces can resuspend and thereby oxygenate surficial sediment or flush the interstices with oxygen-rich water (Riedl et al. 1972, Malan & McLachlan 1991).

Coastal environments are characterised by biogenic structures (mounds, pits, tracks and funnels) created by infaunal and epifaunal organisms and by geological features (ripples) in a variety of morphologies and sizes. These structures strongly affect the small-scale flow regime at the interface, as flow velocity is locally increased or decreased (Vogel 1983, Schlichting 1987, Yager et al. 1993). The velocity gradients generate pressure differences that constitute driving forces for an advective solute transport across the interface of permeable seabeds (Thibodeaux & Boyle 1987, Huettel & Gust 1992). Thus, the topography of the sea-floor can be of importance for the interfacial solute exchange in coastal sediments.

We investigated the role of advective oxygen transport at the sediment surface caused by the interaction of biogenic sediment topography with boundary layer flows. We investigated the distribution of oxygen with polarographic microelectrodes in a natural sediment core characterised by biogenic mounds created by the mud shrimp *Callianassa truncata* (Decapoda, Thalassinidea). Our results show that advective oxygenation effects can reach several centimetres sediment depth, depending on the surface topography, the flow velocity of bottom currents and the sediment permeability.

**MATERIALS AND METHODS**

**Study site and origin of sediments.** The sediment core for the laboratory flume experiments originated from the Bay of Campese at the west coast of Giglio Island in the Mediterranean Sea (Fig. 1). As part of the Tuscany Archipelago, the island is situated ca 150 km northwest of Rome (42° 20' N, 10° 52' E) off the west coast of Italy and has an area of 21 km² with 28 km coastline. The sediment surface in the shallow bay is characterised by conspicuous mounds created by the mud shrimp *Callianassa truncata* (Decapoda, Thalassinidea) (Fig. 2). Thalassinids are burrowing crustaceans that are common and often abundant in soft sediments of temperate and tropical coastal environments (Dworschak 1983, Griffis & Suchanek 1991). While constructing and maintaining its burrow, *C. truncata* ejects excavated sediment in a fountain-like manner through a burrow opening at the sediment surface, forming volcano-shaped mounds with an average height of 4 cm (maximum 9 cm). These biogenic features are abundant throughout the shallow part of the bay (2 to 25 m water depth) and cover the sediment surface in an average density of 120 ± 43 mounds m⁻² (n = 240) (Ziebis unpubl.). The mounds are rebuilt within 1 to 2 h if erased by wave action when storms occasionally occur. Prevailing regional currents passing the island in a south-north direction generate a clockwise gyre within the bay (Fig. 1). From May to August predominant wind directions are NW and W, with 70% of the recorded wind speeds being in the range of 1 to 3 on the Beaufort scale (ca 0.3 to 5.4 m s⁻¹). The bay is sheltered from southerly strong winds prevailing in late autumn, winter and early spring. Boundary flow velocities and directions were measured from May to August
using a mechanical current-meter (Mini Air-Water 2, Schiltknecht) connected to a tripod which was lowered onto the sediment surface at Stns A to C (Fig. 1) at 5, 7, and 12 m water depths. At each water depth the flow velocity was recorded 5 cm above the sediment surface for periods of 12 h and recorded by a 12 bit data-logger in intervals of 2 s. Flow velocities ranged between 2 and 16 cm s\(^{-1}\) with an average current speed of 8.4 cm s\(^{-1}\). The flow changed little in direction (max. 45°) and intensity during each deployment.

**Sediment characteristics.** Analyses of grain size composition within the upper sediment layer of 10 cm showed that the sediment throughout the shallow part of the bay (2 to 15 m water depth) was well sorted, 70 to 95% dry weight consisted of medium sand (200 to 630 μm). Sediment cores for the experimental set-up were recovered at Site A (Fig. 1) at 5 m depth using acrylic cylinders of 20 cm diameter pushed 30 cm into the sediment. At the same site, samples for the analyses of sediment parameters were taken. The median grain size (MD) was 350 μm, the average porosity (water content) was 0.4 ± 0.08 (n = 5) and organic content was 0.8% of dry weight (loss upon ignition at 540°C for 12 h). Permeability (k, numerical constant related to the pore space of a sediment) was determined with a constant head permeameter (Means & Parcher 1964) to be 5.1 × 10\(^{-12}\) m\(^2\).

Shrimps were collected separately because within their deep burrows they are hardly caught by conventional sampling methods.

To investigate the impact of sediment permeability on interfacial exchange processes we used less-permeable North Sea sediment originating from an intertidal flat (Sahlenburg, Germany) for a parallel experimental set-up. The sediment consisted of muddy sand, had a median grain size of 200 μm and an average porosity of 0.38 ± 0.02 (n = 5). The organic content was 1.2% of dry weight. The permeability (k = 5.4 × 10\(^{-12}\) m\(^2\)) was 1 order of magnitude lower than that determined for the Mediterranean sediment.

**Experimental set-up.** Two identical recirculating laboratory flow channels similar to the one described by Vogel (1983) were used to simulate in situ conditions. The open, acrylic channel of the flume was 200 cm long, 30 cm wide and 12 cm deep. The drop box (60 cm long, 30 cm wide and 20 cm deep) holding a sediment core with a surface area of 0.3 m\(^2\) exposed to flow was located 90 cm downstream. The sediment recovered from the 2 study sites was filled into the boxes and the remaining channel floor was covered 1 cm high with natural sediment flush with the core surface. Flow was produced by a rotating propeller situated in the return conduit. Flow velocity was controlled by a mechanical flow-meter (Mini Air-Water 2, Schiltknecht) located 5 cm above the sediment. The flow speed was regulated by adjusting the voltage of the electric motor. The recirculating water was kept at a constant temperature of 19°C by means of a cooling coil in the return conduit. Each flume contained 160 l of sea water, which had been transported from the sampling sites. The salinity was 37% for the Mediterranean set-up and 35% for the North Sea system.

Prior to the experiments, the sediment in both systems was allowed to equilibrate for 6 wk at a flow velocity of 10 cm s\(^{-1}\). Before and between experiments, the channels were protected against light and the overlying water was aerated to keep the oxygen saturation at 97% air saturation.

The Mediterranean sediment core contained 7 individuals of *Callianassa truncata* that constructed 7 mounds (22 mounds m\(^{-2}\)) which were maintained throughout the experiment. We chose a mound situated on the centre line and 110 cm downstream for the measurements to avoid side wall effects.

Because in the North Sea core a biologically produced topography similar to the Mediterranean sediment was lacking, an artificial sediment mound of similar dimensions was built by hand on the centre line 110 cm downstream.

**Small-scale flow velocity profiles.** These were measured using temperature-compensated thermistor probes (LaBarbera & Vogel 1976) with a tip diameter of 0.8 mm and a 12 cm long slanted shaft with a maximum diameter of 1.2 mm. The flow sensors had a response time of 0.1 s. For the vertical profiles of flow velocity, the probes were moved by a micro-manipulator from the water column towards the sediment-water interface. Ten velocity profiles were measured in the Mediterranean set-up along the centre line of the flume starting 4 cm upstream of the *Callianassa truncata* mound and continuing in the direction of flow. Starting at 20 mm height above the sediment surface the flow velocities were measured in 1 mm intervals. For each step the data was recorded for 30 s. The free flow velocity 5 cm above the sediment surface was 6.5 cm s\(^{-1}\).

**Oxygen profiles.** These were measured using Clark-type oxygen microelectrodes with a built-in reference and a guard cathode (Revsbech 1989). They had a tip diameter of 10 μm, a 90% response time of 1 s and showed no stirring sensitivity. Signals were amplified by a picoammeter and recorded on a strip-chart recorder or by a 12 bit data-logger. There was no drift in signal during the measurements. The electrodes were calibrated in air-saturated sea water of known oxygen concentration (Winkler titration) and in N\(_2\)-purged, oxygen-free sea water. The sensors were moved along x, y and z axes by a micro-manipulator. Vertical profiles were measured in intervals of typically 100 to 250 μm. The position of the sediment-water interface was determined visually through a dissecting
microscope as the first contact of the electrode with the sediment surface. The precision of surface detection was in the range of 1 sand grain (±135 μm Giglio sediment; ±200 μm North Sea sediment).

At a constant current speed of 10 cm s⁻¹, 8 profiles of oxygen concentration were measured in an area with a smooth surface in the Mediterranean core, to determine the penetration depth of oxygen in the absence of biotopography.

To assess the effect of topography on oxygen penetration depth, 14 oxygen profiles were measured along a transect starting 10 cm upstream of the 1 cm high mound to 10 cm downstream. At 4 positions, 2 upstream and 2 downstream, oxygen profiles along lines perpendicular to the main transect were measured, in order to document the lateral extension of oxygen intrusion.

To estimate the influence of boundary layer flow velocity on advective solute transport in a permeable seabed with biogenic surface topography, the same series of 14 oxygen profiles along the centre line was measured at flow velocities of 3 and 6 cm s⁻¹. After a change in velocity the sediment was left for 12 h to equilibrate.

Parallel measurements were carried out in the North Sea sediment to assess the impact of sediment permeability on solute exchange across the sediment-water interface. Three series of 14 oxygen profiles were measured at current speeds of 3, 6 and 10 cm s⁻¹ along a transect cross-sectioning the artificial mound.

**RESULTS**

**Small-scale flow regime at a mound**

Fig. 3 shows the flow velocity profiles of the unidirectional flow, as it passed over a 1 cm high Callianassa truncata mound. Mean values of the flow velocity recordings for periods of 30 s in 1 mm intervals were
used to draw each profile. At 4 cm upstream of the mound (position A) the flow was undisturbed and the velocity profile was characterised by an increase of flow speed as the logarithm of the distance from the sediment surface. Closer to the mound (B, C) flow decreased in velocity below 10 mm height above the sediment surface, the same height as the roughness element. As the flow passed over the mound (D, E, F) it accelerated according to the principle of continuity and turbulent fluctuations close to the interface occurred. The maximum disturbance and flow separation were observed at the downstream edge of the mound (position F). At the downstream slope, flow slowed down, low velocities \( U < 4 \text{ cm s}^{-1} \) were measured up to 5 mm above the sediment-water interface (positions G and H). There was an almost stagnant condition at the lee-side of the mound (position I). Due to these velocity gradients, pressure differences built up, with a low pressure area above the mound and high pressure areas upstream and downstream of the mound.

**Effect of biogenic topography on oxygen transport**

At a smooth sediment surface the average oxygen penetration under a current with a velocity of 10 cm s\(^{-1}\) was \( 3.6 \pm 0.57 \text{ mm} \) \( (n = 8) \). Six of the measured profiles are shown in Fig. 4. However, close to the mound the oxygen penetration changed in relation to the distance to the roughness element (Fig. 5). At 60 mm upstream of the mound, the steep decline of oxygen was similar to the smooth-surface profiles and the penetration depth of 6 mm was only slightly deeper. Starting at 50 mm upstream of the mound, oxygen penetrated deeper and the shape of the profiles changed. The gradients measured at the positions 10 mm in front \((x = -10)\), at the foot \((x = 0)\) and at the slope of the mound \((x = +19)\) showed oxygen penetration depths of up to 36 mm, with high values continuing from the overlying water into the sediment. In 20 mm sediment depth there were still concentrations of 120 to 150 \( \mu \text{mol l}^{-1}\). The topography-induced oxygen distribution is illustrated in Fig. 3. In the high pressure areas up- and downstream of the mound, overflowing water was forced into the sediment and the pore space was flushed with oxygen-rich water. In the downstream area the flushing effect was less intensive, but oxygen still reached down to 17 mm sediment depth. In the low pressure area, on top of the mound, anoxic pore-water from deeper layers was transported upward. Consequently a minimum of oxygen penetration was measured at the downstream edge.

We estimated the total oxic volume adjacent to the mound from the oxygen profiles measured along the main transect and along the 4 transects, perpendicular to it (positions: -30, -10, 60 and 75 mm), in the high pressure areas up- and downstream of the mound.

Assuming a 3-dimensional geometry of an elliptical half-sphere, volume \( (V) = \frac{4}{3} \pi a b c / 2 \) (with \( a, b, \) and \( c \) being the half axes of an ellipsoid; \( a \) as the lateral extension, \( b \) as the distance along the centre line and \( c \) as the height).
Fig. 5. Fourteen oxygen profiles were measured along a transect, cross-sectioning the mound (shown in Fig. 3) in flow direction, under a current velocity of 10 cm s⁻¹. Four selected profiles are shown here. Positions are given as distances in mm, where x = 0 is the position at the upstream foot of the mound. Negative values are further upstream, positive values are further downstream.

as the maximum penetration depth), the oxic sediment volumes were estimated as \( V_1 = \frac{4}{3} \pi \times 30 \text{ mm} \times 37.5 \text{ mm} \times 34 \text{ mm} \)/2 = 80 cm³ upstream and \( V_2 = \frac{4}{3} \pi \times 20 \text{ mm} \times 25 \text{ mm} \times 17 \text{ mm} \)/2 = 18 cm³ downstream of the mound.

**Effect of varying flow and sediment permeability**

In the sandy Mediterranean sediment the penetration of oxygen in an area with a smooth sediment surface showed very little variation with flow velocity (Fig. 7). The penetration depth ranged from 4.3 mm at a current speed of 3 cm s⁻¹ to 4.5 and 3.9 mm at current speeds of 6 and 10 cm s⁻¹ respectively. Considering an accuracy of ±0.35 mm of surface determination (grain size: 350 μm), there was no significant increase of oxygen with current speed. The penetration depth of oxygen under stagnant conditions varied between 3 and 8 mm with a mean value of 4.8 mm (n = 6).

In contrast, the topography-induced solute transport varied essentially with flow velocity (Fig. 8). The maximum oxygen penetration measured at the same position (x = 0) in the high pressure area upstream of the mound ranged from 10 mm at 3 cm s⁻¹ to 22 mm at 6 cm s⁻¹ and reached 31 mm at 10 cm s⁻¹. Consequently the sediment volume supplied with oxygen was also clearly increasing with flow speed.

In the North Sea sediment, which consisted of less permeable, muddy sand, the penetration depth at a smooth surface under a flow of 10 cm s⁻¹ was 4 ± 0.65 mm (n = 8). At the sediment mound there was no apparent effect on solute transport at current speeds of 3 and 6 cm s⁻¹ (Fig. 9). Only at a flow velocity of 10 cm s⁻¹ was a 2-fold increase in penetration depth of oxygen recorded in the high pressure area, upstream of the structure. There was no obvious effect on oxygen penetration in the area downstream of the mound. With a height of 8 mm, the artificial mound was slightly lower than the mounds built by *Callianassa truncata* in the Giglio sediment.

![Graph showing oxygen distribution](image)

Fig. 6. Points of equal oxygen concentration were connected to illustrate the oxygen distribution underneath the sediment mound exposed to a flow velocity of 10 cm s⁻¹. Isopleths are shown in 50 μM intervals. Vertical dotted lines indicate the 14 measured oxygen profiles.

![Graph showing oxygen profiles](image)

Fig. 7. At a smooth surface, oxygen profiles were measured at the same position, under 3 different flow velocities.
As the flow was turned off, the oxygen value in 20 mm sediment depth declined to zero within 2 h. In the upper sediment layer, in 3 mm depth, oxygen decreased to a concentration of 10 to 15 μmol l⁻¹, which was maintained over a period of 8 h under no-flow conditions. As the water flow was started again, this oxygen sensor’s signal increased almost instantaneously (within 30 s). The initial value of 216 μmol oxygen l⁻¹ was stable after 50 min and stayed constant. At the depth of 20 mm this effect was delayed, after 1 h 48 min an increase of oxygen was measured. It took another 1 h 20 min until a concentration of ca 90 to 100 μmol l⁻¹ was reached.

The oxygen uptake or respiration (R) in the respective depth could be estimated from the initial (after 30 s) decrease (ΔC) of oxygen with time (Δt): R = ΔC/Δt.

In 3 mm the respiration was 7 x 10⁻⁶ μmol O₂ cm⁻³ s⁻¹ and slightly higher than the oxygen uptake of 5 x 10⁻⁶ μmol O₂ cm⁻³ s⁻¹ in 20 mm sediment depth.

**Dynamics of advective oxygen transport at a mound**

Because in the natural environment flow conditions can vary, we were interested in the time scale of advective oxygen supply to a certain sediment depth after a change of flow velocity. Two electrodes were positioned at fixed sediment depths of 3 and 20 mm at the upstream foot of the mound (x = 0) to follow the oxygen concentration at these particular depths under varying flow conditions (Fig. 10). After equilibration of the oxygen flux at a flow velocity of 10 cm s⁻¹ the flume motor was switched off and the decrease of oxygen concentration in the respective sediment depths were recorded by a data logger at intervals of 1 s. As a steady state of oxygen concentration was reached, the motor was switched on again. At the beginning of the experiment the oxygen concentrations at 3 and 20 mm were 210 and 115 μmol oxygen l⁻¹ respectively; these values corresponded to the oxygen profile measured at this location (x = 0) at a current speed of 10 cm s⁻¹ (Fig. 5). As the flow was turned off, the oxygen value in 20 mm sediment depth declined to zero within 2 h. In the upper sediment layer, in 3 mm depth, oxygen decreased to a concentration of 10 to 15 μmol l⁻¹, which was maintained over a period of 8 h under no-flow conditions. As the water flow was started again, this oxygen sensor’s signal increased almost instantaneously (within 30 s). The initial value of 216 μmol oxygen l⁻¹ was stable after 50 min and stayed constant. At the depth of 20 mm this effect was delayed, after 1 h 48 min an increase of oxygen was measured. It took another 1 h 20 min until a concentration of ca 90 to 100 μmol l⁻¹ was reached.

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**DISCUSSION**

**Advective transport of oxygen**

Diffusive oxygen flux across the sediment-water interface is driven by a concentration gradient be-
between the overlying water and the pore water. It is dependent on the oxygen concentration in the supernatant water (Rasmussen & Jorgensen 1992) and the diffusion coefficient of oxygen in the water and the sediment. The oxygen penetration depth depends on the oxygen uptake of the sediment (Reimers & Smith 1986, Revsbech & Jorgensen 1986) and thus on the organic content. As the O₂ concentration decreases with depth due to biological and chemical consumption (Crank 1983) the microscale measured profiles may show a change in the gradient, allowing the calculation of the oxygen uptake in a defined zone (Crank 1983, Nielsen et al. 1990).

The oxygen gradients we measured in the permeable sand, underneath a smooth surface, corresponded to the profiles measured in other coastal regions. The penetration depth was ca 4 mm and a typical curve of nearly parabolic shape indicated a steep decline of oxygen with depth. At a smooth surface the change of the boundary layer flow velocity did not significantly affect the oxygen transport across the interface (Fig. 4), although minor changes were possibly not detected due to the error of sediment surface detection. The penetration depth of oxygen under stagnant conditions was in the same range of ca 4 mm. In early investigations, Fenchel (1969) also demonstrated that a moderate current of 8 cm s⁻¹ above natural sands of increasing permeability did not result in advective pore water movements below 4 mm sediment depth.

In high-resolution measurements, Jørgensen & Des Marais (1990) showed that oxygen penetration increased 3-fold (from 0.5 mm to 1.5 mm) in a bacterial mat as the flow speed was increased by a factor of 25 (0.3 cm s⁻¹ to 7.7 cm s⁻¹). Their explanation was a reduced thickness of the diffusive boundary layer (DBL). The DBL is a thin layer of water, typically only 0.2 to 1 mm thick (Boudreau & Guinasso 1982, Jørgensen & Revsbech 1985, Gundersen & Jørgensen 1990), covering the sediment surface. Within the DBL the viscous forces exceed the turbulent, and molecular diffusion is the dominant transport mechanism. Oxygen decreases linearly as the sediment surface is approached. With increasing current velocity the thickness of the DBL decreases and as a result oxygen concentration directly at the interface is higher and the solute penetrates deeper into the sediment. In our experiments, in the sandy sediment (median diameter 350 μm) from the Mediterranean Sea, the measured profiles do not show the formation of a DBL. One explanation might be the insufficient resolution of the measurements. We assume that the formation of this layer was most likely affected by the sediment surface roughness. Obstacles protruding more than half of the DBL thickness into the overlying water can influence the formation of this laminar layer (Vogel 1983). The absence of a DBL might indicate some advective flow in the upper few mm of the sediment even in the case of a 'smooth' surface. The average oxygen penetration under stagnant conditions was 4.8 mm (n = 6), so that we assume that advective transport rate at a smooth surface of the sandy sediment was comparable to the diffusive flux of oxygen across the sediment-water interface.

In contrast, hydrodynamic forces determined the interfacial solute transport at the roughness element in the permeable sediment. In the vicinity of the small biogenic mound (1 cm high) the small-scale flow field was altered (Fig. 3) and as a consequence pressure differences were generated. Within the high pressure fields, not only did oxygen reach down to deeper layers but the profiles also showed a characteristic change in shape (Fig. 5). High concentrations persisted up to 20 mm deep into the sediment. The curve of the profile indicates that the oxygen supply is higher than the concurrent uptake at the respective sediment depths. The deep oxygen penetration cannot be explained by diffusion pathways but is due to advection. Consequently, the O₂ uptake cannot be calculated from the profile's shape, as is possible for diffusive oxygen gradients using Fick's first law of diffusion \( J = -D \frac{\partial C}{\partial x} \), where \( J \) is the diffusion flux, \( D \) the apparent diffusion coefficient in the substrate and \( \frac{\partial C}{\partial x} \) is the slope of the concentration profile at depth \( x \).

In contrast to dyes, used as conservative tracers in experiments designed to show advective transport (Huettel & Gust 1992), oxygen is one of the most reactive chemical species. While being transported it is also consumed in biological and chemical processes, thus the measured profiles describe a dynamic balance between oxygen supply and consumption in the specific depth. In dye experiments under similar flow conditions and a structure of comparable size, the solute reached down to more than 5 cm sediment depth (Huettel & Gust 1992).

The depth distribution of oxygen at the obstacle was a function of flow velocity. Penetration depth and thus the sediment volume oxygenated were greatest at the highest flow velocity used in our experiments (10 cm s⁻¹), a current speed commonly observed in the natural environment. A total volume of ca 98 cm³ of sediment was calculated to be oxic next to this mound of 10 mm height. This compares to 20 cm³ of sediment supplied with oxygen by diffusion, considering an equivalent area (51 cm²) of a smooth sediment surface. Thus the oxic volume increased locally by a factor of 4.8. This means a significant increase of oxygen availability for aerobic respiration and oxygen-dependent chemical reactions. In the natural environment the sediment volume supplied with oxygen by advection is related to the density of biogenic structures in a given area. At the observed natural density of 120 callianassid mounds per m², a 3.3-fold increase of oxygenated
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In a permeable sediment with biogenic topography, the oxic zone below the depth of diffusional transport is controlled by boundary flow velocities. Advection transport is initiated as soon as flowing water is deflected by the roughness element and is much faster than diffusional transport. In our experiment, after a change from stagnant water to a boundary layer flow of 10 cm s$^{-1}$ (Fig. 10), it took ca 3 h until the sediment layer in 20 mm depth was continuously supplied with oxygen. For a comparison, the time required for a solute to overcome a distance by diffusional transport can be approximated by using the equation $t = z^2/2D$, derived from the definition of a 1-dimensional diffusion coefficient, where $t$ is the time in s, $z$ is the distance or sediment depth in cm and $D$ the diffusion coefficient of a solute in water at a given salinity and temperature. The diffusion coefficient for oxygen in sea water with a salinity of 37% and a temperature of 19°C would be $D = 1.9214 \times 10^{-5}$ cm$^2$ s$^{-1}$.

According to this calculation it would take 29 h for an oxygen molecule to overcome a distance of 20 mm in sea water by molecular diffusion. In the sediment the time required would be prolonged (ca 3-fold) due to the porosity and tortuosity effects (Berner 1980, Iverson & Jorgensen 1993).

Underneath an irregular surface and within a few centimetres' sediment depth the availability of oxygen can change rapidly with varying flow conditions. Furthermore, the topography of the sea floor is not permanent but varies with faunal activity, which is often seasonal because it is stimulated by the input of organic carbon from the water column and reflects generation cycles. Most biogenic structures are not stable but change in size and are erased by strong currents. In turn, high boundary-layer flow velocities not only render the sediment more permeable but can generate ripples that produce similar advective transport processes (Thibodeaux & Boyle 1987).

Another important aspect of topography-induced solute transport is the upwelling of reduced pore water due to the low pressure field above a mound or ripple. The isopleths (Fig. 6) show that the oxic zones, upstream and downstream of the mound, are separated by an anoxic region underneath the mound, where reduced solutes reach the sediment surface.
Pore water from as deep as 20 cm can be transported to the sediment surface by this suction effect (Huettel & Gust 1992). The presence of this oxygen-free zone next to oxic environments further complicates the zonation pattern and creates horizontal gradients of oxygen concentration within the upper sediment layer. The oxygen distribution in natural environments is heterogeneous and highly variable, thus many factors have to be considered when estimating solute exchange rates.

Implications for the sedimentary environment

Advective oxygen transport can play an important role in the ecology of coastal sediments. Many coastal areas and a large part of the continental shelf (40%) are covered by permeable sediments that are exposed to boundary layer flows and are populated by infaunal organisms or are characterised by ripples. Thus advective transport processes take place that can expand the oxic sediment volume far beyond the zone supplied by diffusion. The increase of free oxygen available for aerobic respiration enhances the mineralisation of organic matter and the subsequent release of regenerated nutrients can be of importance for the ambient environment. Reduced substances are oxidised within the flushed regions or locally at the sediment interface where anoxic pore water is transported upward due to the low pressure on top of elevations. Parallel to the advective solute transport, organic particles are transported into the interstices of the permeable sea bed (Huettel et al. 1996). The co-occurring input of oxygen and organic matter further promotes microbial carbon oxidation and accelerates remineralisation processes within the upper sediment. The oxygen used in surplus during advective transport compared to diffusional supply for respiration and chemical or biological oxidation must also be reflected in the total oxygen uptake of the sediment (Forster et al. unpbl.) Next to food availability, oxygen is the predominant factor determining the habitat conditions for aerobic micro- and meiofauna. The existence of anaerobic life forms is also not possible in isolation from oxic regions, as the essential chemical energy is provided by the processes that take place in the oxic zones. Anaerobic life has therefore been found to be most abundant in the vicinity of aerobic habitats (Fenchel & Finlay 1995). In sandy sediments the numbers of protozoans are highest at the transition zone from anoxic to oxic conditions (Giere 1993). This is also the region where bacterial activity is often found to be highest (Fenchel & Blackburn 1979). Many protozoans are microaerophilic, but are sensitive to higher O2 concentrations, which can be toxic for them. The results of this investigation show that due to topography-induced flow effects the oxic-anoxic transition becomes 3-dimensional, offering an enlarged habitat for gradient organisms. We showed that this region is also characterised by a high spatial and temporal variability. This implies that the organisms have to react with high mobility to meet their metabolic needs or to escape unfavourable conditions, if they are not able to tolerate the changing conditions (Alve & Bernhard 1995). Classification of micro-organisms according to the sediment depth where they have been found is only reliable in combination with the exact description of chemical gradients. Foraminifera, for example, have been observed in ‘anoxic’ habitats, but species with anaerobic metabolism probably do not exist (Bernhard 1989, Bernhard & Reimers 1991). An explanation would be the supply of oxygen to deeper sediment layers. The observed downward migration in Foraminifera as a response to flow (Palmer & Molloy 1986) might be an indication for this.

The presence of biogenic structures at a permeable sea floor exposed to moderate boundary layer flows induces a high spatial and temporal variability of oxygen concentration within the upper layer of the sediment and may also affect the exchange of other dissolved substances between the water column and the sediment. The advective supply of oxygen to a permeable seabed far exceeds diffusional transport and may essentially affect mineralisation processes within the sediment and the distribution of benthic meiofauna and micro-organisms.

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