

Effect of the brittle star *Amphiura filiformis* (Amphiuridae, Echinodermata) on oxygen flux into the sediment

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Abstract

O₂ plays a key role in early sedimentary diagenetic processes, but the effect of most macrofaunal species on the pathways and rates of supply of O₂ into the seabed are not well known. We investigated the effect of the ophiuroid *Amphiura filiformis*, one of the dominant macrobenthic species on soft bottoms in the northeast Atlantic, at depths of ~15–100 m, in a laboratory environment. We determined how the presence of the ophiuroid changed the total O₂ uptake of macrofauna-free sediment by combining measurements from a microcosm approach and an approach that uses microelectrodes and a flushed aquarium. We suggest that natural populations of *A. filiformis* can account for 80% of the total flux of O₂ into the soft bottom. At least 67% of this portion is due to the diffusion of O₂ across additional sediment–water interfaces excavated by the brittle star.

Because O₂ plays a key role in early sedimentary diagenetic processes, pathways and rates of supply of O₂ into the seabed are of interest. Cohesive sediments are supplied with O₂ by molecular diffusion driven by concentration gradients between bottom seawater and the interstitial seawater of the sediment (Gundersen and Jørgensen 1990) and by the advection of seawater as a consequence of infaunal activities (Aller and Yingst 1978; Aller 1980; Gust and Harrison 1981). Larger species create and ventilate burrows and tubes; that is, they expose additional sediment surface area to oxygenated seawater. Many macroinfaunal species continuously rework the sediment and thus increase the oxygenation of the pore water (Marinelli 1992; Krager and Woodin 1993; Rosenberg et al. 1997; Solan and Kennedy 2002). The meiofauna of the surficial sediment and the sediment around macrofaunal burrows apparently contribute to the interfacial flux as well by mixing the pore water through “random walk” within the interstitium of the sediment or by irrigating

microcavities and microtubes (Meyers et al. 1987; Aller and Aller 1992; Pike et al. 2001).

Estimating the overall contribution of benthic communities to the total O₂ flux is a complex issue. This contribution is a function of, for example, the structure of the benthic community, the sizes of the species, the geometries of their burrows, their modes of burrow ventilation and feeding, and their physiological abilities and survival strategies (e.g., Aller and Yingst 1978; Aller et al. 1983). Species’ life histories (population dynamics) and interspecific interactions are additional variables. Larger animals are of particular interest because they can account for the majority of the faunal effect. Populations of the burrowing shrimp *Callinassa subterranea*, for example, can account for 17% of the total oxygen utilization (TOU) of North Sea sediments (de Wilde et al. 1984; Witbaard and Duineveld 1989). Booij et al. (1994) calculated that burrow irrigation by the amphipod *Corophium volutator* and oligochaetes caused ~25% of the total O₂ flux into intertidal sediment of the western Wadden Sea. Forster and Graf (1995) found that *C. subterranea* and the polychaete *Lanice conchilega* increased the TOU of very fine, silty sediment of the Norwegian Trough (698 m, Skagerrak) by 85% over that caused by diffusion across the sediment–water interface. A 2.7-fold increase in solute flux due to the abundant polychaete *Spiochaetopterus* sp. was found by Forster et al. (1999).

Here, we present a laboratory study designed to investigate the impact of the ophiuroid *Amphiura filiformis* (O. F. Müller), one of the dominant macrobenthic species on soft bottoms in the northeast Atlantic at depths of ~15–100 m (O’Connor et al. 1983; Sköld et al. 1994). The population densities of *A. filiformis* are known to be >3,000 individuals m⁻² (Rosenberg 1976, 1995; Josefson 1995). This brittle star

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occupies burrows that extend several centimeters into the sediment. The burrow consists of a disk chamber that is connected to the bottom water through three–four arm channels (Woodley 1975). The size, shape, and positioning of the burrow are consistent, and the inhabitants remain stationary for most of the time (Solan and Kennedy 2002). *A. filiformis* does not move daily in search of food but exhibits density-dependent migratory behavior; that is, the brittle star moves horizontally both on the sediment surface and within the sediment (Rosenberg et al. 1997). Furthermore, this brittle star leaves its position in the sediment during spawning (Woodley 1975) and when $[O_2]$ of the bottom seawater is <13% saturation (Rosenberg et al. 1991).

The arms of an established *Amphiura* serve three main functions: ventilation and respiration, transportation of particles out of the burrow, and the collection of food and its transportation toward the mouth (Ockelmann and Muus 1978). *A. filiformis* usually ventilates its burrow by undulating one arm in the vertical plane (Woodley 1975; Ockelmann and Muus 1978). Undulations pass down the arm from the surface of the sediment toward the disk, forcing water along in the spaces between the upper and lower surface of the arm and the walls of the burrow. The water is drawn down that arm channel to the disk chamber and then flows passively up to the other arm channels. The arms are flanked by arrays of projecting spines to which sediment particles adhere, forming the “respiratory fringe.” The fringe blocks the gaps between the lateral spines and thus prevents a displacement of water during undulation and increases the driving effect of the trunk of the arms. The fringe is constructed with the help of the tube feet, which, in contrast to those of other species, stand free of the fringe and can thus transport material along the arm to the mouth while undulation continues (Woodley 1975).

All previous field and laboratory studies on *A. filiformis* have indicated that the brittle star must have a significant impact on the total O_2 flux and thus on the biogeochemical cycling of organic matter in the sediment. The aim of our study was to quantify this effect. We did enclosure experiments with macrofauna-free sediment as well as experiments with a specific number of ophiuroids added. In addition, detailed microelectrode measurements were done directly in the burrow and through burrow walls in an aquarium with flowing water, where in situ boundary-layer flow conditions could be simulated.

Materials and methods

Locality and sampling—In September 2000, a modified USNEL box corer (0.25 m²) was used to collect organisms and sediment at the mouth of the Gullmarsfjord, west Sweden (58°14.72'N, 11°25.80'E), at 55 m depth. Bottom-water temperatures there vary between 5°C and 12°C, and the salinity is ~34. The sediment is a silty clay with a water content of 73.4% \pm 2.1% and a porosity of 0.83 \pm 0.04 (mean \pm SD, n = 5). The grain-size distribution has two dominant size classes. By weight, 47% of the particles are 2–8 μ m in diameter (i.e., clay-silt), and 38% are 63–125 μ m (i.e., silt–very fine sand) (Sköld et al. 1994).

The sediment in the box corer was gently rinsed with filtered seawater through a 1-mm mesh that removed macrobenthic animals and was used to set up the microcosms and the flushed aquaria described below. During sieving, individuals of the brittle star *A. filiformis* with disk diameters between 6.0 and 7.5 mm were collected with forceps. These individuals were allowed to acclimate for 1 d in a flow-through seawater system filled with sediment from our site at 17 \pm 0.2°C in the dark. The seawater used in all experiments was pumped from 35 m depth.

Microcosm setup—Each of 10 plastic cylinders (length, 24 cm; inner diameter, 9.8 cm), closed at the lower ends with rubber stoppers, was filled two-thirds full with sieved sediment from the study site and completely submerged (upright) in a larger tank filled with 30- μ m filtered seawater (pH, 8.1; salinity, 32). The upper opening of each cylinder was then closed by an O-ring-sealed lid to which a 4-cm-long, Teflon-coated stirring bar was attached. The stirring bar was rotated at ~10 rpm by a rotating external magnet. This gentle stirring prevented the water column from becoming stagnant but did not cause movement of sediment particles. The lid of each cylinder had two ports to which Teflon tubes were connected. A peristaltic pump (Ismatec Laboratoriumstechnik) constantly moved seawater from the cylinder through the first port to a flow-through cell (AMT) and back into the cylinder through the second port. This closed system could be opened by disconnecting the Teflon tube from the second port so that seawater from the surrounding tank was drawn into the cylinder, through the flow-through cell, and back into the tank. The $[O_2]$ of the seawater in the flow-through cell was continuously measured with a Clark-type O_2 microelectrode (AMT) and a miniaturized picoampere meter (AMT) mounted directly on the microelectrode. The signal was digitized by an analog-to-digital converter (DI 220; Dataq Instruments) and analyzed with the software WinDaq/Lite (Dataq Instruments).

Microcosm measurements—The following procedure was repeated for each microcosm. We brought $[O_2]$ in the microcosm to steady state by opening the circulation system (see above). Once the $[O_2]$ was stable, the system was closed, and the decrease of the $[O_2]$ in the seawater of the microcosm was measured for 3 h. Subsequently, the system was opened, to allow flushing with oxygenated seawater from the surrounding tank until $[O_2]$ reached saturation (after ~2 h). Thereafter, 10 of the reserved specimens of *A. filiformis* rinsed with 0.7- μ m filtered seawater were added to the microcosm yielding a density that corresponded to 1,326 individuals m⁻², a realistic natural density. Two hours after the brittle stars had buried themselves, the system was closed, and the decrease of the $[O_2]$ in the seawater of the cylinder was measured again for 3 h. All measurements were made in darkness at 17 \pm 0.2°C. Afterward, the number of openings per burrow and the number of extended arms per individual were estimated visually. The TOU of the microcosm in each treatment was calculated from the rate of decrease of $[O_2]$ in the seawater above the sediment and the volume of the overlying seawater. The rate of decrease in $[O_2]$ was obtained by linear regression of the $[O_2]$ curve (R^2 > 0.937).

Respiration rate of *A. filiformis*—Each group of 10 adult specimens of *A. filiformis* was removed from its cylinder, rinsed in 0.7- μm filtered seawater, and transferred to a 100-ml flask filled with normoxic, 0.7- μm filtered seawater (pH, 8.1; temperature, $17 \pm 0.2^\circ\text{C}$; salinity, 32). No sediment was added. We measured the $[\text{O}_2]$ in the flask at the beginning and at the end of a 4-h (dark) incubation with the O_2 microelectrode by circulating the seawater between the flask and the flow-through cell. Flasks of filtered seawater served as controls. The average individual respiration rate was calculated from the volume of the seawater in a flask and the decrease in its $[\text{O}_2]$. The wet weight and dry weight of the average individual were determined for each of the 10 groups of *A. filiformis*. For wet weight, the 10 brittle stars in each group were rinsed in 0.7- μm filtered seawater, transferred onto a sieve, and weighed. For dry weight, the individuals in each group were rinsed with distilled water, dried at 70°C for 24 h, and weighed again.

Experiments in flow aquaria—Two small aquaria ($19 \times 6 \times 10$ cm) were completely filled with sieved sediment from the study site. These aquaria were submerged in a larger, 60-cm-long aquarium (25×10 cm) filled with seawater (temperature, $17 \pm 0.2^\circ\text{C}$; salinity, 32) and equipped with an outflow on one side and an inflow on the other. The in- and outflow were connected with silicon tubes to a reservoir holding 200 liters seawater that was continuously bubbled with air. This seawater was pumped from the reservoir to the aquarium at a rate of $2.16 \pm 0.03 \text{ L min}^{-1}$ ($n = 5$) and returned to the reservoir by gravity. The resulting flow in the aquarium, measured by tracking of particles ~ 5 cm above the sediment surface, was $\sim 2 \text{ cm s}^{-1}$. After six $[\text{O}_2]$ microprofiles across the sediment–water interface had been measured (see below), 5–10 specimens of *A. filiformis* were placed on the sediment surface of each small aquarium, whereupon they burrowed into the sediment within a few minutes. Some burrows were visible though the sides of the aquaria, so an arm or the disk could be observed. The brittle stars were not fed.

Microelectrode setup—Spatial and temporal variations in $[\text{O}_2]$ of the sediment–water interface and in the burrows of *A. filiformis* were recorded with a Clark-type O_2 microelectrode (MasCom) mounted on a micromanipulator (Märzhäuser) driven by remotely controlled stepping motors and secured to a stable support. The electrode current, measured by a miniaturized picoammeter (MasCom) mounted directly on the shaft of the sensor, was converted to a millivolt signal with a two-channel indication amplifier and digitized by an analog-to-digital converter (DI 220; Dataq Instruments) for data acquisition. The sensor was calibrated at the experimental temperature. Seawater from the tank that had been saturated with O_2 by air bubbled into it was the standard for air saturation. An aliquot that had been nitrogen flushed was the zero- $[\text{O}_2]$ standard. A stereomicroscope (SZ60; Olympus) mounted on a tripod was used to observe the movements of the sensor tip near the surface of the sediment and in the burrows of the brittle stars.

Microscale measurements—We measured one high-resolution $[\text{O}_2]$ profile across the sediment–seawater interface at six randomly chosen locations in the flushed aquaria by advancing the sensor vertically in 0.2-mm increments. Continuous recordings of $[\text{O}_2]$ were made in burrows of *A. filiformis* that were against the walls of the aquaria, so that the position of sensor could be controlled visually. The sensor readings were displayed in real time, and the behavior of the brittle star and the resulting changes in $[\text{O}_2]$ were observed at the same time.

A high-resolution $[\text{O}_2]$ profile was also measured across the channel lumens of the undulating arms of five individuals (Fig. 1, chord B). In each case a second, parallel profile was measured in the surrounding sediment alone (Fig. 1, chord A). These measurements allowed us to estimate the thickness of the oxic halo around the arm channel, the diameter of the channel lumen, and the O_2 consumption of the surrounding sediment. The tip of the microelectrode crossed the oxic halo and the lumen of an arm channel ~ 1.5 cm below the sediment surface at an angle (θ) of 45° , parallel to the vertical radius (Y) of the ellipsoid cross section and perpendicular to the horizontal radius (X). Construction of O_2 profiles in a plane normal to the long axis of the lumen required an estimate of the radial distance (x_{bn}) of each measurement from the center of the lumen. The distance (x_b) of chord B from Y was calculated with Eq. 1.

$$x_b = \{[(B/2)^2 - (A/2)^2] \times \cos^2(90^\circ - \theta) - c^2\}/2c \quad (1)$$

where A and B are the lengths of the chords A and B, respectively, and c is the distance between the chords. The distance (r_{bn}) from the center of the ellipsoid cross section to every measuring point (b_n) along chord B could then be determined with Eq. 2.

$$r_{bn} = (y_n^2 + x_b^2)^{1/2} \quad (2)$$

where y_n is the distance from b_n to the intersection of chord B and the x-axis. The distances X and Y from the center of the lumen to the edge of the oxic halo along the x- and y-axis were calculated with Eqs. 3 and 4, respectively.

$$X = [B^2 \times \cos^2(90^\circ - \theta) + x_b^2]^{1/2} \quad (3)$$

$$Y = X/\cos(90^\circ - \theta) \quad (4)$$

Given X and Y , the length (R_{bn}) of any line through b_n connecting the center and the perimeter of the ellipse can be calculated with Eq. 5.

$$R_{bn} = [(X^2 \times Y^2 \times [1 + y_n^2/x_b^2])/(Y^2 + X^2 \times y_n^2/x_b^2)]^{1/2} \quad (5)$$

Finally, the distance r_{bn} was converted to the distance (x_{bn}) in a plane normal to the long axis of the arm channel with Eq. 6.

$$x_{bn} = X \times r_{bn}/R_{bn} \quad (6)$$

For the construction of the $[\text{O}_2]$ profiles normal to the long axis of the arm tube (see below), the only measurements used were those taken as the sensor moved from the sediment into the channel lumen (not those taken as the sensor moved from the lumen into the sediment).

Calculation of O_2 flux—The diffusive flux (J) of O_2 from the aquarium seawater into the sediment was calculated from

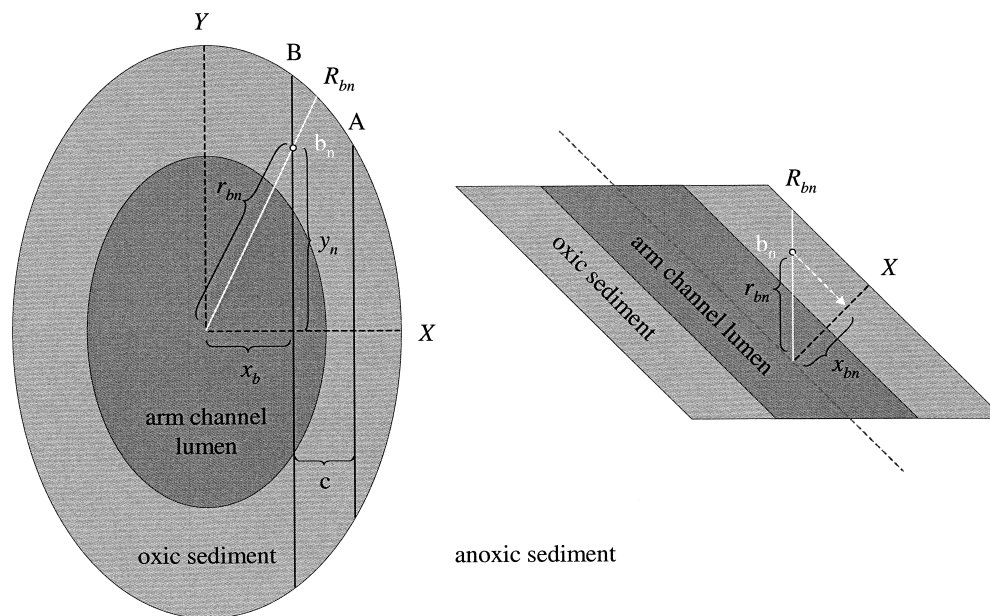


Fig. 1. (Left) Schematic drawing of the plane along which two parallel vertical profiles across the burrow-sediment interface were measured (chords A and B). (Right) Longitudinal section of the arm-channel lumen and its oxic halo. Given the lengths of chords A and B and the distance, c , between the two chords, the shortest distance, x_{bn} , of every measuring point, b_n , from the long axis was calculated. From these values, a pore-water $[O_2]$ profile normal to the long axis was constructed.

the measured steady-state O_2 gradients (dC/dz) in the diffusive boundary layer (Jørgensen and Revsbech 1985):

$$J = -D_0 dC/dz \quad (7)$$

where D_0 is the free-solution diffusion coefficient of O_2 , C is the $[O_2]$, and z is the depth. Values of D were taken from Broecker and Peng (1974) and were recalculated to the ex-

perimental temperature with the Stokes-Einstein relation (Li and Gregory 1974).

The depth-integrated O_2 consumption rate (R) of the sediment was computed from the steady-state, sediment-pore-water profiles according to the method of Berg et al. (1998). The sediment porosity (ϕ) and, thus, the sediment diffusion coefficient (D_s) were assumed to be constant with depth or distance from the burrow wall.

Table 1. Contribution of buried adult *A. filiformis* individuals to the TOU of laboratory microcosms (MC). The contribution of inhabited burrows to the TOU was calculated from the difference between TOU of control microcosms (devoid of macrofauna) and microcosms to which brittle stars had been added. The density of the brittle stars corresponded to the abundance of 1326 ind. m^{-2} . Seawater temperature, $17 \pm 0.2^\circ C$; salinity, 32; pH, 8.1.

MC	TOU ($\mu mol m^{-2} h^{-1}$)		Number of burrow openings (extended arms)	O_2 uptake of one inhabited burrow ($nmol h^{-1}$)
	Control	Treatment		
1	475.21	1290.26	32 (19)	614.79
2	453.87	1045.76	30 (15)	446.46
3	394.20	1359.62	34 (26)	728.21
4	518.45	1103.51	28 (20)	441.31
5	404.72	995.21	34 (23)	445.41
6	801.06	1608.96	31 (20)	609.39
7	852.56	1528.32	38 (22)	509.72
8	384.48	1302.19	26 (11)	692.22
9	406.24	1389.27	34 (27)	700.76
10	518.57	1354.53	32 (21)	630.59
Mean	526.34	1297.76	31.90 (20.40)	581.88
SD	157.04	189.28	3.24 (4.52)	106.71

Sediment porosity and O_2 diffusion coefficients—The porosity of the sediment (ϕ), which accounts for the tortuosity correction (Ullman and Aller 1982), was determined as the weight loss of a known volume of sediment after drying at $105^\circ C$ for 24 h. The sediment diffusion coefficient for O_2 (D_s) was calculated from the temperature-corrected diffusion coefficient (D_0) and the porosity according to

$$D_s = \phi^{(m-1)} D_0$$

where $m = 2$ (Ullman and Aller 1982).

Results

Total O_2 utilization of microcosms—The average TOU of control microcosms without macrofauna was $3.97 \pm 1.18 \mu mol h^{-1}$. In contrast, the average TOU in microcosms containing 10 buried specimens of *A. filiformis* was $9.79 \pm 1.43 \mu mol h^{-1}$ ($n = 10$; here and henceforth the values are given as arithmetic means \pm standard deviation). Given that the area of the sediment surface of each microcosm was $75.43 cm^2$, the TOU were 526 ± 157 and $1298 \pm 189 \mu mol m^{-2} h^{-1}$ for control and *A. filiformis*-populated microcosms, respectively (Tables 1, 2-A1, 2-A2). The average contribution

Table 2. Summary of results from two different approaches.

Result	A: Microcosm with rotating flow	B: Aquaria with unidirectional flow
1. TOU without macrofauna	$526 \pm 157 \mu\text{mol m}^{-2} \text{ h}^{-1}$, measured as decrease in seawater $[\text{O}_2]$	$358 \pm 42 \mu\text{mol m}^{-2} \text{ h}^{-1}$, estimated from $[\text{O}_2]$ profile in DBL $346 \pm 35 \mu\text{mol m}^{-2} \text{ h}^{-1}$, estimated from $[\text{O}_2]$ profile in sediment
2. TOU with density of 1326 ind. m^{-2}	$1298 \pm 157 \mu\text{mol m}^{-2} \text{ h}^{-1}$, measured as decrease in seawater $[\text{O}_2]$	$1110 \mu\text{mol m}^{-2} \text{ h}^{-1}$, calculated from B3 and B1
3. TOU of 1 burrow + inhabitant	$582 \pm 107 \text{ nmol h}^{-1}$, calculated from A2 and A1	$567 \pm 31 \text{ nmol h}^{-1}$, measured as decrease in disc chamber $[\text{O}_2]$
4. Respiration of <i>A. filiformis</i>	$191 \pm 17 \text{ nmol h}^{-1}$, measured as decrease in respiration chamber $[\text{O}_2]$	
5. TOU of burrow	391 nmol h^{-1} ($251 \mu\text{mol m}^{-2} \text{ h}^{-1}$), calculated from A3 and A4	$1451 \pm 301 \mu\text{mol m}^{-2} \text{ h}^{-1}$, flux from arm channel lumen into sediment, calculated from $[\text{O}_2]$ profiles in burrow wall

of one buried *A. filiformis* to the TOU of the brittle-star microcosms was $582 \pm 107 \text{ nmol h}^{-1}$, calculated from the difference between TOU of control microcosms and microcosms containing 10 brittle stars (Tables 1, 2-A3). At the

Table 3. Respiration rate of adult *A. filiformis* specimens at a seawater temperature of $17 \pm 0.2^\circ\text{C}$ and a salinity of 32. The incubation lasted 4 h. The individual values were calculated from the weights and respiration rates of groups of 10 specimens for each replicate. DW, dry weight; MC, microcosm; WW, wet weight.

MC	O_2 consumption (nmol ind. $^{-1} \text{ h}^{-1}$)	WW (mg)	DW (mg)	Weight-specific O_2 consumption	
				$\mu\text{mol g WW}^{-1} \text{ h}^{-1}$	$\mu\text{mol g DW}^{-1} \text{ h}^{-1}$
1	163.23	103.83	48.32	1.57	3.38
2	193.76	109.56	52.68	1.77	3.68
3	172.08	100.39	48.09	1.71	3.58
4	223.45	126.91	59.81	1.76	3.74
5	182.17	111.97	52.92	1.63	3.44
6	205.54	138.92	60.61	1.48	3.39
7	195.59	153.41	64.67	1.27	3.02
8	203.98	172.41	70.67	1.18	2.89
9	187.43	148.78	64.49	1.26	2.91
10	181.65	139.64	58.59	1.30	3.10
Mean	190.89	130.58	58.09	1.49	3.31
SD	16.64	22.77	7.10	0.21	0.30

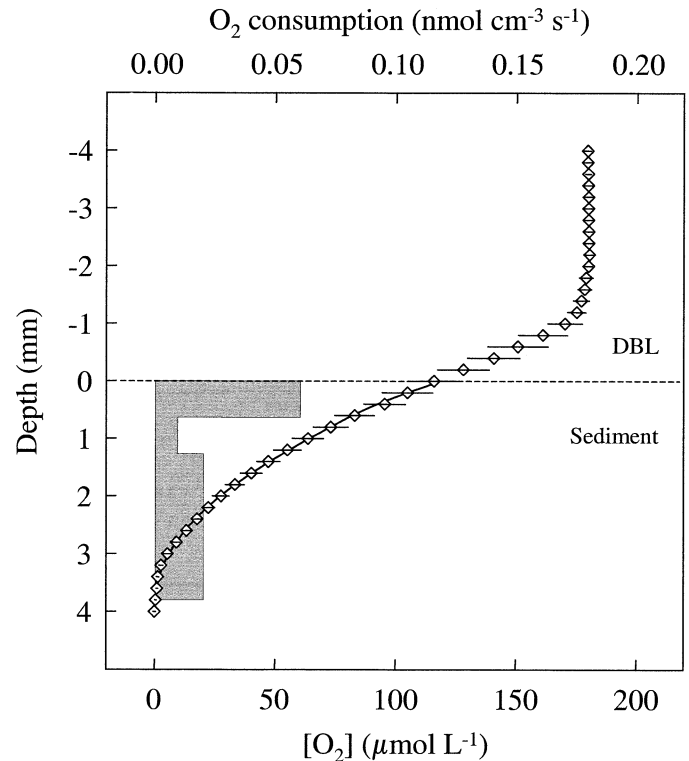


Fig. 2. Vertical $[\text{O}_2]$ profile (diamonds) and O_2 -consumption rates (bars) at the sediment–seawater interface in the aquarium. The O_2 -consumption profile and the fit ($R^2 = 0.9996$) were calculated from the mean $[\text{O}_2]$ profile according to the method of Berg et al. (1998). For $[\text{O}_2]$, symbols indicate the mean ($n = 6$), and horizontal lines indicate standard deviations. Note that concentrations are given per volume of pore water, but consumption rates are given per volume of sediment. The sediment–water interface is located at 0 mm (dashed line). The speed of the overlying water, measured ~ 5 cm above the sediment surface, was $\sim 2 \text{ cm s}^{-1}$. Salinity = 32; temperature = $17 \pm 0.2^\circ\text{C}$.

completion of the measurements, an average of 32 ± 3 burrow openings and 20 ± 5 arms were visible at the sediment surface per treatment microcosm (Table 1); that is, each burrow of *A. filiformis* had three arm channels, and each individual extended two arms. A few disk chambers were visible against the cylinder at a mean sediment depth of $4.75 \pm 0.56 \text{ cm}$ ($n = 6$).

Respiration of *A. filiformis*—The adult specimens of *A. filiformis* recovered from the microcosms had a mean individual wet weight (WW) of $131 \pm 23 \text{ mg}$ and a mean dry weight (DW) of $58 \pm 7 \text{ mg}$ ($n = 10$, Table 3). Their individual O_2 consumption averaged $191 \pm 17 \text{ nmol O}_2 \text{ h}^{-1}$ ($n = 10$, Tables 2-A4, 3). Their weight-specific O_2 consumption was $1.49 \pm 0.21 \mu\text{mol g WW}^{-1} \text{ h}^{-1}$ and $3.31 \pm 0.30 \mu\text{mol g DW}^{-1} \text{ h}^{-1}$.

O_2 flux across the DBL—Figure 2 shows the average $[\text{O}_2]$ profile across the interface between the seawater in the aquarium and the sediment, calculated from arithmetic means of six replicate measurements. The O_2 flux into the sediment was estimated both from the $[\text{O}_2]$ gradients in the

Table 4. Oxygen concentration in different burrow segments of undulating *A. filiformis* individuals. Average values and standard deviations were calculated from means of 1500 data points continuously recorded at a frequency of 25 Hz. The speed of the overlying water, measured ~ 5 cm above the sediment surface, was ~ 2.0 cm s^{-1} .

Burrow region	Arm position	[O ₂] ($\mu\text{mol L}^{-1}$)
Arm-channel entry	On sediment surface	102.8 ± 28.9
Arm-channel lumen, depth ~ 1.5 cm	Upright	220.3 ± 32.6
Disk-chamber lumen	Upright	110.5 ± 27.4

diffusive boundary layer (DBL) and from the pore-water-[O₂] profiles. The thickness of the effective diffusive boundary layer (Jørgensen and Revsbech 1985) was ~ 1 mm, and the average [O₂] gradient in the DBL was 0.547 ± 0.064 $\mu\text{mol cm}^{-4}$. Under the assumption of $D = 1.814 \times 10^{-5}$ cm² s^{-1} at a seawater temperature of 17°C and a salinity of 32, the average O₂ flux from the seawater into the sediment was 358 ± 42 $\mu\text{mol m}^{-2} \text{h}^{-1}$ (Table 2-B1).

O₂ penetrated 4 mm into the sediment. We used the six replicate measurements of pore-water [O₂] to compute the best-fitting concentration profiles and the resulting O₂-consumption profiles. The porosity of the sediment was $\phi = 0.83$, so the diffusivity corrected for tortuosity was $D_s = 1.51 \times 10^{-5}$ cm² s^{-1} . Bioturbation and irrigation by meiofauna were neglected. The calculated concentration profiles closely matched the data points, giving R^2 values >0.999 . The average depth-integrated, O₂-consumption rate (the

equivalent flux across the sediment-water interface) was 346 ± 35 $\mu\text{mol m}^{-2} \text{h}^{-1}$ (Table 2-B1). The highest O₂ consumption rates (0.06 nmol cm⁻³ s^{-1}) were found in the upper zone of the sediment (Fig. 2).

Burrow water [O₂]—A few *A. filiformis* individuals lowered the extended, upright parts of their arms toward the sediment surface at a bottom-water flow of ~ 2 cm s^{-1} . This arm position allowed us to insert the electrode into the opening of the arm channel so that the sensor tip was positioned on one side of the arm, 1 mm below the sediment surface. The [O₂] there averaged 103 ± 29 $\mu\text{mol L}^{-1}$ ($n = 8$) (Table 4; curve 1 in Fig. 3A as an example). Note that we did not take measurements at this position with the extended parts of the arms in an upright position.

Burrows that were partially visible against the wall of the aquarium allowed us to record [O₂] in the burrow lumen with visual control of the sensor-tip position and the behavior of the brittle stars. The [O₂] in the channel lumen of undulating arms that had their tips extended and in upright position averaged 220 ± 33 $\mu\text{mol L}^{-1}$ ($n = 12$) measured ~ 1.5 cm below the sediment surface (Table 4; curve 2–3 in Fig. 3A). In the lumen of the disk chambers of undulating individuals, a mean [O₂] of 111 ± 27 $\mu\text{mol L}^{-1}$ ($n = 8$) was measured (Table 4; curve 4 in Fig. 3A as an example).

Undulation frequency—The continuous recordings in burrow lumens gave rising and falling values (Fig. 3A) because of the undulating movements of the arms of the brittle stars. Depending on the position of the sensor tip, one side or the other of the arm (Fig. 3A, curves 1, 2, and 4; Fig. 3B) or

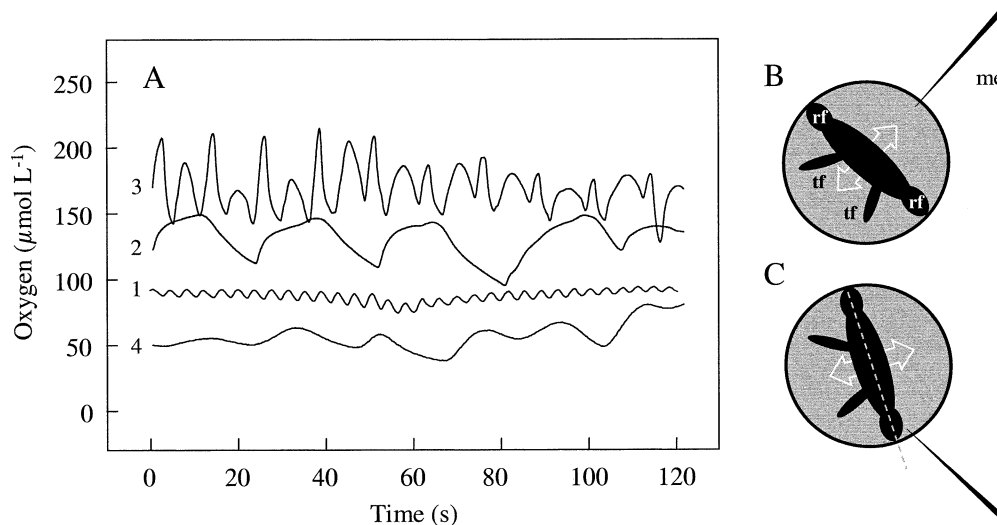


Fig. 3. *A. filiformis*. (A) Recordings of [O₂] (1) at the burrow opening; (2) and (3) in the lumen of an arm channel, ~ 1.5 cm below the sediment surface; and (4) in the disk chamber. (B,C) Schematic drawing of an arm-channel cross section and a microelectrode (me). White arrows indicate the direction of the arm's movement. The arm is flanked by projecting spines, which may account for about half the total width of the arm. The respiratory fringes (rf) are aggregations of substratum particles consolidated with mucus. During undulation, the driving effect of the trunk of the arm would be reduced by the lateral displacement of water through the gaps between the arrays of spines if these gaps were not blocked by these aggregations of particles. The tube feet (tf) project downward, clear of the fringe, during undulation.

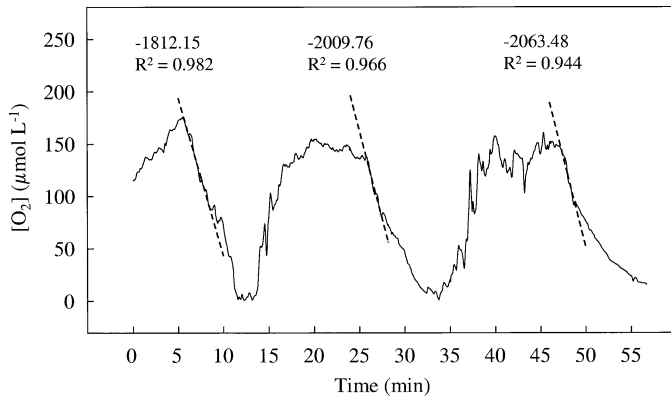


Fig. 4. *A. filiformis* disk chamber $[O_2]$. At 5, 25, and 45 min, the burrow openings were blocked. The slopes of the $[O_2]$ curves immediately after closure are shown ($\mu\text{mol L}^{-1} \text{ h}^{-1}$). From these slopes, the total oxygen consumption of the inhabited burrow was estimated. Salinity = 32; temperature = $17 \pm 0.2^\circ\text{C}$.

the respiratory fringes (Fig. 3A, curve 3; Fig. 3C) disturbed the sensor tip, causing a rapidly decreasing signal once or twice per undulation, respectively. This effect was used to estimate the frequency of undulation. Measurements with the sensor tip positioned ~ 1.5 cm below the sediment surface in the lumen dorsal or ventral of arms whose tips were extended and upright revealed an undulation frequency of $2.4 \pm 0.2 \text{ min}^{-1}$ ($n = 3$). A higher frequency of $4.9 \pm 0.2 \text{ min}^{-1}$ ($n = 9$) was observed shortly after the flow in the aquarium was stopped (Fig. 3A, curve 3). During the latter recordings, the respiratory fringe of the arm passed the sensor tip twice per undulation; that is, the sensor detected the $[O_2]$, for example, for 3.6–6.2 s on one side and 6.2–8.6 s on the other side of the arm. The different durations of the exposures indicated that the sensor tip was not in line with the lateral axis of the arm (Fig. 3C). The durations of the two phases were negatively correlated ($\rho = -0.904$); that is, the exposure of the sensor tip to one side of the arm increased when the exposure to the opposite side decreased. This negative correlation arose because the arm rotated along its longitudinal axis when the extended arm tip moved from an upright position toward the sediment surface. The undulation frequency of the distal end of the buried arm estimated from the $[O_2]$ measurements in the channel opening 1 mm below the sediment surface averaged $15.3 \pm 1.1 \text{ min}^{-1}$ (Fig. 3A, curve 1).

O_2 demand of inhabited burrows—We estimated the O_2 demand of an inhabited burrow by measuring the change of the $[O_2]$ in the disk chamber immediately after plugging the uppermost millimeter of all three arm channels with sediment using a small spatula. A microelectrode was inserted into the disk chamber in such a way that the tip of the electrode was positioned in the seawater-filled space between the disk of the brittle star and the inner surface of the disk chamber. Immediately after the openings of the burrow had been closed, the $[O_2]$ in the disk chamber dropped quasi-linearly ($R^2 = 0.964 \pm 0.016$) at a rate of $1962 \pm 108 \mu\text{mol L}^{-1} \text{ h}^{-1}$ (three trials, same burrow; Fig. 4). The burrow system consisted of three arm channels, each 6.7 cm long and 2.31

mm wide, and a hemispherical disk chamber (diameter = 0.8 cm), so the total surface area and the volume of the burrow were 15.60 cm^2 and 0.977 ml , respectively. Subtracting the volume of the inhabitant (0.688 ml) from the volume of the burrow gives the volume of the seawater in the burrow, 0.289 ml . The total O_2 consumption of the burrow + inhabitant was $567 \pm 31 \text{ nmol h}^{-1}$ (Table 2-B3).

Pore water $[O_2]$ around arm channels—Figure 5B–F shows $[O_2]$ profiles in a plane normal to the long axis of the arm channel, constructed from vertical measurements across the lumens of the arm channels and the surrounding sediment (chords A and B, Fig. 1). An example of such measurements is shown in Fig. 5A. The stepwise $[O_2]$ measurements in the sediment immediately surrounding the arm channels (see below) gave stable readings at each distance from the inner surface of the channel. The lengths of the chords A and B were defined by the points along the profile at which O_2 was detected. The relative position of the inner surface of the arm channel was detected by the onset of oscillating readings and the abrupt change in $[O_2]$. The profiles across the arm channels revealed that O_2 penetrated the surrounding sediment $0.73 \pm 0.18 \text{ mm}$ ($n = 5$). The maximum thickness of the oxic halo was 1.04 mm ; the minimum thickness was 0.53 mm . The average diameter of the arm channels was $2.31 \pm 0.25 \text{ mm}$ (maximum, 2.61 mm ; minimum, 1.95 mm). The $[O_2]$ at the inner surface of the arm channel ranged from 85 (Fig. 5F) to $202 \mu\text{mol L}^{-1}$ (Fig. 5B).

On the simplifying assumption that the oxygenated zone around the arm-channel lumen is planar, the O_2 -consumption rate as a function of the distance from the inner surface of the lumen and the flux across the wall of the lumen can be calculated according to the method of Berg et al. (1998). Irrigation and bioturbation by meiofauna were neglected, and the sediment porosity and thus the sediment diffusion coefficient were assumed to be constant with distance from the burrow wall. The measured $[O_2]$ profiles normal to the long axis of the arm-channel lumen, the calculated best-fitting concentration profiles, and the consumption profiles are shown in Fig. 5B–F. The average integrated O_2 consumption of the burrow wall area $\sim 1.5 \text{ cm}$ below the sediment surface calculated from the five replicate profiles was $1451 \pm 301 \mu\text{mol m}^{-2} \text{ h}^{-1}$ (Table 2-B5). The O_2 consumption rates were at their highest at the interface between the lumen and the burrow wall (Fig. 5D–F) and at the transition between the oxic and anoxic zones (Fig. 5B,C).

Discussion

The aim of our study was to quantify the effect of the ophiuroid *A. filiformis* on the total O_2 flux into the sediment. For this purpose, we measured the O_2 utilization of enclosures of both macrofauna-free sediment and sediment in which brittle stars had buried themselves. These experiments were supplemented by microscale $[O_2]$ measurements in an aquarium with flowing seawater, where in situ boundary-layer flow conditions could be simulated. In the following, we will compare and discuss the results of these two different approaches and then use our data to estimate the contri-

bution of a natural *A. filiformis* population to the O_2 flux into the sediment.

The results from our microcosm experiments incorporate various possible effects of the brittle stars on the O_2 flux. The microelectrode measurements in the flow aquarium, in contrast, allowed the O_2 flux to be measured under more realistic flow conditions and permitted recordings of $[O_2]$ in different regions of the burrow at high temporal and spatial resolution. Because the buried brittle stars remained in the same burrows during our experiments, the possible effects of sediment reworking due to density-dependent migration of the brittle stars could not be considered.

O_2 uptake of macrofauna-free sediment—The diffusive O_2 flux into the sediment of the flow aquarium calculated from O_2 gradients in the DBL agreed well with the O_2 uptake rate modeled from the pore-water $[O_2]$ profile (Table 2-B1). Such consistency was also reported in studies in coastal and deep-sea regions by Rasmussen and Jørgensen (1992) and Glud et al. (1994). The estimated TOU of the control microcosms (without macrofauna) was higher than the O_2 flux into the sediment of the aquaria (by a factor of 1.47; Table 2, compare A1 and B1). This difference probably resulted because, in contrast to the value calculated from microelectrode recordings in the aquaria, the values from our microcosm measurements integrated the O_2 uptake of the seawater overlying the sediment. The latter was independently estimated during the measurement of brittle-star respiration (control) to be $1.36 \mu\text{mol L}^{-1} \text{h}^{-1}$, so it contributed $\sim 20\%$ of the TOU of the control microcosm. The difference between microcosm TOU and the O_2 uptake of the sediment in the aquaria might also have been due to the rotating flow in the microcosms, which prevented the development of natural DBL (~ 1 mm thick). As a consequence, higher $[O_2]$ occurred at the sediment surface, and the sediment therefore consumed more O_2 . The probability of pore-water irrigation by pressure gradients that exist in rotating flow is likely to be negligible in muddy sediment, in contrast to the situation in permeable sediments, where this irrigation increases the O_2 flux significantly (Huettel and Gust 1992; Booi et al. 1994; Glud et al. 1996).

*Impact of *A. filiformis* on the TOU of the sediment*—Buried *A. filiformis* contribute to the total O_2 flux by their respiration and by the O_2 uptake of the additional sediment surface that they create (i.e., the inner surfaces of their burrows). The mounds around their burrow openings are made of sediment from deeper layers ejected to the surface as the feeding arms push up through the sediment–water interface. This sediment can consume more O_2 than the surrounding surficial sediment, as was shown for mounds raised by *C. subterranea* by Forster and Graf (1995). Furthermore, the extended arms of *A. filiformis* can increase the O_2 uptake of the superficial sediment by disturbing the boundary layer flow and by moving particles while sweeping the sediment surface in circles (Duchêne and Rosenberg 2001). We estimated the TOU of an inhabited burrow from (1) the decrease in the $[O_2]$ of the seawater in the microcosms with and without brittle stars (Table 2-A3) and (2) direct measurements of $[O_2]$ in the disk chamber after all burrow openings had been

closed (Table 2-B3). The values from (1) integrate all above-mentioned effects, whereas the microelectrode approach used in (2) accounts only for the $[O_2]$ uptake of the brittle star and the inner burrow surface. Because these two different estimates gave similar results, the possible effects of the excavated sediment (mounds) and the activity of the brittle star arms at and on the sediment surface are likely to be negligible. Given the diffusive O_2 uptake of the sediment surface (Table 2-B1) and the TOU of a buried individual as calculated from our microscale measurements under conditions of unidirectional boundary layer flow in the aquaria (Table 2-B3), the TOU of sediment populated by 1326 individuals m^{-2} would be $1110 \mu\text{mol m}^{-2} \text{h}^{-1}$ (Table 2-B2). This value is only 15% smaller than the value calculated from our microcosm experiments (Table 2-A2).

*Respiration by *A. filiformis**—We measured the mean weight-specific O_2 consumption of *A. filiformis* to be $1.5 \mu\text{mol g WW}^{-1} \text{h}^{-1}$ by incubating the brittle stars in air-free flasks of normoxic seawater without sediment. A similar approach was used by Buchanan (1964), who reported a higher respiration rate of $0.058 \text{ ml } O_2 \text{ g WW}^{-1} \text{h}^{-1} = 2.59 \mu\text{mol g WW}^{-1} \text{h}^{-1}$ at a lower temperature of 6°C . In neither case were conditions natural. Our measurements in the main chamber of the burrow revealed that the disk of the brittle star experienced an $[O_2]$ of only 40%–48% air saturation. At low $[O_2]$, respiration rates of benthic animals decline (Theede et al. 1973), so *A. filiformis* is likely to consume less O_2 in its natural environment than during our respiration measurement. Nevertheless, we use this value (Table 2-A4) to estimate the total O_2 flux across the burrow wall by subtracting it from the calculated burrow TOU (Table 2-A3, see below), because a possible discrepancy between the measured and the actual respiration rate of a buried *A. filiformis* is apparently balanced by the O_2 consumption of the sediment constituting the “respiratory fringe” of the brittle star and of the sediment particles transported along the arms.

O_2 uptake of the inner burrow surface—Given that the TOU of an inhabited burrow was 582 nmol h^{-1} (Table 2-A3) and that the respiration rate measured under normoxic conditions (Table 2-A4) accounted for the O_2 consumption of the buried brittle star, its “respiratory fringe,” and mobile sediment particles, the O_2 demand of the inner burrow surface would be 391 nmol h^{-1} —that is, 67% of burrow TOU (Table 2-A5). A calculation based on the burrow TOU of 567 nmol h^{-1} , as estimated from the change in burrow water $[O_2]$ after irrigation was stopped (Fig. 4; Table 2-B3), gives a marginally lower value of 66% of burrow TOU (376 nmol h^{-1}).

On the assumptions that the O_2 demand of the burrow wall was 391 nmol h^{-1} and that the inner surface area of the burrow was 15.6 cm^2 , the O_2 flux from the burrow lumen into the surrounding sediment would be $251 \mu\text{mol m}^{-2} \text{h}^{-1}$ (Table 2-A5). This flux is 30% lower than the flux estimated for the sediment surface (Table 2-B1). The average O_2 flux calculated from the microelectrode measurements around the arm channels, however, was $1451 \mu\text{mol } O_2 \text{ m}^{-2} \text{h}^{-1}$ —5.8 times higher than the value calculated above. This rate applies only to the upper region of the arm channel, however.

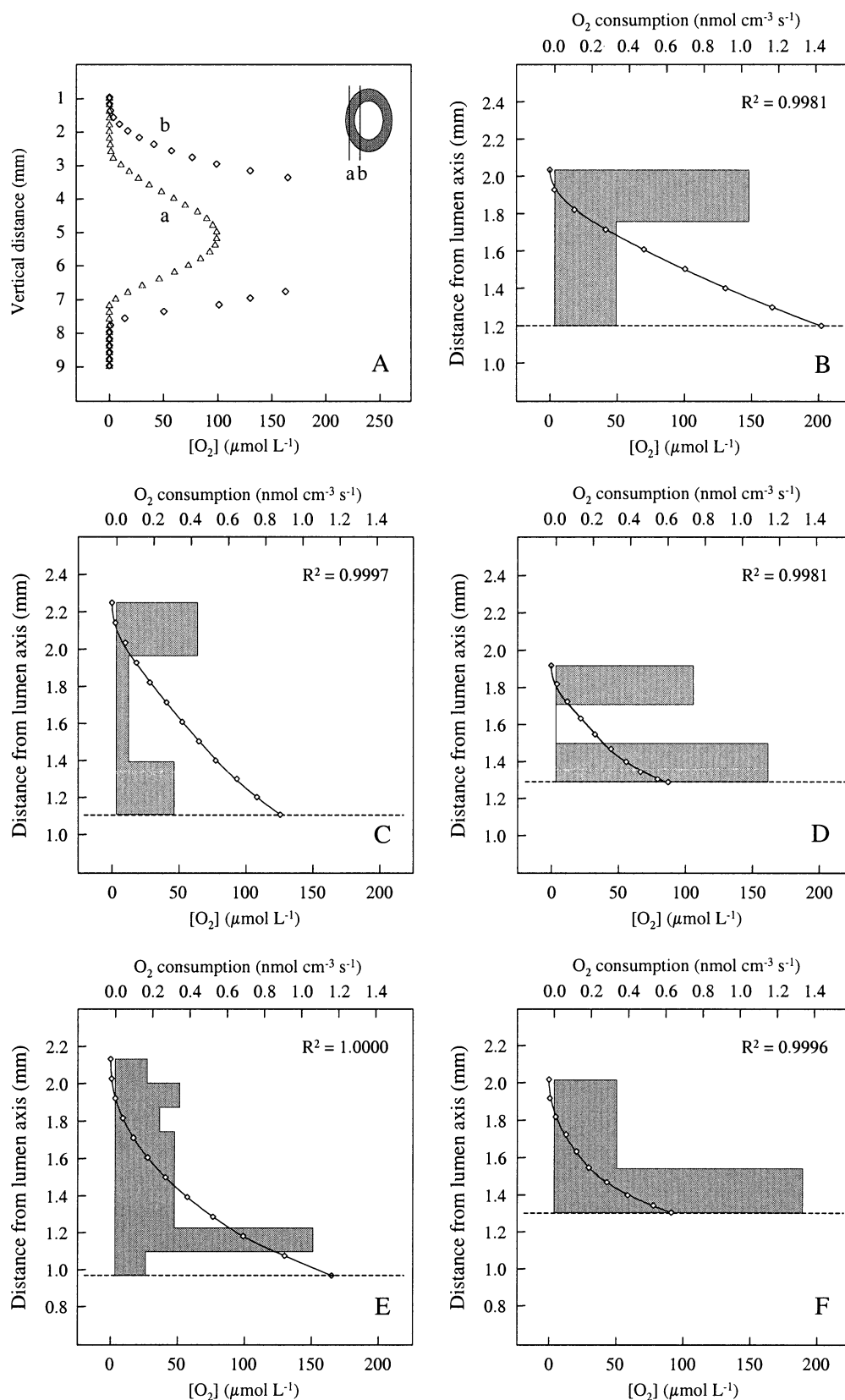


Fig. 5. (A) Example of two parallel, vertical profiles of pore-water $[O_2]$ (a, b) across the sediment immediately surrounding the lumen of an *A. filiformis* arm channel (see inset). The tip of the electrode crossed the long axis of the arm channel lumen ~ 1.5 cm below the sediment surface at

The $[O_2]$ in the channel lumen decreased with increasing sediment depth, and so should the flux into the surrounding sediment. Furthermore, the $[O_2]$ profiles across the burrow wall were only measured in channels of undulating arms. Although *A. filiformis* usually has two arms extended (Table 1; Loo et al. 1996), apparently only one arm ventilates the burrow; seawater is driven down that arm to the disk and then flows passively up the other channels (Ockelmann and Muus 1978), so the $[O_2]$ in the lumen and the O_2 flux into the sediment surrounding the latter channels were likely to be lower. The O_2 -consumption profiles across the sediment surrounding the channel lumen (Fig. 5) were calculated on the assumption that the porosity (and diffusivity) of this sediment equaled the porosity of the bulk sediment. The channel wall, however, was apparently compacted and stabilized with mucus (Buchanan 1964; Woodley 1975). Compaction would decrease the diffusivity for solutes, so our calculation would overestimate the flux. Higher consumption rates near the inner surface of the burrow (Fig. 5) were probably due to the supply of easily degradable material. The higher O_2 consumption at the oxic/anoxic interface can be explained by an oxidation of reduced organic and inorganic compounds from the anaerobic mineralization in the surrounding sediment.

The comparison of our different estimates for the O_2 uptake of the burrow wall shows that, for a realistic estimate of the total O_2 uptake of the inner surface of the burrow system, a large number of $[O_2]$ profiles measured in different parts of the burrow would be required. Combining microscale measurements with enclosure experiments, however, provides the average TOU of the burrow system and detailed information on the behavior of the brittle stars. Our measurement of $[O_2]$ in different sections of the burrow system revealed that, in future studies, microelectrodes can be used to investigate how the behavior associated with its response to changes in boundary layer conditions and food supply of the buried brittle star affects the burrow chemistry. Such studies can be carried out in situ because visual control of the electrode tip within the sediment is not essential.

Behavioral control of solute transport—Oxygenation of the burrow water and the pore water of the sediment surrounding the lumen of the burrow is determined by behavior patterns associated with three main functions of the arms: ventilation and respiration, the transportation of sediment and waste material out of the burrow, and the collection and transportation of food (Woodley 1975; Ockelmann and Muus 1978). The oxygenation of the pore water surrounding the lumen of the burrow is crucial for *A. filiformis* and the associated micro- and meiofauna because it prevents the diffusion of sulphide into the burrow system. Vistisen and Vismann (1997) showed that, al-

though this brittle star tolerates hypoxia very well, even low concentrations of sulfide decrease its survival significantly. *A. filiformis* is apparently able to avoid contact with sulfide by maintaining a seawater flow through the burrow given a bottom-water $[O_2]$ as low as 10% saturation. At lower concentrations, the brittle star leaves its protected position in the sediment and appears at the sediment surface (Rosenberg et al. 1991; Vistisen and Vismann 1997). The aeration of the burrow is controlled by a wavelike undulation of one arm within its channel and by pumping due to raising and lowering of the disk (Woodley 1975). The wavelength and period increase from the burrow opening toward the disk (compare curves 1 and 2 in Fig. 3). Under conditions of bottom-water flow, the wave period measured at the burrow entrance was 4 s. This observation agrees with that of Woodley (1975). Shortly after the flow was stopped, the wave period, measured ~ 1.5 cm below the sediment surface, decreased from 25 to 12 s. Similar behavior was observed by Woodley (1975), who reported that in stagnant water the movement sometimes reached a rate of 100 waves min^{-1} (a period of 0.6 s, most probably measured at the burrow entrance).

A. filiformis can switch between deposit and suspension feeding; that is, the extended arm tips are held low to explore the surface of the sediment for particles or up vertically to a distance of 3–4 cm above the sediment surface to trap both nonliving particulate suspended matter and phytoplankton (Buchanan 1964; Woodley 1975). Our measurements indicated that these different arm positions affected burrow-water oxygenation. Under flow conditions, the average $[O_2]$ at the burrow opening was as low as $103 \mu\text{mol L}^{-1}$ when the extended arms were positioned on the surface of the sediment (Table 4). This value approximated the values measured at the sediment surface under conditions of diffusion across the DBL (Fig. 2). Although we were not able to measure $[O_2]$ at the burrow opening when the arm tip was in the upright position, our recordings in the channel lumen, ~ 1.5 cm below the sediment surface, revealed an average of $220 \mu\text{mol O}_2 \text{ L}^{-1}$ (Table 4), indicating that this arm position results in an advective transport of seawater toward the arm channel opening and therefore in a higher burrow-water $[O_2]$.

Potential impact of *A. filiformis* on TOU of soft bottoms—If bottom seawater is fully oxygenated and the average O_2 demand of a buried adult *A. filiformis* is 582 nmol h^{-1} (Table 2-A3), the diffusional O_2 flux into a square meter of macrofauna-free sediment ($\sim 350 \mu\text{mol h}^{-1}$; Table 2-B1) would be doubled by the presence of only 600 individuals of *A. filiformis*. The densities of natural populations of *A. filiformis* are known to be $>3000 \text{ individuals m}^{-2}$ (Rosenberg 1976, 1995; Josefson 1995). At a somewhat lower density of 2500

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an angle of 45° . From such measurements, an $[O_2]$ profile normal to the long axis of the arm channels was constructed (B–F, symbols). The fits and the O_2 -consumption profiles (bars) in panels B–F were calculated from the $[O_2]$ profiles as described by Berg et al. (1998). Note that $[O_2]$ is given per volume of pore water, but consumption rates are given per volume of sediment. A dashed line indicates the interface between the burrow lumen and the surrounding sediment.

individuals m^{-2} , as reported by Rosenberg (1995) for the east and west slopes (65–90 m depth) of a trench in the Skagerrak, western Sweden, at least 80% of the total O_2 flux into the sediment would be due to *A. filiformis*. Given the additional effects of associated infaunal species on the total O_2 flux, the portion of the total transport attributable to diffusion through the boundary layer of the sediment surface would be <20%. This example emphasizes that information on how key species control their physical microenvironment is crucial for a better understanding of solute exchange across the sediment–water interface.

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