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Ciliate-generated advective seawater transport supplies chemoautotrophic ectosymbionts

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ABSTRACT: Variations of [O_2] and [H_2S] in seawater surrounding laboratory-reared sessile ciliates with ectosymbiotic chemoautotrophic bacteria were studied at high spatial and temporal resolutions using amperometric microsensors. We show how suspension feeding by the colonial *Zoothamnium niveum* and the solitary *Vorticella* sp. in the chemocline (O_2/H_2S-interface) of near-natural and artificial H_2S-releasing substrates generates the physico-chemical microenvironment for the ectobiotic bacteria. Continuous recordings revealed a steep increase of [O_2] and decrease of [H_2S] in the proximal region of *Z. niveum* colonies during rapid stalk contraction. Hydrogen sulphide concentrations 2.5 mm above the substrate (upper end of the fully extended colony) increased when the contracted colony extended, followed by a decrease after the colony attained the fully upright position. Multiple contractions without complete extension successively transported sulphidic seawater upwards. The solitary *Vorticella* sp. maintained high ambient [O_2] and low [H_2S] 350 µm above the H_2S-releasing membrane by generating a vertical flow field that drew seawater from above toward the ciliate. Oxygen concentration at the proximal part of *Vorticella* sp. did not increase during contraction, whereas during slow extension deoxygenated seawater was transported upwards and rapidly mixed with the surrounding oxygenated seawater when the ciliate started to beat its cilia. In both species rapid stalk contraction and subsequent slow extension enhanced the mixing of oxygenated and deoxygenated, H_2S-containing seawater; the feeding currents (toroidal vortices) drew the surrounding seawater within reach of the zooid's external surface at high speed. It is suggested that this advective fluid transport supplies the ectobiotic bacteria with O_2 and H_2S simultaneously. The high fluid velocity may cause a decrease in cell boundary layer thickness, thereby enhancing rates of nutrient uptake by the ectobiotic bacteria.

KEY WORDS: Sessile peritrich ciliates · Suspension feeding · Vortex · Chemoautrophic bacteria · Ectosymbiosis · Oxygen · Hydrogen sulphide

INTRODUCTION

Suspension feeding by sessile peritrich ciliates takes place in chemical and physical gradients along surfaces. Low flow speed near the surface facilitates attachment but only high flow farther away provides sufficient food (Vogel 1996). Species of the peritrich ciliate genera *Vorticella* (Linné) Ehrenberg, 1838 and *Zoothamnium* Bory de Saint Vincent, 1826 grow on stalks, thus elevating their filtration apparatus. The zooids beat their peristomial cilia in a way that puts the animal in the centre of a particle-trapping flow field (toroidal vortex). Feeding is frequently interrupted by animal contraction of an all-or-nothing type involving cell body shrinkage and coiling of the stalk (Hoffmann-Berling 1958, Amos et al. 1976, Katoh & Naitoh 1994).

The solitary *Vorticella* sp. and the colonial *Zoothamnium niveum* (Hemprich & Ehrenberg, 1831) possess white ectobiotic bacteria when growing at point sources

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of H_2S (Ott et al. 1998). In *Z. niveum* ('niveum' = snowy) all but the most basal parts of its feather-shaped colonies are covered with an irregular layer of coccoid and rod-shaped chemolithoautotrophic bacteria (Bauer-Nebelsick et al. 1996a,b). Characteristic and specific ultrastructural affinities between *Z. niveum* and the ectobiotic bacteria compelled Bauer-Nebelsick et al. (1996a) to infer a symbiotic relationship. There is evidence that the ciliates feed on their ectobionts since food vacuoles contain only bacteria having the same characteristic ultrastructure as the symbionts (Bauer-Nebelsick et al. 1986b). In addition the high growth rates in colonies with ectobionts compared to those of aposymbiotic colonies (authors' unpubl. obs.) suggest a trophic relationship. The true nature of a mutualism, however, remains to be determined. The white colour of the bacteria is due to the cellular inclusion of elemental sulphur and makes the bacteria-ciliate association conspicuous: white specimens of both *Zoothamnium* and *Vorticella* grow, for example, on decomposing debris in Mediterranean *Posidonia* meadows and on 'white spots' at the surface of vertical or overhanging walls cut into highly sulphidic mangrove peat of tidal channels in the Belize Barrier Reef system (for a detailed description of the habitat see Ott et al. 1998). The term 'white spot' refers to small sites (mm–cm scale) where the peat surface is disturbed in the vicinity of decomposing rootlets, where the non-stationary transition zone between the O_2-saturated and deoxygenated, H_2S-containing seawater (chemocline) is positioned at or above the peat surface, and where sulphur-oxidising bacteria rapidly proliferate.

The present study aims to examine how the chemical microenvironment for the chemolithoautotrophic ectobionts is generated. A recently proposed model assumes that *Zoothamnium niveum* supplies its ectobiotic bacteria alternately with O_2 and H_2S by moving through sharply defined gradients using rapid contraction and slow expansion (Ott et al. 1998). It was hypothesised that, depending on the state of contraction or expansion, the colonies are bathed in seawater containing H_2S and only a little O_2, or in O_2-saturated, H_2S-free seawater. Due to the small size of the colonies, all motion occurs under low Reynolds numbers at which viscous forces prevail and seawater 'adheres' to moving objects. In order to 'get rid' of the surrounding fluid the ciliates have to move quickly. This increases the Reynolds number and prevents O_2-laden seawater from being dragged along with the colony, which otherwise would push the sulphidic bottom water away before contact with the bacteria. This model is tested by applying fast responding amperometric O_2 and H_2S microelectrodes to 2 different laboratory-reared bacteria-ciliate associations.

MATERIALS AND METHODS

Sampling and experimental set-up. Large colonies of *Zoothamnium niveum* and blocks ($10 \times 10 \times 10$ cm) of red mangrove *Rhizophora mangle* Linnaeus peat were cut off from vertical overhanging walls at the north end (Batfish Point) of the intertidal mangrove island Twin Cays in January 2000. Twin Cays is located inside the Tobacco Reef section of the Belize barrier reef (16° 48′ N, 88° 05′ W). Detailed information about the site and a description of the area are available from Rützler & Macintyre (1982) and Ott et al. (1998). The material was transported 3.5 km seawards to the island Carrie Bow Cay, where the laboratory of the Caribbean Coral Reef Ecosystem program of the National Museum of Natural History (Washington, DC) is located. The peat blocks and the ciliates were kept in small aquaria (seawater temperature 26°C, salinity 34) until swarmers settled on the freshly cut peat and developed into feather-shaped colonies. All measurements on *Z. niveum* were carried out on 3 to 4 mm-large, contracting colonies.

The chemical microenvironment of *Vorticella* sp. was studied in the laboratory of the Department of Marine Biology at the University of Vienna by means of Artificial Gradient Systems. The gradient systems were established by mixing dried seagrass debris with gypsum and reduced sediment in plastic containers capped by a black silicone rubber membrane. The containers were kept in seawater together with seagrass debris taken in the Gulf of Calvi (Mediterranean, Corsica, France) until *Vorticella* sp. populated the surface of the silicone membrane. The seawater temperature was 28°C, the salinity 39.

Microscale measurements. O_2 and H_2S concentrations were recorded under zero flow conditions using amperometric microsensors (ME 11025, ME 15025, MasCom GmbH, Germany) with a sensing tip diameter of <10 and <20 µm, respectively, a 90%-response time of <2 s, and a velocity sensitivity of <1% (Revsbech & Jørgensen 1986, Revsbech 1989, Jeroschewski et al. 1996, Kühl et al. 1998). The sensors were mounted on a micromanipulator (Märzhäuser, Germany) driven by stepping motors, secured to a stable iron frame, and moved vertically at 100 µm increments. A dissection microscope was used to control the movements of the tip near the surface of the peat or membrane of the gradient system, which served as the reference depth for vertical positioning. For continuous measurements in the vicinity of the ciliates the sensors were positioned at an angle of 45° relative to either the peat or membrane surface. The sensor current, measured by a miniaturised picoampere meter (MasCom GmbH) mounted directly on the shaft of the microsensors, was converted to a millivolt signal using a 2 channel-

indication-amplifier and digitised by an analogue-to-digital converter (DI 220, Dataq Instruments, Inc., USA) for PC data acquisition. Calibration of the oxygen microelectrodes was carried out at the experimental temperature, using the output current in the overlying seawater and in nitrogen-flushed seawater for air saturation and zero oxygen, respectively. The amperometric H_2S sensor detects the partial pressure of H_2S gas, which is only one component of the total sulphide equilibrium system. For calibration a buffered system (phosphate buffer, devoid of oxygen, adjusted to pH 6.8) was used, to which increasing amounts of a sulphide stock solution (1 mM) were added in increments. The total sulphide concentration in the stock solution was assayed by iodometric titration.

The relative role of convective to diffusive transport of O_2 was estimated by calculating the (dimensionless) Sherwood number, $1\ v/D$, where 1 is distance to the source of the solutes, v is maximum vertical velocity and D the diffusion coefficient (Vogel 1996).

RESULTS

Zoothamnium niveum (Fig. 1a)

The cut peat surface exposed circular cross-sections of small decomposing rootlets from which H_2S diffused into and mixed with the ambient, oxygen-saturated seawater in a hemispherical zone; maximum $[H_2S]$ at the centre of the rootlet were about 360 and 110 µmol l^{-1} at 0.5 and 1.0 mm above the cut-surface, respectively (Fig. 2). Oxygen concentrations increased with increasing distance from the rootlet's centre. Swarmers of *Zoothamnium niveum* preferentially settled at the edges of this point H_2S source (arrow in Fig. 2). The uncolonised margins of the rootlet's cross-section showed low concentrations of both gases, whereas relatively high $[O_2]$ (~100 µmol l^{-1}) or $[H_2S]$ (~300 µmol l^{-1}) were recorded at 1.0 and 0.5 mm above the colonised margin, respectively. These successive recordings, however, reflect an instantaneous picture. Simultaneous O_2 and H_2S measurements at the distal end of the stalk's basal, non-contractile part (1 mm height of a 3.2 mm-large, contracting colony) revealed rapid temporal variations (Fig. 3a): contraction resulted in a fast increase in $[O_2]$ and decrease in $[H_2S]$ (>20 µmol l^{-1}) of the bottom water. Original conditions were slowly restored during the subsequent extension of the colony. Continuous recordings of $[H_2S]$ 2.5 mm above the substrate (upper end of the fully extended colony) showed a clear, slow increase when the contracted colony extended, followed by a decrease after the colony attained it fully upright position (Fig. 3b). The O_2 concentration in the bottom water returned to the pre-contraction value after peaking and falling below the initial value. During multiple contractions without complete extension H_2S-containing seawater was successively transported upwards (Fig. 3c). In small colonies, straight upward movement followed contrac-

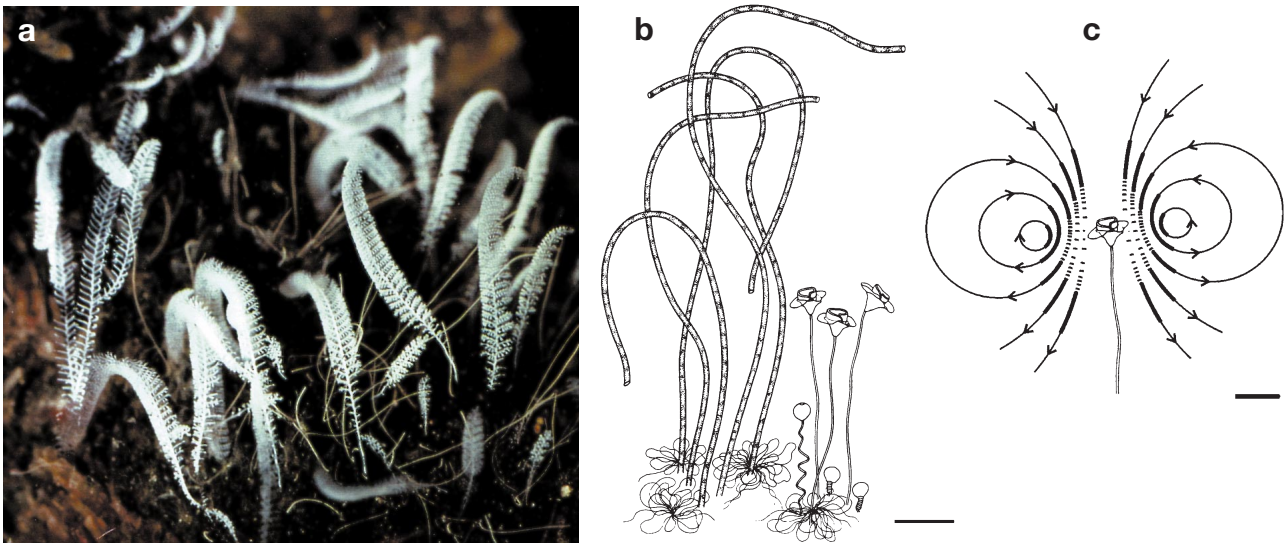

Fig. 1. (a) *Zoothamnium niveum.* Group of colonies on mangrove peat. Twin Cayes, Belize, CA. Largest colonies are 15 mm long. (b) Schematic representation of filamentous sulphur bacteria and *Vorticella* sp. growing on the H_2S-releasing silicone membrane of an Artificial Gradient System. (c) The particle-trapping vortex around an active *Vorticella* sp. Thin and bold lines indicate paths of particles moving at less than 10 µm s^{-1} and between 10 and 75 µm s^{-1}, respectively. Dotted line indicates faster motion: the distance between the dots equals the distance that a particle in that position would move in 0.1 s (redrawn from Sleigh & Barlow 1976). Scale bars = 100 µm

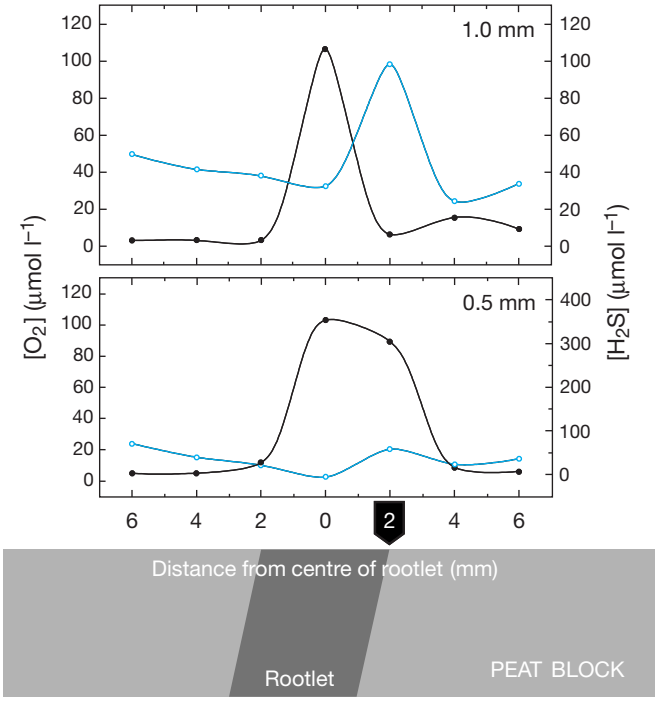

Fig. 2. Horizontal gradients of $[O_2]$ (○) and $[H_2S]$ (•) at 0.5 and 1.0 mm above H_2S-releasing mangrove rootlet (dark grey) cross-section in freshly cut peat (light grey). The 4 gradients were recorded successively. Black arrow indicates the section of the cross-section's margin colonised by colonies of *Zoothamnium niveum*. Note the different scales

tion; large, feather-shaped colonies extended almost horizontally and the fully extended colonies attained their upright position much slower, thus transporting more bottom water.

Vorticella sp. (Fig. 1b)

After an initial period of ageing (several days), the Artificial Gradient Systems created stable O_2 and H_2S fluxes with steep vertical steady-state gradients within a 2 mm-thick layer above the silicone rubber membranes (Fig. 4a). The gradients resulted from molecular diffusion and non-biological reaction of both compounds (to produce mostly $S_2O_3^{2-}$, SO_4^{2-}, and S^0). When kept under low flow conditions, the membranes become populated by a diverse thiobiotic community, consisting mainly of filamentous and unicellular sulphide-oxidising bacteria, heterotrophic flagellates, and ciliates (partly shown in Fig. 1b). *Vorticella* sp. modified the vertical $[O_2]$ and $[H_2S]$ gradients in their immediate surrounding (Fig. 4b) as long as motile sulphur bacteria did not form stable mats that capped the entire membrane and fixed the chemocline in a several µm-thick zone far above the 350 µm-tall ciliates and thus cut off their O_2 supply. Oxygen concentration gradients measured directly next to (horizontal distance ~20 µm) a non-contracting animal show an increased slope between 0.8 and 0.3 mm distance from the membrane surface. The mean $[H_2S]$ gradually increases below 1.1 mm, with a clear reversal between 0.6 to 0.3 mm, followed by a strong increase over the last few micrometers. In a later successional phase of the gradient systems, 300 to 400 µm-thick mats of filamentous sulphide-oxidising bacteria covering the entire membrane exclusively controlled sulphide fluxes.

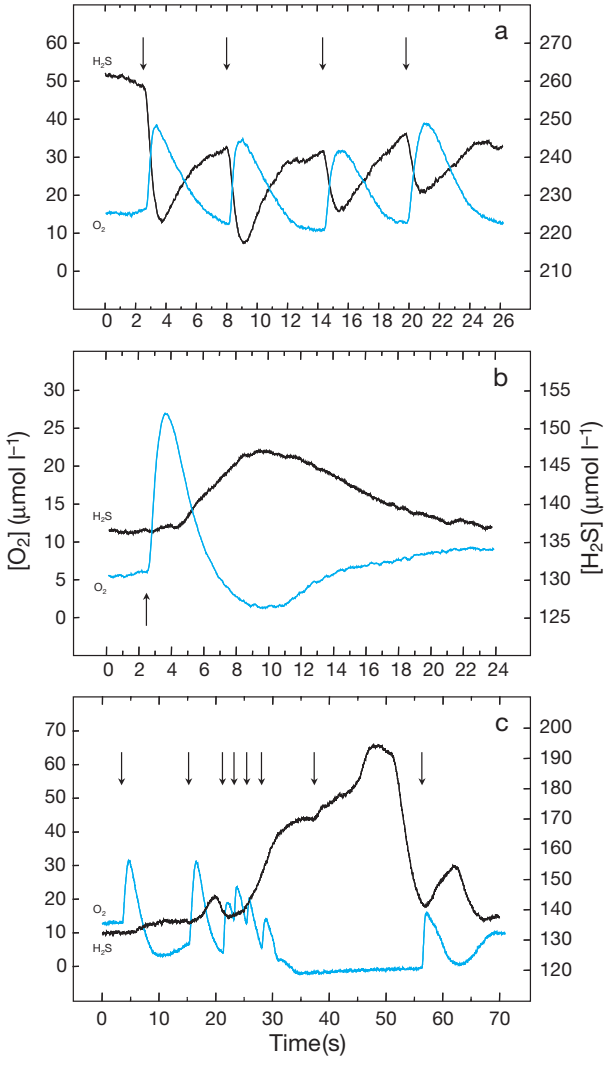

Fig. 3. Simultaneous O_2 (blue line) and H_2S (black line) recordings directly next to a 3.2 mm-large contracting colony of *Zoothamnium niveum*. The measurements were carried out at the edge of an H_2S-releasing mangrove rootlet cross-section in freshly cut peat. The sensor tips were positioned either at the distal end of the stalk's non-contractile proximal part (1 mm height) or at the upper end of the colony (2.5 mm height): (a) both sensors below; (b,c) O_2 sensor at the bottom, H_2S sensor above. Arrows indicate contraction

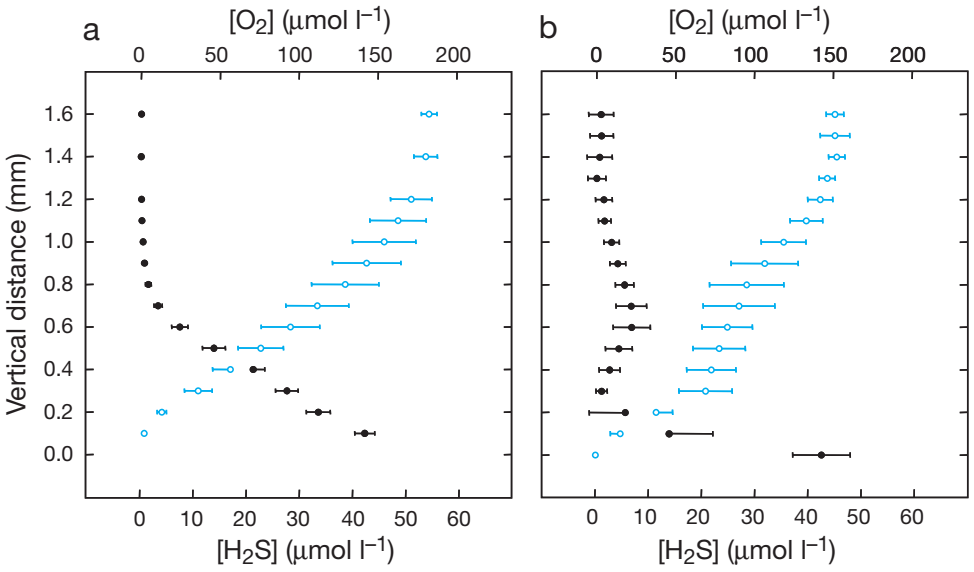

Fig. 4. Vertical $[O_2]$ (○) and $[H_2S]$ (•) gradients above silicone membranes of Artificial Gradient Systems (mean values, SD, n = 10) measured (a) above an uncolonised membrane and (b) directly next to a 350 µm-large *Vorticella* sp.

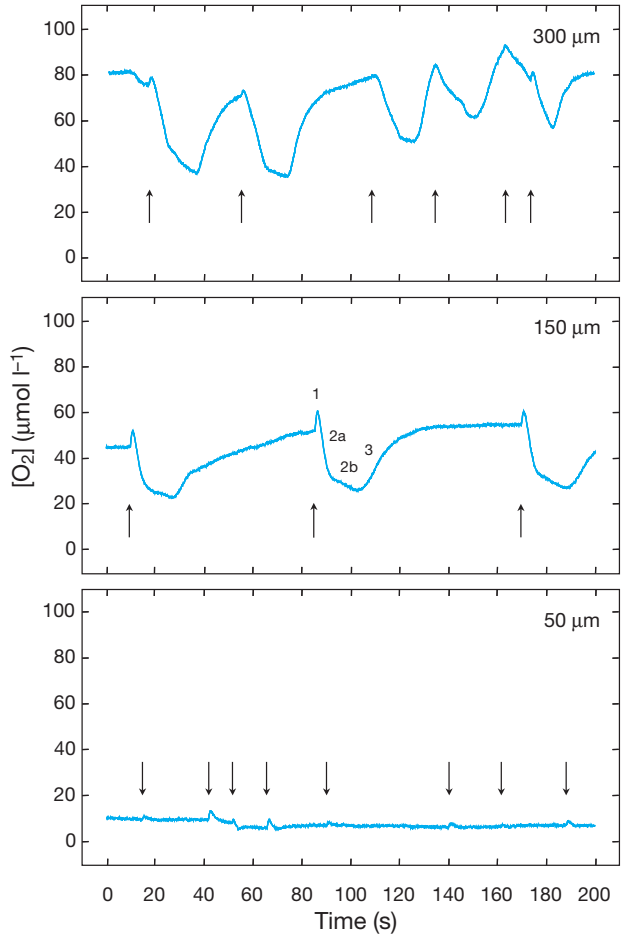

Fig. 5. Continuous oxygen recordings next to (~20 µm distance) a single, contracting, 350 µm-large *Vorticella* sp. and at vertical distances of the electrode from the substrate of 50, 150, and 300 µm. The 3 measurements were carried out successively. Arrows indicate contraction

Three phases of the contraction/extension cycle can be distinguished from continuous O_2 recordings in close proximity to a single, contracting, 350 µm-large specimen with the electrode tip placed 150 µm above the substrate (Fig. 5): (1) a brief, but steep increase in $[O_2]$, (2) a clear decrease which is initially (2a) steep and then (2b) gradually flattens, followed by (3) a lengthier but constant increase. These phases corresponded to the following ciliate activities: (1) lightning contraction, (2a) slow extension, (2b) full upright position without beating cilia, and (3) ciliary action creates vortex. During the last phase the initial conditions were gradually restored unless a further contraction started. The highest fluctuation of up to 40 µmol l^{-1} occurred at the distal end of the ciliate (300 µm distance of the electrode tip from the substrate). The measurements 50 µm above the substrate revealed relatively constant and low $[O_2]$ (<20 µmol l^{-1}) with brief intermediate peaks.

DISCUSSION

Motile swarmer stages of *Zoothamnium niveum* preferentially congregate at the edge of the point H_2S sources where oxygen and hydrogen sulphide coexist at low concentrations (chemocline), apparently by the combined effect of different types of chemosensory motile behaviour recently demonstrated for phagotrophic protists (Fenchel & Blackburn 1999). Once the swarmers settle and grow into large, feather-shaped colonies, they control their chemical microenvironment by frequent contraction and by generating seawater currents, which are strained for food particles. By contracting, *Zoothamnium* and *Vorticella* most prob-

ably ensure that processed fluid does not re-enter the filters (Leeuwenhoek 1713), thereby maintaining an optimal cost-benefit ratio of suspension feeding. The contraction and extension of the feather-shaped colonies of *Z. niveum* is complex compared to the solitary *Vorticella* sp. (see below). The stalk, whose proximal part lacks a spasmoneme, bends at a definitive joint; the remainder coils in a zigzag course and the mass of zooids whips downwards. Our continuous O_2 and H_2S measurements (Fig. 3) show that during contraction of *Z. niveum* the sulphidic bottom water is displaced by oxygenated seawater; the effect increases with increasing colony size. This result is in contrast to the recent model (see 'Introduction'), which suggests that rapid contraction prevents oxygen-containing seawater from being dragged along with the colony. Nevertheless slow extension of the colonies takes H_2S containing seawater upwards as the model suggests (Ott et al. 1998), which is rapidly mixed with the surrounding oxygenated seawater when the zooids start to beat their cilia (Fig. 3). The colonies of *Z. niveum* occur in groups and the stirring action of a single colony affects the chemical environment of the adjoining ciliates (authors' pers. obs.). Frequent contraction within the groups results in permanently changing [O_2] and [H_2S] and, thus, sharply defined steady-state gradients in the surroundings of *Z. niveum* groups can not develop.

An active *Vorticella* with a peristome diameter of 70 µm moves small particles at distances of more than 50 times the ciliate diameter, whereby a maximum particle speed of ca 2.5 mm s^{-1} is reached at the haplokinety ciliary tips (our Fig. 1c, Sleigh & Barlow 1976). Food particles are collected only from a narrow stream of seawater entering at the opening between the paroral membrane and the membranelle (Fenchel 1986). The vortex draws O_2- and H_2S-containing seawater from above along the inside of the torus (Fig. 1b); this water is further transported downwards and mixed with the deoxygenated, H_2S-containing bottom water. The mixture then moves upwards outside the torus (counter-directed flow). This flow field maintains low [H_2S] (~3 µmol l^{-1}) and relatively high [O_2] (~75 µmol l^{-1}) in the surroundings of the zooid that would not coexist under the conditions of a counterdirected diffusional transport of both gases (compare steady state [O_2] and [H_2S] at 350 µm distances from the membrane in Fig. 4a,b).

Since the vortex is maintained at a low Reynolds number of 10^{-1}, it has a proportionally large rotational core, a high energy demand, and immediately grinds to a halt when cell shrinkage and stalk contraction cuts off its energy supply (Vogel 1996). The contraction of the ca 300 µm-long stalk reduces the distance from the zooid to the substratum by about 90% within approximately 9 ms, the maximal contraction velocity of 8.8 cm s^{-1} being observed 2 ms after the onset (Moriyama et al. 1998). A continuous extracellular spasmoneme is responsible for what is probably the most rapid shortening of any contractile element of any animal (Weis-Fogh & Amos 1972, see also Routledge et al. 1975, Katoh & Kikuyama 1997, Moriyama et al. 1999). Full extension requires about 10 s. Calculating Reynolds numbers ($Re = auv^{-1}$) with a = 20 µm, $v = 10^{-6}$ m^2 s^{-1} and either u = 8.8 cm s^{-1} (2200 times the cell diameter s^{-1}) or $u = 3 \times 10^{-3}$ cm s^{-1} suggests that contraction at Re = 1.8 allows only a little oxygenated seawater to adhere to the surface of the zooid, whereas slow extension at $Re = 6 \times 10^{-4}$ takes deoxygenated bottom water upwards due to viscous forces. Our continuous O_2 recordings directly next to the animal at heights of 50, 150 and 300 µm support these calculations (Fig. 5). There is no increase in [O_2] at 50 µm distance due to the contraction of the ciliate; thus, there is no oxygenated seawater carried down during contraction. On the other hand there is a decrease of [O_2] at 150 µm distance when the ciliate extends again; thus, it carries up seawater containing less oxygen (and H_2S, compare gradients in Fig. 4b) from below. The solitary *Vorticella* sp. occur in groups ('pseudocolonies') as colonies of *Zoothamnium niveum* do, and the stirring action of single specimen affects the chemical environment of the adjoining ciliates.

The continuous measurements show that during slow extension of both *Vorticella* sp. and *Zoothamnium niveum* deoxygenated and H_2S-containing seawater is transported upwards. The feeding current (toroidal vortex) enhances the subsequent mixing of this seawater with the surrounding oxygenated seawater and draws O_2 and H_2S within reach of the ciliate's external surface at high speed. High flow velocity should cause a thinning of the diffusive boundary layer and thus enhance uptake of O_2 and H_2S by the ectobiotic bacteria. To increase its food supply by only 10% a free-living bacterium with a radius of 2 µm would have to move at a speed of 0.7 mm s^{-1}, which is 20 times faster than it can actually swim (Purcell 1977). The ectobiotic bacteria of *Vorticella*, e.g., are probably surrounded by seawater moving at a speed of about 2.5 mm s^{-1} (Sleigh & Barlow 1976). A crude measurement of the relative role of convective and diffusive transport of oxygen is the dimensionless expression $l \times v/D$ (Sherwood number). If v = 2.5 mm s^{-1}, l = 0.45 mm (distance above *Vorticella* sp. at which the slope of the gradients changes), and $D = 2.415 \times 10^{-5}$ cm^2 s^{-1} (at 28°C), this works out to ~466, indicating that convective transport is much more important than diffusion for supplying O_2 to the ciliate and its ectobiotic bacteria. The sulphide-oxidising bacterium *Thiovulum majus* generates a convective oxygen transport by collective spinning movements and, thus, maintains flux rates that are about 40 times higher than molecular diffusion (Fenchel & Glud 1998).

CONCLUSION

We suggest that it is not simply the bathing of the ectobiotic bacteria alternately in anoxic, H_2S-containing and O_2-saturated seawater, as previously suggested for *Zoothamnium niveum* (Ott et al. 1998), which supplies the chemoautotrophic ectobionts, but that the ciliate-generated advective seawater transport plays the most important role. The toroidal vortices draw H_2S- and O_2-containing seawater within reach of the cells' external surface at a high flow velocity. This may decrease cell boundary layer thickness and, thus, support nutrient uptake by the chemoautotrophic ectobionts. The feeding currents probably make the surface of the ciliates attractive for sulphur-bacteria even when the ciliates do not grow directly on a H_2S-releasing substrate, e.g., on vertical rocks adjacent to decomposing debris (Mediterranean, west coast of Corsica, France). Here, wave-generated currents draw seawater into the sulphidic debris. The resulting upward current contains both gases at low concentration and passes the vertical rocks.

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