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RESEARCH ARTICLE

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Sulfide fluxes in a microbial mat from the Ebro Delta, Spain

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Abstract The sulfur cycle of Ebro Delta microbial mats was studied in order to determine sulfide production and sulfide consumption. Vertical distribution of two major functional groups involved in the sulfur cycle, anoxygenic phototrophic bacteria and dissimilatory sulfate-reducing bacteria (SRB), was also studied. The former reached up to 2.2×10^8 cfu cm^{-3} sediment in the purple layer, and the latter reached about 1.8×10^5 SRB cm^{-3} sediment in the black layer. From the changes in sulfide concentrations under light-dark cycles it can be inferred that the rate of H_2S production was 6.2 µmol H_2S cm^{-3} day^{-1} at 2.6 mm, and 7.6 µmol H_2S cm^{-3} day^{-1} at 6 mm. Furthermore, sulfide consumption was also assessed, determining rates of 0.04, 0.13 and 0.005 mmol l^{-1} of sulfide oxidized at depths of 2.6, 3 and 6 mm, respectively.

Keywords Sulfide oxidation · Sulfate reduction · Microbial mats

Introduction

Microbial mats are stratified microbial ecosystems characterized by cyclic seasonal fluctuations of flooding and desiccation and also by diel fluctuations in the concentrations of oxygen and sulfide [11, 20, 32]. These ecosystems show a sharp redoxcline less than 1 mm thick due to oxygenic photosynthesis by cyanobacteria developing close to the sulfide-rich zone. In microbial mats, 99% of the photoassimilation of CO_2, sulfate reduction, and the oxidation of sulfide takes place in the upper 5–10 mm of the sediment. Anoxygenic and oxygenic photosynthesis play an important role in sulfide oxidation processes taking place in these sulfidic environments [10].

Microbial mats exhibit very high primary productivity and rapid recycling of organic matter. In these kinds of environments, mineralization processes are mediated by sulfate-reducing bacteria (SRB) [4, 9, 22, 32]. Sulfate reduction is the key process in generating reduced sulfur compounds that are used by chemolithotrophic bacteria, anoxygenic phototrophic bacteria and SRB. Chemolithotrophic bacteria obtain energy by oxidizing reduced sulfur compounds and anoxygenic phototrophic bacteria use reduced sulfur compounds as electron donors to fix CO_2 in the light. Sulfide oxidation and sulfide precipitation proceed efficiently at rates high enough to allow development of diatoms, which are very sensitive to sulfide toxicity, on the surface of the mat.

Iron-bound sulfides or hydrogen sulfide can be reoxidized biologically or chemically to form thiosulfate [8]. Moreover, SRB may play an important role in the regulation of the electron flow in the sulfur cycle of microbial mats due to their metabolic versatility in reducing sulfate and thiosulfate and to disproportionate sulfur compounds [35].

The aim of the present work was to study changes in sulfide concentration, and the vertical distribution of some functional groups of sulfur bacteria (i.e. anoxygenic phototrophic bacteria, dissimilatory SRB), in order to understand their role in the sulfur cycle of Ebro Delta microbial mats.

Materials and methods

Microbial mats and sample collection

The microbial mats studied were located in the Ebro Delta, North-East Spain (40°40′ N, 0°40′ E). The general features of the sampling

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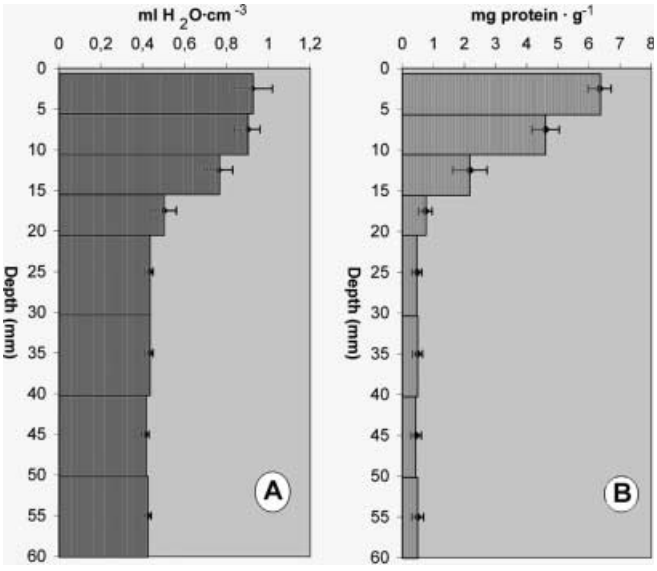

Fig. 1. Depth profiles of water content, and protein content of all sediments used in the experiments. *Error bars* show 99% confidence interval of mean values for 18 samples

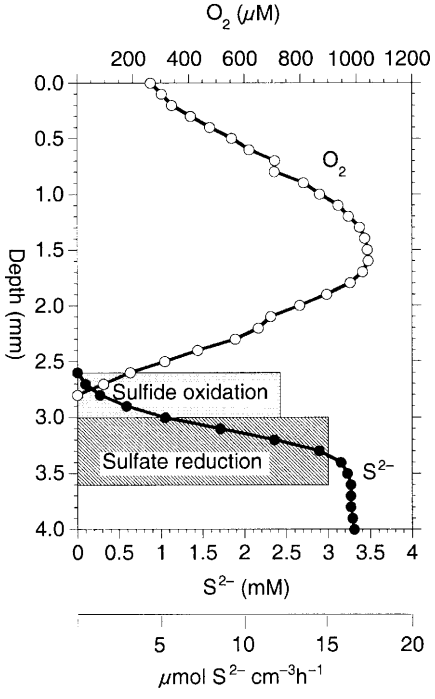

Fig. 2. Profiles of oxygen, sulfide, sulfide oxidation and sulfate reduction in a microbial mat from Ebro Delta, after 4.5 h in the light. The light intensity at the mat surface was 1,000 μE m^{-2} s^{-1}. The specific reaction rates of sulfate reduction and sulfide oxidation were modeled from the measured profiles and are indicated by *boxes*

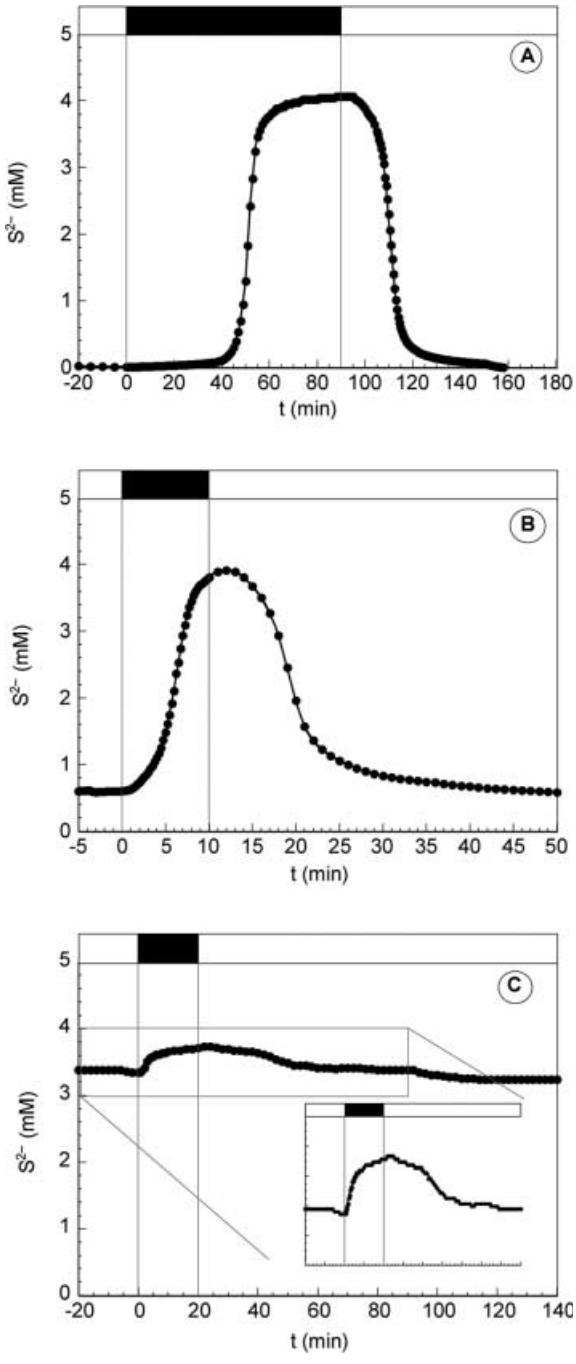

Fig. 3. Time course of hydrogen sulfide concentration at different depths: **A** 2.6 mm; **B** 3 mm; and **C** 6 mm in the Ebro Delta, microbial mat during light-dark cycles. The illuminated and dark periods are indicated at the top of the figures by a *white* and *black* area, respectively. The light intensity at the mat surface was 1,000 μE m^{-2} s^{-1}

area, as well as the dominant phototrophic organisms have been described earlier [13, 24]. Sediment samples for bacterial counts were taken with stainless-steel corers (2.5 cm inner diameter) that were stoppered at both ends immediately after sampling and stored on ice. Samples were processed in the laboratory 2 h after collection. The different pigmented layers were sliced. Sediment samples to study sulfide production and consumption were taken with Plexiglas corers (4.5 cm inner diameter, 34.5 cm long).

Overlying water analysis

Physicochemical variables (temperature, salinity, conductivity and pH) of the water covering the mats were determined. Temperature,

conductivity and salinity were measured using a Yellow Springs Instrument S-C-T Meter model 33. pH was measured with a microPH 2001 Crison pH-meter.

Sediment characterization

The water content of the sediment (pore water) was determined for each slice as the difference between wet weight and dry weight. For the determination of dry weight, samples were dried for 48 h at 105°C. Total sediment porosity was calculated from values of particle and bulk density according to Danielson and Sutherland [7] applying the formula $Pt = [1 - (\rho_b/\rho_p)]$. The bulk density ($\rho_b$) was calculated by weight (dried sample) and volume (fresh sample) in g cm^{-3}. The particle density (ρ_p) was assumed to be 2.65 in g cm^{-3} for mineral particles (71.8%) [6] and 1.08 g cm^{-3} for organic matter (28.2%) [12]. Total porosity was calculated to be 0.947 in the upper part of the mat. Protein content was determined by the method of Bradford [2] after extraction of zero valence sulfur and chlorophylls with methanol and subsequent solubilization of the sediment sample in 1 N NaOH at 100°C for 10 min [14].

Minielectrode measurements

Microprofiles of oxygen and sulfide were measured with needle mini-electrodes according to the method of van Gemerden et al. [34]. Profiles were recorded in the sediment cores during the stepwise lowering of the electrodes using a micromanipulator. The outputs from the electrodes were read on a picoammeter (Keithley 485) or a millivoltmeter (Bioblock 93313). Changes in sulfide concentrations in the mat were studied by placing the minielectrode at different depths [2.6 mm (green layer), 3 mm (purple layer), and 6 mm (black layer)] during light-dark cycles.

Sulfate reduction and sulfide oxidation measurements

The total rate of sulfate reduction was determined as the sulfide flux away from the sulfate reduction zone in the mat. The one-dimensional diffusion flux was calculated from Fick's first law of diffusion as described by Kühl and Jørgensen [21]. We used the profile of sulfide shown in Fig. 2 (see later) to calculate flux of sulfide. The apparent diffusion coefficient for sulfide at 25°C was assumed to be 0.54×10^{-5} cm^2 s^{-1} [28].

Depth distributions of sulfate reduction and sulfide oxidation were obtained by manually fitting parabolic functions to curved sections of the measured sulfide profile as previously described [21, 26] by use of Fick's second law of one-dimensional diffusion. The specific reaction rate in each layer was calculated from the product of the apparent diffusion coefficient and the coefficient of χ^2 for the fitted parabolic function. The integrated specific reaction rate for sulfate reduction was calculated by multiplying the specific rates with the thickness of the depth interval in the mat where the process occurred. Total reaction rate based on flux calculation agreed with the rate calculated from the integrated specific reaction rate.

Bacterial counting procedures

The deep agar shake method [27] was used to estimate the viable counts of anoxygenic phototrophic bacteria. The tubes were incubated at 23°C at continuous light intensity of 3 μE m^{-2} s^{-1}. Each lamination of the mat had been previously introduced into a screw cap tube with 5 ml of a saline solution (3% NaCl and 0.1% Na ascorbate). SRB were counted using the most probable number (MPN) method with three replicates per dilution. The sediment was first diluted in saline solution, followed by serial dilution in modified Baar's culture medium. The inoculated tubes were incubated at 23°C in the dark.

Results

Sediment characterization

Prior to the experiments on sulfide production and consumption, the physical and chemical characteristics of the mat were determined. The temperature of the water overlying the mat was 28°C, conductivity was 99 mS cm^{-1}, salinity was 63‰ and the pH was 8.6. Sediment cores used to carry out the experiments

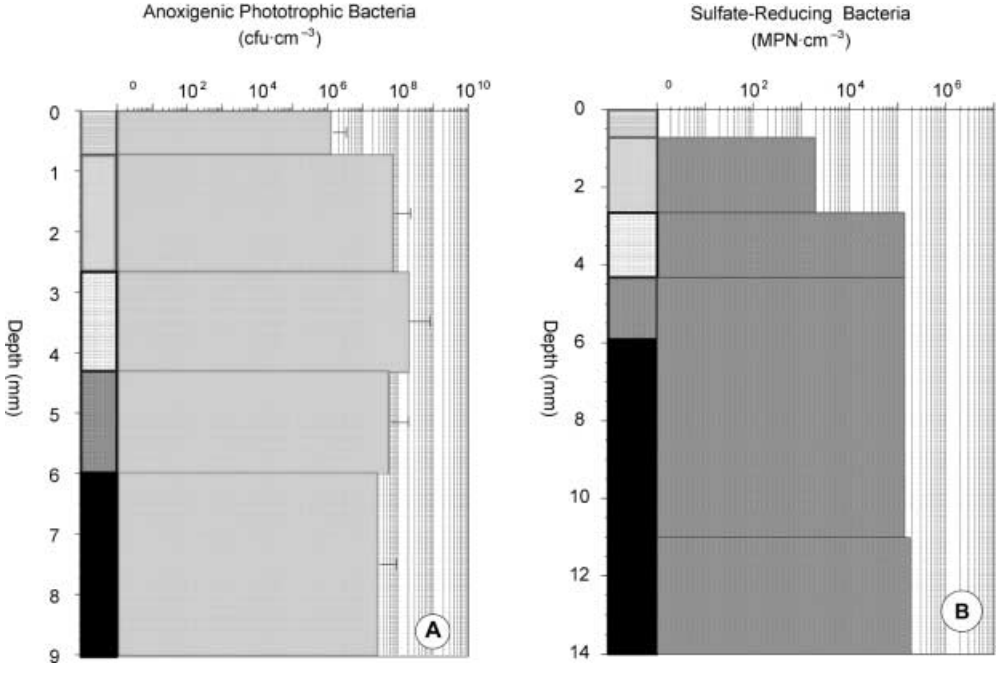

Fig. 4. Depth profiles of the number of bacteria from a mature Ebro Delta microbial mat. **A** Anoxygenic phototrophic bacteria viable counts; **B** sulfate reducing bacteria most probable number. The distinct colored layers of the mat are designated by different symbols in the diagram on the left. Yellow-brown layer: 0–0.72 mm; green layer: 0.72–2.67 mm; purple layer: 2.67–4.31 mm; compact black layer: 4.31–6 mm; and sandy black layer (sediment): below 6 mm. Horizontal bars indicate standard error of mean values for triplicate samples

Table 1. Sulfate reduction rates (maximum rate and sulfate reduction per unit area) and most probable number (MPN) of sulfate-reducing bacteria (SRB) in sediments of different microbial mats environments

Location of microbial mat	Depth (mm)	nmol SO_4^{2-} cm^{-3} day^{-1}	mmol H_2S m^{-2} day^{-1}	MPN SRB cm^{-3}	Reference
Experimental hypersaline pond, Red Sea	8–10	10,000	–	–	[17]
Experimental hypersaline pond, Red Sea	0–12.5	–	9.5–33[a]	–	[10]
Hypersaline pond Salins de Giraud, France	0–60	200–17,000[a]	400–450	10^4–10^5	[5]
Cai, Bonaire, Netherlands Antilles	0–10	800	–	–	[23]
Ebro Delta, Spain	6	7,560[b]	–	1×10^5	This study
Ebro Delta, Spain	2.9–3.3	–	261[c]	–	This study
Great Sippewisselt, Massachusetts	0–20	7,500	540	–	[16]
Guerrero Negro, Baja California Sur, Mexico	0–5	1,152 to >13,000	5–30[a]	–	[3]
Kalo Lagoon, Denmark	0–10	1,200	62	–	[33]
Pekelmeer, Bonaire, Netherlands Antilles	0–10	950	–	–	[33]
Shark Bay, Australia	0–50	–	10	–	[31]
Solar Lake, Sinai	Surface	5,400	67	2.5×10^6	[18]
Spencer Gulf, Australia	0–50	–	103	–	[31]
Texel (Frisian Island) Salt marsh sediments	0–5	567	9.66	1.1×10^6	[35]
Belle Baruch, South Carolina	20–40	317	68–94	–	[19]
Chapman's, New Hampshire	0–200	1,000	75	–	[15]
Kenan Field, Sapelo Island, Georgia	30	2,000	–	–	[16]
Saltmarsh creek, United Kingdom	0–100	1.5–315	–	–	[25]
Saltmarsh pan, United Kingdom	0–100	1.7–190	–	–	[25]

[a]Temporary variations
[b]Sulfide production
[c]Estimated flux of sulfide

showed two distinctive zones. In the upper part (0–15 mm) the water content and the protein content were higher than in the bottom part (15–60 mm) (Fig. 1A). The maximum protein content was detected at the mat surface (0–5 mm) (6.3 mg protein g^{-1} sediment) and decreased with depth (Fig. 1B).

Sulfide production and consumption

In order to determine the position of the O_2–H_2S interface, vertical profiles of oxygen and sulfide concentrations were established (Fig. 2). Oxygen reached a maximum concentration of 1.04 mM at 1.6 mm, and penetrated 2.7 mm into the mat, down to the upper boundary of the sulfide zone. Oxygen and sulfide overlapped over a 0.2 mm layer. Sulfide was oxidized within a narrow zone (2.6–3.0 mm), where the specific activity of sulfide oxidation was 12.1 μmol cm^{-3} h^{-1}. Sulfide was produced by sulfate reduction 3.0–3.6 mm below the mat surface at a specific rate of 15 μmol cm^{-3} h^{-1}.

To study the dynamics of the sulfide production and consumption at different depths within the microbial mat, the sulfide mini-electrodes were placed at three different depths within the mat: (1) at 2.6 mm, in the aerobic zone (green layer) close to the upper part of the O_2-H_2S interface; (2) at 3 mm (purple layer), where the sulfide concentration profile showed a clinograde function close to the bottom part of the O_2-H_2S interface; (3) at 6 mm, in the anaerobic zone (black layer) (Fig. 3). At a depth of 2.6 mm, sulfide was not detected when the core was illuminated, but it appeared after 40 min incubation in the dark at an initial rate of 476 μmol l^{-1} min^{-1}. In the last 20 min of darkness, the rate decreased to 4.3 μmol l^{-1} min^{-1}. When the light was switched on, the initial sulfide oxidation rate was 45 μmol l^{-1} min^{-1} increasing to 446 μmol l^{-1} min^{-1} after 19 min of incubation in the light (Fig. 3A). The concentration of sulfide at 3 mm depth was 0.6 mM. When the light was switched off, the initial rate of sulfide appearance was 470 μmol l^{-1} min^{-1}. After 10 min, when sulfide reached 3.8 mM, the light was switched on and the initial sulfide disappearance rate was 130 μmol l^{-1} min^{-1}, but it increased to 403 μmol l^{-1} min^{-1} after 7 min of illumination (Fig. 3B). At a depth of 6 mm, the initial rate of sulfide appearance was 54 μmol l^{-1} min^{-1} during

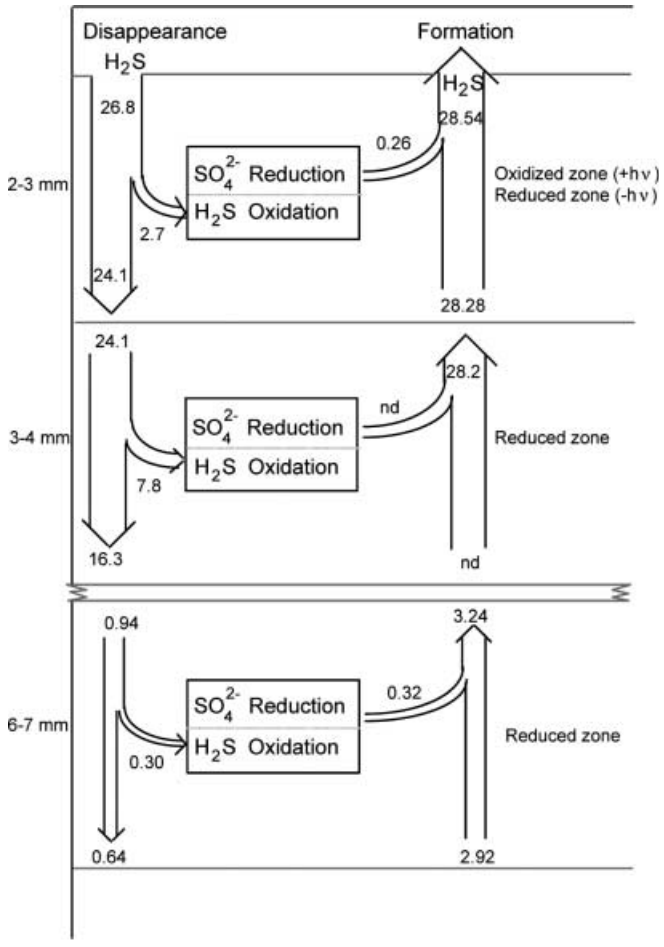

Fig. 5. Flow diagram of sulfide in Ebro Delta, microbial mats. Numbers indicate transfer rates in mmol m^{-2} h^{-1}. *nd* Not determined, *+hv* illuminated conditions, *–hv* dark conditions

the first 6 min of incubation in the dark. After this initial period, the rate of sulfide production was 5.25 μmol l^{-1} min^{-1}. When the sulfide concentration was 3.7 mM the core was illuminated again and a small decrease in the concentration of sulfide could be detected with an initial rate of 5 μmol l^{-1} min^{-1} for 23 min and then a decrease down to 15.6 μmol l^{-1} min^{-1} (Fig. 3C).

Bacterial counts

Depth distribution of viable anoxygenic phototrophic bacteria showed a peak of 2.2×10^8 cfu cm^{-3} in the purple layer of the mat, and decreased with increasing depth (Fig. 4A). SRB were not detected in the upper lamination of the mat, but their numbers increased with depth, reaching 1.8×10^5 SRB cm^{-3} in the black layer (Fig. 4B).

Discussion

When sulfide is measured in the light, rates of sulfide oxidation can be considered a measure of anoxygenic photosynthesis. Thus, the anoxygenic photosynthetic activity at 3 mm depth was measured at 130 μmol sulfide l^{-1} min^{-1}. This value found in the purple layer of Ebro Delta microbial mats is similar to rates reported in other microbial mats. For example, Caumette et al. [5] determined rates of 200–300 μmol sulfide l^{-1} min^{-1} in microbial mats from Salins-de-Giraud (France).

Respiration, in which sulfate is reduced to hydrogen sulfide, is a very important process in microbial mats [5, 9, 30]. Usually, sulfate reduction rates are quantified by using radioactively labeled sulfate [1, 8, 17]. This method is very sensitive, but it has limitations when oxidized layers are found close to the zones where sulfate reduction take place, because a significant proportion of the radiolabeled sulfide formed during incubation may then be reoxidized during the same period thus resulting in an underestimation of sulfate-reducing activity [18]. Also, this method overestimates the rate of sulfate reduction, as pointed out by Revsbech et al. [29], because, using microelectrodes, they detected only 15% of the flux of sulfide that would be expected from measurements of the sulfate reduction in the same mat using radiolabeled sulfate.

Sulfate reduction may be studied using micro- or mini-electrodes [21]. Sulfide diffuses upward from deeper layers and it is oxidized at the oxic-anoxic interface. Assuming a steady-state situation, the flux of sulfide just below the oxic-anoxic interface must equal the integrated rate of sulfate reduction in the layers below. In Ebro Delta mats, the flux was estimated to be 261 mmol H_2S m^{-2} day^{-1}. This value is similar to those calculated in other microbial mats. It is higher than the rate found in microbial mats of Solar Lake (Sinai) or Shark Bay (Australia) and it is lower than those determined in microbial mats of hypersaline ponds in Salins-de-Giraud (France) or Great Sippewissett (Mass., USA) (Table 1).

The simplified flow diagram of sulfide in Fig. 5 shows the sulfate reduction rates, measured as sulfide production, sulfide oxidation rate and sulfide fluxes from diffusion and chemical oxidation. From 2 to 3 mm depth, the biological sulfide oxidation rates were 10-fold higher than sulfate reduction rates; however, from 6 to 7 mm depth the sulfate reduction rates were slightly higher than the biological sulfide oxidation rates. In the green layer higher values of the sulfide oxidation flux (24 mmol m^{-2} h^{-1}) were detected, probably corresponding to chemical oxidation. On the other hand, the diagram shows a flux of sulfide production, probably due to molecular diffusion, mainly in the upper layers where the light-dark shift produces a sharp gradient. This observation can be explained either because sulfide is not oxidized by anoxygenic phototrophic bacteria in the dark, or because the O_2–H_2S interface extends to the surface. However, from 6 to 7 mm depth, the sulfide gradient is negligible, and the outflux of sulfide cannot be explained by molecular diffusion alone; additional transport mechanisms must be involved, as pointed out by Jørgensen and Cohen [18] for the outflux of sulfide in Solar Lake mats.

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