Small-scale patchiness in the chemistry and microbiology of sediments in Lake Geneva, Switzerland

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Lake Geneva is a large, holomictic, eutrophic lake with a maximum depth of about 300 m. The sediments in the central basin have a pillow-like appearance. The soft elevations containing the major portion of the recently sedimented detritus are separated by trenches of 5 to 15 cm depth in which the top sediment layers seem to be missing. Bottom-dwelling fishes (*Lota lota*) prefer the trenches as their habitat and might partly be responsible for the turbation of the trench sediment layers. Thus, within distances of 10 to 30 cm two sediment types can clearly be distinguished. They differ with respect to morphology and chemical stratification. Concentration depth profiles of nitrate, manganese(II), iron(II), sulphate, and methane dissolved in the interstitial water reveal the location within the sediment of microbially catalysed redox processes. The redox transition zone (RTZ) from aerobic to anaerobic is located only a few millimetres below the sediment surface in the pillow sediments, which contain the bulk of the organic detritus. The RTZ is at a depth of approximately 6 cm in the trench sediments, which are poor in oxidizable organic matter. The same thermodynamic sequence of microbially catalysed redox reactions can be observed in both sediment types. As a consequence, microbial activities as well as diffusion fluxes of dissolved substances in and out of the different sediment regions vary greatly. This leads to small-scale horizontal differences in the sediment's abilities to supply nutrients to the bottom water, which is probably a major controlling factor for sediment-borne eutrophication of this lake.

Introduction

At the boundary layer between the water column and the sediment of an aquatic ecosystem many physical and chemical parameters vary within extremely short vertical distances (Hanselmann, 1985). Due to environmental conditions such as the availability of organic carbon and electron acceptors, rates of microbial processes show pronounced vertical gradients and are responsible for the stratification of the sediments (Brandl *et al.*, 1990; Brandl & Hanselmann, 1991; Hakanson & Jansson, 1983; Stumm & Morgan, 1981; Mortimer, 1941, 1942). While these spatial vertical heterogeneities are well documented and seasonal changes have been described, little has been reported on horizontal patchiness in sediments, especially within short distances (Downing & Rath, 1988). Staub (1981) found extensive variability at different sites when determining diffusion fluxes of dissolved compounds through the water–sediment interface in Lake Lucerne. This indicates pronounced horizontal heterogeneity. To study horizontal patchiness of

chemistry and microbiology of sediments, porewater and sediment samples were collected at specific sites in Lake Geneva at a depth of 250 m (Brandl *et al.*, 1990). The objectives of the work described here were (i) the collection and chemical analysis of interstitial water and sediment samples from morphologically different sediments, (ii) to describe small-scale horizontal heterogeneities in the chemistry and the microbiological activities of sediments, and (iii) to determine quantitatively microbial conversion rates under *in situ* conditions in the different sediment types.

Methods

Study site. All sediment sampling was carried out in 250 m depth of water in the central basin of Lake Geneva, Switzerland. The sampling site is described elsewhere (Brandl *et al.*, 1990). Using a small manned research submarine, pillow-like structures which extend over an area of approximately 200 to 250 km² could be observed at the sediment surface (Fig. 1a). Soft elevations are separated by trenches of 5 to 15 cm depth. Therefore, within distances of 10 to 30 cm two sediment types can clearly be distinguished. Evidence of macrofaunal activity (snails, fish) is apparent on the sediment surface. The structures were described for the first time by Vernet (1966). We have seen them in water depths from as little as 30 m down to the deepest point of the lake

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(309 m). To establish a permanent experimental station, a nylon rope (200 m) was laid out on the sediment surface. This allowed repeated dives at the same sampling site and provided a guide for relocating the porewater samplers. Porewater samples as well as sediment cores were collected on 3 March 1984, 22 March 1984, 17 December 1985, 1 April 1986, 23 April 1986, and 30 April 1986. Usually six cores and up to four porewater profiles were taken on each sampling day.

Sampling methods. Interstitial water samples were collected from sediments by a dialysis equilibrium technique (Fig. 1*b*). The samplers consisted of an 80 × 12 × 1.5 cm Plexiglas sheet containing 41 rows of cylindrical dialysis chambers, each 1.5 cm in diameter and 1.5 cm deep. The chambers were covered on both sides with dialysis membranes (cellulose acetate; thickness 80 µm; Union Carbide) held in place by 3 mm thick Plexiglas overlays (Brandl & Hanselmann, 1991). Up to five individual samples of 2.6 ml were collected from each row. Further details of the sampling methods are published elsewhere (Brandl *et al.*, 1990; Brandl & Hanselmann, 1991). All porewater samples were processed within 60 to 90 min of retrieval of the samplers. Samplers were transported to the sediment surface using the research submarine and inserted into the sediment at the experimental site with the aid of a manipulation arm.

Transparent PVC tubes (length 50 cm, inner diameter 6.3 cm) were used to collect undisturbed sediment cores. A ball valve prevented loss of the sampled material during retrieval of the core. The external manipulation arm of the submarine allowed the vertical insertion into the sediment as well as the collection of porewater and sediment samples from exactly defined locations (both the top of sediment pillows and the trench between the pillows).

Analytical methods. Nitrate and sulphate were determined by ion chromatography (Hertz & Baltensperger, 1984; Brandl *et al.*, 1990). ICP-AES analysis (inductively coupled plasma atomic emission spectroscopy) was used to determine simultaneously the following

elements: Ca, Fe, K, Mg, Mn, Na, P, S and Si (Bolliger *et al.*, 1992). In addition to the chemical analysis of the porewater, the water content of the sediment cores was determined gravimetrically and their porosity was calculated (Håkanson & Jansson, 1983). The amount of organic material was determined from the weight loss of dried sediment samples after combustion at 550 °C for 1 h.

Results and Discussion

Cores taken from sediment pillows showed a heterogeneous stratification. Cores from the top of pillows showed only a narrow oxidized layer, whereas this zone was broad when the core was taken from a trench. Distinct yearly deposits cannot be located in these sediment cores. Determination of the water content and the porosity (Fig. 2) also provided evidence for the different structures at the two different sites: the sediment in the trench was more compact, more dense and contained less organic material than the top of a pillow. These physical differences probably strongly influence exchange reactions and transport phenomena within the sediment.

To obtain information on the relationship between the nature of the surface and microbial activities in the sediments, different geochemical species and microbial metabolites dissolved in the interstitial water were determined quantitatively.

Profiles of electron acceptors such as sulphate (Fig. 3*a*), the reduced forms of iron or manganese (Fig. 3*b*),

Fig. 1. (*a*) View of pillow-like sediment structures in the central basin of Lake Geneva, Switzerland, at water depths between 250 and 300 m. Soft elevations (pillows) with a diameter of approximately 0.5 to 1 m are separated by trenches 5 to 15 cm deep. The rope which aids orientation near the experimental sites was placed exactly in an east-west direction. For comparison of the dimensions the metal ring on the left (handle of a sampling device) has a diameter of 6 cm. (*b*) Dialysis porewater samplers were positioned by the aid of a research submarine precisely on both the top of a sediment pillow and in the trench between the pillows.

Fig. 2. Representative profiles of water content (a), porosity (b), and amount of organic matter (c) as determined by weight loss after combustion (●, sediment pillow; ○, trench between sediment pillows). Values show means from duplicate determinations.

Fig. 3. Representative concentration profiles of sulphate (a), manganese(II) (b), methane (c), phosphorus (d), sodium (e), and silicon (f) in the interstitial water at the sediment-water interface of the two different sediment structures in Lake Geneva (●, sediment pillow; ○, trench between sediment pillows). Samples of interstitial water were obtained by a dialysis equilibrium technique. Values show means from duplicate determinations.

products of anaerobic microbial metabolism such as methane (Fig. 3c), or components which are indirectly involved in microbially mediated redox reactions such as

phosphorus (Fig. 3d) showed distinct differences between the top of a pillow and the trench. In contrast, geomicrobiologically inert compounds such as sodium or

Table 1. *In situ* microbial conversion rates at 5 °C per volume of interstitial water in two different sediment types of Lake Geneva according to the thermodynamic redox sequence (Stumm & Morgan, 1981; Hanselmann, 1985)

Conversion rates were calculated according to the model described by Brandl *et al.* (1990). First, diffusion fluxes were determined by numerical differentiation according to Fick's first law. According to a model already described (Brandl *et al.*, 1990), maximal diffusion flux changes are proportional to maximal microbial conversion rates. Rates of microbial substrate utilization and product formation were estimated from maximal diffusion fluxes. The results are means $\pm$ SD, with the number of independent experiments in parentheses. An asterisk (*) denotes a significant difference between the sediment types according to the *t*-test ($P = 0.01$).

Sediment type	Mean rates† (nmol cm ⁻³ d ⁻¹)				
	NO ₃ ⁻ -ΣR	ΣMn ²⁺ ‡ +ΣR	ΣFe ²⁺ ‡ +ΣR	SO ₄ ²⁻ -ΣR	CH ₄ +ΣR
Pillow	8.3 $\pm$ 3.4 (4)	11.5 $\pm$ 5.8 (5)	0.7 $\pm$ 0.5 (5)	21.8 $\pm$ 2.2 (5)	12.5 $\pm$ 7.4 (5)
Trench	3.6 $\pm$ 1.4 (3)*	4.8 $\pm$ 0.9 (4)*	0.4 $\pm$ 0.2 (4)	10.8 $\pm$ 2.2 (3)*	4.1 $\pm$ 2.8 (4)*

† +ΣR is an overall production rate, -ΣR an overall consumption rate.

‡ ΣMn²⁺ is the sum of mobile Mn(II) species under the prevailing pH and pe conditions; ΣFe²⁺ is the sum of mobile Fe(II) species under the prevailing pH and pe conditions.

silicon (Fig. 3e,f) showed identical profiles. Thus, electron transport activities were probably much greater in the higher parts of the pillow-like structures, leading to a rapid loss of electron accepting compounds in the uppermost layer of the sediment.

In situ conversion rates were calculated from the concentration profiles (Brandl *et al.*, 1990). Diffusion fluxes were determined by numerical differentiation according to Fick's first law. According to a model already described (Brandl *et al.*, 1990), maximal diffusion flux changes are proportional to maximal microbial conversion rates. Rates of microbial substrate utilization and product formation were estimated from maximal diffusion fluxes. From the results, it became obvious that the microbial ecosystem at the top of the pillow was metabolically two to three times more active than that in the trench (Table 1). Within a few centimetres, distinctly different microbial activities can be recognized in surface sediments. Microbial metabolic activities affect the magnitude of chemical fluxes in and out of the sediment as well as the solubility and therefore the retention of compounds within the sediment. The steeper chemical gradients indicate a higher exchange rate of dissolved substances through the sediment-water interface in sediment pillows than in the trenches between the pillows.

In general, sedimentation in lakes is thought to be a relatively homogeneous process giving rise to only large-scale differences. Heterogeneities may result from the non-uniform distribution of materials brought into the lake by rivers or from autochthonous material produced locally in the epilimnion. In reality, large differences in biomass production per square metre at different sites are seen in lakes as well as in the ocean (Hakanson &

Jansson, 1983; Mann, 1982; Overbeck, 1972; Parsons & Strickland, 1962). However such differences would never result in the small-scale compartmentation described for the bottom of Lake Geneva. An explanation for the existence of these pillow-like structures is still lacking, but possible causes such as interferences of water streams near the bottom, bioturbation (e.g. by fish), local convection by thermal differences, or oscillations in the whole water system have been suggested (Vernet, 1966; Brandl & Hanselmann, 1985). At certain sites, bottom-dwelling fishes (*Lota lota*) prefer the trenches as their habitat. Through their activities they might be partly responsible for the conservation and stabilization of these unusual sediment structures.

Differences between pillows and trenches are also seen in the ¹³⁷Cs activity profiles in the solid phase of the sediment, where a layer of higher activity results from the fallout in 1964. This layer is clearly lacking in the sediment below the trench, indicating either heterogeneous sedimentation or secondary removal and transport of sediments from these sites (Sturm *et al.*, 1984). On a macroscopic scale, the abundance of mesotrophic and eutrophic worm communities was significantly higher on sediment pillows, suggesting a higher sedimentation rate on the pillow compared to the trench (Lang, 1989). Our observations confirm these results.

Distinct horizontal heterogeneities show that results of studies on microbial activities in sediments at just a few randomly chosen sites cannot be extrapolated to draw conclusions about microbially mediated biogeochemical processes occurring at the total sediment-water interface of a lake, especially when sediment profiles are taken blindly from a boat. The small-scale horizontal hetero-

geneities of freshwater lake sediments force the investigator to probe the bottom of a lake at a large number of sites and use statistical treatment of the data (Downing & Rath, 1988).

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