

Effect of macrozoobenthos on two-dimensional small-scale heterogeneity of pore water phosphorus concentrations in lake sediments: A laboratory study

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Abstract

We used mesocosms equipped with two-dimensional (2D) pore water samplers (24 rows × 24 columns, 9-mm spatial resolution) to resolve and quantify some of the complex spatial patterns in diagenetic reactions produced by irrigated biogenic structures. The mesocosms were filled with an organic-, iron-, and phosphorus-rich sediment, and chironomids and oligochaetes were added in high densities to three of six mesocosms; the other three mesocosms served as controls. In the mesocosms without macrozoobenthos, a classic redox zonation developed. In the mesocosms with macrozoobenthos, profiles of redox-sensitive dissolved species were less steep in the vicinity of the sediment–water interface, and more irregular throughout the sediment, than in the mesocosms without macrozoobenthos. Furthermore, pore water P concentrations were decreased overall and showed much more small-scale 2D heterogeneity in the mesocosms with macrozoobenthos than in the controls. A comparison of the calculated heterogeneity indices of pore water P concentrations (the ratio of horizontal to vertical flux components) of this laboratory study with in situ-determined indices of previous studies indicates that the presence of macrozoobenthos is the major factor causing heterogeneity. A conceptual model of the effects of macrozoobenthos on biogeochemistry along with pore water and sediment analysis showed a close coupling of P cycling with iron and sulfur cycling. This led to the conclusion that pore water P concentrations and heterogeneity were mainly redox-controlled by association of P with iron oxyhydroxides precipitating along oxidized burrow walls, and not a consequence of mineralization processes occurring in organic-rich “hot spots” of increased P turnover. Decreased P release rates accompanied addition of macrozoobenthos and indicated that redox control of P release by iron oxyhydroxide precipitation and dissolution was of major importance.

Pore water phosphorus (P) concentration gradients in the upper zone of lake sediments are used to estimate the magnitude of internal P loading to lakes. In addition, they provide insight into early diagenetic processes (Urban et al. 1997). Although the existence of microniches (Wilson 1978) and spatial heterogeneity (Rhoads 1974) in sediment was already reported in the 1970s, lake sediments are often still assumed to be one-dimensional (1D) systems with a sequentially layered, laterally uniform redox zonation. For example, in many studies, the time series of soluble reactive P (SRP) pore water concentrations are discussed without considering small-scale spatial variability, which might be more important than temporal variability (e.g., de Vicente et al. 2003). This simplified view has persisted. Previously, an increasing number of authors have shown that most turnover does not occur in sequentially layered zones, but instead occurs in discrete, highly reactive sites (Brandes and Devol 1995;

Harper et al. 1999), and that a 1D concept of lake sediments, which presupposes laterally uniform layers, is often insufficient to model diagenetic processes (Jahnke 1985; Meile et al. 2003).

Different causes of microniches and small-scale horizontal heterogeneity are reported in the literature: benthivorous fish digging in the sediment change the local sediment structure (Breukelaar et al. 1994); an irregular distribution of microbial mats causes variability of the pore water P concentrations (since growing microorganisms have high P uptake rates overcompensating for the increased P release due to stimulated mineralization [Tezuka 1990]); and sedimentation of fecal pellets (Brandes and Devol 1995), living or dead organisms (Jahnke 1985), macroscopic organic aggregates (“lake snow”) (Grossart et al. 1997), and resuspended sediment (Weyhenmeyer 1998) result in a heterogeneous distribution of particles rich in organic matter that are hot spots of microbial activity, and sources of nutrient remobilization (Jahnke 1985; Harper et al. 1999). Organic detritus finer than the previously mentioned particles settles more homogeneously, but is likely to be redistributed heterogeneously by the actions of bioturbating macrozoobenthos reworking the sediment. Furthermore, bioturbation results in an upwardly directed transport of chemically reduced sediment particles from deeper sediment layers to the sediment surface (Brandes and Devol 1995). The transfer of sediment particles equilibrated at high concentrations might result in a local release of sorbed P species in regions of lower concentrations (Schink and Guinasso 1978). Bioirrigation, the process by which tube-dwelling animals pump down oxic water for respiration, causes spatial heterogeneity of pore water P concentrations and cylindrical redox zonation around the tubes (Aller 1994).

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Lewandowski et al. (2002) observed that the small-scale horizontal variability of pore water P concentrations was higher in lakes with high macrozoobenthos abundances than in lakes with low macrozoobenthos abundances. Thus, they assumed that there was a direct link between the presence of macrozoobenthos and small-scale horizontal variability. However, they could not rule out that the variation of other factors, such as benthivorous fishes, microbial mats, heterogeneous sedimentation, lake snow, sediment resuspension, lake depth, restoration techniques, and sediment characteristics may have caused the different amounts of small-scale horizontal variability occurring in the different lakes studied in their field investigations. Thus, we conducted a laboratory experiment using mesocosms with and without chironomids and oligochaetes. In fact, this is the first laboratory study on two-dimensional (2D) small-scale heterogeneity of pore water P concentrations.

The major aim of the study was (1) to clarify in a laboratory study whether macrozoobenthos causes the 2D small-scale heterogeneity of pore water P concentrations in lake sediments observed in previous field studies. Additional aims were (2) to describe possible mechanisms controlling pore water P concentrations and causing the observed heterogeneity in macrozoobenthos-inhabited sediments, and (3) to draw conclusions on the contradictory findings reported in literature that the presence of macrozoobenthos leads to a decreased or increased P release to the overlying water.

Material and methods

Experimental setup—Each of six mesocosms used in the experiment was a Perspex container (40 cm high; 24.5 cm wide; 10 cm deep). A 2D pore water sampler (peeper) made up of a Perspex plate (38 cm high; 24.3 cm wide; 2.2 cm deep) was inserted directly against one interior wall of each container guided by a rail. The design of the 2D peeper was based on Hesslein's (1976) 1D peeper. In contrast to Hesslein's peeper, the 2D peeper contains 24 columns and 23 rows (approximately 540 chambers), to investigate the horizontal as well as the vertical distribution of pore water concentrations. The 2D peeper is similar to the one described by Lewandowski et al. (2002), and provides a horizontal as well as vertical resolution of 9 mm. The drill holes in the Perspex plate were 7 mm in diameter and 17 mm deep, resulting in a volume of 650 μl . The sampler was initially filled with oxygen-free distilled water, and coated with a polysulfone membrane with a pore size of 0.2 μm (HT-Tuffryn 200; Pall Gelman Laboratory).

Sediment for the laboratory experiment was collected from the eutrophic, mono- to dimictic Lake Arendsee (northern Germany, 52°53.4'N, 11°27.5'E). This lake was chosen because its deeper profundal is uninhabited by meio- and macrozoobenthos (Wilhelmy and Scharf 1996). About 50 sediment cores (5.8 cm in diameter, 40 cm long) were collected in Perspex tubes using a modified Kajak sampler (Uwitec) on 22 January 2003 at a water depth of 48 m. The sediment cores were sectioned and pooled immediately after collection into three layers: 0 to 1 cm, 1 to 4 cm, and 15 to 35 cm. The layer 4 to 15 cm was discarded because a re-

Table 1. Sediment characterization at beginning of the experiment (arithmetic means).

Sediment characterization	Layer (cm)		
	0–1 (n = 2)	1–4 (n = 2)	15–35 (n = 4)
Dry matter (%)	2.3	6.5	11.9
Loss on ignition (%)	30.8	18.6	18.4
Total P ($\mu\text{mol g}^{-1}$ dry wt)	68.5	39.1	19.9
Calcium ($\mu\text{mol g}^{-1}$ dry wt)	4439	5821	3992
Aluminum ($\mu\text{mol g}^{-1}$ dry wt)	124	109	199
Iron ($\mu\text{mol g}^{-1}$ dry wt)	95	88	373
Manganese ($\mu\text{mol g}^{-1}$ dry wt)	9.5	8.5	27.0

distribution of littoral calcite-rich deposits (Seekreide) applied in 1995 as a restoration measure resulted in a visibly distinct layer of calcareous mud in this horizon. Including this layer would have limited the transferability of the results of this experiment to other lakes. The chemical characteristics of the three layers are shown in Table 1. The sediment of the pooled layers was thoroughly homogenized and stored at about 10°C.

To prepare the six mesocosms, the three sediments (Table 1) were added in layers of original thickness (20 cm bottom layer, 3 cm middle layer, and 1 cm top layer) into the Perspex containers already equipped with 2D peepers. Afterwards, water from Lake Arendsee was carefully siphoned on top, avoiding any disturbance of the sediment. In each mesocosm, a bubbler was installed about 1 cm above the sediment. Gentle bubbling of air should have prevented oxygen depletion in the overlying water, kept the overlying water in slow circulation to avoid concentration differences, and assured a natural thickness of the diffusive boundary layer. The latter is important since a thick diffusive boundary represents an unnatural resistance toward molecular diffusion (Jørgensen and Revsbech 1985). All incubations were performed in darkness at 10°C.

Macrozoobenthos—Three mesocosms were run without addition of macrozoobenthos. In the other three mesocosms, chironomids and oligochaetes were used since they represent typical macrozoobenthos in eutrophied lakes (Walshe 1947; Davis 1974; Andersson et al. 1988). Chironomids were obtained by sieving profundal sediments collected in January 2003 from Lake Müggelsee (southeast Berlin) by an Ekman grab through a 250- μm mesh screen. The chironomids were collected from the sieve residue using forceps. To acclimatize the chironomids to the experimental conditions, they were stored at 10°C for about a week in a vessel containing a small amount of Lake Arendsee sediment and continuously aerated Lake Arendsee water. Oligochaetes bought from a fish food seller were also carefully acclimatized to experimental conditions like chironomids, but without sediment addition. When required for experimentation, chironomids and oligochaetes were collected by hand picking with a Pasteur pipette.

Experimental procedure and sampling—After a preincubation of 3 d, the water in all mesocosms was replaced by

new water from Lake Arendsee. The experiment was started by adding 210 chironomids (*Chironomus plumosus*) and 200 oligochaetes (approximately 40% *Tubifex tubifex* and 60% *Limnodrilus hoffmeisteri*) to each of three mesocosms, whereas the other three mesocosms served as controls without macrozoobenthos. The numbers of invertebrates added simulated population densities of about 11,000 chironomids m^{-2} and 10,500 oligochaetes m^{-2} , which are at the high end of the range of densities found in situ (Gallepp 1979; Fisher et al. 1980; Fukuhara and Sakamoto 1987). At 35 d after addition of the macrozoobenthos, the sediment of each mesocosm was passed through a 250- μm mesh screen, and the remaining chironomids and oligochaetes were identified and counted.

During the first 16 d of the experiment, the water in the mesocosms was replaced three times (day 2, 7, and 11) by new water from Lake Arendsee by siphoning. At day 16, the 2D peepers were removed, after first inserting thin Perspex plates in front of each 2D peeper, to retrieve the peeper without disturbing the sediment. Subsequently, 1D minipeepers with a larger sample volume than the 2D peepers were exposed in the laboratory mesocosms for 19 d (days 16 to 35 of the experiment) to determine pore water concentration gradients of nitrate (NO_3^-), ammonium (NH_4^+), dissolved manganese (Mn^{2+}), dissolved iron (Fe^{2+}), sulfate (SO_4^{2-}), and SRP. These minipeepers contained 30 round chambers of 0.7-cm diameter and 1-cm spatial resolution, and were prepared similarly to the 2D peepers. The water in the mesocosms was replaced once (day 25) with fresh water from Lake Arendsee during the incubation of the minipeepers.

To calculate the P balance of the overlying water, SRP and total phosphorus (TP) in the water were measured before each water exchange. At the end of the experiment, two 20-cm-long cores with a diameter of 5.8 cm were taken from each mesocosm. One was used for a P fractionation of the upper 3 cm; the other was sectioned for a TP depth profile with a resolution of 1 cm. The P pools of the sediment above and below 3 cm were calculated taking into account the TP content and sediment dry weight of the single layers. To balance the P translocation, P pools of the sediment at the start of the experiment were calculated analogously.

Chemical analysis—The photometrical SRP analysis of the pore water samples collected with the 2D peepers were conducted in microtiter plates directly after removal of each 2D peeper, using a scaled-down molybdenum blue method (Lewandowski et al. 2002), and were completed within 3 h after removal of the 2D peepers from the mesocosm. Replicates for seven different phosphate concentrations showed a coefficient of variation below 10% in the range 1.5 to 5 $\mu mol L^{-1}$ ($n = 100$), and below 3% in the range 5 to 30 $\mu mol L^{-1}$ ($n = 100$).

In contrast to the pore water samples, SRP in the water samples was measured using a segmented flow analyzer (Skalar San^{plus}) based on the photometrical molybdenum-blue method. TP in water samples and in extracts of the P fractionation was determined as SRP after digestion at 121°C and 0.12 MPa using peroxodisulfate. Ammonium was determined photometrically using a segmented flow analyzer with a modified indophenol method (Skalar San^{plus}). Nitrate and

sulfate were determined with an ion chromatograph (Dionex), and dissolved iron and dissolved manganese were measured with a flame atomic absorption spectrometer (Perkin Elmer). Sediment dry weight was measured after drying at 105°C to constant weight, and organic matter was measured as loss on ignition after 3 h of ignition at 450°C. The TP in sediment samples was obtained as SRP after 12-h sulfuric acid digestion with peroxide at 150°C. Total metal concentrations were analyzed with a flame atomic absorption spectrometer after an aqua regia digestion. Particulate P binding forms in sediment samples were determined by extracting P according to the sequential fractionation scheme proposed by Psenner and Pucsko (1988) and modified by Jensen and Thamdrup (1993) and Hupfer et al. (1995). The applied scheme allows six major fractions to be distinguished (NH_4Cl -P, BD-P, NaOH-SRP, NaOH-NRP, HCl-P, Rest-P). In this study, we are only interested in redox-sensitive P, which is released with the elution medium bicarbonate dithionite (BD). To assure that iron was the binding partner of P in that fraction, iron concentrations as well as P concentrations were measured in the BD fraction.

Data analysis—For 2D isoconcentration diagrams of SRP, Surfer V 5.01 (Golden Software) was used. Data gaps at screw positions were filled using linear kriging as the gridding method to achieve the homogeneous grid of SRP concentrations necessary for the program. Diffusive SRP fluxes were calculated using Fick's first law of diffusion:

$$J_i = \frac{\varphi}{\Theta^2} \cdot D_i \cdot \frac{dC_i}{dz}$$

with J_i , diffusional flux of ion i ($\mu mol cm^{-2} s^{-1}$); φ , porosity of the sediment (); Θ , tortuosity of the sediment (); D_i , molecular coefficient of diffusion for ion i ($cm^2 s^{-1}$); dC_i/dz , concentration gradient of ion i ($\mu mol cm^{-4}$). To apply Fick's first law (1) a steady state should have been reached, and (2) molecular diffusion should be the only transport mechanism for solutes. However, as long as macrozoobenthos live in the sediment, other transport mechanisms besides molecular diffusion will exist (for example, bioirrigation), and macrozoobenthos will cause local changes so that a complete steady state cannot be reached. Owing to the lack of other applicable method, Fick's first law was used, although both prerequisites are insufficiently fulfilled.

The porosity of the sediment φ was calculated by

$$\varphi = \frac{\rho_{ws} \cdot w}{\rho_{wat}}$$

with ρ_{ws} , density of the wet sediment ($g cm^{-3}$); ρ_{wat} , density of water at ambient temperature ($g cm^{-3}$); w , water content (weight-%/100). The density of water ρ_{wat} can be found in tables, and the density of wet sediment ρ_{ws} was calculated by

$$\rho_{ws} = \left[\frac{w}{\rho_{wat}} + \frac{(1-w)}{\rho_{ds}} \right]^{-1}$$

with ρ_{ds} , density of the dry sediment ($g cm^{-3}$). The density of the dry sediment ρ_{ds} was calculated by

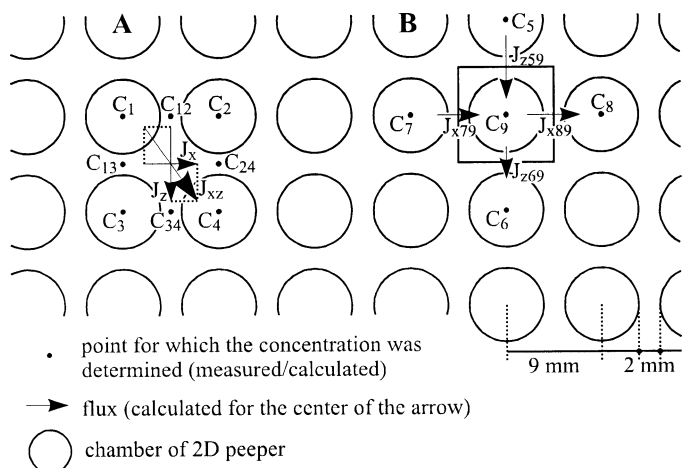


Fig. 1. (A) Procedure for flux calculations: It is assumed that the concentration determined for a peeper chamber is valid for the center of the chamber (C_1 , C_2 , C_3 , and C_4). For the midpoint between neighboring chambers, the concentration is calculated as arithmetic mean in both horizontal (C_{13} and C_{24}) and vertical (C_{12} and C_{34}) directions. The horizontal flux J_x between C_{13} and C_{14} is calculated with Fick's first law of diffusion as described in the text. The vertical flux J_z is calculated analogously. Finally, the horizontal and the vertical fluxes are added to the 2D vector J_{xz} . (B) Procedure for calculation of turnover rates (difference between P mobilization and P fixation rate): The turnover rates are calculated for squares with 9-mm-long edges. The fluxes across each of the four borders (J_{z59} , J_{x79} , J_{x89} , and J_{z69}) are calculated as described above, added together, and divided by the area of the square.

$$\rho_{ds} = \left[\frac{loi}{\rho_{org}} + \frac{(1 - loi)}{\rho_{min}} \right]^{-1}$$

with loi , loss on ignition (weight-%/100); ρ_{org} , density of organic matter (1.4 g cm^{-3}); ρ_{min} , density of mineral components (2.65 g cm^{-3}). The tortuosity Θ was calculated according to Boudreau (1996):

$$\Theta = \sqrt{1 - \ln(\varphi^2)}$$

Since the diffusion coefficients of the different dissociation levels of phosphoric acid are different, the degree of proteolysis α was calculated according to Stumm and Morgan (1996), taking pH and temperature into account. With the Stokes–Einstein relation, tabulated values of the diffusion coefficient were transferred to the temperature of the laboratory experiment:

$$D_i = D_{i,25^\circ\text{C}} \cdot \frac{v_{25^\circ\text{C}} \cdot T}{v_T \cdot T_{25^\circ\text{C}}}$$

with $D_{i,25^\circ\text{C}}$ molecular coefficient of diffusion of ion i at 25°C (H_2PO_4^- : $8.46 \times 10^{-6} \text{ cm}^2 \text{ s}^{-1}$; HPO_4^{2-} : $7.34 \times 10^{-6} \text{ cm}^2 \text{ s}^{-1}$; PO_4^{3-} : $6.12 \times 10^{-6} \text{ cm}^2 \text{ s}^{-1}$) (Li and Gregory 1974); T , temperature of the laboratory experiment (283.15 K); $T_{25^\circ\text{C}}$, temperature 25°C in Kelvin (298.15 K); $v_{25^\circ\text{C}}$, dynamic viscosity of water at 25°C ($0.8903 \text{ g m}^{-1} \text{ s}^{-1}$); v_T , dynamic viscosity of water at temperature T ($\text{g m}^{-1} \text{ s}^{-1}$). Fluxes in horizontal and vertical directions were calculated unidimensionally and then converted into a flux vector on a 2D plane as shown in Fig. 1A. Turnover rates were calculated for squares with 9-

mm-long edges by adding up the fluxes across the borders of the square (Fig. 1B). The insufficiently fulfilled prerequisites (steady state, transport only by diffusion) resulted in incorrect flux calculations. Since the turnover was calculated as the difference of the fluxes across the four borders of a square, the susceptibility to insufficient fulfilled prerequisites was worse than for absolute flux calculations.

To calculate an index for the observed heterogeneity, Lewandowski et al. (2002) suggested dividing the summed absolute values of the vertical flux components at 0- to 10-cm sediment depth by the equivalent sum of the horizontal flux components at that depth. To match the word heterogeneity index more precisely we changed to the inverse of the originally suggested quotient:

$$HI = \frac{\sum |J_{x,i,j}|}{\sum |J_{z,i,j}|}$$

with HI , heterogeneity index (); $J_{x,i,j}$, horizontal flux components in 0- to 10-cm sediment depth ($\mu\text{mol cm}^{-2} \text{ s}^{-1}$); $J_{z,i,j}$, vertical flux components in 0- to 10-cm sediment depth ($\mu\text{mol cm}^{-2} \text{ s}^{-1}$). The heterogeneity index is a measure of the importance of the horizontal concentration gradients relative to the importance of the vertical concentration gradients. In a sediment corresponding to the classical 1D view of sediments, the index would be zero. In a sediment with random (or systematic) scattering of concentrations, the index would be close to one, since the importance of the horizontal fluxes would be similar to that of the vertical fluxes. In such sediments, a 2D or three-dimensional (3D) view should be preferred to a 1D view.

Results

Within a few minutes of being introduced into the mesocosms, the oligochaetes and the chironomids dug down into the sediment. Within several hours the color of the sediment around the chironomid burrows changed from nearly black to light brown due to oxidization of the sediment (Fig. 2) (because oxygen penetrates only a few millimeters into the anoxic sediment, chironomids pump oxic water down into their burrows). Gradually, more and more oxidized burrows appeared. Most of these oxidized burrows were located in the upper 15 cm of the sediment. In contrast, the burrows of the oligochaetes did not have oxidized walls. However, the oligochaete burrows could easily be seen through the transparent walls of the Perspex containers. Some oligochaetes even burrowed down to the base of the sediment (about 25 cm). At the end of the experiment, approximately 11% of the chironomids and 12% of the oligochaetes had died. Thus, mortality during the experiment was low.

After 16 d of incubation in the mesocosms without macrozoobenthos, the SRP concentrations at the sediment–water interface increased sharply compared to the concentrations in the water above sediment and roughly 2 cm below the surface the concentration maximum of about 130 to 200 $\mu\text{mol L}^{-1}$ was reached (Fig. 3A). Beneath this depth, SRP concentrations decreased to approximately 100 $\mu\text{mol L}^{-1}$. After 16 d of incubation in the mesocosms with macrozoobenthos, a completely different distribution of SRP concen-

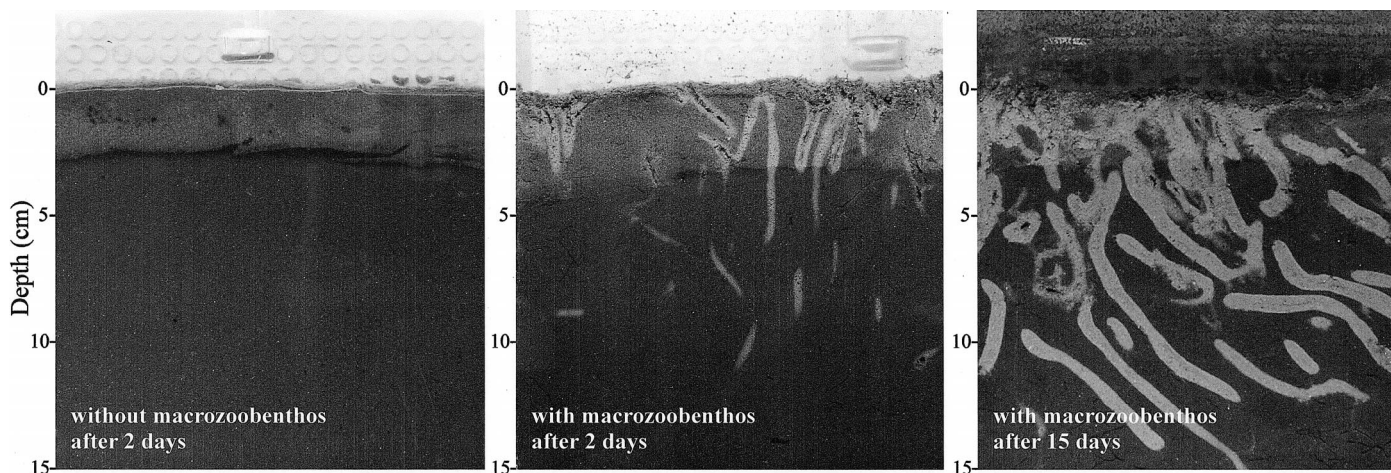


Fig. 2. Photographs of laboratory mesocosms without and with macrozoobenthos 2 and 15 d after start of the experiment. The light reddish-brown colored sediment areas are oxidized zones around the chironomid burrows.

trations was seen. At the sediment–water interface lowest SRP concentrations of the 2D peeper were observed. The concentrations were even lower than in the overlying water. About 3 cm below the sediment–water interface, there was a steep increase of SRP concentrations to values of approximately $40 \mu\text{mol L}^{-1}$, and roughly 15 cm below surface the concentration gradient became steeper again, reaching values of about $100 \mu\text{mol L}^{-1}$. In the mesocosms with macrozoobenthos, the SRP concentration distributions were much more heterogeneous than in the mesocosms without macrozoobenthos (compare upper and lower rows in Fig. 3A). The 2D isoconcentration diagram showed small localized zones of low SRP concentrations (6 to $20 \mu\text{mol L}^{-1}$) down to about 14 cm of sediment depth in the mesocosms with macrozoobenthos, but these were not seen in the mesocosms without macrozoobenthos.

The calculated 2D SRP flux diagrams of the mesocosms with and without macrozoobenthos show the highest diffusive fluxes in the vicinity of the sediment–water interface (Fig. 3B). In the mesocosms with macrozoobenthos the direction and intensity of the fluxes is much more heterogeneous than in the mesocosms without macrozoobenthos. The 2D SRP isoturnover diagrams show that the mesocosms without macrozoobenthos exhibit the highest P turnover rates directly below the sediment–water interface (Fig. 3B). In contrast, in mesocosms with macrozoobenthos, highest P turnover rates occur distributed over the upper 10 cm of the sediment; there was a much more patchy pattern of P turnover, and maximum rates are lower than in mesocosms without macrozoobenthos. P sinks with high immobilization rates ($>30 \text{ mmol m}^{-3} \text{ d}^{-1}$) are located in the upper 10 cm of the sediment in the mesocosms with macrozoobenthos. The maximum immobilization rates of these sinks are even greater than the rates occurring in the mesocosms without macrozoobenthos. Although the uncertainties of the calculated turnover rates arising from the not completely steady-state pattern are high, the basic trend of turnover rates is probably correct.

The results of pore water analysis in the mesocosms after 35 d are shown in Figs. 4 and 5. There was a clear difference

in the SRP, Fe^{2+} , and SO_4^{2-} gradients in mesocosms without and with macrozoobenthos (Fig. 4). In the mesocosms without macrozoobenthos, there was a peak of SRP concentrations directly below the sediment–water interface (upper 5 cm), whereas in the mesocosms with macrozoobenthos, SRP concentrations were extremely low in the upper 10 cm and increased only moderately with further depth. In the mesocosms without macrozoobenthos, Fe^{2+} concentrations increased sharply below the sediment–water interface, and in the mesocosms with macrozoobenthos, Fe^{2+} concentrations were below the detection limit in the upper 5 cm of the sediment and increased with further depth. In the mesocosms without macrozoobenthos, SO_4^{2-} decreased sharply 2 to 3 cm below the sediment–water interface, and was not detected at deeper layers. In contrast, in the mesocosms with macrozoobenthos, SO_4^{2-} in the upper 10 cm was as high as in the overlying water, and decreased moderately in deeper layers. Furthermore, for all three parameters there were negligible differences between the replicates in the macrozoobenthos-free mesocosms, whereas there was great variation between replicates in the mesocosms with macrozoobenthos. In the mesocosms without macrozoobenthos, there was only a small variation in the concentration of each of the five ions NO_3^- , NH_4^+ , Mn^{2+} , Fe^{2+} , and SO_4^{2-} , and we could identify a depth sequence of oxygen, nitrate, manganese, iron, and sulfate reduction zones (Fig. 5). The maximum SRP concentration was reached in, or directly below, the sulfate reduction zone.

At the end of the experiment, P fractionation in the upper 3 cm of the sediment showed a drastic increase of the BD-P fraction in the mesocosms with macrozoobenthos compared to the mesocosms without macrozoobenthos. BD-P was 13.9 ± 0.4 (standard error) $\mu\text{mol g}^{-1}$ dry wt in the mesocosms without macrozoobenthos and $44.0 \pm 2.0 \mu\text{mol g}^{-1}$ dry wt in the mesocosms with macrozoobenthos. Iron in the BD extract was $27.5 \pm 0.2 \mu\text{mol g}^{-1}$ dry wt in the mesocosms without macrozoobenthos and $103.7 \pm 4.6 \mu\text{mol g}^{-1}$ dry wt in the mesocosms with macrozoobenthos. In contrast, the other P fractions of Psenner's sequential P extrac-

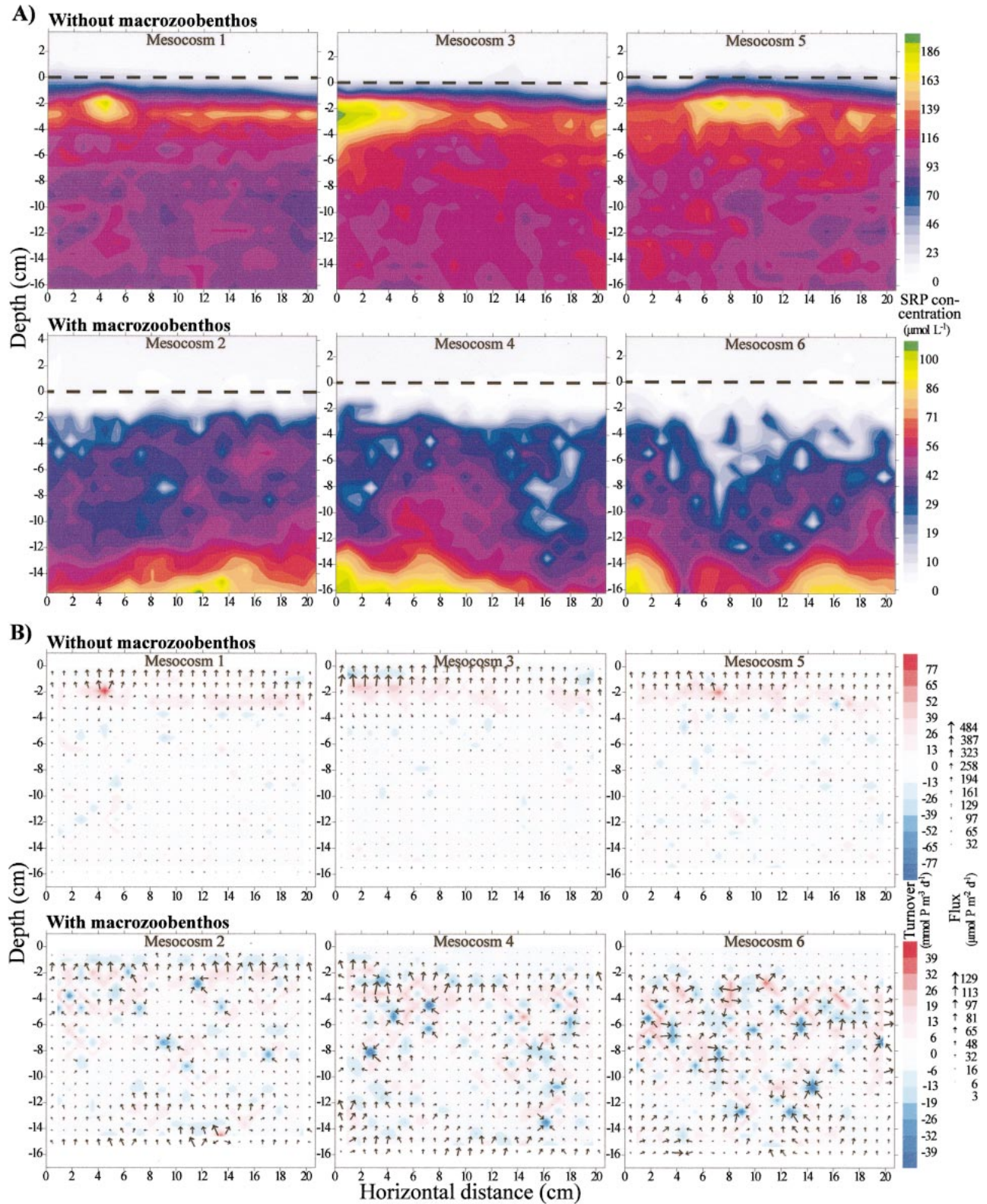


Fig. 3. (A) Two-dimensional (2D) soluble reactive phosphorus (SRP) isoconcentration diagrams of the mesocosm experiments after 16 d. Three replicates performed without macrozoobenthos and three with macrozoobenthos. Positions of sediment–water interface are marked with dashed lines. (B) Combined 2D SRP fluxes and isoturnover diagrams of the mesocosm experiments after 16 d. Note different scales for concentration, turnover, and flux for upper and lower rows within both A and B.

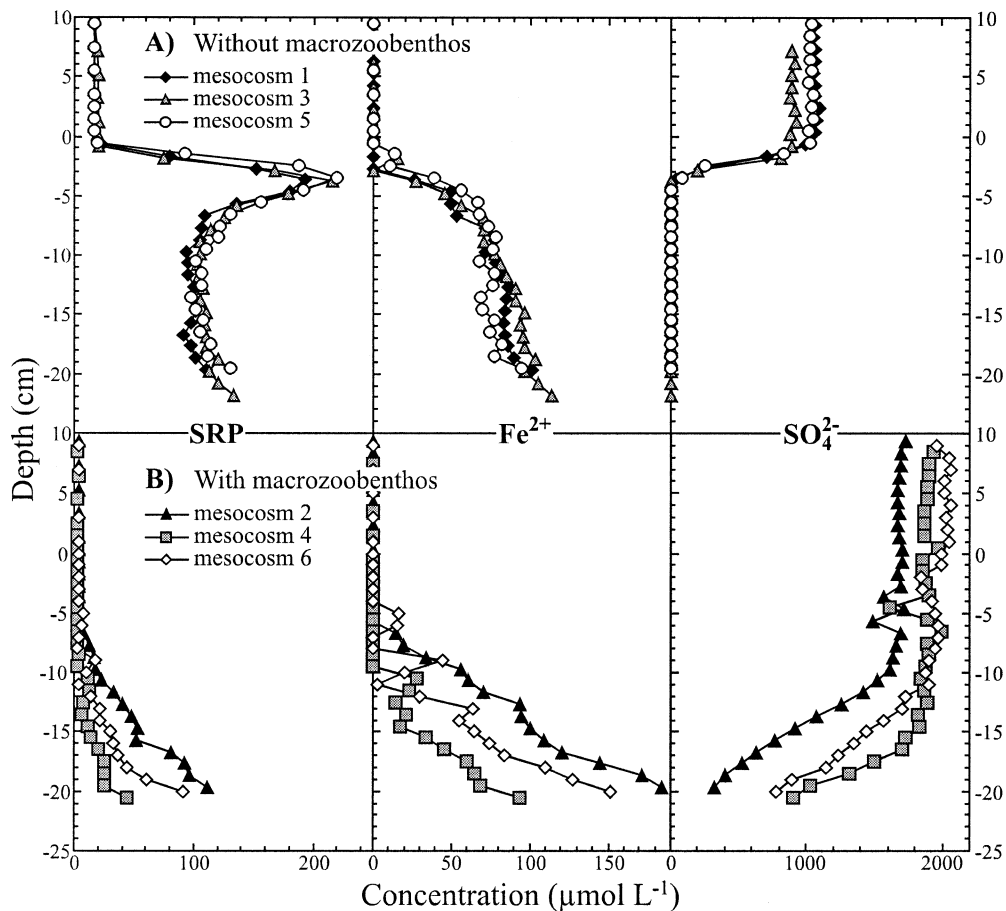


Fig. 4. Pore water gradients taken with minipeepers at the end of the experiment after 35 d, for soluble reactive phosphorus, dissolved iron, and sulfate in (A) mesocosms without macrozoobenthos, and (B) with macrozoobenthos. Zero used for values below detection limits: 9 $\mu\text{mol L}^{-1}$ for Fe^{2+} , and 20 $\mu\text{mol L}^{-1}$ for SO_4^{2-} .

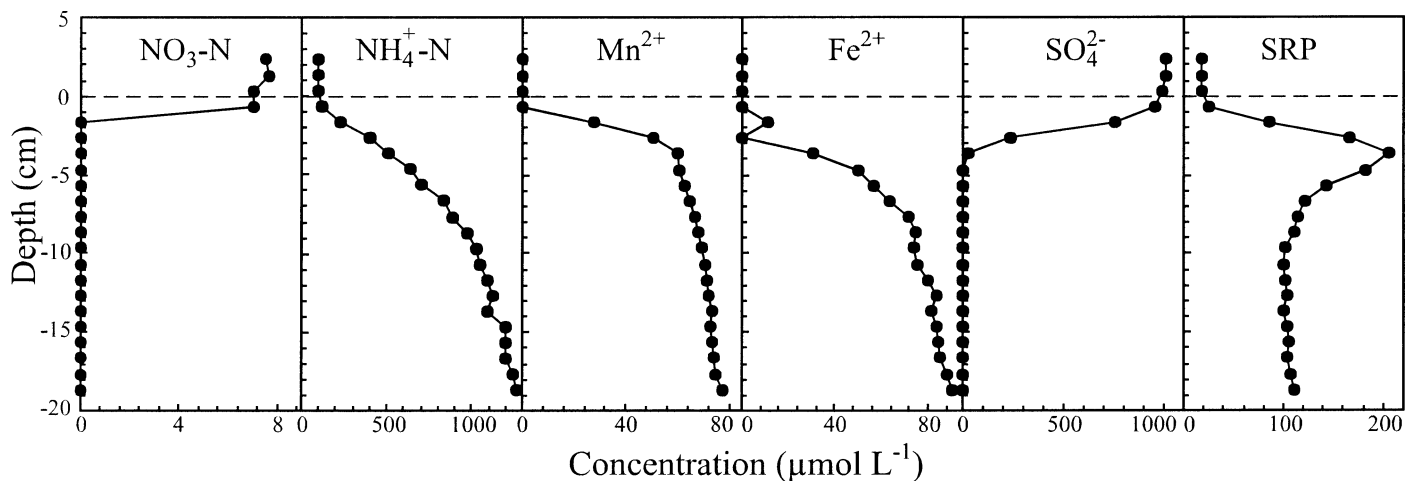


Fig. 5. Pore water profiles taken with minipeepers after 35 d for nitrate, ammonium, dissolved manganese, dissolved iron, sulfate, and soluble reactive phosphorus in mesocosms without macrozoobenthos. Arithmetic mean of three replicates. Zero used for values below detection limits: 0.8 $\mu\text{mol L}^{-1}$ for NO_3^- , 4.5 $\mu\text{mol L}^{-1}$ for Mn^{2+} , 9 $\mu\text{mol L}^{-1}$ for Fe^{2+} , and 20 $\mu\text{mol L}^{-1}$ for SO_4^{2-} .

tion were roughly the same in the mesocosms with and without macrozoobenthos.

In the mesocosms with macrozoobenthos, the increased P content in the upper 3 cm of the sediment ($+1,319 \pm 95 \mu\text{mol}$) might have originated from a decrease of P stored in deeper (>3 cm) sediment layers ($-1,681 \pm 587 \mu\text{mol}$), and a decrease of P in the overlying water ($-246 \pm 17 \mu\text{mol}$). In the mesocosms without macrozoobenthos, P released in sediment layers below 3 cm ($-1,506 \pm 192 \mu\text{mol}$) diffused into the water above the sediment ($+484 \pm 33 \mu\text{mol}$), while the P amount in the upper 3 cm of the sediment remained approximately constant ($-82 \pm 126 \mu\text{mol}$). The arithmetical imbalances of these data contradicting mass conservation are due to the imprecise measurements when determining a relatively small change of the high TP content in the deep sediment layers (>3 cm) with their high amount of dry matter.

Discussion

Spatial and temporal resolution of the 2D peeper—Spatial variations less than a centimeter and larger than a decimeter were hardly visible because of the resolution of the 2D peeper (9 mm) (Lewandowski et al. 2002). Although the chironomid tubes are only a few millimeters in diameter, and even with the oxidized zones around them less than 1 cm in diameter, the region affected by the burrows is enlarged beyond this by diffusion of solutes. Thus, influences of burrows on pore water concentrations and pore water heterogeneity can be detected with our 2D peeper. However, the spatial resolution of the 2D peeper did not allow sampling of water from only a burrow or burrow lining; the sampled pore water was always a mixture of water from the burrow, the burrow lining, and the surrounding pore water due to the chamber diameter of 7 mm. Since the chironomid burrows may extend a few decimeters into the sediment, the resolution of the 2D peeper was well suited to investigate the effects of the burrows on the pore water surrounding the burrows down to this maximum depth.

Temporal variations of the pore water composition interfere with the equilibration of the 2D peeper. The peeper was more sensitive to changes during the last days of its exposure since equilibration of the water in the peeper chambers was always directed toward the actual outside composition. After a change of the outside composition, the initial diffusive flux was high and was driven by a large concentration difference, whereas the flux rapidly decreased with progress of equilibration. Thus, some features might reflect biological activity during an earlier phase of deployment, and other features might be caused by more recent activity. Steady-state conditions are desirable throughout the equilibration time. Because of a chamber depth of 1.7 cm, we calculated an equilibration time of approximately 7 d to reach 95% of the outside concentrations in the peeper chambers, whereas the whole exposure lasted 16 d. The first 9 d were available to reestablish equilibrium conditions in the pore water after its dilution with distilled water originating from the water in the peeper chambers and to allow the chironomids to build their tubes. Through the front plate of the mesocosm, we could

observe that most of the chironomid burrows were built during the first few days of the experiment and that there were only minor changes in the burrow courses afterwards. Nevertheless, real steady conditions will never be reached in a highly dynamic system such as a sediment inhabited by macrozoobenthos. The measured concentration distribution is an undefined mixture of the pore water concentrations at the termination of the experiment and during the last days of the peeper exposure.

Mesocosms without macrozoobenthos—In the mesocosms without macrozoobenthos, horizontal variability of SRP pore water concentrations was low (Fig. 3A). Thus, it is reasonable to consider the sediment as 1D system with laterally uniform layers, and to calculate mean pore water concentrations for each depth (Fig. 5) (Lewandowski et al. in press). A classic, sequentially layered redox zonation had established in the sediment with steep concentration gradients at the borders of the redox zones. SRP is released by the dissolution of iron-bound P and mineralization of organic matter, resulting in a peak of SRP concentrations in the upper sediment layers (<4 cm). In these layers, intensive mineralization occurs because of the freshly settled, easily degradable organic matter and sufficient availability of electron acceptors. For deeper layers of the laboratory mesocosms (>4 cm), old sediment was used with poorly degradable organic matter and thus, mineralization and P release were less intensive than in the upper sediment layers. In summary, the pore water P concentrations in mesocosms without macrozoobenthos are mostly homogenous in a lateral direction, with a classic redox zonation.

Mesocosms with macrozoobenthos—The chironomid burrows can be regarded as an increase of the sediment–water interface area per unit of mesocosm base or lake bottom. Since the amount of oxic sediment, as well as the diffusional exchange of solutes between sediment and overlying water, depend on the area of the sediment–water interface, both the amount of oxic sediment and the diffusional exchange of solutes are increased in the presence of chironomids reducing pore water P concentrations and altering P release rates. However, this simplified view neglects the spatial heterogeneity that is introduced by the 3D geometry of the burrow (Matisoff et al. 1985). The local chemical milieu surrounding the tubes differs considerably from the chemical milieu existing at the same depth but at larger distances from a burrow. The irregular pattern of mineralization, of synthesis of new compounds, and of other diagenetic reactions is linked to an irregular pattern of SRP turnover (Fig. 3B). Consequently, SRP fluxes caused by molecular diffusion are also irregular (Fig. 3B), resulting in a patchy distribution of SRP concentrations (Fig. 3A).

To quantify the observed heterogeneity we calculated the heterogeneity index. The indices of earlier studies (Lewandowski et al. 2002, 2003, in press) and the indices of the present laboratory mesocosms are presented in Table 2. The quotient of the mesocosms without macrozoobenthos (0.27) is similar to the quotients determined at deep locations of Lake Arendsee (0.28 and 0.38), where there is no macrozoobenthos. The quotient of the mesocosms with chirono-

Table 2. Patchiness of flux pattern, represented by heterogeneity index, in 0- to 10-cm sediment depth in different ecosystems.

Lake	Depth of sampling site (m)	Mixis	Anoxia*	Macrozoobenthos†	Heterogeneity index‡		Literature source
					Macrozoobenthos†	Heterogeneity index‡	
Arendsee	(Mesocosm experiment)		No	No		0.27	Present study
Arendsee	48.7	Mono- to dimictic	Yes	No		0.28	Lewandowski et al. (2002)
Arendsee	48.0	Mono- to dimictic	Yes	No		0.38	Lewandowski et al. (in press)
Stechlin	68.5	Dimictic	No	Yes		0.61	Lewandowski et al. (2003)
Süsser See	7.5	Polymictic	No	Yes		0.67	Lewandowski et al. (2002)
Arendsee	14.0	Mono- to dimictic	No	Yes		0.69	Lewandowski et al. (in press)
Arendsee	(Mesocosm experiment)		No	Yes		0.81	Present study
Müllrose	5.2	Polymictic	No	Yes		0.81	Lewandowski et al. (2002)

* Anoxic water above sediment at the end of summer stratification, or during the laboratory experiment.

† Macrozoobenthos observed at the sampling site.

‡ Compare Eq. 7.

mids and oligochaetes (0.81) is similar to that of Lake Müllrose (0.81), a lake with high densities of macrozoobenthos. The quotients of Lake Müllrose and the mesocosm experiment were a little bit higher than the quotients of Lake Süsser See (0.67) and Lake Stechlin (0.61). Both lakes have lower macrozoobenthos densities than Lake Müllrose and the mesocosm experiment. The fact that the in situ quotients of Lake Müllrose and Lake Arendsee were similar to the quotients of the laboratory mesocosms (with or without macrozoobenthos, respectively) suggests that in situ in the investigated type of eutrophic lake sediments, no other major factors besides macrozoobenthos controlled small-scale spatial heterogeneity (whereas in shallow areas of eutrophic lakes, roots of macrophytes might cause additional small-scale spatial heterogeneity by transporting oxygen into the sediment [Christensen 1997; Hupfer and Dollan 2003]).

Effects of oligochaetes and chironomids on their sediment environment—Since the 1970s a number of researchers focused on the effects of macrozoobenthos in marine sediments (for example, Rhoads 1974; Aller 1978); however, there were only a few studies on the equivalent effects in freshwater systems, and only a small part of these freshwater studies investigated the effects of macrozoobenthos on phosphorus (for example, Gallepp 1979; Matisoff et al. 1985). The overall result of the marine and freshwater studies was that macrozoobenthos affect their sediment environment via several different pathways. Oligochaetes and chironomids, the organisms used in our study, influence the chemical, physical, and microbiological sediment characteristics by bioirrigation, bioturbation, resuspension, ingestion, digestion, defecation, excretion, and secretion. The effects of these influences on sediment biogeochemistry, with a focus on P cycling in freshwater sediments, are described below. The conceptual model we present (Fig. 6) was based on review of the literature considering the data of the present study.

Oligochaetes and chironomids bioturbate the sediment (Fig. 6A); that is to say they mix the sediment by burrowing; sediment can fall down into vacated burrows, and they drag particles through the sediment by locomotory activities (Fisher et al. 1980; McCall and Tevesz 1982). In the mesocosm experiment, some oligochaetes even burrowed to the base of the sediment (about 25 cm). According to Davis (1974), oligochaetes might burrow deeper than 35 cm but over 95% occur in the upper 16 cm. Oligochaetes ingest sediment at certain sediment depths (for example, peek feeding occurs at 2 to 7 cm according to Davis [1974], or at 6 to 9 cm according to Fisher et al. [1980]), and expel this material at the sediment–water interface. Thus, they displace large volumes of sediment upward (Davis 1974). Therefore, Rhoads (1974) called them “conveyer belt species.” The uppermost sediment layers move slowly downward as a discrete unit, to the depth of peak feeding, before the material is transported to the top again. According to Fisher et al. (1980), the particle reworking rate of oligochaetes is $59.7 \pm 10.1 \times 10^{-5} \text{ cm}^3 \text{ h}^{-1} \text{ individual}^{-1}$. With a population of 10,500 oligochaetes m^{-2} in the mesocosms, the downward velocity of the upper sediment layer due to oligochaete feeding was 0.15 mm d^{-1} , corresponding to 2.4 mm until removal of the 2D

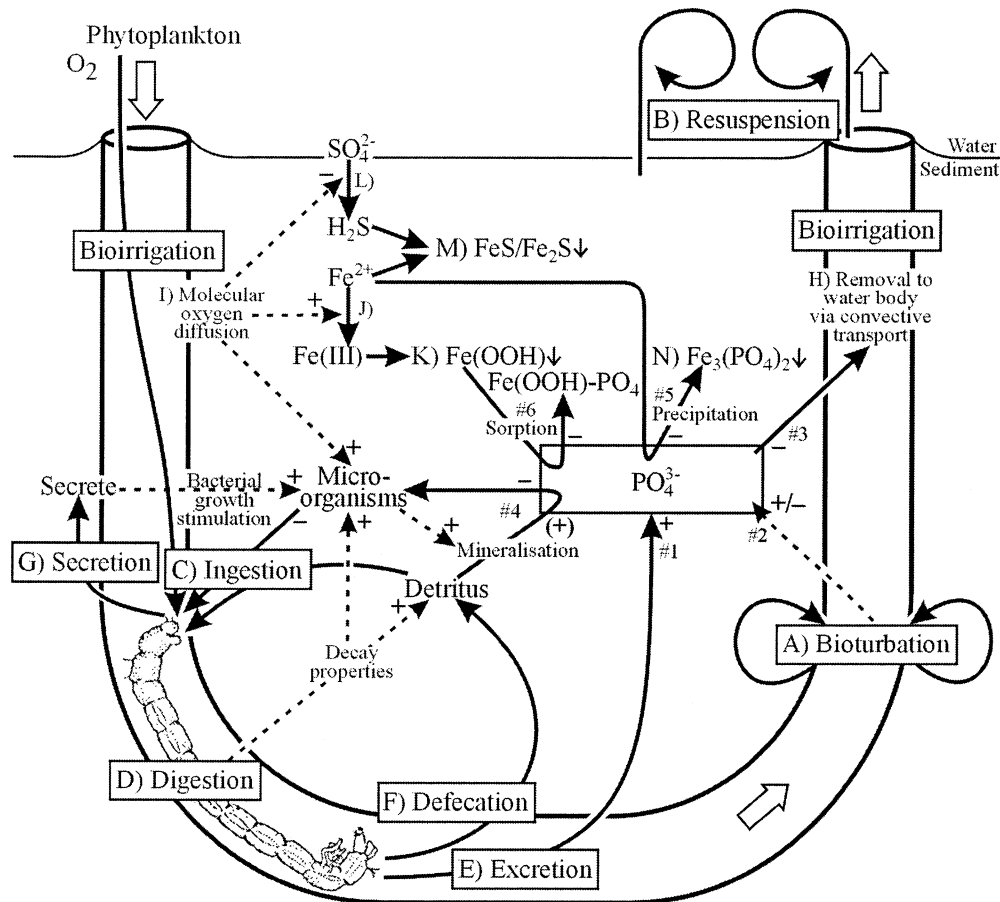


Fig. 6. Effect of macrozoobenthos (chironomid used as symbol for macrozoobenthos) on P cycling in iron-rich, organic-rich sediments with high total P content. Solid arrows, fluxes; dashed arrows, influences; +, positive influence; -, negative influence. Processes with letters or numbers are discussed in the text.

peepers at day 16, and 5.3 mm during the whole experiment after 35 d. The particle redistribution by bioturbation changes the local biogeochemistry, and transfer of particles between redox zones causes increased mineralization due to redox alternation (Aller 1994; Aller and Aller 1998; Kristensen and Mikkelsen 2003).

The burrowing activity of macrozoobenthos at the sediment-water interface may result in resuspension of sediment particles (Fig. 6B) (Gosselin and Hare 2003), resulting in a change of their chemical properties. Oligochaetes ingest sediment bacteria and chironomids graze on sediment bacteria and filter feed on phytoplankton (Walshe 1947). The ingested particles are digested (Fig. 6D) and a part of the uptaken P is excreted (Fig. 6E). The quantitative importance of this direct P release is still not clear (Gallepp 1979; Andersson et al. 1988). A further part of the ingested particles is defecated with altered structure, chemical properties, and microbiological characteristics (Fig. 6F). Furthermore, secretions of chironomids to build tube linings alter the diffusive permeability of the sediment (Aller 1983) and probably stimulate bacterial growth, and thus, mineralization (Fig. 6G) (Aller and Aller 1998).

Additionally, burrows and fecal pellets enhance diffusion by shortening the path length within the sediment (McCall

and Tevesz 1982). Furthermore, oligochaetes might cause an increase of the oxidized sediment layer by respiratory irrigation mediated through undulating movements of their posterior end (Andersson et al. 1988). However, their oxidizing effect on the sediment is limited, and no oxidized oligochaete burrow walls were observed (Fig. 2). In contrast, chironomid larvae pump water through their U-shaped burrows. The enhanced solute exchange between overlying water and pore water due to bioirrigation removes metabolites of mineralization processes to the overlying water (Fig. 6H), and supplies dissolved reactants (electron acceptors) from the overlying water (Fukuhara and Sakamoto 1987; Aller and Aller 1998). Imported oxygen diffuses through the burrow walls into the surrounding sediment (Fig. 6I), resulting in redox zones spherically layered around the tubes (Aller 1994) and stimulating bacterial growth.

Fe^{2+} ions diffusing from the surrounding sediment toward the burrows are oxidized (Fig. 6J) and precipitated (Fig. 6K) within the oxidized zone before reaching the interior of the burrow tube. The light reddish-brown color of the zone around the burrows that we observed (Fig. 2) might indicate the precipitation of $Fe(III)$ oxyhydroxides as described by Matisoff et al. (1985). The oxidation and precipitation of iron in the upper 10 cm is confirmed by the results of the

dialysis samplers showing significantly lower pore water Fe^{2+} concentrations (*t*-test, $\alpha < 0.01$) in the mesocosms with macrozoobenthos compared to the mesocosms without macrozoobenthos (Fig. 4). We assume that the SRP concentrations in the pore water of the mesocosms with macrozoobenthos were drastically decreased because of incorporation of phosphate during formation of Fe(III) oxyhydroxides (Gunnars et al. 2002) and sorption of phosphate on freshly precipitated Fe(III) oxyhydroxides. This supposition is confirmed by the results of the P fractionation, which showed a significant increase (*t*-test, $\alpha < 0.01$) of the iron-bound P in the mesocosms with macrozoobenthos (P and Fe increased in BD-P fraction), whereas P in all other fractions remained constant. The depth profile and the P balance of the water above the sediment showed that the major part of this P sorbed in the upper sediment layers as BD-P had been released in deeper sediment layers, whereas only a minor part originated from the overlying water.

A further P release mechanism is based on the close coupling of Fe, S, and P cycling. In sediments without macrozoobenthos, sulfate diffuses from the sulfate-rich overlying water (0.76 mmol L^{-1}) into the sediment (Fig. 4) and is reduced in the upper 3 cm of the sediment. The sulfate reduction rate is high ($176 \text{ mmol SO}_4 \text{ m}^{-3} \text{ d}^{-1}$, calculated from sulfate pore water gradients without macrozoobenthos although it might be quite inaccurate because of unsteady state conditions, Fig. 4). The produced H_2S might diffuse upward into the oxic sediment where it is reoxidized, or it might precipitate in the anoxic sediment as Fe(II) sulfide. In anoxic sediment, even at high phosphate concentrations, Fe(II) sulfide formation inhibits precipitation of Fe^{2+} as ferrous phosphates such as $\text{Fe}_3(\text{PO}_4)_2 \cdot 8 \text{ H}_2\text{O}$ (vivianite) (Roden and Edmonds 1997; Gächter and Müller 2003). Thus, SRP concentrations in the pore water reach high values (Fig. 4). In contrast, in mesocosms with macrozoobenthos, bioirrigation causes a decreased net sulfate reduction (Fig. 6L) (and an increased sulfide oxidation), visible as significantly increased sulfate concentrations in the overlying water of the mesocosms with macrozoobenthos compared to mesocosms without macrozoobenthos (*t*-test, $\alpha < 0.01$) (Fig. 4). Furthermore, there is a downward shift of sulfate consumption in the sediment with macrozoobenthos compared to the mesocosms without macrozoobenthos (Fig. 4). This results in less precipitation of Fe^{2+} as Fe(II) sulfide (Fig. 6M) in the mesocosms with macrozoobenthos than in the mesocosms without macrozoobenthos. A part of the additional Fe^{2+} might diffuse into oxic zones where it is oxidized (Fig. 6J) and precipitates as Fe(III) oxyhydroxide (Fig. 6K). The other part of Fe^{2+} , under anoxic conditions, might precipitate as ferrous phosphates (Fig. 6N) when the corresponding solubility products are exceeded.

Evaluation of the different processes controlling SRP pore water concentrations—According to Fig. 3A, the presence of macrozoobenthos resulted in a significant decrease (*t*-test, $\alpha < 0.01$) of SRP pore water concentrations in the upper sediment layers of the Arendsee sediment. In Fig. 6 we show eight effects (A to H) of macrozoobenthos on its sediment environment, which could have jointly controlled P concentrations. Six processes (Fig. 6 [#1 to #6]) directly affect

phosphate pore water concentration, as follows. (1) SRP excretions of chironomids will have increased SRP pore water concentrations, and thus were not a cause of the decreased SRP concentrations we observed (Fig. 6 [#1]). (2) Bioturbation of chironomids and oligochaetes resulted in a redistribution of the sediment, with a patchy pattern of both increases and decreases of SRP pore water concentrations. Since decreases of SRP concentrations clearly predominated in the mesocosm experiment (Fig. 3A), bioturbation is also a factor of only minor importance for SRP pore water concentrations and their spatial heterogeneity (Fig. 6 [#2]). (3) The removal of SRP from the pore water to the overlying water by bioirrigation might have a phosphate-decreasing effect but cannot account for the size of the phosphate decrease (Fig. 6 [#3]). Pore water SRP concentrations in the upper sediment layers were even lower than in the overlying water (Fig. 3A). Furthermore, the P balance of the overlying water in the mesocosm experiment showed that there was a smaller increase of the TP concentrations in the mesocosms with macrozoobenthos than in the mesocosms without macrozoobenthos (whereas an increased convective P release would have resulted in higher TP concentrations in the overlying water). (4) Increase in numbers and metabolic activity of bacteria stimulated by chironomid activities increase mineralization of detritus. In spite of increased biodegradation of organic matter, P release is probably decreased (Fig. 6 [#4]) because of high P uptake rates of growing microorganisms (Tezuka 1990). The incorporated P might be released after death of the microorganisms or excreted by chironomids feeding on sediment bacteria. An increased SRP excretion would result in increased SRP concentrations in the water above the sediment. Thus, increased mineralization was probably not the main cause of the decreased SRP pore water concentrations we observed. (5) Precipitation of ferrous phosphates such as vivianite requires high Fe^{2+} concentrations, the absence of sulfide, and high phosphate concentrations. In the upper sediment layers (<10 cm) of the mesocosms with macrozoobenthos where no sulfate reduction occurs (Fig. 4) the solubility product of vivianite was not exceeded. Thus, precipitation of Fe(II) phosphate compounds is probably only of minor importance for the observed SRP decrease in the mesocosms with macrozoobenthos (Fig. 6 [#5]), although it might play a role in microenvironments, which was undetectable with the resolution of the 2D peeper. (6) The significantly decreased SRP concentration in the mesocosms with macrozoobenthos compared with the mesocosms without macrozoobenthos that we observed was probably a consequence of bioirrigation delivering oxidizing agents into the sediment, resulting in an oxidation of Fe^{2+} diffusing from the surrounding sediment into the burrow walls, and sorption of P on Fe(III) oxyhydroxide phases (Fig. 6 [#6]). Evidently, chironomids decrease pore water P concentration by P coprecipitation of Fe(III) oxyhydroxides. In other words, the low SRP pore water concentration in the mesocosms with macrozoobenthos might be explained by an increase of the redox potential visualized as altered redox zonation in Fig. 4. Like the low SRP concentrations, the heterogeneity of the SRP concentrations (Fig. 3A) was also a consequence of the increased redox potential around the heterogeneous distributed burrow tubes.

The thesis of Brandes and Devol (1995) and Harper et al. (1999), that most turnover does not occur in sequentially layered zones but in highly reactive, discrete sites, was not supported by our results. In our mesocosms without macrozoobenthos, the turnover either occurred in the whole layer, or there were many hot spots so close to each other that the resolution of the 2D peeper was insufficient to record them. If there were hot spots only in the mesocosms with macrozoobenthos, their SRP concentrations should be higher than concentrations in the control without macrozoobenthos. In fact, SRP concentrations were decreased in the presence of macrozoobenthos. Therefore, we assume that hot spots are more important in sediments with low P concentrations and little organic matter. Lewandowski et al. (in press) exposed a 2D peeper in a sandy sediment of Lake Arendsee with much lower P concentrations and less organic matter than the sediment used in our study. In that sediment, hot spots with very high P turnover were found and attributed to secretion, digestion, and bioturbation of macrozoobenthos, whereas P sorption caused by bioirrigation might only have been of minor importance due to already low SRP concentrations. The high P coprecipitation capacity of Fe(III) oxyhydroxides can only be important in iron-rich sediments.

Influences of macrozoobenthos on P release rates—The influence of macrozoobenthos on P release rates depends on life habits and feeding groups of the macrozoobenthos species involved, as well as on sediment characteristics. In our mesocosm experiment, the sediment was inhabited by both oligochaetes and chironomids. The most important influence of macrozoobenthos on P cycling in our experiment was identified as the change of the redox conditions by bioirrigation. Since oligochaetes do not bioirrigate the sediment, their influence on P release was negligible in our mesocosm experiment, and therefore, our discussion focuses on chironomids. In our experiment, P release across the sediment-water interface was decreased by chironomids. This observation warrants a reevaluation of the well-accepted opinion that P release from the sediment into the overlying water is in principle increased by chironomids. The basis for this common opinion are observations of many authors, for example, Gallepp 1979 and Andersson et al. 1988. Few authors report no (Matisoff et al. 1985) or a decreasing effect of chironomids on P release (Andersen and Jensen 1991). The contrasting results have been discussed in the literature (Fukuhara and Sakamoto 1987; Andersen and Jensen 1991; Wetzel 2001); however, as far as we know, there is yet no definite answer concerning in which cases which macrozoobenthos species increase, and in which cases they decrease, P release.

In the iron-rich sediments used in our study and probably also in other iron-rich sediments of eutrophic lakes, the effects of the import of oxidizing agents into the sediment by chironomids is dominant over the effects of convective pore water exchange, increased mineralization, and direct P excretion, resulting in a decrease of P release. In contrast, in iron-poor sediments where the P-binding capacity of the precipitating Fe(III) oxyhydroxide is insufficient to bind a great portion of the released P, chironomid activities might cause an increase of P release. The results of the presented study

suggest that in iron-rich sediments, chironomids influence P release by a redox-controlled P-fixation due to the high P coprecipitation capacity of Fe(III) oxyhydroxides.

Implications of the present study—Macrozoobenthos are the decisive factor controlling heterogeneity of pore water phosphorus concentrations in lake sediments uninhabited by macrophytes. To date, small-scale 2D variability of phosphate in pore water has been poorly investigated because of the lack of adequate methodology. Applying the novel 2D pore water sampler introduced by Lewandowski et al. (2002), this is the first laboratory study that systematically investigates the influence of macrozoobenthos on spatial distribution of pore water phosphorus concentrations. The results of the laboratory experiment showed that there is increased retention of P in the sediment in the presence of macrozoobenthos. This may help us to understand the processes by which macrozoobenthos affect P turnover in sediments and P cycling in lakes (Fig. 6). Identification of the basic mechanisms of increased or decreased P release may help interpretation of the contradictory findings reported in literature that macrozoobenthos usually lead to an increase or decrease of P release.

The present study emphasizes that the traditional 1D view of lake sediments is insufficient in sediments inhabited by macrozoobenthos. This knowledge has far-reaching consequences since in many scientific studies, only single pore water profiles are used for sediment investigations, and are assumed to be representative—neglecting the occurrence of horizontal variability at a specific sampling site. In future, collecting additional profiles will be essential in study design, and heterogeneity has to be carefully considered in data interpretation.

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