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Contribution of bacteria to release and fixation of phosphorus in lake sediments

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Abstract

Cycling of phosphorus at the sediment–water interface is traditionally considered to be controlled by pH- and redox-dependent, abiotic processes, such as formation and dissolution of FeOOH-PO_4 complexes. In this study, however, a large part of total P in sediments of Lake Sempach, an 87-m deep eutrophic lake, was estimated to be incorporated in bacterial biomass. Laboratory experiments indicated that sediment microorganisms can rapidly take up and release soluble reactive P (SRP), depending on redox conditions, and that sterilization of oxic sediments decreased their SRP sorption capacity. In an in situ experiment conducted in the lake, bacteria also contributed considerably to SRP fixation when water enclosed within a sediment flux chamber was reoxygenated following anoxia. Moreover, in that experiment and in data sets from several other lakes, anoxic releases of Fe and P from sediments appeared to be partly uncoupled. As part of an ongoing revision of the classical model for P exchange across the sediment–water interface, these results provide direct evidence that fixation and release of SRP may be controlled partly by redox-dependent changes in microbial physiology, as well as by production and decomposition of microbial biomass.

In addition to external loading and loss through the outflow, net sedimentation affects the cycling of phosphorus in lakes. The sediment–water interface may act either as a permanent sink or as a transient source for P. According to classical theory based on studies of Mortimer (1941, 1942) and Einsele (1936), P flux at the sediment–water interface is controlled primarily by ferric iron [Fe(III)], to which PO_4^{3-} adsorbs to form solid FeOOH-PO_4 complexes. Mortimer (1941) mentioned the possibility and Davison and Tipping (1984) provided evidence that organic constituents also form a part of the PO_4^{3-}-adsorbing ferric complex. When hypolimnetic water becomes anoxic and sediment redox potential decreases, these ferric complexes dissolve, and Fe and PO_4^{3-} are released into the hypolimnion. In this traditional model, sedimentary microorganisms only play an indirect role by consuming O_2 and NO_3^- during organic matter decomposition, thus providing necessary conditions for abiotic or biotic reduction of Fe(III) and subsequent release of PO_4^{3-} (Jansson 1987).

Although numerous field and laboratory studies support the classical model, it has not yet been clearly demonstrated in any lake that a substantial part of the PO_4^{3-} released under anoxic conditions was previously bound to Fe(III). Based on results from recent laboratory experiments and studies conducted in shallow lakes, Boström et al. (1982, 1988) discussed additional physical and chemical mechanisms controlling P cycling at the sediment–water interface. They especially emphasized that living microorganisms can play a direct role by acting as either a sink or a source for PO_4^{3-}. In deep-water lakes, however, evidence for similar biotic uptake and release controlling P cycling is limited.

Lake sediments are complex systems, and it is not easy to separate the contribution of microorganisms to either fixation or production of PO_4^{3-} from the postulated abiotic coupling between Fe and P cycles. For this reason, we conducted laboratory experiments with cultures of sedimentary bacteria and with sterilized sediments, in order

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to identify conditions under which sedimentary microorganisms might contribute to PO_4^{3-} uptake and release. We also conducted an in situ experiment with bottom water to test whether microbial processes observed in the laboratory contribute considerably to P fluxes across the profundal sediment–water interface. Finally, we measured bacterial biovolume in sediment from Lake Sempach, an 87-m-deep, eutrophic lake in north-central Switzerland, and estimated the amount of P incorporated in bacteria. Our results show that the apparent simultaneous release of Fe and PO_4^{3-} from anoxic sediments is not conclusive proof that the two elements were associated before the onset of anoxia, as is assumed in the classical model. Furthermore, in some deep-water lakes, Fe and PO_4^{3-} are not even released simultaneously into bottom water. These findings suggest that in sediments of deep-water eutrophic lakes, microorganisms responding to variations in redox potential and nutrient concentrations may also contribute considerably to uptake and release of P.

Methods

Chemical analyses—Unless stated otherwise, all filtered samples were passed through 0.45-μm Sartorious CA membrane filters. Soluble reactive P (SRP) was determined after filtration, according to Vogler (1965). Concentrations of total P in unfiltered (TP) and filtered samples (DP) were determined by the same method after digestion with $K_2S_2O_8$ at 120°C for 2 h. The concentration of particulate P (PP) was calculated as the difference between TP and DP.

Dissolved organic C (DOC) was analyzed in filtered water with an autoanalyzer (Technicon). To determine particulate organic C (POC), we filtered samples through Whatman GF/F glass-fiber filters (preheated to 500°C). The filters were then moistened with 1 M HCl and dried at 40°C to remove inorganic C before analysis in a Heraeus CHN analyzer (CHN Rapid). Total inorganic C (TIC) was calculated from pH and alkalinity measurements according to Harvey and Rodhe (1955).

NO_3^- and NH_4^+ in filtered water were determined as described by Müller and Widemann (1955) and Wagner (1969), respectively. O_2, Ca^{2+} (complexometric titration), and pH were analyzed according to Deutsche Einheitsverfahren zur Wasser-, Abwasser- und Schlammuntersuchung (VCH Verlagsges.). Concentrations of dissolved (DFe and DMn) and total (TFe and TMn) Fe and Mn were determined by graphite furnace atomic absorption. Concentrations of particulate Fe and Mn (PFe and PMn) were calculated as the difference between their respective dissolved and total concentrations. Samples for DFe and DMn were filtered immediately after collection and acidified with HCl to about pH 3.

Wet sediments were dried to constant weight at 80°C for percent moisture analyses. POC analysis of wet sediment was the same as described for aqueous samples. Calcium in dried sediment was determined by complexometric titration after combustion (550°C) and dissolution in HCl. After acidic digestion of dried sediment (H_2SO_4/H_2O_2 at 260°C), TFe, TMn, and TP were determined as described for the aqueous procedure.

Laboratory experiments with sedimentary microorganisms—Two identical experiments were conducted about 1 month apart in fall 1986. In each experiment, culture medium containing 6.7 g of standard 1 nutrient broth (Merck), 10 g of glucose, and 2.7 g of NH_4Cl was prepared in 10 liters of lake water, then filtered (0.2-μm Sartorius CA membrane filter) and sterilized at 120°C for 20 min. After cooling, the medium was bubbled with air and inoculated with 100 mg of surface sediment collected at 87 m in the lake. When the approximately 150 μmol liter^{-1} of SRP in the medium was exhausted, the culture was subdivided and placed in two glass carboys. To one carboy about 10 μmol liter^{-1} of PFe in the form of freshly precipitated FeOOH flocs was added; nothing was added to the other carboy. Since little SRP was in solution at that time, the added Fe was unable to bind large amounts of SRP. The cultures in both carboys were then bubbled with N_2 gas for about 3 d, after which they were again aerated. SRP, TP, DP, DFe, TFe, POC, and pH were measured frequently during the first 8 h of anoxia and oxia and later at daily intervals.

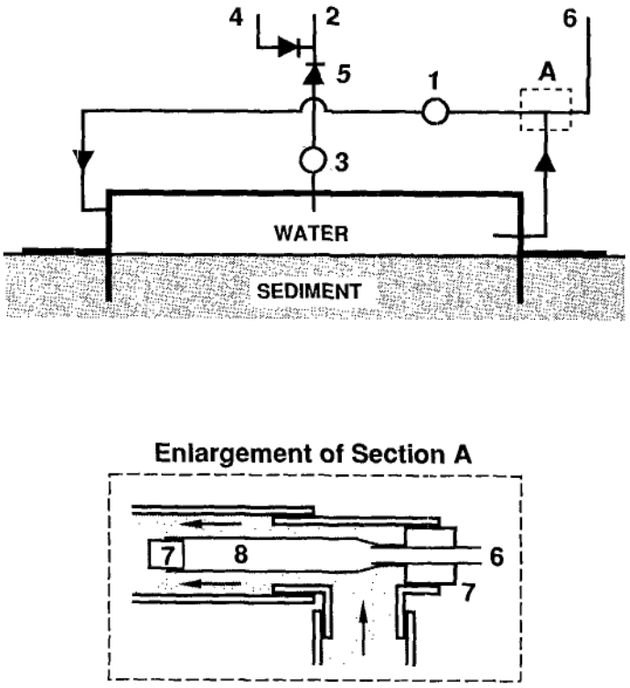

Fig. 1. Schematic presentation of sediment flux chamber (enlargement shows Tygon tubing used to add oxygen). 1—Pump to circulate water through flux chamber; 2—tubing for sampling; 3—sampling pump; 4—tubing to add formaldehyde to sampling tube; 5—one-way valves; 6—tubing for supply of pressurized oxygen; 7—stoppers; 8—inflated Tygon tubing.

Laboratory experiment with sterilized sediment—The upper 1 cm of sediment was collected from about 10 cores taken on 2 September 1987 at 85 m in the lake. Ten grams of homogenized sediment were diluted with filtered hypolimnetic water (0.2-μm Sartorius CA membrane filter) containing 200 μg SRP liter^{-1} to a volume of 450 ml in each of 12 1-liter bottles. Then 50 ml of Formalin were added to six of the bottles and 50 ml of distilled H_2O to the other six, producing a 4% formaldehyde concentration in the sterilized treatments. These sediment suspensions were aerated overnight at 20°C on a rotary shaker. Five bottles in each series were then spiked with additional PO_4^{3-} (as KH_2PO_4) at 0, 800, 1,200, 1,600, and 2,000 μg P liter^{-1}. The sixth bottle in each series was spiked with 2,000 μg P liter^{-1} plus 200 mg C liter^{-1} (as glucose) and 40 mg N liter^{-1} (as NH_4Cl). Aeration and agitation continued for 96 h. Samples were collected at 2, 4, 8, 24, 48, and 96 h after the addition of PO_4^{3-} and analyzed for pH and SRP. TP was measured to demonstrate that removed SRP was not adsorbed onto the glass surfaces.

In situ experiment with flux chamber—On 3 June 1986, a flux chamber was lowered onto the sediment surface at 87 m in the lake. The flux chamber (Fig. 1) is a large stainless-steel cylinder (1.5-m diam) with a lid that closes after the chamber reaches the sediment surface. When fully implanted in the sediment, it encloses 440 liters of overlying water. Water enclosed within the chamber is continuously circulated with a pump at a flow rate of 5.3 liters min^{-1} to ensure uniform mixing; no visible resuspension of sediment occurs at this low mixing rate. Molecular oxygen can be added to the water by diffusion when 50 cm of Tygon tubing inserted in the recirculation loop is inflated with pressurized O_2 supplied from the lake surface (Fig. 1, enlargement). When O_2 pressure in the Tygon tubing is decreased below the hydrostatic pressure in the flux chamber, the tubing compresses and no O_2 diffuses into the circulating water.

Water samples from the flux chamber were collected at about daily intervals by pumping them to the lake surface through carefully rinsed Tygon tubing. We prevented growth of bacteria in the tubing by filling it with a 4% formaldehyde solution between samplings. Fluxes of chemical species through the sediment–water interface were calculated from changes in concentration in the overlying water, the volume of the enclosed water, and the surface area of sediment enclosed by the flux chamber.

Estimating microbial biovolume—For each aqueous sample, 100 ml of water were pumped directly from the flux chamber into a sterile 125-ml serum bottle and kept in the dark in a cooling box. About 2 h after collection, acridine orange was added to the bottle; 30 min later, aliquots were filtered through 0.2-μm Nuclepore filters prestained with Sudan Black B. Fluorescing bacteria were counted with an epifluorescence microscope and grouped into the following size classes: rods (range of diameter, range of length expressed in μm) 0.25–0.5, 0.25–0.5; <0.5, 0.5–1.5; 0.5–1.5, 1.5–2.5; 0.5–1.5, 2.5–5.5; 1.5–2.5, 2.5–5.5; filaments with a diameter of 0.25–1.0 and 1.0–2.0; and cocci with a diameter 0.5–1.5. Total microbial biovolume was estimated from number and average volume of each size class as described by Laczko (1988).

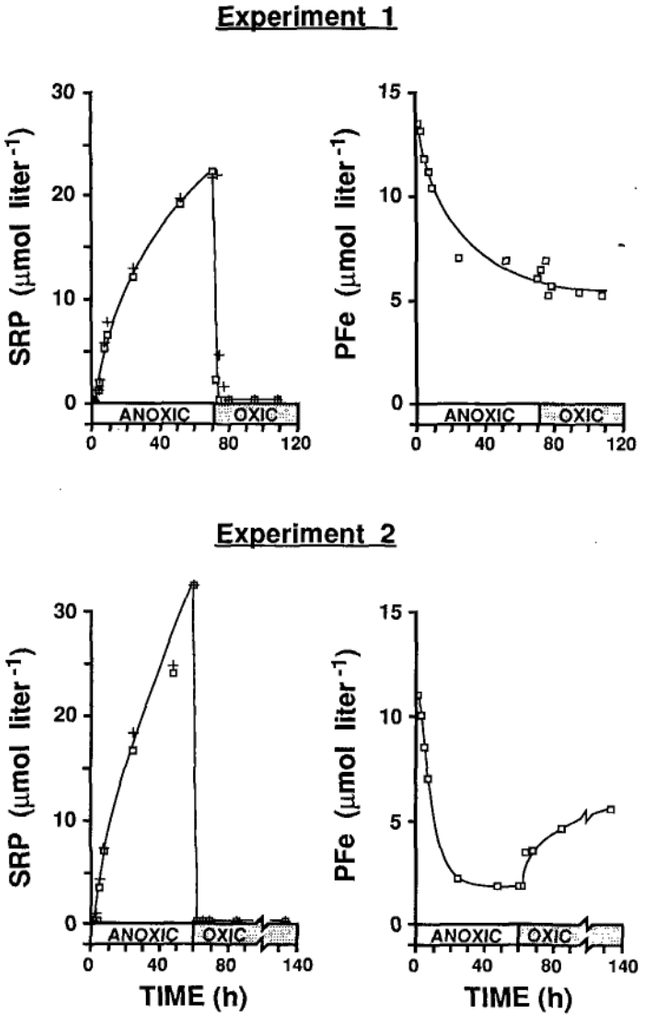

Fig. 2. Results of two experiments on the mobilization and immobilization of SRP and the dissolution and formation of PFe in anoxic and oxic cultures of bacteria with (□) and without (+) added FeOOH flocs. In experiment 1, initial (t = 0 h) TP and PP concentrations were 174 and 169 μmol liter^{-1}; in experiment 2, corresponding values were 148 and 135 μmol liter^{-1}.

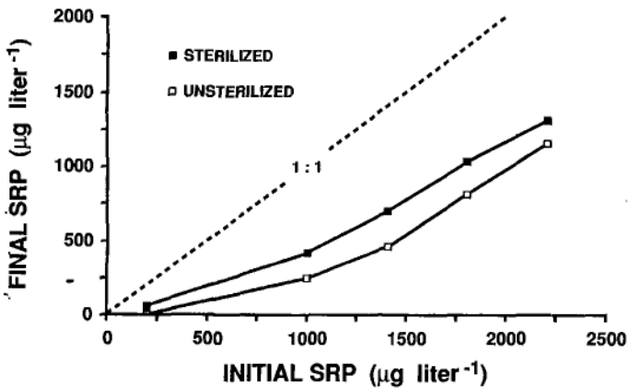

Fig. 3. SRP concentrations in sediment-water suspensions (10 g of sediment per 500 ml of suspension) after 48 h, with (sterilized) and without formaldehyde (unsterilized). The 1 : 1 line represents SRP concentrations if none of the initial SRP had been sorbed.

For the sediment sample, a core was taken on 1 September 1986 at 87 m in the lake, near the location of the flux chamber experiment. It was sectioned at 0.5, 1, 2, 3, and 4 cm, and weighed subsamples of each section were diluted ~1 : 10,000 with filtered hypolimnetic water (0.2-μm Sartorius CA membrane filter), stained, and processed as described above.

Results

Laboratory experiments with sedimentary microorganisms—Sedimentary bacteria grown in P-limited aerobic medium depleted SRP concentrations from about 150 to between 0.01 and 0.1 μmol liter^{-1}. When those cultures subsequently became anoxic, the bacteria released 14% (experiment 1) and 25% (experiment 2) of their P as SRP after 71 and 60 h of anoxia without attaining a plateau in SRP concentration (Fig. 2). In cultures to which FeOOH flocs were added, >50% of the Fe precipitate dissolved simultaneously with the increase of SRP. The culture with added FeOOH flocs and the control without such a precipitate released SRP at equal rates in both experiments. When air was again bubbled through the cultures, all of the released SRP was immediately (<2–4 h) reconverted into PP, and the molar PP : POC ratio in the solid phase increased from 0.012 to 0.015. Contrary to P, the Fe dissolved during anoxia remained to a large extent in solution when aerobic conditions were restored, or it may have formed colloids or very small particles which passed the 0.45-μm filter (Davison and Tipping 1984).

Laboratory experiment with sterilized sediment—In all sterilized and unsterilized sediment suspensions, SRP was removed from solution rapidly during the first 2 h. Removal was faster in unsterilized suspensions than in corresponding sterilized suspensions, and it continued until the SRP concentrations were minimal at 48 h. Considerably more SRP remained in solution at 48 h in bottles containing formaldehyde than in bottles without formaldehyde (Fig. 3). The vertical distance between the "sterilized" and "unsterilized" curves in Fig. 3 represents the amount of SRP removed due to microbial uptake, whereas the vertical difference between the 1 : 1 line and the "unsterilized" curve is the total

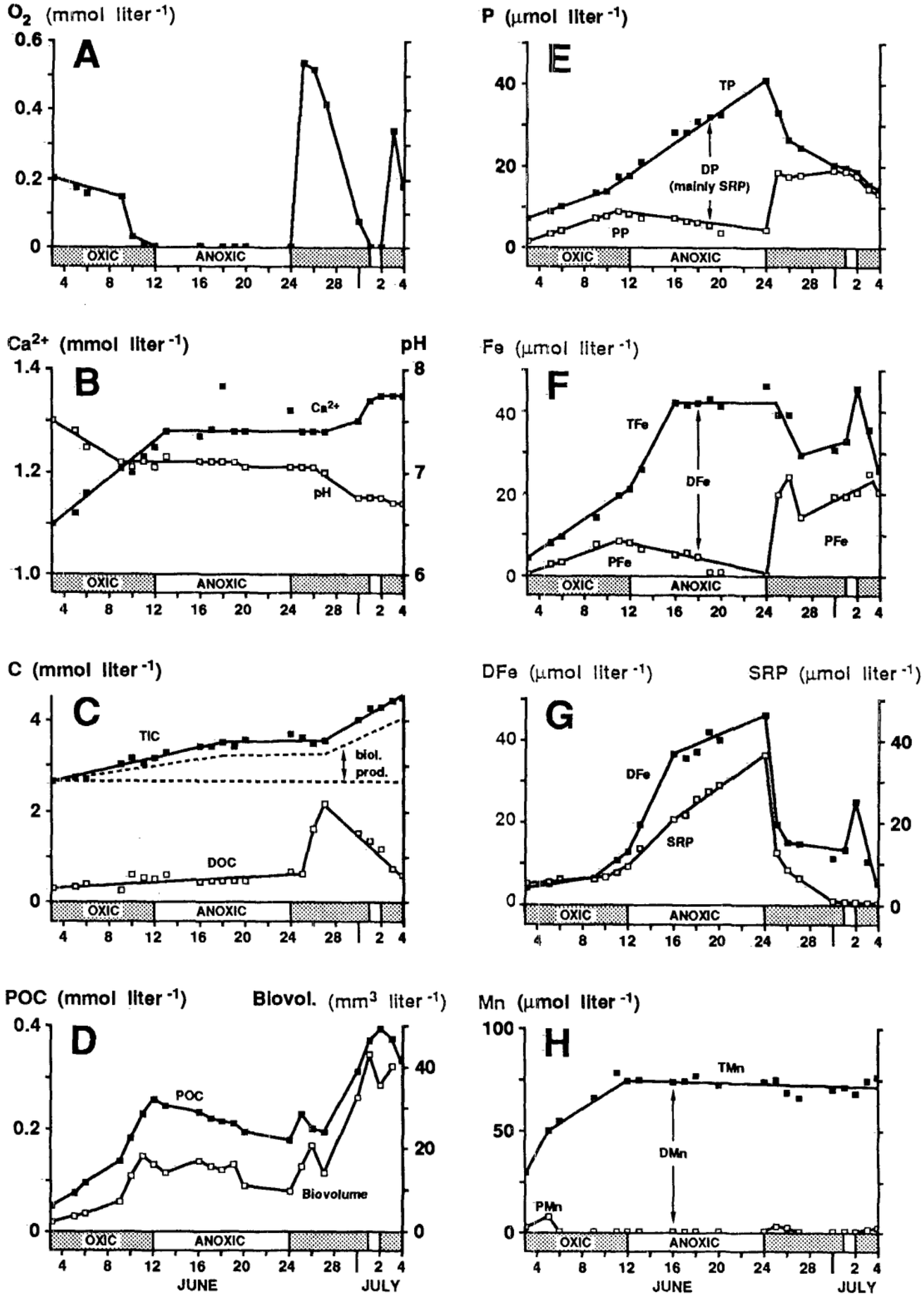

Fig. 4. Variation of concentrations in enclosed water from 3 June to 4 July 1986 in the flux chamber experiment.

amount of SRP removed from solution. Hence, the relative contribution of microorganisms to removal of SRP (the ratio of those two vertical distances) ranged between 14 and 31%. The pH values were similar in all bottles (8.3–8.4), and preliminary tests showed that the amount of SRP adsorbed to FeOOH does not change when 4% formaldehyde is added to lake water containing FeOOH flocs, if a constant pH is maintained.

In the bottles with glucose, NH_4^+, and 2,000 μg P liter^{-1} added, all SRP was removed from solution in the unsterilized bottle after 24 h, but 1,160 μg SRP liter^{-1} remained in solution in the sterilized bottle. The pH was 7.6 in the unsterilized bottle and 8.0 in the sterilized bottle. Plating of these suspensions on agar showed no viable microbial colonies in sterilized treatments.

In situ experiment with flux chamber—O_2 concentration decreased slowly during the first 6 d of the flux chamber experiment (Fig. 4A) despite a continuous O_2 supply. On 9 June, this supply was interrupted and the enclosed water became anoxic within 3 d. After an anoxic phase of 12 d, an O_2 pulse was applied on 24 June. After a second anoxic phase (1–2 July), a second O_2 pulse was applied on 2 July. In periods when no O_2 was supplied, O_2 consumption was similar to the average seasonal O_2 consumption rate of 18 mmol m^{-2} d^{-1} estimated from mass balance calculations for the hypolimnion of Lake Sempach (R. Gächter and W. Stumm EAWAG/ETH unpubl. rep.).

Dissolution of $CaCO_3$ was estimated from the increase of Ca^{2+} concentration in the water enclosed within the flux chamber (Fig. 4B). Total TIC production minus TIC originating from $CaCO_3$ dissolution was taken as a measure of biologically produced inorganic C. TIC production was mainly due to biotic processes and not to the dissolution of $CaCO_3$ (Fig. 4C). Net production of DOC increased sharply immediately after the first O_2 pulse (25–27 June), then decreased at a constant rate during the remainder of the experiment (Fig. 4C). POC content increased during the first oxic phase, then decreased during the subsequent anoxic phase (Fig. 4D). Simultaneously with the increase in TIC production and onset of DOC consumption, the POC production rate increased rapidly after 27 June.

Bacterial biovolume also increased during the first oxic phase, decreased during the first anoxic phase, and finally increased to about 40 mm^3 liter^{-1} at the end of the experiment (Fig. 4D). The high bacterial biovolumes in the enclosed water resulted from relatively high densities of bacteria (3–40 $\times$ 10^9 cells liter^{-1}) and from relatively large average cell sizes (0.53–1.42 μm^3). Although Hobbie and Wright (1979) stated 1–2 $\times$ 10^9 cells liter^{-1} to be typical bacterial densities for eutrophic lakes, values up to 18 $\times$ 10^9 cells liter^{-1} have been reported (Riemann et al. 1982). Additionally, average cell sizes of bacteria grown in the flux chamber fall in the upper range of values estimated by others: 0.08–0.28 μm^3 (Bell et al. 1983), 0.06–0.74 μm^3 (Riemann et al. 1987), and 0.001–1.99 μm^3 (Edwards 1987). Since in the case of filamentous forms we counted filaments instead of individual cells, our average cell sizes may not, however, be directly comparable to values reported by others. We attribute the relatively large average volume of bacteria grown in the flux chamber primarily to the presence of large filaments (2–36% of the total biovolume). Also, growth conditions were more favorable than in the free water column, because bacteria growing above the sediment–water interface and nutrients released from the sediment were not transported into the hypolimnion by turbulent diffusion. Finally, the low temperature (~5°C) in the hypolimnion of the lake might have favored large cell sizes, since Riemann et al. (1987) reported that average cell volume of bacteria at 5°C was more than three times larger than average cell volume at 30°C.

The POC : bacterial biovolume ratio showed a decreasing trend throughout the experiment, starting at 0.25 mg POC mm^{-3} and ending at 0.11; the average ratio was 0.18 mg POC mm^{-3}. It is not surprising that the ratio varied, because nutrient supply and redox potential within the flux chamber were not constant. As shown by Bratbak (1985), POC : bacterial biovolume ratio is affected by changing nutritional status and community structure. Our average ratio falls in the midrange of literature values (0.12–0.35

mg POC mm^{-3}) discussed by Bell and Ahlgren (1987).

TP concentration in the enclosed water increased slowly during the first oxic phase (Fig. 4E). After 10 June, though, when O_2 concentration decreased to <0.03 mmol $liter^{-1}$, TP concentration increased rapidly until the first O_2 pulse was delivered on 24 June. Then TP decreased with a first-order rate constant of about 0.11 d^{-1} until the end of the experiment. The concentration of suspended PP also increased during the first oxic phase, decreased during anoxia, and then increased sharply immediately after the first O_2 pulse. DP concentration (mainly SRP) was practically constant from the beginning of the experiment until 10 June. Under anoxic conditions, however, SRP concentration increased rapidly to a maximum value of 37.4 μmol $liter^{-1}$ on 24 June (Fig. 4G). After the first O_2 pulse, it decreased within 1 d, to less than half of the maximum value and finally stabilized at about 1 μmol $liter^{-1}$.

At the beginning of the experiment, even under oxic conditions, concentrations of TFe, PFe, and DFe increased (Fig. 4F and G), although SRP concentration remained practically constant. Under anoxic conditions, TFe concentration increased rapidly beginning on 12 June. This switch occurred 2 d later (i.e. at a lower redox potential) than the increase in rate of TP release. In addition, the release of Fe ceased on 16 June (as indicated by a plateau of TFe concentration), whereas the sediment continued to release P until the O_2 pulse was applied on 24 June. Under anoxic conditions, PFe concentration decreased steadily to zero, but PFe increased and DFe decreased quickly as soon as O_2 concentration increased again. TFe concentration decreased during the second oxic period, probably due to deposition of PFe onto the sediment surface. A second maximum of DFe was observed on 2 July during the second anoxic period, immediately before the second O_2 pulse; this increase in DFe was not accompanied by an increase in SRP. The second O_2 pulse was again followed by a decrease in DFe and TFe concentrations.

At the end of the first anoxic phase (24 June), no PFe was suspended in the water but the PP concentration equaled 4.6 μmol $liter^{-1}$. At the same time, POC concentration equaled 177 μmol $liter^{-1}$. If we assume that most of this PP and POC was incorporated in microorganisms, their atomic P : C ratio was 0.026 (wt ratio of 0.068). For comparison, Fenchel and Blackburn (1979) reported a typical P : C atomic ratio of 0.021 for bacteria, and Bratbak (1985) reported atomic P : C ratios varying between 0.018 and 0.13 for mixed bacterial cultures, depending on whether P or C limited growth.

As shown in the laboratory experiment, it is likely that under oxic conditions the P : C ratio was higher than under anoxic conditions. Thus, a minimum estimate of PP fixed in microorganisms in the enclosed water on each sampling date can be calculated by multiplying measured POC concentrations times the atomic P : C ratio estimated above. On the basis of these estimates (Table 1), bacterial PP contributed 28–100% of total suspended PP. Subtracting total PP minus bacterial PP yields a maximum estimate of PP associated with Fe (nonbacterial PP in Table 1). Hence, minimum Fe : P ratios can be estimated for the nonbacterial solid phase in the enclosed water (Table 1). These results show that it is very likely that, even in the presence of high concentrations of PFe, more than half of the PP was fixed in microbial biomass.

Sediment core analysis—Bacterial biovolume, POC, TP, and TMn decreased as sediment depth increased, whereas TFe and TCa concentrations remained about constant (Table 2). In the layer 0–1 cm below the sediment surface, average bacterial cell volume was 1.7 μm^3, and it decreased with increasing sample depth to 0.4 μm^3 in the layer between 3 and 4 cm deep. The large average cell volume at the sediment surface was mainly due to filamentous forms with a diameter of 1–2 μm and an average length of 11 μm. In deeper layers, these large forms contributed <10% to the estimated biovolume. Similar bacterial sizes and a decreasing trend of average cell volume with increasing depth were also observed in the sediments of oligo-mesotrophic Lake Lucerne (Laczko 1988). An average bacterial cell volume 5–10 times smaller (0.157 μm^3 $cell^{-1}$) was reported by Bell and Ahlgren

Table 1. Estimated partitioning of total particulate phosphorus in enclosed water into PP fixed in bacteria and nonbacterial PP during the flux chamber experiment.

1986	POC	Total PP	PFe	PP in bacteria*	Nonbacterial PP†	PFe/ nonbacterial PP	Total PP in bacteria (%)
	(μmol liter^{-1})						
3 Jun	51	1.8	0.3	1.3	0.5	0.6	72
5 Jun	75	3.4	3.0	1.9	1.5	2.0	56
6 Jun	96	4.2	3.6	2.5	1.7	2.0	60
9 Jun	136	7.3	7.7	3.5	3.8	2.0	48
10 Jun	180	7.8	8.0	4.7	3.1	2.5	60
11 Jun	228	9.2	8.6	5.9	3.3	2.5	64
12 Jun	258	8.4	8.1	6.7	1.7	5.0	80
13 Jun	245	7.5	6.6	6.4	1.1	5.0	85
16 Jun	233	7.3	5.4	6.1	1.2	5.0	83
17 Jun	221	6.5	5.9	5.7	0.8	10.0	88
18 Jun	214	6.2	4.7	5.6	0.6	10.0	90
19 Jun	211	5.5	1.1	5.5	0.0	—	100
20 Jun	194	3.7	1.3	5.0	0.0	—	100
24 Jun	177	4.6	0.0	4.6	0.0	—	100
25 Jun	228	18.6	19.9	5.9	12.7	1.7	31
26 Jun	201	17.7	24.2	5.2	12.5	2.0	30
27 Jun	194	18.1	14.6	5.1	13.0	1.1	28
30 Jun	313	19.1	19.4	8.1	11.0	1.4	42
1 Jul	371	18.8	19.4	9.7	9.1	2.0	52
2 Jul	396	17.9	20.4	10.3	7.6	2.5	57
3 Jul	376	14.7	25.1	9.8	4.9	5.0	67
4 Jul	333	13.6	20.4	8.7	4.9	5.0	64

* POC × 0.026 μmol PP (μmol POC)$^{-1}$.
† Total PP − PP in bacteria.

(1987), however, for the sediments of hypereutrophic Vallentunasjön. In those sediments, few filamentous bacteria were observed (R. Bell pers. comm.) and larger bacteria growing on freshly settled material may have been "diluted" with smaller forms resuspended by physical mixing of the upper 5–10 cm of sediment. Additionally, the constantly low temperature of sediments in Lake Sempach (~5°C) might have caused cell sizes to be larger than in the shallow, seldom stratified Vallentunasjön where sediment temperature in summer is higher (up to 20°C). Bacterial abundance in Lake Sempach sediment also decreased with depth from 4.9–3.0 × 10^{10} cells (g DW)$^{-1}$. These abundances rank in the lower range of values reported for sediment of Vallentunasjön [4–20 × 10^{10} bacteria (g DW)$^{-1}$: Bell and Ahlgren 1987] and for sediments of four eutrophic Cumbrian lakes [4–9 × 10^{10} bacteria (g DW)$^{-1}$: Jones et al. 1979].

Using the average POC : bacterial biovolume ratio (0.18 mg C mm^{-3}) and the PP : POC weight ratio [0.068 mg P (mg C)$^{-1}$] determined for bacteria in enclosed water during the flux chamber experiment, we estimated the amounts of organic C and P contained in sediment bacteria (Bio POC and Bio PP) from the bacterial biovolume column in Table 2. These values decreased as sediment depth increased, as did percentage of TP contained in bacterial biomass, ranging between 22 and 80% (Table 2). Even if a more conservative POC : bacterial biovolume ratio of 0.1 mg C mm^{-3} (Sorokin and Kadota 1972) had been used for these calculations, the percentage of TP contained in bacterial biomass still would have ranged between 12 and 45%.

The PP : POC ratio used for our estimates was calculated from bacteria suspended in the flux chamber water under anoxic conditions. As discussed above, this ratio was probably higher under oxic conditions. Since such conditions likely occurred in the upper few millimeters of the sediment core, the Bio PP value for the 0–0.5-cm section may underestimate the contribution of bacteria to TP in that layer. On the other hand, the values for the upper 1 cm of sediment may overestimate Bio PP because of the sedi-

Table 2. Estimated amounts of particulate organic carbon and total phosphorus associated with bacteria in a sediment core from Lake Sempach.

Sediment layer (cm)	DW* (%)	Bacterial biovolume [mm^3 (g DW)$^{-1}$]	POC	TP	TFe	TMn	TCa	Bio POC†	Bio PP‡	POC in bacteria (%)	TP in bacteria (%)
			[mg (g DW)$^{-1}$]								
0–0.5	8.1	83.5	92.2	1.94	12.6	3.1	258	15.0	>1.02	16	>53
0.5–1	9.6	72.1	74.7	1.10	10.8	1.8	265	13.0	0.88	17	80
1–2	10.1	30.5	63.7	0.82	14.1	1.4	257	5.5	0.37	9	45
2–3	10.5	25.1	64.4	0.78	16.1	1.2	250	4.5	0.31	7	40
3–4	13.4	12.5	52.7	0.69	13.5	1.1	245	2.2	0.15	4	22

* Dry weight expressed as percentage of fresh weight.
† POC associated with bacteria (=bacterial biovolume × 0.18 mg POC mm^{-3}).
‡ TP associated with bacteria [=Bio POC × 0.068 mg PP (mg POC)$^{-1}$].

mentary bacterial composition. Specifically, if the larger filamentous forms that dominated the biovolume of the surface-sediment community contained considerably less PP per unit of biovolume than bacteria in the enclosed water (dominated by nonfilamentous forms), then the estimated percentage of Bio PP would decrease.

Discussion

Despite lack of replication in the sediment sterilization and flux chamber experiments and in the sediment core analysis, the internal consistency of our results and their compatibility with a cross section of earlier findings leads us to suggest a revision of the traditional view of Fe and P cycling in lakes. According to the classical Mortimer-Einsele model, a substantial part of the inorganic PP in oxic sediments is associated with Fe. If such sediment layers are rendered anoxic, this solid phase dissolves due to reduction of Fe(III). As a consequence, Fe(II) and PO_4^{3-} ions diffuse down their concentration gradients toward the sediment surface and into the hypolimnion. At a higher redox potential, either still in the sediment or in the overlying water, Fe and PO_4^{3-} may form solid FeOOH-PO_4 adsorption complexes again. In most studies on the release of P from sediments, bacteria are either totally neglected or are treated only as catalyzers accelerating the oxidation of organic detritus and the reduction of various electron acceptors. For example, Jansson (1987) recently showed that nitrate-reducing bacteria enzymatically can catalyze the reduction of extracellular FeOOH-PO_4 complexes and thus indirectly may enhance the release of PO_4^{3-} from sediments.

Bacteria can also act as a sink or a source of PO_4^{3-}, however, and thus play a more direct role in uptake and release of P in sediments. Levine and Schindler (1980) Lean (1984), and Currie and Kalff (1984) presented experimental evidence that bacteria may outcompete phytoplankton in the uptake of SRP, especially at low SRP concentrations. Thus, it is not surprising in our experiment that sedimentary microorganisms depleted SRP concentrations from >100 μmol liter^{-1} initially to <0.1 μmol liter^{-1}, when grown in aerated, P-limited medium. More importantly, the same microbial cultures released considerable amounts of SRP when the O_2 supply was interrupted and PFe consequently began to dissolve. Fleischer (1983) reported a similar pattern of P uptake and release by facultative anaerobic microorganisms cultured under alternating aerobic-anaerobic conditions, but he did not correlate that pattern with Fe cycling. Our results demonstrate that the simultaneous dissolution or precipitation of Fe and PO_4^{3-}, which is often also observed in the hypolimnion of lakes, does not necessarily prove that the cycles of the two elements are coupled.

It is well known that bacteria, yeast, fungi, and algae can accumulate and store PO_4^{3-} in the form of polyphosphate (poly-P) when excess PO_4^{3-} is available (Kulaev 1979). For example, poly-P can constitute up to about 20% of the dry weight in *Acinetobacter* spp. (Deinema et al. 1980). According to Wentzel et al. (1986), the ATP : ADP ratio is a key parameter controlling poly-P synthesis and degradation in sewage-sludge bacteria. Under aerobic conditions with abundant PO_4^{3-} and organic C available, oxidative

phosphorylation increases the ATP : ADP ratio, thus stimulating poly-P production. Under anaerobic conditions, when O_2 and NO_3^- are not available as electron acceptors, the ATP : ADP ratio decreases due to the lack of oxidative phosphorylation. This decrease stimulates ATP production via hydrolysis of stored poly-P. The ATP can then be used by some bacteria to synthesize acetyl coenzyme A (acetyl CoA) from acetate (or other short-chain organic acids) and CoA. Acetyl CoA is then converted to acetoacetyl CoA, which subsequently serves as an acceptor for electrons that otherwise would accumulate along with protons as products of catabolism under anaerobic conditions. PO_4^{3-} accumulates intracellularly due to ATP hydrolysis during formation of acetyl CoA and eventually is transported out of the cells, thus increasing the extracellular PO_4^{3-} concentration. Without this capacity to synthesize an organic electron acceptor with energy stored in poly-P, bacteria incapable of glycolysis and fermentation could not survive anaerobiosis (Wentzel et al. 1986).

Similar biochemical processes leading to uptake and release of PO_4^{3-} have not yet been demonstrated for sedimentary microorganisms, but results of our laboratory experiments and those of Fleischer (1983) are consistent with the model of Wentzel et al. (1986). Based on the known occurrence of poly-P storage in some sedimentary microorganisms, Boström et al. (1988) also speculated that PO_4^{3-} mobilization as a result of altered physiology in living cells could contribute to P release from anaerobic sediments.

From our experiments with microbial cultures, it is impossible to determine whether microorganisms successfully competed with Fe for SRP or merely took up the remaining SRP after FeOOH sorption sites were quickly saturated. Moreover, laboratory experiments in which C and N are added to culture medium may select for only a small portion of the sedimentary microbial community, thus biasing subsequent interpretations. Therefore, in an additional SRP uptake experiment in the laboratory, we demonstrated that unsterilized sediments from Lake Sempach could sorb up to 31% more SRP than could sterilized sediments, with no C or N added to the sediment suspensions. Furthermore, uptake of SRP in unsterilized sediments was more rapid than in sterilized sediments. These results indicate the presence of simultaneous biotic and abiotic processes for SRP uptake in the upper 1 cm of a eutrophic lake sediment. Doremus and Clesceri (1982) reported similar results for the flocculent uppermost layer of sediments from an oligotrophic lake, but it is impossible to determine from their figure 4 how much $^{32}PO_4^{3-}$ was removed from solution by abiotic adsorption and biotic uptake and how much was only exchanged with stable $^{31}PO_4^{3-}$, producing no net removal of PO_4^{3-} from solution.

For several reasons, our sterilization experiment may have underestimated in situ SRP uptake capacity of sedimentary microbes relative to the sorption capacity of abiotic sites. First, when the black sediment (indicating low enough redox potential for FeS formation) was aerated, it became oxidized and changed color to light brown. Hence, considerably more FeOOH surfaces capable of sorbing SRP were present in the experiment than in the original sediment. We do not know, however, to what extent bacterial density also increased during aeration. Second, conditions for microbial uptake of SRP were less favorable because substrate concentrations in the interstitial water were diluted by mixing the sediment 1 : 50 with hypolimnetic water, and microorganisms no longer received the continuous supply of substrate particles that settle out of the hypolimnion in Lake Sempach. In support of this contention, microorganisms in an enriched sediment suspension demonstrated a high potential for SRP uptake, similar to that observed in our laboratory cultures with sedimentary microorganisms. Most likely, in situ microbial uptake capacity for SRP is somewhere between the extremes obtained with and without C and N additions.

Flux chamber results, if unbiased, should help evaluate whether the laboratory-documented role of bacteria in P exchange is important in the field. Disturbance of the sediment surface should have been greatest

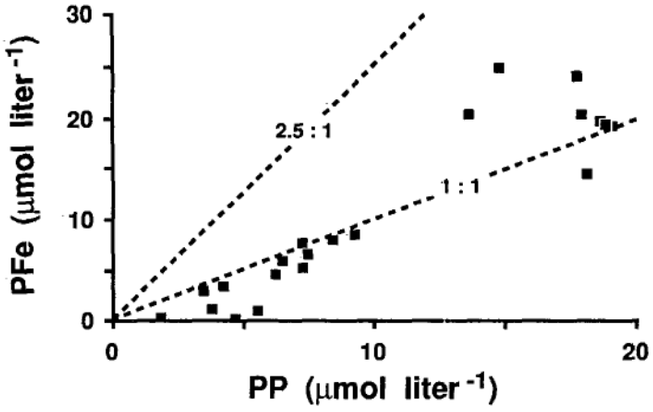

Fig. 5. Particulate iron and phosphorus concentrations in enclosed water during the flux chamber experiment. Dashed lines represent molar Fe : P ratios of 1 : 1 and 2.5 : 1. The equation for the least-squares regression of PFe on PP (not shown) is PFe = 1.31 × PP − 2.87 (r^2 = 0.86).

at the beginning of the experiment, immediately after implanting the flux chamber and starting the circulation pump. Since we did not observe any turbidity in water samples collected at that time, we assume that resuspension of sediment particles can be neglected. Thus, in water enclosed within the flux chamber, only three P species were important: SRP (concentration of dissolved nonreactive P was negligibly small compared to SRP); PP incorporated in bacteria grown in this compartment (no input of detrital organic P due to isolation from settling seston); and PP associated with freshly precipitated FeOOH (no input of solid carbonates of silicates due to isolation from settling seston). Even if a small amount of flocculent material, including ferric complexes and bacterial cells, was swept off the sediment surface by mixing turbulence or during sample extraction, our conclusions regarding the relative contributions of Fe and bacteria to P cycling would not be altered, as long as either Fe or bacteria were not selectively resuspended.

Therefore, the simultaneous investigation of production or decay of microbial biomass, the cycling of P, and the cycling of Fe in the enclosed water permits at least semiquantitative evaluation of the contribution of microorganisms to P cycling in sediments. Since experimental conditions in a flux chamber are much closer to those in real sediments than in the laboratory experiments described above, we believe that the study of P cycling in this experimental system can serve as a useful link between laboratory systems and real sediments.

During the flux chamber experiment, O_2 supply was controlled in order to investigate formation and dissolution of solid Fe species and the production of bacterial biomass in the enclosed water under oxic and anoxic conditions. Consistent with the classical theory of Fe and P cycling, concentrations of dissolved and total Fe and P began to increase rapidly when all oxygen was consumed. At the end of the first anoxic period (24 June), all the Fe in the sediment-overlying water and 90% of the TP were dissolved (≤0.45 μm). When the water was reoxygenated, PFe and PP quickly formed. Thereafter, ~40% of the TFe and 50% of the TP either diffused into the sediment or settled out of the water, and by 30 June only 5% of the TP remaining in the enclosed water was in dissolved form.

There is even an excellent correlation between PFe and PP in the enclosed water during the oxic and anoxic phases of the flux chamber experiment (Fig. 5). At first glance, this finding seems to support the assumption that the cycles of Fe and P are strongly coupled. A closer examination of the results shows, however, several inconsistencies. Based on experimental results (Lijklema 1977; Meyer unpubl. data), the Fe : P atomic ratio for adsorption of PO_4^{3-} to FeOOH flocs at pH 7 should be about 10 : 1. Yet the PFe : PP ratio in enclosed water was always ≤1.7 : 1, and often <1.0 : 1, indicating that there must have been a large pool of PP contained in something other than FeOOH-PO_4 adsorption complexes. Moreover, the atomic ratio of the rates of increase in DFe and SRP (ΔDFe : ΔSRP) at the beginning of the first anoxic period (12–16 June) was 2.0 : 1, and the atomic ratio of newly formed PFe to newly formed PP (ΔPFe : ΔPP) during the first day of the subsequent oxic period (24–25 June) equaled only 1.4 : 1. In a different flux chamber experiment conducted at 87 m in the lake during July 1987 (unpubl. data), the corresponding ΔDFe : ΔSRP ratio at the beginning of the anoxic period was 0.8 : 1 and the ΔPFe : ΔPP ratio during the first day of the subsequent oxic period was 1.6 : 1.

Thus, fluxes of SRP must also have been at least partly controlled by processes other than adsorption to and reductive dissolution of FeOOH.

Even if $FePO_4 \cdot Fe(OH)_3$ complexes form when Fe(II) is oxidized in the presence of PO_4^{3-}, as reported by Tessenow (1974), the Fe : P atomic ratio of an Fe-P complex formed at neutral pH will not be <2.0 : 1. Given an initial DFe : SRP atomic ratio of 1.3 : 1 at the end of the first anoxic period, we would expect an Fe : P atomic ratio of >2.5 : 1 in Fe-P precipitates based on figure 4 of Tessenow (1974). Yet the observed ΔPFe : ΔPP ratio during the first day of the subsequent oxic period equaled only 1.4 : 1, and all of the points in Fig. 5 plot well below the 2.5 : 1 line. Hence, the low PFe : PP, ΔDFe : ΔSRP, and ΔPFe : ΔPP ratios observed in the flux chamber experiment indicate that, apart from formation of Fe-P complexes, additional PP-forming mechanisms must be considered in the enclosed water.

As demonstrated in the laboratory experiments with sediment bacteria, an additional possibility for PP formation is uptake of SRP by microorganisms. In the flux chamber experiment, DOC released from sediments diffused into the overlying water and appeared to serve as substrate for microbial production. During the oxic phases of the experiment, net increases of POC and bacterial biovolume were observed, indicating that the sediment–water interface is not only the place of decomposition of planktonic biomass but that in this layer there is simultaneous production of microbial biomass. Since P is an essential nutrient for all organisms, this biomass production must have been coupled with the formation of PP. For example, we estimate that between 30% (based on a minimum PP : POC ratio determined for bacteria in anoxic water: Table 1) and 60% (based on a ΔPFe : ΔPP ratio of 2.5 : 1 for the formation of particulate Fe-P complexes from the DFe and SRP concentrations shown in Fig. 4G) of the PP formed during the O_2 pulse following the first anoxic period was incorporated in bacteria. These estimates suggest that bacteria competed successfully with FeOOH for SRP after reoxygenation of flux chamber water and therefore may also have contributed significantly to the immobilization of PO_4^{3-} at the sediment–water interface.

In addition, microbial contribution to release of SRP from sediment can be inferred from another line of evidence. There was a 2-d interval between the beginning of the rapid increase in TP concentration (10 June) and the beginning of the rapid increase in TFe concentration (12 June). This lack of synchrony in Fe and P releases would not be predicted from classical theory, because reductive dissolution of $FeOOH\text{-}PO_4$ complexes should initially result in simultaneous, stoichiometric Fe and P releases, unless redox potential is already low enough for formation of insoluble FeS. At first, it might seem that the accelerated release of P without a concomitant release of Fe could be explained by retention of Fe as sulfides in the sediment. The accelerated release of Fe 2 d later (probably at an even lower redox potential), however, is inconsistent with this explanation. On the other hand, the sudden halt in Fe release on 16 June could be explained by FeS precipitation. From these results, we conclude that accelerated release of P between 10 and 12 June cannot be explained by reductive dissolution of $FeOOH\text{-}PO_4$ complexes.

There was no similar 2-d interval between the increases in SRP and DFe concentrations in enclosed water at the end of the first oxic period (10–12 June). Although at first this absence might seem to support a strong coupling between Fe and P releases from the sediment, this result is consistent with the previous argument because the enclosed water was still oxic on 10 and 11 June. SRP diffusing from anoxic sediment into the overlying water therefore was probably adsorbed to suspended FeOOH particles or taken up by bacteria until the water became anoxic (12 June). Only then could DFe and SRP concentrations increase rapidly because of redox-dependent release from bacteria and Fe-P complexes. Thus, comparison of concentrations of the two dissolved species (DFe and SRP) in the enclosed water cannot be used to identify their sources in the sediment.

Dissolution of Mn-P and Ca-P complexes must also be considered as expla-

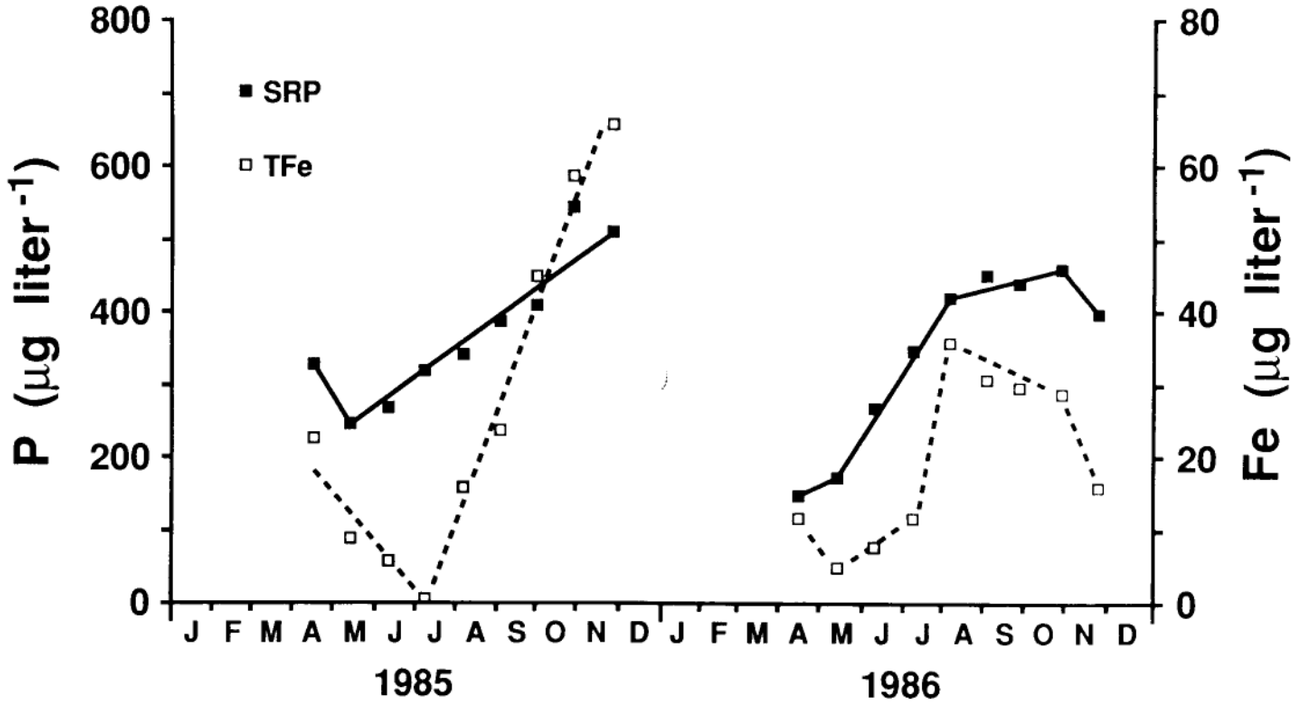

Fig. 6. Concentrations of SRP and TFe in bottom water (45 m) of Lake Hallwil from April to November 1985 and 1986 (M. Schmid and A. Stoeckli unpubl. data).

nations for the early release of P. After steadily increasing from the beginning of the experiment until 11 June, however, DMn and TMn concentrations in the enclosed water decreased slightly during the first anoxic period (Fig. 4H), just as TP and SRP releases accelerated. Hence, Mn and P releases also appeared to be uncoupled. Similarly, Ca^{2+} concentration increased most rapidly during the initial oxic period, when the release rate of P was at a minimum, and then stabilized during the subsequent anoxic period, when the release rate of P was at a maximum (Fig. 4B). Thus, dissolution of Ca-P complexes can probably also be discounted as a dominant mechanism for P release.

Observations of changes in Fe and P concentrations in hypolimnetic waters just above the sediments in several other lakes support our flux chamber results. For example, in Lake Hallwil (a 45-m-deep eutrophic lake in north-central Switzerland) there was a 2-month lag in the onset of Fe release (July–August) compared to the onset of SRP release (May–June) in 1985 (Fig. 6); similarly in 1986, there was a 3-month lag in the onset of Fe release (July–August) compared to the onset of SRP release (April–May). In Greifensee (a 30-m-deep eutrophic lake in northeastern Switzerland) there was a 1-month interval between the onset of SRP (April–May) and Fe (May–June) releases in 1985 and a 3-month interval between the onset of SRP (April–May) and Fe (July–August) releases in 1986 (Fig. 7).

There even appeared to be a 10-d interval between the releases of P_2O_5 and Fe [TFe and Fe(II)] in Mortimer's results for Esthwaite Water at the onset of anoxia during late July and early August 1940 (Fig. 8; redrawn from figure 29 of Mortimer 1942). Moreover, based on concentrations for the 12 sampling dates from mid-July to mid-October (including the entire period when O_2 concentration in the sediment and overlying water was <1 mg liter $^{-1}$), the correlation between Fe(II) and P_2O_5 concentrations is not significant. Mortimer (1942) suggested that the large fluctuations in Fe and P concentrations during summer 1940 were due to unstable conditions in the hypolimnion; however, the releases of P_2O_5 and Fe(II) during late July and early August still should have been synchronous if they are to be explained by reductive dissolution of Fe-P complexes. Contrary to the expected synchrony, P_2O_5 concentration decreased sharply between 3 and 13 August, whereas TFe and Fe(II) concentrations in-

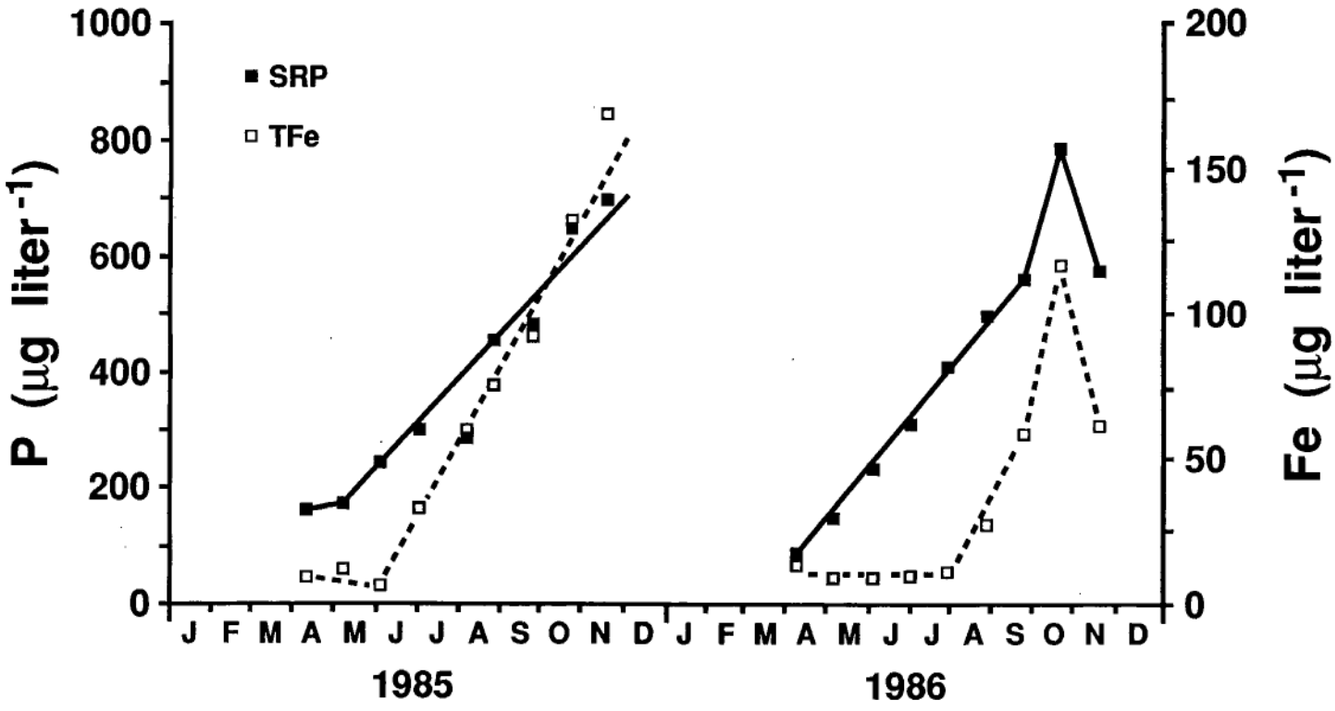

Fig. 7. Concentrations of SRP and TFe in bottom water (30 m) of Greifensee from April to November 1985 and 1986 (H. Ambühl unpubl. data).

creased (and all Fe was in the reduced form). Thus, these results indicate that not all P released from Esthwaite Water sediment was tightly coupled with Fe. Unfortunately, the coupling between Fe and P release cannot be investigated in the 1939 data set for Esthwaite Water because P_2O_5 concentration was estimated in only a few water samples (Mortimer 1941).

Processes occurring in the flux chamber seem to mimic (at a highly accelerated rate) processes that naturally occur at the sediment–water interface in eutrophic lakes. Therefore, on a relative basis, the 2-d lag between P and Fe releases in the flux chamber seems to be equivalent to the lags of several weeks to several months observed in Lake Hallwil, Greifensee, and Esthwaite Water. All of those observations are consistent with a microbial contribution to PO_4^{3-} release from sediments, but not all eutrophic lakes exhibit this pattern. For example, no lag between P and Fe releases is apparent in data for Schleinsee during the anoxic period in summer 1935 (figures 15 and 16 of Einsele and Vetter 1938), and there is a high correlation between Fe and PO_4^{3-} concentrations ($r^2 = 0.96$, $P < 0.001$). This strong correlation suggests that reductive dissolution of Fe may have played a major part in PO_4^{3-} release from Schleinsee sediment, although on the basis of those data alone there is no way of testing whether microorganisms also contributed directly to PO_4^{3-} release.

Another result from the flux chamber experiment further suggests that Fe and P releases were not completely coupled. During the second anoxic period (1–2 July), TFe and DFe concentrations increased by about 40 and 90%, indicating that redox potential was low enough for reductive dissolution of FeOOH. SRP concentration remained constant (1 µmol liter^{-1}) however, and TP concentration decreased by 5%, contrary to what might be predicted from the classical model.

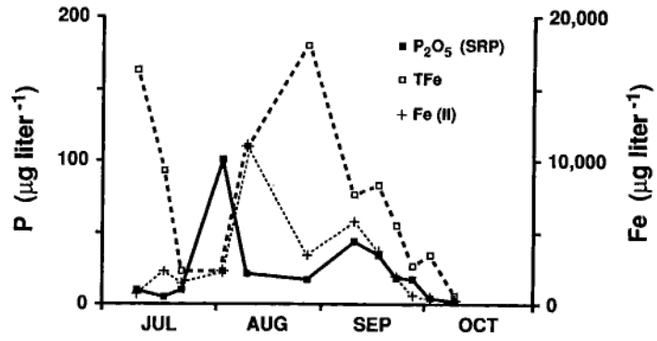

Fig. 8. Concentrations of P_2O_5, TFe, and Fe(II) in bottom water (14 m) of Esthwaite Water from July to October 1940 (redrawn from figure 29 of Mortimer 1942).

One explanation would be that all of the SRP released during reductive dissolution of Fe-P complexes was rapidly taken up by P-starved bacteria. Yet before the end of the oxic period, SRP had already stabilized at a concentration of 1.0 μmol liter^{-1}, and it remained constant during the subsequent anoxic period. Because that concentration was over 10 times greater than concentrations to which our laboratory cultures of sedimentary bacteria depleted SRP (<0.1 μmol liter^{-1}), the bacteria were probably not P starved. Thus, it is unlikely that they then took up additional SRP released from Fe-P complexes during anoxia.

Although at first glance the absence of an increase in SRP concentration also appears inconsistent with microbial release of PO_4^{3-} during anoxia, bacteria do not necessarily release PO_4^{3-} under all anoxic conditions. When the enclosed water was reoxygenated after the first anoxic period, SRP concentration decreased sharply and biovolume in the enclosed water increased threefold. If bacteria used most of the SRP taken up for biomass production, little would have been stored as poly-P. Hence, little SRP would have been released during the subsequent anoxic period.

Moreover, even if considerable SRP was still incorporated in bacteria as poly-P, conditions may not have been favorable for poly-P utilization during the second anoxic period. Florentz et al. (1984) and Iwema and Meunier (1985) showed that anoxic release of P from activated sludge microorganisms stops when easily degradable short-chain organic acids (required substrate for these bacteria) are not available, and it is decreased even in the presence of suitable DOC if denitrifying bacteria compete with poly-P bacteria for the available substrate (Iwema and Meunier 1985). Neither possibility can be tested with the flux chamber data, but these microbial mechanisms are consistent with the absence of SRP release during the second anoxic period. They also provide possible explanations for why PO_4^{3-} concentrations did not increase greatly with the onset of anoxia under winter ice cover in the hypolimnia of oligotrophic Canadian Shield Lakes 227 and 302, even though most of the SRP taken up during oxic conditions was incorporated into decomposers (Schindler et al. 1973; Levine and Schindler 1980).

Our conclusions concerning bacterial contributions to SRP uptake and release in the flux chamber thus far have been based on chemical concentrations and bacterial counts in the enclosed water. In order to conclude that bacteria in the sediment contributed considerably to P fluxes, it is also necessary to demonstrate that they contained enough P to account for the observed release and uptake in the flux chamber. We estimated that a substantial part (up to 80%) of TP in the upper 1 cm of Lake Sempach sediment was incorporated in bacterial biomass. Since this indirect estimate of Bio PP is based on several assumptions (e.g. PP:POC ratio of sediment bacteria was the same as PP:POC ratio determined for bacteria in the enclosed water), it is not precise. It strongly suggests, however, that bacterial PP may be a significant fraction of the total PP in aerobic surface sediment.

Laczko (1988) found similar results in sediment of oligo-mesotrophic Lake Lucerne. Boström et al. (1985) found that ~75% of TP in surface sediments of eutrophic Vallentunasjön could be classified as residual P, using a chemical fractionation procedure in which that category consists primarily of organic P. Moreover, about 50% of the residual P was rapidly released from the sediment within 1 week, at the same time that O_2 concentration in the hypolimnion decreased from about 10 mg liter^{-1} to about 2. Residual P in the sediment increased to its original concentration when O_2 in the hypolimnion later increased to about 10 mg liter^{-1}, indicating that release and uptake were reversible, redox-dependent processes. These observations are consistent with P release and uptake by microorganisms.

Although we did not monitor P content of sediment inside the flux chamber during the oxic and anoxic phases, the total amount of P released into the enclosed water during the first anoxic period was about 200 mg m^{-2}. We estimate that >500 mg P m^{-2} was incorporated in bacterial biomass in the upper 0.5 cm of sediment, given the values listed in Table 2. Thus, the released P was

equivalent to <40% of the bacterial P in the upper sediment layer. On the basis of results of our laboratory experiments, sedimentary bacteria easily could have accounted for a large part of the observed P release.

Our laboratory and field experiments indicate that uptake and release of SRP by bacteria and precipitation and dissolution of FeOOH seem to occur at about the same redox potential. This coincidence might explain why direct microbial contributions to uptake and release of P have been overlooked since the very convincing, purely abiotic model was proposed more than 40 yr ago.

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