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Nutrient cycling in shallow, oligotrophic Lake Kvie, Denmark

II: Effects of isoetids on the exchange of phosphorus between sediment and water

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Abstract

The importance of isoetids for the exchange of phosphorus between sediment and water was studied in the shallow Lake Kvie, Denmark. Vegetated sediments from the littoral zone (55% of lake area) were compared to unvegetated sediments from the littoral and profundal zone. Porewater concentration of soluble reactive phosphate (SRP) was in general low, however, different distributions were found in the three sediments. The vegetated littoral sediment showed highest conc. of SRP just below the surface and decreasing conc. with sediment depth. The SRP release was low on all stations (<40 μmol m^{-2} d^{-1}). The observed release of SRP on the vegetated station was much lower than the calculated diffusional flux probably due to assimilation of P by isoetids and binding of SRP to oxidized Fe. The high redox potential in the rhizosphere was probably caused by oxygen excretion from roots. The annual P release from vegetated sediments were only 5% of the P requirements of the macrophytes. The efficient plant assimilation of SRP from the porewater resulted in a small SRP pool with a very fast turnover of P of 500–900 times per year. Both the effects of isoetids on the P cycle in littoral sediments and on the P budget of the entire lake indicate that this plant group is important for keeping lakes in an oligotrophic state.

Introduction

A large number of studies have dealt with the relationship between macrophyte growth and P concentrations in water and sediment (e.g. Carignan & Kalff, 1980; Smith & Adams, 1986; Moeller *et al.*, 1988). Other studies have involved the importance of macrophytes for P cycling in lakes (Howard-Williams & Allanson, 1981; Graneli & Solander, 1988). The significance of the littoral zone for the phosphorus dynamics in lakes has been reviewed by Wetzel (1983).

However, very few have investigated the interactions between the isoetid species growing in oligotrophic, softwater lakes and P. Sand-Jensen & Søndergaard (1979) studied the growth of macrophytes in relation to sediment parameters in an oligotrophic lake and found an enhanced biomass of isoetids at shallow depths with increasing porewater concentrations of exchangeable P, inorganic N and CO_2. Christiansen *et al.* (1985) showed that growth of the isoetid species *Littorella uniflora* (L.) Aschers. and its tissue content of P was elevated after sediment enrichment with P, indicating that P might be limiting for *Littorella* growth.

Oligotrophic lakes not situated in remote places may be threatened by eutrophication which may

reduce the abundance of isoetids in these lakes. It is therefore crucial to get a better knowledge of the importance of the isoetids for the nutrient cycling in oligotrophic lakes.

The present study compares the P-cycle in isoetid dominated sediments in a shallow, oligotrophic lake with unvegetated littoral and profundal sediments. Furthermore, we evaluate the importance of isoetids for the P budget of the entire lake. Annual variations in porewater concentration of SRP, redox potential and sediment-water exchange of SRP and O_2 are presented. A parallel investigation was made on the N-cycle (Olsen & Andersen, 1994).

Study site

The study was carried out in oligotrophic, Lake Kvie, situated in Western Jutland, Denmark. The lake is shallow (mean depth 1.2 m, max. depth 2.6 m) and has an area of 30.0 ha. There are no permanent tributaries. This caused a fluctuation in water level (50 cm in 1989) and a high hydraulic retention time (1–2 years). The lake bottom may be classified in the following types: sandy littoral sediment vegetated by isoetids (55% of lake area), littoral sediment without macrophytes (8%, this type is denoted 'unvegetated'), sediment with emergent vegetation (1%) and peaty profundal sediment (36%). The isoetid species were *Isoetes echinospora* Durieu, *I. lacustris* L., *Littorella uniflora* (L.) Aschers. and *Lobelia dortmanna* L. See Olsen & Andersen (1994) for a more detailed description of Lake Kvie.

The phytoplankton biomass showed peaks in April and in July–August (9–10 $\mu l\, l^{-1}$), whereas zooplankton peaked in May–June (5 $\mu l\, l^{-1}$) after the spring phytoplankton bloom (Ribe County Council, unpublished data). Seasonal variation of plankton biomass and nitrogen concentrations is shown in Olsen & Andersen (1994).

Materials and methods

Undisturbed sediment samples were collected in clear acrylic tubes (52 mm inner diam.) on three stations representing vegetated (with *Littorella uniflora*) and unvegetated littoral, and profundal sediment. Fluxes between sediment and water of O_2 and soluble reactive phosphate (SRP) were measured in six cores from each station. Cores from all stations were incubated at 30–50 cm water depth in the littoral zone. Three cores were incubated at ambient light condition (light/dark cores) and the other three cores were covered by black plastic and incubated in darkness (dark cores). All cores were incubated for about 24 h. The cores were closed with a top containing a magnetic stirrer that ensured mixing of the water above the sediment during incubations. No gas headspaces were present in the cores during incubations. Flux calculations were based on initial and final concentrations and the volume of the water column in the cores. Oxygen was measured with an electrode (YSI model 58). Samples for chemical analysis were immediately filtered and kept at 0 °C during transport to the laboratory where the samples were frozen. SRP was measured by the stannous chloride method on a flow injection analyzer (Tecator FIAstar 5010, Application Note 60-01/83). Detection limit for SRP was 0.16 μM.

Three sediment cores from each station were sectioned at six depths and porewater was retrieved by centrifugation in double bottomed centrifugation tubes (Andersen & Kristensen, 1988). The porewater was kept frozen until analyzed. Diffusive fluxes of SRP were calculated on the basis of porewater concentrations according to Ficks first law (Lerman, 1979; Li, Y. & S. Gregory, 1974; Sinke *et al.*, 1990). Sediment from each slice was dried at 105 °C for 24 h before carbon and total nitrogen analysis (Hewlett-Packard CHN-analyzer, 185-B). Subsamples of the dried material were ignited at 550 °C after which total-P was measured as SRP on HCl-extracts of the remaining ash. Total-Fe was measured on the same extracts by atomic absorption spectrometry (Perkin-Elmer 2380). Measurements of redox profiles and calculation of Eh were performed according to Hargrave (1972) on 3 cores from each station using a platinum electrode with a calomel electrode as a reference.

Water samples from a mid-lake station were analyzed for SRP as described under flux measurements and total-P was measured on unfiltered samples as SRP after autoclaving with persulphate (Koroleff, 1968). The mid-lake water samples were considered representative for the water column in the entire lake due to the shallow depths and thorough mixing.

Precipitation was collected for every 12 h period at a climate station situated 1.7 km south of the lake. Samples of the precipitation was immediately filtered (Whatman GF/C) and stored frozen until analysis.

Results

Seasonal variation of temperature, pH, SRP and total-P are shown in Fig. 1. It appears that the lake is acidic with pH varying from 5.0 to 6.0. The SRP concentration in the lake was in general low.

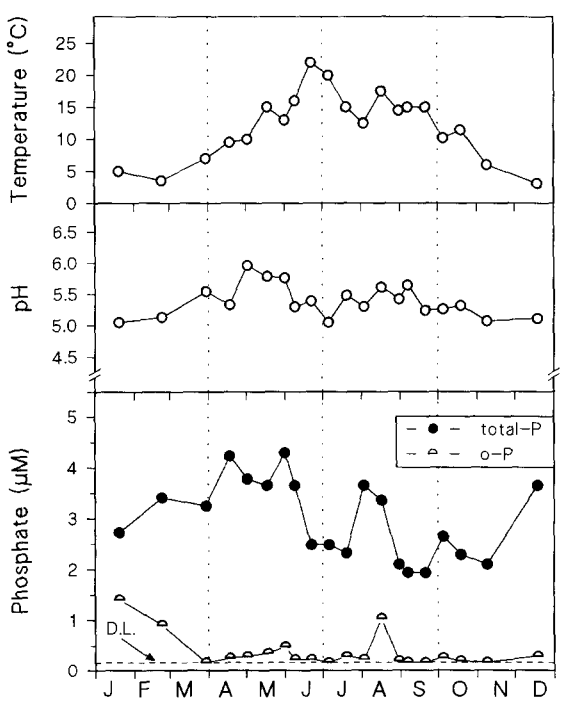

Fig. 1. Seasonal variation of temperature, pH, SRP and total-P in Lake Kvie during 1989. Broken line marked by D.L. indicates the detection limit for SRP.

Winter values were about 1.5 μmol l^{-1} and summer values were close to the detection limit, except for a small peak in August. Total-P in contrast were relatively high, varying from 2 to 4.4 μmol l^{-1}.

The sediments of the three stations differed considerably. Loss on ignition (LOI) was very low in the unvegetated littoral sediment (< 0.25% of DW), whereas the vegetated sediment showed 1.6% LOI at the surface and 0.25% at 5–10 cm depth. In contrast, the peaty profundal sediment showed 32% LOI at the surface and 7–16% deeper in the sediment. The total-P content of the surface sediments was 0.019, 0.092 and 2.3 mg P g DW^{-1} at the unvegetated littoral, vegetated littoral, and profundal stations, respectively (Fig. 2). The iron content of the sediments showed a distribution fairly similar to that of phosphorus (Fig. 2).

In contrast to the large differences in total-P content, the Fe:P ratios in the surface sediment were of the same order: 6.8, 4.6 and 6.1 in vegetated littoral, unvegetated: profundal sediments, respectively. The vegetated sediment showed high ratios at 3 and 15 cm (12.5 and 10.3, respectively), whereas the unvegetated station showed only a small variation in this ratio with depth. In the profundal sediment, increasing ratios were found below 5 cm depth (14.3 at 12 cm). An analysis with sequential extraction of the P-fractions (according to Hieltes & Lijklema 1980) in the profundal sediment showed that iron-bound P and residual P each constituted about 50% of total-P and that only insignificant amounts of adsorbed- and calcium bound P were present in the sediment between 4 and 24 cm depth (unpublished data from Ribe County Administration). The upper very flocculent 4 cm of the sediment was unfortunately lost at their sampling.

The SRP release was low at all three stations throughout the year (< 40 μmol m^{-2} d^{-1}) and often of the same magnitude as the detection limit ($\pm$ 5 μmol m^{-2} d^{-1}) (Fig. 3A, 4A, 5A). Uptake of SRP by the sediment was also observed. There was no clear effect of light when comparing light/dark cores to dark cores. The SRP fluxes at the vegetated station were in general of similar size as

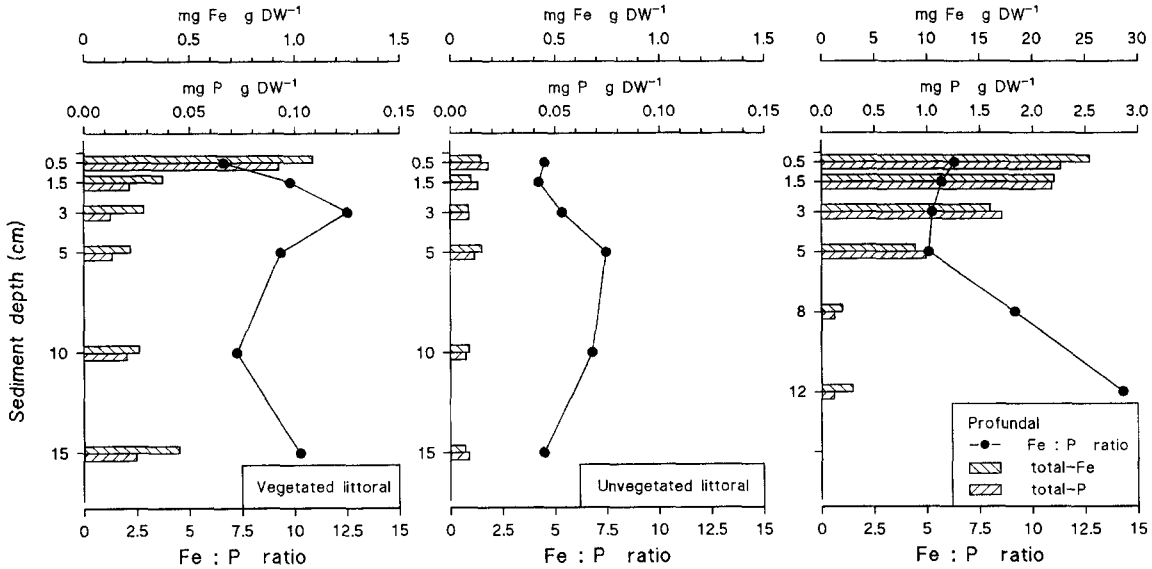

Fig. 2. Total-P and total-Fe concentration, and their molar ratio in the sediment from the three stations.

the fluxes measured on the other stations. The profundal station, however, showed an elevated SRP release during September–November (Fig. 5A).

The measured SRP release on the vegetated station was much lower than the calculated diffusive flux based on porewater concentrations. The unvegetated station also showed a lower measured release than the calculated, but the differences were smaller than at the vegetated station. At the profundal station, measured and calculated flux rates usually were of similar magnitude, except during August to November when the measured release was higher than that calculated.

Porewater concentrations of SRP were in general low at all stations (< 5–6 μmol l^{-1}), but different patterns of distribution with sediment depth and time were observed (Fig. 3C, 4C, 5C). The vegetated station had the highest SRP concentration in a subsurface layer of the sediment (~ 1 cm depth) below which the concentration gradually decreased to less than 0.5 μmol l^{-1} below 5 cm depth (Fig. 3C). This distribution was fairly constant over the year. In contrast, the unvegetated station showed lower concentrations and a more variable pattern (Fig. 4C). Subsurface maxima were only developed for shorter periods in May and late July–early August. The profundal sediment showed slightly increasing concentrations with depth (Fig. 5C).

The three stations had very different redox conditions in the sediment (Fig. 3D, 4D, 5D). The vegetated station in general showed higher redox potentials than the other stations (Fig. 3D). A minimum at 1 cm depth ($+310$ mV) was observed, whereas the redox potential was high from the maximum at 7 cm ($\sim +400$ mV) to the core bottom. The unvegetated station showed decreasing redox potentials with depth (175 mV at 11 cm depth) and less seasonal variation than the vegetated sediment. In the profundal sediment a very steep redoxcline was found in the upper 1.5 cm, below which the redox was very constant (~ 235 mV) with both depth and time.

All stations exhibited a net uptake of O_2 by the sediment or a very low release (Fig. 3B, 4B, 5B). The highest O_2 uptake was observed on the vegetated and the profundal station (max. 70 and 60 mmol O_2 m^{-2} d^{-1}, respectively), while the unvegetated littoral station showed a significant lower uptake (max. 20 mmol O_2 m^{-2} d^{-1}). The O_2 uptake was usually higher in the dark than in the light/dark cores. This difference was most

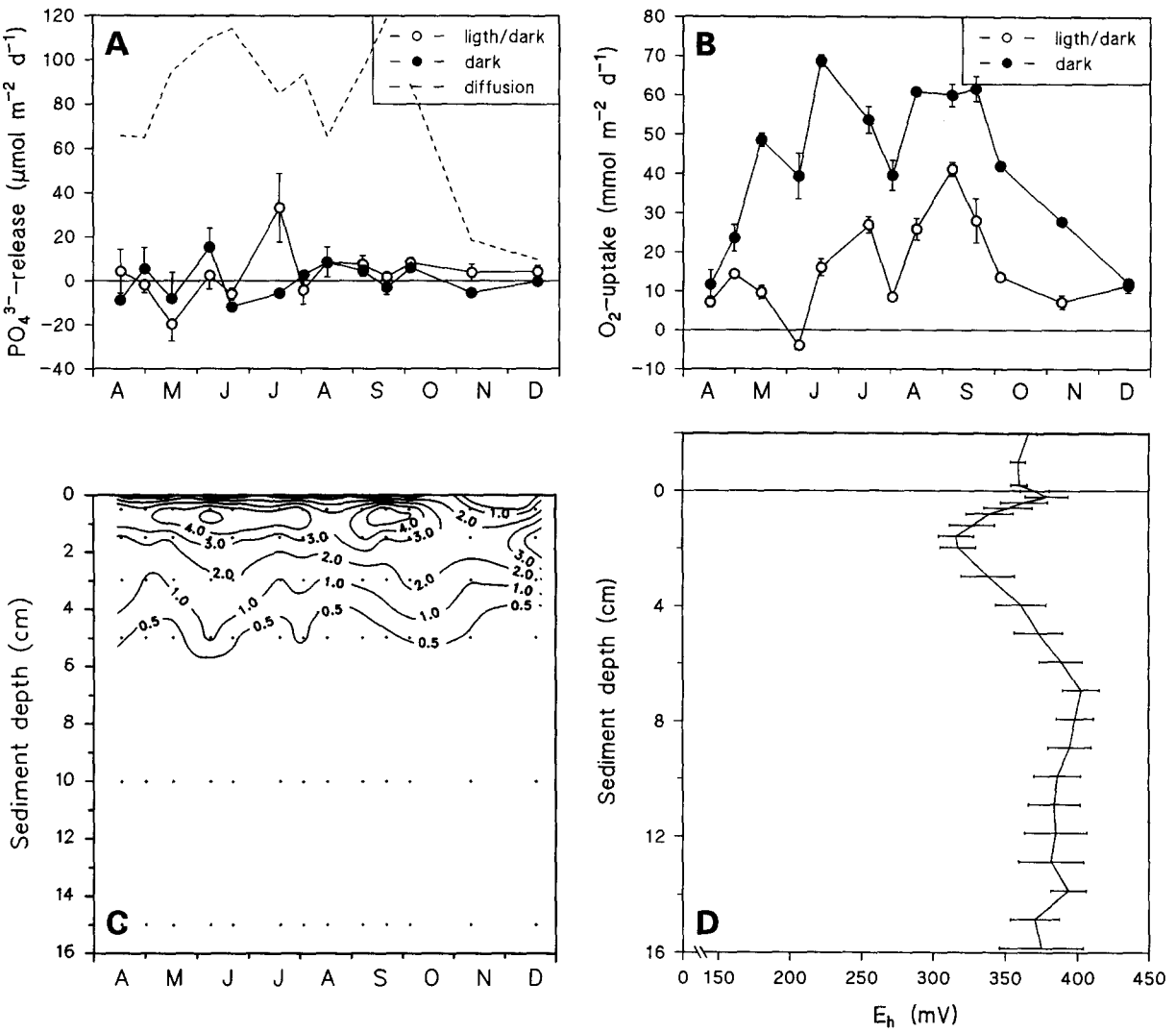

Fig. 3. In situ flux rates of SRP (A) and O_2 (B) over the sediment-water interface at the vegetated littoral station; SRP concentration (µM) of sediment pore water (C); and redox potential (mV) of the sediment (D). Mean ± SE ($n = 3$) are shown for fluxes measured at ambient light and in darkness. The broken line on (A) indicates the calculated diffusive flux of SRP.

pronounced in cores from the vegetated station (Fig. 3B) as a result of photosynthetis.

An estimate of the turnover of SRP in the porewater may be made on the basis of data on P in plant biomass and the integrated content of P in the porewater per unit area. The P content in *Littorella* leaves and roots on May 31 was 0.47 and 0.65% of DW, respectively, and the P content in living leaf and root biomass was 23.9 mmol P m^{-2}. Sand-Jensen & Søndergaard (1978) have estimated the annual renewal of *Littorella* leaf biomass to be 150%, which means that the annual P requirement of the plants is 35.9 mmol P m^{-2}. The annual mean content of SRP in the porewater is estimated to be 38.2 µmol m^{-2}. A comparison of this value with the P requirements of the *Littorella* biomass gives a 940-fold turnover of the porewater SRP per year.

The turnover of the porewater may also be estimated from the rate of P mineralization from

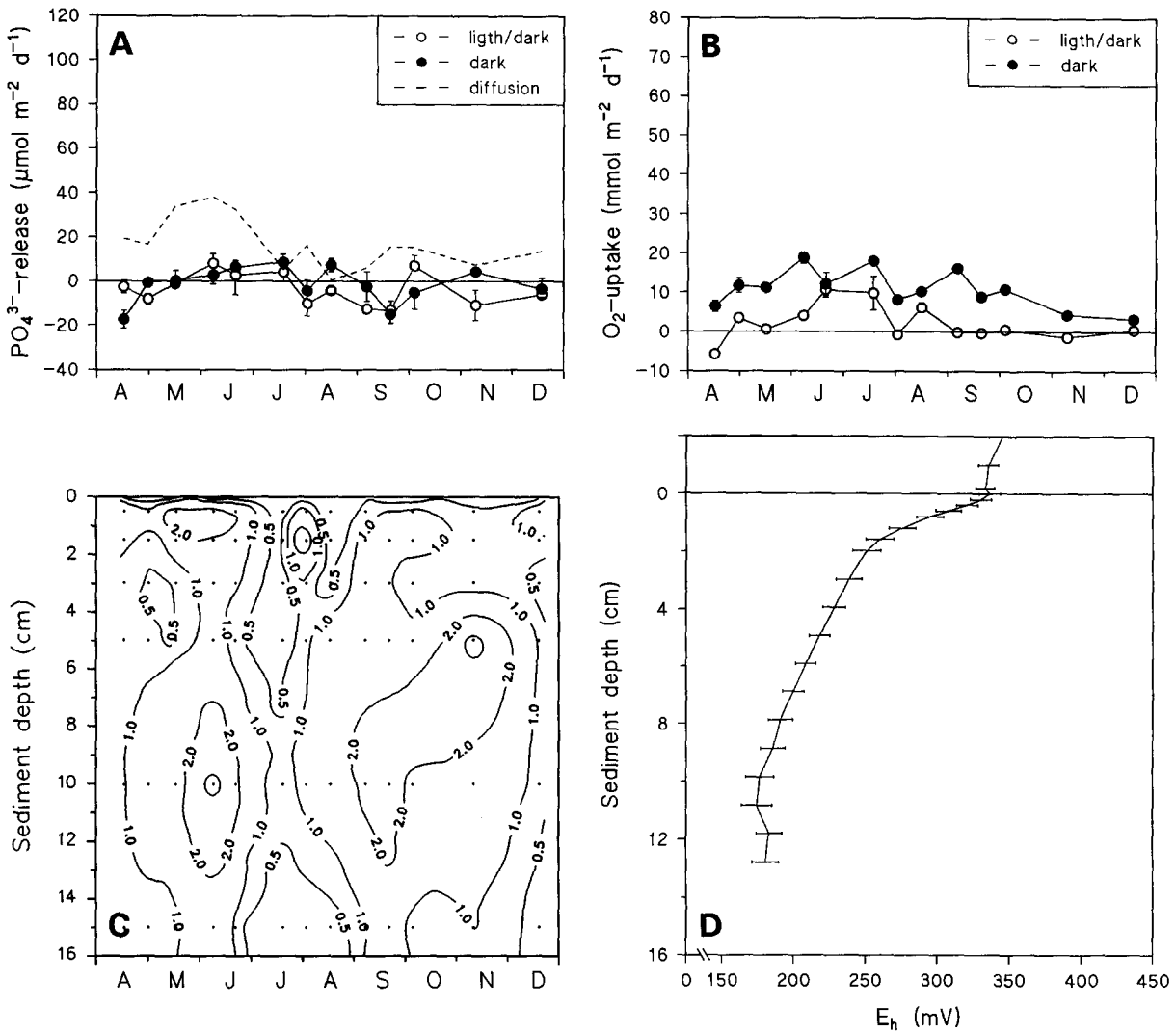

Fig. 4. Same as Fig. 3, but for the unvegetated station.

organic matter. Based on a measured C:P ratio of the surface sediment of 234 and the O_2 uptake measurements, a P mineralization of 21.5 mmol P m^{-2} y^{-1} can be estimated (assuming an RQ of 1). The turnover of porewater SRP calculated in this way is 560 y^{-1}.

Based on measurements in precipitation, tributaries and the lake outlet a P-budget for Lake Kvie can be estimated (Fig. 6). The precipitation was relatively low in 1989. From April 17 to December 18, precipitation was 362 mm compared to 576 mm normally. The concentration of SRP in the precipitation showed a high variation (mean 2.1, SD 4.7, min. 0.1, max. 28.7 µmol l^{-1}). Based on these figures an annual deposition of 8.1 kg P y^{-1} (2.4 µmol m^{-2} d^{-1}) for the lake was calculated. This figure might be an underestimate because total-P was not measured. The estimated contribution from the catchment area to the lake was 6.1 kg P y^{-1}.

This estimation was based on export values (0.16 kg P ha^{-1} y^{-1}) measured in another catchment area with similar soil types and land use. The external input thus totalled 14.2 kg P y^{-1}.

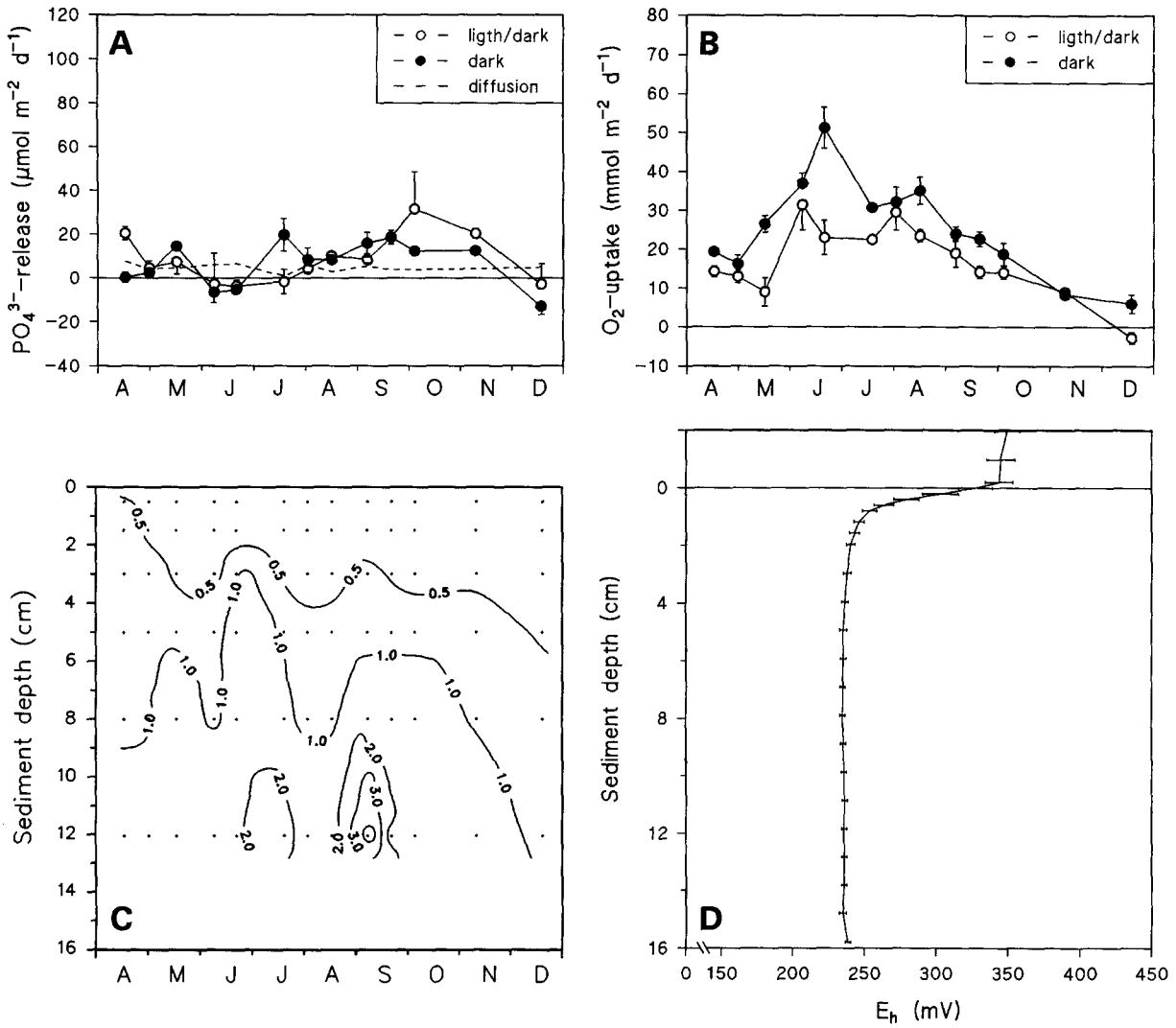

Fig. 5. Same as Fig. 3, but for the profundal station.

The output of P from the lake was estimated at 10.2 kg P y^{-1} by measuring water flow and P concentration at the weir controlling the outlet from the lake. The retention of P in the lake, as calculated by the difference between input and output, was 4.0 kg P y^{-1}.

Discussion

The SRP fluxes across the sediment-water interface were generally low in Lake Kvie because of low porewater SRP concentrations and oxic conditions in overlying water. The SRP release was of the same order as that found in other oligotrophic or P-poor lakes (19–55 µmol PO_4^{3-} m^{-2} d^{-1}; Kamp-Nielsen, 1974; Twinch & Peters,1984; Nürnberg *et al.*, 1986; Jensen *et al.*, 1992).

The lack of significant differences between incubations in light/dark and continuous darkness indicate that a photosynthetic effect on sediment conditions from the earlier light/dark incubation continues for some time during dark incubations.

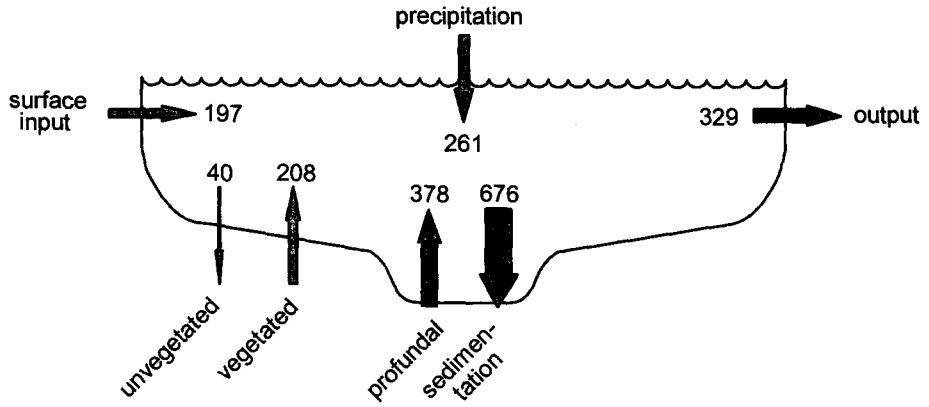

Fig. 6. Phosphorus budget for Lake Kvie. Figures indicate annual fluxes to and from the lake in mol PO_4^{3-}. Sedimentation was calculated as the difference between input and output minus the net release of P from the sediment.

Andersen & Kristensen (1988) found a similar sustained effect of benthic microalgae on NH_4^+ efflux from a marine sediment incubated in darkness. However, Carlton and Wetzel (1988) demonstrated a reduced P-release from a hardwater, oligotrophic lake sediment during light periods because of microalgal P-assimilation.

In contrast to the P fluxes, O_2 fluxes were significantly different under light/dark and dark conditions, indicating a photosynthetic O_2 production in all three types of sediments. However, for the isoetid covered sediment, it should be emphasized that this difference is not a precise measure of the photosynthesis of the isoetids because they may release significant amounts of O_2 through the root system (Sand-Jensen *et al.*, 1982; Robe & Griffiths, 1990). The O_2 production by the profundal sediment is overestimated because the sediment was incubated in shallow water and thus at higher light intensities.

The calculated diffusional fluxes showed good agreement with the measured fluxes in the unvegetated littoral and the profundal sediment, although the diffusional fluxes were calculated on the basis of porewater SRP profiles with a rather crude depth resolution. At the vegetated station, however, the observed fluxes during April to October were significantly lower than the calculated diffusional fluxes. The efficient retention of P in the upper layer of the sediment was probably due to sorption of P to oxidized Fe. This is stressed by the facts that the surface of the vegetated sediment had the highest Fe:P ratio and redox potential of the three studied sediments, indicating a higher capacity for binding of P. Iron will be oxidized at high redox potentials which implies that phosphate may be removed from solution and bound to iron as ferric hydroxides or as insoluble ferric phosphate (e.g. Jensen *et al.*, 1992; Jensen & Andersen, 1992). Correlations between Fe and P in interstitial water of sediments have also been shown by Bortleson & Lee (1974). The redox maximum observed at the surface may be due to photosynthetic activity of epilithic or epiphytic algae at or just above the sediment-water interface. Assimilation of P by these algae may also have contributed to diminish the P release to overlying water.

The different patterns of porewater SRP concentration found in vegetated and unvegetated sediments show a significant influence of *Littorella* on the P cycle in the sediment. The very low concentrations of SRP found below 5 cm sediment depth are primarily a result of both assimilation of P through the root system of *Littorella*, but also of oxidation of the sediment due to oxygen excretion from the roots. The oxidative effect of the roots is evident from the high redox potentials measured in sediments below *Littorella*-stands in the present study and by Wium-Andersen & Andersen (1972). The binding of P in insoluble forms due to oxidation in the rhizo-

sphere may be a disadvantage for the isoetids living in an environment with low P concentrations.

In spite of low concentrations in the rhizosphere of *Littorella*, the P concentration in leaves (0.47%) is well above the critical level (0.28%) found for this species (Christiansen *et al.*, 1985). The plants requirements for P were higher than the calculated P mineralization in the sediment. This leaves no surplus P for diffusion to overlying water. Accordingly, the annual P release is only about 5% of the P assimilation by *Littorella*. Similarly, Howard-Williams & Allanson (1981) found a closed P cycle within a *Potamogeton pectinatus* L. bed. Comparisons of porewater SRP with plant uptake of P or with P mineralization in the sediment show a very fast turnover of 500–900 times y^{-1} for the pool of porewater SRP. Barko & Smart (1980) similarly reported a more than 1000-fold turnover of interstitial SRP over a three-month period in sediments with macrophytes.

The unvegetated sediment showed a small net uptake of P which may be due to benthic microalgae assimilation (Carlton & Wetzel, 1988) or to formation of amorphous FeOOH in the sediment caused by groundwater seepage. However, P was not accumulated in the sediment which may be due to resuspension caused by the bathers.

It cannot be concluded from the comparison of the two littoral sediments that the internal loading of the lake would decrease if the isoetid vegetation declined. The unvegetated sediment for example caused by eutrophication due to limited light penetration would be of another character than the small area on which vegetation was destroyed by bathers. The P budget summarized on Fig. 6 shows that net fluxes in general are very low in Lake Kvie. The large fraction of the lake bottom made up by littoral sediments which exhibited low release (vegetated) or uptake rates (unvegetated) was important for lowering the mean net release from the sediment to 5.0 μmol PO_4^{3-} m^{-2} d^{-1} for the entire lake. The low release from the sediment compared to the external loading (4.2 μmol PO_4^{3-} m^{-2} d^{-1}) in this oligotrophic lake is in contrast to studies from eutrophic lakes. Jensen & Andersen (1992) thus reported area-specific releases of 2.1–53 times the external loadings in four shallow, eutrophic, Danish lakes. Nürnberg *et al.* (1986) similarly found that P release rates from the sediment were positively correlated to the trophic state of the lake as indicated by the P concentration.

Oligotrophic lakes not situated in remote places may be endangered by eutrophication due to excessive use of fertilizers, waste water and atmospheric deposition. Eutrophication will cause a reduction of isoetid growth and probably an increase in the more organic soft bottom. This will imply an enhancement of the internal P-loading because the latter sediment type has a significantly higher release of P to the water column and eutrophication may therefore be accelerated. Most of the P mineralized in the vegetated sediment was trapped in the macrophyte biomass. The vegetation of isoetids is therefore crucial for preservation of oligotrophic lakes like Lake Kvie.

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