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Direct and Indirect Influences of Aquatic Macrophyte Communities on Phosphorus Mobilization from Littoral Sediments of an Inlet Region in Lake Delavan, Wisconsin

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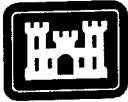
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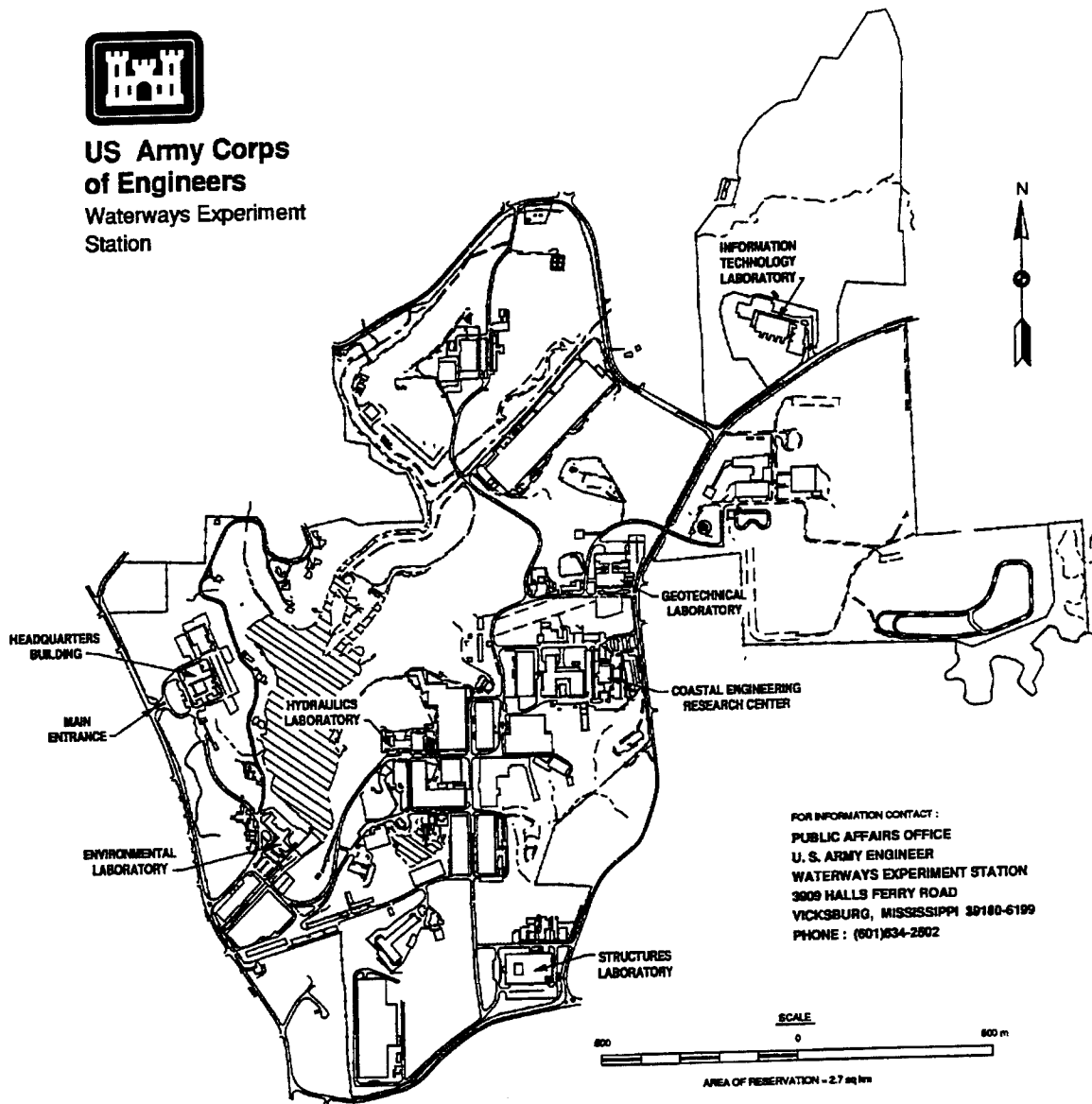
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Preface

This study was conducted in response to a request from the State of Wisconsin, Department of Natural Resources (WI-DNR), Milwaukee, to the U.S. Army Engineer District, St. Paul, for planning assistance under Section 22 of the Water Resources Development Act (Public Law 93-251).

The work reported herein was sponsored by the WI-DNR, the St. Paul District, and the Headquarters, U.S. Army Corps of Engineers (HQUSACE), as part of the Water Operations Technical Support (WOTS), Work Unit 004419. The WOTS is assigned to the U.S. Army Engineer Waterways Experiment Station (WES) under the purview of the Environmental Laboratory (EL). Funding was provided under Department of the Army Appropriation No. 96X3123, Operations and Maintenance. The WOTS is managed under the Environmental Resources Research and Assistance Programs (ERRAP), Mr. J. L. Decell, Manager. Mr. Robert C. Gunkel, Jr., was Assistant Manager, ERRAP, for the WOTS. Technical Monitors during this study were Messrs. Frederick B. Juhle and Rixie Hardy, HQUSACE.

This study was conducted and the report prepared by Mr. William F. James and Drs. Craig S. Smith and John W. Barko, Environmental Processes and Effects Division (EPED), EL, WES, and by Mr. Stephen Field, U.S. Geological Survey (USGS), Madison, WI. We gratefully acknowledge the assistance of Mr. D. Helsel, WI-DNR, in collecting sediment cores and deploying sediment peepers; Mr. G. Goddard, USGS, for deploying and maintaining the in situ water quality monitor and providing the authors with the data; Drs. D. Robertson and J. Elder, USGS, for insightful discussions and information on external phosphorus loading to Lake Delavan; Mr. K. MacKinnon, Delavan Lake Sanitary District, for providing logistical support; Ms. S. Fox, WES, for analysis of sediment P fractions; and Messrs. A. Albrightson, A. Budelis, D. Dressel, H. Eakin, and E. Isherwood, and Meses. M. Huppert, S. Krause, and S. Riddick, U.S. Army Corps of Engineers Eau Galle Aquatic Ecology Laboratory, for processing sediment cores and conducting phosphorus release studies.

This investigation was conducted under the general supervision of Dr. John W. Keeley, Director, EL, and Mr. Donald L. Robey, Chief, EPED, and under the direct supervision of Dr. Richard E. Price, Chief, Ecosystem Processes and Effects Branch, EPED.

At the time of publication of this report, Director of WES was Dr. Robert W. Whalin. Commander was COL Bruce K. Howard, EN.

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1 Introduction

Lake Delavan, Wisconsin, has been the subject of extensive lake restoration to control phosphorus (P) and reverse eutrophication (O'Reilly 1992). Efforts over a 5-year period (1986-1991) to improve deteriorating water quality in this lake have included diversion of septic systems and control of nonpoint sources of P in the watershed, construction of an in-lake dike and modification of the dam and outlet structure to divert external P and sediment loads from the main body of the lake, the development of wetlands and sedimentation pools along the main tributary inflow of the lake to reduce sediment loading, a hypolimnetic alum treatment, and complete eradication and restocking of the fishery to promote top-down control of phytoplankton biomass. While the preliminary results of these actions have indicated a marked improvement in the trophic state of the lake, concerns have arisen over the development of extensive submersed macrophyte beds in the inlet region of the lake following restoration and improved water clarity. Associated with the macrophytes in the inlet region of the lake, oftentimes extremely high total P concentrations (range = 0.09 to 0.87 mg/l; Holmstrom, Kammerer, and Ellefson 1994) have been measured during the summer.

Macrophytes can mobilize sediment P via root uptake and senescence (Barko and Smart 1980; Carpenter 1980; Smith and Adams 1986) and by altering water chemistry in ways that affect rates of P release from the sediments (James and Barko 1991). Species composition, biomass, and nutrient content of submersed macrophytes in the inlet region of Lake Delavan were evaluated at the approximate peak in biomass to estimate the macrophyte P pool and its potential for P loading to the inlet region. The possibility was examined that by regulating pH and dissolved oxygen concentrations in their surrounding environment, submersed macrophytes may be indirectly enhancing P release from the littoral sediments. Laboratory sediment systems were used to estimate rates of P release from littoral sediments under various redox and pH conditions. Ranges in these rates were then combined with a continuous record of in situ dissolved oxygen concentrations and pH, measured in the inlet region, to estimate rates of P release from the sediments on a daily basis. Finally, these estimates were compared with in situ measurements of Fickian diffusional fluxes determined using sediment peepers to examine the overall importance of littoral sediments as a source of P to the inlet region of Lake Delavan.

2 Methods

Study Site

Lake Delavan, located in southeastern Wisconsin, is an 840-ha natural lake with a mean and maximum depth of 7.6 and 16.5 m, respectively. Jackson Creek, the major tributary inflow to the lake, drains a predominantly agricultural watershed (100 km²). The shallow (mean depth = 0.5 m; area = 590 ha) inlet region (Figure 1) enters the northeastern corner of the lake and receives drainage from Jackson Creek watershed. The inlet region was typically turbid and devoid of measurable aquatic macrophyte growth until 1991; after lake rehabilitation and improved water clarity, macrophytes were first observed in great numbers.

Area Coverage, Biomass, and Nutrient Content of Submersed Macrophytes

The land-water boundary and boundaries between emergent macrophytes, open water, and three submersed macrophyte zones (upper, middle, and lower; Figure 1) were traced from aerial photographs. The tracings were digitized into a computer-aided drawing program (FastCAD, Evolution Computing) and imported into the EPPL7 Geographic Information System (Minnesota State Planning Agency) to calculate the areas of the three zones of submersed plants, the open water, and the emergent vegetation.

Plant biomass was measured on 08 August 1994 via harvesting 0.25-m² quadrats. Each submersed macrophyte zone was subdivided into 10 approximately equal areas, with one sample quadrat being harvested from each area. To minimize bias, quadrat locations were selected randomly within each area by dropping the sampling quadrat from a moving boat without looking at the plant community. All plants rooted in the quadrat were then harvested. For unrooted species (*Ceratophyllum* sp., duckweed and filamentous algae), all plant material within the horizontal limits of the quadrat was harvested. Biomass samples were washed under running water and separated according to species. Above-sediment parts were removed and dried at 80 °C to a constant mass. Below-sediment parts were discarded. The P content (milligrams per

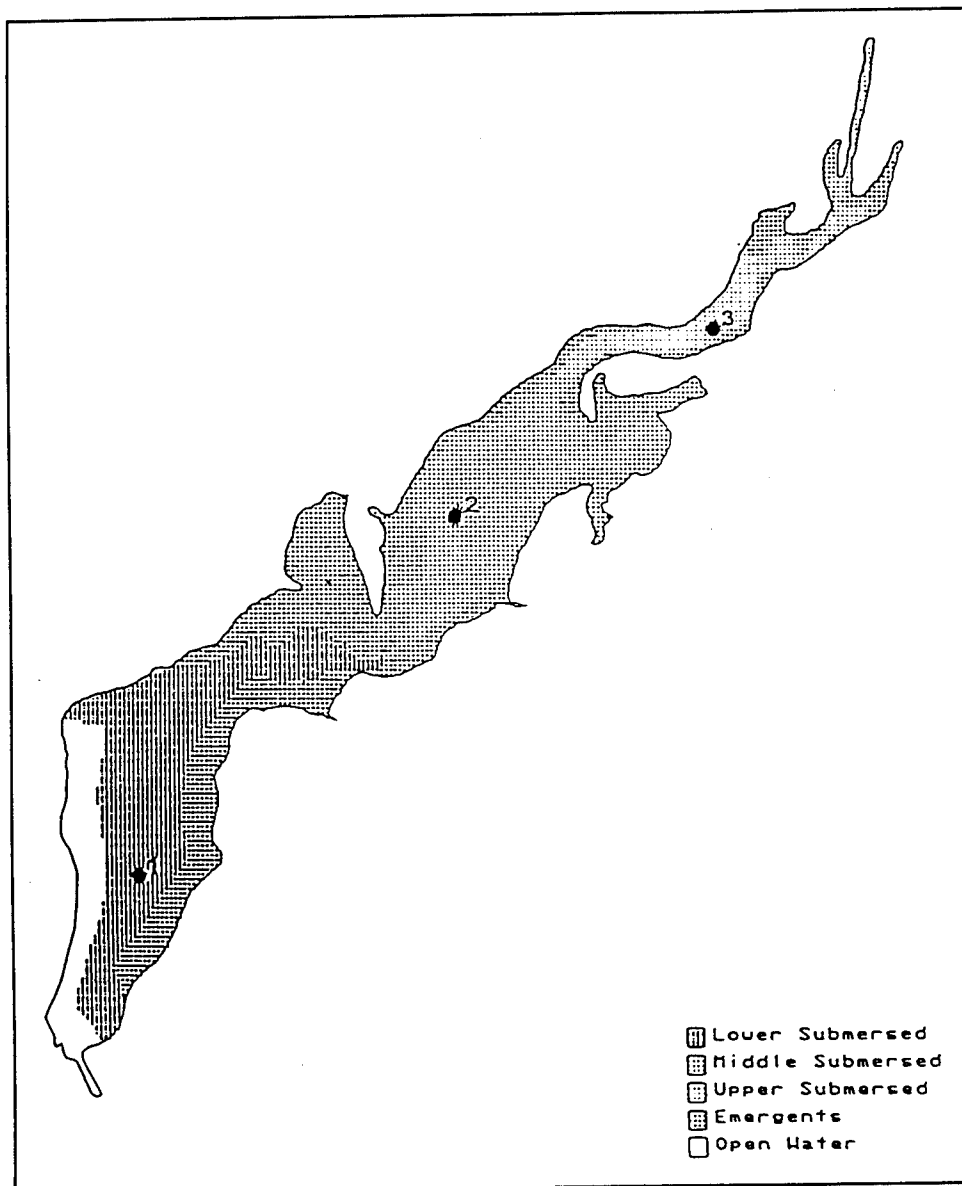


Figure 1. Map of Lake Delavan showing inlet region and sediment core and sediment peeper sampling stations (The in situ water temperature, pH, and dissolved oxygen monitoring station was located near Station 2)

gram dry weight) of dried plant tissue was determined colorimetrically (Lachat QuickChem; Method 13-115-01-1-B) after grinding in a Wiley Mill (40 mesh size) and digestion according to Allen et al. (1974).

Pools of Sediment Phosphorus

Replicate (3) sediment cores were collected at each of three stations in the inlet region of Lake Delavan (Figure 1) for the determination of sediment total

P and sediment P fractions. The upper 8 cm of surficial sediment were collected with a Wildco KB sediment core sampler (5.1-cm ID and 50-cm length; Wildco Wildlife Supply Co.), immediately extruded into an airtight container, and sealed to preserve the redox integrity of the sediments. In the laboratory, the sediment was sectioned at 2-cm intervals in a nitrogen atmosphere. Sediment total P (total-P) was analyzed colorimetrically using automated Lachat procedures (American Public Health Association (APHA) 1992), following digestion with sulfuric acid, potassium sulfate, and red mercuric oxide (Plumb 1981). Sequential fractionation of inorganic phosphorus in sediment subsamples was performed according to Hieltjes and Lijklema (1980). Wet sediment (~ 50 mg) was extracted for 2 hr with 1 M NH_4Cl for determination of loosely bound plus CaCO_3 -adsorbed P (NH_4Cl -P). The same sediment was then extracted with 0.1 N NaOH for 17 hr for determination of iron and aluminum-bound P (NaOH-P). Finally, the same sediment was extracted with 0.5 N HCl for determination of calcium-bound P (HCl-P). Each extract was filtered through a 0.45- μm filter under a nitrogen atmosphere, adjusted to pH 7, and analyzed for soluble reactive P (SRP). SRP was measured colorimetrically using the ascorbic acid method (APHA 1992). Sediment total inorganic P was calculated as the sum of the measured sediment inorganic P extracts. Sediment organic P was calculated as the difference between sediment total-P and sediment total inorganic-P.

In Situ Measurements of Water Temperature, Dissolved Oxygen, and pH

Water temperature, dissolved oxygen (DO), and pH were measured in situ in the bottom waters of the inlet region of Lake Delavan every hour at Station 2 from April through September 1994 using a recording YSI 6000. The probes were positioned about 20 cm above the sediment interface by securing the sonde unit to a platform permanently anchored into the sediments (Figure 1). At biweekly intervals, the sonde unit was removed from the water column for data retrieval and servicing. At that time, the combination DO/temperature probe was replaced with a clean probe. The DO/temperature probe was calibrated against saturated air concentrations, while the pH probe was cleaned gently with distilled water and calibrated against known buffers before redeployment.

Laboratory Determinations of Rates of P Release from Littoral Sediments

Replicate (six) sediment cores (6.5-cm ID) were collected at three sampling stations located in the inlet region of Lake Delavan (Figure 1) for the determination of P release from littoral sediments as a function of oxidation-reduction (redox) condition. The upper 10-cm section of sediment and filtered lake water (Gelman A/E glass fiber) were used to construct sediment systems

according to the methods of James and Barko (1991). The redox environment was controlled by gently bubbling either air or nitrogen through an air stone (15- to 20- μ m nominal pore size) that was placed just above the sediment interface. A set of nine sediment systems (three replicates from each station) was subjected to an oxic environment, while another set of nine was subjected to an anoxic environment. Bubbling air through the systems resulted in an equilibrium pH of about 8.5, while bubbling nitrogen through the systems resulted in an equilibrium pH of about 9.0.

Nine additional sediment cores were collected from each station (a total of 27 sediment cores) to examine the effects of elevated pH on P release from littoral sediments under oxic conditions. The pH levels in these oxic systems were altered either by the addition of NaOH or by bubbling the systems with CO₂-free air. An automated recording pH controller (New Brunswick) was used to maintain the pH at 9.0 or 10.0 in each of nine systems (three replicates from each station) through additions of 0.1 M NaOH. The pH was adjusted to about 9.0 (actually 9.1) in an additional nine systems (three replicates from each station) via bubbling with CO₂-free air.

All sediment systems were placed in a darkened environmental chamber (Psychrotherm) and incubated at a constant temperature of 20 °C for 1 to 2 weeks, which reflected approximately mean water temperature conditions in the bottom waters of the inlet region during the summer. Water samples for SRP determination were collected daily from the center of each sediment system using an acid-washed syringe and immediately filtered through a 0.45- μ m membrane syringe filter (Nalge). The water volume removed from each system during sampling was replaced by additions of filtered lake water pre-adjusted to the proper redox and pH conditions. Rates of SRP release from the littoral sediment (milligrams per square meter per day) were calculated as the linear change in concentration in the overlying water divided by time and the area of the incubation core liner.

Rates of P release from littoral sediments were estimated on a daily basis for the period April through September as a function of pH and redox condition (i.e., oxic or anoxic) using ranges in laboratory-derived rates of P release and in situ measurements of pH and DO. From in situ measurements, the mean daily pH and the proportion (percent) of the day that the bottom waters in the littoral inlet region were either oxic (i.e., DO > 0.5 mg/l) or anoxic (i.e., DO \leq 0.5 mg/l) were calculated. For portions of the day when DO > 0.5 mg/l, a rate of P release under oxic conditions was estimated as a linear function of pH using the equation, rate of P release (milligrams per square meter per day) = pH(6.2) - 49.9 (see Chapter 3). The equation was derived from results obtained from laboratory sediment systems that were preadjusted to a pH of either 8.5 or 9.1 via additions or removal of CO₂ from the overlying water. When in situ mean daily pH values were greater than 9.1 or less than 8.5, rates of P release from our linear equation were extrapolated based on results of earlier studies demonstrating linearity over a broad range in pH values (range = 8.3 to 10; James and Barko 1991). For portions of the day when DO was \leq 0.5 mg/l, the laboratory-derived rate of P release determined

under anoxic conditions was applied. The rate of P release was assumed to be constant during periods of anoxia. Incremental estimates of rates of P release under oxic and anoxic conditions were then summed to obtain an integrated daily rate of P release from the littoral sediments of the inlet region.

In Situ Determinations of Fickian Diffusional Fluxes and P Gradients in the Pore Water

Phosphorus gradients in the sediment pore water were determined in situ at three stations (Figure 1) in the inlet region of Lake Delavan using sediment peepers (dialysis techniques). The sediment peepers were deployed in triplicate at these stations in May, June, July, August, and September. Acrylic sediment peepers had 12 chambers spaced at 2-cm intervals that were covered by a dialysis membrane (2- μ m pore size; Nucleopore, Corporation). The procedures of Carignan (1984) and Shaw and Prepas (1989) and those outlined in James and Barko (1991) were followed for the preparation, deployment, and retrieval of the peepers.

Fickian diffusional fluxes (J , milligrams per square meter per day) of P across the sediment-water interface were calculated as $J = -\phi \cdot D \cdot \Theta^{-2} \cdot dC/dx$ (Berner 1980), where ϕ is the porosity of the sediment, D (square meters per day) is the areal sediment diffusion coefficient for phosphorus (Li and Gregory 1974), Θ^{-2} is the tortuosity of the sediment, and dC/dx is the phosphorus gradient across the sediment interface. The variable, D , was corrected to the mean water temperature of the inlet during peeper deployment periods using the regression equations of Krom and Berner (1980). Sediment porosity (0.88) was determined as the water mass in the upper 2 cm of the sediment divided by the wet sediment volume. Sediment tortuosity was estimated from reported relationships between the formation factor, F , and sediment porosity (Ullman and Aller 1982; Sweerts et al. 1991). The variable, dC/dx , was calculated from concentrations immediately above and below (2-cm interval) the sediment interface.

3 Results

Macrophyte Biomass and P Content

Aquatic vegetation (emergent and submersed) covered approximately 92 percent of the inlet; submersed vegetation accounted for 52 percent, and the remaining 40 percent was emergent (Table 1). Six submersed plant species and one floating species (duckweed) occurred in samples from the inlet (Table 2). A mat of unidentified filamentous algae was also present in many locations, particularly in the middle region. The upper region was dominated by two pondweed species and coontail; the middle was dominated by filamentous algae, coontail, and elodea; and the lower region was dominated by elodea and northern watermilfoil (Figure 2). The contribution of duckweed to total plant biomass was negligible. The total biomass of submersed plants increased from 161 to 236 and 344 g/m² from the upper region to the middle and lower regions, respectively. The P content of submersed plants increased from the upper through the middle and lower regions of the inlet (Table 3), coinciding with increases in both the area and biomass of submersed vegetation. Approximately one-third of the P was contained in unrooted plants (algae and coontail); the remainder was in rooted plants (Figure 3).

Category	Area, ha	% Coverage
Open (harvested)	4.9	8
Submersed		
Upper	4.3	
Middle	11.9	
Lower	14.3	
Total Submersed	30.5	52
Emergent	23.9	40
Inlet Total	59.3	100

Common Name	Scientific Name
Aquatic Buttercup	<i>Ranunculus</i> sp.
Coontail	<i>Ceratophyllum demersum</i>
Elodea	<i>Elodea canadensis</i>
Northern Watermilfoil	<i>Myriophyllum sibiricum</i>
Narrow-leaved Pondweed	<i>Potamogeton pusillus</i>
Sago Pondweed	<i>Potamogeton pectinatus</i>
Filamentous Algae	Unknown

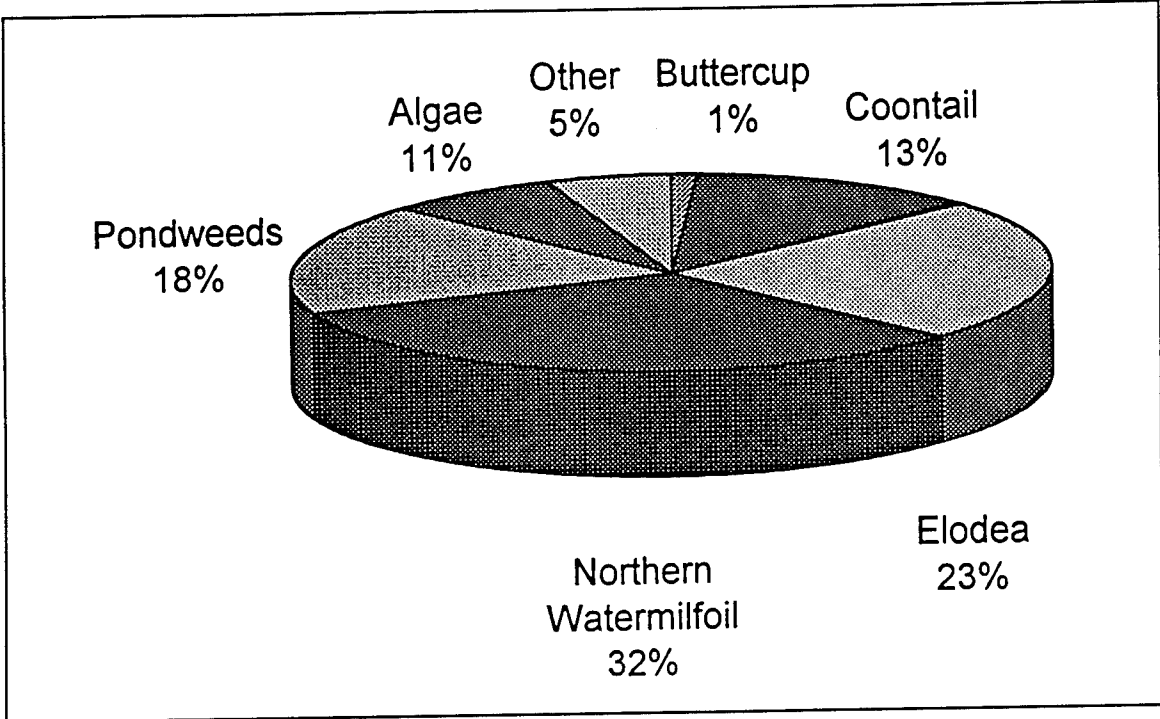


Figure 2. Species composition of submersed macrophyte above-sediment biomass in three regions of Delavan inlet (Each bar is mean of measurements from ten 0.25-m² quadrats. Error bars indicate standard errors)

Sediment P Content

There were no significant differences in sediment P fractions as a function of depth or station location, so all values were pooled to estimate mean concentrations for sediment of the inlet region of Lake Delavan (Table 4). Inorganic fractions of P accounted for about 70 percent of the total P in the

Table 3 Phosphorus (P) Content of Submersed Plants (above-sediment parts only) in Delavan Inlet	
Region	P, kg
Upper	42
Middle	212
Lower	332
Total	585

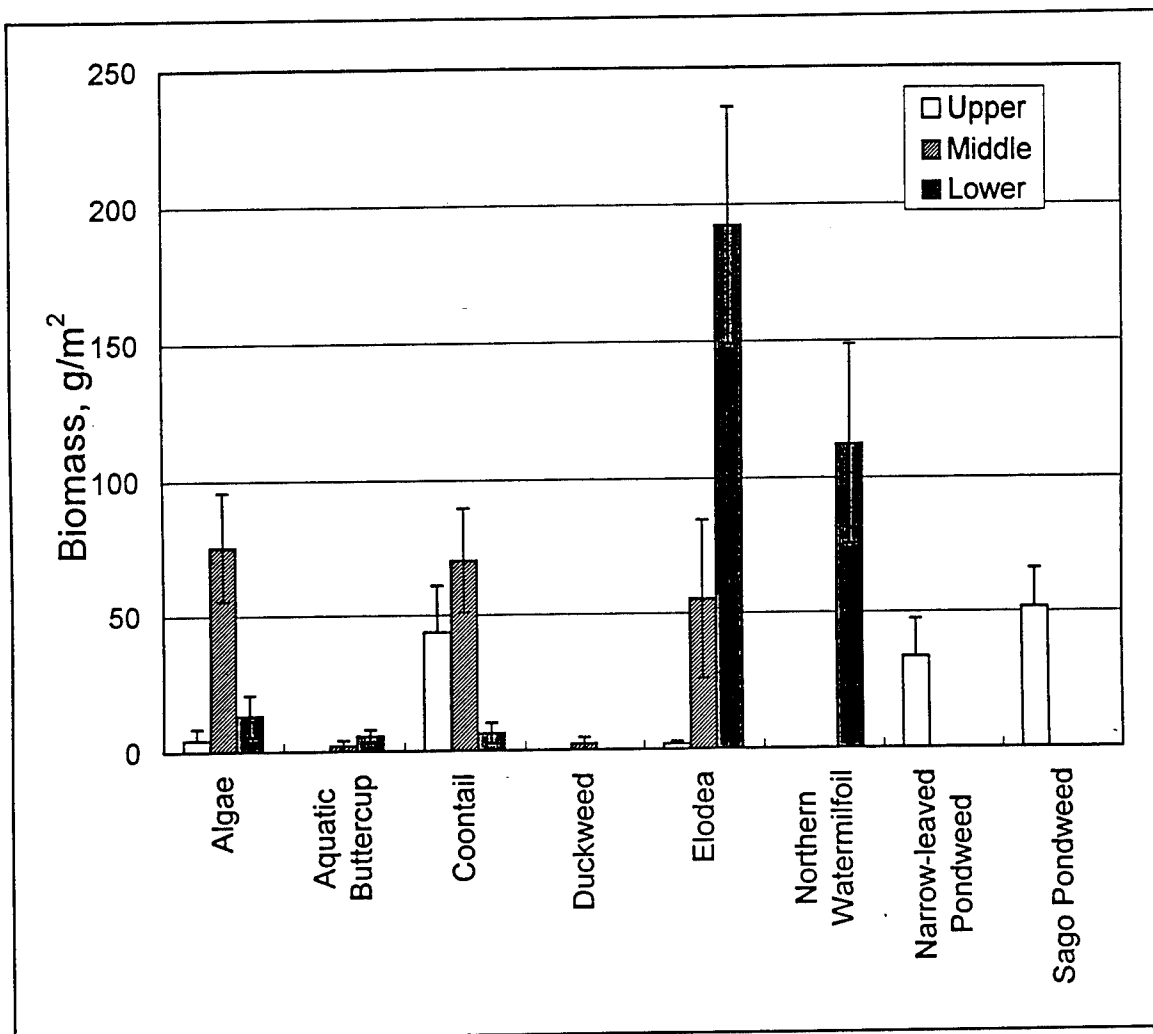


Figure 3. Distribution of phosphorus among submersed plant species in inlet

surficial sediments. The dominant inorganic P fractions were HCl-P and NaOH-P, indicating that most of the inorganic P was associated with iron, aluminum, and calcium compounds. NH_4Cl -P accounted for < 5 percent of the sediment inorganic P. In general, mean concentrations of sediment total P,

Sediment P Fraction	Mean, mg/g dry weight	1 S.E.
Loosely Bound P (NH ₄ Cl-P)	0.031	0.004
Fe- and Al-Bound P (NaOH-P)	0.444	0.014
Ca-Bound P (HCl-P)	0.506	0.020
Total Inorganic P	0.981	0.019
Total Organic P	0.411	0.017
Total P	1.392	0.019

NH₄Cl-P, and NaOH-P were low ($p < 0.05$; t-test; SAS 1988) when compared with mean concentrations estimated for a variety of lakes in eastern North America (Ostrofsky 1987).

Sediment P Release as a Function of pH and Redox Conditions

Rates of P release from littoral sediments measured in the laboratory increased significantly ($p < 0.05$; ANOVA; SAS 1988) as a function of elevated pH under oxic conditions (Table 5). The method of pH adjustment was

Redox (pH Method)	pH	Mean Rate (mg m ⁻² d ⁻¹)	1 S.E.	ANOVA
Oxic	8.5	3.4	0.4	d
Oxic (CO ₂ Removal)	9.1	7.1	1.9	c
Oxic (NaOH Addition)	9.0	10.6	1.3	b
Oxic (NaOH Addition)	10.0	26.4	1.8	a
Anoxic	9.0	23.0	1.7	a

Note: Rates of P release were measured in the laboratory under different pH and redox conditions. Under oxic conditions, pH was adjusted to about 9 and 10 by additions of 0.1 N NaOH (NaOH addition). The pH was also adjusted to about 9 under oxic conditions by removal of CO₂ from the overlying water (CO₂ removal). The method of pH adjustment is indicated in parentheses for each redox treatment. Different letters indicate significant differences ($p < 0.05$; ANOVA; Duncan's Multiple Range Analysis; SAS 1988) between treatments. Rates of P release were logarithmically transformed prior to statistical analysis to stabilize the variance.

an important factor, as rates of P release were significantly greater when NaOH was used to adjust the pH to about 9.0 rather than using CO₂-free air. The rate of P release increased linearly as a function of pH (Rate of P Release, milligrams per square meter per day = pH(13.8) - 122.3; R² = 0.83; SAS 1988) over values ranging from 8.5 to about 10.0 adjusted via additions of NaOH. The mean rate of P release from littoral sediments (at pH 9.0) was markedly higher (p < 0.05; ANOVA; SAS 1988) under anoxic conditions than under oxic conditions (Table 5).

Marked seasonal variations in DO and pH occurred in the inlet region during April through September. Mean daily pH increased to a peak of 9.9 in late May and then remained near 9 (except during storms) between June and September (Figure 4a). Notably, pH minima in late April, early August, and late September coincided with elevated storm inflows to the inlet region. The mean daily pH for the entire study period was 8.9 (range = 7.7 to 9.9). Anoxic conditions occurred on 21 days during the study period, primarily in June and late July (Figure 4a) and averaged about 4.8 hr per day (range = 2.4 to 14.4 hr).

Estimated daily rates of P release from the littoral sediments fluctuated between April through early June primarily as a function of pH, reaching a peak of 11.5 mg m⁻² d⁻¹ (Figure 4b). In mid and late June and late July, estimated daily rates of P release were more strongly influenced by the occurrence of anoxic conditions. A maximum rate of 15.7 mg m⁻² d⁻¹ was estimated for 07 July, when anoxic conditions prevailed for about 14 hr. Overall, the estimated mean rate of P release from the littoral sediments in the inlet region of Lake Delavan was 5.7 mg m⁻² d⁻¹ (range = 0 to 15.7 mg m⁻² d⁻¹; 1 S.E. = 0.2), or about 3.4 kg P d⁻¹ over the entire surface area.

Pore water concentrations of SRP increased from May to a peak in July, then declined and remained nearly constant in August and September (Figure 5). Marked gradients (mean = 1.377 µg/ml · cm; 1 S.E. = 0.154) in SRP concentration occurred across the sediment interface throughout the summer, resulting in the development of high concentrations of SRP in the overlying water at a depth of 1 cm above the sediment-water interface (range in SRP = 0.116 to 7.215 mg/l; mean = 1.552; 1 S.E. = 0.253).

Mean Fickian diffusional fluxes, representing an average over the deployment period, exhibited a seasonal pattern, with rates increasing to a maximum in late June, coincident with the occurrence of frequent anoxia, and then declining to a fairly uniform rate of 5 to 7 mg m⁻² d⁻¹ from July through September (Table 6). Only in May was the mean Fickian diffusional flux significantly lower than the estimated laboratory rate of P release (Table 6; p < 0.05; t test; SAS 1988). This discrepancy occurred during a period when mean water temperature in the inlet was approximately 4 °C cooler (15.7 °C) than the temperature of 20 °C used for incubating the laboratory sediment systems, suggesting possible temperature effects. Otherwise, there were no significant differences (p > 0.05; t test; SAS 1988) between results of the two methods for estimating rates of P release.

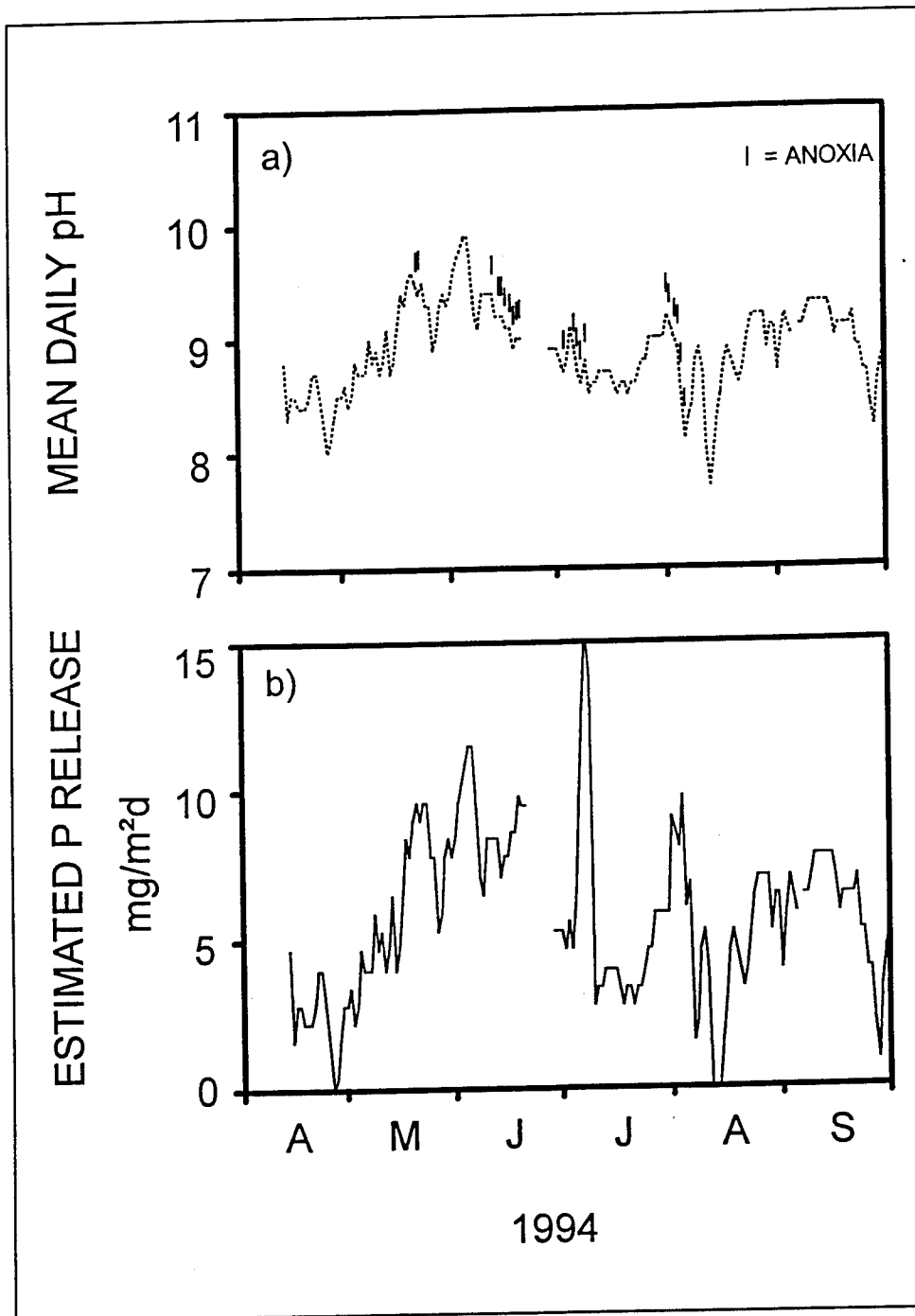


Figure 4. Seasonal variations in (a) mean daily pH and occurrence of anoxia (dissolved oxygen < 0.5 mg l⁻¹) and (b) estimated rates of P release from littoral sediments of inlet region (Rates of P release were estimated from ranges measured in laboratory sediment systems under different redox and pH conditions and from in situ records of pH and dissolved oxygen in inlet region)

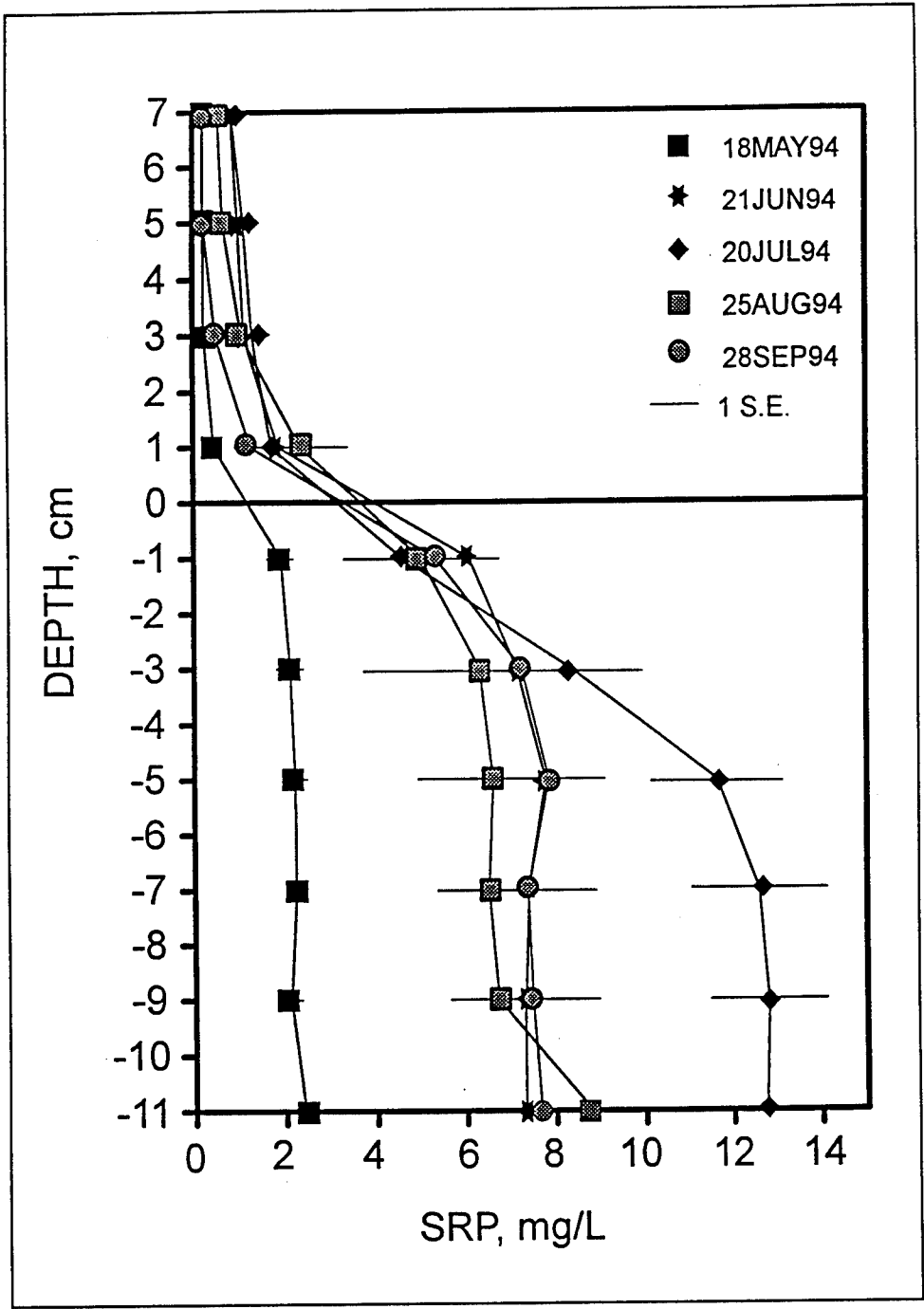


Figure 5. Seasonal variations in mean (± 1 S.E.; $n = 7$ to 9) concentrations of soluble reactive phosphorus measured in situ at 2-cm intervals above and below sediment interface in inlet region of Lake Delavan

Table 6
A Comparison of Mean (± 1 S.E.) Seasonal Variations in Rates of P Release Measured Using Sediment Peepers and Laboratory Sediment Systems

Deployment Period	Sediment Peeper Rate $\text{mg m}^{-2} \text{d}^{-1}$	Laboratory Rate $\text{mg m}^{-2} \text{d}^{-1}$
02-18 May	2.6 (0.4)	5.0 (0.4)
08-21 Jun	8.6 (1.3)	8.4 (0.3)
05-20 Jul	4.6 (1.4)	5.8 (1.1)
03-25 Aug	4.5 (1.6)	4.2 (0.5)
14-28 Sep	6.5 (1.5)	5.3 (0.5)

Note: Rates of P release from sediment peepers were calculated as Fickian diffusional fluxes, using a diffusion coefficient corrected for mean in situ water temperature (Krom and Berner 1980). Rates of P release from laboratory sediment systems, determined at a water temperature of 20 °C, were estimated over the ranges of mean daily pH and redox conditions of the inlet region of Lake Delavan (see methods) during the sediment peeper deployment periods.

4 Discussion

It is widely recognized that elevated hydroxyl ion concentrations (high pH) in lake water can have a strong influence on rates of P release from sediments, especially under oxic conditions, by enhancing the desorption of P via ligand exchange on iron hydroxide particles (Andersen 1975; Lee, Sonzogni, and Spear 1977; Lijklema 1980; Boström, Jansson, and Forsberg 1982; Boström et al. 1988; Drake and Heaney 1987; Jenson and Anderson 1992). The sediment fraction that is most likely mobilized at high pH values is the NaOH-extractable fraction (Boström 1984), which is prevalent, although not unusually high in concentration, in the inlet region of Lake Delavan. This mechanism of P release from sediments, coupled with high productivity by aquatic plants (macrophytes and periphyton) in littoral regions, can result in considerable internal P loading to lakes and reservoirs (James and Barko 1991, 1993).

Adjustments in pH via additions of NaOH to experimental laboratory systems were found to result in significantly greater rates of P release from sediments than pH adjustments via removal of CO₂. Boers (1991) contends that the former technique of pH adjustment can artificially stimulate P release from sediments by increasing alkalinity and flux of hydroxyl ions into the sediment, whereas the latter technique more closely simulates the effects of aquatic plant photosynthesis on pH and alkalinity. Results of this study appear to support this contention as well, as pH adjustments from 8.5 to 9.0 via CO₂ removal resulted in only a doubling, while pH adjustments to 9.0 via additions of NaOH resulted in a tripling of mean rates of P release from sediments.

As oxic conditions prevailed throughout most of the summer in the inlet region, marked fluctuations in pH occurred, which significantly affected rates of P release from the littoral sediments, probably because of macrophyte (and periphyton) metabolism. As anoxia occurred in the inlet region, estimated rates of P release from littoral sediments were extremely high, significantly greater ($p < 0.05$; *t* test; SAS 1988) than rates observed from profundal sediments of a variety of eutrophic lakes (Nürnberg et al. 1986).

Rates of P release from littoral sediments, combined here with *in situ* measurements of pH and DO, provided valuable information on the dynamic nature of P mobilization, which to the knowledge of these authors has not been demonstrated as a function of these variables in such detail before. However, the predictive model could have been improved somewhat with attention to the

potential effects of water temperature on P release from sediments, as has been demonstrated by others (Jenson and Andersen 1992). Nevertheless, in this study, seasonal patterns in laboratory-estimated rates of P release from littoral sediments were very similar to the rates based on Fickian diffusional fluxes measured in situ during the warm summer months (June through September). Thus, these two methods of measuring P release from sediments appear to provide comparable results under similar temperature, pH, and DO regimes.

These authors estimate that submersed plants (including duckweed and filamentous algae) in the inlet region incorporated a maximum of about 600 kg of P into their tissues during the summer, which can potentially be recycled to the water column during senescence (Carpenter 1980; Smith and Adams 1986). Since rooted macrophytes represented 70 percent of the total submersed plant P pool, these authors suggest that much of this P was derived directly from the sediment via root uptake (Barko and Smart 1980; Carignan and Kalff 1980; Barko and Smart 1981; Smith and Adams 1986). This mass of P in rooted plant tissues was approximately equivalent to P release from sediments of the inlet region (at 3.4 kg day^{-1}) between April and September 1994. Together, plant tissue P plus P released from sediments amounted to about twice the external P load contributed to the inlet by Jackson Creek during the same period in Lake Delavan (Holmstrom, Kammerer, Ellefson 1995). Clearly, internal P loads generated in the littoral zone, even those under oxic conditions, can be high and play an important role in the P budget of this and other aquatic systems.

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