The role of submerged macrophyte beds in phosphorus and sediment accumulation in Lake Memphremagog, Quebec, Canada

Neil Rooney,[1] *Jacob Kalff, and Catherine Habel*

Department of Biology, McGill University, 1205 Av. Drive, Penfield, Montreal, Quebec H3A 1B1, Canada

Abstract

The relationships between long-term (~115-year) phosphorus and sediment accumulation and submerged macrophyte biomass were determined both within a submerged macrophyte bed and among beds in Lake Memphremagog, Quebec, Canada. Strong relationships between present submerged macrophyte biomass and littoral-zone sediment and phosphorus accumulation rates both within and among macrophyte beds yielded simple models for estimating long-term littoral-zone accumulation rates. Mean sediment particle size at the depth of maximum submerged macrophyte biomass, estimated from water content, was comparable with the mean particle size in profundal zone of Lake Memphremagog, suggesting that energy environments differ little between vegetated littoral zones and profundal zones. The mean total sediment-accumulation rate of 1.2 mm yr^{-1} in the macrophyte beds was indistinguishable from average profundal rates of sediment accumulation in North American lakes. Although dense beds accumulated twice as much bulk sediment per unit area (g m^{-2} yr^{-1}) compared with their profundal counterparts, phosphorus accumulation per unit bulk sediment in macrophyte beds with a biomass of 1,000 g m^{-2} (wet weight) was one sixth that measured in profundal sediments, pointing to large postdepositional losses of sedimented phosphorus (>70%) from macrophyte beds. Finally, extrapolation of the present results to five nearby lakes suggests, based on still-limited data, that, in lakes in which half of the sediment surface is colonized by submerged macrophytes, the littoral zone accounts for roughly one third of whole-lake phosphorus and two thirds of whole-lake bulk sediment accumulated annually.

The distribution, transport, and ultimate fate of sediments have large effects on phosphorus (P) cycling in lakes (Canfield et al. 1982; Kalff 2001). With respect to the composition and long-term accumulation of sediments, stratified lakes can be divided into three zones. The zone of sediment accumulation (ZSA) located in deep sites of low underwater slope and energy is dominated by fine, low-density inorganic and organic particles (Håkanson and Jansson 1983; Rowan et al. 1992*a*), and is characterized by disproportionately high rates of sediment accumulation. Located just above the ZSA is the zone of discontinuous sediment accumulation (ZDA), where the accumulation of fine sediment particles is interrupted by periodic resuspension and transport during rare storm events. Finally, the zone of sediment erosion (ZSE), located in high-energy, shallow environments, is characterized by coarse-grained, dense inorganic sediments and low sediment-accretion rates. This pattern, however, does not hold where the littoral zone is colonized by submerged vegetation (James and Barko 1990; Benoy and Kalff 1999; Bindler et al. 2001).

Submerged macrophytes modify near-bed water flow and sediment composition, increasing the sedimentation rates of fine inorganic and organic particles, and associated nitrogen, phosphorus, and trace metals (Petticrew and Kalff 1992; Sand-Jensen 1998; Benoy and Kalff 1999). Long-term sediment-accumulation rates measured over periods of decades to centuries are therefore high within the low-turbulence vegetated littoral zone, declining sharply to a minimum in the zone of highest turbulence beyond macrophyte beds, and rising to a second maximum in deeper profundal regions of lakes and reservoirs characterized by low turbulence (Moeller and Wetzel 1988; James and Barko 1990). The role of macrophyte beds in long-term sediment accumulation and retention was dramatically demonstrated during the eutrophication of Lake Constance when an increase in algal turbidity lead to the disappearance of beds, and the loss of the extensive sediment shelves deposited over centuries, as the result of increased nearshore turbulence (Schröder 1988). Apparently, only one study has examined relationships between macrophyte bed characteristics and long-term sediment accumulation. In Lake Memphremagog, Quebec, total, bulk, organic, and anthropogenic lead accumulation rates at the depth of maximum submerged macrophyte biomass (MSMB) rise linearly with plant biomass (g m^{-2}) and biomass density (g m^{-3}) (Benoy and Kalff 1999). Increased long-term sediment accumulation in macrophyte beds results from the deposition and retention of water column and catchment-derived particles as well as the production and retention of organic matter produced within the littoral zone by macrophytes and periphyton. Because these processes result in the import of external P to macrophyte beds, the extent to which such beds accumulate and retain P should be a function of macrophyte bed attributes such as biomass and biomass density.

Both biomass and biomass density vary within macro-

phyte beds. Submerged macrophyte distribution in larger lakes is limited by turbulence near shore (Chambers and Kalff 1987) and by light in deeper water (Chambers and Kalff 1985). Within beds, slope, sediment characteristics, and the light regime interact to determine plant biomass and its distribution (Duarte and Kalff 1986; Anderson and Kalff 1988). With plant biomass attributes being the primary determinant of lead and sediment accrual among beds, determined at the depth of maximum submerged macrophyte biomass (Benoy and Kalff 1999), it seems plausible that there be an equivalent link between plant biomass and the sediment and P accumulation rates not only at the depth of MSMB but also at different depths within macrophyte beds. As much of the P entering lakes is sorbed to particles (Prairie and Kalff 1988) or converted to particulate form by organisms, littoral-zone sediment accumulation should be linked to P accumulation. Moreover, the extent to which macrophyte beds are a sink for P should be a function of bed characteristics such as biomass and biomass density.

It is clear that submerged macrophyte beds can act as a source or sink of P depending on the stage of plant development (Granéli and Solander 1988; Barko and James 1998). However, most studies that have quantified the influence of submerged macrophyte beds on P cycling have been carried out over short time periods (weeks–months) during the growing season only, ignoring nutrient cycling during the remainder of the year. Yet macrophyte stands are capable of acquiring and retaining nutrients even during periods of ice cover (Wetzel and Søndergaard 1998). One advantage of measuring long-term accumulation rates in macrophyte beds is, therefore, that accumulation outside of the growing season is taken into account. Further, interyear variation in macrophyte biomass and distribution (Rooney and Kalff 2000) and associated sedimentation rates are averaged over longer time periods, allowing for the development of predictive models not confounded by seasonal and interannual variation.

A problem associated with measuring long-term sediment P accrual using a sediment marker technique is the potential mobility of P across the marker in the sediment column (Carignan and Flett 1981), as well as the potential for sediment P loss to the overlying water. Counteracting sediment processes do, however, allow for sediment P immobilization in vegetated sediments. Precipitated calcite in hard-water lakes (Carignan 1985) and iron oxyhydroxide complexes that sorb soluble P in oxygenated surface sediments (see Kalff 2001) help prevent the upward diffusion of soluble P from anoxic sediments below to the overlying water. Retention is further enhanced through a diffusion of dissolved oxygen from plant roots into the surrounding sediments. Thus P, Fe, and Mn retention rates are 2–5 times higher in a *Littorella uniflora* bed than in nearby bare sediments (Christensen et al. 1997). Furthermore, a high C:P ratio observed in littoral sediments (Moeller and Wetzel 1988) points to an incomplete microbial mineralization of the organic matter, shown directly by the presence of plant fragments in macrophyte bed sediments (LaZerte 1983).

Here we use a sediment marker (stable lead) to determine long-term (~115-year) P accumulation within and among Lake Memphremagog macrophyte beds to estimate their im-
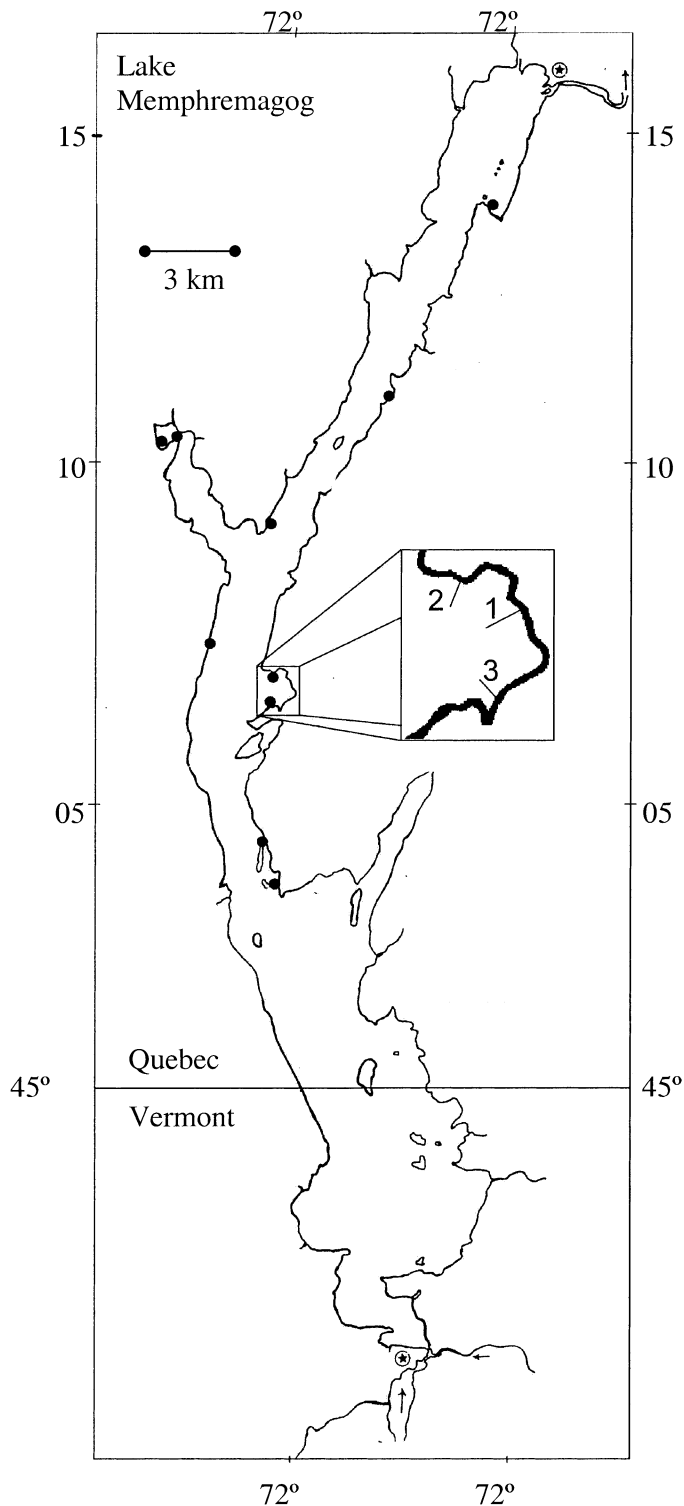

Fig. 1. Map of Lake Memphremagog (Quebec–Vermont), showing study sites. Sites for the among-macrophyte bed portion of the study are shown with black circles, and the site for the within-macrophyte bed portion of the study is shown in the inset.

Table 1. Summary statistics for within and among portions of the study, including mean, minimum, maximum, and standard deviation of all variables measured within and among macrophyte beds in Lake Memphremagog, Quebec.

Variable	Mean		Minimum		Maximum		Standard deviation	
	Among	Within	Among	Within	Among	Within	Among	Within
Mean biomass, g m^{-2}	845	987	78	0	1,767	2,603	567	597
Mean biomass density (g m^{-3})	530	280	39	0	876	759	268	213
Slope (%)	7.9	4.1	2.1	2.7	28.4	7.5	7.4	1.7
Water content (%)	76	68	62	24	88	84	7	18
TSAR, mm yr^{-1}	1.2	1.1	0.1	0	1.8	2.0	0.7	0.5
BSAR g m^{-2} yr^{-1}	588	507	88	0	1,130	1,167	371	248
OSAR g m^{-2} yr^{-1}	57	51	2	0	139	123	47	33
PSAR, mg m^{-2} yr^{-1}	193	246	14	0	498	616	154	149
Min PSAR mg m^{-2} yr^{-1}	114	120	14	0	276	287	100	79

portance as P traps and to use the relationships developed between plant biomass and the specific P and sediment-accumulation rates (mg m^{-2} yr^{-1}) to provide a first estimate of the importance of such beds as sinks for P and sediments. Some of the P in the ~115-year profile may be derived from earlier deposited sediments which, following the deposition of additional sediment, created anoxic conditions that allowed a solubilization and migration within the profile. If so, this would lead to an overestimation of P accumulation unless offset by an equivalent loss of P from the surface sediment to the overlying water as a result of periodic surface sediment anoxia (James et al. 1996). While anoxia is unlikely at the macrophyte densities encountered (Table 1), it cannot be precluded. Not knowing the magnitude of the above processes, we calculate both P accumulation and what we call, for lack of a better term, a minimum P accumulation rate (see Methods and Materials).

The goal of this investigation was to quantify the role of macrophytes in the accumulation of sediments and the infilling of lakes and to test two previously untested hypotheses. The first is that macrophyte biomass and biomass density are linked to long-term P accumulation within and among submerged macrophyte beds. The second is that relationships between macrophyte biomass characteristics and sediment and P accumulation rates at different depths within a single macrophyte bed are not significantly different from those observed among beds at the depth of maximum submerged macrophyte biomass. If correct, this would greatly facilitate the modeling of sediment and P accumulation rates in the littoral zones of lakes.

Methods and materials

Field work was conducted in oligo-mesotrophic Lake Memphremagog (Quebec, Canada–Vermont, USA), which provides a wide variety of littoral environments for comparative work (e.g., Duarte and Kalff 1986; Rasmussen 1988; Benoy and Kalff 1999). Lake Memphremagog is a long (45 km), narrow (1–4 km), and deep ($Z_{mean} = 20$ m, $Z_{max} = 107$ m) dimictic lake (Fig. 1).

Among macrophyte beds—Sampling for the among-bed portion of the study took place in October 1998. Ten sites were selected to examine among-macrophyte bed variation

in sediment and P accumulation patterns (Fig. 1), with the sites a subset of those examined by Benoy and Kalff (1999). Macrophyte biomass (g m^{-2}), biomass density (g m^{-3}), and the depth of the sediment marker (lead horizon, see below) at each of the sites were taken from Benoy and Kalff (1999). We used the biomass data from the previous study for two reasons. First, by October, the biomass of the macrophytes in Lake Memphremagog is far less than peak biomass in August (Jackson et al. 1994). Second, the lack of systematic differences between surface and deeper core sediment characteristics and the absence of discontinuities in Pb profiles are both consistent with the hypothesis that macrophyte beds have remained relatively constant over the past century (Benoy and Kalff 1999), but do not preclude modest interyear differences in macrophyte biomass and linked sediment accumulation.

At each site, sediment cores (tube inner diameter, 5.7 cm, length 70 cm) were collected by SCUBA divers from the depth of maximum submerged macrophyte biomass (MSMB), determined to be 2.7 ± 0.5 m using an empirical relationship between Secchi depth and MSMB derived by Chambers and Kalff (1985). The cores, ranging in length from 3 cm to 25 cm, were immediately returned to the laboratory and extruded using a vertical extrusion system at one of three section intervals (1, 1.5, or 2 cm), with section intervals consistent within cores, to obtain at least 10 sections per core where possible. Sediments were transferred to clean, preweighed 25-ml polyethylene vials and weighed to the nearest 0.1 g to obtain sediment wet weight. Sediments were dried at 85°C until constant weight (~48 h) to determine water content (%) and bulk sediment weight. Subsamples (~1 g) were burned for 2 h at 550°C to determine loss on ignition (LOI) to estimate the organic content (Dean 1974).

Phosphorus (P) analysis was carried out following a modification of the ignition method (Anderson 1976). Between 3 and 10 mg of burnt sediment was boiled in 10 ml of 1 N HCl for 15 min. Each sample was then diluted to 40 ml with double-distilled deionized water and assayed for P using the ascorbic acid method following persulfate digestion (Griesbach and Peters 1991).

Within macrophyte bed—Sampling for the within-bed portion of the study was done in August 1999. Three transects were sampled within a macrophyte bed located in

MacPherson Bay, a large ($\sim$1 km^2) embayment on the eastern shore of Lake Memphremagog (Fig. 1 inset). Macrophyte composition was heterogeneous, with plants nearest the shore dominated by isoetids and sequentially moving away from shore, by *Myriophyllum spicatum, Potamogeton* spp., and *Elodea canadensis*. Sampling for accumulation rates (ARs) and aboveground macrophyte biomass was done at seven sites along each of three transects, for a total of 21 sites. Two (Transect 2, cores 1 and 2, nearest the shore) were later eliminated because they lacked identifiable lead horizons.

Triplicate quadrats (0.25 m^2) were placed at each site, and plant height was measured in situ, providing estimates of macrophyte bed canopy height to be used to calculate macrophyte biomass density (g m^{-3}; Benoy and Kalff 1999). All plants within quadrats were harvested, taken back to the laboratory, and processed within 24 h of collection. Plants were washed free of epiphytes, detritus, and invertebrates; roots were pinched off; and plants were then spun in a lettuce spinner to remove excess water. Plant biomass was weighed to the nearest 0.1 g to obtain fresh weight.

Sediment cores (inner diameter 5.7 cm) were taken from a fourth quadrat at each site. Cores varied in length from 4 to 32 cm. The 19 cores were returned immediately to the laboratory and processed as in the among-macrophyte bed portion of the study (see above).

Sediment analysis—Stable Pb was selected as the most suitable marker for dating sediment cores, as it has been shown to be a replicable and reliable marker for both profundal and littoral sediments in lakes in this region (Blais and Kalff 1995; Benoy and Kalff 1999). The subsurface enrichment of stable Pb is the result of coal burning and mining and smelting activities in southern Quebec and adjacent regions starting in the mid 1880s. Consequently, all ARs are based on a $\sim$115-year interval (Blais et al. 1995; Benoy and Kalff 1999). There is a high degree of agreement between accumulation rates determined using stable lead and other markers (^{210}Pb, *Ambrosia* pollen, ^{137}Cs) in Quebec and Ontario lakes (Blais and Kalff 1995).

All laboratory glassware used for Pb analysis was acid washed in 15% HCl and twice rinsed in double-distilled deionized water. All reagents were AnalaR grade acids from BDH. Dried sediment samples ($\sim$1 g) were crushed by mortar and pestle and digested in a dilute aqua regia (3HCl: 3H$_2$O: HNO$_3$) at 85°C for 1 h. After digestion, samples were cooled and brought to a final volume of 25 ml in polyethylene volumetric flasks using double-distilled deionized water. Samples were centrifuged at 3,000 rpm for 10 min to remove suspended solids. Concentrations of Pb were measured using a flame atomic absorption spectrometer (Perkin Elmer 3100). Pb extraction efficiencies were assessed using standard reference material (Buffalo River sediment, No. 2704, U.S. National Bureau of Standards). The extraction efficiency of the medium for Pb was 100%, and the extraction reproducibility was 10%, both of which are within limits set by the U.S. National Bureau of Standards.

Accumulation rate determination—The depth used to calculate accumulation rates (ARs) was, as in Blais et al. (1995)

and Benoy and Kalff (1999), the point in the sediment profile where anthropogenic Pb burden was greater than background burden by a factor of two. When two or more points of inflection were encountered in cores, shallower rather than deeper points were selected to avoid artificially inflating of the depth of the sediment marker.

Five measures of accumulation were used. Total sediment-accumulation rate (TSAR, mm yr^{-1}) refers to the depth of material that has accumulated with respect to the lead horizon. TSAR was corrected for compaction by using elastic bands placed at the sediment–water interface at the time of core collection to indicate the difference between the sediment depth in the core tube and the surrounding sediment. The undisturbed depth of sediments accumulated since the 1880s was calculated as the sum of the sediment sections from the surface down to and including the section at the inflection point (in mm) multiplied by the distance from the elastic band to the bottom of the core tube divided by the distance from the top of the sediments to the bottom of the core tube. The average TSAR (mm yr^{-1}) was obtained by dividing the above-corrected depth (mm) by 115 yr.

The bulk sediment-accumulation rate (BSAR) was calculated by summing the dry weights (g) of the sediment sections again from the surface down to and including the section at the inflection point. Because the tube had an area of 25.5 cm^2, the sum was multiplied by 392 to convert to m^2 and divided by 115 yr to obtain the average BSAR (g m^{-2} yr^{-1}). The organic sediment-accumulation rate (OSAR) was found in the same manner but summing the loss on ignition values for each section instead of the dry weights.

Two measures of phosphorus accumulation were developed. The phosphorus sediment-accumulation rate (PSAR) was calculated by multiplying the bulk dry weight (g) times the sediment P content (mg g^{-1}) for each section, again starting at the sediment surface down to and including the section at the inflection point. The values were summed, multiplied by 392, and divided by 115 yr to find the average PSAR (mg m^{-2} yr^{-1}). The minimum phosphorus sediment-accumulation rate (MinPSAR) was calculated by multiplying the background concentration of P (mg g^{-1}) as determined by the deep ($>$115 yr) portion of the cores (Fig. 2b) by the BSAR. Like the PSAR, the units are in mg m^{-2} yr^{-1}.

Statistical analyses were performed using SYSTAT software (1998). Correlation and regression analysis were used to develop predictive models for the measured accumulation rates as a function of macrophyte biomass.

Results

The large ranges of underwater slope, biomass, and sediment water content show that a wide variety of littoral environments were considered (Table 1). Including all sediment cores, peak Pb concentrations (mean = 20.4 μg g^{-1}, SE = 9.2, n = 19) were significantly higher than background levels (mean = 8.8 μg g^{-1}, SE = 5.9, n = 19) according to a paired *t*-test ($P < 0.0001$). Figure 2 shows profiles of Pb, organic content, and P in sediment cores taken at different sites from the within-macrophyte bed portion of the study.

Macrophyte bed sediment-accumulation rates were com-
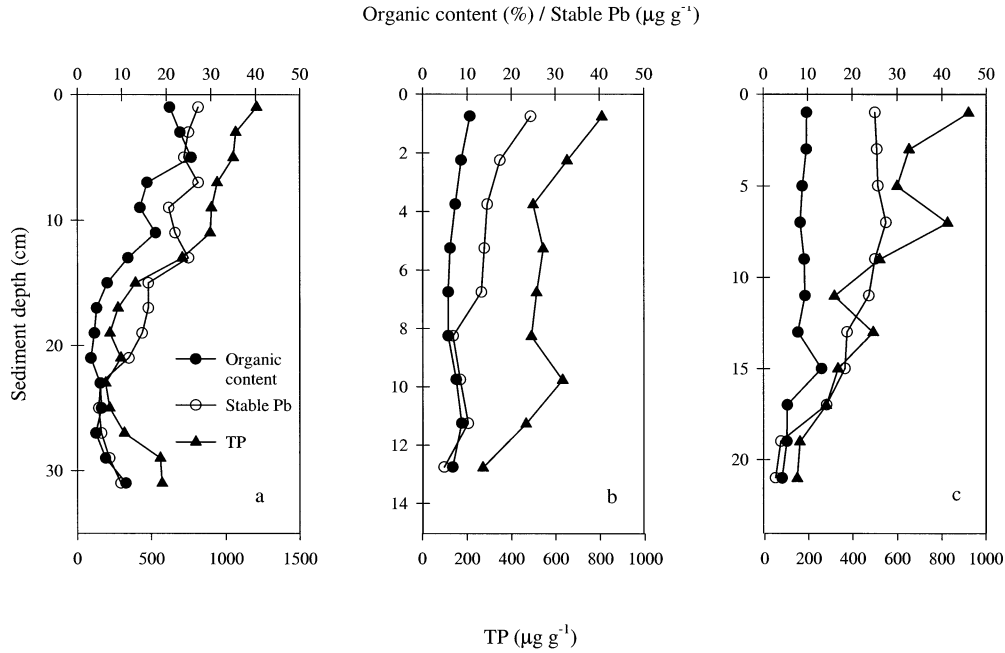
Organic content (%) / Stable Pb (µg g⁻¹)

Fig. 2.   Three example profiles taken from the within-macrophyte bed portion of the study: (a) transect 1, quadrat 5; (b) transect 2, quadrat 6; (c) transect 3, quadrat 2. Figures for each site include organic content (%), Pb concentrations (μg g^{-1}), and TP concentration (μg g^{-1} dry weight).

parable among the three within-bed transects measured. In general, macrophyte biomass increased from the near-shore sites to a peak in the center (and densest portion) of the bed, and then declined toward the open water (Fig. 3a–c). Sediment ARs followed a similar pattern, with most rates attain-

ing their highest values in the middle (densest portion) of the macrophyte bed (Fig. 3d–i).

Of the three predictor variables (biomass, biomass density, and underwater slope), only biomass was coupled to within-macrophyte bed sediment accumulation (Table 2). Sediment
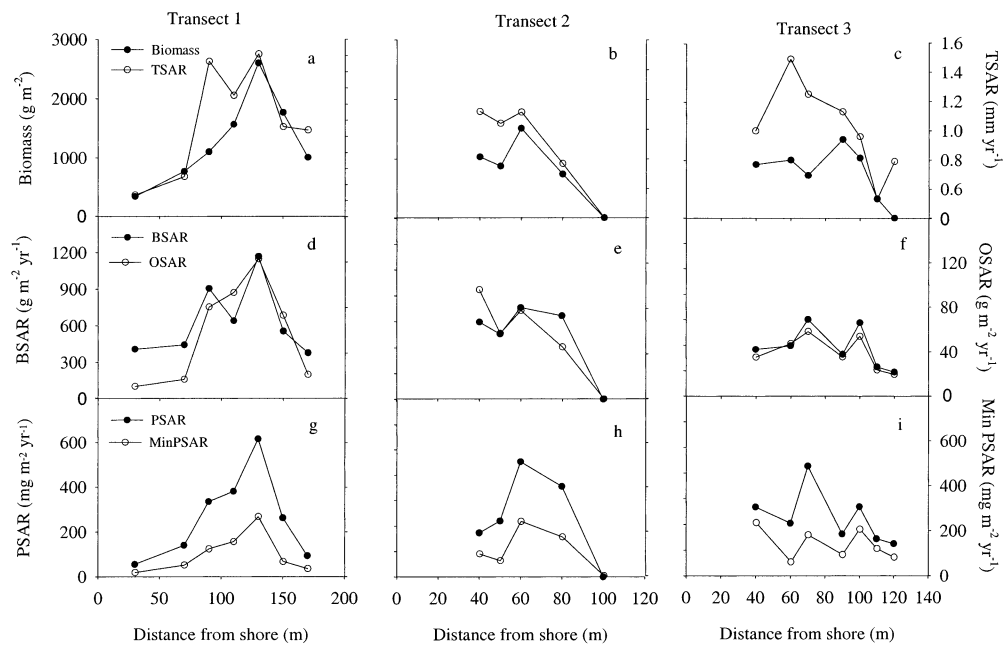
Fig. 3.   Relation of macrophyte bed characteristics to distance from shore for each of the three transects. The top row (a, b, c) shows macrophyte biomass and total sediment-accumulation rate (TSAR). The second row (d, e, f) shows bulk (BSAR) and organic (OSAR) sediment-accumulation rates. The third row (g, h, i) shows phosphorus (PSAR) and minimum phosphorus (MinPSAR) sediment-accumulation rates. See text for explanation of abbreviations.

Table 2. Correlation matrix of all measured variables from the within-macrophyte bed portion of the study.

	Biomass	Biomass density	Slope	Water content	TSAR	BSAR	OSAR	PSAR	MinPSAR
Biomass	1.00								
Biomass density	—	1.00							
Slope	—	—	1.00						
Water content	0.52*			1.00					
TSAR	0.73***	—	—	0.77***	1.00				
BSAR	0.79***	—	—	0.48*	0.78***	1.00			
OSAR	0.82***	—	—	0.70**	0.88***	0.86***	1.00		
PSAR	0.74***	—	—	0.61**	0.72**	0.86***	0.81***	1.00	
MinPSAR	0.54*	—	—	0.52*	0.52*	0.64**	0.60**	0.85***	1.00

— Not significant.
* $P<0.05$.
** $P<0.01$.
*** $P<0.001$.

water content (%) was correlated with biomass and accumulation rates (Table 2). Organic sediment accumulation (OSAR) showed the highest correlation with biomass, whereas MinPSAR was least correlated, although the correlation coefficient was significant at the $P = 0.05$ level (Table 2). Whereas neither underwater slope nor biomass density were linked to any of the ARs, all accumulation rates were correlated with each other (Table 2).

Among beds, biomass was again the overall best predictor of ARs, being significantly related to TSAR, OSAR, PSAR, and MinPSAR (Table 3). Water content was not significantly correlated with biomass or any ARs among sites. Biomass density (g m^{-3}) was correlated only with TSAR (Table 3). As in Table 2, variation in underwater slope was too small to allow it to be a significant predictor of any ARs.

ANCOVA of the within and among portions of the study showed no significant differences between grand means and slopes of the relationships between biomass and sediment ARs for TSAR, BSAR, and PSAR (Fig. 4a,b,d), allowing the data to be pooled for regression analysis.

Linear regression analysis was used to construct models predicting sediment accumulation within macrophyte beds, among macrophyte beds, and for pooled data where AN-COVA allowed. Biomass was a significant predictor of all

ARs within the bed, accounting for the largest variation in OSAR, followed by BSAR, PSAR, TSAR, and finally MinPSAR (Table 4). Prediction of ARs among beds was generally better than those within the single bed, with the exception of BSAR (Table 4). Pooling data from the two portions of the study decreased the SE$_{est}$ and increased significance of the regression models for TSAR and PSAR, although it did not increase the R^2 of the relationships (Table 4).

Discussion

The results show macrophyte biomass to be a good predictor of long-term sediment and phosphorus (P) accumulation in the littoral zone of Lake Memphremagog. It is particularly noteworthy that models predicting among-bed total (TSAR), bulk (BSAR), and P (PSAR) measured at the depth of maximum submerged macrophyte biomass (MSMB) do not differ significantly from the within-macrophyte bed ARs measured over a similar range of biomass (Fig. 4). This shows accumulation rates (ARs) to be a function of local biomass rather than of where along transects within a bed or where in the lake measurements were made. That patterns among macrophyte beds emerged despite having combined

Table 3. Correlation matrix of all measured variables from the among-macrophyte bed portion of the study.

	Biomass	Biomass density	Slope	Water content	TSAR	BSAR	OSAR	PSAR	MinPSAR
Biomass	1.00								
Biomass density	—	1.00							
Slope	—	—	1.00						
Water content	—	—	—	1.00					
TSAR	0.81*	0.72*	—	—	1.00				
BSAR	—	—	—	—	0.81*	1.00			
OSAR	0.87**	—	—	—	0.89**	—	1.00		
PSAR	0.79*	—	—	—	0.90**	0.76*	0.92**	1.00	
MinPSAR	0.92**	—	—	—	0.83*	—	0.94***	0.93**	1.00

— Not significant.
* $P<0.05$.
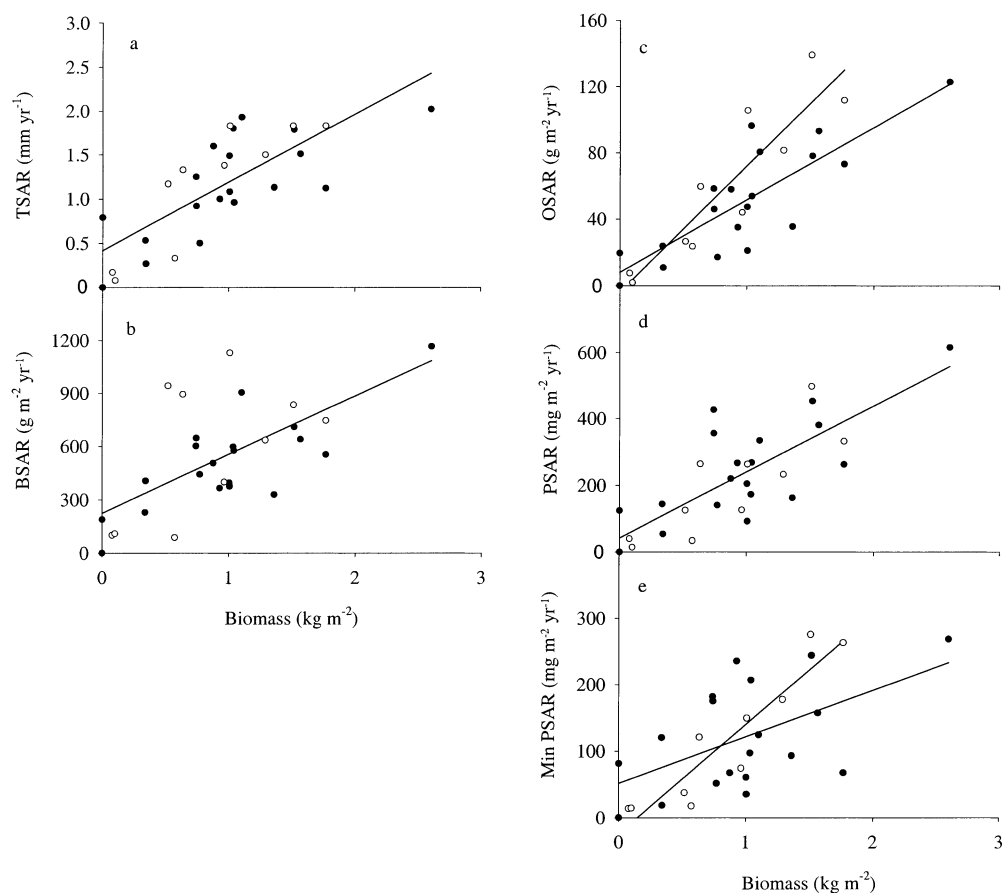** $P<0.01$.
*** $P<0.001$.

Fig. 4. Bivariate plots of the relationship between five SARs and macrophyte biomass. Black circles represent measurements for the within-macrophyte bed portion of the study and open circles represent measurements taken among macrophyte beds at the depth of maximum submerged macrophyte biomass. (a) Total sediment-accumulation rate (TSAR), (b) bulk sediment-accumulation rate (BSAR), (c) organic sediment-accumulation rate (OSAR), (d) phosphorus sediment-accumulation rate (PSAR), and (e) minimum phosphorus sediment-accumulation rate (MinPSAR). Linear regressions are plotted for pooled data when allowed for by ANCOVA, and separately for each portion of the study when slopes are significantly different. Regression equations are given in Table 4.

sediment core data collected in 1998 with macrophyte biomass data collected 3 yr earlier (Benoy and Kalff 1999) is an indication of the robustness of the relationships.

The total sediment-accumulation rate (TSAR) is low ($\sim$0.4 mm yr^{-1}), but not negligible, just outside macrophyte beds, rising systematically with increasing plant biomass to a maximum of nearly 2 mm yr^{-1} in the densest beds (Fig. 4a). The overall average TSAR (1.2 mm yr^{-1}, SD = 0.55) was indistinguishable from the average profundal TSAR reported by Blais (1995) for 143 North American lakes (1.4 mm yr^{-1}, SD = 0.56). Littoral TSARs are sufficient to have a large impact on shallow embayments of Lake Memphremagog and the morphometry of lakes with large shallow water zones. A large impact of macrophyte beds on the long-term accumulation of sediment was observed in Lake Constance, on the border of Germany, Switzerland, and Austria, following eutrophication. The increased turbidity led to the disappearance of submerged macrophyte beds, increased littoral-zone turbulence, and the loss of sediments accumulated by macrophyte beds over millennia (Shröder 1988). Based

on the underwater emergence of a near-shore Neolithic house (2800 B.P.) following the loss of 1.5–2 m of sediments, we estimated the loss of sediment to represent a long-term accumulation of $\sim$0.5–0.7 mm yr^{-1}, a rate sufficient to modify lake geomorphometry over millennial time scales. Lakes therefore fill in not only in the profundal zone but also from the edges in littoral regions with slopes of less than 15% where submerged macrophyte beds establish (Duarte and Kalff 1986). Given time, macrophyte beds therefore act as "biological engineers," using a term coined by Sand-Jensen (1997) with reference to seasonal effects of macrophytes on lowlands streams, but here applied to their long-term impact on lakes.

The minimum estimate of P accumulation (MinPSAR) places a lower limit on the amount of P accumulated during the past 115 yr because, with a known mobility of P, at least following complete mixing of sediments (Carignan and Flett 1981), there is a possibility that some of the total P accumulated (PSAR) is the result of a migration from below the lead horizon. However, if P mobility was responsible for the

Table 4. Regression models of sediment accumulation rates (SARs) with macrophyte biomass as the independent variable. Models are given for within-macrophyte bed, among-macrophyte beds, and where allowed by ANCOVA, the pooled data. SE_{est} is the standard error of the estimate for each model. Significant intercepts for the models are denoted with an asterisk. Units are biomass (kg m^{-2}), total SAR (mm yr^{-1}), bulk SAR (g m^{-2} yr^{-1}), organic SAR (g m^{-2} yr^{-1}), phosphorus SAR (mg m^{-2} yr^{-1}), and min phosphorus SAR (mg m^{-2} yr^{-1}).

Dependent variable	n	Coefficient (biomass)	SE_{est}	Intercept	R^2	Regression P value
Total SAR						
Within	19	0.67	0.15	0.49*	0.50	<0.001
Among	10	1.05	0.21	0.24	0.73	<0.001
Pooled	29	0.77	0.13	0.42	0.57	<0.001
Bulk SAR						
Within	19	330	63	181*	0.59	<0.001
Among	ns	ns	ns	ns	ns	ns
Pooled	29	330	75	225	0.39	<0.001
Organic SAR						
Within	19	44	7.4	8.1	0.65	<0.001
Among	10	76	12.5	−4.0	0.80	<0.001
Pooled	nd	nd	nd	nd	nd	nd
Phosphorus SAR						
Within	19	184	40	65.3	0.53	<0.001
Among	10	225	53	2.6	0.65	0.003
Pooled	29	198	31	42.1	0.58	<0.001
Min Phosphorus SAR						
Within	19	70	26	51.4	0.25	0.016
Among	10	164	23	−24.4	0.84	<0.001
Pooled	nd	nd	nd	nd	nd	nd

ns, not significant; nd, not done.

observed biomass–PSAR relationships, one would expect macrophyte biomass and background P concentration (>115 yr) to be correlated, which they were not ($r = -0.2$, $P = 0.43$). Further, PSAR was better correlated with other measures of sediment accumulation than was MinPSAR (Table 3), indicating that the total P accumulated during the 115-yr period was associated with sedimenting particles. Even though MinPSAR sets a lower limit on P accumulation, estimates were of the same magnitude as those of PSAR (Table 1), both showing macrophyte beds to be long-term net sinks for P.

The high correlation between P accumulation rates and the other measures of sediment accumulation (TSAR, BSAR, OSAR; Tables 2 and 3) shows P accumulation to be closely linked to other long-term rates of littoral-zone sedimentation. Yet within individual cores, the amount of P (g m^{-2}) per stratum was not correlated with bulk sediment (g m^{-2}) for pooled strata ($r = 0.01$, $p = 0.93$), indicating that P accumulation is decoupled from the physical building of the sediments. The decoupling reflects an increase in bulk weight per stratum in deeper sections as a result of compaction, and a decrease in [P] (μg g^{-1}) with increasing sediment depth, presumably the result of an upward diffusion of soluble P under anoxic conditions in deeper sediment (Carignan and Flett 1981) and high rates of P recycling at the sediment water interface. With the largest pool of P near the sediment surface (Fig. 2), P is susceptible to loss to the overlying water, resulting from surface sediment anoxia (James et al. 1996) or biological activity at the sediment–water interface (see below). Nonetheless, the results show that, over long

periods, increased sedimentation of particles and associated P is proportional to macrophyte biomass and outweigh P losses (Fig. 4e).

Submerged macrophytes not only influence sedimentation rates (Benoy and Kalff 1999) but also surficial sediment particle-size distribution, with plant surface area a significant predictor of surface sediment clay content (Petticrew and Kalff 1992). This finding is particularly relevant because small particles with their large surface area to volume ratio disproportionately sorb P (Clay and Wilhm 1979). An analysis of surficial sediment (0–5 cm) water content allows for a comparison of macrophyte bed sediments with profundal and bare littoral sediments, as water content is an excellent predictor of mean surface sediment particle size (Phi = $-0.93 + 0.09 \times$ water content, $r^2 = 0.93$; Rowan et al. 1992a). The estimated mean sediment particle diameter at higher biomass sites (>1 kg m^{-2}) was 12 μm (range 7–41 μm, $n = 14$) and much closer to reported profundal values averaging 7 μm for glacial lakes in the region (Rowan et al. 1992b) than to bare littoral sediments in Lake Memphremagog (~300 μm, Benoy 1997). Even at lower biomass sites (<1 kg m^{-2}), mean sediment particle size, although much more variable, was much smaller (mean = 52 μm, range 4–323 μm, $n = 15$) than in bare littoral sediment. Consequently, although the finest particles are accumulated in littoral areas of greatest macrophyte biomass, even a modest plant density reduces turbulence sufficiently to allow for the permanent sedimentation of relatively fine particles.

While mean sediment particle size in dense macrophyte beds is similar to that of profundal sediment, there are no-
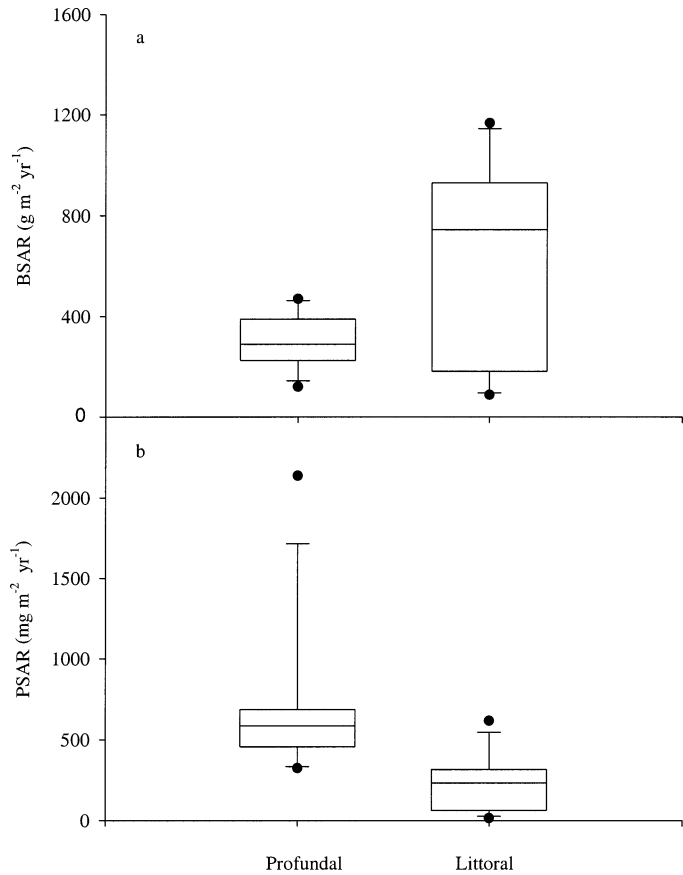
Fig. 5. Box plots of sediment-accumulation rates in the vegetated littoral and profundal zones of Lake Memphremagog. The horizontal bars indicate the median and the 25th and 75th percentiles and the error bars represent the 10th and 90th percentiles for (a) bulk sediment-accumulation rate and (b) phosphorus sediment-accumulation rate. Profundal data from Flett and Marshall (1983).

table differences between ARs in the profundal zone of Lake Memphremagog (Flett and Marshall 1983) and those measured in the macrophyte beds. First, the mean bulk sediment-accumulation rate (BSAR) among beds was more than double that of mean BSARs measured in two profundal basins of Lake Memphremagog, with the densest beds having BSARs almost fourfold higher than mean profundal zone rates (Fig. 5a). In contrast, PSARs in the macrophyte beds

were on average less than half that of profundal rates of P accumulation (Fig. 5b), with only the densest macrophyte beds exhibiting PSARs similar to profundal rates. Therefore, macrophyte beds accumulate far less P per unit bulk sediment than their profundal counterparts even though mean particle size is roughly the same. In fact, P accumulation per unit bulk sediment was more than six times greater in profundal sediments than in dense macrophyte beds (biomass $> 1,000$ g m^{-2}). The fine particles retained in both the macrophyte beds and the profundal zone are, based on the loss on ignition of surface sediments, overwhelmingly inorganic (macrophyte bed mean 12% organic, profundal mean 13% organic; Flett and Marshall 1983). Assuming the origin of these inorganic particles to the catchment (Rowan et al. 1992*b*), and an almost total P retention by the aerobic profundal sediment surface, the much lower PSAR : BSAR ratio in the macrophyte bed cores implies a large P loss following sedimentation in the macrophyte beds. For example, assuming bulk sediment to P ratios of 515 : 1 in Lake Mephremagog (Flett and Marshal 1983), the average macrophyte bed in this study loses about three quarters (range 72%–90%) of sedimented P. Lake Memphremagog macrophyte beds, therefore, by retaining a fraction of incoming P are net sinks, with the balance of the originally sedimented P exported to the open water, linking the littoral and pelagic zones in the process.

Although the mechanisms cannot be resolved here, there are many plausible means for postdepositional export of P from macrophyte beds. Summer organic matter mineralization rates in the warmer littoral zone are about threefold higher than in profundal sediments (den Heyer and Kalff 1998) and, with the highest rates of nutrient recycling at the sediment-water interface, recently sedimented P is rapidly recycled and made available to the algae and bacteria living in or above the sediments of macrophyte beds, leaving behind P-depleted sediments. Furthermore, phosphorus losses from macrophyte beds to the open water can be linked not only to a direct loading from macrophyte bed sediments (James et al. 1996), but also to both the export of macrophyte detritus containing P obtained primarily via root uptake (Carignan and Kalff 1980), and sloughed off periphyton containing, directly or indirectly, sediment-derived P. Finally, fish feeding on the disproportionately abundant macrobenthos (Rasmussen and Rowan 1997; Vadeboncoeur et al. 2002) and horizontally migrating zooplankton (Jeppesen et

Table 5. Morphometric and macrophyte characteristics of five lakes in the Eastern Townships, Quebec, used in the whole-lake sediment accumulation simulation. Estimates of the proportion of bulk (BSAR) and phosphorus (PSAR) are given, using estimates of accumulation in vegetated and bare lake sediments.

| Lake | Measured variables | | | | | Predicted | |
	Area (ha)	Z_{max} (m)	Z_{mean} (m)	% of lake colonized	Mean biomass (g m^{-2})	% BSAR in macrophyte bed	% PSAR in macrophyte beds
Waterloo	150	6	2.9	11	143	26	7
Brome	1,417	12	5.8	18	195	33	10
Magog	927	18	7.7	19	675	35	10
D'Argent	108	16	5.4	28	212	58	23
Hertel	29	9	4.7	66	890	80	47

al. 1999) provide yet another vector for P transport from macrophyte beds to the open water (e.g., Schindler et al. 1996).

While the above discussion addresses specific rates (mg m^{-2} yr^{-1}) of long-term sediment accumulation, the relative importance of littoral and profundal sediments as sites of P accumulation (% zone^{-1}) is a function of lake morphometry and the associated size of the vegetated littoral and the profundal zones. Large and deep Lake Memphremagog is, except for shallow embayments, characterized by generally steep underwater slopes and submerged macrophytes cover <2% of the surface area, making the littoral zone an insignificant sink for P and bulk sediment in absolute terms. The importance of macrophyte beds as net sinks for P and sediment will, on a whole-lake basis, be much greater in shallow lakes with a much larger fraction of the bottom covered by macrophytes.

Whole-lake accumulation rates: An exploration—We extrapolated the per-unit area estimates of littoral and profundal bulk and P accumulation rates as a function of macrophyte biomass in Lake Memphremagog to five nearby lakes for which we collected macrophyte biomass and distribution data (Table 5). The lakes share a similar climate, geology, and land use, but differ appreciably in morphometry and littoral characteristics, thereby providing a first indication of the relative impact of macrophyte beds on sediment accumulation among lakes. The extrapolation, albeit based on a small data set, suggests that macrophyte beds in such lakes could account for more than half of the annual bulk sedimentation when greater than one third of the sediment surface is colonized by submerged macrophytes, with the balance sedimented in the profundal zone. The same analysis for P suggests that macrophytes must cover a much larger fraction (about two thirds) of the sediment surface in such lakes for the littoral zone to retain half of the P accumulated in sediments (Table 5). The primary value of the simple models lies not in the relevance of the estimated impacts to lakes everywhere, but rather to serve as a first indication of the magnitude of macrophyte cover required to have a major impact on sediment and P distribution in lakes. In the same vein, the estimated impacts serve as an indication of the importance of vegetated littoral zones as traps for sediments, nutrients, and contaminants, something generally overlooked as the result of the emphasis in limnology on pelagic zones and profundal sediments.

In summary, our results highlight the importance of submerged macrophyte beds in the long-term accumulation of sediment and P in the near-shore regions of lakes. Although macrophyte beds can act alternatively as sources and sinks of water column P over short time scales (Granéli and Solander 1988; Barko and James 1998), the present study supports the hypothesis that submerged macrophyte beds are net sediment, trace metal (Pb), and P sinks, with rates of total, bulk, organic matter, and P accumulation linked to macrophyte biomass. In general, the relationships between macrophyte biomass and sediment and P accumulation rates at different depths within a single weedbed in Lake Memphremagog are not significantly different from those observed among beds at the depth of maximum submerged macro-

phyte biomass. Although both submerged macrophyte beds and the profundal zone accumulate fine particles, macrophyte beds accumulate far more (bulk) sediment per unit area than their profundal counterparts, while retaining about six times less P per unit bulk sediment (Fig. 5). The results show that macrophyte beds serve as important sediment traps, but that a large portion of initially sediment-associated P is subsequently lost to the open water. Extrapolations of the specific accumulation rates to five nearby lakes for which macrophyte cover is known points to a major role of submerged macrophyte beds in the trapping and cycling of phosphorus in shallow lakes.

References

ANDERSON, J. M. 1976. An ignition method for determination of total phosphorus in lake sediments. Water Res. **10:** 329–331.

ANDERSON, M. R., AND J. KALFF. 1988. Submerged aquatic macrophyte biomass in relation to sediment characteristics in ten temperate lakes. Freshw. Biol. **19:** 115–121.

BARKO, J. W., AND W. F. JAMES. 1998. Effects of submerged aquatic macrophytes on nutrient dynamics, sedimentation and resuspension, p. 197–214. *In* E. Jeppesen, M. Søndergaard, M. Søndergaard, and K. Christofferson [eds.], The structuring role of submerged macrophytes in lakes. Ecological Studies, V. 131. Springer.

BENOY, G. 1997. Sediment accumulation and retention in the littoral zone of lakes. M.Sc. thesis, McGill University.

———, AND J. KALFF. 1999. Sediment accumulation and Pb burdens in submerged macrophyte communities. Limnol. Oceanogr. **44:** 1081–1090.

BINDLER, R., I. RENBERG, M. BRÄNNVALL, O. EMTERYD, AND F. ELDAOUSHY. 2001. A whole-basin study of sediment accumulation using stable lead isotopes and flyash particles in an acidified lake, Sweden. Limnol. Oceanogr. **46:** 178–188.

BLAIS, J. M. 1995. The distribution and dynamics of heavy metals in lake sediments. Ph.D. thesis, McGill University.

———, J. CORNETT, AND R. D. EVANS. 1995. Evaluation of ^{210}Pb dating in lake sediments using stable Pb, *Ambrosia* pollen, and ^{137}Cs. J. Paleolimnol. **13:** 169–175.

———, AND J. KALFF. 1995. The influence of lake morphometry on sediment focusing patterns. Limnol. Oceanogr. **40:** 582–588.

CANFIELD, D. E., J. R. JONES, AND R. W. BACHMAN. 1982. Sedimentary losses of phosphorus in some natural and artificial Iowa lakes. Hydrobiology **87:** 65–76.

CARIGNAN, R. 1985. Nutrient dynamics in a littoral sediment colonized by the submersed macrophyte *Myriophyllum spicatum*. Can. J. Fish. Aquat. Sci. **42:** 1303–1311.

———, AND R. J. FLETT. 1981. Postdepositional mobility of phosphorus in lake sediments. Limnol. Oceanogr. **26:** 361–366.

———, AND J. KALFF. 1980. Phosphorus sources for aquatic weeds: Water or sediment? Science **207:** 987–989.

CHAMBERS, P. A., AND J. KALFF. 1985. Depth distribution and biomass of submersed aquatic macrophyte communities in relation to Secchi depth. Can. J. Fish. Aquat. Sci. **42:** 701–709.

———, AND ———. 1987. Nearshore occurrence of submersed aquatic macrophytes in relation to wave action. Can. J. Fish. Aquat. Sci. **44:** 1666–1669.

CHRISTENSEN, K. K., F. Ø ANDERSEN, AND H. S. JENSEN. 1997. Comparison of iron, manganese, and phosphorus retention in freshwater littoral sediment with growth of *Littorella uniflora* and benthic microalgae. Biogeochemistry **38:** 149–171.

CLAY, E. M., AND J. WILHM. 1979. Particle size, percent organic

carbon, phosphorus, mineralogy, and deposition of sediments in Ham's and Arbuckle lakes. Hydrobiology **65:** 33–38.

DEAN, W. E., JR. 1974. Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: Comparisons with other methods. J. Sediment. Petrol. **44:** 242–248.

DEN HEYER, C. AND J. KALFF. 1998. Organic matter mineralization rates in sediments: A within and among lake study. Limnol. Oceanogr. **43:** 695–705.

DUARTE, C. M., AND J. KALFF. 1986. Littoral slope as a predictor of maximum biomass of submerged macrophyte communities. Limnol. Oceanogr. **31:** 1072–1080.

FLETT, R. J., AND H. MARSHAL. 1983. The accumulation and distribution of phosphorus, organic and inorganic matter in lake sediments as determined by ^{210}Pb. Report to Lake Memphremagog Project, Limnology Research Centre of McGill University.

GRANÉLI, W., AND D. SOLANDER. 1988. Influence of aquatic macrophytes on phosphorus cycling in lakes. Hydrobiology **170:** 245–266.

GRIESBACH, L. R., AND R. H. PETERS. 1991. The effects of analytical variations on estimates of phosphorus concentration in surface waters. Lake Res. Manag. **7:** 97–106.

HÅKANSON, L., AND M. JANSSON. 1983. Principles of lake sedimentology. Springer.

JACKSON, L. J., J. B. RASMUSSEN, AND J. KALFF. 1994. A mass-balance analysis of trace metals in two weedbeds. Water Air and Soil Pollution **75:** 107–119.

JAMES, W. F., AND J. W. BARKO. 1990. Macrophyte influences on the zonation of sediment accretion and composition in a north-temperate reservoir. Arch. Hydrobiol. **120:** 129–142.

———, ———, AND S. J. FIELD. 1996. Phosphorus mobilization from littoral sediments of an inlet region in Lake Delavan. Arch. Hydrobiol. **138:** 245–257.

JEPPESEN, E., T. L. LAURIDSEN, T. KAIRESALO, AND M. R. PERROW. 1999. Impact of macrophytes on fish-zooplankton interactions in lakes, p. 91–114. *In* E. Jeppesen, M. Søndergaard, M. Søndergaard, and K. Christofferson [eds.], The structuring role of submerged macrophytes in lakes. Ecological Studies, V. 131. Springer.

KALFF, J. 2001. Limnology. Prentice Hall.

LAZERTE, B. D. 1983. Stable carbon isotope ratios: Implications for the source of sediment carbon and for phytoplankton carbon assimilation in Lake Memphremagog, Quebec. Can. J. Fish Aquat. Sci. **40:** 1658–1666.

MOELLER, R. E., AND R. G. WETZEL. 1988. Littoral vs profundal components of sediment accumulation: Contrasting roles as phosphorus sinks. Verh. Internat. Verein. Limnol. **23:** 386–393.

PETTICREW, E. L., AND J. KALFF. 1992. Water flow and clay retention in submerged macrophyte beds. Can. J. Fish. Aquat. Sci. **49:** 2483–2489.

PRAIRIE, Y. T., AND J. KALFF. 1988. Particulate phosphorus dynamics in headwater streams. Can. J. Fish. Aquat. Sci. **45:** 210–215.

RASMUSSEN, J. B. 1988. Littoral zoobenthic biomass in lakes, and its relationship with physical, chemical, and trophic factors. Can. J. Fish. Aquat. Sci. **45:** 1436–1447.

———, AND D. J. ROWAN. 1997. Wave velocity thresholds for fine sediment accumulation in lakes, and their effect on zoobenthic biomass and composition. J. N. Am. Benthol. Soc. **16:** 449–465.

ROONEY, N., AND J. KALFF. 2000. Inter-annual variation in submerged macrophyte community biomass and distribution: The influence of temperature and lake morphometry. Aquat. Bot. **68**(4): 321–335.

ROWAN, D. J., J. KALFF, AND J. B. RASMUSSEN. 1992a. Estimating the mud deposition boundary depth in lakes from wave theory. Can. J. Fish. Aquat. Sci. **45:** 1436–1447.

———, ———, AND ———. 1992b. Profundal sediment organic content and physical character do not reflect lake trophic status, but rather reflect inorganic sedimentation and exposure. Can. J. Fish Aquat. Sci. **49:** 1431–1438.

SAND-JENSEN, K. 1998. Influence of submerged macrophytes on sediment composition and near-bed flow in lowland streams. Freshw. Biol. **36:** 663–679.

———. 1997. Macrophytes as biological engineers in the ecology of Danish streams, p. 74–101. *In* K. Sand-Jensen and O. Pedersen [eds.], Freshwater biology—priorities and development in Danish research. University of Copenhagen and G. E. C. Gad Publishers.

SCHINDLER, D. E., S. R. CARPENTER, K. L. COTTINGHAM, X. HE, J. R. HODGSON, J. F. KITCHELL, AND P. A. SORANNO. 1996. Food web structure and littoral zone coupling to pelagic trophic cascades, p. 96–205. *In* G. A. Polis and K. O. Winemiller [eds.], Food webs: Integration of patterns and dynamics. Chapman and Hall.

SCHRÖDER, R. 1988. Sublittoral erosion of Untersee (Lake Constance): Late consequences of eutrophication and hydrological phenomenon. Arch. Hydrobiol. **12:** 265–277.

SYSTAT. 1998. SYSTAT for Windows: Statistics, 9th ed. SYSTAT.

Vadeboncoeur, Y., M. J. Vander Zanden, and D. Lodge. 2002. Putting the lake back together: Reintegrating benthic pathways into lake food web models. BioScience **52:** 44–54.

WETZEL, R. G., AND M. SØNDERGAARD. 1998. Role of submerged macrophytes for the microbial community and dynamics of dissolved organic carbon in aquatic ecosystems, p. 133–148. *In* E. Jeppesen, M. Søndergaard, M. Søndergaard, and K. Christofferson [eds.], The structuring role of submerged macrophytes in lakes. Ecological Studies, V. 131. Springer.