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Sediment accumulation and Pb burdens in submerged macrophyte beds

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Abstract

This study quantifies the role of lake morphometry and submerged macrophyte beds on the accumulation of sediments in the littoral zone. Stable Pb, a historical marker of lacustrine sediments in southern Quebec, was used to date the sediments (~110 yr) and to calculate three long-term sediment accumulation rates (SARs) in Lake Memphremagog (located in Quebec and Vermont). The anthropogenic Pb burden in the littoral zone of Lake Memphremagog was found to be two to eight times greater (per m^2) than the Pb burdens in the profundal zone of surrounding eastern township lakes. Pb concentrations were nearly fourfold higher than background Pb concentrations (115 and 31 $\mu g\ g^{-1}$, respectively), providing a reliable marker for littoral sediment core analysis. Lake morphometry is related to the three accumulation rates measured by providing distinct threshold limits (i.e., littoral slope, $>10\%$; exposure, $>10\ km^2$) where sediments are unable to accumulate. Macrophyte beds are shown to disproportionately accumulate sediments at rates 2 to 20 times greater (per m^2) than in the profundal zone. Linear regression models show that both the total SAR (mean, 1.7 mm yr^{-1}) and organic SAR (mean, 83.1 g $m^{-2}\ yr^{-1}$) are best predicted by the biomass density of the macrophytes, closely followed by plant mean biomass. Bulk SAR, principally representing the larger, inorganic fraction of sediments, is least predictable. Biomass density, but not mean biomass, was related to the accumulation rate of stable Pb (mean, 37.7 mg $m^{-2}\ yr^{-1}$), supporting empirical models that show growth form to be an important determinant of both sediment and plant tissue elemental concentrations. The variety of macrophyte communities sampled across Lake Memphremagog demonstrates that the conclusions drawn are not restricted to monospecific stands but to assemblages as a whole.

It has long been recognized that the ultimate fate of sediments retained by lakes is deposition in the deep-water profundal zone. Paleolimnological sediment core analysis has benefited not only from uninterrupted long-term records of accumulation but also from a sedimentary environment that is both conducive to the preservation of sediments and resistant to disturbance and resuspension. Determining the fate of sediments in the near-shore region of lakes is more challenging, because the high-energy littoral environment and associated biotic communities are far more complex and dynamic. Identifying and quantifying the exchange of materials between the pelagic and littoral zones have been elusive goals, with some research identifying the littoral zone as a source of materials to the pelagic over the short term (Landers 1982; Pieczynska 1993; Kairesalo and Matilainen 1994; Schindler et al. 1996) and other research showing that the littoral zone is able to trap materials over longer time periods (Moeller and Wetzel 1988; Schröder 1988). Quantification of the effects of macrophytes and littoral morphometry on the distribution and accumulation of sediments is a prerequisite to understanding the role of the littoral zone in lakewide processes and contaminant distribution.

Submerged macrophytes attenuate energy associated with waves and currents to permit the sedimentation of particles out of the water column. Although the mechanisms of littoral sediment accumulation have only recently been examined in lacustrine systems (Petticrew and Kalff 1992; Losee and Wetzel 1993), extensive research in coastal (Ginsburg and Lowenstam 1958; Scoffin 1970; Fonseca and Fisher 1986) and riverine (Gregg and Rose 1982; Madsen and Warncke 1983) environments has long demonstrated that quantifiable characteristics of submerged vegetation are linked to wave baffling, current reduction, and surficial sediment composition. In the littoral zone, the low-energy environment within submerged macrophyte beds allows for the entrapment of fine-grained sediments (clays and silts with a diameter of $<64\ \mu m$) that otherwise accumulate only in the profundal zone (Lehman 1975; Hilton 1985; Blais and Kalff 1995). Nutrients, contaminants, and heavy metals are most readily adsorbed or bound to the same fine particles (Gibbs 1973; Lick 1982). Petticrew and Kalff (1992) found that the proportion of clay in surficial sediments was higher in low-energy macrophyte beds because of diminished current flow and wave energy. Where lakes contain extensive macrophyte beds, the opportunity for littoral sediment interception and accretion is substantial.

Several factors, based on creating a local energy environment that can trap and retain particles, may affect the ability of the littoral zone to accumulate sediments. Littoral slope (Duarte and Kalff 1986) and exposure (Spence 1982; Chambers and Kalff 1987) have been identified as morphometric variables that govern the distribution and biomass of submerged macrophyte beds, which in turn have been implicated in the zonation and composition of littoral sediments (Keddy 1982; Petticrew and Kalff 1991, 1992; Rowan et al.

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1992). Measures of submerged plants have ranged from simple presence or absence of littoral vegetation (Petticrew and Kalff 1991) to complex variables that reflect the flow obstruction and community architecture of macrophyte beds in the water column, such as leaf area index (Petticrew and Kalff 1992) and biomass density (Duarte and Kalff 1990).

Characterizing the littoral zone for sediment accumulation rates (SARs) requires both a reliable historical marker and inclusion of the parameters that govern the sedimentary environment in macrophyte beds. Although it is unlikely that the accuracy and precision achieved in profundal paleolimnology can be matched in the littoral zone, there are examples of efficacious sediment core analysis in the near-shore zone of lakes using *Ambrosia* pollen (Moeller and Wetzel 1988) and reservoir preimpoundment soil (James and Barko 1990). In the present study, we used stable Pb, a geochemical marker of lacustrine sediments in southern Quebec corresponding to the onset of coal mining and fossil fuel combustion more than a century ago. To date, there has been no attempt to quantify the role of macrophyte bed structure and littoral morphometry on actual rates of sediment accumulation. The wide variety of macrophyte beds and littoral habitat available in Lake Memphremagog, which is located in Quebec and Vermont, make it possible to assess among-site patterns of sediment and Pb accumulation as a function of lake morphometry and macrophyte bed structure. We propose that a combination of these factors can be used to predict the accumulation of littoral zone sediments over time, supporting the hypothesis that submerged macrophyte beds serve as major sinks of materials in lakes.

Methods and materials

Study site—Field work was conducted at Lake Memphremagog (45°00′N, 72°10′W) in the eastern townships of southern Quebec during the summer of 1995 (Fig. 1). Lake Memphremagog is a long (45 km), narrow (1–4 km), and deep ($Z_{\text{mean}} = 20$ m; $Z_{\text{max}} = 107$ m) dimictic lake. It is oligotrophic throughout most of the Quebec portion and slightly more mesotrophic in Vermont. Previous studies have identified Lake Memphremagog as an excellent system for littoral research owing to a wide range of morphometry and wind exposure, providing a variety of near-shore environments (e.g., Duarte and Kalff 1986; Rasmussen 1988; Petticrew and Kalff 1991).

Study sites were selected during May 1995 (Fig. 1), before macrophyte growth reached seasonal maturation, and were based on estimates of littoral slope and effective length, a surrogate of exposure (Håkanson 1981). Potential sites proximate to stream inflows or shoreline development were excluded.

Sampling was conducted from late July until early September to coincide with the period of maximum submerged macrophyte biomass (MSMB). At each site, samples were collected by means of scuba diving from the depth of MSMB to standardize the protocol among sites and to eliminate any confounding depth effects, such as wave action, ice scouring, and natural changes in lake level (Duarte and Kalff 1988; Duarte and Roff 1991). The depth of MSMB was estimated to be 2.7 ± 0.5 m using empirical relationships derived by Chambers and Kalff (1985). In Lake Memphremagog, the depth of MSMB is readily identifiable because it coincides with a littoral shelf established by the intersection of the euphotic zone and the wave transition depth.

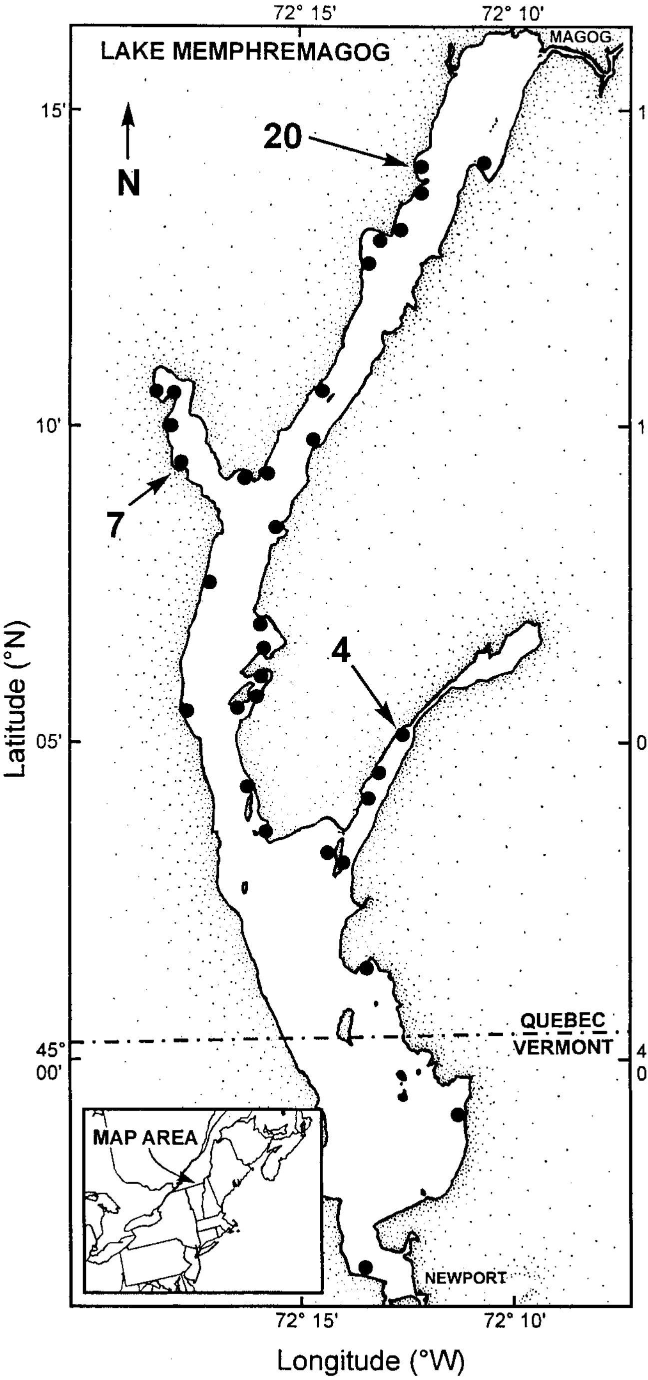

Fig. 1. Map of Lake Memphremagog (Quebec–Vermont) showing sites used for analysis in this study. All sites were selected according to slope and exposure estimations before seasonal macrophyte development.

Physical environment—The littoral slope of each site was determined using echo sounder printouts (Si-Tex Honda HE-357), following a perpendicular transect to the shoreline, by dividing the water depth by the distance of the site to the shoreline and expressed as a percentage. Site exposure was measured by planimetry, using the 1985 Canadian Hydrographic Service map for Lake Memphremagog (No. 1361), and expressed as effective area (E_{area}, km^2) to integrate all impinging effects of waves, currents, and wind on a particular site (Duarte and Kalff 1988).

Macrophyte beds—Triplicate quadrats (0.64 m^2) were randomly placed a minimum of 5 m apart, and all plants within each quadrat were harvested. Average plant height within each quadrat was measured in situ, providing an estimate of the height of the canopy in the water column. Plants were processed within 2 d of collection. For each quadrat, the roots were pinched off, and plants were rinsed of loose sediments and invertebrates. Samples were then spun dry in a lettuce spinner to remove excess water and weighed to the nearest 0.1 g to get a measure of fresh weight. Quadrat areal biomass values were all converted to grams per square meter. Biomass density ($\mathrm{g\ m^{-3}}$), a measure of the distribution of the biomass in the water column, was calculated by dividing the mean biomass of the three quadrats by the heights of the dominant macrophyte species (Duarte and Kalff 1990). All plants were keyed to species following Fassett (1957) and Ogden et al. (1976). Two-thirds of the sites comprised heterogeneous mixed-species weed beds. The other sites were identified as monospecific by virtue of having one species dominate the total biomass by $>90\%$.

Sediment core collection—Sediment cores were taken from the three quadrats using beveled acrylic core tubes (diameter, 7 cm; length, 70 cm). Immediately upon retrieval, each core was extruded on shore using a vertical extrusion system at one of three section intervals (1.0, 1.5, or 2.0 cm) to achieve a desired minimum of 10 sections per core. Sediments were stored in clean, preweighed polyethylene scintillation vials and measured for wet weight to the nearest 0.01 g. The longest of the three cores was used for analysis; in a subset of study sites (5 of 30), all three cores were processed to estimate the reproducibility of the sediment analyses. Where sediments were too thin for coring, surficial sediments were collected.

Sediments were dried at 75°C until a constant weight was achieved to estimate the water content or dry weight. Subsamples (0.5–1.0 g) of the dried mud was then burned at 550°C for 2 h to determine the loss on ignition as an estimate of the organic content of the sediment section (Dean 1974).

Sediment analyses and SAR determination—Stable Pb was selected from a variety of chemical and biological markers (e.g., $^{14}\mathrm{C}$, $^{210}\mathrm{Pb}$, $^{137}\mathrm{Cs}$, and *Ambrosia* pollen) as the most suitable sediment marker for dating littoral cores. Blais and Kalff (1995) found stable Pb to be a highly replicable and reliable marker of sediment accumulation, mainly because most anthropogenic Pb arrives via direct deposition. Subsurface enrichment in stable Pb is routinely observed in profundal sediment cores, resulting from increases in coal combustion and mining and smelting activities in the late 19th century in southern Quebec and adjacent regions. For the eastern townships, the onset of increases in anthropogenic Pb occurred during the mid-1880s, meaning that all accumulation rates (ARs) are based on a 110-yr interval (Blais et al. 1995). The anthropogenic Pb burden is further enhanced by the widespread combustion of leaded gasoline starting in the 1920s (Nriagu 1990). Agreement between results obtained with use of stable Pb as a geochemical tracer of inferred accumulation and those obtained with other tracers of accumulation is close, confirming that the procedure is robust (Blais et al. 1995).

Table 1. Acronyms used to describe each of the accumulation rates.

Measure	Unit	Type of accumulation
Total SAR	$\mathrm{mm\ yr^{-1}}$	Total sediment accumulation rate
Bulk SAR	$\mathrm{g\ m^{-2}\ yr^{-1}}$	Bulk sediment accumulation rate
Organic SAR	$\mathrm{g\ m^{-2}\ yr^{-1}}$	Organic sediment accumulation rate
Pb AR	$\mathrm{mg\ m^{-2}\ yr^{-1}}$	Anthropogenic Pb accumulation rate

Sediment section subsamples (1.0–1.3 g) were crushed with a mortar and pestle and digested in dilute aqua regia ($\mathrm{3HCl : 3H_2O : HNO_3}$) for 1 h at 85°C. All laboratory equipment used for Pb analysis was washed in a 10% HCl acid bath and rinsed at least twice in double-distilled, deionized water. All reagents used in the analysis were AnalaR-grade acids from BDH. After digestion, extracts were cooled and brought to a final volume of 25 ml in polyethylene volumetric flasks and centrifuged at 2,800 rpm to remove suspended solids. Concentrations of Pb were measured with 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.

Four measures of accumulation were developed, all based on the stable Pb peak (Table 1). The depth used to calculate ARs was the point in the sediment profile where the anthropogenic Pb burden was greater than the background Pb concentration by a factor of 2 (Fig. 2). The first three measures make use of the anthropogenic Pb horizon only as a point of reference by which to date the sediments, whereas the Pb AR integrates the actual amount of Pb that has accumulated as a result of human activities.

Total SAR refers to the total amount of material that has been accumulated with respect to the Pb horizon. It is a depth measure (expressed in $\mathrm{mm\ yr^{-1}}$) calculated by dividing the depth of the Pb horizon by 110 yr. Total SAR is 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 mud depth in the core tube and the surrounding sediment depth of the macrophyte bed:

$$\text{Total SAR} = \frac{[(\Sigma s_i) \times \mathrm{si_a} \times (\mathrm{td} - \mathrm{md})]}{110\ \mathrm{yr}} \tag{1}$$

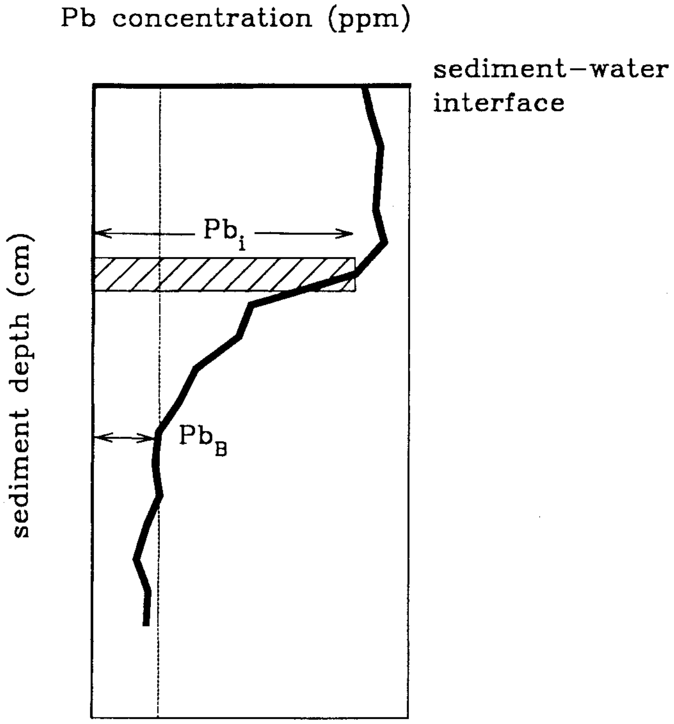

Fig. 2. Idealized Pb profile showing parameters used (1) to determine the depth where anthropogenically derived stable Pb is initiated and (2) to calculate the Pb AR. Pb$_i$ denotes the Pb concentration at a specific sediment depth (*i*th section), and Pb$_B$ refers to the natural background Pb level.

where s_i = *i*th section, si_a = section interval, td = total depth (mm), and md = mud depth. Bulk and organic SAR measures of accumulation were calculated using the dry weight and ashed weight (loss on ignition) of the sediment sections, respectively. Both ARs are expressed in mass units (g m^{-2} yr^{-1}):

$$\text{Bulk and organic SAR} = \frac{(\Sigma m_i) \times si_b \times 392}{110 \text{ yr}} \qquad (2)$$

where m_i = mass at the *i*th section, either dry weight (g) or organic content (g), and si_b = corrected section interval (si_a × td/md). The value of 392 converts the areal measure of accumulation from that of a standard core tube area (25.5 cm^2) to square meters. Finally, the anthropogenic Pb AR was determined by calculating the anthropogenic Pb burden at each site. For each core at a particular site, the surplus anthropogenic Pb (*see* Fig. 2) was summed from each section following a procedure outlined by Blais and Kalff (1995):

$$Pb_A = \frac{\Sigma(Pb_i - Pb_B) \times W_D}{A_c} \qquad (3)$$

where Pb_A = anthropogenic Pb burden (μg per section), Pb_i = Pb concentration at the *i*th horizontal section of a core (μ g^{-1}), Pb_B = natural background Pb concentration (μ g^{-1}), W_D = dry weight of the *i*th section (g), and A_c = area of the core (cm^2). Pb AR is expressed in milligrams per square meter per year and again is divided by 110 yr:

$$\text{PbAR} = \frac{(\Sigma Pb_{Ai}) \times si_b \times 392}{110 \text{ yr}} \qquad (4)$$

where Pb_{Ai} = anthropogenic Pb burden (μg per section) and si_b = corrected section interval (si_a × td/md).

All statistical analyses were performed using SYSTAT software (1992). Correlation and regression analyses were used to determine predictive models for all four measures of accumulation. Multiple regression models were constructed using the stepwise regression procedure of the general linear model function of SYSTAT. Where applicable, variables were evaluated for log transformation to improve homoscedasticity of the variance (Zar 1996).

Results

Summary of observations—Thirty-four sites were initially selected for study. Four were eliminated because they lacked an identifiable Pb horizon. Biomass values and species composition at these sites were similar to other sites, suggesting that localized disturbance, such as sediment slumping, dredging, or shoreline development, may have prevented the development of a Pb profile. Of the remaining 30 sites, 4 others had no appreciable sediment accumulation. Here, sediment parameters and ARs were based on surficial sediments.

Observed sediment profiles ranged from those with obvious points of inflection where the anthropogenic Pb burden was evident to those for which detection of the rise in Pb was complicated by background variability. To avoid artificial inflation of the depth of the historical marker, ambiguous points of inflection were considered shallower rather than deeper in the mud, and Pb concentrations were never inferred deeper than the depth of the bottom sediment section. Figure 3 presents three exemplary profiles. Background Pb levels were easily discerned in 67% of all sites; at the remaining sites, increases in stable Pb were undetectable. Including all sites, peak Pb concentrations (mean = 115.2 μ g^{-1}, SE_{est} = 18.3, $n = 30$) were significantly higher than background levels (mean = 31.4 μ g^{-1}, SE_{est} = 5.7, $n = 30$), as shown by a paired *t*-test ($t_{crit} = -5.919$, $n = 30$, $P < 0.001$).

The large ranges of slope, exposure, and biomass show that a wide variety of littoral environments were encompassed (Table 2). The orthogonality of slope and exposure, needed to ensure that the field design was unbiased, is upheld by the low correlation coefficient between them (Table 3; $r = 0.12$, $n = 30$, $P > 0.05$). Similarly, the low correlation coefficients between littoral morphometry (slope and exposure) and macrophytes (biomass and biomass density) indicate that the location of macrophyte beds is relatively independent of littoral morphometry, except at extreme sites characterized by very high slope (>10%) or exposure (>10 km^2). Macrophyte communities ranged from high-biomass (1,888 g m^{-2}), monospecific *Myriophyllum spicatum* stands to low-biomass (78 g m^{-2}), monospecific patches of isoetids. In between were more diverse communities that contained a variety of pond weeds (*Potamogeton* spp.) and relatively

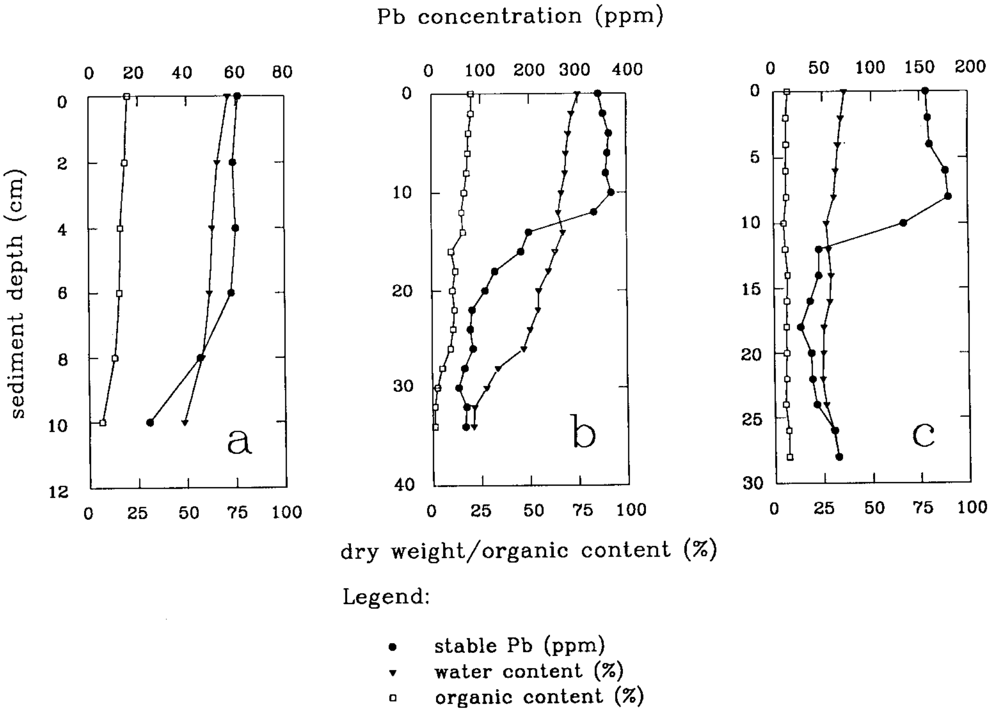

Fig. 3. Three exemplary Pb profiles from a variety of littoral sites: site 4, Middle Fitch Bay (a); site 7, Sargeant's Bay, Penfield Point (b); and site 20, Point Green North (c). The figure for each site includes Pb concentrations (μg/g), dry weight (%), and organic content (%).

slow-growing species (e.g., *Ceratophyllum demersum* and *Elodea canadensis*).

SARs and Pb ARs vary widely (Table 2). Analysis of the subset of study sites, including all three sediment cores from each site, showed that for each SAR and Pb AR, there was greater variation among sites than within sites (Kruskal-Wallis tests, df $= 3$, all $P < 0.05$). Among sites, total SAR and organic SAR have lower coefficients of variation (54 and 60%, respectively) than bulk SAR and Pb AR (85 and 99%, respectively), meaning that the accumulation of all particles and stable Pb is more variable than the accumulation of flocculent organic matter and associated water content. Bulk SAR incorporates between 71 and 98% of the mass of the sediments, on average 10 times that of the organic content, indicating that the bulk of the sediments are inorganic and likely eroded from the shoreline. These larger, heavier particles are much less vulnerable to waves and currents. In contrast, the flocculent and easily resuspended organic particles are represented by the total and organic SARs.

Table 2. Summary statistics for the 30 Lake Memphremagog among-bed sites, including mean, range, and coefficient of variation (CV). Bulk SAR is based on 29 sites; an identified outlier is omitted (*see text*).

Variable	Mean	Minimum	Maximum	CV
Slope, %	7.1	0.1	46.9	130.7
Exposure, km^2	4.9	0.2	25.4	119.0
Mean biomass, g m^{-2}	1,042.6	0.0	2,218.9	57.2
Biomass density, g m^{-3}	559.0	0.0	1,006.5	48.7
Total SAR, mm yr^{-1}	1.7	0.2	3.6	54.0
Bulk SAR, g m^{-2} yr^{-1}	743.8	38.8	1,669.8	54.8
Organic SAR, g m^{-2} yr^{-1}	83.1	4.3	188.8	60.3
Pb AR, mg m^{-2} yr^{-1}	37.7	0.0	133.7	99.4

The composition of surficial sediments (top 1–2 cm) in macrophyte beds reflects processes that have shaped the character of accumulated sediments over the past season or few years. To infer that SARs are based on existing morphometric and macrophytic features of the littoral zone requires that the temporal and spatial distributions of the macrophyte beds not vary greatly. The similarity between the surficial and mean organic contents and between the surficial and mean dry weights implies that the littoral sedimentary environment has remained remarkably constant over the temporal scale of 110 yr, as defined by stable Pb (Table 4). Residuals from these relationships were plotted against the number of sections used per site to check for autocorrelation. No pattern or influence was found in either plot, confirming the strength of the relationship (Fig. 4a,b). In contrast, the anthropogenic Pb burden, expressed as Pb AR, varied substantially over the same time period (Table 4). The independence of Pb AR against the measured sediment parameters of dry weight and organic content reflects the changing stable Pb burden over time against a relatively constant littoral sediment composition.

Correlation and regression analyses—Both mean biomass and biomass density are better coupled with all rates of sediment accumulation than either slope or exposure (Ta-

Table 3. Correlation matrix of slope, exposure, mean biomass (MB), biomass density (BD), total SAR, bulk SAR, organic SAR, and anthropogenic Pb AR. For correlations with bulk SAR, site 30 is removed because of an identified outlier (*see text*).

	Slope	Exposure	MB	BD	Total SAR	Bulk SAR	Organic SAR	Pb AR
Slope	1.00							
Exposure	0.12†	1.00						
MB	−0.42*	−0.41*	1.00					
BD	−0.44*	−0.47**	0.69***	1.00				
Total SAR	−0.49**	−0.48**	0.81***	0.87***	1.00			
Bulk SAR	−0.39*	−0.26†	0.48**	0.46*	0.51**	1.00		
Organic SAR	−0.38*	−0.53**	0.71***	0.79***	0.84***	0.25†	1.00	
Pb AR	−0.31†	−0.26†	0.21†	0.67***	0.50**	0.38*	0.39*	1.00

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

ble 3). Bulk SAR is the least predictable of the ARs, having low correlation coefficients with mean biomass and biomass density, even after an obvious outlier is omitted (Fig. 5c,d). This outlier (site 30), corresponding to a location in the south basin of Lake Memphremagog closest to the principle river inflow, was subsequently removed from all analyses involving bulk SAR. Extensive emergent macrophyte beds, nearly contiguous shoreline development, and comparatively low mean depth in the south basin may contribute to the anomalous bulk AR observed at this one site. Similarly, Rowan et al. (1992) reported inorganic (bulk) sedimentation rates in the south basin to be four times higher than in the rest of the lake.

At the depth of MSMB, site exposure has an insignificant effect on bulk SAR in macrophyte beds, whereas littoral slope has a significant, although small, effect. Total and organic SARs are most strongly related to biomass density (Fig. 5b,f) and secondly to mean biomass (Fig. 5a,e). The degree of packing of macrophyte biomass in the water column evidently has an important effect on the conservation of flocculent organic particles that are associated with high water content sediments. Generally poor agreement among the independent variables indicates that the presence of macrophyte beds encourages long-term sediment accumulation, followed by the secondary effects of slope and exposure on the sedimentary environment but not on the plants. Finally, only the biomass density of macrophyte beds is significantly related to the Pb AR (Table 3). The finding that the two plant measures are correlated ($r = 0.69$) supports the hypothesis that the growth form and packing of weeds in the water column rather than the biomass itself is related to the sequestering of metals and nutrients in littoral sediments over time.

Table 4. Correlation matrix of sediment parameters with Pb AR ($n = 26$). All terms are highly significant ($P < 0.001$), except for those with Pb AR, which are not significant at $P > 0.05$.*

	SDW (%)	MDW (%)	SOC (%)	MOC (%)	Pb AR
SDW (%)	1.00				
MDW (%)	0.94	1.00			
SOC (%)	−0.84	−0.83	1.00		
MOC (%)	−0.81	−0.87	0.94	1.00	
Pb AR	−0.14	−0.09	0.10	0.01	1.00

* SDW, surficial dry weight; MDW, mean dry weight; SOC, surficial organic content; MOC, mean organic content. *See text* for further explanations.

Stepwise multiple regression analysis was used to construct models including the independent variables. Although the correlation matrix showed low but significant relationships between the ARs and the morphometric measures, slope and exposure were largely unimportant contributors to the multiple regression models (Table 5). Models that include biomass density explain most of the observed variance in total SAR, organic SAR, and Pb AR. Model R^2 values were particularly high for both total and organic SAR owing to the overwhelming dominance of the macrophyte bed parameters. Only for organic SAR was there a second significant variable incorporated into a model. Site exposure, when combined with either mean biomass or biomass density, explained a small portion of the variance in the accumulation of organic material. R^2 values for models with Pb AR were significant only when biomass density was included. The difference between the two Pb AR models is mainly due to the overwhelming influence of biomass density (Fig. 5h) rather than mean biomass (Fig. 5g).

Discussion

Core analysis in the littoral zone—That littoral sediment cores were not retrievable from all sites attests to the variability of sedimentary processes in the near-shore region of lakes. For the littoral zone, compared to the profundal zone, different factors need to be evaluated to determine rates of sediment accumulation. The detail and resolution common to deep-water core analysis have yet to be demonstrated with littoral sediments. Physical forces and seasonally dynamic macrophyte communities combine to maintain a variable sedimentary environment in the littoral zone. Nonetheless, the accumulation of sediments over ecologically long time frames is predictable among submerged macrophyte beds. The 110-yr period defined by the stable Pb profile integrates seasonal and interannual variability in sediment accumulation, allowing clear patterns to be seen.

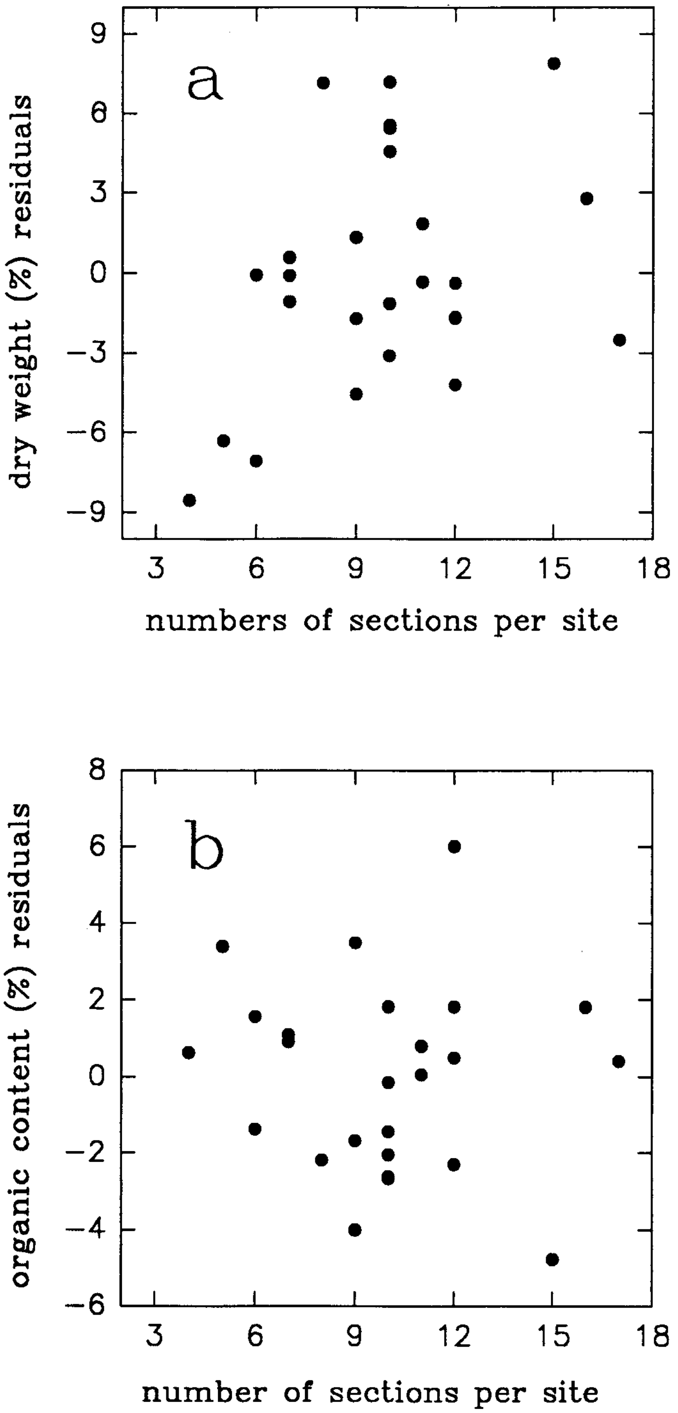

Fig. 4. Plots of the sediment parameter residuals against the number of sections per core required to achieve the stable Pb horizon depth. $n = 26$ because sites where only surficial sediments were collected are not included. a. Dry weight measures versus number of sections. b. Organic content measures versus number of sections.

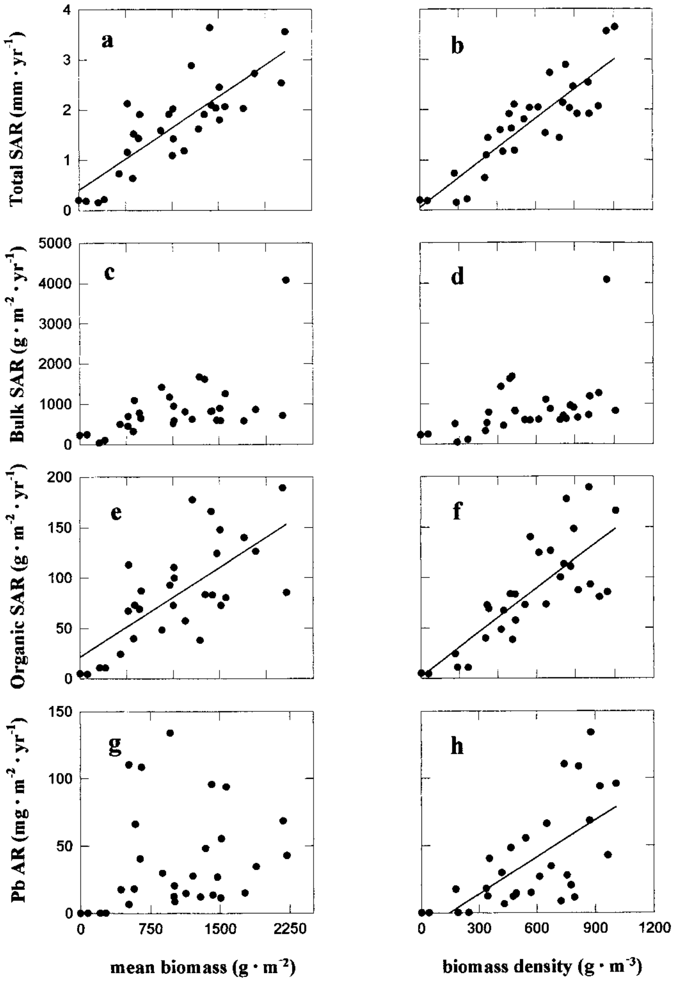

Fig. 5. Bivariate plots for the four measures of SARs as related to either mean biomass or biomass density. a,b. Total SAR. c,d. Bulk SAR. e,f. Organic SAR. g,h. Anthropogenic Pb AR.

The independence of Pb accumulation against a historical backdrop of relatively constant sediment composition supports an implicit assumption of SAR models. The agreement between surficial and deeper core sediment characteristics and the lack of discontinuities in most stable Pb profiles is consistent with the hypothesis that the submerged macrophyte beds have remained relatively constant over the last century despite climate variation, moderate shoreline development, changes in catchment land use, and invasion of *M. spicatum.* This relative stability is supported by paleolimnological records of Lake Memphremagog, which show, through carbon isotope analysis, that water chemistry and primary production over the past 350 yr have remained relatively constant, well before the anthropogenic increase in stable Pb 110 yr ago (LaZerte 1983).

Relying on stable Pb as a historical record of sediment accumulation requires that any deposited Pb remain unaffected by chemical and biological processes that could distort the profile. Jackson et al. (1993) listed three possible causes of subsurface peaks in metal concentrations in sediments, including an increase in atmospheric metal deposition, a decrease in watershed pH with a concomitant increase in metal mobility, and diffusion and/or precipitation along sediment redox gradients. The same subsurface (10 cm) sediment profile also encompasses the rooting zone of most submerged macrophytes. The hypothesis that metal bioavail-

Table 5. Comparison of stepwise multiple regression models for four AR measures separated according to mean biomass (MB, g m^{-2}) or biomass density (BD, g m^{-3}) ($n = 30$, except for bulk SAR, for which $n = 29$; *see text* for identification of outlier).

Dependent variable	R^2	F ratio	SE_{est}	Intercept	B_1 (slope)	B_2 (exposure)	B_{3A} (MB)	B_{3B} (BD)
Total SAR (mm yr^{-1})								
MB	0.66	53.21***	0.55	0.40†	†	†	0.0012***	
BD	0.76	90.31***	0.45	0.05†	†	†		0.0029***
Bulk SAR (g m^{-2} yr^{-1})								
MB	0.23	7.90**	364.75	398.84**	†	†	0.34**	
BD	0.21	7.25*	368.20	359.47*	†	†		0.71*
Organic SAR (g m^{-2} yr^{-1})								
MB	0.57	17.75***	34.14	43.94*	†	−2.48*	0.049***	
BD	0.66	25.86***	30.42	19.87†	†	−1.70*		0.13***
Pb AR (mg m^{-2} yr^{-1})								
MB	0.10	3.01†	36.22	46.61***	−1.26†	†	†	
BD	0.44	22.18***	28.48	−13.49†	†	†		0.090***

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

ability is affected by the sediment physicochemical environment was rejected for eastern township lakes, including Lake Memphremagog, by Jackson et al. (1991), who showed that above-ground concentrations of elements in macrophytes reflected the total concentration of the element in the underlying sediment. Consequently, the effects of rooted macrophytes on sediment metal concentrations is minimal. Metal profiles in the sediments thus reflect increased anthropogenic burdens and are independent of plant–sediment interactions.

Predicting ARs and littoral zone ecology—This study is the first to combine lake morphometry and quantifiable aspects of macrophyte beds in the prediction of SARs and Pb ARs in the littoral zone of lakes. The variables that were selected and shown to be useful predictors are not causal mechanisms but rather surrogate variables that integrate several mechanisms and processes that determine the fate of sediments in the littoral zone. Extrapolation of the models to other lakes is possible because of the wide range of slopes and exposures present in Lake Memphremagog. In addition, the morphometric and macrophytic variables used to predict SARs are based on physical factors that are not limited to lakes and should be equally useful in other aquatic systems, such as estuaries and sea grass beds.

Although site slope and exposure each play a provisional role in setting the potential for sediment and Pb accumulation, the observed among-site patterns are primarily governed by quantifiable aspects of the macrophyte beds. The relationships between morphometry and SAR are consequential though, because they define distinct accumulation thresholds. All sites with high exposure (>10 km^2) and/or high slope (>10%) had negligible sediment accumulation. The remaining sites within these physical extremes all exhibited appreciable sediment accumulation, but they were not linked to slope and exposure. Duarte and Kalff (1986), who also sampled at the depth of MSMB in Lake Memphremagog, found an equivalent threshold in the relationship between submerged macrophyte biomass and littoral slope. Submerged vegetation at these more favorable sites is able to entrap and retain sediments within the limits imposed by the littoral morphometry. Conventional morphometric definitions in lakes, such as wave transition depth (Håkanson and Jansson 1983) and mud deposition boundary depth (Rowan et al. 1992), do not apply to submerged macrophyte beds. At the depth of MSMB, even severe waves and currents were unable to overcome the presence of rooted vegetation and disturb the accumulated sediments.

Both macrophyte parameters were useful in the prediction of all SARs but not Pb AR, for which only biomass density was significant. For the SARs, biomass density always had a greater predictive power than macrophyte biomass. Evidently, the distribution of stems and leaves in the water column has a strong effect on the ability of macrophyte beds to attenuate energy and in turn accumulate and retain sediments (Petticrew and Kalff 1992). Stands dominated by canopy-forming species, characterized by a lower biomass density (*see* Duarte and Kalff 1990), intercept more water, and in turn more seston, than understory stands. Although the resulting attenuation of turbulence increases the sediment load to the macrophyte bed, the material does not necessarily accumulate interannually. Conversely, understory species (e.g., *Potamogeton robbinsii* and *E. canadensis*), which have a higher biomass density, occupy a smaller fraction of the water column but are much more effective at retaining any captured sediment and lead. Species that have a high root-to-shoot ratio (e.g., *Potamogeton* spp. and isoetids; Wetzel 1983) should retain sediments better than species that have a low root biomass. Roots and rhizomes further chemically alter the rooting zone of the sediments by agglutinating and binding sediments to roots, facilitating sediment stabilization (Jaynes and Carpenter 1986). Consequently, some of the unexplained variance in macrophyte–SAR relationships may be attributable to unexamined differences in root-to-shoot ratios at the different sites.

Total SAR most completely describes macrophyte bed sediments, including all particles, organic and inorganic, and associated water content. It is negatively affected by slope and exposure but positively related to plant biomass and biomass density (Table 3), indicating that littoral sediments are sensitive to changes in macrophyte community structure and the local energy environment. A dramatic manifestation of this sensitivity was seen in Lake Constance, where the disappearance of macrophytes, induced by eutrophication and increased turbidity, resulted in a massive loss of littoral sediments (Schröder 1988). In Lake Memphremagog, the two plant measures were the most important determinants of sediment accumulation, overshadowing the importance of lake morphometry. Although slope and exposure determine the potential for sediment accumulation, the presence of rooted vegetation allows for long-term retention.

Bulk SAR represents the dry weight accumulation of all particles and consists predominantly of inorganic material. The relatively small fraction of organic material contained within the bulk SAR measure (~10%) is of minor importance in determining the general pattern of SARs. Estimated inorganic SARs in profundal Lake Memphremagog range from 15 to 78 g m^{-2} yr^{-1} (Rowan et al. 1992). In comparison, most macrophyte beds have bulk SARs that are 2 to 20 times higher (Table 2), meaning that vegetated littoral zones disproportionately accumulate lakewide sediments.

Organic SAR, characterized by flocculent sediments with a particularly high water content, is more vulnerable to waves and currents than bulk SAR, which is typified by larger particles with higher bulk density. Macrophyte beds and associated epiphytic and benthic communities undoubtedly contribute to the sedimentary organic pool during the growing season. However, the physical presence of the submerged plants permits the retention of organic material (Landers 1982). Our results show that macrophytes have a greater effect in counteracting the influence of slope than of exposure (Table 3). At sites with a similar macrophyte biomass, those having relatively higher exposure are, therefore, more subject to the resuspension and loss of organic sediments than sites of higher slope.

Organic particles come from one of three sources: the catchment, the pelagic zone, and the vegetated littoral zone. Sediments at low-growing, high–biomass density sites may be expected to retain relatively higher proportions of autochthonous organic matter than canopy-forming stands, which should have relatively higher amounts of allochthonous organic matter from the pelagic zone. In Quinn Bay, Lake Memphremagog, LaZerte (1983) concluded that the sediments beneath canopy-forming *M. spicatum* and *Vallisneria americana* macrophyte beds contained insignificant quantities of macrophyte-derived carbon, attributable to low–biomass density growth forms. We hypothesize that if low–biomass density macrophyte beds conservatively retain carbon and other essential nutrients, then the opportunity for filtration and sequestration of lakewide particles is low. Conversely, if high–biomass density macrophyte beds retain disproportionately high amounts of organic material derived from the catchment and the pelagic zone, then they would serve as net sinks of sediments and associated nutrients and contaminants.

The anthropogenic Pb burden in the littoral zone of Lake Memphremagog is, on average, almost 4.5 times greater than the profundal Pb burden calculated for nine eastern townships lakes (Blais and Kalff 1993). Quantifying the stable Pb burden at littoral sites allows macrophyte beds to be compared according to how well they sequester stable Pb, which is relevant to other biogeochemically similar elements and contaminants (e.g., Ni, Cd, and polycyclic aromatic hydrocarbons) that are also disproportionately sorbed to fine sediment particles (Gibbs 1973). Plant growth form, in turn, is indeed strongly coupled to trace metal concentrations of both rooted macrophytes and their underlying surficial sediments (Jackson et al. 1991). The relationship between biomass density and Pb accumulation provides a new perspective on the empirical evidence that sediment and plant tissue elemental concentrations are correlated. The highest Pb ARs were observed at littoral sites occupied by macrophytes with high biomass densities. No equivalent relationship was found between Pb AR and mean biomass despite a very strong correlation between mean biomass and biomass density. Similarly, site slope and exposure were unrelated to Pb accumulation, further emphasizing the importance of the plant–sediment complex in contaminant retention. Thus, over the 110-yr time scale defined by stable Pb, macrophyte communities characterized by high–biomass density species (e.g., *P. robinsii* and *E. canadensis*) have disproportionately sequestered fine sediments carrying the highest associated concentrations of nutrients, metals, and contaminants.

The littoral zone has been largely overlooked by limnologists concerned with temporal patterns of lake processes. The much greater SARs and Pb ARs, per unit area, in macrophyte beds over the profundal zone ARs of other eastern township lakes show the importance of littoral zones in the retention of particles and their associated nutrients and contaminants. Other comparative research in the same region has showed that organic matter mineralization rates per unit area in macrophyte beds are, on average, nearly four times those in the profundal zone and sufficiently elevated to also dominate on a whole-lake basis (den Heyer and Kalff 1998). This, together with the fact that most lakes worldwide are shallow with extensive submerged vegetation, implies that an understanding of whole-lake functioning requires explicit consideration of littoral zones.

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