

# A MASS-BALANCE ANALYSIS OF TRACE METALS IN TWO WEEDBEDS

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**Abstract.** A mass-balance approach was used to examine the role of macrophyte beds as a sink or source for 7 metals over time scales varying from two months (the growing season of the plants) to one year. During the growing season the macrophyte beds were found to be net sinks for particulate metals but were net sources of dissolved metals. During senescence, ca. 15–20% of the Al, Fe, and Mn and ca. 25–30% of the Cr, Cu, Ni and Zn within the macrophyte tissues at maximum seasonal biomass was lost to the surrounding waters in a dissolved form. The export of metals from the weeds during senescence was a very small fraction (<0.01% of Al, Fe to 3.5% of Zn) of the annual allochthonous metal loading to Fitch Bay in L. Memphremagog, Quebec. In L. Weedon however, metal export during senescence was 34% (Mn) to 57% (Cu) of the annual allochthonous load. The time estimated for the plants to recycle the metals within the rooting zone of the sediments was on the order of hundreds of years. These results demonstrate that while weedbeds are net sources of metals during the summer, only a small fraction of metals in littoral sediments are not permanently buried over the longer term.

## Introduction

Rooted aquatic macrophytes obtain a substantial amount of their nutrition from their sediments (Huebert and Gorham, 1983; Barko and Smart, 1980, 1981, 1982; Carignan and Kalff, 1980; Bole and Allen, 1978). Radio-tracer studies have demonstrated that many elements (e.g., P: Carignan and Kalff, 1980; Demarte and Hartman, 1974; Bristow and Whitcombe, 1971; N: Nichols and Keeney, 1976; Ca and Fe: Demarte and Hartman, 1974) are absorbed by the roots and translocated to above-ground tissues. Element uptake from the sediments followed by translocation to macrophyte shoots represents a mechanism by which macrophytes retrieve a portion of the large potential reservoir of elements from the sediment profile.

The role rooted aquatic macrophytes play in the cycling of elements in the littoral zone, and indeed, within the lake, depends upon the fate of the elements contained within the above-ground tissues of the plants. Four possible fates for elements include: (1) return to the sediment bound to shoot fragments (Landers, 1982); (2) transfer to attached epiphytes (Jackson, 1992; Carignan and Kalff, 1982; Hough and Wetzel, 1975; Wetzel and Manny, 1972); (3) transfer to herbivores by grazing (Lodge, 1991; Carpenter and Lodge, 1986); and (4) release to the surrounding water during senescence (Carpenter and Lodge, 1986; Moore *et al.*, 1984; Carpenter, 1983; Landers, 1982; Lie, 1979; Prentki *et al.*, 1979). The first fate represents an internal loop within the littoral, with elements moving from the

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sediments, to the macrophytes, and back to the sediments. The second and third fates represent cycling that occurs within the littoral, but may extend to the pelagic, depending on the mobility and behavior of the grazers present (e.g., invertebrates or fish). The last fate represents a source of internal loading of elements to the lake.

The importance of rooted macrophytes as a source of internal loading depends upon the amount of a particular element released relative to other internal and allochthonous loading sources. Internal loading of C (Wetzel and Manny, 1972; Wetzel, 1969), N (Landers, 1982; Lie, 1979; Wetzel and Manny, 1972), and P (Moore *et al.*, 1984; Landers, 1982; Lie, 1979) by aquatic macrophytes is well documented. The release of these elements by macrophytes can aid growth of epiphytes during the summer (Allen, 1971), and late season pulses in chlorophyll *a* have been linked to nutrient release by macrophytes (Landers, 1982; Gibbons, 1981). Adams and Prentki (1982) calculated the internal loading of senescing macrophytes to be about 25% of the annual loading of C and P to L. Wingra, Wisconsin, and exceeded allochthonous loading of P during the summer. Thus, the role of rooted aquatic macrophytes in lake functioning extends beyond the traditional notion of primary producer.

No studies have quantified the role rooted aquatic macrophytes play in the internal loading of trace metals to lakes. Because the trace metal content of many macrophytes is roughly proportional to the metal's content in the sediments (Jackson *et al.*, 1991), and the sediments represent a large reservoir of metals, the macrophytes may be a significant source of trace metals to the lake. The purpose of this study is to quantify the loss of metals from naturally occurring rooted freshwater macrophytes from mid-June to early October. This encompasses the period when macrophyte productivity is highest through to the early stages of senescence (Cattaneo and Kalff, 1980). In addition, we consider the inputs of particulate matter during the peak macrophyte production period, and over the annual cycle, in order to evaluate the net metal flux to the weedbeds over both time scales.

## Materials and Methods

### THE STUDY SITES AND SAMPLING PROTOCOL

Between 18 June and 6 October 1991 we sampled 2 sites in the eastern townships of Quebec (Figure 1) approximately every 10 days (12 samples per site). The sites were chosen because they featured uni-directional water flow through the weedbeds at rates that were measurable. Lake Weedon (45°45'N, 71°24'W) is a shallow (max. depth 2 m) widening of the Saint-Francois River. *Myriophyllum spicatum* was the predominant macrophyte species by biomass (ca. 80–85%), with some *Potamogeton perfoliatus* and *Vallisneria americana*. The second site was a dense, nearly monospecific bed of *M. spicatum* located at the north end of Fitch Bay (45°05'N, 72°13'W) in L. Memphremagog. Minor species at this site (5–10% of total biomass) included *Potamogeton amplifolius* and *P. robbinsii*.

On each sampling date we collected duplicate water samples upstream and

downstream from the sites. We also sampled 6 quadrats of plants ( $30 \times 30$  cm each), chosen to represent as much as possible the variability in each weedbed. Plants were separated by species, washed, spun-dried in a plastic salad spinner, weighed to determine fresh weight, and frozen. We froze only *M. spicatum* for future metal analyses because it accounted for such a large fraction of the total biomass at both sites and because a previous study had shown metal content of *P. perfoliatus* and *P. amplifolius* not to differ from that of *M. spicatum* at the same sites (Jackson and Kalf, 1993). Water samples were filtered through  $0.45 \mu\text{m}$  membrane filters (Millipore HA) to remove suspended sediments (the filters were then frozen), acidified to 2% with ultrapure  $\text{HNO}_3^-$ , and stored in the dark at  $4^\circ\text{C}$  until analysis (10–60 days).

#### METAL ANALYSES

All labware was acid washed (10% HCl) and rinsed a minimum 3 times in double distilled deionized water. Acids used for washing were Analar grade (BDH Inc.). To assess extraction efficiencies, methodological variation between dates and possible contamination we extracted National Bureau of Standards Buffalo River sediment, citrus leaves, and water as reference sediment, plant and water materials, respectively. Concentrated  $\text{HNO}_3^-$  extracted all plant metals with 100% efficiency (the C.V. ranged from 3–8%). Dilute aqua regia extracted the sediment Cu, Mn, Ni and Zn with 100% efficiency while Al, Fe and Cr were extracted with 18, 52, and 55% efficiency, respectively (the C.V. for all sediment metals ranged from 3–9%). We tested our analytical procedure for contamination by performing our laboratory protocol on reference water samples of known composition.

Dried suspended sediments on the filters were digested with dilute aqua regia (3:3:1  $\text{H}_2\text{O}:\text{HCl}:\text{HNO}_3^-$ ); dried plants were digested with concentrated  $\text{HNO}_3^-$ , and the acidified water samples were aspirated directly. Sediments and plants were digested with an acid:dry weight ratio of 15 mL: 1 g in 50 mL teflon tubes at room temperature overnight (ca.  $20^\circ\text{C}$ ), heated to  $90 \pm 5^\circ\text{C}$  for 2 hr, and allowed to cool. Cooled extracts were brought to 25 mL final volume in polyethylene volumetric flasks, spun at 2800 rpm to remove suspended solids, then analysed for Al, Cr, Cu, Fe, Mn, Ni and Zn by either flame atomic absorption spectroscopy (plant material; Perkin Elmer model #5100 with deuterium background correction for Fe) or inductively coupled plasma-mass spectroscopy (sediment and water material; Jerrell-Ash model #975). Metal values for duplicate samples were averaged to yield one metal concentration estimate for plant, water and sediment for each sampling date.

#### DISCHARGE CALCULATIONS

Upstream from the Fitch Bay site in L. Memphremagog and in the small Riviere au Canard (Figure 1) we estimated discharge with the salt dilution (gulp) technique (Hersch, 1982). This technique involves injecting a tracer (we used NaCl) of known concentration and volume into the channel and measuring the pulse of

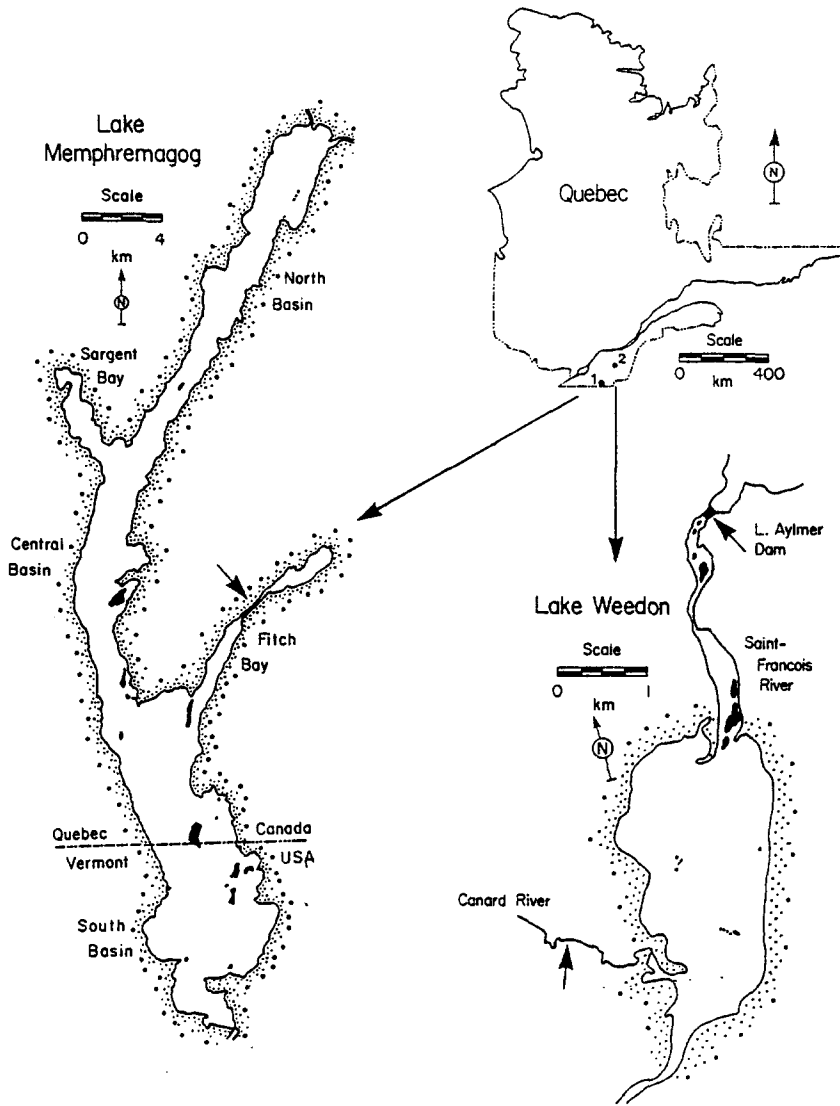


Fig. 1. Location of Lakes Memphremagog (1) and Weedon (2), Quebec. The short arrows indicate the locations where discharge was determined (by Environment Quebec at the L. Aylmer dam and by the salt technique in the Riviere au Canard and above the Fitch Bay weedbed). Water flow in Fitch Bay is to the south, but to the north in the main part of L. Memphremagog, and to the south in L. Weedon.

tracer downstream. A plot of relative concentration versus time is integrated and the discharge is calculated as the volume of solution injected divided by the time of passage of the tracer pulse (the area under the curve).

Discharge is regulated with a dam at the outflow to L. Aylmer, approximately 2 km upstream from L. Weedon (Figure 1). Daily discharge values were provided by

the water resources branch of Environment Quebec. The only potential additional inflow to L. Weedon other than the Saint-Francois River is the small Riviere au Canard. Because the latter had very low discharge throughout the study period (amounting to less than 1% of the discharge of the Saint-Francois River) we ignored it in our calculations.

#### MASS BALANCE CALCULATIONS

We used a mass-balance approach to examine the role of the weedbeds as a source or sink for metals over seasonal (the study period) and annual periods (raw data are available from Jackson, 1992). We calculated dissolved metal export from the sites by multiplying the difference in the upstream and downstream (relative to the sampling sites) dissolved metal concentrations ( $\mu\text{g L}^{-1}$ ) by the discharge ( $\text{L day}^{-1}$ ). The largest difference between upstream and downstream dissolved metal concentrations varied from  $0.06 \mu\text{g L}^{-1}$  (Cu) to  $4.49 \mu\text{g L}^{-1}$  (Al) at the Fitch Bay site. We assumed that discharge on the sampling dates represented the mean value for an interval centred on the sampling dates at the Fitch Bay site, and used values averaged over the time intervals between sampling for L. Weedon. We summed the daily net metal export over the duration of the study period to yield a seasonal net metal export value. We calculated the average metal content of *M. spicatum* on 27 July, the date for which the maximum seasonal biomass was obtained, and compared this estimate of plant metal content with the net seasonal export calculated as above. The ratio of these two values was used as an estimate of the percent of metal lost from the plants during the growing season.

For each sampling date we calculated the daily suspended particulate metal import to each site by multiplying the difference in suspended particulate matter concentration above and below the sites ( $\text{g L}^{-1}$ ) by the discharge ( $\text{L day}^{-1}$ ) and the particulate matter metal content ( $\mu\text{g g}^{-1}$ ) to yield  $\mu\text{g metal day}^{-1}$ . The seasonal suspended particulate metal import to the sites was calculated by summing the daily values, assuming a linear change in values between sampling dates. The ratio of the net seasonal metal import to the net seasonal dissolved metal export was calculated to determine what proportion of the net dissolved metal export (i.e., plant metal export) from the site could be accounted for by the net particulate metal import to the site. The net annual import of particulate metals to both sites was estimated by multiplying the gross annual sediment load (from Environment Quebec open files) in the inflows by a particle retention coefficient estimated for the sites by Rowan (1992), and the average metal concentration of surficial sediments. The latter was determined as the average metal content of surficial sediments for these sites (Fitch Bay:  $n = 12$ ; L. Weedon  $n = 7$ ) previously reported elsewhere (Rowan 1992). We then calculated the ratio of the metal export during our study period to the annual loading (import) to assess the degree to which L. Weedon and Fitch Bay are sources or sinks for metals on an annual basis.

To estimate the turnover rates of sediment metals by the plants we took the ratio of the net seasonal dissolved metal export to the amount available for uptake in

TABLE I

Seasonal dissolved metal export (daily export summed over the study period), metal standing stock, and percent standing stock exported from 2 sites in southern Quebec. The metal standing stock was estimated by multiplying the average metal content ( $\mu\text{g g}^{-1}$  dry wt $^{-1}$ ) by the estimated dry weight standing stock (dry wt m $^{-2}$ ), which was assumed to be 15% of the fresh weight

Metal	Seasonal metal export ( $\mu\text{g m}^{-2}$ )	Plant metal content ( $\mu\text{g m}^{-2}$ )	% export
<i>Fitch Bay – L. Memphremagog</i>			
Al	$3.0 \times 10^5$	$1.7 \times 10^6$	17
Cr	$2.8 \times 10^3$	$1.0 \times 10^4$	27
Cu	$2.4 \times 10^3$	$8.7 \times 10^3$	28
Fe	$1.2 \times 10^5$	$7.6 \times 10^5$	15
Mn	$2.2 \times 10^5$	$1.5 \times 10^6$	14
Ni	$2.5 \times 10^3$	$9.5 \times 10^3$	26
Zn	$2.3 \times 10^3$	$7.8 \times 10^3$	30
<i>L. Weedon</i>			
Al	$1.5 \times 10^5$	$7.2 \times 10^5$	21
Cr	$2.1 \times 10^3$	$6.5 \times 10^3$	32
Cu	$4.7 \times 10^3$	$1.6 \times 10^4$	29
Fe	$3.4 \times 10^5$	$1.9 \times 10^6$	18
Mn	$2.3 \times 10^4$	$1.0 \times 10^5$	22
Ni	$2.4 \times 10^3$	$7.6 \times 10^3$	31
Zn	$4.0 \times 10^3$	$1.3 \times 10^4$	31

the plant's rooting zone. We assumed the plant's roots extended to 25 cm depth, a sediment bulk density of  $1.4 \text{ g mL}^{-1}$  (Hakanson and Jansson 1983), and metal concentrations in the sediments as above.

## Results

### FITCH BAY – L. MEMPHRETAGOG

Between 15–30% of the metal inventory present in *Myriophyllum spicatum* at peak seasonal biomass was lost to the surrounding water as dissolved metals between mid-June and the first week in October (Table I). The percent metal exported fell into two groupings: ca. 15% for Al, Fe and Mn and ca. 25–30% for Cr, Cu, Ni and Zn. Because we detected no differences in the metal content of the suspended particles, the lower percent export for Al, Fe and Mn was not due to adsorption of these metals to suspended particles travelling through the site. The net particulate

TABLE II

Net annual and seasonal particulate metal import ( $\mu\text{g m}^{-2}$ ), seasonal dissolved metal export ( $\mu\text{g m}^{-2}$ ), percent net export that the net import could account for, seasonal export from macrophytes as a percent of the annual loading, and seasonal export as a percent of the available metals in the sediments for two sites in southern Quebec

Metal	Net annual import	Net seasonal import	Seasonal export	Seasonal export as a % of annual load	Seasonal import as a % of export	% recycled from sediments
<i>Fitch Bay – L. Memphremagog</i>						
Al	$9.0 \times 10^8$	$2.1 \times 10^{-3}$	$3.0 \times 10^5$	<0.01	0.7	0.25
Cr	$4.6 \times 10^6$	$1.5 \times 10^{-4}$	$2.8 \times 10^3$	0.05	5.3	0.45
Cu	$2.6 \times 10^6$	$5.1 \times 10^{-5}$	$2.4 \times 10^3$	0.09	2.1	0.69
Fe	$3.0 \times 10^9$	$3.2 \times 10^{-3}$	$1.2 \times 10^5$	<0.01	2.8	0.03
Mn	$1.0 \times 10^8$	$1.4 \times 10^{-3}$	$2.2 \times 10^5$	0.22	0.6	1.6
Ni	$6.9 \times 10^6$	$8.3 \times 10^{-5}$	$2.5 \times 10^3$	<0.01	3.4	0.27
Zn	$8.6 \times 10^6$	$1.3 \times 10^{-4}$	$2.3 \times 10^3$	3.5	5.7	0.20
<i>L. Weedon</i>						
Al	$3.1 \times 10^5$	$1.5 \times 10^{-3}$	$1.5 \times 10^5$	48	1.0	0.22
Cr	$3.8 \times 10^3$	$5.7 \times 10^{-5}$	$2.1 \times 10^3$	54	2.8	0.55
Cu	$8.3 \times 10^3$	$2.0 \times 10^{-5}$	$4.7 \times 10^3$	57	0.4	1.2
Fe	$8.9 \times 10^5$	$1.9 \times 10^{-3}$	$3.4 \times 10^5$	39	0.6	0.30
Mn	$6.8 \times 10^4$	$1.7 \times 10^{-4}$	$2.3 \times 10^4$	34	0.7	0.70
Ni	$4.8 \times 10^3$	$1.9 \times 10^{-5}$	$2.4 \times 10^3$	50	0.8	0.47
Zn	$8.7 \times 10^3$	$5.5 \times 10^{-5}$	$4.0 \times 10^3$	46	1.5	0.44

input to the Fitch Bay weedbed was minor, varying only between 0.63% (Mn) and 5.7% (Zn) of the dissolved metal export over the study period (Table II).

The loss of metals from the Fitch Bay weedbed during the study period represented a very small fraction of the estimated net annual metal input to the bay (Table II). The export ranged from <0.01% (Al and Fe) to 3.5% (Cr).

There was a similar pattern of metal loss from the plants for all metals studied (Figure 2). The daily export rate was initially undetectable (mid-June). By July, differences in dissolved metal concentrations of the water samples upstream and downstream from the weedbeds were detected. The peak loss was measured on 16 August and generally dropped steadily to 27 September when daily export reached very low (Al, Fe and Mn) to undetectable (Cr, Cu, Ni and Zn) levels.

The maximum standing stock (grams fresh weight  $\text{m}^{-2}$ ) of *M. spicatum* at the Fitch Bay site occurred by late July. The mean biomass declined slightly thereafter but was not significantly lower until the 6 September sampling date (Figure 3). The mean export of metals from the weedbed therefore occurred approximately 1

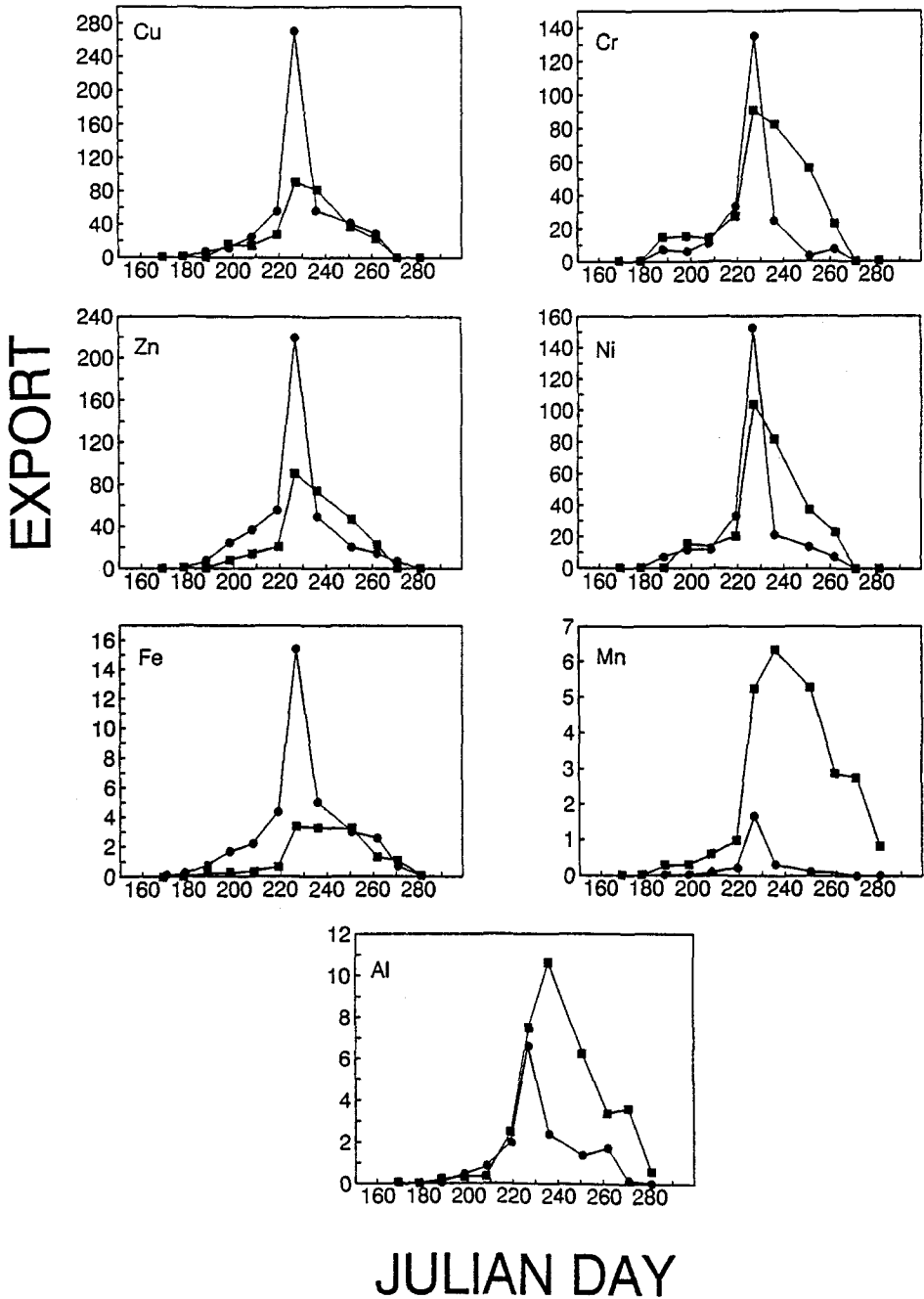


Fig. 2. The areal rate of daily export of dissolved metals from mid-June to early October from Fitch Bay, L. Memphremagog (■) and L. Weedon (●) Quebec, as determined with a mass-balance approach. The units are  $\mu\text{g m}^{-2} \text{ day}^{-1}$  for Cr, Cu, Ni and Zn and  $\text{mg m}^{-2} \text{ day}^{-1}$  for Al, Fe and Mn.



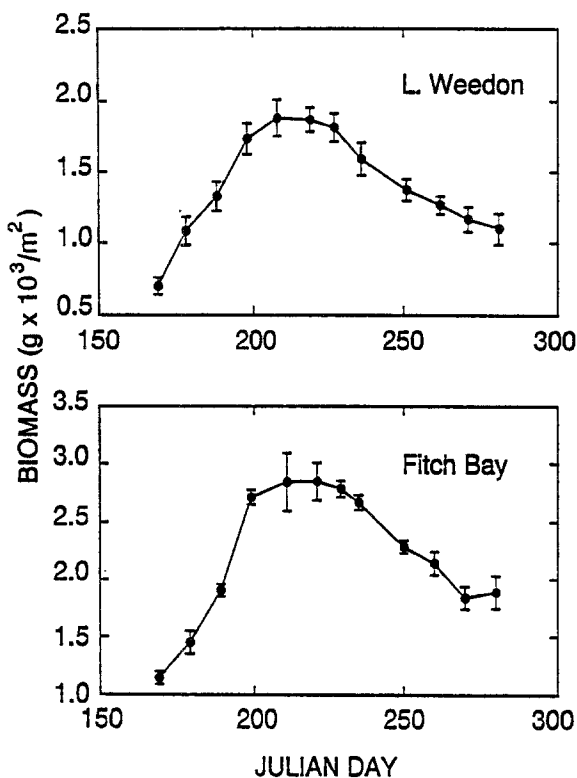


Fig. 3. Mean biomass (error bars represent 2 standard errors) of *M. spicatum* from mid-June to early October at one site in Fitch Bay, L. Memphremagog and in L. Weedon, Quebec.

month after the plants attained their maximum seasonal biomass.

#### LAKE WEEDON

The metal export from the plants in L. Weedon followed a similar pattern to that of the Fitch Bay site. Similar values were calculated for the percent metal inventory lost through the study period (Table I) and as in Fitch Bay, the percent export appeared to fall into 2 distinct groupings. In L. Weedon the shape of the metal export curves was somewhat smoother than for Fitch Bay, indicating a less abrupt pulse of metals with the onset of senescence. The amount of particulate metal loading to the weedbed during the study period, as a function of the metal exported, was roughly the same as the Fitch Bay site (0.01% for Mn and 0.53% for Zn).

The loss of metals from L. Weedon during the study period varied between 33% (Mn) and 56% (Cu) of the annual net allochthonous loading (Table II). Lake Weedon is therefore a net sink for metals annually, but the recycling of metals by the macrophytes represents a large source of internal loading during the late summer period.

The pattern of whole-lake standing stock was similar to that of Fitch Bay; however, the biomass only reached ca  $1.9 \text{ kg m}^{-2}$ , approximately 65% the biomass at the Fitch Bay site. Plant Cr, Cu, Fe, Ni and Zn was higher, but Al and Mn was lower in the plants in L. Weedon than those in Fitch Bay.

### Discussion

One of the most fundamental questions concerning the role of aquatic macrophytes in lake ecosystems centres around the degree to which weedbeds are sources or sinks for materials. Carpenter and Lodge (1986) suggested that the measured effect of weedbeds on material flow should depend upon the material examined (i.e., dissolved or particulate) and the time scale of the examination. Processes in the littoral vary over time scales of hours (e.g., exudation of photosynthetic products) to years (e.g., trapping and incorporation of particles into the sediments). We have attempted to quantify our two sites as metal sources or sinks on time scales ranging from a relatively short seasonal scale (the macrophyte's growing season) to a longer (annual) scale. Weedbeds can serve as sinks for particles, and their associated metals, for centuries (Schroder 1988) as long as the integrity of the beds are maintained.

During our seasonal study the Fitch Bay and L. Weedon weedbeds were net sources of all dissolved metals to the surrounding waters. The loss of dissolved metals was far in excess of the particulate metal trapped by the beds even though the weedbeds were net sinks for suspended sediments during this period. A possibility exists that metals adsorbed to the suspended sediment load to the weedbeds was, upon sedimentation, desorbed and released such that the release was responsible for the observed pulse in dissolved metals. However, our calculations indicate that the particulate metal input trapped at both sites, even if completely desorbed and exported, could not possibly account for the pulses in dissolved metals measured. This clearly shows that during the study period the export of dissolved metals out of Fitch Bay and L. Weedon far exceeded particle sedimentation; therefore, both weedbeds are net sources of metals over the course of the study period. However, on an annual basis both sites are a net sink for metals because the maximum estimated metal loss during senescence was only 56% (Cu in L. Weedon) of the net annual metal loading to the lake via particulate inputs. This, and other values for L. Weedon are probably maximum annual estimates because the particle retention coefficient of Rowan (1992) considers basin morphometry but not any particle trapping by macrophytes and would therefore be a minimum annual estimate of particle trapping by the lake. Our calculation of metal export by the plants as a fraction of annual metal input to the lake would contain this same error.

Both sites were dominated by *M. spicatum*, but the quantitative effect of the weedbeds on the lake or bay metal mass balance is very different. The Fitch Bay weedbed accounts for a very small fraction of the bay surface area ( $1.8 \times 10^{-7}$ ) and the weedbed has a very small effect on the annual metal loading to the water mass

(<0.5%). In contrast, approximately 90% of the L. Weedon surface area supports macrophytes and the plants there account for 33–56% of the annual loading to the water mass. The effect of the macrophytes on the annual metal inputs is therefore a function of the amount of littoral zone, but would also be affected by macrophyte biomass and allochthonous loading. We have demonstrated that in at least 1 shallow lake harbouring abundant macrophyte biomass the plants can play a major role on the metal dynamics within the lake and in outflowing water. On an areal basis, both weedbeds have similar metal exports as the differences varied by factors of 2–10. The percent of sediment metal recycled by the macrophytes varied less, with maximum differences about a factor of 1.5.

The export of dissolved metals from the littoral zone could represent a significant source of metals on the lake's biota. The metals are released from the macrophytes in a dissolved form (possibly bound to organic compounds), and therefore are potentially more bioavailable than sediment bound metals. Landers (1982) measured pulses in chlorophyll *a* resulting from the release of P by senescing macrophytes in Monroe Reservoir, thus indicating the potential importance of elements released during macrophyte senescence. The use of metals by e.g., phytoplankton would depend upon release from the plants preceding the fall phytoplankton bloom. This would likely be the case for systems dominated by *M. spicatum*, but might not for those dominated by species that senesce in September and October (e.g., *V. americana*; Carpenter 1980a, b).

Since there was no increase in the metal content of suspended particles during the study period, the metals lost by the plants and exported from the weedbed were in the dissolved phase. The lower % export of Al, Fe and Mn from the weedbeds could result in two ways. First, metals affected by large changes in redox potential (Fe and Mn) could, upon leaching, precipitate as insoluble hydrous oxides and sink from the water column. Al would likely co-precipitate with the insoluble oxides. An alternative hypothesis is that Al, Fe and Mn within the above-ground macrophyte tissues are associated with tissue pools that are less soluble (e.g., bound within cell walls) than those of the trace metals and therefore require more complete tissue breakdown to be released.

The diverse macrophyte community in L. Weedon may explain the more protracted metal export pulse in this lake. At both sites we have measured a community event but the Fitch Bay site is predominantly *M. spicatum*. In L. Weedon we measured a community event where the minor species (*P. perfoliatus* and *V. americana*) might have senesced at different times than *M. spicatum*, effectively smearing the measured pulse.

There has historically been difficulty in measuring element fluxes from macrophyte beds because water exchange between the littoral and pelagic zones is difficult to quantify. The use of enclosures to isolate water around the macrophytes is also problematic because temperature, light, grazer composition etc., tends to deviate, with time, from the conditions outside the enclosures. The 2 sites we chose allowed an accurate determination of water exchange, and required no artificial measures to

isolate water masses. Expressing our calculations on an areal ( $\text{m}^2$ ) basis facilitates between-site comparisons that would otherwise be very difficult. The magnitude of the fluxes calculated ( $\text{per m}^2$ ) shows that the amount of recycling of the estimated available sediment metal (the 'active' layer) was similar between our sites. Thus we feel our results are relevant to the majority of weedbeds where water exchange is difficult to quantify, and is the best information concerning metal fluxes in weedbeds currently available.

Our results also have important implications for the cycling of contaminants in lakes because they show that only a small fraction of the metals incorporated into littoral sediments are not permanently buried. Our calculations show that it would require roughly 100–200 yr for the plants to retrieve and export the available metals in their rooting zone (this is approximately 10 times the time required to deplete the available phosphorus in Chemung Lake; Wile *et al.*, 1979). Thus, for all but highly toxic or concentrated metal deposits, the risk to the lake posed by the recycling of metals from the sediments by the macrophytes is probably small.

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### References

- Adams, M. S. and Prentki, R. T.: 1982, *Arch. Hydrobiol. (Suppl.)* **62**, 333.  
Allen, H. L.: 1971, *Ecol. Monogr.* **41**, 97.  
Barko, J. W. and Smart, R. M.: 1980, *Freshwat. Biol.* **10**, 229.  
Barko, J. W. and Smart, R. M.: 1981, *Aquat. Bot.* **10**, 339.  
Barko, J. W. and Smart, R. M.: 1982, *Aquat. Bot.* **12**, 157.  
Bole, J. B. and Allen, J. R.: 1978, *Water Res.* **12**, 353.  
Bristow, J. M. and Whitcombe, M.: 1971, *Am. J. Bot.* **58**, 8.  
Carignan, R. C. and Kalff, J.: 1980, *Science* **207**, 987.  
Carignan, R. C. and Kalff, J.: 1982, *Limnol. Oceanogr.* **27**, 419.  
Carpenter, S. R.: 1983, in J. Taggart (ed.), *Lake Restoration, Protection and Management*, U.S.E.P.A., Washington, D.C., pp. 105–111.  
Carpenter, S. R.: 1980a, *Ecology* **61**, 1145.  
Carpenter, S. R.: 1980b, *Am. Mid. Nat.* **104**, 163.  
Carpenter, S. R. and Lodge, D. M.: 1986, *Aquat. Bot.* **26**, 341.  
Cattaneo, A. and Kalff, J.: 1980, *Limnol. Oceanogr.* **25**, 280.  
DeMarte, J. A. and Hartman, R. T.: 1974, *Ecology* **55**, 188.  
Gibbons, H. L.: 1981, 'Phytoplankton Production and Regulating Factors in Liberty Lake, Washington with Possible Implication of Restoration Activities on the Primary Productivity', Ph. D. thesis, Washington State Univ.  
Hakanson, L. and Jansson, L.: 1983, *Principles of Lake Sedimentology*, Springer-Verlag, New York, 316 p.

- Hersch, R. W.: 1982, in R. W. W. Scott (ed.), *Developments in Flow Measurement* – 1. Applied Science Publishers, Englewood, New Jersey, U.S.A., pp. 253–305.
- Hough, R. A. and Wetzel, R. G.: 1975, *Verh. Int. Verein. Limnol.* **19**, 939.
- Huebert, D. B. and Gorham, P. R.: 1983, *Aquat. Bot.* **16**, 269.
- Jackson, L. J.: 1992, 'Rooted Aquatic Macrophytes and the Cycling of Littoral Zone Metals', Ph.D. Thesis, McGill University, 191 pp.
- Jackson, L. J. and Kalff, J.: 1991, *Freshwat. Biol.* **29**, 351.
- Jackson, L. J., Rasmussen, J. B., Peters, R. H., and Kalff, J.: 1991, *Biogeochemistry* **12**, 71.
- Landers, D. H.: 1982, *Limnol. Oceanogr.* **27**, 428.
- Lie, G. B.: 1979, in J. E. Breck, R. T. Prentki and O. L. Loucks (eds.), *Aquatic Plants, Lake Management, and Ecosystem Consequences of Lake Harvesting*, Proceedings of Conference at Madison, Wisconsin, pp. 101–126.
- Lodge, D. M.: 1991, *Aquat. Bot.* **41**, 195.
- Moore, B. C., Gibbons, H. L., Funk, W. H., McKarns, T., Nyznyk, J., and Gibbons, M. V.: 1984, in *Lake and Reservoir Management, Proceedings of the third Annual Conference, North American Lake Management Society*, U.S.E.P.A., Washington, D. C., pp. 113–117.
- Nichols, D. S., and Keeny, D. R.: 1973, *Hydrobiologia* **42**, 509.
- Prentky, R. T., Adams, M. S., Carpenter, S. R., Gasith, A., Smith, C. S., and Weiler, P. R.: 1979, *Arch. Hydrobiol. (Suppl.)*, **57**, 221.
- Rowan, D. J.: 1992, 'The Distribution, Texture and Trace Element Concentrations of Lake Sediments', Ph. D. Thesis, McGill University, 225 pp.
- Schroder, V. R.: 1988, *Arch. Hydrobiol.* **112**, 265.
- Wetzel, R. G.: 1969, *Verh. Int. Verein. Limnol.* **17**, 72.
- Wetzel, R. G. and Manny, B. A.: 1972, *Verh. Int. Verein. Limnol.* **18**, 162.
- Wile, I., Hitchin, G., and Beggs, G.: 1979, in: J. E. Breck, R. T. Prentki and O. L. Loucks (eds.), *Aquatic Plants, Lake Management, and Ecosystem Consequences of Lake Harvesting*, Proceedings of Conference at Madison, Wisconsin, pp. 145–159.