



## Seepage patterns, pore water, and aquatic plants: hydrological and biogeochemical relationships in lakes

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Received 24 April 2002; accepted in revised form 23 May 2003

**Key words:** Aquatic macrophyte, Coupled hydrological and biogeochemical processes, Lake hydrology, Lakeshore seepage, Pore water chemistry

**Abstract.** This study documented linkages between lakeshore seepage fluxes, pore water chemistry, and aquatic plants in several lakes of the Adirondack Mountains region of New York, USA. Three replicate stations were set up along each of four different lake shorelines. From June through September 1998 and from snowmelt in April through August 1999, seepage flux was measured with seepage meters. Throughout this time period, lake surface water and pore water chemistry were monitored weekly to biweekly. At each station, leaf tissue chemistry of the water lily *Nuphar variegatum* was measured once in each year. Sediment chemistry and plant abundance were also measured once in 1998. We found that pore water concentrations of base cations, iron, and zinc were related to the direction, magnitude, and variability of seepage fluxes. Concentrations of base cations, iron, and zinc were both highest and most variable where seepage was low (0 to 50 mL m<sup>-2</sup> h<sup>-1</sup>) in contrast to being more stable where seepage was highest and variable (–608 to 612 mL m<sup>-2</sup> h<sup>-1</sup>). Leaf tissue chemistry and plant abundance were also related to seepage patterns. *N. variegatum* leaves had elevated zinc content at stations with low average discharge. Knowledge of seepage patterns helped to explain spatial patterns of elevated trace metal content in both pore water and plant tissues. Our work suggests that the hydrological process of lakeshore seepage exerts important controls on lakeshore biogeochemistry.

### Introduction

Research over the past quarter century reveals that the seepage of water through sediments occurs along nearly all lakeshores although this ‘invisible’ process is frequently overlooked (McBride and Pfannkuch 1975; Lee 1977; Winter 1978; Mitchell et al. 1988; Shaw and Prepas 1990; Winter 1999). The locations of recharge or discharge zones and the actual seepage flux magnitudes vary considerably among different lakes as well as at sub-meter spatial scales within lakes (McBride and Pfannkuch 1975; Lee 1977; Brock et al. 1982; Mitchell et al. 1988; Asbury 1990; Schafran and Driscoll 1990; Shaw and Prepas 1990; Belanger and Kirkner 1994). Seepage also varies temporally across days, seasons, and years (Asbury 1990; Shaw and Prepas 1990; Snucins et al. 1992; Schneider 1994; Sebestyen and Schneider 2001). Despite these

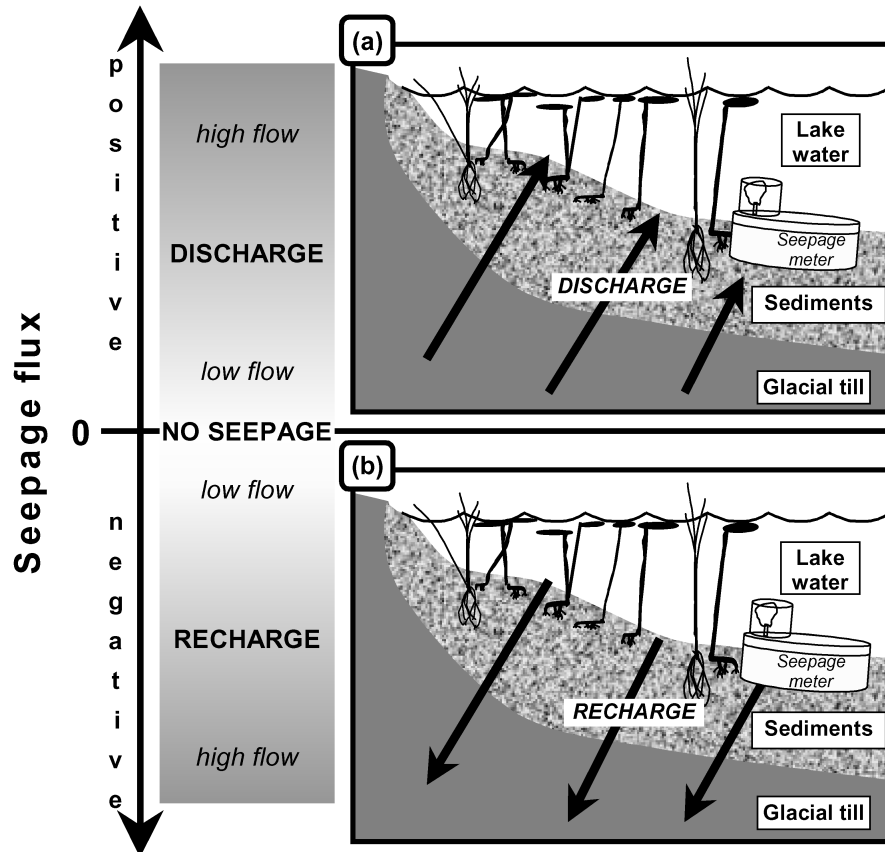


Figure 1. Seepage, the advective movement of water through the sediment profile, passes through the dynamic interface of lake surface water, groundwater, sediments, macrophyte roots, and till, soils, or bedrock. A seepage flux expresses both magnitude and direction: a positive seepage flux indicates discharge of groundwater to the lake (a), and a negative seepage flux indicates recharge of lake water to a groundwater system (b). 'High' and 'low' flow can refer to the relative magnitude of either discharging or recharging seepage fluxes.

inherent variabilities, studies consistently find seepage in the shoreline littoral zones that coincide with communities of highly productive aquatic plants and associated fish, macro-invertebrate, and amphibian inhabitants (Wetzel 1990; Kalff 2002). Therefore, the dynamic seepage process links hydrology to lakeshore ecosystems where and when water seeps through the interface of lake surface water, groundwater, pore water, sediments, and rooted aquatic macrophytes (Figure 1).

Evidence from a number of studies supports a hypothesis that changes of pore water chemistry with seepage flux can influence lakeshore ecosystems (Connor and Belanger 1981; Loeb and Hackley 1988; Asbury 1990; Schafran

and Driscoll 1990; Schneider 1994). The transport of solutes and dissolved gases with seepage has the potential to influence biogeochemistry of pore waters as well as the broader lakeshore environment (Lee et al. 1980; Frape and Patterson 1981; Brock et al. 1982; Schafran and Driscoll 1990, 1993). Namely, pore water biogeochemistry will logically change when seepage fluxes affect the transport of gases and other dissolved solutes. Such interactions become particularly relevant when nutrients or toxic substances carried by seepage bathe plant roots that are interspersed throughout shoreline sediments.

A few studies have already documented positive relationships between macrophyte or benthic algae biomass and seepage (Loeb and Hackley 1988; Lodge et al. 1989; Lillie and Barko 1990; Schneider 1994; Hagerthey and Kerfoot 1998; Rosenberry et al. 2000). However, seepage has not been comprehensively considered in relation to the availability of nutrients and toxic elements to aquatic macrophytes.

This paper describes part of a two-component study of the hydrology (Sebestyen and Schneider 2001) and biogeochemistry of lakes in the Adirondack Mountains of New York, USA. In the Adirondack Mountains, element cycles in nearshore areas of lakes have been altered by acidification, an associated decline in base cation ( $C_B$ ) concentrations, and the accumulation of trace metals in sediments (Galloway and Likens 1979; Likens et al. 1998; Stoddard et al. 1998; Lawrence et al. 1999; Driscoll et al. 2001). Trace metals have also accumulated in the tissue of aquatic macrophytes that are common in Adirondack lakes (Campbell et al. 1985; Reimer and Duthie 1993; Thompson-Roberts et al. 1997). Recent declines of aquatic macrophytes in Adirondack region lakes, specifically the yellow spatterdock water lily (*Nuphar variegatum*) may be associated with the continuing declines of base cation concentrations and elevated trace metals in the environment (Schneider 1997; R.L. Schneider, unpublished data). Past studies of hydrology have identified seepage flowpaths to Adirondack lakes (Peters and Driscoll 1987; Staubitz and Zarriello 1989; Schafran and Driscoll 1990, 1993) but have not investigated patterns of seepage that influence solute availability in pore water and lakeshore vegetation.

The primary objective of this study was to determine if pore water chemistry varied with seepage patterns along different lakeshores. The secondary objectives were: (1) to determine if *Nuphar* leaf tissue chemistry was related to pore water chemistry, and (2) to investigate relationships of seepage patterns to macrophyte abundance and to levels of elements in leaf tissue of *N. variegatum*.

### Site description

Seepage was measured and water samples were obtained along four shorelines located in Lower Sylvan Pond, Dart Lake, and Wilmurt Lake near Old Forge, NY, USA, in the southwest region of the Adirondack Mountains (Figure 2). These temperate forested watersheds contain a mix of hardwoods and conifers (Cronan et al. 1987) that drain to the Hudson or St. Lawrence Rivers and

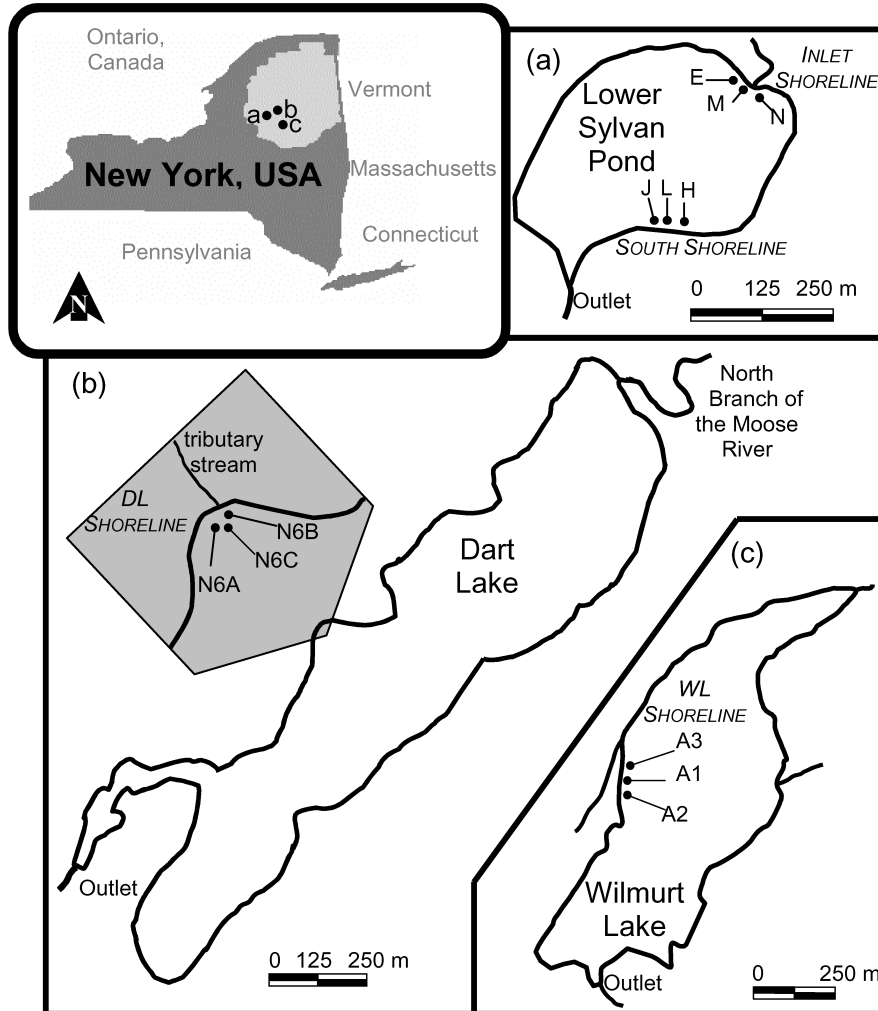


Figure 2. The New York State map (USA) shows the locations of the Adirondack Park and the study lakes. Lake shoreline maps show locations of the sampling stations at Lower Sylvan Pond ( $43^{\circ}36'$ ,  $74^{\circ}56'$ ), Dart Lake ( $43^{\circ}47.25'$ ,  $74^{\circ}52'$ ), and Wilmurt Lake ( $43^{\circ}27'$ ,  $74^{\circ}44.25'$ ). The gray shaded inset above Dart Lake gives an enlarged view of the shoreline segment.

ultimately to the Atlantic Ocean. Metamorphic bedrock inhibits deep infiltration of groundwater and flowpaths are limited to shallow glacial tills (Peters and Murdoch 1985; Peters and Driscoll 1987; Staubitz and Zarriello 1989). The average annual precipitation of about 1000 mm is spread evenly throughout the year (Shepard et al. 1989) and a snow pack develops over winter. Snowmelt generates the largest surface runoff event during a typical year.

Lower Sylvan Pond is a 5.9 ha lake with a mean water depth of 2.5 m, a maximum depth of 4.9 m, and an elevation of 622 m above mean sea level. A single second order stream originates in an undeveloped 48.7 ha watershed, passes through Upper Sylvan Pond, and then discharges into Lower Sylvan Pond along the north shore. We studied two sections of the shoreline at Lower Sylvan Pond, the South (stations H, J, and L) and Inlet shorelines (stations E, M, and N).

The North Branch of the Moose River flows through Dart Lake and several small tributaries enter around the perimeter of the lake. The lake has a surface area of 51.8 ha, a watershed area of 10,800 ha (ALSC 2002), a maximum depth of 17.7 m, a mean depth of 7.3 m, and an elevation of 536 m. Dart Lake has been investigated in numerous biogeochemical studies (Rudd et al. 1986; Schafran and Driscoll 1987a,b; White and Driscoll 1987a,b; White et al. 1989; Schafran and Driscoll 1990, 1993) and surface water chemistry has been routinely monitored as part of the Adirondack Long Term Monitoring program (Driscoll and Van Dreaseon 1993). The lake margins are forested except for a portion occupied by a camp and the contributing watershed includes many lakes. The study area, DL shoreline (stations N6A, N6B, and N6C), was in an embayment on the north shore near an area where Schafran and Driscoll (1990) previously measured seepage flux.

In 1998, limited work was done at Wilmurt Lake, a 39 ha mountain-top lake. Several first and second order tributaries enter the lake and the watershed is undeveloped except for recreational cabins along a portion of the shoreline. The lake has a watershed area of 270 ha (ALSC 2002), a maximum depth of 10.7 m, a mean depth of 3.6 m, an elevation of 752 m, thermally stratifies in summer, and lime has been applied yearly during snowmelt to maintain a circumneutral pH. The study area, WL shoreline (stations N6A, N6B, and N6C), was along the west shore.

Throughout this paper, we refer to the study units by lake name (Lower Sylvan Pond, Dart Lake, and Wilmurt Lake), as sections of the shoreline (South and Inlet at Lower Sylvan Pond, DL, and WL), or as the individual stations that are nested within shorelines (e.g. stations A1, A2, and A3 at the WL shoreline).

## Methods

Shoreline segments were chosen to include sites where *N. variegatum* grew in the past (personal communications May 1998: H. Hawley, Wilmurt Lake Club; D.C. Josephson, Cornell University, Little Moose Field Station; P. Meneilly, Camp Gorham YMCA). However, we had no *a priori* knowledge of seepage fluxes or macrophyte abundance at these sites because plants were only beginning to grow at the time of site selection. We placed three replicate sampling stations along each shoreline to avoid submerged detritus and rocks, for ease of site access by wading from shore, with sediments that could support walking,

and to have similar water depths at stations. The stations were installed on planar, shallowly sloping lake bottoms along each 50 m (or shorter) section of shoreline. Stations were between 4 and 16 m from the shore and water depths were 0.45–0.6 m at the time of equipment installation.

Equipment at each station included a single seepage meter (Lee 1977), a control seepage device (Schneider 1994), and pore water samplers. Within a station, the seepage meter, control device, and pore water samplers were equidistant from the shore in order to reduce spatial variability associated with reported exponential decreases of seepage flux with increasing distance from shorelines (McBride and Pfannkuch 1975; Shaw and Prepas 1990).

#### *Seepage flux measurement*

Seepage fluxes were measured with seepage meters based on the design of Lee (1977) and described by Sebestyen and Schneider (2001). Briefly, the seepage meters were 0.52 m diameter and made of stainless steel. Flexible plastic bags (light density polyethylene) were attached to the top ports (1.3 cm diameter) on the seepage meters to measure water fluxes. The bags (4 L capacity) were pre-filled with 1.0 L of lake water to prevent anomalous influxes of water as observed by Shaw and Prepas (1989) and air was expelled from the bags before attachment. The seepage meters were permitted to flush for at least one day before the first measurement and remained stationary throughout the study.

Seepage flux ( $Q$ ) was calculated using the formula

$$Q = \frac{V_f - V_o}{\Delta t \cdot A}$$

The initial volume of water placed in a bag is  $V_o$ ,  $V_f$  is the bag volume at the time of removal from a seepage meter,  $\Delta t$  is the time that a bag was attached to the seepage meter (typically 22–26 h), and  $A$  is the surface area covered by the meter (0.21 m<sup>2</sup>). Positive seepage flux values indicate discharge and negative seepage flux values indicate recharge (Figure 1). We did not attempt to quantify or correct for potential underestimates of seepage discharge (Asbury 1990; Belanger and Montgomery 1992). Regardless, if our measured values are underestimated, our interpretations are based on relative magnitudes of seepage fluxes and do not change. Also, we compare our data to several others studies in which seepage fluxes were not adjusted.

During a drought in 1999, water levels were unusually low throughout the Adirondack region. Lake water levels substantially dropped at Dart Lake as the drought intensified and water depths at the sampling stations were less than 0.10 m at times. Seepage measurements were not made when water levels at a station were less than 0.1 m deep (Dart Lake, 30 June to 2 July and after 28 July 1999).

Schneider (1994) noted that seepage meters may ineffectively quantify seepage fluxes under low flow due to physical characteristics of bags and

sediments (Shaw and Prepas 1989; Asbury 1990) and pioneered the use of control devices. A control device was located and monitored in conjunction with each seepage meter. Control device design and use are detailed in Schneider (1994; see also Sebestyen and Schneider 2001). Briefly, control devices consisted of pre-filled bags (identical to those of seepage meters) that were suspended 0.15 m above the lake bottom so that the bags measure volume changes due to other factors but not seepage. Comparison of control device and seepage meter data indicated that seepage meters effectively quantified seepage patterns in our study (Sebestyen 2000; Sebestyen and Schneider 2001).

#### *Lake surface water and pore water sampling*

Surface and pore water samples were collected for chemical analyses. Lake surface water samples were collected approximately 0.1 m beneath the water surface at each station. Shallow pore water samples were collected from the rhizosphere (0.15 m) and deep pore water samples were collected below the rooting zone (0.30–0.50 m) with *in situ* pore water samplers (Schneider 1994). A pore water sampler consisted of a Luerlock<sup>®</sup> valve connected to the above-sediment end of a flexible plastic tube (0.32 cm diameter, vinyl) that passed lengthwise through a structural PVC pipe and terminated inside a tip made of Delrin<sup>®</sup> plastic. The below-sediment end of a tube was perforated over 10 cm and wrapped in a polyethylene filter that fit inside the permeable tip. A seal above the tip prevented lake water from infiltrating through the PVC tube to the sediments. The pore water samplers were pushed or pounded into the sediments. Only shallow pore water samplers were used at Dart Lake because a dense till layer encountered at about a depth of 0.3 m precluded deeper insertion of the devices.

Immediately after installation, at least 60 mL of pore water were extracted and the samplers then equilibrated for at least 3 days prior to the first sampling. The pore water samplers were removed, refurbished, and reinstalled at the stations before sampling reconvened in 1999. Sampler integrity was periodically tested using dye tracers to ensure that lake water was not moving into the tips.

Pore water samplers were placed 0.5–2 m from seepage meters (depending upon submerged debris) to maintain a nested design and minimize the effects of spatial variability of seepage (McBride and Pfannkuch 1975; Shaw and Prepas 1990; Belanger and Montgomery 1992). To prevent seepage meters from influencing pore water samples, buffer zones at least 0.5 m wide were left between pore water samplers and seepage meters (e.g. seepage meters may influence sediment redox chemistry, Brock et al. 1982; Belanger and Mikutel 1985; Belanger et al. 1985; Zimmerman et al. 1985).

Pore water samples were extracted with 60 mL syringes. Before sampling, syringes and connection points (Luerlock<sup>®</sup> valves) were rinsed with NANO-pure deionized water. Each time before collecting samples for chemical

analysis, 60 mL of pore water were evacuated and discarded to purge the pore water samplers that had approximate tube volumes of 20 mL. Subsequent volumes of pore water were collected for chemical analyses.

We measured pH potentiometrically on unfiltered water samples in the field except during snowmelt (measured within 24 h at a field laboratory). Additional samples were filtered through 1  $\mu\text{m}$  glass fiber filters (Whatman GF/B filters in Millipore Swinex filter holders) and directly transferred to new 60 mL Nalgene high density polyethylene sample bottles. Samples were placed in an iced cooler, acidified to pH less than 2.0 within 24 h of collection, and then stored frozen until analyzed for total solute concentrations. Concentrations of  $C_B$  (the sum of calcium, magnesium, potassium, and sodium concentrations), total dissolved phosphorus (TDP), and trace metals were determined with inductively coupled plasma spectrophotometry (ICP, Thermo Jarrell Ash) within 10 months of sample collection. In this paper, trace metal data are presented for aluminum (Al), iron (Fe), and zinc (Zn).

To monitor for sample contamination during collection, filtering, and storage, NANOpure deionized water was collected from a beaker with a syringe, filtered, transferred to sample bottles, acidified, and subsequently analyzed by ICP. These blank samples were collected in the field in June, July, and August 1999 (three at Lower Sylvan Pond and two at Dart Lake on every date that pore water was sampled). Water sample blanks indicated that the surface and pore water sampling technique did not contaminate water samples (Sebestyen 2000).

#### *Seepage and water chemistry sampling regime*

In 1998, seepage was measured more frequently and over a shorter time period than in 1999 to characterize the hydrologic patterns with great detail at Lower Sylvan Pond and Dart Lake. From July to August 1998, seepage was measured 5–7 times a week and water samples were collected once or twice a week. Sample collection was initiated immediately prior to the final spring snowmelt event in April 1999 but only at Lower Sylvan Pond (South and Inlet shorelines) due to inherent difficulties in accessing the other snow and ice covered lakes. Seepage was measured daily and seepage meters and pore water samplers were accessed through holes cut in the lake ice. Water samples were collected once before and 4 times during the 3-week snowmelt. After snowmelt sampling, seepage meters were monitored again at both Lower Sylvan Pond (South and Inlet shorelines) and Dart Lake. From May to August 1998, seepage was measured for 3 consecutive days every other week and samples were collected once during each 3-day period.

Wilmurt Lake was sampled less frequently and only in 1998 due to limited site accessibility. Seepage was generally measured only on the day of sample collection and samples were collected every 6–10 days from July through August 1998. Although less data were collected, the Wilmurt Lake observations offer considerable insight and provide information for an additional shoreline.



*Sediment and leaf tissue sampling*

Two replicate sediment cores were collected from each station once in late July 1998 with a sediment corer (0.06 m diameter PVC) inserted until reaching an impenetrable layer. The sediment cores were taken from the center of two different randomly selected 0.1 m<sup>2</sup> cells of a 3.0 m<sup>2</sup> quadrat. Sediment cores were sectioned into 0.10 m segments from top to bottom in the field (maximum core length = 0.48 m), but the Dart Lake sediment cores (0.08–0.14 m) were too short to segment.

The aquatic plants emerge from the sediments in June, the plants senesce in September or October, and winter ice cover removes the standing biomass each year. Once in late July 1998, stems of all floating leaved and emergent species were counted in three 0.1 m<sup>2</sup> cells of a 3.0 m<sup>2</sup> quadrat to estimate macrophyte abundance adjacent to each station. Stems were counted in the cell closest to the pore water samplers and two other randomly selected cells. At stations with sparse macrophyte growth (approximately 50 or fewer stems), all stems within the quadrat were counted. Plant abundance was calculated for each station as an average stem abundance of the three cells or for the entire quadrat, accordingly.

We collected samples of *Nuphar* to document leaf tissue chemistry of a native water lily that is undergoing a regional decline and to assess relationships of seepage patterns to leaf tissue chemistry. *Nuphar* was collected at stations H and J (South shoreline at Lower Sylvan Pond), N (Inlet shoreline at Lower Sylvan Pond), N6A and N6B (DL shoreline), and A1 and A2 (WL shoreline). The closest *Nuphar* leaves were collected once each field season in late July. *Nuphar* grew within three meters of stations except at J (within 11 m) and N (within 15–20 m). *Nuphar* did not grow at four of the stations: L (South shoreline), M (Inlet shoreline), N6C (DL shoreline), or A3 (WL shoreline). At least three replicate leaves per station (from different rhizomes if possible) were removed from the petioles, wiped to remove epiphytes, and rinsed with NA-NOpure deionized water. Consumption of leaves by unidentified macro-invertebrates prevented sampling at station N in 1998 and station N6A in 1999 (note that *Nuphar* at these stations grew outside the quadrat and loss to herbivory did not affect abundance estimates).

Sediment and *Nuphar* leaf tissue samples were placed in plastic storage bags and immediately placed in an iced cooler. Sediment samples were refrigerated and *Nuphar* leaf samples were frozen within 6 h of collection upon return from the field. The samples were later dried for 24 h in a convection oven, sediment at 105 °C and *Nuphar* leaves at 60 °C. Coarse woody debris and pebbles were removed from sediment samples. A subsample of each sediment core segment was homogenized after drying to determine the percentages of sand, silt and clay (Bouyoucos hydrometer, Gee and Bauder 1986).

Sediment and *Nuphar* leaf samples were ground with a mortar and pestle, placed in quartz tubes, and ashed in a muffle furnace at 450 °C for 4 h. Percent organic content of sediment samples was measured as loss on ignition (LOI).

Samples were then digested by adding 30% hydrogen peroxide, re-ashing at 450 °C for 2 h, and adding nitric acid. Three replicate 0.50 g subsamples of each sediment core segment were digested, and up to three replicate 0.20 g subsamples of leaf samples were digested. A single leaf generally provided enough sample for digestion, but the three leaf samples from a station were aggregated if individual leaves did not yield enough sample mass (leaf lengths varied from 4.8 to 19.8 cm). Total concentrations of  $C_B$ , P, and trace metals were determined by ICP. Empty quartz tubes were processed with the samples to serve as blanks and provide evidence that sediment and *Nuphar* leaf tissue digests were not contaminated through the digestion process (Sebestyen 2000).

We ran a standard reference leaf (National Institute of Standards and Technology Standard Reference Material<sup>®</sup> 1573a, Tomato leaves) with our *Nuphar* leaf samples and reference soil (NIST Standard Reference Material<sup>®</sup> 2709, San Joaquin soil) with our sediment samples. Our recoveries were less than 100% and varied by element so we standardized our leaf and sediment element contents accordingly.

#### *Data interpretation*

Due to the sampling regime and occasional equipment malfunctions, the number of seepage flux measurements, chemistry samples, *Nuphar* leaf samples, and sediment samples collected were different among shorelines (Table 1).

Patterns of seepage flux, solute concentrations with seepage flux, and *Nuphar* chemistry with seepage flux were first assessed graphically. To retain a consistent visual presentation of seepage data, seepage fluxes are always plotted on the y-axis. The suite of three seepage measurements (measured a day prior to, at the time of, and a day after collection of water samples) was averaged per station to determine an average seepage flux for each sample collection date. These average seepage fluxes were plotted against pore water solute concentrations.

To assess relationships of *Nuphar* chemistry and seepage, we calculated a metric of seepage by averaging seepage fluxes at each station in each year. Additionally, the natural log of the standard deviation of seepage fluxes ( $\ln SD_{\text{seep}}$ ) was used as an index of seepage variability at a station. For example, a station with a large relative range of seepage fluxes had a higher relative  $\ln SD_{\text{seep}}$  (approximately 3–6) than a station with a more stable and narrow range of seepage fluxes ( $\ln SD_{\text{seep}} < 3$ ). Linear regression models were also used to test relationships of stem abundance to average 1998 seepage fluxes and the variability of seepage (SAS PROC REG, SAS Institute 1989). A *P*-value of 0.05 was used as a level of significance.

Statistical relationships of *Nuphar* chemistry to lake surface water, pore water, or sediment chemistry were tested with linear regression models (SAS PROC GLM, SAS Institute 1989) to determine pools of elements that were associated with *Nuphar* leaf chemistry. Only 1998 data were included in the

Table 1. Number of seepage flux measurements, chemistry (lake surface water, shallow pore water, and deep pore water), leaf tissue, and sediment samples collected in 1998 and 1999.

Shoreline	Seepage flux	Chemistry samples			<i>Nuphar</i> leaf tissue	Sediment core segments
		Surface	Shallow	Deep		
South	259	81	75	81	14	21
Inlet	259	83	81	80	3	22
Dart	116	57	58	n/a	6	6
Wilmurt	35	21	18	18	9	26

regression models because sediments were only collected in 1998. When leaf chemistry parameters ( $C_B$ , P, Al, Fe, and Zn) were tested, levels of significance were adjusted to a  $P$ -value of 0.01 for multiple comparisons (Bonferonni adjustment, Neter et al. 1996).

The SAS mixed procedure (PROC MIXED) was used to test for differences of sand, silt, and clay percentages between replicate cores, among shorelines, and among depths (treated as repeated measures as per McKone and Lively 1993; SAS Institute 1996). For sediment data, a  $P$ -value of 0.05 was used as a level of significance.

## Results

### *Seepage hydrology*

Temporal and spatial patterns of seepage for the shorelines differed as follows (terminology is consistent with Sebestyen and Schneider 2001):

- (1) seepage was highly variable over time and included both recharge and discharge. This temporal pattern is referred to as 'dynamic' and only occurred at the South shoreline of Lower Sylvan Pond.
- (2) low discharge generally occurred at the Inlet (Lower Sylvan Pond), DL, and WL shorelines.

The widest ranges of seepage fluxes were measured along the South shoreline of Lower Sylvan Pond. Station J ( $-608$  to  $612 \text{ mL m}^{-2} \text{ h}^{-1}$ ) had a greater range than station H ( $-112$  to  $176 \text{ mL m}^{-2} \text{ h}^{-1}$ ) or L ( $-118$  to  $108 \text{ mL m}^{-2} \text{ h}^{-1}$ ). Nonetheless, the temporal seepage patterns were similar among these three stations (Figure 3). That is, seepage fluxes increased, decreased, and changed direction at the same time among the three stations in both 1998 and 1999 creating a unique and dynamic temporal pattern of seepage that has not been reported for other lakes (Figure 3, also see Sebestyen and Schneider 2001). In particular, seepage fluxes increased immediately in response to large rainfall events and spring snowmelt. Notably, the magnitudes of highest discharge and recharge seepage fluxes were

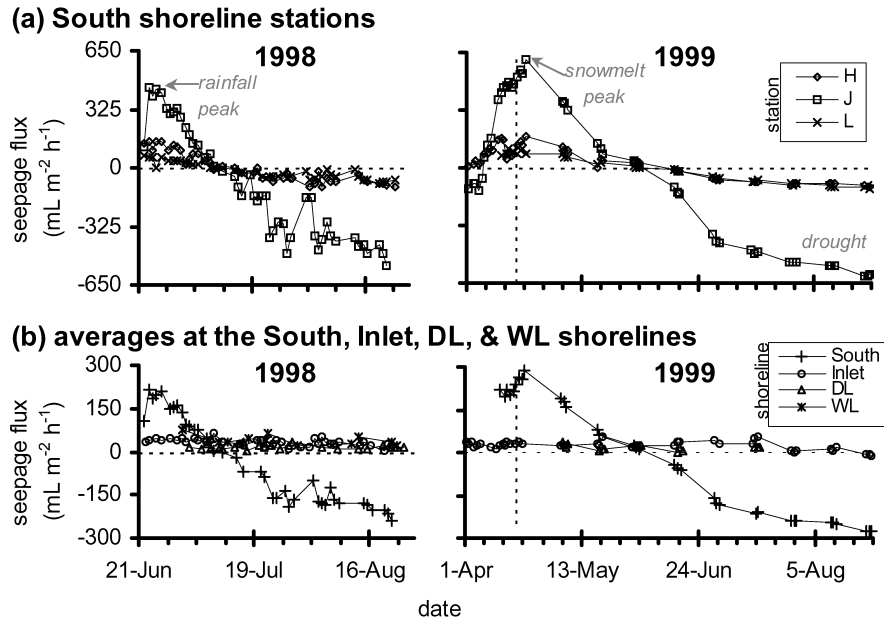


Figure 3. Seepage flux hydrographs. Distinct patterns of seepage were evident for the different shorelines. In (a), the three stations along the South shoreline had consistent temporal patterns of seepage, although magnitudes varied among the stations. Each point is a single measurement at a station and dates in 1999 to the left of the vertical dotted line indicate ice cover. Seepage fluxes at the Inlet, DL, and WL shorelines were less variable than the South shoreline. Hence, in (b), data for the three stations within a shoreline were averaged per date. Notably, only South Shoreline stations responded to rainfall and snowmelt.

nearly equal for individual South shoreline stations. For example, the absolute values of maximum recharge ( $-608 \text{ mL m}^{-2} \text{ h}^{-1}$ ) and discharge ( $612 \text{ mL m}^{-2} \text{ h}^{-1}$ ) at station J were both about  $610 \text{ mL m}^{-2} \text{ h}^{-1}$ .

Patterns of seepage were similar among the Inlet (Lower Sylvan Pond), DL, and WL shorelines relative to patterns observed at the South (Lower Sylvan Pond) shoreline (Figure 3). Low discharge usually occurred at the Inlet, DL, and WL shorelines, but seepage at the Inlet (stations E and N) and DL (stations N6A and N6B) shorelines occasionally shifted to recharge for several days. The narrowest ranges of seepage fluxes were measured at the DL shoreline stations ( $-14$  to  $49 \text{ mL m}^{-2} \text{ h}^{-1}$ ) and ranges were larger at the Inlet ( $-64$  to  $103 \text{ mL m}^{-2} \text{ h}^{-1}$ ) and Wilmurt ( $2$  to  $154 \text{ mL m}^{-2} \text{ h}^{-1}$ ) shorelines.

#### *Lake surface water and pore water chemistry*

Lake surface water pH was more variable over time than pore water pH that ranged between 5.5 and 6.8 for all stations. Lake water pH remained between

Table 2. Range of lake surface water, shallow pore water, and deep pore water solute concentrations. The average concentrations  $\pm$  1 standard deviation (SD) are in the parentheses.

Shoreline	$C_B$ (meq L <sup>-1</sup> )	TDP ( $\mu$ mol L <sup>-1</sup> )	Al ( $\mu$ mol L <sup>-1</sup> )	Fe ( $\mu$ mol L <sup>-1</sup> )	Zn ( $\mu$ mol L <sup>-1</sup> )
Lake surface water					
South	0.03–0.39 (0.15 $\pm$ 0.05)	0.01–0.43 (0.14 $\pm$ 0.12)	0.05–5.73 (1.43 $\pm$ 1.17)	0.4–3.9 (1.39 $\pm$ 0.67)	0.1–1.75 (0.68 $\pm$ 0.31)
Inlet	0.03–0.44 (0.15 $\pm$ 0.06)	0.02–0.44 (0.19 $\pm$ 0.12)	0.26–9.49 (1.63 $\pm$ 1.47)	0.2–3.3 (1.24 $\pm$ 0.59)	0.05–1.77 (0.69 $\pm$ 0.3)
DL	0.1–0.26 (0.15 $\pm$ 0.04)	0.03–0.16 (0.09 $\pm$ 0.05)	1.74–24.13 (8.22 $\pm$ 4.57)	1–14.3 (4.41 $\pm$ 2.98)	0.75–2.8 (1.52 $\pm$ 0.45)
WL	0.11–0.16 (0.13 $\pm$ 0.01)	0.01–0.45 (0.21 $\pm$ 0.12)	2.36–4.11 (3.28 $\pm$ 0.54)	0.6–1.6 (0.91 $\pm$ 0.25)	0–2.01 (1.13 $\pm$ 0.52)
Shallow pore water					
South	0.20–1.17 (0.40 $\pm$ 0.17)	0–0.99 (0.28 $\pm$ 0.24)	0.92–18.94 (4.41 $\pm$ 3.77)	20.0–183.7 (65.2 $\pm$ 24.9)	0.21–2.07 (0.82 $\pm$ 0.33)
Inlet	0.20–1.17 (0.45 $\pm$ 0.18)	0–1.49 (0.60 $\pm$ 0.42)	0.69–6.45 (1.98 $\pm$ 1.06)	7.6–189.0 (53.4 $\pm$ 36.6)	0.03–2.54 (0.76 $\pm$ 0.42)
DL	0.25–1.62 (0.61 $\pm$ 0.24)	0–0.70 (0.31 $\pm$ 0.19)	1.26–20.52 (5.43 $\pm$ 5.15)	5.5–521.6 (136.5 $\pm$ 109.0)	1.07–4.25 (1.84 $\pm$ 0.63)
WL	0.29–1.15 (0.54 $\pm$ 0.22)	0–0.45 (0.31 $\pm$ 0.24)	1.96–5.77 (2.87 $\pm$ 1.31)	15.1–139.7 (68.5 $\pm$ 41.6)	0.56–2.01 (0.95 $\pm$ 0.44)
Deep pore water					
South	0.19–0.95 (0.44 $\pm$ 0.22)	0.01–1.16 (0.42 $\pm$ 0.31)	0.35–4.75 (1.32 $\pm$ 0.73)	4.2–407.3 (70.5 $\pm$ 62.3)	0.18–2.19 (0.70 $\pm$ 0.39)
Inlet	0.16–1.16 (0.44 $\pm$ 0.18)	0.02–2.39 (0.67 $\pm$ 0.47)	0.42–45.77 (3.17 $\pm$ 6.11)	0.9–113.4 (28.2 $\pm$ 14.9)	0.07–1.81 (0.58 $\pm$ 0.30)
WL	0.31–0.68 (0.51 $\pm$ 0.14)	0–0.26 (0.02 $\pm$ 0.06)	0.96–4.16 (2.52 $\pm$ 0.90)	0.3–125.9 (60.0 $\pm$ 48.3)	0.03–0.93 (0.63 $\pm$ 0.18)

6.0 and 7.2 except during snowmelt ( $\text{pH}_{\text{minimum}} = 4.6$ ) at Lower Sylvan Pond, remained below 6.5 and dropped below 5.0 on five different dates at Dart Lake, and ranged from 6.3 to 7.0 at Wilmurt Lake (only sampled in 1998).

In contrast, pore water base cation and trace metal concentrations were consistently greater than and more variable than lake surface water (Table 2). As a point of reference to other studies, our measured concentrations of  $C_B$ ,  $H^+$ , Al, Fe, and Zn are consistent with concentration ranges reported for pore waters of Adirondack lakes (Gubala et al. 1990; Schafran and Driscoll 1990).

Concentrations of  $C_B$ ,  $H^+$ , Fe, and Zn in shallow pore water samples were consistently highest and most variable where seepage flow was low (0 to  $50 \text{ mL m}^{-2} \text{ h}^{-1}$ ) and more stable where flow was highest and most variable (Figure 4). This general pattern was clearest for Fe and Zn. For example, the DL shoreline had the narrowest range of seepage fluxes and had the widest ranges of concentrations. At the Inlet shoreline, the range of shallow pore water concentrations was narrower than the DL shoreline, but the range of concentrations did increase slightly as seepage discharge approached zero.

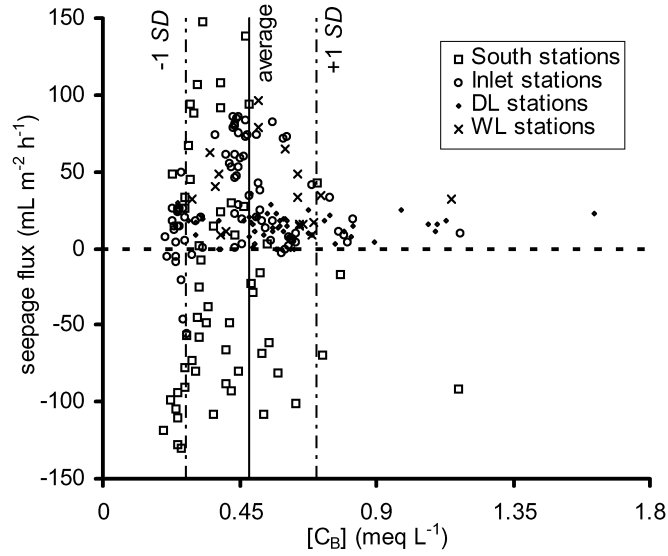
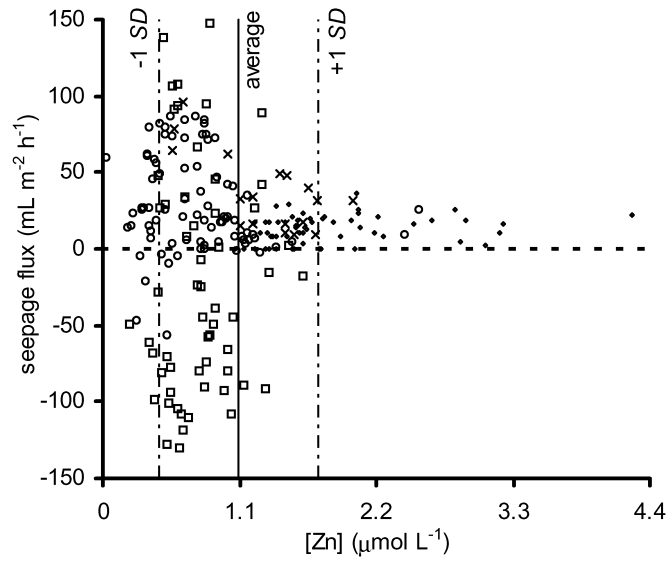
**(a) base cations****(b) zinc**

Figure 4. Shallow pore water  $C_B$  and Zn concentrations versus seepage flux ( $n_{\text{discharge}} = 159$ ,  $n_{\text{recharge}} = 46$ ). Every data point is a measurement from a station on a particular date but a unique symbol is used for each shoreline. The hashed vertical lines indicate  $\pm 1$  standard deviation around average concentrations (solid line). The pattern of higher and more variable solute concentrations with low flow was also similar for  $\text{H}^+$  and Fe as well.

### Station J, South shoreline of Lower Sylvan Pond

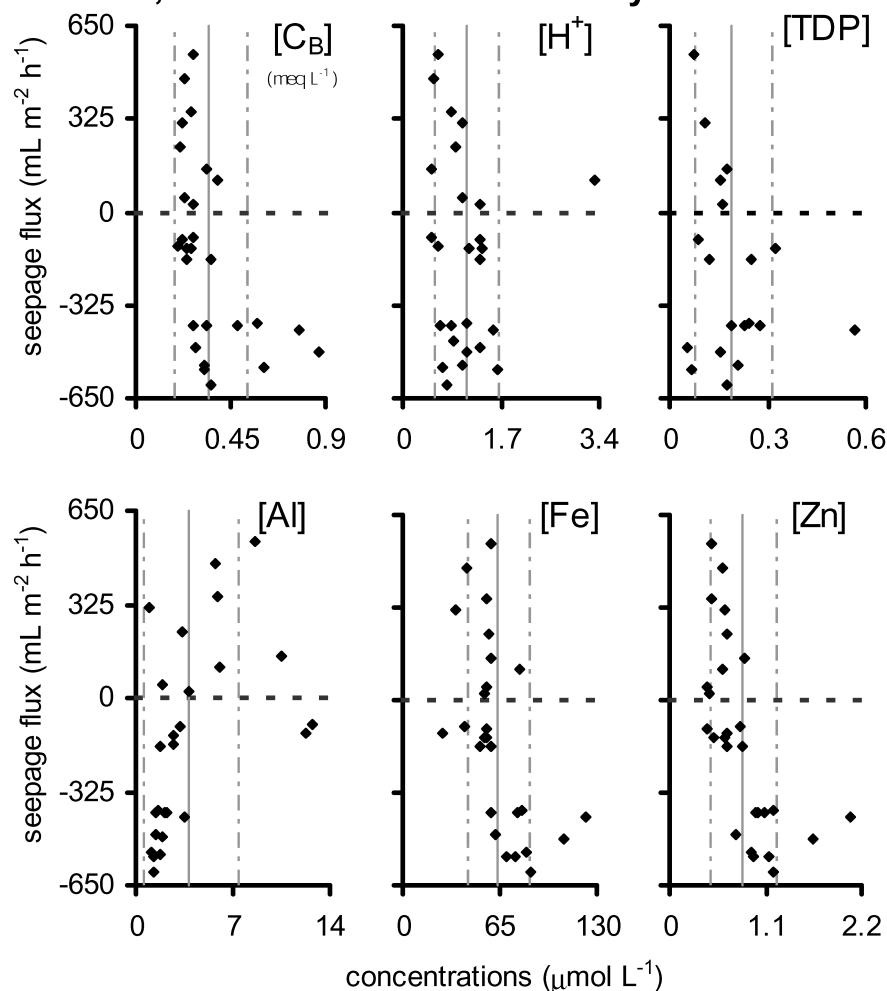


Figure 5. Shallow pore water solute concentrations versus average seepage fluxes for each sampling date at station J ( $n_{\text{discharge}} = 18$ ,  $n_{\text{recharge}} = 36$ ). The dashed vertical lines indicate  $\pm 1$  standard deviation around the average concentration (solid line). All units are  $\mu\text{mol L}^{-1}$  except  $C_B$  ( $\text{meq L}^{-1}$ ).

At the South, Inlet, and WL shorelines where deep pore water samples were collected, deep pore water  $C_B$ , Fe, and Zn concentration ranges and patterns were similar to the shallow pore water concentrations (Table 2). The ranges of observed concentrations were slightly larger than concentrations of these solutes in shallow pore water.

Several exceptions to the chemical and seepage flux patterns occurred. Total dissolved P concentrations were highly variable and did not have any

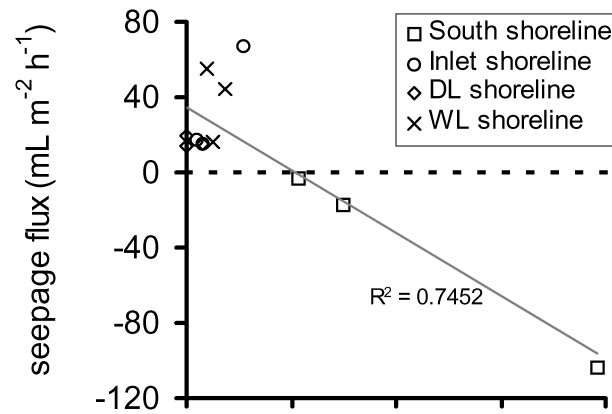
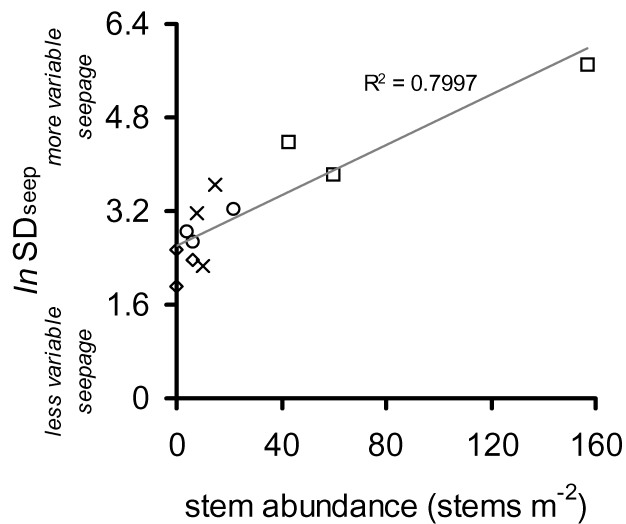
**(a) average seepage flux & stem abundance****(b) seepage variability & stem abundance**

Figure 6. Stem abundance (1998) versus average seepage flux (a) and the variability of seepage,  $\ln \text{SD}_{\text{seep}}$  (b). Seepage fluxes are means calculated for each station over the 1998 field season.

discernable pattern over the range of observed seepage fluxes (Sebestyen 2000). Solute concentration ranges were similar among all three South shoreline stations, but the patterns of pore water chemistry at station J substantially differed from all other stations (Figure 5). At this station, concentrations of  $C_B$ , TDP, Fe, and Zn (shallow and deep pore waters) were greatest and had broader ranges when seepage fluxes were less than  $-250 \text{ mL m}^{-2} \text{h}^{-1}$ .



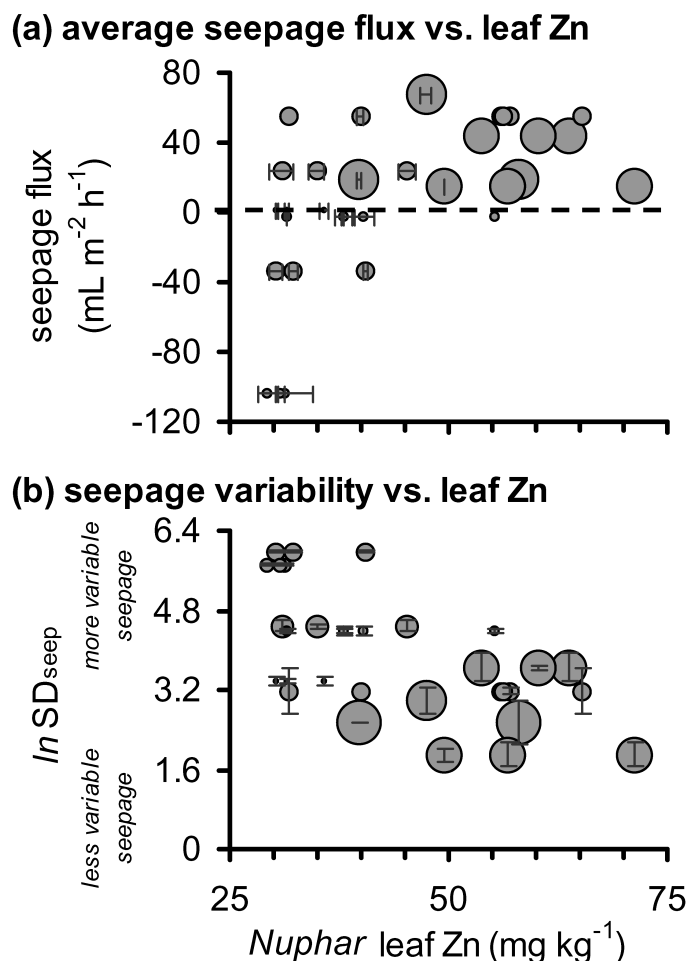


Figure 7. Seepage versus *Nuphar* Zn content. Each circle represents a single *Nuphar* leaf at a station and the size represents the magnitude of the average pore water Zn concentration (range = 0.37–2.07  $\mu\text{mol L}^{-1}$ ) at that same station. Data for both years are shown and seepage fluxes were averaged over each field season. Leaf Zn content was highest at stations having both low flow and high pore water concentrations of Zn (a). The horizontal error bars in (a) show  $\pm 1$  standard deviation of the leaf Zn content (the absence of error bars indicates samples with insufficient sample volume for analytical repetitions). Leaf Zn content was also highest where seepage fluxes were least variable (low  $\ln \text{SD}_{\text{seep}}$ ) and pore water Zn concentrations were highest (b). The vertical error bars in (b) show  $\pm 1$  standard deviation of pore water Zn concentrations.

### Sediments

The sediment cores predominantly consisted of sands (84.2–91.4%) with minor fractions of silt and clay. Percentages of sand were not statistically different

among shorelines, among depths, or between replicate cores, and likewise for both silt and clay content. Sediment loss on ignition was higher at Wilmurt Lake (3.28–13.92%) than Lower Sylvan Pond (0.63–2.94%) or Dart Lake (3.38–5.17%). Sediment C<sub>B</sub>, P, Al, Fe, and Zn contents were similar among the South, Inlet, and DL shoreline sediments, but were 2–5 times greater at the WL shoreline (Sebestyen 2000). Sediment element content did not have consistent patterns with depth increment (e.g. no zones of enrichment or depletion at the coarse scale of 10 cm core segments).

#### *Lake surface water, pore water, sediment, and leaf tissue relationships*

Three species of water lilies (water shield, *Brasenia schreberi*; water heart, *Nymphoides cordata*; and *N. variegatum*) and several emergent species grew along the shorelines. These species were present in all the lakes, but never simultaneously at individual stations. Stem abundance increased with decreasing average recharge flux ( $P = 0.0003$ ,  $R^2 = 0.75$ ) and was highest at stations that had the most variable seepage ( $\ln SD_{\text{seep}}$ ,  $P < 0.0001$ ,  $R^2 = 0.80$ , Figure 6). Shorelines with low discharge and little seepage flux variability (low  $\ln SD_{\text{seep}}$ ) had low stem densities or no stems.

Element contents of *Nuphar* leaves were not correlated with sediment element contents. Instead, *Nuphar* leaf Fe ( $P < 0.0001$ ,  $R^2 = 0.68$ ) and Zn ( $P = 0.0076$ ,  $R^2 = 0.31$ ) were positively related to pore water concentrations. Also, Al ( $P < 0.0020$ ,  $R^2 = 0.39$ ) and Fe ( $P < 0.0001$ ,  $R^2 = 0.73$ ) content were positively related to surface water solute concentrations. *Nuphar* leaf Fe and Zn were highest at stations where yearly average seepage discharge was between 0 and  $60 \text{ mL m}^{-2} \text{ h}^{-1}$  (Figure 7(a)) and seepage variability was low ( $\ln SD_{\text{seep}} < 3$ , Figure 7(b)). In other words, elevated leaf Fe and Zn contents coincided with stations having nearly constant, low discharge that also had the highest average pore water concentrations. With regard to other studies, trace metal content of *Nuphar* was similar to values reported by Adams et al. (1973) for whole plant samples in polluted environments and to values reported by Campbell et al. (1985) for Zn in stems and rhizomes.

#### **Discussion**

The results of this research, in agreement with other studies, reveal the complex spatial and temporal nature of lakeshore seepage fluxes (Meyboom 1967; Winter 1981; Cherkauer and Zager 1989; Krabbenhoft and Webster 1995; Norrström and Jacks 1996; Lee 2000; Rosenberry 2000; Genereux and Bandopadhyay 2001; Sebestyen and Schneider 2001). As a new contribution, this study further documents that seepage flux patterns are related to pore water chemistry and aquatic macrophyte communities. The highest trace metal concentrations of pore water and content of *Nuphar* leaves occurred where

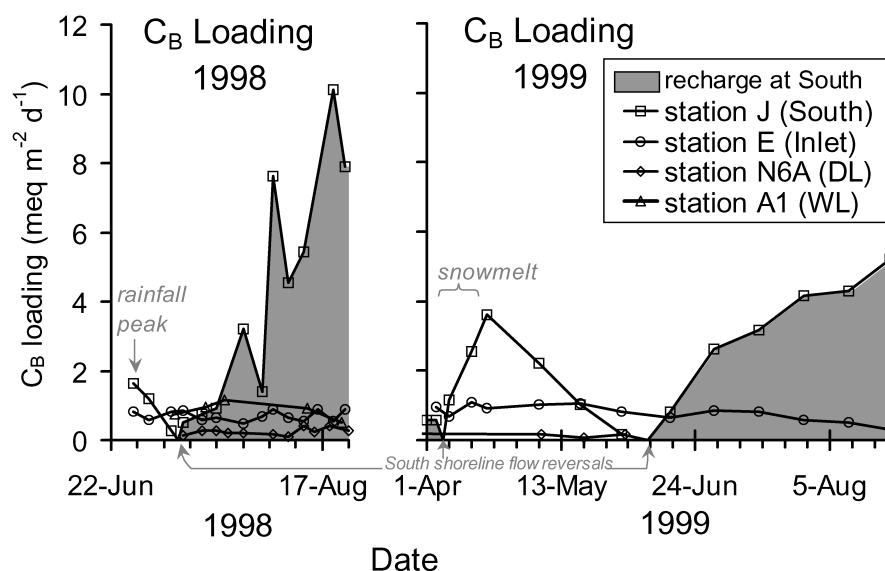


Figure 8. Mass loading of base cations at the shallow pore water depth (concentration multiplied by seepage flux). An example station from each shoreline is shown; South (J), Inlet (E), DL (N6A), (1998 mean) and WL (A1) shorelines. The filled areas beneath the South shoreline data indicate time periods when recharge occurred at the South shoreline whereas the non-filled areas indicate discharge.

discharge was low. Seepage appeared to influence shorelines differently depending upon: (1) flow direction and magnitude, (2) the magnitude of solute transport, and (3) biogeochemical transformations. In the following sections, we discuss the importance of seepage flux and how seepage is coupled to pore water chemistry, macrophyte abundance, and plant tissue chemistry for the water lily, *N. variegatum*.

#### *Seepage hydrology and solute transport*

The fluxes of water with seepage control the movement of nutrients and other solutes through shoreline substrates. Since the magnitude of solute loading is a function of both solute concentration and seepage fluxes, solute transport to and from lakes was greatest with high discharge or recharge seepage (Figure 8). This process is best demonstrated by the dynamic flow pattern observed at the South shoreline and the associated solute mass loadings (loading = pore water concentration \* seepage flux). Here, base cation and trace metal loading within the plant root zone were high with recharge in mid to late summer when recharging lake water was the source of solutes to pore water (e.g. base cation loading from July to August 1998, Figure 8). Recharge most likely reflects the

typical mid to late growing season conditions at this site because seepage only reversed direction after large rainfall events and spring snowmelt (Sebestyen and Schneider 2001). During the hydrologically important snowmelt period when lake waters acidified, pore water pH and  $C_B$  concentrations were stable at the South shoreline suggesting that enhanced base cation loading with discharge during snowmelt could help to maintain stable conditions in sediments and contribute to surface water buffering (Baker et al. 1986; Kenoyer and Anderson 1989).

In contrast, seepage fluxes along the Inlet (Lower Sylvan Pond), DL, and WL shorelines are among the lowest of the reported values that have ranged from  $< -10^4$  to 0 to  $> 10^4 \text{ mL m}^{-2} \text{ h}^{-1}$  (Lee 1977; Downing and Peterka 1978; Asbury 1990; Belanger and Walker 1990; Schafran and Driscoll 1990; Shaw and Prepas 1990; Belanger and Kirkner 1994; Blanchfield and Ridgway 1996; Isiorho et al. 1996; Rosenberry 2000). Although seepage was relatively stable, the solute loadings along these shorelines accordingly are much lower than those of the dynamic seepage patterns along the South shoreline of Lower Sylvan Pond.

#### *Chemical transformations occurring with seepage fluxes*

We observed a pattern of broad pore water concentration ranges for solutes under low flow. Base cation, Zn, and Fe concentrations were up to 5 fold greater under stable low flow than under high flow. Such coupling of solute concentrations to low flow has been documented in other lakeshore seepage studies for chloride (Connor and Belanger 1981),  $C_B$  and ammonium (Schafran and Driscoll 1990; Schneider 1994), and to phosphorus, several nitrogen species, and dissolved organic carbon (Asbury 1990). One of these studies actually occurred at Dart Lake (Schafran and Driscoll 1990) and also documented low  $C_B$  pore water concentrations at seepage fluxes that ranged as high as  $2000 \text{ mL m}^{-2} \text{ h}^{-1}$ .

Several different geochemical and biogeochemical processes may contribute to this linkage between seepage and pore water chemistry. Slow transmission of water through sediment profiles under low flow allows more time for decomposition, geochemical weathering along flowpaths, and exchange reactions to enrich solutes in groundwater. In contrast, water passing through sediments during high flow flushes pore waters by carrying away these reaction products and replacing them with solute concentration signatures of flowing water.

The development of anoxia in sediments under low flow conditions may explain the high pore water concentrations of redox sensitive species such as Fe (White et al. 1989; Schafran and Driscoll 1990; Jackson et al. 1993). Schafran and Driscoll (1990) and Schneider (1994) found evidence of anoxia when seepage fluxes were between  $-250$  and  $250 \text{ mL m}^{-2} \text{ h}^{-1}$ . In this study, the threshold seepage flux for a shift in biogeochemical conditions appeared to be narrower (between about  $-100$  and  $100 \text{ mL m}^{-2} \text{ h}^{-1}$ ). Hence, the reduction of

ferric to ferrous Fe is favored at low discharge and pore water Fe concentrations would increase as we observed. Additionally, redox insensitive elements such as Zn may be controlled by Fe reduction (Bostick et al. 2001) to produce nearly identical concentration profiles as we observed in this study. Redox reactions can also be important for other biogeochemical transformations such as denitrification and dissimilatory sulfate reduction. Schafran and Driscoll (1990) described concentration patterns of nitrate and sulfate in Dart Lake pore waters that are consistent with denitrification and sulfate reduction during low flow anoxic conditions (e.g. highest concentrations when discharge was high and lowest concentrations with low discharge).

These processes may also help to explain why the seepage versus concentration pattern at station J (South Shoreline of Lower Sylvan Pond) was an exception to the low flow and high solute concentration pattern. In both years, this site exhibited the greatest range in seepage fluxes, peaking in late spring at  $> 400 \text{ mL m}^{-2} \text{ h}^{-1}$ , declining through zero flow, and then recharging at  $< -400 \text{ mL m}^{-2} \text{ h}^{-1}$  through August. Importantly, low flow conditions lasted for only several days in both in 1998 and 1999. This short period of low flow may not have been sufficient for anaerobic microbial communities to develop and pore water concentrations to increase due to decomposition or reduction reactions. Additionally, although P availability often increases with anoxia, TDP concentrations did not increase under low flow conditions at any of the sites. Both of these findings suggest that more research is needed to examine biogeochemical processes under different seepage flow regimes.

#### *Aquatic plants*

Several lines of evidence suggested important links of seepage flux to pore waters and plants in nearshore areas. First, stem abundance was strongly correlated with the magnitude and variability of seepage fluxes. Others have found correlations between plant biomass and seepage discharge, although none have described influences of temporally variable seepage (Loeb and Hackley 1988; Lodge et al. 1989; Lillie and Barko 1990; Schneider 1994; Rosenberry et al. 2000). These patterns of increased plant productivity (stem abundance) with higher seepage (recharge or discharge) may be explained by the increased volume of water and associated nutrients flowing through the sediment profile as well as by seepage dependent concentration patterns of pore water chemistry.

Additionally, our study found two other links between seepage and aquatic macrophytes: relationships of pore water chemistry with element content of *Nuphar* leaf tissue and elevated trace metals in *Nuphar* under low flow conditions. In this study, the patterns of pore water chemistry that varied among stations better explained *Nuphar* tissue content of Fe and Zn than did sediment or surface water chemistry patterns. Documenting links between seepage patterns, pore water, and aquatic plants expands upon previous studies of

macrophyte communities because past studies have usually focused on other sources of aquatic plant nutrition and toxicity. Sediment chemistry and texture were not significantly related to macrophyte abundance or *Nuphar* chemistry in this study, but sediments have been shown to be sources of nutrients and trace metals for some rooted aquatic macrophytes (Carignan and Kalff 1980; Barko and Smart 1981; Campbell et al. 1985; Lehtonen 1989; Sprenger and McIntosh 1989; Jackson et al. 1991, 1993; Reimer and Duthie 1993; Jackson 1998). Lake surface waters are occasionally element sources for submerged species (Jackson 1998) and lake water concentrations of Fe were correlated with *Nuphar* leaf Fe in this study. However, surface water chemistry was homogenous among all the stations in Lower Sylvan Pond and *Nuphar* chemistry varied among sites in patterns that are more consistent with pore waters serving as the source of Fe and Zn.

Interpreting connections between macrophytes and seepage variability is more challenging. We hypothesize that the availability of elements to aquatic plants is dynamic and influenced not just by average flow conditions but also by the timing of specific seepage events. Temporally variable seepage can provide pulses of critical nutrients or alternatively elevate potentially toxic element concentrations at certain times during the growing season or the overall plant life cycle. Average seepage fluxes that correlated with *Nuphar* leaf chemistry indicate typical flow conditions yet do not convey the temporal and spatial complexities of the flow patterns observed in this study. The dynamic patterns of seepage flux that were related to snowmelt, rainfall, and drought conditions emphasize a need to understand how variability of seepage patterns may influence plant communities. For example, high discharge during and after snowmelt at the South shoreline may sustain nutrient loading through leaf emergence and vigorous plant growth in late spring and early summer (Figure 8). Therefore, a low snowmelt year could potentially reduce water and solute fluxes through the rhizosphere in late spring. More research is needed to examine the influence of pulse events versus chronic conditions in terms of relative contributions to long-term plant health.

Overall, seepage may play a particularly important role in controlling the availability of both nutrients and toxic substances to aquatic macrophytes in nutrient-poor or stressed systems (Loeb and Hackley 1988; Lillie and Barko 1990). Adirondack watersheds are chronically stressed by acidification, declining concentrations of base cations, and elevated concentrations of trace metals (Galloway and Likens 1979; Likens et al. 1998; Stoddard et al. 1998; Lawrence et al. 1999; Driscoll et al. 2001). We hypothesize that the low macrophyte densities at the Inlet, DL, and WL shorelines may be associated with the interacting effects of decreased base cation loadings and increased availability of potentially toxic trace metals (e.g. elevated pore water concentrations of Zn). Similar relationships have been documented for leaf tissue cadmium content of *N. variegatum* and alkalinity (Thompson et al. 1997). With enhanced macrophyte uptake of trace metals under low discharge when base cation loading is low, trace metals could accumulate, approach or surpass toxic

thresholds. Alternatively, calcium limitation due to trace metal competition for root binding sites could lead to decreased water lily productivity (Smits et al. 1992). Continued research is needed to address the relative importance of variable pore water chemistry and solute loading as a function of seepage to toxicity and the nutrition of rooted aquatic macrophytes.

### Conclusions

Seepage occurs along lakeshores and varies over space and time. In this study, the direction, magnitude, and variability of seepage influenced biogeochemical cycles of pore waters, the abundance of aquatic plants along lakeshores, and the chemistry of *Nuphar* leaf tissue. Solute sources and fluxes were related to seepage patterns and these relationships suggest that coupled hydrologic and biogeochemical processes influence lakeshores and associated plant communities. Our study identifying pore water and leaf tissue linkages to seepage adds to the literature that suggests seepage is important in lake ecosystems (Winter 1978; Fellows and Brezonik 1981; Brock et al. 1982; Asbury 1990; Belanger and Walker 1990; Hagerthey and Kerfoot 1998; Winter 1999). Recent findings of epibenthic algal biomass related to seepage (Hagerthey and Kerfoot 1998) also strongly suggest seepage as a control on nearshore biological communities.

Since seepage is a ubiquitous process that occurs along lake margins, our findings suggest that quantifying seepage may provide considerable insight into plant communities that grow along lakeshores. Variable solute concentrations within and among shorelines suggested multiple and complex processes coupled to seepage, but specific mechanisms of biogeochemical transformations need further study. To advance our knowledge of seepage linkages to biogeochemical processes, investigations are needed across diverse geomorphologic settings and trophic levels to gain a broader understanding of seepage relationships to pore water chemistry, aquatic plant communities, and lake surface water chemistry and to determine the generality of our findings.

### Acknowledgements

We wish to thank H. and S. Hawley, N.L. Holtmeier, H.M. Moore, M.J. Nemeth, T.J. Patronski, K.A. Smemo, M.M. Traynor, C.C. Wafer, B. Webster, and B.C. Weidel for field assistance, the Cornell University Cold Water Fishery Research Program (D.C. Josephson) for use of field facilities and logistical support, M.A. Rutzke for lab assistance and use of the ICP. The Adirondack League Club, the Wilmurt Lake Club, and P. Meneilly and the administration at Camp Gorham are gratefully acknowledged for providing access to the study sites. This manuscript benefited greatly from comments made by L.O. Hedin, C.C. Krueger, D.I. Siegel, S.L. Loeb, and two anonymous reviewers. Funding was provided by the Kieckhefer Adirondack

Fellowship, the Cornell University Research Training Grant in Biogeochemistry and Environmental Change, the Department of Natural Resources, Cornell University, and an USDA hatch grant.

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