

# Phosphorus and land-use changes are significant drivers of cladoceran community composition and diversity: an analysis over spatial and temporal scales

Marc Richard Albert, Guangjie Chen, Graham K. MacDonald, Jesse C. Vermaire, Elena M. Bennett, and Irene Gregory-Eaves

**Abstract:** We conducted paleolimnological studies over spatial and temporal gradients to define the responses of subfossil cladoceran community composition and diversity to changes in land use and phosphorus concentrations in shallow lakes. We predicted that watershed disturbance by humans, through its impact on water quality, would explain significant variation in cladoceran diversity and composition. Across lakes, water-column total phosphorus concentration was a significant ( $p < 0.05$ ) predictor of the subfossil cladoceran community composition. Chydorid diversity was also found to be related significantly to phosphorus concentration ( $r = -0.55$ ,  $p < 0.05$ ) and the proportion of disturbed land in the watershed ( $r = -0.47$ ,  $p < 0.05$ ). However, net load of phosphorus to the watershed rather than proportion of watershed disturbance was a significant predictor of chydorid diversity ( $r = -0.86$ ,  $p < 0.001$ ) in our temporal analysis of an eutrophying lake. Given that phosphorus loading to surface waters is often related to phosphorus concentrations in soils, we suggest that the net phosphorus load to the watershed is a more sensitive metric of land-use change and necessary for detecting ecological responses in time series data.

**Résumé :** Des études paléolimnologiques le long de gradients spatiaux et temporels nous ont servi à définir les réactions de la composition et de la diversité de la communauté subfossile de cladocères aux changements d'utilisation des terres et de concentrations de phosphore dans des lacs peu profonds. Nous avons prédit que la perturbation des bassins versants par les humains, par son impact sur la qualité de l'eau, expliquerait une partie importante de la variation de la composition et de la diversité des cladocères. Dans l'ensemble des lacs, la concentration de phosphore total dans la colonne d'eau est une variable prédictive significative ( $p < 0,05$ ) de la composition de la communauté subfossile de cladocères. La diversité des chydoridés est aussi reliée significativement à la concentration de phosphore ( $r = -0,55$ ,  $p < 0,05$ ) et à la proportion de terres perturbées dans le bassin versant ( $r = -0,47$ ,  $p < 0,05$ ). Cependant, dans notre analyse temporelle d'un lac en voie d'eutrophisation, la charge nette de phosphore dans le bassin versant, plutôt que le pourcentage de perturbation du bassin versant, est une variable prédictive significative de la diversité des chydoridés ( $r = -0,86$ ,  $p < 0,001$ ). Étant donné que la charge de phosphore vers les eaux de surface est souvent reliée aux concentrations de phosphore dans le sol, nous croyons que la charge nette de phosphore vers le bassin versant est une métrique plus sensible au changement d'utilisation des terres et qu'elle est nécessaire pour détecter les réponses écologiques dans les séries chronologiques de données.

[Traduit par la Rédaction]

## Introduction

Nutrient enrichment of freshwaters is one of the most widespread forms of anthropogenically induced global change (Carpenter et al. 1998; Tilman et al. 2001). Elevated loading of nutrients to shallow lakes, mainly in the form of phosphorus and nitrogen, results in increased phytoplankton biomass and decreased water clarity, which in turn can fundamentally alter lake food webs (e.g., Scheffer et al. 1993, 2001; Vadeboncoeur et al. 2008). Since the 1970s, many governments have regulated the discharge of nutrients to

surface waters, but non-point sources in the form of runoff from agricultural and urban areas continue to be a major source of nutrients to lakes (Carpenter et al. 1998; Bennett et al. 1999). A current focus of eutrophication research is to define the interactions among land use – land cover, water quality dynamics, and aquatic community structure (e.g., Gélinas and Pinel-Alloul 2008). To date, this research has largely been focused on lake survey analyses (Hoffmann and Dodson 2005). However, it is not yet clear whether we can assume that biodiversity patterns derived over spatial

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gradients can be used to predict what might occur within a single lake over time (Dodson et al. 2000). We believe that comparative paleolimnological and land use – land cover analyses, which can be conducted across both spatial and temporal gradients, are particularly insightful as they can allow investigators to fully evaluate how applicable results are across these different scales.

Subfossil cladoceran assemblages provide valuable insight into how eutrophication has altered the structure and functioning of aquatic systems (e.g., Frey 1960; Manca et al. 2007). In particular, planktonic Cladocera play a key role in controlling phytoplankton biomass as they actively graze small-sized phytoplankton and sequester limiting nutrients from ungrazed algae (Sommer and Sommer 2006). Furthermore, the community structure of the littoral Cladocera (i.e., chydorids) is known to be very sensitive to changes in nutrient levels (e.g., Whiteside 1970; de Eyto et al. 2003) and macrophyte coverage (e.g., Quade 1969; Duigan and Kovach 1994). Planktonic and littoral cladoceran communities differ, however, in their sensitivities to fish predation where the community structure of planktonic taxa is more strongly controlled by planktivory pressure (Jeppesen et al. 1996).

In this study, we first conducted paleolimnological analyses across a spatial gradient (i.e., an among-lake surface sediment survey) to define the nutrient autecologies of cladoceran taxa in northeastern North American shallow lakes. We predicted that nutrients (total phosphorus (TP)) and factors related to habitat quality (e.g., depth and turbidity) would explain a significant amount of variation in the cladoceran community structure. We then conducted a detailed lake study and used the results from the spatial analysis to interpret the sediment core data so that we could define the lake's responses to land-use change.

A second objective of this paper was to test the generality of a principle proposed by Dodson et al. (2007), who suggested that watershed land use, through its impact on water quality, was a key factor structuring zooplankton diversity and composition in field settings. Dodson et al.'s (2005, 2007) research was based on a large spatial survey of pelagic zooplankton from 73 lakes. Here we use paleolimnology, land use, and historical census data to evaluate this principle over spatial and temporal gradients. To our knowledge, the relationship between watershed land use and cladoceran diversity and composition in shallow lakes has not been tested quantitatively over a centennial time scale.

## Materials and methods

### Study sites and paleolimnological analyses

The Environmental Monitoring and Assessment Program (EMAP) has created a valuable database that includes physicochemical and environmental data for 257 randomly selected northeastern North American lakes (available from [www.epa.gov/emap/](http://www.epa.gov/emap/)). A subset of 20 randomly selected, primarily shallow lakes (i.e.,  $Z_{\text{mean}} = 3.2 \pm 2.8$  m, mean  $\pm$  standard deviation (SD)), spanning a large phosphorus gradient (mean TP = 0.9–154.5  $\mu\text{g}\cdot\text{L}^{-1}$ ) was included in our surface sediment analysis (Fig. 1; for a more complete limnological description, see Appendix A, Table A1). Surface sediments from each lake were collected using a gravity corer (see Dixit et al. 1999). We analysed the top 0–1 cm

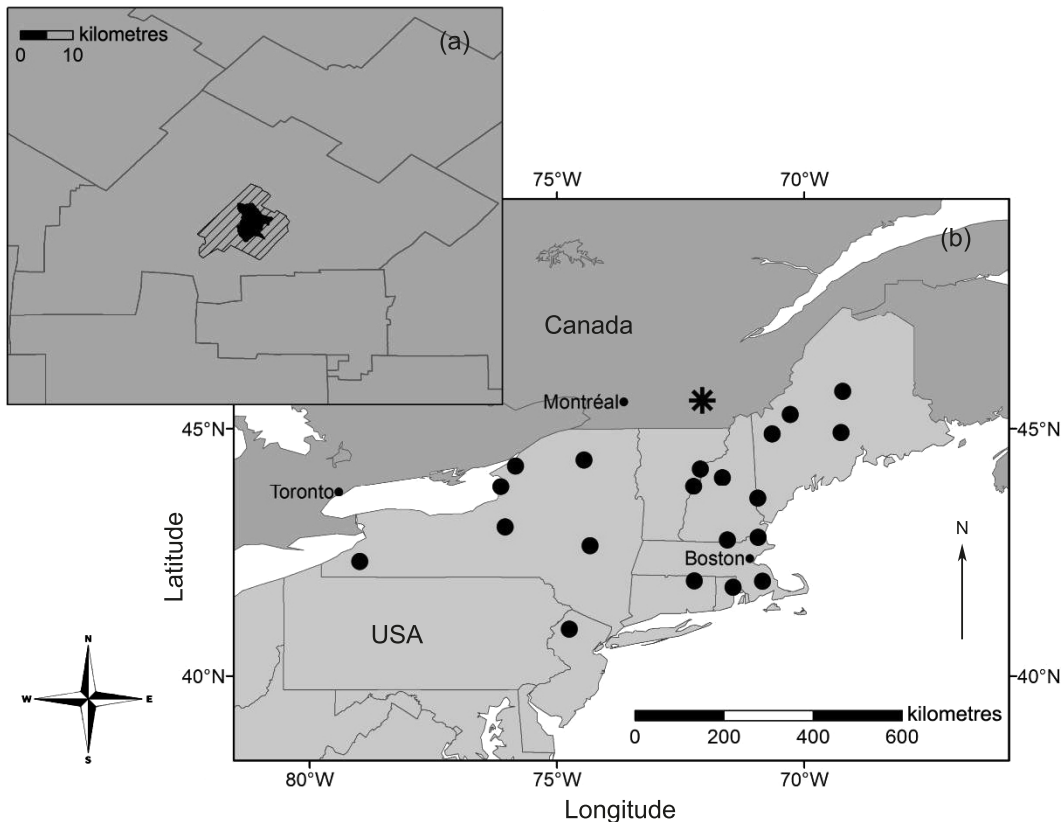
of each sediment core, which represents an integrated sample of the entire lake's production over the past ~1–4 years (Smol 2008).

We also conducted a detailed analysis of a sediment core from a shallow lake in northeastern North America to reconstruct the response of cladocerans to environmental change over the past ~150 years (Fig. 1). Petit Lac Saint-François (aka Tomcod Lake) is a hypereutrophic (mean summer TP = 193  $\mu\text{g}\cdot\text{L}^{-1}$ ) shallow lake ( $Z_{\text{mean}} = 0.9$  m) that flushes quickly (water residence time of 0.06 years). The phytoplankton of Petit Lac Saint-François is dominated by cyanobacteria (I. Gregory-Eaves, personal observation) and was found to have the highest epilimnetic microcystin concentrations relative to other lakes in the region (Giani et al. 2005). The lake is set within a relatively large, but gently sloping, watershed that is underlain by sedimentary bedrock (mean catchment slope = 2.5% and drainage area – lake area ratio (DA:LA) = 24). A sediment core was retrieved from the deeper portion of the lake using a modified Kajak–Brinkhurst gravity corer (Glew 1989). The core was subsampled in the field at 1 cm resolution using a vertical extruder (Glew 1988). Samples were freeze-dried and processed for  $^{210}\text{Pb}$  dating. The radioisotope activities of  $^{210}\text{Pb}$ ,  $^{214}\text{Pb}$ , and  $^{214}\text{Bi}$  from a known mass (0.4 to 1 g) and volume of freeze-dried sediment were measured for 24 h using a Canberra well-detector gamma ray spectrometer. Sediment ages were calculated using the constant-rate-of-supply (CRS) model (Binford 1990). Based on the derived sedimentation rates, we calculated fluxes (aka the accumulation rate of remains per defined area and time period, i.e., a standardized paleolimnological indicator of production) for several cladoceran groups to take into account differences in sedimentation rates between samples.

Counts and identifications of cladoceran remains were done using a Leica DM2500 compound microscope (200–400 $\times$  magnification) with the aid of taxonomic keys (Frey (1985), Smirnov (1996), and Bos (2000) and references cited therein). All remains were identified down to the lowest possible taxonomic level. *Daphnia* were identified to the species group level (*D. pulex* and *D. longispina* groups), and *Bosmina* and chydorids were identified to the species level when possible. Following standard methods, we adjusted counts of remains to be representative of the cladoceran population as individuals are comprised of two halves forming the carapace, one headshield and one postabdomen, which are often found separately (Korhola and Rautio 2001). The most abundant remain is used to represent each individual until at least 60 individuals of the chydorid group have been counted (Frey 1986).

To describe the geochemical changes of the sediment core collected from Petit Lac Saint-François, we conducted measurements of loss-on-ignition at 550 °C (LOI 550; Heiri et al. 2001) and magnetic susceptibility (Sandgren and Snowball 2001). The LOI 550 measurements describe the changes in the relative amount of organic matter (vs. inorganic matter) across the core. Magnetic susceptibility measurements quantify the relative abundance of magnetic minerals present in the sample (e.g., iron and manganese carbonates), which are often transported to a lake via catchment erosion (Sandgren and Snowball 2001).

**Fig. 1.** Maps of our study sites: (a) high spatial resolution map showing the delineation of the Petit Lac Saint-François watershed (black) set within the smaller census subdivision (hatched) and the larger census division boundaries (lines); (b) map of the northeastern US and southeastern Canada showing the location of the EMAP study sites (solid circles) and Petit Lac Saint-François (star).



### Quantifying land-use change in the Petit Lac Saint-François region

To define land-use changes in the region surrounding Petit Lac Saint-François, we compiled agriculture and population census data from the Government of Canada dating from the earliest periods available (i.e., 1851 for human population and 1871 for agriculture) until 2001 (Canada Department of Agriculture 1851, 1861, 1873, 1883, 1893, 1901; Canada Census and Statistics Office 1911; Canada Dominion Bureau of Statistics 1922, 1932, 1942, 1952, 1962; Statistics Canada 1972, 1982, 1992, 2003). Data on the extent of cropland and pastureland, as well as human population trends, were available at both census division (coarse) and census subdivision (fine) scales (Fig. 1). The historical agricultural census data includes inventories of annual fertilizer purchases, livestock numbers, and crop production. We used these data to estimate the amount of phosphorus (P) fertilizer and livestock manure P applied to croplands in this region historically, as well as the P removed by harvested crops (see MacDonald and Bennett 2009). Specifically, we defined changes in the regional P budget (i.e., net P load to the watershed soils, a metric of agricultural intensity) as the difference between annual P inputs (fertilizer P and P derived from livestock manure,  $\text{kg P}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ ) and P removed in harvested crops ( $\text{kg P}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ ). The regional P budget was calculated at the census division scale because fertilizer and livestock density data were available only at this scale over most of the study period. We found, however, that time series data on the ex-

tent of cropland at the census division and subdivision scales were significantly correlated ( $r = 0.80$ ,  $p = 0.001$ ,  $n = 13$ ), which suggests that the census division data accurately tracked temporal trends in land use at both spatial scales.

### Statistical analyses

#### Surface sediment analyses

We first conducted a series of ordination analyses to define both qualitatively and quantitatively the relationships between environmental variables and modern sedimentary cladoceran assemblages. Cladoceran species that were present in at least two sites at  $>2\%$  relative abundance were used in all ordinations. Species data were square root transformed to reduce the influence of dominant taxa and stabilize the variation. We first applied detrended correspondence analysis (DCA) to quantify the length of gradient represented by our surface sediment samples. Given that this preliminary analysis revealed a relatively short gradient length (i.e., 0.95 SD units), we subsequently applied linear ordination techniques (Lepš and Šmilauer 2003).

Redundancy analysis (RDA) was performed to quantify relationships between the full cladoceran assemblages and measured physical and environmental variables (chlorophyll *a*, colour, conductivity, dissolved organic carbon, dissolved inorganic carbon, TN, TP, pH, turbidity, mean depth, lake surface area, lake volume, percent watershed disturbance) (Appendix A, Table A1). All values were either square root or natural log transformed to generate nor-

malized distributions. Prior to running the RDA with forward selection, however, we identified collinear variables with a Pearson's correlation and only included one of the variables from a correlated group (i.e.,  $r > 0.8$ ) in our RDA (Lepš and Šmilauer 2003). Specifically, the variable that explained the most variation in the cladoceran assemblage when run as a single variable in a preliminary RDA was included in the final RDA. All ordination analyses were performed using CANOCO software (version 4.5; ter Braak and Šmilauer 2004).

To quantify subfossil cladoceran diversity within our sediment samples, we applied two metrics: Simpson's diversity index (Simpson 1949) and rarefied species richness estimates (Hurlbert 1971). For both metrics, we calculated diversity exclusively within the chydorids because this is a species-rich group that is known to preserve well in lake sediments (Korhola and Rautio 2001). For the species richness estimates, we applied rarefaction to standardize chydorid counts to 60 individuals. All diversity metrics were calculated using the "vegan" package in the statistical program R (R Development Core Team 2007).

Correlation analyses were run to assess the strength of the relationship between chydorid species richness estimates and TP, the proportion of disturbed watershed area (i.e., percent disturbance, which is the sum of percent agricultural land and percent urban land), or lake surface area. Lake surface area, TP, and species richness data were log-transformed, and percent disturbance data were arcsine square root transformed to normalize distributions. Correlation analyses were performed using JMP (version 7; SAS Institute Inc. 2007). We also verified whether there was significant spatial autocorrelation in any of our variables to ensure that our correlation  $p$  values were not artificially low. Following methods similar to those of MacDonald and Bennett (2009), we used OpenGeoDa for Windows (version 0.9.8.14; GeoData Center for Geospatial Analysis and Computation, Tempe, Arizona) to test for spatial dependence in the variables listed above but failed to detect any strong or significant spatial effects (based on interpretation of Moran's  $I$  or Lagrange multiplier values, where appropriate, all with  $p > 0.05$ ).

### *Sediment core and historical analyses*

We used correlation analyses to quantify the strength of the relationship between land-use metrics based on our census data collection and the flux of different cladoceran groups or chydorid diversity. Prior to running correlation analyses, the normality of all variables was assessed.  $\text{Log}(x + 1)$  transformation was applied to LOI 550 data, as well as to *Bosmina*, *Daphnia*, and chydorid flux data.

Similar to our spatial analyses, we conducted an assessment to evaluate whether there was significant autocorrelation in our time series data that could bias correlation  $p$  values that were derived from statistical tables. We detected significant lag-1 correlations for all time series data and thus followed the approach outlined in Keller et al. (2008). In particular, we conducted a randomization test to calculate a  $p$  value for each set of covariates. We first created 9999 randomly reshuffled time series of one of our variables (e.g., *Bosmina* flux) and then correlated each of these time series with a nonrandomized time series (e.g., net P load to the

watershed) such that we had calculated 9999 correlation coefficients for each set of covariates. The  $p$  value was then calculated as the number of randomization-based correlations plus the observed correlation that were equal to or larger than the observed correlation, divided by the total number of correlations (i.e., the number divided by 10 000). We also adopted a conservative alpha level for our temporal analyses where only  $p$  values  $< 0.01$  were considered significant.

For our diversity analyses, we followed the same approach as described above in the spatial survey, but with two exceptions. We presented species-richness profiles from the sediment core samples based on individual samples, as well as on integrated samples that represent similar time intervals. This latter step was taken to address the issue raised by Smol (1981), who cautioned that alpha diversity indices (i.e., species richness) need to account for changes in sedimentation over the course of paleolimnological records to provide an unbiased perspective of change over time (i.e., sediment intervals from different parts of the core may be integrating different amounts of time, which could have an impact on diversity estimates). For the integrated sample profile, we pooled data across equally spaced time steps (i.e., 20–30 years) and then conducted rarefaction on these pooled samples. Rarefaction of the sediment core samples was standardized to chydorid counts of 60 individuals.

We also conducted an RDA analysis in which we plotted the fossil samples (i.e., core samples from Lac Petit Saint-François) passively in the ordination space based on the surface sediment and associated environmental data from the spatial lake survey. The goal of this analysis was to show the trajectory of change in the core samples relative to the environmentally defined axes of cladoceran community composition collected over a broader spatial scale.

## Results

### Modern spatial survey

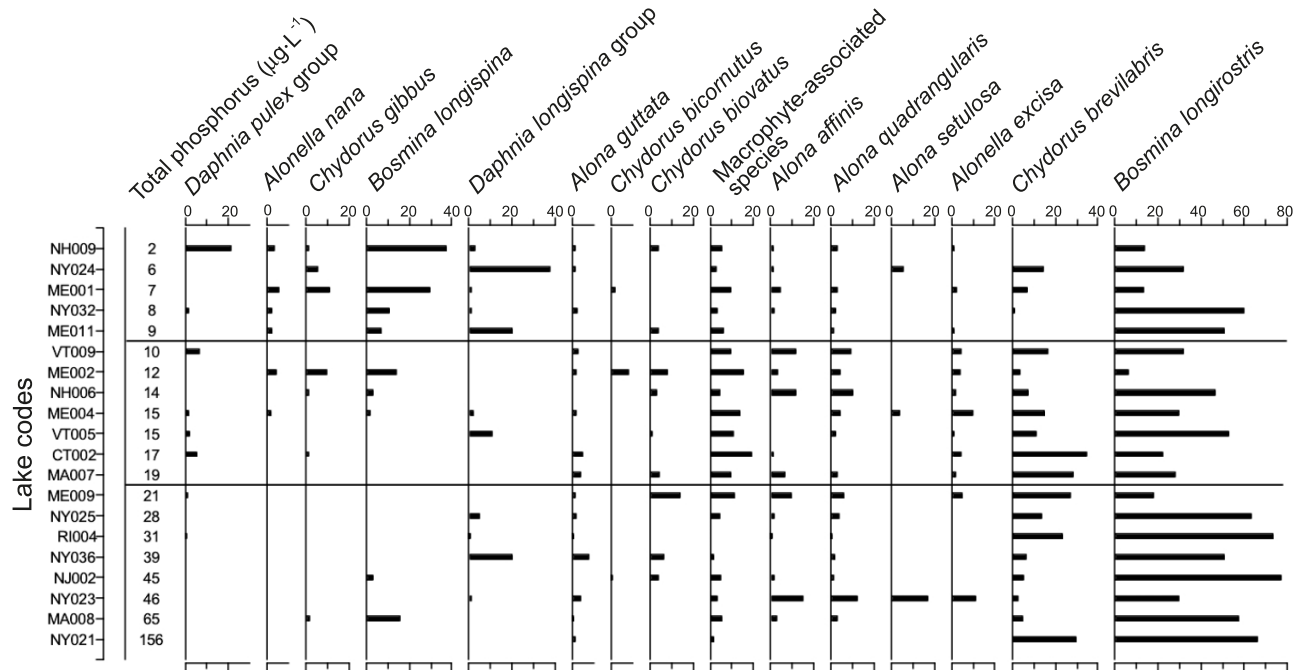
A total of 50 Cladocera taxa were identified in the 20-lake EMAP data set. Of these, 35 taxa had  $>2\%$  abundance in at least two different sites and were included in ordination analysis (Appendix B, Table B1). *Bosmina longirostris* was the most abundant taxon, occurring in all lakes with a relative abundance of  $41.2\% \pm 2.14\%$  (mean  $\pm$  SD). The remaining assemblage was largely comprised of the predominantly littoral Chydoridae family (mean relative abundance  $44.1\% \pm 1.08\%$ ) of which *Chydorus brevilabris* was dominant (mean relative abundance of  $12.6\% \pm 2.13\%$ ).

The RDA, with forward selection, of the surface sediment cladoceran community assemblages identified three significant ( $p < 0.05$ ) environmental predictors: TP, pH, and mean depth. Total phosphorus explained the largest portion of the variation (13.3%) in the cladoceran assemblages. TP was also highly correlated with chlorophyll  $a$  ( $r = 0.82$ ,  $p < 0.01$ ) and turbidity ( $r = 0.82$ ,  $p < 0.01$ ). pH and mean depth explained a further 12.7% and 9.8%, respectively, of the variation in the modern cladoceran assemblages.

Across a large TP gradient, it is clear that there are specialist taxa that are abundant within a fairly narrow TP range, whereas others are more broadly distributed (Fig. 2). For example, the *Daphnia pulex* group, *Alonella nana* and *Chydorus gibbus*, were primarily found in oligotrophic to



**Fig. 2.** Cladoceran species assemblages found in surface sediments from 20 northeastern North American EMAP lakes (data are expressed as percent relative abundance). Only taxa that were present in greater than 5% are shown. Lake trophic status is categorized based on total phosphorus (TP) measurements. Note that the taxa included in the macrophyte-associated group are *Alona rustica*, *Alona intermedia*, *Eurycercus lamellatus*, *Pleuroxus* spp., and *Sida crystallina*.



mesotrophic waters. Conversely, the dominant *Bosmina longirostris* was present across the entire gradient but showed increased relative abundance at higher TP levels. *Chydorus brevilabris* was also a taxon with a widespread distribution (present in 19 of the 20 sites) but occurred at higher relative abundances in mesotrophic to hypereutrophic waters. Macrophyte-associated taxa (a group comprised of *Alona rustica*, *Alona intermedia*, *Pleuroxus* spp., *Eurycercus lamellatus*, and *Sida crystallina* (Smirnov 1996)) were most abundant in mesotrophic sites.

With both the Simpson's and species-richness estimates of diversity, we found that chydorid diversity was negatively correlated with TP concentrations (Fig. 3a for species richness; for the Simpson's diversity estimate,  $r = -0.52$ ,  $p = 0.02$ ). There was also a significant relationship when percent disturbance was used as a predictor variable for species richness (Fig. 3b) but not for Simpson's diversity estimates ( $r = -0.36$ ,  $p = 0.12$ ). Unlike many other studies (e.g., Dodson et al. 2000), we failed to detect a significant relationship between alpha diversity and lake area (Fig. 3c for species richness; for the Simpson's diversity estimate,  $r = -0.34$ ,  $p = 0.15$ ) or depth (for species richness,  $r = 0.38$ ,  $p = 0.10$ ; for the Simpson's diversity estimate,  $r = 0.36$ ,  $p = 0.12$ ). However, because we chose to focus on shallow lakes, the range of lake sizes was limited (1.8–77.8 ha and 0.56–10.9 m  $Z_{max}$ ), and in turn, this may have precluded our ability to detect a significant effect of lake morphometry.

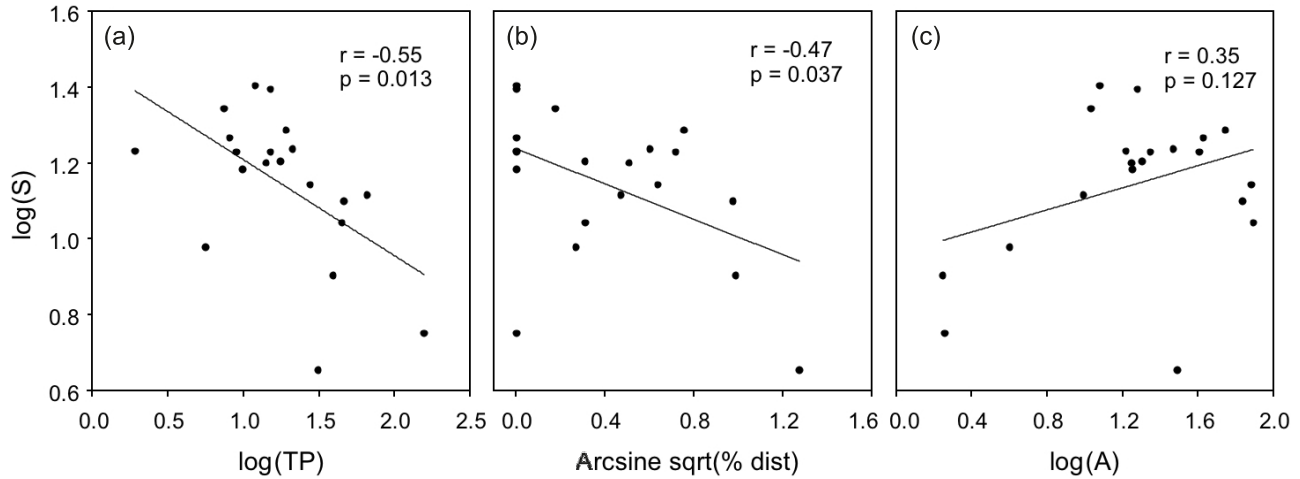
### Historical and paleolimnological analyses

The first census division and subdivision land-use data for the Petit Lac Saint-François region were collected in 1871. At that time, the amount of land cleared for cropland and pastureland comprised 17% and 13% of the census division

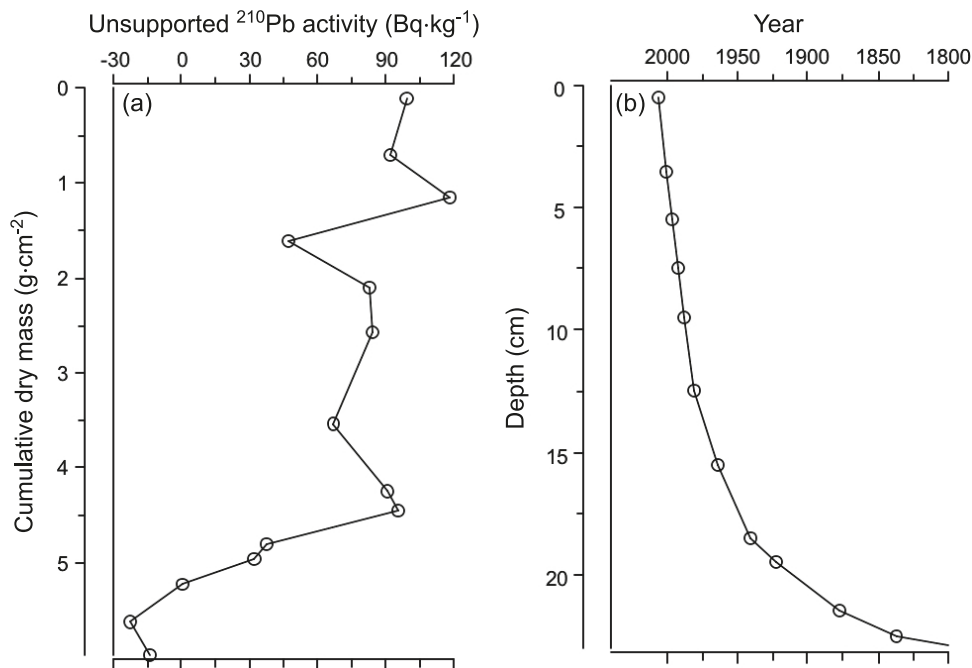
and subdivision, respectively. The spatial extent of these agricultural lands, however, peaked in the mid-1900s and then subsequently declined. The intensity of agriculture, measured by the change in the census division's net P load to watershed soils, peaked later (i.e., between 1971 and 1991). Most of the P inputs (on average, 80%) have come in the form of manure-derived P. Based on aerial photograph analyses, we know that the proportion of urban land at both the census division and census subdivision scale has always been very low (~5%; G.K. MacDonald, unpublished data).

Our  $^{210}\text{Pb}$  data suggest that the sediment record covers the entire historical period (Fig. 4), and over this time period, the geochemical and biological analyses show strong changes, many of which are synchronous with land-use change. For example, the sedimentation rates to the lake have been accelerated since ~1950 (Fig. 4b). The sedimentary organic carbon content (measured as LOI 550) showed a strong decline between 1890 and 1940 in Petit Lac Saint-François and has remained relatively low since 1940 (Fig. 5). The magnetic susceptibility profile shows an opposite trajectory compared with the LOI 550 profile, with a trend towards increasing values between 1870 and 1950 and then values remaining high between 1950 and the present (Fig. 5). The fluxes of cladoceran remains, indicators of secondary production, increased markedly over the past ~20–30 years (Fig. 5). The changes in LOI 550 and magnetic susceptibility, as well as changes in the fluxes of *Bosmina* and chydorids, are all significantly correlated with one another ( $r > |0.87|$ ,  $p < 0.001$ ,  $n > 14$ ). Similar to the surface sediments where the strongest predictor of cladoceran community composition was TP, we found that the strongest environmental predictor of *Bosmina* or chydorid flux was net P load to soils ( $r = 0.93$  and  $0.89$ , respectively,  $p < 0.001$ ,  $n = 14$ ). The sum of percent cropland and percent

**Fig. 3.** The relationship between rarefied chydorid species richness ( $S$ , 4.5–25.4 species, log-transformed) and (a) total phosphorus (TP, 0.9–154.5  $\mu\text{g}\cdot\text{L}^{-1}$ , log-transformed), (b) the proportion of disturbed watershed area (i.e., percent agricultural and urban lands (denoted as % dist), 0%–91.5%, arcsine square root (Arcsine sqrt) transformed), and (c) lake surface area ( $A$ , 1.8–77.8 ha, log-transformed) of the 20-lake EMAP surface sediment analysis.



**Fig. 4.** (a) Changes in  $^{210}\text{Pb}$  activity vs. sediment cumulative dry mass; (b) changes in sedimentation rate.



pastureland was not significantly related to either *Bosmina* or chydorid flux ( $p > 0.05$ ).

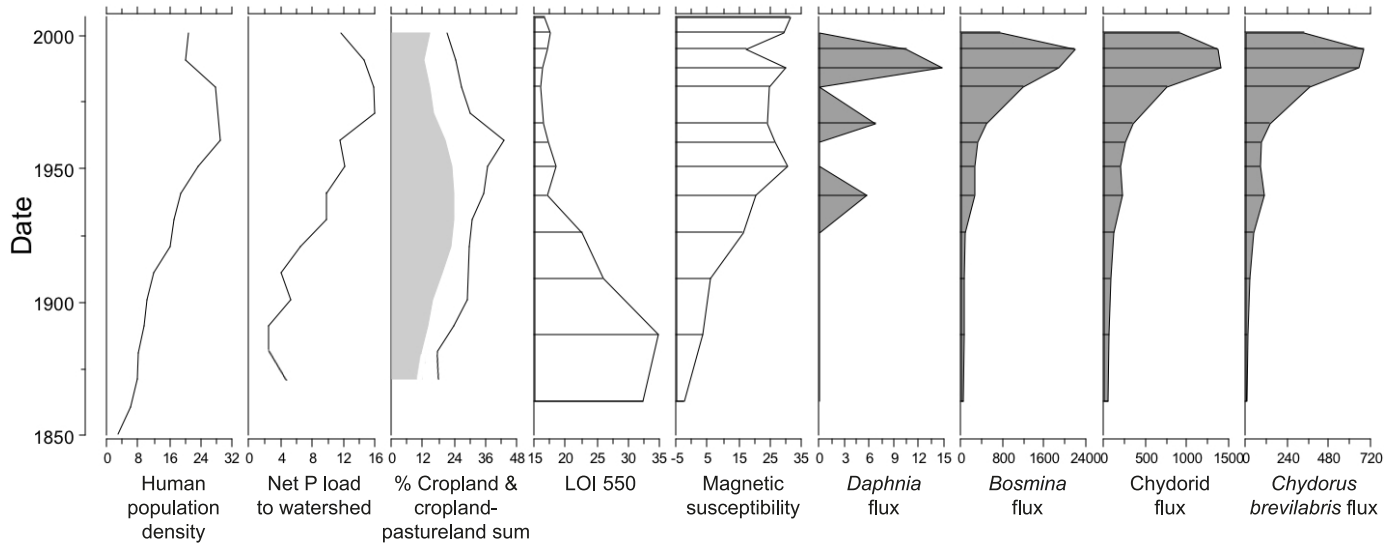
The large changes in cladoceran fluxes were mirrored by pronounced shifts in cladoceran species composition and diversity. Specifically, *Alonella nana*, an oligotrophic indicator, showed a sharp decline in relative abundance in the early 1900s. Macrophyte-associated taxa also showed a decline towards the top of the core. These taxa are replaced by large expansions in the mesotrophic- and hypereutrophic-tolerant *Chydorus biovatus* and *Chydorus brevilabris* (Fig. 6). Plotting the cladoceran sediment core intervals passively in the RDA (which was developed based on modern cladoceran and environmental data) reveals that the Petit Lac Saint-François samples follow along the TP and pH vectors (Fig. 7).

The cladoceran assemblage shift also represents a major change in chydorid species richness. Rarefied species richness estimates show a significant decline from a maximum of  $20.2 \pm 1.6$  species to a low of  $10.5 \pm 1.6$  species at the surface, when comparing individual intervals (Fig. 6). The integrated-sample species richness and Simpson's index measures also show the same declining trend in species diversity (Fig. 6). Correlation analyses between the diversity metrics and net P load were all strongly negatively related ( $r < -0.86$ ,  $p < 0.001$ ,  $n = 14$ ).

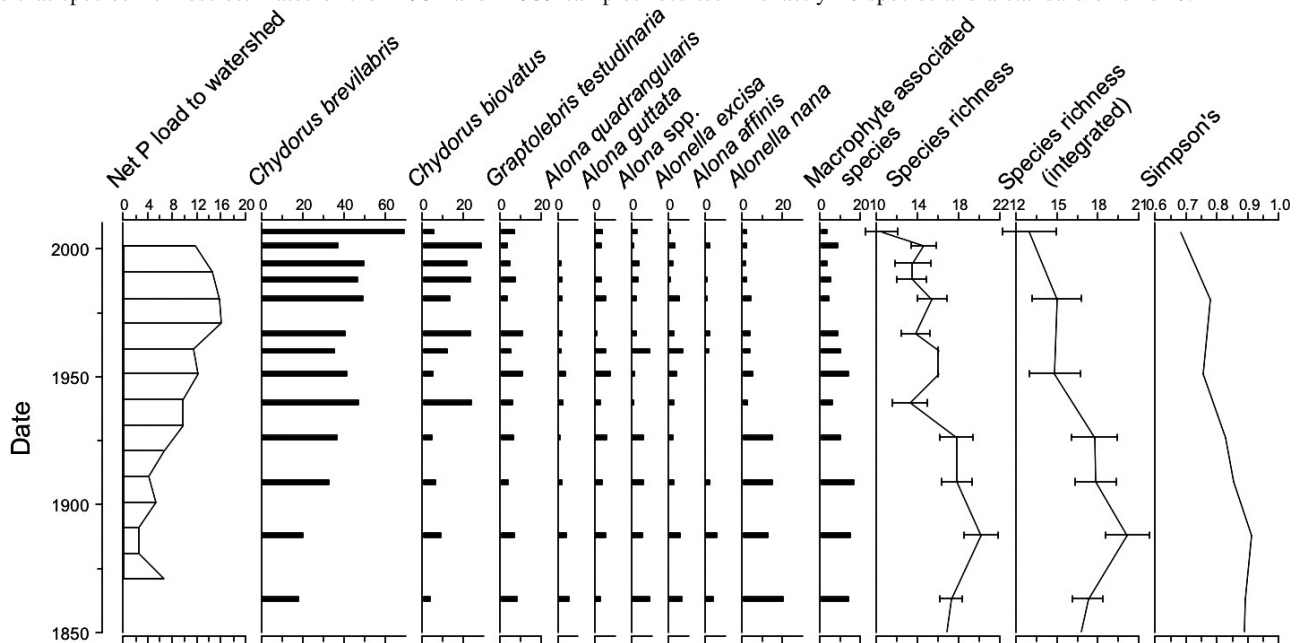
## Discussion

Across spatial and temporal gradients, lake-water TP concentration and P load to watershed soils were significant

**Fig. 5.** Historical census division data and paleolimnological analyses from Petit Lac Saint-François. Human population densities represent measurements of number of people-km<sup>-2</sup>. The sums of cropland and pastureland data are expressed as percentages of the entire census division, with the shaded area representing the percent area dedicated to cropland alone. The net P load to the watershed soils is the difference between P inputs (i.e., fertilizer P and P derived from livestock manure) and outputs (i.e., P removed in harvested crops), expressed as kg P·ha<sup>-1</sup>·year<sup>-1</sup>. LOI 550 is a measure of the percent organic content of the sediment. The units for magnetic susceptibility and fluxes of Cladocera groups are SI units·g<sup>-1</sup> and individuals·cm<sup>-2</sup>·year<sup>-1</sup>, respectively. Because cladoceran flux and accumulation data (individuals·g dry weight<sup>-1</sup>) were very similar, we have not shown the accumulation data (i.e., significant correlations were detected between flux and accumulation for each group of cladocerans). *Daphnia* remains may not preserve as well as other cladocerans, and thus we have focused our quantitative analyses on *Bosmina* and chydorids.



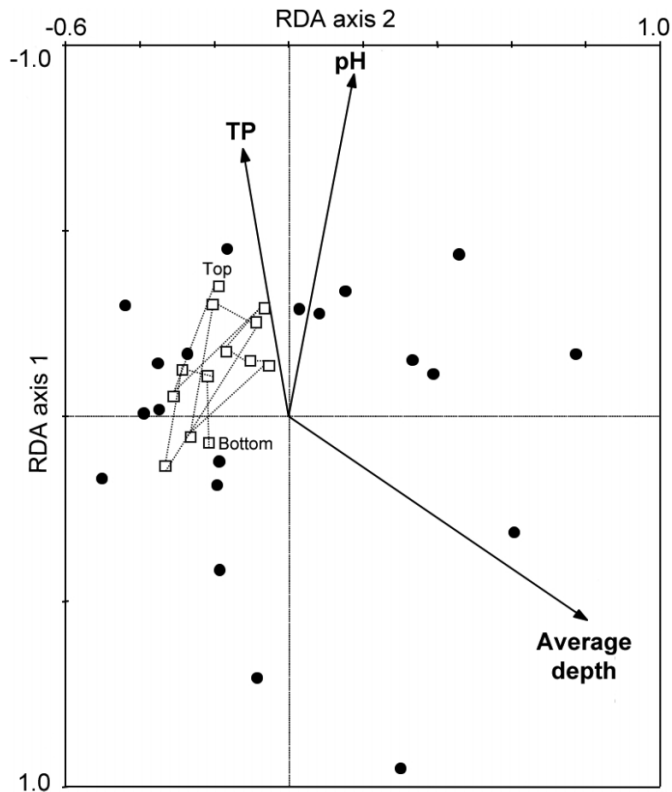
**Fig. 6.** Changes in the relative abundance (%) of chydorid species and diversity in the ~150-year sediment core record from Petit Lac Saint-François plotted alongside the net P load to the watershed. With the relative abundance data, only taxa that were present at greater than 5% abundance are shown. The taxa included in the macrophyte-associated cladoceran group are *Alona rustica*, *Alona intermedia*, *Pleuroxus* spp., *Eurycercus lamellatus*, and *Sida crystallina* (note that not all of these taxa are chydorids). Species richness was measured by individual-based rarefaction of raw chydorid counts ( $n = 60$ ) for both individual and integrated sample assemblages to correct for changing sedimentation rate. Note that species richness estimates of the ~1951 and ~1959 samples resulted in exactly 16 species and a standard error of 0.



predictors of cladoceran community composition, diversity, and (or) secondary production (measured as changes in flux to the sediments). These results are consistent with previous ecological surveys and paleolimnological studies that have

demonstrated significant relationships between phosphorus and Cladocera. Specifically, phosphorus is known to impact cladocerans directly as it is an essential nutrient and a component of several key biochemicals (Sterner and Hessen

**Fig. 7.** Redundancy analysis (RDA) of the EMAP surface sediment cladoceran assemblages (solid circles) with samples from Petit Lac Saint-François (open squares) plotted passively. The dotted lines connect sequential sediment intervals from the bottom (~1860) to the top of the core (2007).



1994). As such, phosphorus influences individual cladoceran growth when it is found in low concentrations in cladoceran food (i.e., algae; Urabe et al. 1997). Phosphorus also has an indirect influence on cladocerans, as it strongly controls the amount of algal growth. As has been found in many other studies (e.g., Prairie et al. 1989), we noted that TP is a significant predictor of chlorophyll *a* levels in the spatial survey, which in turn is a proxy for primary production (Dillon and Rigler 1974), an important food resource for herbivorous grazers such as cladocerans. TP may also affect the quality of prey for cladocerans by altering phytoplankton community composition, but this mechanism could not be addressed with the data available.

Pronounced ecological changes can occur in shallow lakes at elevated TP levels when phytoplankton biomass becomes so dense that it shades out submerged macrophytes (Scheffer et al. 1993, 2001). Submerged macrophytes are vital for certain littoral species (namely, *Alona rustica*, *Alona intermedia*, *Pleuroxus* spp., *Eurycercus lamellatus*, and *Sida crystallina*) that feed on epiphytes or require them as a substrate (Fryer 1968; Korhola and Rautio 2001). These taxa were predominantly found in mesotrophic waters in our spatial survey and were much less abundant in eutrophic waters, most likely due to the loss of macrophytes in nutrient-rich waters. In our sediment record of Petit Lac Saint-François, there is a discernable decrease in relative abundance of macrophyte-associated species that is broadly concurrent with the changes in net P load to the watershed

soils. Based on our preliminary macrofossil analyses of this same core, there is also evidence to suggest that macrophytes were once very abundant in this lake (J.C. Vermaire, personal observation). Given that there are now very few macrophytes growing in Petit Lac Saint-François, we believe that the eutrophication of this lake resulted in a loss of macrophytes and associated epiphytic taxa.

Change in predation pressure is another important factor to consider when interpreting changes in Cladocera community structure (e.g., Jeppesen et al. 1996). Across our survey of lakes, it is likely that planktivorous predation pressure plays some role in shaping overall cladoceran community composition, but unfortunately, fish data were not available for our subset of EMAP lakes. In the Petit Lac Saint-François record, we suggest that chydorid composition is primarily reflecting changes in nutrients and macrophytes because these variables are stronger predictors of littoral community composition than fish predation (Jeppesen et al. 1996). Furthermore, the trajectory of our core data, within the context of the RDA derived from our spatial survey, suggests that the cladoceran assemblage, over time, shifted to one reflecting a more nutrient-rich community. Likewise, the consistent pattern evident across all flux profiles suggests that predation pressure is not the primary driver, as these groups differ in their sensitivity to planktivores.

Similar to previous work by Dodson et al. (2005, 2007), we detected a significant negative relationship between cladoceran diversity and the proportion of disturbed land in the watershed across lakes. This may be due, in part, to the dominance of eutrophic-tolerant taxa such as *Chydorus brevilabris* that are better able to compete at high nutrient levels or are not affected by toxic cyanobacteria and can exclude other species. A shift in the phytoplankton community towards larger, inedible filamentous primary producers, a phenomenon that can occur in more nutrient-rich waters (Kalff 2002), could also hamper the ability of some filter-feeding cladoceran taxa. Furthermore, eutrophication can lead to a decline or loss of macrophytes and their associated communities, which in turn, can decrease cladoceran diversity in nutrient-rich lakes.

In our temporal analysis, we found that land-use intensity rather than land cover was a significant predictor of chydorid diversity, as well as *Bosmina* and chydorid flux. Consistent with this finding, we note that previous paleolimnological studies have found that the clearing of vegetation from a watershed on its own may not result in a large or sustained change in lake-water P concentration (e.g., Räsänen et al. 2007). However, when land is cleared for agriculture and a sufficient amount of fertilizer is applied to watershed soils (either from animal manure or commercial fertilizer with applications that are in excess of crop requirements), the export of nutrients to surface waters is enhanced (Carpenter 2008). In our study, we found that increases in net P load to the watershed soils lagged behind increases in agricultural land cover. Net P load to regional soils, however, was correlated with both LOI 550 and magnetic susceptibility. The LOI 550 and magnetic susceptibility profiles reflect a progressive increase in minerogenic content of lake sediments, which is indicative of soil erosion (Boyle 2001; Sandgren and Snowball 2001). Given that LOI 550 is a relative measure, it would appear as though the increases in inorganic matter arising from the catchment outweigh any increased autochthonous organic matter production. The



strong correlations between LOI 550, magnetic susceptibility, or net P load to the watershed and cladoceran production or diversity imply that changes in the ecological functioning of Petit Lac Saint-François were driven by shifts in the intensity of agricultural activities rather than the spatial extent of agricultural land. We suggest that a spatial survey approach may be more apt to detect a strong interaction between biological indicators and the proportion of land use dedicated to agriculture, particularly in regions where land-use practices have not changed much in the past decade or more, because spatial surveys can provide a temporally integrated perspective of cumulative phosphorus loads.

Overall, our study has shown that changes in land use within the watershed, in particular those changes that result in increased phosphorus loading, can have a significant effect on the cladoceran community that ultimately results in the reduction of biodiversity. Our findings are consistent with those of Dodson et al. (2005, 2007) and demonstrate that watershed land use is a key structuring factor of cladoceran diversity and community composition. Our results also highlight that metrics of land-use intensity rather than cover may be more appropriate for defining the responses of aquatic ecosystems to land-use change.

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## Appendix A

**Table A1.** Summary of ecological variables of the 20-lake EMAP data set.

Lake code	Lake name	Latitude (°N)	Longitude (°W)	Chlorophyll <i>a</i> (µg·L <sup>-1</sup> )	Conductivity (µS·cm <sup>-1</sup> )	Dissolved organic carbon (mg·L <sup>-1</sup> )	pH
CT002	Bissonette Pond	41.92	72.22	8.1	101	5.2	7.9
MA007	Upper Artichoke Reservoir	42.8	70.93	3.9	176	7.4	8.2
MA008	Savery Pond	41.91	70.84	11.1	81	5.6	7.3
ME001	Moose Pond	43.59	70.93	1.5	48	2.9	7.8
ME002	Mountain Pond	44.9	70.64	2.6	16	4.1	6.7
ME004	Shaw Pond	45.29	70.28	4.1	32	7.3	7.6
ME009	Alder Brook Stream	44.92	69.25	3.5	124	7.5	8.4
ME011	Female Pond	45.75	69.22	3.4	32	6.9	7.6
NH006	Flints Pond	42.75	71.55	4.1	143	6.4	8.2
NH009	Russell	44.01	71.65	2.0	21	1.9	6.8
NJ002	Cranberry Lake	40.95	74.75	22.8	142	5.1	8.2
NY021	Gerlach Pond	42.32	78.98	34.9	87	6.2	8.1
NY023	Crystal Lake	43.83	76.13	15.1	236	4.2	8.5
NY024	White Lake	43.01	76.04	1.2	1073	2.1	8.5
NY025	Hyde Lake	44.24	75.83	26.8	122	3.4	8.1
NY032	Windfall Pond	44.36	74.45	4.8	24	3.6	7.3
NY036	Masick's Pond	42.63	74.32	6.0	136	4.7	8.4
RI004	Mashapoag	41.79	71.43	21.4	345	5.2	8.3
VT005	Ticklenaked	44.19	72.1	6.3	180	4.3	8.4
VT009	Abanaki	43.83	72.23	4.2	72	4.7	8.1

Note: NTU, nephelometric turbidity units.

## Appendix B

**Table B1.** List of all identified Cladocera species.

EMAP data set species list	PSF core species list
<i>Acroperus harpae</i>	<i>Acroperus harpae</i>
<i>Alona affinis</i>	<i>Alona affinis</i>
<i>Alona barbabulata</i>	<i>Alona circumfibrata</i>
<i>Alona bicolor</i>	<i>Alona costata</i>
<i>Alona circumfibrata</i>	<i>Alona guttata</i>
<i>Alona costata</i>	<i>Alona intermedia</i>
<i>Alona guttata</i>	<i>Alona quadrangularis</i>
<i>Alona intermedia</i>	<i>Alona rustica</i>
<i>Alona quadrangularis</i>	<i>Alona</i> spp.
<i>Alona rustica</i>	<i>Alonella dentifera</i>
<i>Alona setulosa</i>	<i>Alonella excisa</i>
<i>Alona</i> spp.	<i>Alonella exigua</i>
<i>Alonella dentifera</i>	<i>Alonella nana</i>
<i>Alonella excisa</i>	<i>Bosmina longirostris</i>
<i>Alonella exigua</i>	<i>Bosmina longispina</i>
<i>Alonella nana</i>	<i>Camptocercus</i> spp.
<i>Bosmina longirostris</i>	<i>Chydorus biovatus</i>
<i>Bosmina longispina</i>	<i>Chydorus brevilabris</i>
<i>Camptocercus</i> spp.	<i>Chydorus faviformis</i>
<i>Chydorus bicornutus</i>	<i>Chydorus gibbus</i>
<i>Chydorus biovatus</i>	<i>Chydorus piger</i>
<i>Chydorus brevilabris</i>	<i>Daphnia pulex</i>
<i>Chydorus faviformis</i>	<i>Daphnia</i> spp.
<i>Chydorus gibbus</i>	<i>Disparalona leei</i>
<i>Chydorus piger</i>	<i>Eurycerus lamellatus</i>
<i>Daphnia longispina</i>	<i>Graptolebris testudinaria</i>

**Table B1 (concluded).**

EMAP data set species list	PSF core species list
<i>Daphnia pulex</i>	<i>Kurzia latissima</i>
<i>Daphnia</i> spp.	<i>Latona setifera</i>
<i>Diaphanosoma brachyurum</i>	<i>Leydigia leydigii</i>
<i>Disparalona acutirostris</i>	<i>Monospilus dispar</i>
<i>Disparalona rostrata</i>	<i>Pleuroxus aduncus</i>
<i>Dunhvedia crassa</i>	<i>Pleuroxus denticulatus</i>
<i>Eurycerus lamellatus</i>	<i>Pleuroxus laevis</i>
<i>Graptolebris testudinaria</i>	<i>Pleuroxus procurvus</i>
<i>Kurzia latissima</i>	<i>Pleuroxus</i> spp.
<i>Latona setifera</i>	<i>Pleuroxus striatus</i>
<i>Leptodora kindti</i>	<i>Pleuroxus trigonellus</i>
<i>Leydigia leydigii</i>	<i>Pleuroxus truncatus</i>
<i>Monospilus dispar</i>	<i>Pleuroxus uncinatus</i>
<i>Oxyurella tenuicaudis</i>	<i>Sida crystallina</i>
<i>Pleuroxus aduncus</i>	
<i>Pleuroxus denticulatus</i>	
<i>Pleuroxus laevis</i>	
<i>Pleuroxus procurvus</i>	
<i>Pleuroxus</i> spp.	
<i>Pleuroxus trigonellus</i>	
<i>Pleuroxus truncatus</i>	
<i>Pleuroxus uncinatus</i>	
<i>Pseudochydorus globosus</i>	
<i>Rhynchotalona falcata</i>	
<i>Sida crystallina</i>	

Total nitrogen ( $\mu\text{g}\cdot\text{L}^{-1}$ )	Total phosphorus ( $\mu\text{g}\cdot\text{L}^{-1}$ )	Turbidity (NTU)	Mean depth (m)	Lake surface area (ha)	Agriculture in watershed (%)	Disturbance in watershed (%)	Estimated watershed slope (%/100)
400	16.5	1.3	1.3	20.1	3.1	9.2	0.04
500	18.0	1.0	1.4	55.3	44.9	47.0	0.02
550	64.3	9.4	1.4	9.8	18.2	20.5	0.01
300	6.4	0.4	2.6	10.7	0.0	3.1	0.03
300	10.9	0.7	3.8	11.9	0.0	0.0	0.14
400	14.0	0.9	1.2	18.9	0.0	0.0	0.06
500	20.0	1.4	0.8	29.3	30.6	32.0	0.01
300	7.9	0.7	8.4	40.2	0.0	0.0	0.06
470	13.0	1.9	1.3	17.5	20.0	23.5	0.03
300	0.9	0.2	10.9	16.4	0.0	0.0	0.16
600	43.5	3.0	1.9	77.8	0.0	9.4	0.04
900	154.5	7.8	0.6	1.8	0.0	0.0	0.10
600	45.0	1.4	3.1	68.1	68.5	68.5	0.01
1060	4.6	0.2	5.5	4.0	0.0	7.0	0.08
500	26.5	2.8	3.4	75.9	34.0	35.4	0.01
300	7.0	0.7	3.0	42.3	0.0	0.0	0.07
500	37.9	1.4	2.1	1.8	69.6	69.6	0.15
800	30.0	6.8	1.9	30.8	0.0	91.5	0.01
400	14.0	2.1	7.2	22.2	42.1	43.2	0.04
400	8.8	0.5	1.6	17.7	0.0	0.0	0.08