Primary determinants of macrophyte community structure in 62 marshes across the Great Lakes basin: latitude, land use, and water quality effects

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Abstract: We collected water quality, land use, and aquatic macrophyte information from 62 coastal and inland wetlands in the Great Lakes basin and found that species richness and community structure of macrophytes were a function of geographic location and water quality. For inland wetlands, the primary source of water quality degradation was inputs of nutrients and sediment associated with altered land use, whereas for coastal wetlands, water quality was also influenced by exposure and mixing with the respective Great Lakes. Wetlands within the subbasins of the less developed, more exposed upper Great Lakes had unique physical and ecological characteristics compared with the more developed, less sheltered wetlands of the lower Great Lakes and those located inland. Turbid, nutrient-rich wetlands were characterized by a fringe of emergent vegetation, with a few sparsely distributed submergent plant species. High-quality wetlands had clearer water and lower nutrient levels and contained a mix of emergent and floating-leaf taxa with a diverse and dense submergent plant community. Certain macrophyte taxa were identified as intolerant of turbid, nutrient-rich conditions (e.g., *Pontederia cordata*, *Najas flaxilis*), while others were tolerant of a wide range of conditions (e.g., *Typha* spp., *Potamogeton pectinatus*) occurring in both degraded and pristine wetlands.

Résumé : Des données recueillies sur la qualité de l'eau, l'utilisation des terres et les macrophytes aquatiques dans 62 terres humides des régions côtières et intérieures du bassin des Grands Lacs indiquent que la richesse spécifique et la structure des communautés de macrophytes dépendent de la situation géographique et de la qualité de l'eau. Dans les terres humides intérieures, la source principale de dégradation de la qualité de l'eau est l'apport de nutriments et de sédiments causé par les changements dans l'utilisation des terres, alors que, dans les terres humides côtières, la qualité de l'eau est aussi influencée par le contact avec le Grand Lac adjacent et les mélanges d'eau qui s'y produisent. Les terres humides des sous-bassins des Grands Lacs d'amont, qui ont subi moins de développement et qui sont plus exposés, possèdent des caractéristiques physiques et écologiques tout à fait particulières, par comparaison avec les terres humides des Grands Lacs d'aval qui sont plus développés et moins protégés, et les terres humides intérieures. Les terres humides turbides et riches en nutriments sont caractérisées par le développement d'une ceinture de végétation émergente et la présence sporadique de quelques plantes submergées. Les terres humides de grande qualité possèdent une eau plus claire, des concentrations plus faibles de nutriments et une combinaison de taxons de plantes émergentes et de plantes à feuilles flottantes, d'une part, et d'une communauté diversifiée et dense de plantes submergées, d'autre part. Certains taxons de macrophytes se sont révélés intolérants aux conditions de turbidité et de richesse en éléments nutritifs élevées (e.g., *Pontederia cordata, Najas flexilis*), alors que d'autres tolèrent une gamme étendue de conditions (e.g., *Typha* spp., *Potamogeton pectinatus*) et se retrouvent dans les terres humides tant dégradées qu'intactes.

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Introduction

Long-term changes in the macrophyte communities of individual Great Lakes coastal marshes, especially those located in settled areas of Lakes Erie and Ontario, have been well documented over the past two decades (e.g., Crowder and Bristow

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1986; Klarer and Millie 1992; Chow-Fraser et al. 1998); however, the underlying factors causing these changes have rarely been investigated. These preliminary studies have indicated that year-to-year changes in areal cover of emergent vegetation are probably controlled by fluctuating water levels (Keddy and Reznicek 1986; Chow-Fraser et al. 1998), whereas growth and diversity of submergent vegetation are more likely controlled by water clarity (Lougheed et al. 1998).

The combined effects of hydrology, local bedrock geology, and wetland morphology, referred to jointly as hydrogeomorphic factors, tend to be the primary regional determinants of plant community structure in wetlands and littoral systems (e.g., Minc 1997; Thiébaut and Muller 1998; Keough et al. 1999). Where the Great Lakes basin is concerned, hydrogeomorphic variation and climatic differences associated with a total shoreline length of 12 017 km contribute to a great diversity of physical environments (Smith et al. 1991; Keough et al. 1999). These regional differences have impor-

tant consequences for human settlement and land use patterns, with the most productive agricultural land and largest urban centers occurring south of the 46th parallel (Environment Canada and U.S. Environmental Protection Agency 1995). Consequently, although wetlands throughout the entire Great Lakes basin are at risk from non-point-source pollution (Crosbie and Chow-Fraser 1999), water level regulation (Keddy and Reznicek 1986), disturbance by nuisance exotic species such as common carp (*Cyprinus carpio*) (Lougheed et al. 1998), and internal loading of phosphorus (Chow-Fraser 1998; Mayer et al. 1999), these disturbance factors tend to predominate in the lower lakes. In particular, agricultural and urban land use in wetland catchments of the lower lakes has been shown to affect nutrient enrichment, water clarity and sediment quality (Crosbie and Chow-Fraser 1999) and will therefore likely have profound effects on submersed macrophyte growth (e.g., Phillips et al. 1978; Barko and Smart 1983; Magee et al. 1999) and distribution (Lougheed et al. 1998; Crosbie and Chow-Fraser 1999).

Macrophyte growth is limited by both water quality and sediment quality (Day et al. 1988; Barko et al. 1991). Light availability is a primary factor determining photosynthetic potential and can be reduced by nonalgal and algal turbidity, including periphytic growth (Phillips et al. 1978). As such, details on the nutrient status, sediment quality, and particulate content of the water are required to make conclusions regarding the causative effects of macrophyte community changes. Although taxonomic surveys of macrophyte communities in individual Great Lakes coastal wetlands exist (e.g., Crowder and Bristow 1986; Klarer and Millie 1992; Chow-Fraser et al. 1998), there have been no published studies that account for all of these variables and their roles in causing species replacement in the macrophyte community on a basin-wide scale. The most comprehensive study that we have found was a report by Minc (1997), who analyzed macrophyte data from 110 coastal wetlands in the U.S. waters of the Great Lakes and listed the primary determinants of macrophyte distribution as latitude, soil pH, water temperature, and turbidity; however, several important factors were excluded from this study, including trophic state and sediment fertility. In Canadian waters, Smith et al. (1991) published a study that described the differences in the physical attributes of 160 coastal wetlands in the three southernmost Canadian Great Lakes. Their study provided evidence that geology, exposure, and disturbance vary statistically among the three lakes but provided no information on water quality and taxonomic composition of submerged macrophytes that could be affected by changes in sediment and nutrient load.

The challenge facing managers is to determine the degree to which each of these hydrogeomorphic, climatic, and disturbance factors individually or in combination alters wetland plant communities. In this paper, we compare the macrophyte community composition of 62 wetlands in the Canadian part of the Great Lakes basin to examine how water quality and sediment quality affect the taxonomic composition and community structure of the macrophyte community and relate these to land use in their watershed. In addition to the 22 marshes sampled by Crosbie and Chow-Fraser (1999), located primarily along the shoreline of the lower lakes, our data set includes 40 additional coastal and inland

wetlands covering all four Canadian Great Lakes. This study will contribute much needed information to help wetland managers determine the relative importance of these various factors in structuring the aquatic macrophyte community on a basin-wide scale.

Methods

Sixty-two marshes in the Great Lakes basin were visited between 1995 and 1999 and sampled for water quality and macrophyte community information. These wetlands were selected based on the amount of agricultural, urban, and forested land in their watersheds to ensure a sufficient gradient of disturbance (Crosbie and Chow-Fraser 1999). In addition, wetlands were chosen from a broad geographic range: from the St. Lawrence River just east of Cornwall, down to the Windsor–Detroit area and Lake St. Clair, and up to Lake Superior and the Ontario–Minnesota border (Fig. 1). Forty-six of these were coastal marshes (within 2 km of the Great Lakes shoreline but not separated hydrologically from the lake due to dams or waterfalls) of the upper (Huron, Superior) and lower (Ontario, Erie) lakes, while the remaining 16 wetlands were located inland within the Great Lakes – St. Lawrence River basin. All wetlands were visited once in midsummer (June 18 to July 30).

To choose the sampling location, the general character of each marsh was first assessed with a brief inspection of accessible nearshore areas. Subsequently, we selected a sheltered location (if available) containing relatively dense submergent plants (if present). All water and sediment samples were collected during daylight hours from the middle of the water column at an open-water site 3 m from the edge of macrophyte beds. Because of the large site-to-site, year-to-year, and seasonal variation in water levels, which are characteristic of Great Lakes coastal marshes (Chow-Fraser 1999), water depths in this study ranged from 5 to 260 cm, depending on wetland, time of year, and the sampling year in question; however, there were no observed effects of depth on any other parameter measured in this study.

The protocol for sampling and analysis of water samples has been documented elsewhere (V.L. Lougheed and P. Chow-Fraser, unpublished data). For each wetland, we analyzed samples for total phosphorus (TP), soluble reactive phosphorus (SRP), total nitrogen (TN) (sum of total Kjeldahl nitrogen (TKN) and total nitrate nitrogen (TNN)), total suspended solids (TSS), total inorganic suspended solids (TISS), and planktonic chlorophyll *a* corrected for phaeopigments (CHL*a*). Temperature, pH, dissolved oxygen, and conductivity were measured with an H2O® Hydrolab. Turbidity readings were taken using a portable Hach turbidimeter (model 2100P).

Sediment samples were collected using either an Ekman grab sampler or a 5-cm Plexiglas tube with plunger and analyzed to determine the proportion of inorganic matter (INORG$_{SED}$) and total phosphorus (TP$_{SED}$) in the sediment (Crosbie and Chow-Fraser 1999). The maximum and dominant grain size in each sediment sample (20–70 g dry sediment) was classified according to the Wentworth scale (Wotton 1990); wetlands visited by Crosbie and Chow-Fraser (1999) were not analyzed for sediment size ($n = 22$).

We counted every species of submergent, emergent, and floating-leaf vegetation encountered within a 3-m radius of the selected vegetated site. In wetlands where submergent plant distribution was sparse (estimated as <5 plants·m^{-2}), we conducted an expanded survey along approximately 100 m of shoreline. Keys by Fassett (1940) and Newmaster et al. (1997) were used to identify the macrophyte specimens to species where possible. Because many wetlands were visited only once, and because certain species are difficult to identify accurately without flowering parts, many taxa were identified to genus only. Most submergent taxa were identified to genus, except for several common species that were keyed to species. All emergent taxa encountered were identified at

Fig. 1. Map of the Great Lakes of North America showing the location of the 62 wetlands sampled between 1995 and 1999.
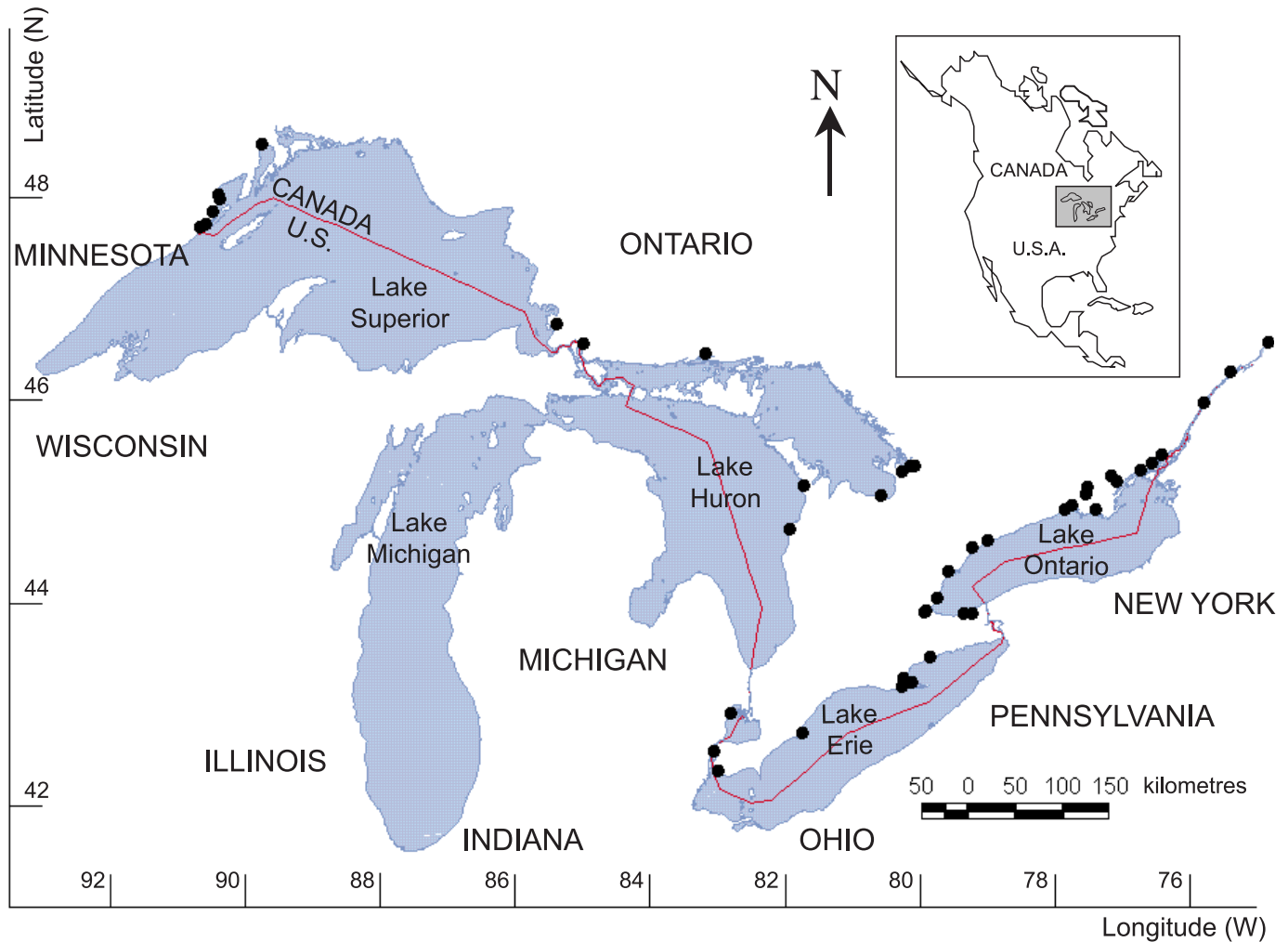
least to genus, and the dominant taxa were noted. The objective of this plant survey was not meant to be exhaustive but rather to obtain floristic information on common taxa in a structurally diverse plant community that would include emergent, submergent, and floating-leaf components. Consequently, we did not sample along parallel transects of a systematic grid, an approach employed in studies designed to produce comprehensive species lists (e.g., Minc 1997; Magee et al. 1999). Our approach therefore likely excluded rare species and many grasses, rushes, and sedges that would have been more common in wet meadow environments (e.g., Minc 1997).

Proportion of agricultural, urban, and forested land was determined as described in Crosbie and Chow-Fraser (1999); however, for the three largest watersheds (>1500 km²), land use was estimated from Detenbeck et al. (1999) (Goulais and Spanish River) and the Grand River Conservation Authority (Cambridge, Ont.; www.grandriver.on.ca). Wetlands were classified into land use categories as follows: (*i*) wetlands were assigned to the dominant land use category if the majority (>50%) of their watershed was of that land use and if <30% of the remaining catchment area was of another land use, (*ii*) wetlands were assigned to a combined land use category (e.g., agriculture/forested) if no land use type accounted for >50% of the total catchment area and the difference between any two types was <20%, and (*iii*) wetlands that occurred as fringes along the Great Lakes shoreline and did not have any obvious inflows were not classified to any land use (*n* = 11).

All statistical analyses were performed using SAS.Jmp software

(SAS Institute Inc., Cary, N.C.), except for canonical correspondence analysis (CCA), which was performed using CANOCO version 4.0 (ter Braak and Smilauer 1998). Principal components analysis (PCA) was used to create linear combinations of the environmental data to describe the underlying environmental gradients in the data. Environmental data were $\log_{10}$ transformed (excluding pH) to approximate normal distributions and standardized to zero mean and unit variance. CCA was used to determine the best environmental factors to describe aquatic macrophyte distribution and has been used in similar studies relating macrophytes to their environment (e.g., Toivonen and Huttunen 1995; Bini et al. 1999; Magee et al. 1999). CCA maximizes the separation of species optima along synthetic axes, which represent linear combinations of environmental variables. CCA was appropriate in this study because the gradient lengths obtained from detrended correspondence analysis (CANOCO 4.0) indicated that the species data were moderately unimodal (ter Braak and Smilauer 1998).

Variables entered into the CCA included the presence of macrophyte taxa encountered in >10% of wetlands as well as accompanying environmental variables (i.e., TP, TN, TSS, CHL*a*, pH, conductivity (COND), TP$_{SED}$, INORG$_{SED}$, latitude (LATITUDE) (in decimal degrees)). We excluded turbidity, SRP, TISS, TKN, and TNN from the CCA because they showed a high degree of collinearity with chosen variables ($r > 0.90$) and contributed less to explaining the variation in the data set. All included variables had variance inflation factors <20, indicating that they contributed uniquely to the analysis (ter Braak and Smilauer 1998). The statis-

tical significance of the relationship between the species data and environmental gradients was determined using Monte Carlo permutations (199 random permutations) (ter Braak and Smilauer 1998).

Results

Water and sediment quality

Wetlands in this study correspond to a wide range of environmental conditions, ranging from very clear and nutrient poor (e.g., TP = 16.3 $\mu g \cdot L^{-1}$, TN = 920 $\mu g \cdot L^{-1}$, CHLa ≥ 0 $\mu g \cdot L^{-1}$, TSS = 3.4 $mg \cdot L^{-1}$) to turbid and hypereutrophic (e.g., TP = 670 $\mu g \cdot L^{-1}$, TN = 9164 $\mu g \cdot L^{-1}$, CHLa = 239 $\mu g \cdot L^{-1}$, TSS = 209 $mg \cdot L^{-1}$) (Table 1). PCA was initially used to determine which environmental variables explained the greatest amount of variation in the data set (Table 2). The first three axes explained 72% of the variation in the data (Table 2), with nearly 50% being explained by PC axis 1. This axis was highly and positively correlated with variables associated with nutrient status (TN, TP, TNN) and particulate content (TSS, TISS, turbidity, CHLa) of the water. Conductivity, an indication of the ionic strength of the water, was also highly correlated with this axis. The second axis explained 16% of the variance and was positively correlated with INORG$_{SED}$ and negatively correlated with the phosphorus in the sediment. Wetlands with high PC axis 2 scores also had relatively high pH. PC axis 3, which explained only 10% of the variation in the data, was positively correlated with SRP and temperature.

Since PC axis 1 is associated with a nutrient–turbidity gradient, wetlands to the extreme right in Fig. 2 are turbid, hypereutrophic marshes, whereas those to the left are clear, nutrient-poor marshes. The majority of turbid, nutrient-rich wetlands in our data set are coastal wetlands of the lower Great Lakes, while clear, nutrient-poor wetlands correspond to inland wetlands and coastal wetlands of the upper Great Lakes. The second PC axis, which separates wetlands with largely organic, fertile sediment and low pH from those with inorganic, infertile sediment and high pH, is a good discriminator for inland and upper coastal wetlands. Coastal wetlands in the upper lakes (Huron, Superior) tend to have a higher pH and a greater proportion of INORG$_{SED}$ (analysis of variance (ANOVA), Tukey–Kramer, $p < 0.05$), while inland wetlands tend to have more organic sediment and higher TP$_{SED}$ (ANOVA, Tukey–Kramer, $p < 0.05$).

Land use

Given development patterns in the Great Lakes basin over the past century, it was not surprising that the proportion of agricultural ($r^2 = 0.50$, $p < 0.0001$) and urban ($r^2 = 0.08$, $p < 0.05$) land in wetland watersheds decreased significantly with latitude, while the proportion of forested land increased ($r^2 = 0.72$, $p < 0.001$). To determine the effect of land use on water and sediment quality, we regressed PC axis 1 scores against the proportion of the three different land use categories. PC axis 1 scores were positively related to percent agricultural land ($r^2 = 0.39$) (Fig. 3a) and negatively correlated with percent forested land ($r^2 = 0.40$) (Fig. 3b). Although we found no significant relationship between PC axis 1 scores and the proportion of urban land use, likely due to the small number of wetlands with >10% urban land in their watershed ($n = 6$), we found a significant regression when both

Table 1. Range of environmental variables observed at 62 wetlands in the Great Lakes basin.

Variable	Mean	Range
TP ($\mu g \cdot L^{-1}$)	101	16.3–670
TN ($\mu g \cdot L^{-1}$)	2351	920–9164
TSS ($mg \cdot L^{-1}$)	23.3	3.4–209
Turbidity (NTU)	17.4	1.3–260
CHLa ($\mu g \cdot L^{-1}$)	20.2	0–239
Temperature (°C)	23.5	16.5–28.9
Dissolved oxygen ($mg \cdot L^{-1}$)	8.46	1.55–15
pH	7.54	6.0–8.7
COND ($\mu S \cdot cm^{-1}$)	388	39–1387
% INORD$_{SED}$	79.2	22.3–99.44
TP$_{SED}$ ($mg \cdot g^{-1}$)	0.78	0.12–2.17
No. of submergent plant taxa	6	0–15

Note: CHLa determined from up to 500 mL of water filtered through GF/C filters. Zero values likely reflect insufficient sample volume.

percent agricultural and percent urban land were combined ($r^2 = 0.48$) (Fig. 3c).

The wetlands were further divided into three groups according to their location in the Great Lakes basin: inland wetlands, coastal wetlands of the lower Great Lakes, and coastal wetlands of the upper Great Lakes. For inland wetlands, land use explained a large amount of variation in PC axis 1 (indicative of water quality) and PC axis 2 (indicative of sediment quality). By contrast, land use was not as good a predictor for water quality in lower coastal wetlands and was not a significant predictor for upper coastal wetlands (Table 3).

Sediment grain size and organic content of the sediment also can be affected by land use as well as by geological factors and exposure. Because the PCA showed that sediment characteristics tended to vary by location, wetlands were again divided into the three groups according to their location. For inland wetlands, agricultural watersheds had a significantly higher proportion of INORG$_{SED}$ relative to forested watersheds (Wilcoxon rank sum, $p < 0.05$), while forested wetlands had a somewhat larger maximum sediment grain size (Wilcoxon rank sum, $p < 0.10$) (Table 4). There were no significant trends observed for the more exposed lower and upper coastal wetlands, where all wetlands contained significantly more inorganic soils relative to inland wetlands, especially in the upper lakes (ANOVA, Tukey–Kramer, $p < 0.05$).

Submergent plant species richness

The number of submergent plant species in the wetlands varied inversely with both PC axes 1 and 2 scores, although there was a great deal of scatter about the best-fit line ($r^2 = 0.32$ and 0.15, respectively) (Figs. 4a and 4b). A greater amount of the variation in the species richness data was explained by turbidity alone ($r^2 = 0.45$, $p < 0.0001$) (Fig. 4c). When data were sorted according to location, the percent variance explained by turbidity increased for inland ($r^2 = 0.67$, $p < 0.0001$) and lower ($r^2 = 0.54$, $p < 0.0001$) coastal wetlands but was not significant for upper lakes ($r^2 = 0.27$, $p = 0.0554$). Similarly, PC axis 2 explained 51% of the variance in species richness for inland wetlands but was not significant for either lower or upper wetlands. Figure 4 also

Table 2. Correlation coefficients between PC axes 1, 2, and 3 scores and environmental variables.

	Variance explained (%)	Environmental variable	r
PC axis 1	45.7	TSS	0.92
		Turbidity	0.89
		TN	0.88
		TP	0.87
		TISS	0.87
		CHLa	0.83
		COND	0.76
		TNN	0.71
PC axis 2	15.8	TP$_{SED}$	−0.85
		% INORG$_{SED}$	0.78
		pH	0.68
PC axis 3	10.4	Temperature	0.68
		SRP	0.52

Fig. 2. Plot of PC axis 1 versus PC axis 2 scores including inland (□), lower coastal (+), and upper coastal (○) wetlands.


shows that there were generally fewer submergent species in upper compared with lower and inland wetlands with similar turbidity PC axis 1 or PC axis 2 scores.

Macrophyte community structure

Submergent taxa that occurred in >50% of the wetlands included *Ceratophyllum*, *Elodea*, *Myriophyllum*, *Potamogeton pectinatus*, *Potamogeton richardsonii*, and *Vallisneria*. *Typha*, *Scirpus*, and *Lythrum salicaria* were the most prevalent emergents; *Nymphaea* and *Nuphar* also occurred in at least half of the wetlands. As explained in the methods, these emergent species are only representative of the dominant forms encountered in these wetlands.

We performed a CCA to determine the association between environmental variables and the distribution of macrophytes (Fig. 5). Sixty-two percent of the variation in macrophyte distribution could be explained by the first two synthetic environmental gradients. The most important predictors of macrophyte distribution, as indicated by their correlation with CCA axis 1, were TSS ($r = 0.79$), TP ($r = 0.73$), CHLa ($r = 0.70$), TN ($r = 0.65$), and COND ($r = 0.61$) (Fig. 5a). The second CCA axis was correlated with variables indicative of sediment quality (TP$_{SED}$ ($r = -0.54$), INORG$_{SED}$ ($r = 0.34$), pH ($r = 0.41$)), although the strength of these correlations was weaker than that for CCA axis 1 scores. Not surprisingly, these variables were also the primary descriptors of the PC axes and those describing most of the variation in the submerged macrophyte species richness data. LATITUDE was moderately correlated with both CCA axes 1 ($r = -0.38$) and 2 ($r = 0.38$) and therefore confirms the distinction between higher latitude sites (clearer water, less nutrient- and organic-rich sediment) and lower latitude marshes (more turbid water, nutrient-rich, higher organic content sediment).

Location of plant taxa to the right of the origin in the biplot suggests that these plants tolerate a turbid, nutrient-rich water column (Fig. 5a). These included the emergent taxa *Typha*, *Sagittaria*, and *Lythrum*, submergent taxa *Potamogeton pectinatus* and *Potamogeton crispus*, and the floating taxa *Nuphar variegatum* and *Nymphaea odorata*. Those taxa that were least tolerant of turbidity and eutrophication
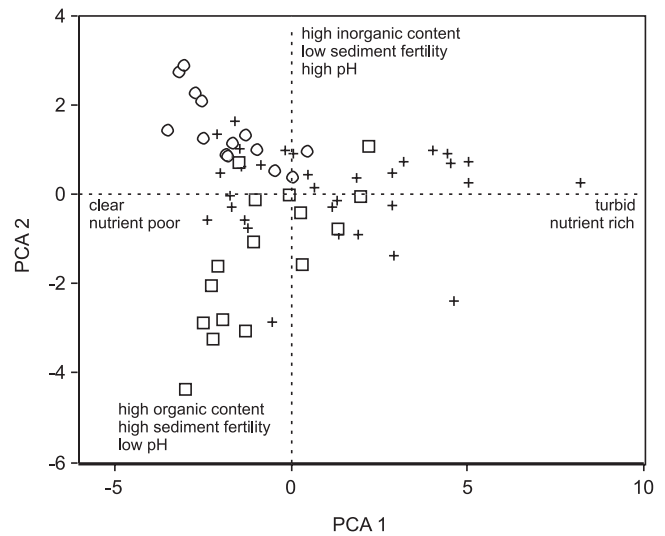
included the emergent taxa *Pontederia cordata* and *Sparganium* sp., the majority of the submergent taxa (e.g., *Potamogeton richardsonii*, *Najas flexilis*, *Utricularia* sp.), and the floating-leaf species *Potamogeton natans*. Submergent taxa that were moderately tolerant of turbid water included *Elodea canadensis* and *Ceratophyllum demersum*. Taxa more influenced by CCA axis 2 and common in more inorganic, infertile soils at higher latitudes included *Scirpus* sp. and *Potamogeton richardsonii*. Several taxa were excluded from the CCA because of their rare occurrence, and some of these taxa displayed obvious trends in their distribution. Most notably, *Potamogeton gramineus*, *Eleocharis smallii*, *Isoetes* sp., and *Zizania palustris* were found north of 44° latitude in wetlands with relatively low water turbidity and nutrient concentrations.

Figure 5b displays the location of the site scores for the CCA analysis. In general, CCA axis 1 separates the turbid, nutrient-rich wetlands in highly agricultural and urban watersheds from the clearer, more oligotrophic wetlands located in moderately to largely forested watersheds. CCA axis 2 separates higher latitude forested sites from all other sites. Three main macrophyte community types are apparent. In the upper left quadrant of the CCA biplot are higher latitude sites in forested watersheds where the emergent vegetation is often dominated by *Scirpus* sp., *Eleocharis smallii*, *Potamogeton gramineus*, and *Potamogeton richardsonii*. The mean number of submergent taxa found in these wetlands was 6.5, and one quarter of the wetlands in this quadrant had a low stem density of submergents (<5 stems·m^{-2}). By contrast, *Typha* was the dominant emergent in the lower latitude sites, which are plotted in the lower half of the biplot. Wetlands located in the lower left quadrant correspond to relatively high-quality wetlands in forested watersheds with relatively high species richness of submergent taxa (mean = 10.3 species) where the submergents formed dense mats (all wetlands >5 stems·m^{-2}). Wetlands located on the right-hand side of the biplot, however, correspond to turbid, nutrient-rich wetlands with highly developed watersheds. These contain relatively few submergent taxa (mean = 3.6 taxa), with

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Fig. 3. PC axis 1 scores against arcsine-transformed percent (*a*) agricultural land, (*b*) forested land, and (*c*) agricultural and urban land.
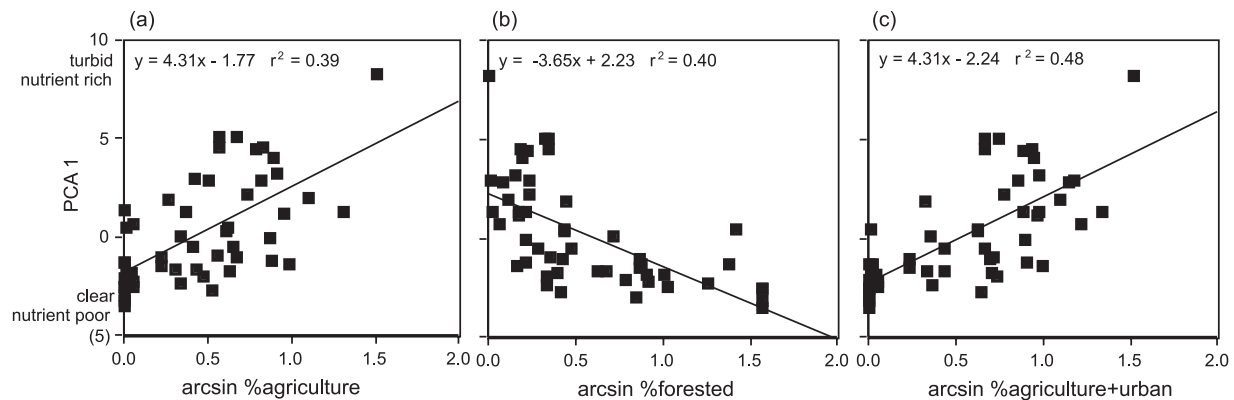
Table 3. Characteristics of the regression relating land use (agricultural, agricultural and urban, forested) in each region (inland, lower coastal, upper coastal) to PCA axes 1 and 2.

		PCA axis 1		PCA axis 2	
		r^2	p	r^2	p
% agricultural	Inland	0.67	0.0003	0.34	0.0284
	Lower	0.16	0.0489	—	—
	Upper	—	—	—	—
% agricultural and urban	Inland	0.61	0.0009	0.29	0.0457
	Lower	0.22	0.0181	—	—
	Upper	—	—	—	—
% forested	Inland	0.60	0.0012	0.23	0.08
	Lower	0.16	0.0511	—	—
	Upper	—	—	—	—

45% of the wetlands containing a low stem density of submergents (<5 stems·m^{-2}) and only a fringe of *Typha*.

Discussion

The species richness and community structure of aquatic macrophytes in wetlands of the Great Lakes basin appeared to be a function of the geographic location of the wetland (i.e., whether they are associated with the upper or lower Great Lakes or located inland) and the degree of water quality degradation. For inland wetlands, the primary source of water quality degradation was excess inputs of nutrients and sediment associated with agricultural development in the watershed. For coastal wetlands, however, water quality may have also been influenced by mixing with water in the lake proper. In particular, wetlands in the less developed and more exposed upper Great Lakes had unique physical and ecological characteristics when compared with more developed and less exposed wetlands of the lower Great Lakes and inland locations.

The proportion of agricultural and urban land in wetland watersheds was a highly significant predictor of water quality (PC axis 1), explaining almost half of the variation in the dependent variables. These results are consistent with previous studies where water quality was related to land use in the watershed (Johnson et al. 1997; Crosbie and Chow-Fraser 1999). There was, however, a great deal of variability observed due to climatic and geological differences associated with different latitudes (upper versus lower lakes) and

exposure (inland versus coastal). Water quality in inland wetlands was substantially degraded by urban and agricultural land use. Inland wetlands that received a disproportionate amount of agricultural runoff tended to have a greater proportion of fine, inorganic silts and clays in their sediment compared with those in mainly forested watersheds that have a deep layer of organic muck and larger gravels in their substrate (Minc 1997). The presence of high silt and clay content in the sediment is undesirable, since plants grow better in organic than in inorganic substrates (Day et al. 1988), and small inorganic particles in the sediment can become easily resuspended and stay in suspension (Hamilton and Mitchell 1997), thus keeping the water column turbid and light limited for macrophytes. Conversely, forested land appeared to attenuate the delivery of sediment from the watershed to inland wetlands and can apparently contribute to a greater level of organic matter in these wetlands.

It is noteworthy that land use effects were greatest on water and sediment quality in inland systems that do not have direct hydrological links with the Great Lakes. In coastal wetlands, the flow of water between the marsh and the Great Lake in question can be reversed depending on watershed inputs, wind direction, and water level (Chow-Fraser 1999; Botts 1999); hence, mixing with lake water may ameliorate the effects of upstream pollution, while wind and wave action in exposed coastal marshes may lead to export of organic matter from the wetland to the lake (Day et al. 1988). The geomorphological characteristics of the Canadian shorelines of the Great Lakes have produced largely exposed shorelines and lacustrine embayments along the upper lakes as compared with a large number of riverine-type wetlands and a smaller proportion of protected lacustrine embayments in Lakes Erie and Ontario (Smith et al. 1991; Chow-Fraser and Albert 1999). In our study, 70% of our upper lake wetlands and only 33% of the lower lake wetlands were classified as lacustrine. Consequently, intrusion by lake water and exposure to wave action may play an even larger role in affecting wetland water quality in the upper lakes than in the more protected wetlands of the lower lakes.

Many studies have shown that nutrient enrichment can cause substantial changes in the species richness, composition, and density of aquatic vegetation in lakes (e.g., Toivonen and Huttunen 1995; Bini et al. 1999; Magee et al. 1999). Our results confirm that submergent macrophyte biodiversity in Great Lakes wetlands declines with deterioration

Fig. 4. Number of submersed plant taxa plotted against (*a*) PC axis 1 scores, (*b*) PC axis 2 scores, and (*c*) log turbidity (nephelometric turbidity units) including inland (□), lower coastal (+), and upper coastal (○) wetlands.
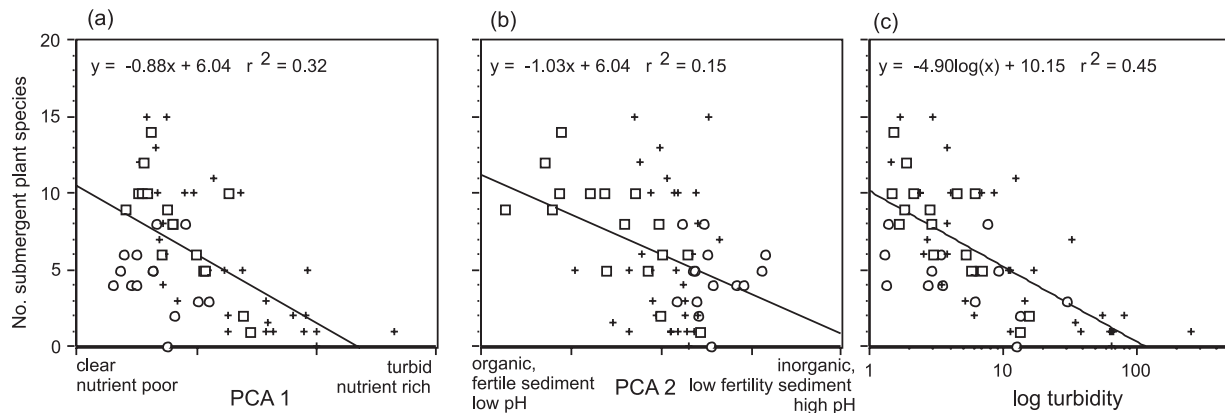
Table 4. Comparisons of means (and standard errors) of the percent organic composition of the sediment and the maximum sediment size observed in wetlands characterized by different land use types (agricultural, forested, agricultural/forested, urban) in inland, lower coastal, and upper coastal systems.

		n	% organic	Maximum sediment size (μm)
Inland	Agricultural	4	16.5 (4.3)*	0.156 (0.094)*
	Forest	8	49.8 (6.8)*	16 (0)*
	Agricultural/forested	2	76.1 (1.7)	0.0039 (0)
Lower	Agricultural	17	17.2 (4.3)	0.094 (1.98)
	Forest	2	23.9 (14.8)	8.03 (7.97)
	Agricultural/forested	2	21.8 (0.6)	0.25 (0)
	Urban	4	29.1 (11.4)	0.125 (0)
Upper	Agricultural	1	6.62 (0)	0.0625 (0)
	Forest	8	3.0 (0.8)	9 (2.91)
	Agricultural/forested	2	8.73 (7.58)	8.03 (7.97)

**Note:** Asterisks indicate significant differences among inland sites (Wilcoxon rank sum, $p < 0.05$).

in water quality. This is consistent with a study by Findlay and Houlahan (1997), who also found reduced species richness of both aquatic and terrestrial organisms with increasing development in wetland watersheds of southeastern Ontario. In particular, we found that 45% of the variation in submergent plant species richness could be explained by turbidity alone. The tolerance of aquatic macrophytes to reduced light availability is tightly linked to their structural characteristics. While emergent and floating-leaf macrophytes are not generally affected by light availability (Day et al. 1988; Toivonen and Huttunen 1995; Bini et al. 1999), submergents tend to be greatly influenced by reduced water clarity. Our results confirm that submerged macrophytes that are canopy-formers such as *Potamogeton pectinatus*, *Myriophyllum* sp., and *Ceratophyllum* are able to survive in situations of light limitation, as opposed to species such as *Chara* and other *Potamogeton* spp., whose leaves grow below the surface (Chambers and Kalff 1987; Minc 1997).

The synergistic effects of many factors including eutrophication and algal and nonalgal turbidity (Phillips et al. 1978) and sediment characteristics (Carignan and Kalff 1980; Barko and Smart 1983; Day et al. 1988) can all affect macrophyte growth. Because of their sensitivity to this large

suite of physical and chemical variables, many macrophyte taxa have been used as indicators of trophic state in other systems (e.g., Grasmück et al. 1995; Thiébaut and Muller 1998). In this study, there appears to be certain taxa that are intolerant of turbid, nutrient-rich conditions (e.g., *Pontederia cordata*, *Potamogeton richardsonii*, *Najas flexilis*, *Utricularia* sp.) but none that occur exclusively in degraded sites. Although some taxa appear to be more tolerant of water and sediment quality degradation (e.g., *Typha*, *Sagittaria*, *Potamogeton pectinatus*, *Nuphar*, *Nymphaea*), including exotic species such as purple loosestrife (*Lythrum salicaria*) and curly-leaf pondweed (*Potamogeton crispus*), even these taxa can be found in high-quality wetlands that are not turbid and eutrophic. What appears to be a better indicator of wetland quality is the type of community present rather than the presence of certain indicator species. The presence of a fringe emergent community with only a few sparsely distributed submergent taxa is highly indicative of a turbid, nutrient-rich wetland, whereas a mix of emergent and floating-leaf taxa with a diverse and dense submergent community is highly indicative of a high-quality wetland.

Species richness and plant density tend to be low in oligotrophic systems. As nutrient concentrations increase in these impoverished systems, both the stem density and the diversity of macrophytes increase until such time as light becomes limiting and plant abundance starts to level off (Lachavanne 1985; Toivonen and Huttunen 1995). The most oligotrophic sites in this study tended to be associated with the upper lakes, where species richness and density were substantially lower than in the lower lakes; however, inland wetlands of similar trophic state showed greater species richness and plant density. In the Great Lakes basin, the relationship between water quality and the macrophyte community is definitely confounded by the strong latitudinal gradient that exists from the southern- to northernmost points (Smith et al. 1991). The macrophyte communities in the upper and lower lakes differed substantially in their dominant species. In lower latitudes, emergent marshes tended to be dominated by *Typha* sp., while in the upper lakes the dominant emergent tended to be *Scirpus* sp. or *Eleocharis smallii*. There were fewer submergent taxa overall in the upper lakes, with the most frequently observed being relatively sparse beds of *Potamogeton gramineus*, *Potamogeton richardsonii*, and

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Fig. 5. Biplot of the CCA. (*a*) Environmental vectors and common macrophyte species (occurred in >10% of the wetlands sampled): submergent (✱), emergent (△), and floating (○); (*b*) location of site scores classified into land use categories: agricultural (□), forested (◇), agricultural/forested (◆), urban (+), and unknown (■). Submergent species: *Ceratophyllum demersum* (DE), *Chara* sp. (CH), *Elodea Canadensis* (EL), *Myriophyllum* sp. (MY), *Najas flexilis* (NA), *Potamogeton* sp. (PS), *Potamogeton crispus* (PC), *Potamogeton pectinatus* (PP), *Potamogeton richarsonii* (PR), *Ranunculus* sp. (RA), *Utricularia* sp. (UT), *Vallisneria americana* (VA). Emergent species: *Lythrum salicaria* (LY), *Pontederia cordata* (PO), *Sagittaria latifolia* (SA), *Scirpus* sp. (SC), *Typha* sp. (TY). Floating-leaf species: *Nuphar variegatum* (NU), *Nymphaea odorata* (NY), *Potamogeton natans* (PN).
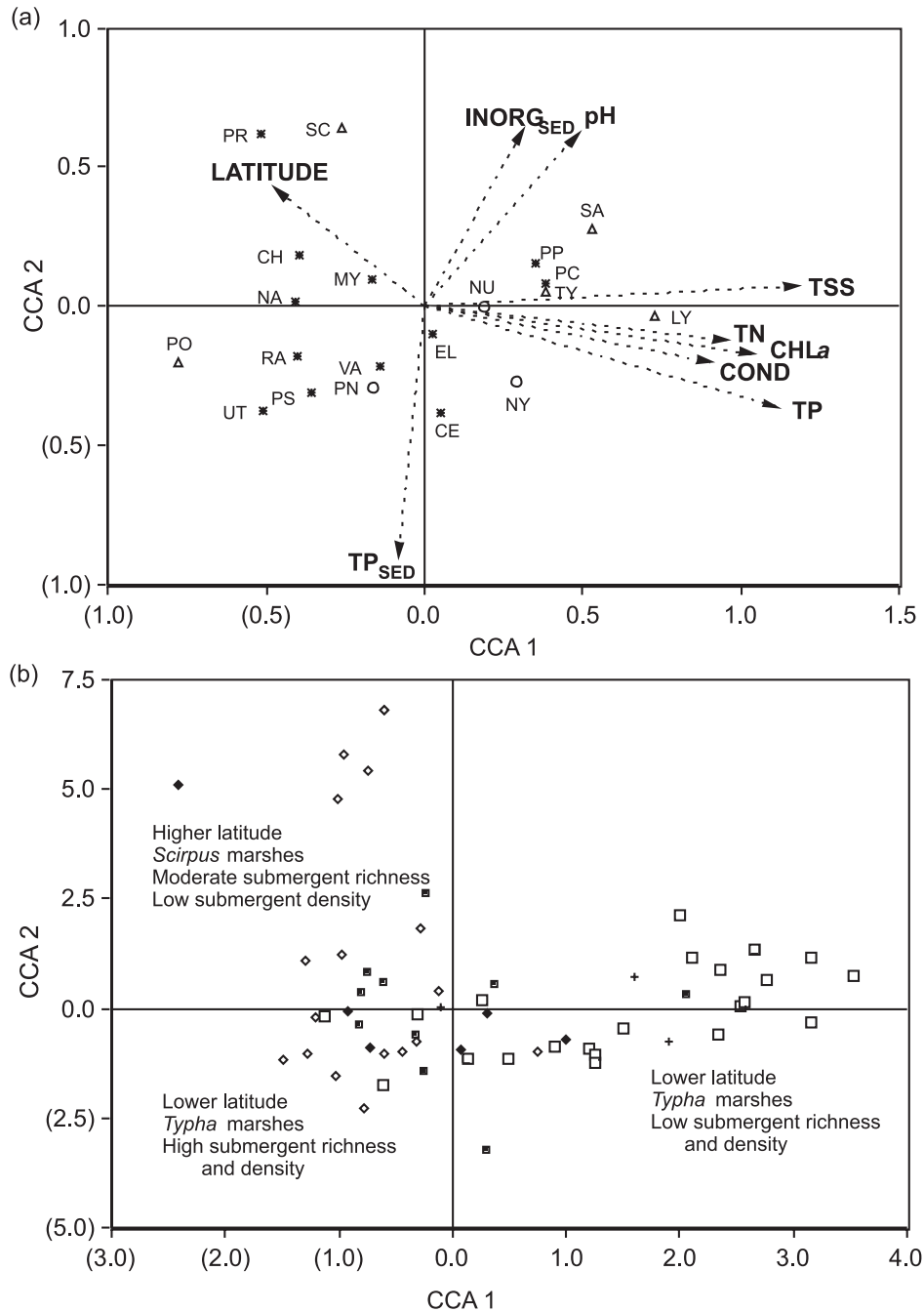
Isoetes sp. Conversely, there was a more diverse, dense, and variable submergent plant community in the high-quality wetlands of the lower lakes and fewer submergent species present in more turbid, sparsely vegetated wetlands.

The importance of latitude in structuring the macrophyte community in the Great Lakes basin is due to several fac-

tors, including climate and geology (Smith et al. 1991; Minc 1997). A strong latitudinal gradient exists between the upper and lower lakes, which affects the length of the growing season and the annual input of solar radiation. Furthermore, the soft sedimentary rock underlying the lower lakes provides expansive areas of shallow water and fine-textured sub-

strates favorable for marsh development, while the older igneous and metamorphic bedrock in Lake Superior and Georgian Bay (Lake Huron) results in a deeper and more exposed shoreline with large-textured inorganic substrates. Plants grow best in organically rich and fertile substrates (Barko and Smart 1983), which are generally lacking in the upper lakes. Consequently, we saw sparse vegetative communities consisting of species better adapted to the shorter growing season and lower substrate fertility of the northern lakes such as *Scirpus*, *Eleocharis*, *Equisetum*, *Potamogeton gramineus*, and *Isoetes* (Day et al. 1988; Minc 1997). These taxa were largely absent from the lower lakes and were replaced by taxa more indicative of a southern community such as *Ceratophyllum* (Minc 1997).

In conclusion, as has been observed in several other large-scale studies (Smith et al. 1991; Minc 1997), physical factors largely related to geology and latitude such as exposure, sediment composition, and length of growing season may be important determinants of macrophyte community composition in coastal wetlands of the Great Lakes. In lower coastal and inland wetlands, plants are distributed according to a nutrient and clarity gradient, which was inextricably linked to land use in the watershed. In coastal lacustrine wetlands, especially in the upper lakes, land use plays less of a role in affecting water and sediment quality than mixing with the lake proper. Because aquatic plants are tightly linked to the functional capacity of wetlands, providing habitat and a sink for sediment and nutrients, the cumulative impacts of altered land use may reduce these important wetland values. We echo the management challenge issued to all levels of government at the State of the Lake Ecosystem Conference (e.g., Bertram and Statler-Salt 1999) to promote land use that is both efficient and protective of high-value nearshore habitat in the Great Lakes.

Acknowledgements

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