Relative importance of macrophyte community versus water quality variables for predicting fish assemblages in coastal wetlands of the Laurentian Great Lakes

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ABSTRACT

Fish have been shown to be sensitive indicators of environmental quality in Great Lakes coastal wetlands. Fish composition also reflects aquatic macrophyte communities, which provide them with critical habitat. Although investigators have shown that the relationship between water quality and fish community structure can be used to indicate wetland health, we speculate that this relationship is a result of the stronger, more direct relationship between water quality and macrophytes, together with the ensuing interconnection between macrophyte and fish assemblages. In this study, we use data collected from 115 Great Lakes coastal marshes to test the hypothesis that plants are better predictors of fish species composition than is water quality. First we use canonical correspondence analysis (CCA) to conduct an ordination of the fish community constrained by water quality parameters. We then use co-correspondence analysis (COCA) to conduct a direct ordination of the fish community with the plant community data. By comparing the statistic 'percent fit,' which refers to the cumulative percentage variance of the species data, we show that plants are consistently better predictors of the fish community than are water quality variables in three separate trials: all wetlands in the Great Lakes basin (whole: 21.2% vs 14.0%; $n = 60$), all wetlands in Lakes Huron and Superior (Upper: 20.3% vs 18.8%; $n = 32$), and all wetlands in Georgian Bay and the North Channel (Georgian Bay: 18% vs 17%; $n = 70$). This is the largest study to directly examine plant–fish interactions in wetlands of the Great Lakes basin.

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Introduction

Recent studies on coastal wetlands of the Laurentian Great Lakes have shown that fish communities are affected by water quality, specifically those parameters that reflect anthropogenic activities within their watersheds (e.g., water turbidity, conductivity, and nutrient input; Brazner and Beals, 1997; Seilheimer and Chow-Fraser, 2006, 2007; Bhagat et al., 2007; Danz et al., 2007; Sharma and Jackson, 2007). Seilheimer and Chow-Fraser (2006, 2007) used this information to guide their development of the Wetland Fish Index (WFI), an index based on the statistical relationship between a species' intolerance to increased level of pollutants, indicating wetland degradation, and the consistency of this response across all sites. They demonstrated that WFI scores were significantly correlated with an indicator of water quality impairment, the Water Quality Index (WQI; Chow-Fraser, 2006), and confirmed that wetlands associated with less disturbed areas of the Great Lakes basin had correspondingly better WFI scores than those associated with agricultural and urban development.

Fish distribution in Great Lakes wetlands is also significantly affected by the type and abundance of aquatic macrophytes that are present. Studies have consistently shown a positive relationship between fish diversity and abundance and macrophyte diversity and coverage (Minns et al., 1994; Randall et al., 1996; Brazner and Beals, 1997; Weaver et al., 1997; Hook et al., 2001). Aquatic plants are essential for fish by providing (1) substrate for invertebrates that are food for foraging species and juvenile piscivores, (2) refugia for small fish from predators, (3) a barrier from wave and wind disturbance, and (4) shade and cooler temperatures (French, 1988; Savino and Stein, 1989; Jude and Pappas, 1992; Hook et al., 2001; Lougheed et al., 2001). Some investigators have therefore included information on aquatic vegetation to develop multi-metric indices of biotic integrity for coastal wetlands (e.g., Randall et al., 1996; Uzarski et al., 2005).

By comparison, the relationship between water quality and the aquatic plant community in Great Lakes coastal wetlands is more poorly documented. Nevertheless, abundance of macrophytes is known to depend on clear, low-nutrient water (Lougheed et al., 2001; McNair, 2006; Croft and Chow-Fraser, 2007), and their presence, richness and species diversity has been used as an indicator of water quality conditions. Recently, Croft and Chow-Fraser (2007) used the statistical relationship between plant species and certain water quality parameters to develop the basin-wide Wetland

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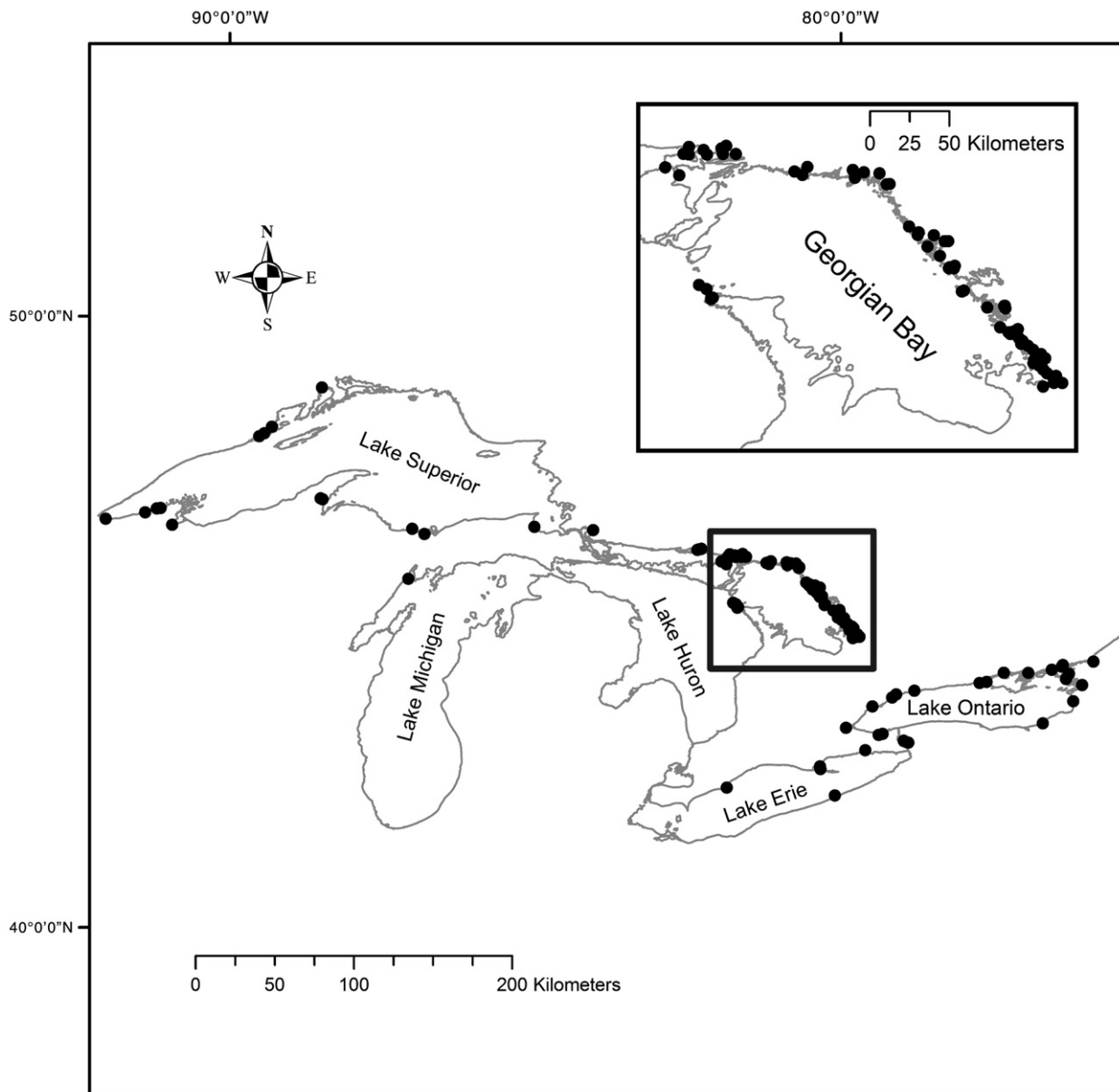
Fig. 1. Location of all of the Great Lakes sites used in this study. Inset shows a close-up of Georgian Bay.

Macrophyte Index (WMI), which is similar to the WFI in that a species' score is based on its tolerance or intolerance to water quality deterioration. This index is also highly significantly correlated with the WQI; in fact, in a direct comparison, Seilheimer et al. (2009) found a slightly stronger relationship between WMI and WQI than that between WFI and WQI.

There have been few direct assessments of fish and plant communities in the literature, and the WFI and WMI have not been directly and statistically compared. Both Croft and Chow-Fraser (2007) and Seilheimer and Chow-Fraser (2007), however, reported that water quality variables and geographic location (i.e., longitude and latitude) were the principal variables driving species composition

Table 1
Summary of values of percent fit produced by the CCA and COCA for three regions within the Great Lakes basin: Whole Basin, Upper Lakes, and Georgian Bay.

Geographic coverage	Wetlands (n)	Trial #	Fish species (n)	Plant species (n)	CCA % fit of fish*	COCA % fit of plant**	COCA% fit of fish***
Whole Basin	60	1	72	60	11.9	15.5	17.0
		2	57	49	14.0	17.2	21.2
Upper Lakes	32	1	63	53	18.8	22.3	20.3
Georgian Bay	70	1	41	69	17.0	18.1	18.0
		2	41	68	17.0	18.3	18.0

Rare species are included in Trial 1 and excluded in Trial 2.
  * CCA % fit of fish: cumulative percentage variance of fish data explained by first two axes.
 ** COCA % fit of plant: cumulative percentage variance of plant data explained by first two fish-derived axes.
*** COCA% fit of fish: cumulative percentage variance of fish data explained by first two plant-derived axes.

in their studies; hence, there is evidence that both fish and plant communities have a similar relationship with water quality parameters. In addition, both studies were able to distinguish among species of low, mid, and high tolerance in relation to axes of degradation. It is possible that macrophyte and fish taxa that have similar tolerance to degradation will co-occur and are positively associated; on the other hand, species interrelationships are likely much more complicated and are probably shaped by many other factors including macrophyte cover and density, water level fluctuations, degree of exposure, etc. (Janecek, 1990; Randall et al., 1996). Given that empirical studies evaluating the co-occurrence of fish and macrophyte taxa are scarce (see Janecek, 1990; McNair, 2006), there is a demand for papers that advance this branch of fish habitat research in order to gain a more detailed understanding of the complex connections between macrophyte and fish communities (Randall et al., 1996; Brazner and Beals, 1997; Trebitz et al., 2009).

It is apparent that these three variables, water quality, fish, and macrophytes are highly correlated; yet the exact nature of the relationships is still unclear. There is no doubt that land-use alteration and point source pollution can lead to water quality impairment in wetlands (Chow-Fraser, 2006; Danz et al., 2007; Trebitz et al., 2007), and this can in turn lead to predictable changes in both the plant and fish communities. This evidence implies that a change in fish community should be a synergistic consequence of the effect of changes in water quality, and the effect of water quality on plants and the subsequent impact on fish. While recent studies have shown the importance of both water quality (described in terms of water clarity) and aquatic vegetation assemblages to the Great Lakes fish community (Trebitz et al., 2009), no studies to our knowledge have directly investigated which of these two factors, water quality or macrophyte community, has a more prominent influence on fish composition. Ultimately, such investigations could refocus research efforts to improve wetland sampling and monitoring programs and provide enhancement of wetland restoration projects.

In this study we tested the hypothesis that species composition of macrophyte communities is better than water quality variables for explaining fish distribution in coastal wetlands. Our study sites included 115 coastal marshes from the entire Great Lakes shoreline, and this ensured that a wide distribution of taxa was incorporated. Our large sample size allowed us to determine whether results obtained at a local or regional scale for relatively similar wetlands can be applied to a basin-wide scale, where there is a greater degree of variation in human disturbance.

To make this a rigorous test, we included a large number of wetlands that are in reference condition, that is, where watersheds are primarily forested, and where the water quality, fish and plant communities have only been minimally affected by human activities. This includes the many wetlands of Georgian Bay, as well as Lake Huron and Lake Superior. At the other extreme, we also included wetlands that are highly degraded, where watersheds have been severely altered and where water quality has been highly degraded by human activities. The majority of these marshes are found in the lower Great Lakes. We speculate that the fish community is primarily responding to the type of plant community in a wetland rather than to water quality conditions, since the plant community integrates both environmental parameters and habitat complexity.

Methods

Description of dataset

Although data used in this study correspond to coastal marshes distributed throughout the five Great Lakes, most of them are located along the shoreline of Lakes Ontario, Superior and Georgian Bay (see Fig. 1). Sampling occurred in the summer between early June and late

Table 2
List of all fish taxa used in this study, including the common name and species code. WB = Whole Basin, UL = Upper Lakes, GB = Georgian Bay.

Taxon	Common name	Species code	Trial
Alosa pseudoharengus *	Alewife	ALPS	WB, GB
Ambloplites rupestris	Rock Bass	AMRU	WB, UL, GB
Ameiurus melas	Black Bullhead	AMME	WB, UL
Ameiurus nebulosus	Brown Bullhead	AMNE	WB, UL, GB
Ameiurus sp.	Bullhead	UNAM	WB, UL, GB
Amia calva	Bowfin	AMCA	WB, UL, GB
Anguilla rostrata	American eel	ANRO	WB
Apeltes quadracus	Fourspine stickleback	APQU	WB, UL
Aplodinotus grunniens	Freshwater drum	APGR	WB, UL
Carassius auratus *	Goldfish	CAAU	WB
Catostomus catostomus	Longnose sucker	CACA	WB
Catostomus commersonii	White sucker	CACO	WB, UL, GB
Cottus bairdii	Mottled sculpin	COBA	WB, UL
Cottus cognatus	Slimy sculpin	COCO	WB, UL
Couesius plumbeus	Lake chub	COPL	WB, UL
Culaea inconstans	Brook stickleback	CUIN	WB, GB
Cyprinella spiloptera	Spotfin shiner	CYSP	WB, UL, GB
Cyprinus carpio *	Common carp	CYCA	WB, UL, GB
Dorosoma cepedianum	Gizzard shad	DOCE	WB
Esox americanus	Redfin pickerel	ESAA	WB
Esox lucius	Northern pike	ESLU	WB, UL, GB
Esox masquinongy	Muskellunge	ESMA	WB
Etheostoma exile	Iowa darter	ETEX	WB, GB
Etheostoma microperca	Least darter	ETMI	WB, UL
Etheostoma nigrum	Johnny darter	ETNI	WB, UL, GB
Fundulus diaphanus	Banded killifish	FUDI	WB, UL, GB
Gasterosteus aculeatus	Threespine stickleback	GAAC	WB, UL
Gymnocephalus cernua	Ruffe	GYCE	WB
Hybognathus hankinsoni	Brassy minnow	HYHA	WB
Ictalurus punctatus	Channel catfish	ICPU	WB, UL
Labidesthes sicculus	Brook silverside	LASI	WB, UL, GB
Lepisosteus osseus	Longnose gar	LEOS	WB, UL, GB
Lepomis cyanellus	Green sunfish	LECY	WB, UL
Lepomis gibbosus	Pumpkinseed	LEGI	WB, UL, GB
Lepomis macrochirus	Bluegill	LEMA	WB, UL, GB
Lepomis megalotis	Longear sunfish	LEME	WB, GB
Lepomis sp.	Sunfish	UNLE	WB, UL, GB
Luxilus cornutus	Common shiner	LUCO	WB, UL, GB
Micropterus dolomieu	Smallmouth bass	MIDO	WB, UL, GB
Micropterus salmoides	Largemouth bass	MISA	WB, UL, GB
Micropterus sp.	Bass sp.	UNMI	WB, UL
Morone americana *	White perch	MOAM	WB, UL
Morone chrysops	White bass	MOCH	WB
Moxostoma macrolepidotum	Shorthead redhorse	MOMA	WB, GB
Notemigonus crysoleucas	Golden shiner	NOCR	WB, UL, GB
Notropis atherinoides	Emerald shiner	NOAT	WB, UL, GB
Notropis heterodon	Blackchin shiner	NOHN	WB, UL, GB
Notropis heterolepis	Blacknose shiner	NOHE	WB, UL, GB
Notropis hudsonius	Spottail shiner	NOHU	WB, UL, GB
Notropis stramineus	Sand shiner	NOST	WB
Notropis volucellus	Mimic shiner	NOVO	WB, UL, GB
Noturus gyrinus	Tadpole madtom	NOGY	WB, UL, GB
Oncorhynchus tshawytscha	Chinook salmon	ONTS	WB, UL
Osmerus mordax *	Rainbow smelt	OSMO	WB, UL
Perca flavescens	Yellow perch	PEFL	WB, UL, GB
Percina caprodes	Logperch	PECA	WB, UL, GB
Percopsis omiscomaycus	Trout-perch	PEOM	WB, UL
Petromyzon marinus	Sea lamprey	PEMA	WB, UL
Phoxinus eos	Northern redbelly dace	PHEO	WB, GB
Pimephales notatus	Bluntnose minnow	PINO	WB, UL, GB
Pimephales promelas	Fathead minnow	PIPR	WB
Pomoxis annularis	White crappie	POAN	WB, UL, GB
Pomoxis nigromaculatus	Black crappie	PONI	WB, UL, GB
Pomoxis sp.	Crappie	UNPO	GB
Prosopium cylindraceum	Round whitefish	PRCY	WB, UL
Pungitius pungitius	Ninespine stickleback	PUPU	WB, GB
Sander vitreus	Walleye	SAVI	WB
Scardinius erythrophthalmus	Rudd	SCER	WB, UL
Semotilus atromaculatus	Creek chub	SEAT	WB, UL, GB
Umbra limi	Central mudminnow	UMLI	WB, UL, GB

Species followed by asterisks are non-native to the Great Lakes.

Table 3
List of all macrophyte species used in this study, including species code, taxon, common name, and type (e.g., emergent, floating, or submergent).

Taxon	Common name	Type	Species code	Trial
Bidens beckii	Beck's marsh marigold	Submergent	BIbe/MEbe	GB
Brasenia schreberi	Water shield	Floating	BRsc	WB, UL, GB
Callitriche sp.	Water starwort	Submergent	CAsp	WB, UL, GB
Ceratophyllum demersum	Coontail	Submergent	CEde	WB, UL, GB
Chara sp.	Muskgrass	Submergent	CHsp/CHss	WB, UL, GB
Eleocharis acicularis	Needle spike rush	Emergent	ELac	WB, UL, GB
Eleocharis smallii	Marsh spike rush	Emergent	ELsm	GB
Elodea canadensis	Canadian waterweed	Submergent	ELca/EDca	WB, UL, GB
Equisetum fluviatile	Water horsetail	Emergent	EQfl	GB
Eriocaulon aquaticum	Pipewort	Emergent	ERaq	WB, UL, GB
Freshwater sponges	Sponges	Submergent	SPon	WB, UL, GB
Hippuris vulgaris	Mare's tail	Submergent	HIvu	WB, UL
Hydrocharis morsus-ranae *	Frogbit	Floating	HYmo	WB, GB
Isoetes sp.	Quillwort	Submergent	ISsp	WB, UL, GB
Lemna minor	Lesser duckweed	Floating	LEmi	WB, UL
Lemna trisulca	Ivy duckweed	Floating	LEtr	WB, UL
Lobelia dortmanna	Water lobelia	Submergent	LOdo	WB, UL, GB
Myriophyllum alterniflorum	Alternate water-milfoil	Submergent	MYal	WB, UL, GB
Myriophyllum farwellii	Farwell's water-milfoil	Submergent	MYfa	WB, UL
Myriophyllum heterophyllum	Two-leaf water-milfoil	Submergent	MYhe	WB, UL, GB
Myriophyllum sibiricum	Common water-milfoil	Submergent	MYsi	WB, UL, GB
Myriophyllum sp.	Water-milfoil	Submergent	MYsp	WB, UL, GB
Myriophyllum spicatum *	Eurasian water-milfoil	Submergent	MYsc	WB, UL, GB
Myriophyllum tenellum	Slender water-milfoil	Submergent	MYte	WB, UL, GB
Myriophyllum verticillatum L.	Whorled water-milfoil	Submergent	MYve	WB, UL
Najas flexilis	Slender water nymph	Submergent	NAfl	WB, UL, GB
Nitella sp.	Stonewort	Submergent	NIsp	WB, UL, GB
Nuphar advena	Spatterdock	Floating	NUad	WB,
Nuphar pumila	Yellow water lily	Floating	NUpu	WB, UL, GB
Nuphar variegata	Common yellow pond lily	Floating	NUva	WB, UL, GB
Nymphaea odorata	Fragrant water lily (white)	Floating	NYod	WB, UL, GB
Nymphaea tetragona	Pygmy water lily	Floating	NYte	GB
Nymphoides cordata	Little floating hearts	Floating	NYco	GB
Pistia stratiotes L. *	Water lettuce	Floating	PIst	WB
Pontederia cordata	Pickerelweed	Emergent	POco	GB
Potamogeton amplifolius	Large-leaved pondweed	Submergent	POam	WB, UL, GB
Potamogeton crispus *	Curly-leaf pondweed	Submergent	POcr	WB, UL, GB
Potamogeton epihydrus	Ribbon-leaf pondweed	Submergent	POep	WB, UL, GB
Potamogeton friesii	Fries' pondweed	Submergent	POfr	GB
Potamogeton gramineus	Variable pondweed	Submergent	POgr	WB, UL, GB
Potamogeton illinoensis	Illinois pondweed	Submergent	POil	WB, UL, GB
Potamogeton natans	Broad-leaved pondweed	Floating	POna	WB, UL, GB
Potamogeton pusillus	"Slender" pondweed	Submergent	POpu/POsl	WB, UL, GB
Potamogeton richardsonii	Clasping-leaved pondweed	Submergent	POri	WB, UL, GB
Potamogeton robbinsii	Fern-leaf pondweed	Submergent	POro	WB, UL, GB
Potamogeton sp.	Pondweed	Submergent	POsp	WB, UL, GB
Potamogeton spirillus	Northern snailseed pondweed	Submergent	POsr	WB, UL, GB
Potamogeton vaseyi	Vaseyi pondweed	Submergent	POva	WB,
Potamogeton zosteriformis	Flat-stemmed pondweed	Submergent	POzo	WB, UL, GB
Ranunculus longirostris	Buttercup, crowfoot	Submergent	RAlo	WB, UL, GB
Ranunculus sp.	Crowfoot	Submergent	RAsp	GB
Sagittaria cuneata	Small arrowhead	Emergent	SGcu	WB, UL, GB
Sagittaria graminea	Grassy arrowhead	Submergent	SGgr	GB
Sagittaria latifolia	Broad arrowhead	Emergent	SGla	GB
Sagittaria sp.	Arrowhead species	Emergent	SGsp	GB
Schoenoplectus acutus	Hardstem bulrush	Emergent	SCac	GB
Schoenoplectus americanus	Three-square bulrush	Emergent	SCam	GB
Schoenoplectus cyperinus	Wool-grass	Emergent	SCcy	GB
Schoenoplectus sp.	Bulrush	Emergent	SCsp	GB
Schoenoplectus subterminalis	Water bulrush	Submergent	SCsu	WB, UL, GB
Schoenoplectus validus	Softstem bulrush	Emergent	SCva	GB
Sparganium androcladum	Branched burreed	Emergent	SPad	GB
Sparganium angustifolium	Narrow-leaf burreed	Emergent	SPan	WB, UL
Sparganium eurycarpum	Giant burreed	Emergent	SPeu	GB
Sparganium fluctuans	Floating burreed	Floating	SPfl	WB, UL, GB
Sparganium sp.	Burreed	Emergent	SPsp	GB
Spirodela sp.	Greater duckweed	Floating	SRss	WB
Stuckenia pectinata	Sago pondweed	Submergent	STpe	WB, UL, GB
Stuckenia vaginata	Sheathed pondweed	Submergent	STva	WB, UL
Trapa natans L. *	Water chestnut	Floating	TRna	WB
Typha angustifolia *	Narrow-leaf cattail	Emergent	TYan	GB
Typha latifolia	Broadleaf cattail	Emergent	TYla	GB
Typha sp.	Cattail	Emergent	TYsp	GB
Utricularia cornuta	Horned bladderwort	Emergent	UTco	GB

Table 3 (*continued*)

Taxon	Common name	Type	Species code	Trial
Utricularia geminiscapa	Hidden fruit bladderwort	Submergent	UTge	WB, UL, GB
Utricularia intermedia	Flat-leaved bladderwort	Submergent	UTin	WB, UL, GB
Utricularia rare	Rare bladderwort	Submergent	UTra	UL, GB
Utricularia sp.	Bladderwort	Submergent	UTsp	WB, UL, GB
Utricularia vulgaris	Common bladderwort	Submergent	UTvu	WB, UL, GB
Vallisneria americana	Tape grass, eel grass	Submergent	VAam	WB, UL, GB
Wolffia sp.	Horkel/Water meal	Floating	WFss	WB
Zizania sp.	Wild rice	Submergent	ZIpa/ZIss	WB, UL, GB
Zosterella dubia	Water stargrass	Submergent	ZOdu	WB, UL, GB

WB = Whole Basin, UL = Upper Lakes, and GB = Georgian Bay. Species followed by asterisks are non-native to the Great Lakes.

August from 2002 to 2007, inclusive. For most sites, water quality sampling and measurements, as well as collection of fish, and macrophyte identification, were performed on consecutive days in a given year.

We performed statistical analyses for three different subsets: (1) Whole Basin (60 sites), (2) Upper Lakes (32 sites) including Lakes Superior, Huron, and Georgian Bay (14, 3, and 15 sites respectively), and (3) Georgian Bay and the North Channel (70 sites) (Fig. 1). We included only 60 sites in the Whole Basin subset because we sought to have an even distribution of upper and lower lakes sites, and low and high quality sites. Georgian Bay wetlands were evaluated as a separate subset because of recent studies that have noted their high water quality and high diversity (Chow-Fraser, 2006; Croft and Chow-Fraser, 2007; Seilheimer and Chow-Fraser, 2007), and we were interested in how the interrelationships in this region would compare against the rest of the basin.

Field sampling and analyses

Water quality sampling and analytical methods are described in detail in Chow-Fraser (2006). Thirteen environmental parameters were included in this study, and these were chosen on the basis of parameters included in the development of the WFI and WMI (see Seilheimer and Chow-Fraser, 2007; Croft and Chow-Fraser, 2007). These included latitude, longitude, total phosphorus (TP), soluble reactive phosphorus (SRP), total nitrate nitrogen (TNN), total ammonia nitrogen (TAN), turbidity (TURB), total suspended solids (TSS), total inorganic suspended solids (TISS), total organic suspended solids (TOSS), conductivity (COND), pH, and chlorophyll (CHL).

Plant sampling occurred from late June to late August, when adequate time had passed for the majority of taxa to develop and for flowers to mature, allowing for easier and more accurate identification. Samplers walked random transects along the shoreline, and identified all species in flooded areas using a 0.75×0.75 m quadrant (see Croft and Chow-Fraser, 2009, for more details). Deeper portions of the wetland were accessed via canoe or boat, where submergent vegetation was sampled with the aid of a rake. All forms of macrophytes were identified, including shoreline emergents, shallow emergents, floating (rooted and unrooted), and submergents. Meadow species were excluded because they are not used by the fish community. We noted only the presence of taxa and did not identify other variables such as percent cover or abundance. Generally 10–15 quadrants were completed at each wetland, and sampling stopped after no new species were found in two consecutive quadrants. Sampling time ranged from 20 min to several hours depending on the site. Plants were identified to species whenever possible following Newmaster et al. (1997), Crow and Helquist (2000), and Chaade (2002).

All of the fish information was collected with the same gear and identical protocol. Two sets of large paired fyke nets (13 and 4 mm bar mesh, 4.25 m length, 1 m × 1.25 m front opening) and one set of small paired fyke nets (4 mm bar mesh, 2.1 m length, 0.5 m × 1.0 m front opening) were deployed overnight at each site (approximately 24-h).

The fyke nets had 2.5 m long wings on each side and were connected by a 7 m lead. They were placed parallel to shore, in depths of 1 m (large nets) and 0.5 m (small nets), and in contact with submergent or floating vegetation whenever possible. Upon return, the fish in each net were counted and identified to species according to Scott and Crossman (1998) and then released.

Description of multivariate analyses

We used two different types of multivariate analyses to test our hypothesis. The first one, canonical correspondence analysis (CCA), is widely used in community ecology to analyze biological communities in relation to environmental parameters. It is appropriate when the dataset is large and the species in the community show a unimodal response to the environmental variables (ter Braak and Verdonschot, 1995). It is often used to identify underlying environmental gradients and associated key variables that influence the distribution of species. It has also been used to develop ecological indices, by pairing species with scores that are indicative of their tolerance to degradation (e.g., Lougheed and Chow-Fraser, 2002; Seilheimer and Chow-Fraser, 2006, 2007; Croft and Chow-Fraser 2007). In this study, we were interested in quantifying the degree to which environmental variables (i.e., water quality parameters) could predict the fish community. The program we used, CANOCO™ 4.5 (ter Braak and Smilauer, 1998), generates a statistic for the cumulative percent variance of the species data, which refers to the amount of variability that could potentially be explained out of the total variation (McCune and Grace, 2002).

All variables were $\log_{10}$ transformed to normalize the variance. Abundance data were log-transformed and normalized to have a mean of zero and a standard deviation of 1.0. We used the standard method in CANOCO 4.5 and tested for significance using the full model and Monte Carlo permutations. We used the cumulative percent variance of the first two axes when reporting our results.

The second multivariate analysis we used is co-correspondence analysis (COCA). It is a relatively new ordination method that can directly relate two different communities, such as plants and fish at specific sites (ter Braak and Schaffers, 2004). Before COCA was introduced, comparison of communities could only be done indirectly. With COCA however, direct comparison of the two biotic communities can be made by maximizing the weighted covariance between weighted averaged species scores of one community with the weighted averaged species scores of the other community (ter Braak and Schaffers, 2004). We used MATLAB™ software (MATLAB 2000) and a program provided by A.P. Schaffers (personal communication) to generate a statistic called "percent fit," that conveys the extent to which one community (i.e., plants) can explain the variation in the other community (i.e., fish). This statistic is analogous to the total percentage variance reported in CANOCO v.4.5 for CCA.

Since canonical correspondence analysis and co-correspondence analysis are similarly derived (ter Braak and Schaffers, 2004; Schaffers et al., 2008), we were able to directly compare the two relevant statistics to determine which of the biotic (macrophyte species) or
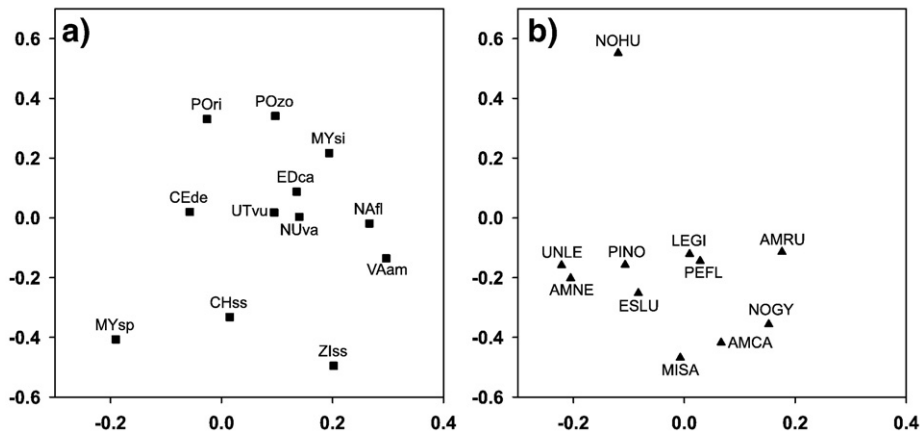
Fig. 2. Bi-plot showing results from co-correspondence analysis of (a) plant and (b) fish taxa in coastal wetlands of the Great Lakes (Whole Basin subset), after ter Braak and Schaffers (2004). Total percent fit of fish (%FISH) by plant-derived axes equaled 21.2%. Only species occurring at more than two-thirds of sites are included here. Plant and fish codes can be located in Tables 2 and 3.

abiotic (water quality data) variables better explained fish distribution for wetlands at the three spatial scales.

Results

For Whole Basin, Upper Lakes, and Georgian Bay, there were a total of 72, 63, and 41 fish species, respectively (Tables 1 and 2). Since rare species tend to be overemphasized in CCA, we conducted a second trial, where we excluded taxa that occurred only once, and this reduced the number of fish species to 57, 49 and 41 in the three subsets, respectively (Table 1). For all CCA analyses, we used both fish species data and water quality variables. Prior to running a CCA, we ran a detrended correspondence analysis (DCA) on the species data to ensure that there was a unimodal distribution across the environmental gradient to meet the assumptions of the statistical test (ter Braak and Smilauer, 1998). Fish presence/absence data were used for Whole Basin and Upper Lakes sites. We used fish abundance for DCA on Georgian Bay sites because presence/absence data did not meet the unimodal assumption required for DCA.

The two sets of community data used in the COCA were fish and macrophyte species, where we tested how well the plant community predicted the fish community at a common set of sites. Similar to the CCA we ran two separate COCA trials, one that included rare species and one excluding rare species. The fish data for the COCA analyses were the same that we used in the CCA. Macrophyte species for Whole

Basin, Upper Lakes, and Georgian Bay sites equaled 60, 53, and 69, respectively, in the first trial, and 49, 45, and 68, respectively, in the second trial (Tables 1 and 3).

In the first trial, where all species were included, plant-derived COCA axes (%FISH) yielded a higher percent fit than CCA for all three subsets: Whole Basin (17.0% macrophyte–fish vs. 11.9% water quality–fish), Upper Lakes (20.3% macrophyte–fish vs. 18.8% water quality–fish), and Georgian Bay (18.0% macrophyte–fish vs. 17.0% water quality–fish) (see Table 1).

Bi-plots of fish–plant associations for Whole Basin, Upper Lakes, and Georgian Bay are shown in Figs. 2–4. We included only those taxa occurring in at least two-thirds of the sites when plotting the graphs. This allowed us to focus on the predominant species and helped simplify the initial COCA output figures. By visually comparing the graphs we can make general inferences on which species seem to be correlated by identifying their locations within the axes. Generally, the majority of plant and fish taxa are clustered in the same vicinity, for all subsets. In preliminary analyses of basin-wide fish–plant communities, McNair (2006) was able to discern fish–plant groups that were indicative of ecoregion and extent of degradation. We attempted to establish fish–plant groups for the Georgian Bay region using similar methods but were unable to successfully tease out any clear species relationships at this regional level.

CCA results showed that TURB, TSS, TISS, and TOSS had high inflation factors and hence were redundant variables; however after
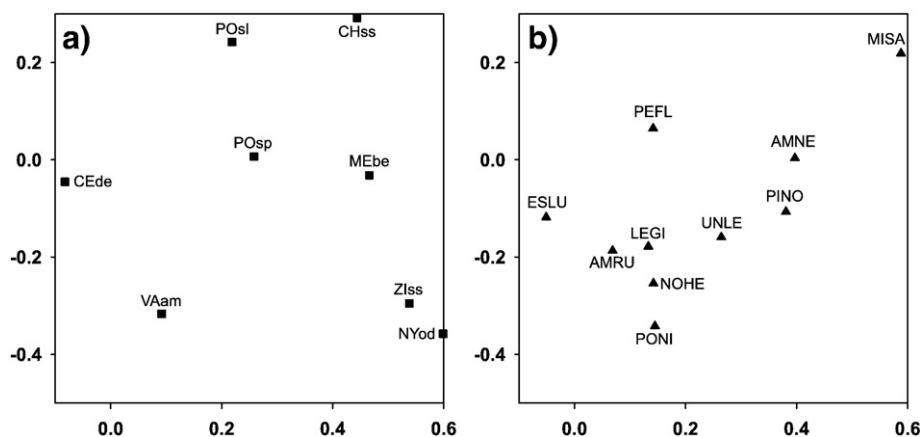

Fig. 3. Bi-plot showing results from co-correspondence analysis of (a) plant and (b) fish taxa (right) in coastal wetlands of the Great Lakes (Upper Lakes subset) after ter Braak and Schaffers (2004). Total percent fit of fish (%FISH) by plant-derived axes equaled 20.3%. Only species occurring at more than two-thirds of sites are included here. Plant and fish codes can be located in Tables 2 and 3.
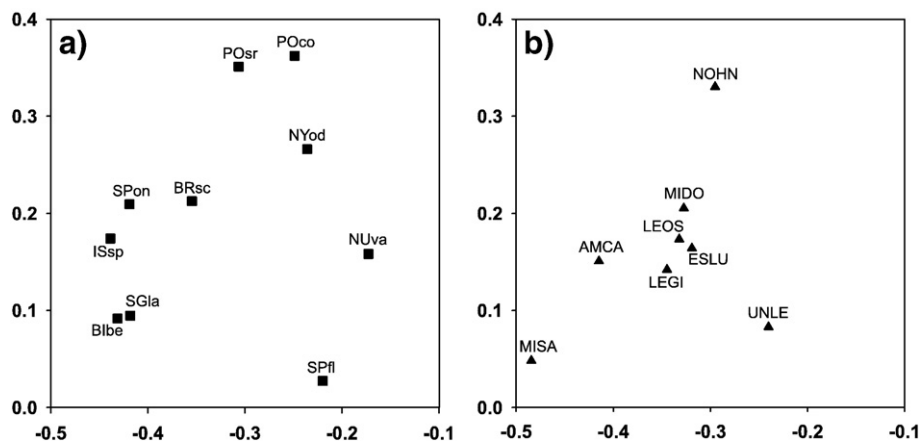
Fig. 4. Bi-plot showing results from co-correspondence analysis of (a) plant and (b) fish taxa (right) in coastal wetlands of the Great Lakes (Georgian Bay subset) after ter Braak and Schaffers (2004). Total percent fit of fish (%FISH) by plant-derived axes equaled 18.0%. Only species occurring at more than two-thirds of sites are included here. Plant and fish codes can be located in Tables 2 and 3.

running subsequent CCAs that excluded suspended solids parameters, our results showed essentially identical models (i.e., with similar fits of axes and Monte Carlo significance values), and we opted to keep all 13 parameters in the model to allow for easier comparisons with previous WFI and WMI publications. We found many of the water quality variables to be positively and strongly (i.e., >0.5) correlated, particularly in the Whole Basin. In all three subsets TP was correlated with SRP and TURB. In the Whole Basin TP, TURB, COND, CHL, TAN and TNN were correlated, while TP was also associated with TNN, and COND was negatively associated with latitude. In the Upper Lakes both TP and SRP were negatively correlated with longitude. These associations generally show that if one parameter increases as a result of anthropogenic impact, other parameters sensitive to human degradation are affected as well.

Weighted correlation matrix results in the CCA showed that species axes were mainly associated with water clarity, nutrients, and geographic location (Table 4). Generally, the greater the spatial scale (i.e., Whole Basin), the greater the number of parameters that were strongly correlated with the species axes, likely due to the presence of a larger environmental gradient. Within the Whole Basin, latitude, longitude, water clarity (TURB, TSS), conductivity, nutrients (TP and TAN), and productivity (CHL) were strongly correlated with the species axes (see Table 4). Similarly, latitude and nutrients (TP and TAN) were most predictive of species in the Upper Lakes sites. Within Georgian Bay, latitude and water clarity were the most consistent predictors of species (Table 4). We will not report specific details on relationships between fish taxa and various environmental parameters from CCA results because this has been documented elsewhere (see Seilheimer and Chow-Fraser, 2006, 2007).

Table 4
Summary of weighted correlation matrix values showing relationships between environmental parameters and multiple fish species axes based on CCA results for sites within the Whole Basin, Upper Lakes, and Georgian Bay.

Parameter	Whole Basin	Upper Lakes	Georgian Bay
Latitude	0.51	0.84	0.55
Longitude	0.75	0.78	–
TURB (NTU)	0.58	–	0.68
TSS (mg/L)	0.56	–	0.63
TISS (mg/L)	0.57	–	0.69
COND (μS/cm)	0.76	–	–
CHL (μg/L)	0.61	–	–
TP (μg/L)	0.79	0.56	–
TAN (mg/L)	0.66	0.55	–

Only absolute values of correlations greater than 0.50 are presented. TURB = turbidity, TSS = total suspended solids, TISS = total inorganic suspended solids, COND = conductivity, CHL = chlorophyll, TP = total phosphorus, TAN = total ammonia nitrogen.

In the second trial, we ran CCA and COCA only for the Whole Basin and Georgian Bay subsets because DCA results indicated that the Upper Lakes dataset did not have a unimodal distribution. Our results again showed a higher percent fit with plant-derived COCA axes (%FISH) than CCA in both cases (Whole Basin: 21.2% macrophyte–fish vs. 14.0% water quality–fish, Georgian Bay: 18.0% macrophyte–fish vs. 17.0% water quality–fish) (Table 1). COCA bi-plots (Figs. 2–4) were comparable to those in the first trial. Species data responded similarly to water quality parameters in the CCA as in the first trial.

Discussion

Our results show that regardless of lake origin, region, and water quality, fish taxa associated with coastal marshes of the Great Lakes had a more pronounced response to plant composition than to water quality parameters. In all cases, the percent fit associated with the COCA (i.e., macrophyte–fish relationships) was higher than that for the CCA (i.e., water quality–fish relationships) for Whole Basin, Upper Lakes, and Georgian Bay, confirming that macrophytes explain a greater proportion of the variation in fish community than does water chemistry.

Our results support preliminary findings of McNair (2006), who first hypothesized that species composition of aquatic vegetation can better explain fish communities than abiotic factors such as water quality information. We found this to be true on both a regional (e.g., Georgian Bay) and basin-wide scale. These results are not surprising given the many functional roles plants provide for fish, which in essence incorporates both habitat and environmental quality factors, including structural complexity, water clarity and nutrient concentrations.

Macrophytes as habitat

The species composition, abundance, and density of the plant community is a reflection of the water quality condition in a wetland and is a good indicator of overall quality of fish habitat. Consistent with our results, numerous studies have found that submersed aquatic vegetation are negatively affected by water turbidity because of light limitation (Chow-Fraser, 1998; Brazner and Beals, 1997; Lougheed et al., 2001; Ibelings et al., 2007; Trebitz et al., 2009). When wetlands become enriched with primary nutrients (phosphorus and nitrogen), the plant communities tend to shift from species that require high light and low-nutrient conditions (e.g., rooted rosettes) to those that can tolerate low light and require high-nutrient conditions (e.g., unrooted, floating and canopy species) (Lougheed et al., 2001; Edvardsen and Okland, 2006; Croft and Chow-Fraser, 2007; Trebitz et al., 2007).

The macrophyte community also reflects the physical conditions in a wetland (Lougheed et al., 2001; Croft and Chow-Fraser, 2007; Trebitz et al., 2009), as well as climatic and geological factors (Smith et al., 1991; Lougheed et al., 2001; De Catanzaro et al., 2009). In addition, morphology of the wetland will influence the type of aquatic vegetation, as high exposure and fetch can prevent establishment of many macrophyte species at a site, both directly through disturbance by wave action and burial by sediment, and indirectly through slow organic soil accretion (Keddy, 1983, 1985; Randall et al., 1996; Wei, 2007; Cvetkovic, 2008; Trebitz et al., 2009). We did not examine this factor directly in this study, but we anticipate that wave and wind exposure would play an important role in shaping the macrophyte community in exposed wetlands of eastern and northern Georgian Bay, Lake Huron (Cvetkovic, 2008).

Many studies have recognized that a diverse fish community (both species richness and abundance) depends on the type and diversity of aquatic vegetation in the wetland (Randall et al., 1996; Weaver et al., 1997; Hook et al., 2001; Pratt and Smokorowski, 2003; Pelicice et al., 2008). A diverse plant community provides high structural complexity for both predators and prey (Savino and Stein, 1989; Weaver et al., 1997; Sass et al., 2006; Padial et al., 2009). These studies have emphasized the importance of habitat heterogeneity in providing refuge for prey. These vegetated habitats also support a higher density of invertebrates, which is a vital food source for the juvenile fish (e.g., Batzer et al., 2000).

While a few studies have looked at the influence of plant species richness on fish communities (Fernandez et al., 1998; McNair, 2006; Pelicice et al., 2008) the majority have focused on quantitative data such as presence/absence (Lougheed et al., 2001; Croft and Chow-Fraser, 2007), percent cover (Randall et al., 1996; Brazner and Beals, 1997; Hook et al., 2001; Trebitz et al., 2009), biomass (Pelicice et al., 2008), patchiness (Weaver et al., 1997), as well as the inclusion of characteristics such as plant morphometric type (Janecek, 1990; McNair, 2006; Trebitz et al., 2009). We agree with the conclusions of Lougheed et al. (2001) that the type of assemblage present in a wetland is likely a better indicator of wetland quality than certain indicator species. We suspect that the presence of high quality macrophyte taxa, unless occurring in high densities, are likely acting more as an indicator of wetland quality and contributing to the overall habitat complexity for the fish community, than acting as a sole niche for a particular fish species.

CCA results were consistent with other studies relating fish to anthropogenic stressors, and largely showed that water clarity and nutrients were the predominant factors affecting fish distribution (Brazner and Beals, 1997; Seilheimer and Chow-Fraser, 2007, Trebitz et al., 2009). In the Georgian Bay region, where eutrophication has yet to reach levels associated with highly impacted wetlands such as those found in the lower lakes, water clarity was the major factor in predicting fish species assemblages. This is consistent with Brazner and Beals (1997) assertion that turbidity and macrophytes were the two dominant factors structuring the fish community in coastal wetlands of Green Bay, Lake Michigan.

Even after we simplified the COCA cluster diagrams to display only those taxa found in more than two thirds of the sites, a large proportion of fish and macrophyte species seemed to be closely associated judging by their placements on the axes. This is particularly true for Georgian Bay, a region that has relatively undisturbed coastal marshes of high quality. In-depth statistical explorations of COCA scores did not reveal any useful fish–plant associations for this region. This suggests that a high degree of similarity exists between fish and macrophyte communities throughout Georgian Bay. Whether this means that the majority of these fish taxa are generalists benefiting from the presence of the overall vegetation, rather than being specialists that are mainly associated with specific plant taxa, remains to be determined. We believe that future studies concentrating on more quantitative plant data including percent cover, relative abundance, and growth form categories, will lead to more comprehensible information regarding plant–fish interrelationships (Cvetkovic, 2008).

Sampling and analyses

In this study we were forced to compare fish presence/absence data (Whole Basin and Upper Lakes sites) and fish abundance data (Georgian Bay sites), and are aware that this may have introduced a source of error, since we assumed that the two were directly comparable; however, the fact that Georgian Bay presence data were not unimodally distributed prevented us from performing further statistical analyses with that particular dataset. The high similarities in fish communities for this region required us to use abundance information as a means of site discrimination. The resulting Georgian Bay CCA and COCA percent scores were similar in magnitude and difference when compared to the Whole Basin and Upper Lakes scores, and this reinforced our decision to use abundance values for Georgian Bay.

Macrophyte surveys were strictly based on taxa identification in this study. Since we only collected presence/absence information on the macrophyte community, our ability to provide meaningful interpretations is limited when dominance of the various species differs from site to site. Therefore, future studies should attempt to tease out fish–plant associations using more quantitative data such as relative abundance of plant taxa or percent cover for more accurate descriptions. In a literature review of fish and macrophyte interactions in the Upper Mississippi river, Janecek (1990) suggested that cover densities of plants can neither be too dense nor too sparse to support specific fish assemblages, and this seems to be supported by other studies that have followed (French, 1988; Hook et al., 2001).

Plant surveys can usually be completed by two samplers with minimal equipment, (e.g., waders, a canoe, some type of depth measuring device, and a quadrant) and are best conducted during July and August when plant growth is at a maximum. A recent study that compared three common wetland vegetation survey methods, the grid, transect, and the proposed 'stratified' method, found that the stratified method was more efficient in locating rare or unique species, identifying greater species richness, and took fewer quadrants and thus less time and effort to sample than the other two methods (see Croft and Chow-Fraser, 2009). We recommend the stratified method as a valuable survey protocol, as it ensures that all aquatic vegetation zones and habitat features are sampled and is typically completed in less than two hours. In comparison, water quality, while quick to collect, can be time-consuming to analyse and requires trained professionals and expensive laboratory equipment. Fish sampling on the other hand, can often take a whole day's worth of work (e.g., seining or electrofishing) or more when nets are set overnight (e.g., fyke nets, trap nets, or gill nets). When appropriate, plant surveying can be used as a convenient surrogate to water quality sampling to obtain a general idea of the health of the habitat, especially if resources are limited (Croft and Chow-Fraser, 2007). Similarly, we have also shown that aquatic plant taxa may one day have the potential to elucidate the general fish composition, which may be desirable to wetland conservationists depending on their overall project objectives.

Future work and management implications

The statistical correspondence shown between plant and fish data suggest that after continual investigation into plant–fish associations, the habitat availability for specific fish species or assemblages may be indicated by specific plant taxa. This would be advantageous in situations where budgets do not allow for intensive fish sampling, since plant surveys require less time and money to complete than fish surveys that require the use of nets, traps or electrofishing gear. Since

plant assemblages revealed more information about the fish community than expensive water quality analyses, managers whose goals are to track changes in quality of wetland fish habitat could benefit by using plant-based (e.g., WMI) rather than water quality-based (e.g., WQI) indices if cost is the major concern. Obviously, if fish composition is the primary study objective, no surrogate sampling method will adequately compare to the information obtained by classic and appropriate fishing methods for the coastal wetlands in question. In order to obtain the most complete and accurate representation of the entire marsh ecosystem, all possible components should be sampled, both physical and biological, whenever economically feasible.

By establishing a direct link between plant and fish communities we have provided justification for mapping aquatic vegetation that can be used in accordance with available fish information to provide further insight into relationships between fish and plant taxa, cover, and growth forms. It is now possible to map fish habitat at the scale of an entire Great Lake using high-resolution satellite imagery (e.g., IKONOS) and remote-sensing technology (see Wei and Chow-Fraser, 2007). Future studies should therefore focus on the development of detailed fish–plant relationships by judicious mapping of wetland vegetation in representative wetlands that can be statistically associated with specific fish species or guilds.

Knowledge of fish and plant associations can be very useful for restoration projects. In the future, organizations may use fish–plant relationships to guide restoration of degraded aquatic ecosystems by planting macrophytes that have proven to be beneficial for fish populations of interest (Chow-Fraser, 1998; Miller and Provenza, 2007; Ibelings et al., 2007). There will also be a need to create wetland habitat when existing fish habitats are developed. For example, Fisheries and Oceans Canada currently has a "no net loss" policy of productive fish habitats which states that "like-for-like" habitat must be created if an alternate productive habitat is destroyed (DFO, 1986; Pratt and Smokorowski, 2003). The success of habitat creation and enhancement will largely depend on the initial species chosen for establishment.

Conclusions

Throughout this study, we have stressed the importance of various factors that affect ichthyofauna composition in coastal wetlands, especially the composition of aquatic plants. We have shown that macrophyte species composition was a consistently better predictor of fish distribution than were water quality variables, and this was demonstrated at the regional scale for the entire Georgian Bay, and at the basin-wide scale for the Upper Lakes, and the Whole Basin. This is the first study that has quantified these factors and compared their relationships to fish communities at such large spatial scales. Our results support the hypothesis that there are plant–fish associations and that plant information alone can potentially be used to map fish habitat. We have also suggested other ecological factors such as physical disturbance (i.e., exposure) that may act to structure ichthyofauna communities in coastal marshes, and recommend alternate methods of sampling and analyzing plant–fish relationships to advance this area of research.

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