

Geographic, anthropogenic, and habitat influences on Great Lakes coastal wetland fish assemblages

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Abstract: We analyzed data from coastal wetlands across the Laurentian Great Lakes to identify fish assemblage patterns and relationships to habitat, watershed condition, and regional setting. Nonmetric multidimensional scaling (NMDS) ordination of electrofishing catch-per-effort data revealed an overriding geographic and anthropogenic stressor gradient that appeared to structure fish composition via impacts on water clarity and vegetation structure. Wetlands in Lakes Erie and Michigan with agricultural watersheds, turbid water, little submerged vegetation, and a preponderance of generalist, tolerant fishes occupied one end of this gradient, while wetlands in Lake Superior with largely natural watersheds, clear water, abundant submerged vegetation, and diverse fishes occupied the other. Fish composition was also related to wetland morphology, hydrology, exposure, and substrate, but this was only evident within low-disturbance wetlands. Anthropogenic stress appears to homogenize fish composition among wetlands and mask other fish–habitat associations. Because land use is strongly spatially patterned across the Great Lakes and aquatic vegetation is a key habitat element that responds to both biogeography and disturbance, it is difficult to disentangle natural from anthropogenic drivers of coastal wetland fish composition.

Résumé : Nous analysons des données provenant de terres humides riveraines réparties sur l'ensemble des Grands Lacs laurentiens afin d'identifier les patrons d'associations de poissons et leurs relations avec les habitats, les conditions du bassin versant et l'environnement régional. Une ordination de cadrage non métrique multidimensionnel (NMDS) de données de captures par unité d'effort de pêche électrique révèle l'existence d'un gradient prédominant de facteurs de stress géographiques et anthropiques qui semble structurer la composition des peuplements de poissons par son impact sur la clarté de l'eau et la structure de la végétation. Les terres humides aux lacs Érié et Michigan avec des bassins versants agricoles, de l'eau turbide, une végétation submergée rare et une prépondérance de poissons généralistes et tolérants, occupent une extrémité de ce gradient; en revanche, les terres humides du lac Supérieur avec des bassins versants en grande partie naturels, de l'eau claire, une végétation submergée abondante et une diversité de poissons, occupent l'autre extrémité. La composition des peuplements de poissons est aussi en relation avec la morphologie des terres humides, l'hydrologie, l'exposition et le substrat, mais la relation n'est évidente que dans les terres humides peu perturbées. Le stress anthropique semble homogénéiser la composition des peuplements de poissons dans les différentes terres humides et masquer les autres associations poissons–habitats. Parce que l'utilisation des terres dans la région des Grands Lacs forme un patron spatial bien marqué et que la végétation est un élément essentiel de l'habitat qui réagit à la fois à la biogéographie et aux perturbations, il est difficile de démêler les facteurs explicatifs naturels et anthropiques de la composition des peuplements de poissons dans les terres humides riveraines.

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Introduction

Coastal wetlands of the Laurentian Great Lakes provide crucial habitat for a wide variety of resident and migrant fish species (Jude and Pappas 1992; Wei et al. 2004; Minns and Wichert 2005). Key aspects governing the use of these wetlands by fishes are thought to be their productivity, connectivity, structural complexity, and water clarity (Wilcox 1995; Randall et al. 1996; Brazner and Beals 1997). Compared with the adjacent Great Lakes, coastal wetlands have warmer water, reduced wave energy, higher primary productivity, and an abundance of vegetated habitat that supports invertebrate forage items and provides spawning substrate, nursery habitat, and predation refuge. Anthropogenic activities such as agriculture and urban development have resulted in the historic loss of large portions of the wetlands in the Great Lakes (e.g., Bosley 1978; Whillians 1982) and continue to threaten habitat quality for fish and other biota via adverse impacts on hydrologic regime, water clarity, and aquatic vegetation (Whillians 1992; Loughheed et al. 2001; Jude et al. 2005).

Studies examining fish–habitat relationships in Great Lakes coastal wetlands have primarily focused on local scales (individual or small groups of wetlands) using a species-by-species approach (e.g., Chubb and Liston 1986; Tanner et al. 2004; Jacobus and Ivan 2005), and habitat preferences of individual species are generally well understood (e.g., Becker 1983, Lane et al. 1996; Coker et al. 2001). Over broader scales, however (e.g., the Great Lakes basin), environmental influences on fishes are more appropriately addressed with whole assemblage data (Poff and Allan 1995) and ordination techniques (Gauch 1982). Studies in streams (e.g., Wang et al. 2003; Brazner et al. 2005), lakes (e.g., Rodríguez and Lewis 1997; Weaver et al. 1997), and estuaries (e.g., Vorwerk et al. 2003; Saintilan 2004) have used ordination analyses of fish assemblage data to examine the interplay among local-scale habitat descriptors and broader-scale geographic features, to elucidate the role of type and scale of anthropogenic disturbance in molding physical habitat, and to identify which of a potentially large and related suite of habitat variables are most strongly associated with fish composition. In the Great Lakes, ordination analyses have been successful in identifying environmental factors structuring fishes in wetlands in Lake Michigan's Green Bay (Brazner and Beals 1997). Across broader geographic scales, however, ordination analyses of Great Lakes coastal wetland fishes have been conducted only for the narrower purposes of evaluating whether fish composition indices are sensitive to water quality parameters (Seilheimer and Chow-Fraser 2007) and whether they require biogeographic classification (Uzarski et al. 2005).

Our objectives here are to use ordination techniques to examine coastal wetland fish assemblage patterns and their associations to wetland conditions across the Great Lakes basin. Specifically, we describe fish composition at the whole-wetland scale and relate that to a broad suite of variables describing geographic setting, anthropogenic impacts, and wetland habitat elements, such as hydromorphology, water quality, and vegetation structure. A companion paper (Trebitz et al. 2009) examines patterns of fish composition at the subwetland scale, with a focus on differences in fish

composition among microhabitats, predictors of homogeneity or heterogeneity in fish composition within wetlands, and implications for sampling design. Data for both papers were collected as part of a larger study with the goals of investigating effects of nutrient enrichment and habitat degradation on wetland water quality and biota.

Materials and methods

Over the summers of 2002, 2003, and 2004, we sampled 58 coastal wetlands along the US shore of the Laurentian Great Lakes (Fig. 1). Four of the wetlands were sampled in 2 years each, for a total of 62 wetland sampling events. Wetlands were selected according to a design that distributed them across a gradient of watershed agricultural intensity within combinations of biogeographic ecoprovince (Laurentian Mixed Forest or Eastern Broadleaf Forest; Keys et al. 1995) and wetland type. Agricultural intensity was measured as the first principal component combination of variables describing agricultural activity in the watershed (rates of fertilizer application, nutrient and sediment runoff, etc.), developed as part of a basin-wide stressor characterization (Danz et al. 2005, 2007). Sites were distributed across the basin in all 3 years to minimize confounding geography with possible interannual variability in water levels, fish recruitment, etc.

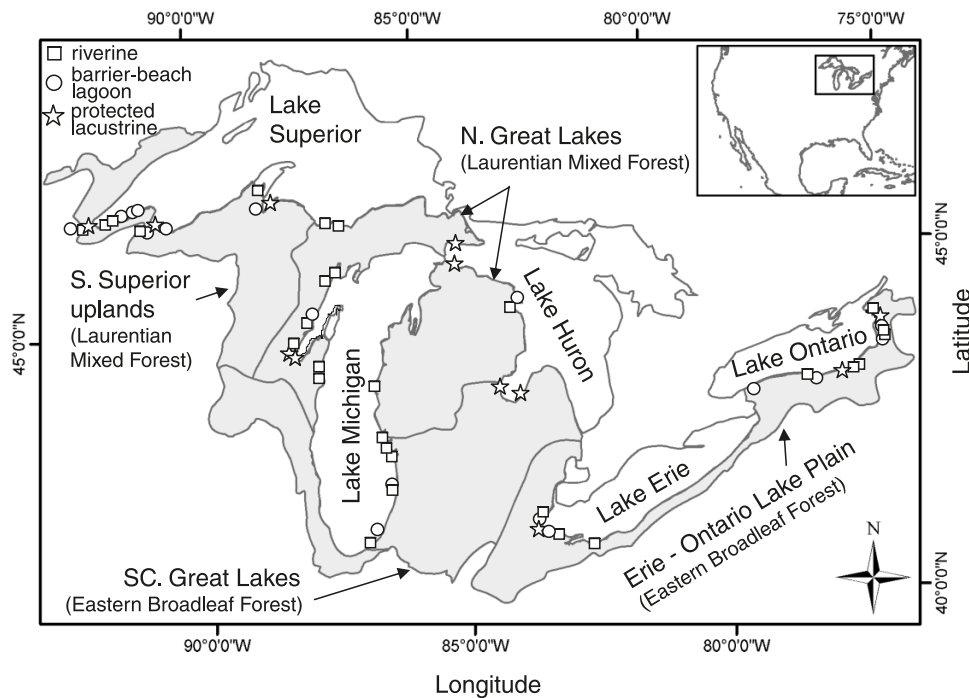
For site selection, wetland type categories used were “riverine” and “protected” (after Keough et al. 1999). Riverine coastal wetlands form near the lake terminus of rivers and streams and are substantially influenced by lotic flow and water quality, whereas protected wetlands have the adjacent lake as their primary water source and physical influence. For analysis, we further divided protected wetlands into “barrier-beach lagoon” and “lacustrine-protected” categories (after Albert et al. 2005). Both of these wetland types are sheltered from the open lake to some degree, but lacustrine-protected wetlands have much larger openings and less permanent barrier beaches and therefore typically experience greater wind and wave energy and stronger exchanges of water with the lake than do barrier-beach lagoons. While some riverine and barrier-beach lagoon wetlands have only intermittently open mouths, all wetlands we sampled had a surface hydrologic connection to the adjacent lake.

Sampling took place during July or August, a period during which aquatic vegetation growth is typically at its peak and water chemistry, hydrology, and fish composition are stable. Anthropogenic stressors and some hydromorphology descriptors were characterized for entire wetlands or watersheds, while water quality, vegetation structure, fish composition, substrate, and other hydromorphology descriptors were measured at multiple stations within wetlands and aggregated to the whole-wetland scale for analysis (Table 1). All field data were obtained from a 1-day visit per wetland, with the exception of the water level time series used to characterize seiche.

Anthropogenic stressors

The percentage of the wetland shoreline that was hardened (marina wall, riprap, etc.) was estimated to the nearest 5% in the field. Boating impacts were scored according to

Fig. 1. Map showing wetlands sampled around the Laurentian Great Lakes (inset: location of Great Lakes region in North America). Associated geographic ecoregions and ecoprovinces (the latter in parentheses) are indicated in grey. Wetland names and coordinates are available in Trebitz and Taylor (2007).



the number of docks or boat slips observed per kilometre of shoreline (1 if there were none, 2 if <1 dock or slip- km^{-1} , 3 if <5 , 4 if <10 , and 5 if >10), with the additional criteria that wetlands having a substantial boat launch (paved, multiple parking spaces, etc.) received a minimum score of 2, and wetlands in which we observed activities such as jet boating or water-skiing received a minimum score of 4. No wetlands received a boat impact score of zero, since all were accessed by boat.

Data describing land cover around the wetlands were extracted from the 30 m resolution 2001 National Land Cover Data set (NLCD — Homer et al. 2004) as amended by Wolter et al. (2006) to incorporate more detailed road data and correct some data gaps and classification errors. We used a geographic information system (GIS) to generate polygons for each wetland watershed and for 100 and 500 m buffers around each wetland inundated area and intersected these with the Wolter et al. (2006) version of NLCD 2001 to obtain the proportion of the area by land cover category. The proportions were computed after excluding the wetland-inundated areas and any areas where the buffers extended out into Great Lakes waters. Categories analyzed were developed lands (residential, commercial–industrial, roads, quarries–mines–gravel), agricultural lands (orchard, pasture–hay, row crop, small grains, urban–recreational grasses), and natural lands (all other terrestrial categories). We did not separately analyze intense agriculture or impervious development because these were highly correlated with overall percentages of agricultural or developed lands. We noted some misclassification of naturally bare areas (beaches) as commercial–industrial land but made no correction, as these constituted $<0.1\%$ of the area of any buffer or watershed.

Wetland-scale habitat data

Wetland-inundated area and shoreline complexity (ratio of shoreline length to that of a circle of the same area) were obtained from wetland outlines digitized over orthophotographs. Wetland mouth size was measured in the field (if small) or estimated from orthophotographs (if large). Wetland hydrology was characterized by the flow of tributary streams as gauged on the day we sampled and by the summed daily water level change due to seiche extracted (method in Trebitz 2006) from hourly water level time series collected with automated recorders deployed in wetlands for ~ 4 weeks. Wetlands without streams or gaugeable flow were assigned a minimal discharge of $0.001 \text{ m}^3\cdot\text{s}^{-1}$ to avoid missing values in analyses. Surveys of water depth and plant cover on a 30–50 point grid across each wetland were used to establish mean water depth, maximum depth at which submerged vegetation grew (average of the three deepest observations), and percentage of points bare of vegetation.

Station-scale habitat data

Prior to site visits, we used GIS software to establish five to seven sampling stations per wetland (depending on size), spaced at even intervals around the shoreline. Morphological descriptors recorded at each station included nearshore bottom slope (depth divided by distance offshore of the outer edge of the emergent plant zone) and fetch (cosine-weighted average of distance to the opposite shore at 45° , 90° , and 135° angles; Burton et al. 2004). Station surface water quality was characterized for a broad suite of parameters (Trebitz et al. 2007b), of which this paper considers water temperature, dissolved oxygen (midmorning), and water clarity as measured by Secchi (using a transparency tube), total suspended solids (TSS), and turbidity. Sediments were

Table 1. Summary of environmental variables analyzed.

Variable	Description	Distribution		Associations to fish		
		Mean±SD	Range	All 62	Low 38	High 24
Physical setting (wetland and station scale)						
InunArea	Inundated area (ha)	43.7±39.0	2.9–184.8		M	
ShapeCpx	Shape complexity	3.8±2.2	1.1–10.4			
WetZav	Mean water depth (m)	0.9±0.3	0.32–1.74	M	M	M
MthSize	Mouth cross-section area (m ²)	122±198	0.2–1000			
ShedArea_log	log ₁₀ watershed area (ha)	3.7±1.1	1.9–6.2			
TribIn_log	log ₁₀ tributary inflow (m ³ ·s ⁻¹)	-1.3±1.6	-3.0–1.6		M	
SechSum	Total daily seiche-driven water level change (m)	0.29±0.29	0.01–1.21		M	M
Fetch_log	log ₁₀ fetch (m)	2.3±0.5	1.5–4.1			
ShoreSlope	Nearshore slope (%)	16.8±13.4	0.4–58.8			
SedDens	Sediment density (g·mL ⁻¹)	1.5±0.2	1.1–2.0		MB	
Vegetation (station scale)						
VegZmx3	Maximum plant depth (m)	1.4±0.4	0.4–2.3	M	M	M
%Bare	Percentage of points lacking vegetation	36±26	0–91			
AlgCovP	Periphyton cover on macrophytes (index)	2.4±0.7	1.0–4.0			
VegCovF	Floating cover (index)	1.6±1.0	0.0–3.6	M	M	M
VegCovS	Submerged cover (index)	2.7±0.8	0.9–4.0	M	M	
VegFrmSF	Submerged–floating growth forms (% of max.)	61±20	10–90	M		
VegCpxSF	Submerged–floating complexity index	0.37±0.20	0.03–0.71	M	M	
EmgWidth	Emergent zone width (m)	14±22	1–141			
VegCovE	Emergent cover (index)	3.2±0.6	1.2–4.0			
VegFrmE	Emergent growth forms (% of max.)	70±18	25–100		M	
VegCpxE	Emergent complexity index	0.57±0.17	0.2–1.0		MB	
Water quality (station scale)						
Temp	Water temperature (°C)	22.3±3.0	13.9–27.0	M	M	
DO	Dissolved oxygen (mg·L ⁻¹)	6.7±1.8	3.0–11.9			
Secchi	Secchi tube depth (cm)	83±38	8–120	MB		M
Turb	Turbidity (NTU)	16.7±19.5	0.05–85.9	B		M
TSS	Total suspended solids (mg·L ⁻¹)	12.0±16.4	1.0–97.0	MB		M
Anthropogenic stressors (wetland and watershed scale)						
BoatAct	Boating activity score	2.2±1.2	1–5			
Shore%Armor	% wetland shoreline that is armored	6±13	0–60			M
Shed%Ag	% agricultural land in watershed	32±29	0–86	M		
B500%Ag	% agricultural land in 500 m buffer	18±21	0–82	M	M	
B100%Ag	% agricultural land in 100 m buffer	15±18	0–67	M	M	
Shed%Dev	% developed land in watershed	10±8	0–37	M	M	
B500%Dev	% developed land in 500 m buffer	18±17	0–79	M		
B100%Dev	% developed land in 100 m buffer	17±16	0–67			
Shed%Nat	% natural land in watershed	59±30	7–100	M	M	
B500%Nat	% natural land in 500 m buffer	63±27	9–99	M	M	M
B100%Nat	% natural land in 100 m buffer	68±24	15–100	M		M

Note: Statistics reported for variables measured at the station scale are wetland averages. Associations with fish composition patterns are reported separately across all 62 wetlands, the 38 low-disturbance wetlands, or the 24 high-disturbance wetlands; “M” signifies a monotonic relationship to the ordination (vector length ≥ 0.5 in overlay plots), and “B” signifies a match in pattern to multivariate fish composition ($\rho > 0.35$ in BEST analyses).

characterized by wet density (weight per unit volume) averaged across all vegetation zones per station from which an Ekman dredge sample could be obtained. Higher sediment density corresponds to sandier, less organic sediments.

Vegetation cover and composition at each station were surveyed over an area that extended along 100 m of shoreline and across the full width of the relevant vegetation zone (details in Treibitz and Taylor 2007). All macrophyte taxa found growing in the water were recorded, and total emergent cover, floating-leaf cover, and submerged cover were

each assigned a score using a scale of 0 (none), 1 (<10% cover), 2 (10%–33% cover), 3 (33%–66% cover), and 4 (>66% cover). Periphyton growth on plant stems was scored as 0 (none), 1 (stems slimy), 2 (visible layer < 0.5 cm thick), 3 (layer 0.5–2 cm thick), and 4 (layer > 2 cm thick) (modified from Stevenson and Bahls 1999). To focus on the habitat structure the plants provided, we assigned each taxa to a growth form and computed the proportion of possible growth forms present at each station and a structural complexity index that multiplies the proportion of

growth forms present by the proportion of the maximum cover score (after Brazner and Beals 1997). Submerged and floating-leaf vegetation were combined in these indices because they broadly overlap in their zonation and some taxa have both kinds of leaves. The four emergent growth forms used were broadleaf monocot (e.g., *Sagittaria*, *Pontederia*), robust monocot (e.g., *Typha*, *Schoenoplectus*), slender monocot (e.g., *Juncus*, *Carex*), and dicot (e.g., *Polygonum*, *Potentilla*), while the seven submerged and floating forms used were large floating (*Brasenia*, *Nymphaeaceae*), tiny free-floating (*Lemnaceae*), ribbon (e.g., *Vallisneria*, *Sparganium fluctuans*), dissected (e.g., *Myriophyllum*, *Ceratophyllum*), broadleaf pondweed (e.g., *Potamogeton amplifolius*, *Potamogeton richardsonii*), narrow-leaf pondweed (e.g., *Potamogeton foliosus*, *Stuckenia pectinata*), and ground cover (e.g., *Elodea*, *Characeae*).

Fish data

Fish were surveyed at the same spatial scale as aquatic vegetation, namely across 100 m stretches of shoreline at each sampling station. Fish were collected by daytime electrofishing (5 m metal boat, 5000 W generator, 1 m Wisconsin ring with stainless steel droppers, 6.0 to 8.0 A DC current depending on conductivity), enumerated to species (using Becker 1983 as the primary reference), classified by life stage (young of year, juvenile, or adult), measured and weighed, and released. Ten minutes of electrofishing effort were expended at each stretch of shoreline, distributed across the emergent, submerged–floating, and open-water zones in proportion to their relative size. Fish data were recorded by station and vegetation zone sampled and aggregated to wetland scale by summation.

Fish composition was variously expressed as number caught, catch per unit effort (per minute electrofishing), percent relative abundance, and presence or absence. Numbers caught were used to compute a variety of trait metrics, including species richness, Shannon–Wiener diversity, and percentage of individuals by age (young of year), origin (exotic), feeding guild (omnivore, top carnivore), turbidity tolerance (tolerant, intolerant), spawning behavior (nest guarding, lithophilic spawner, vegetation spawner), swimming style (benthic), body size (large), and desirability to anglers (game or panfish). Because of redundancy among mutually exclusive categories, not all possible trait metrics were evaluated (e.g., omnivore and top carnivore but not invertivore). Turbidity tolerances were assigned according to Trebitz et al. (2007a), while other trait designations (see Appendix A, Table A1) were compiled from various sources (e.g., Becker 1983; Coker et al. 2001). Young-of-year sunfish (very small *Lepomis* that could not be identified to species in the field) were omitted from richness calculations to avoid double counting but were treated as a species in ordinations and computation of trait metrics.

Analyses

We used nonmetric multidimensional scaling (NMDS) ordination based on Bray–Curtis similarity to summarize fish species patterns at the wetland scale. NMDS is well suited to examining patterns in complex ecological data because it identifies a low-dimensional ordination space that preserves the pattern of dissimilarity among sites in the full species

space without requiring any assumption of linearity in responses (Gauch 1982). Preliminary ordinations were made using catch per effort (raw CPE, \log_{10} -transformed CPE), relative abundance (RA), and presence or absence (PA) forms of the fish data, each with rare species (those found at less than three wetlands and never >1% of the catch at any wetland) either included or excluded to examine their influence (Gauch 1982). Comparisons among the ordinations (visually and via the PRIMER software 2d-stage NMDS procedure — Clarke and Warwick 2001) revealed only small differences among raw CPE, log CPE, and RA data, while PA differed somewhat from the other three. Removal of rare species made no difference for RA and raw CPE ordinations and had only a minor influence on PA and log CPE ordinations. Stress statistics (McCune et al. 2002) suggested that 3D ordinations were called for. However, the correlation between Euclidean distances among sites in 2D versus 3D ordinations was high (>0.9), and the fish species, trait metrics, and environmental variables identified as most closely related to the pattern of sites in species space (via BEST analyses, details below) were essentially the same whether the full similarity matrix or a 3D or 2D ordination matrix was evaluated. Based on these results, we selected untransformed CPE data with rare species included for final analyses and restricted ordinations to two dimensions to facilitate depiction of results.

Relationships of fish composition to categorical environmental variables (describing wetland geography and type) were examined via coding of points in ordination plots and via PRIMER's analysis of similarity (ANOSIM) procedure, which tests for group structure with a nonparametric analogue of analysis of variance (ANOVA; Clarke and Warwick 2001). Relationships of fish composition to continuous variables (describing fish trait metrics, abundances of non-rare species, wetland environment) were examined both by means of vector overlay plots (McCune et al. 2002) and by using PRIMER's BEST procedure coupled with bubbleplot interpretation to look more generally for matches between the respective wetland similarity matrices (Clarke and Warwick 2001). We used this dual approach because vector plots enable a compact visual display of monotonic relationships, whereas BEST analyses can also detect nonmonotonic relationships that are more difficult to depict and because the former work with a reduced-dimension space (i.e., the ordination), whereas the latter work with the full species space. We used Spearman rank correlations as the metric of association, with values ≥ 0.5 as a conservative criteria for reporting vector associations and values ≥ 0.35 as a conservative criteria for reporting BEST associations. Environmental data and species trait metrics were normalized (i.e., mean = 0 and standard deviation = 1) prior to BEST calculations.

Results

The 62 coastal wetlands sampled were distributed approximately equally among ecoprovinces, ecoregions, and riverine versus protected wetland types, although there were more barrier-beach lagoon than lacustrine-protected systems (Fig. 1). The wetlands had quite diverse physical characteristics, with a five orders of magnitude range in watershed

Table 2. Summary of fish trait metrics computed for wetland-scale catch data.

Variable	Description	Distribution		Association to fish		
		Mean±SD	Range	All 62	Low 38	High 24
TotCPE	Catch per effort (fish·min ⁻¹)	18.2±33.9	2–183	MB	M	MB
Richness	Species richness	16±3	8–26			
SWdiv	Shannon–Wiener diversity	1.6±0.6	0.1–2.4	B		MB
%YOY	% young-of-year fish	56±33	1–100		M	MB
%Benth	% benthic fish	28±23	1–98	M		
%Exot	% exotic fish	13±22	0–96	M		M
%GamePan	% game and panfish	37±30	0–88	M	MB	M
%Large	% large-bodied fish	37±30	1–100	B	M	MB
%Lith	% lithophilic spawners	22±25	0–96		B	M
%Nest	% nest-guarding fish	39±27	0–95	M		M
%Omni	% omnivores	46±30	2–99	MB	MB	MB
%Carn	% top carnivores	35±26	1–85		M	M
%TurbTol	% turbidity-tolerant fish	45±33	3–100	MB		M
%TurbInt	% turbidity-intolerant fish	5±9	0–44	M		M
%Veg	% vegetation spawners	34±27	0–97		M	

Note: Associations with fish composition patterns are reported separately across all 62 wetlands, the 38 low-disturbance wetlands, or the 24 high-disturbance wetlands; “M” signifies a monotonic relationship to the ordination (vector length ≥ 0.5 in overlay plots), and “B” signifies a match in pattern to multivariate fish composition ($\rho > 0.35$ in BEST analyses).

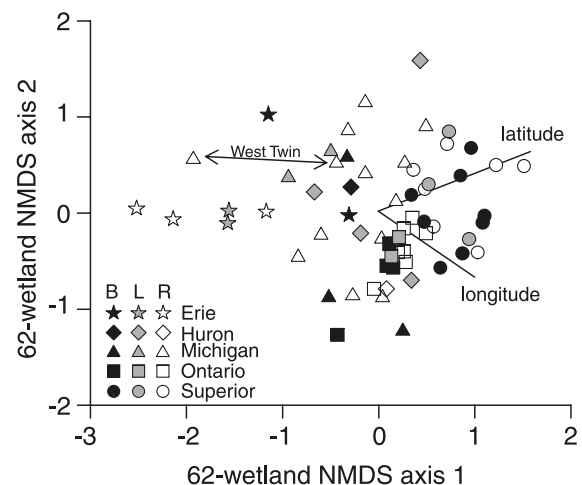
area and a three orders of magnitude range in inundated area, mouth size, fetch, and tributary inputs (Table 1). The wetlands also varied considerably in water clarity and aquatic vegetation structure (Table 1). Landuse–landcover in the wetland watersheds ranged from heavily agricultural and developed (up to 86% and 37%, respectively) to almost completely natural (Table 1).

We captured >69 000 individuals and 76 species of fish from 21 families across all the wetlands. Catches at any one wetland ranged from <100 to >10 000 fish, while species richness ranged from 8 to 26 (Table 2). The most common species were yellow perch (at 84% of wetlands) and pumpkinseed (77% of wetlands), with golden shiner, brown bullhead, common carp, white sucker, largemouth bass, northern pike, rock bass, bluegill, and bluntnose minnow also each found at over half the wetlands (scientific names given in Appendix A, Table A1). Twelve species fit our designation of rare, and 22 species did not occur in all five Great Lakes (listed in Appendix A, Table A1). Species occasionally caught in very large numbers included gizzard shad (>12 000 at one wetland), goldfish (>3000), common carp, yellow perch, common shiner, alewife, emerald shiner, white sucker, and brown bullhead (each >500); and black crappie, bluegill, golden shiner, and bluntnose minnow (each >200). Gizzard shad made up over 50% of the individuals caught over the study, even though they were found at only one-third of the wetlands; yellow perch was the next most numerically abundant species but made up only 7% of the overall catch.

Basin-wide fish patterns and habitat associations

Geography described much of the structure in fish composition across the basin. A two-dimensional NMDS ordination spread sites in a roughly triangular pattern, with wetlands in Lake Erie forming the left-hand point of the triangle and wetlands in Lake Superior defining the triangle’s right-hand side (Fig. 2). Lake Ontario wetlands were the most tightly clustered, while Lake Michigan sites had the greatest hori-

Fig. 2. Patterns in fish composition across all 62 wetlands, as expressed in a two-dimensional nonmetric multidimensional scaling (NMDS) ordination of catch-per-effort data (stress = 0.22; variation explained = 52%). Symbols indicate parent lake (symbol shape) and wetland type (symbol fill; B = barrier-beach lagoon, L = lacustrine-protected, R = riverine). Latitude and longitude are depicted as vectors whose angle and length reflect their correlation to the ordination axes. The position of West Twin wetland in year 1 (left open triangle) versus year 2 (right open triangle) is highlighted.



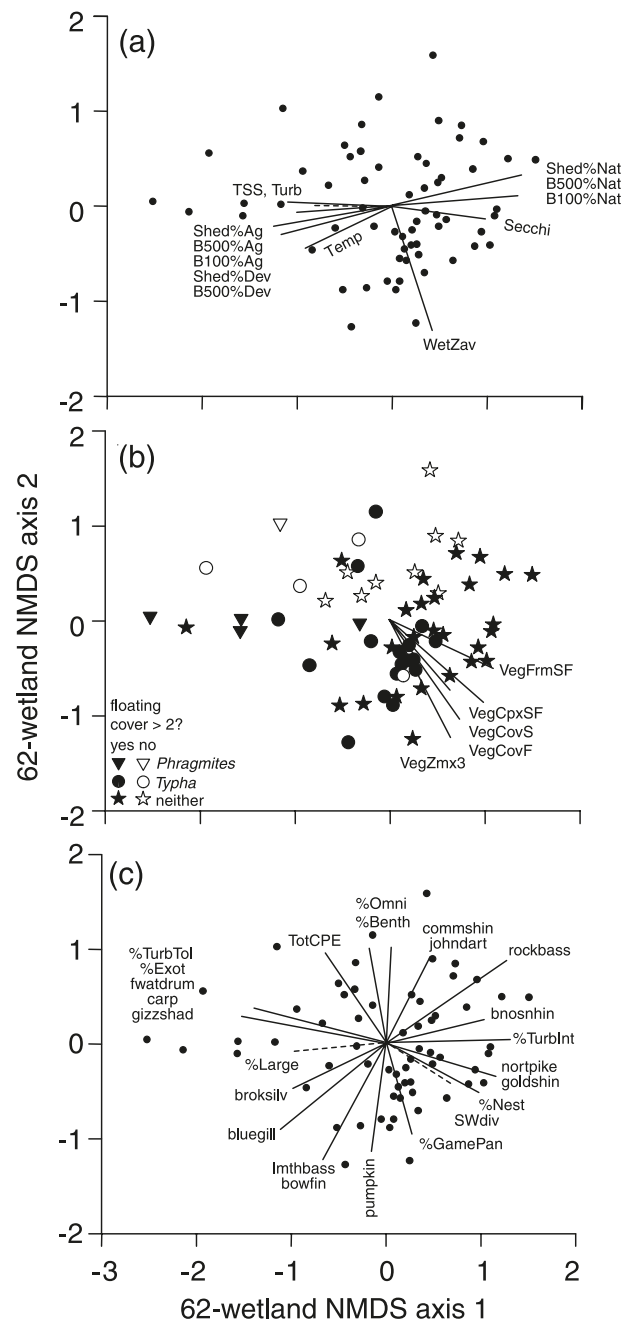
zontal and vertical spread (Fig. 2). Within Lake Michigan, wetlands from Green Bay and the western shore were largely separated from sites along the eastern shore (respectively plotting above and below the zero-line on the vertical axis in Fig. 2). Fish composition differed significantly between ecoprovinces, between the South Superior Uplands and the other three ecosections, and between all lake pairs except Lakes Michigan and Huron (all ANOSIM $p < 0.02$). Fish composition did not differ among wetland types either across the basin or within lakes.

Plots superimposing vectors for fish and environmental variables on the ordinations suggested that species composition was strongly related to anthropogenic disturbance. Increasing anthropogenic stressor levels along axis 1 were associated with reduced water clarity, higher fish catches, and increasing prevalence of exotic, omnivorous, turbidity-tolerant species, such as common carp, gizzard shad, and freshwater drum (Fig. 3). In contrast, sites in largely natural watersheds had clear water, more diverse fish taxa, and proportionally more nest-guarding or turbidity-intolerant species, such as golden shiner and northern pike (Fig. 3). BEST-bubbleplot analyses indicated that a few Lake Superior wetlands in red-clay soil watersheds had somewhat different fish composition associated with elevated turbidity (Fig. 3) in the absence of major anthropogenic disturbance. Correlations to the ordination were highest at the 500 m buffer and watershed scale, but all anthropogenic stressor vectors were aligned in the same generally horizontal plane (shoreline hardening, boating impact, and percent developed land in the 100 m buffer had vector lengths below the 0.5 threshold for plotting in Fig. 3). Vectors for latitude (Fig. 2) and water temperature (Fig. 3a) were also aligned more or less horizontally.

The vertical gradient among wetlands was truncated relative to the horizontal gradient (note the difference in *x* versus *y* axis scales in Figs. 2 and 3), and there was a conspicuous lack of vertical dispersion among the most anthropogenically disturbed wetlands. The vertical distribution of sites seemed to reflect water depth and submerged and floating vegetation structure (Fig. 3). Deeper wetlands tended to have higher vegetation cover and complexity and were characterized by larger predator and gamefish taxa such as centrarchids and bowfin, while shallower wetlands had more benthic taxa like common shiner and johnny darter, less submerged vegetation, and sometimes little or no floating-leaf vegetation (Fig. 3). Emergent vegetation structure (cover score, growth forms present) was not correlated with the ordination, but dominance by emergent taxa with very dense stand architecture (i.e., *Phragmites* and *Typha*) characterized many wetlands on the disturbed end of the stressor gradient (Fig. 3b).

We confirmed that the geographic patterning of the ordination was not simply driven by the limited distribution of some fish taxa by repeating the ordination after excluding the 12 species that were rare in our data and the 22 species whose range did not include all five Great Lakes (after Underhill 1986; Page and Burr 1991). The horizontal position of wetlands in this ordination (not shown) was essentially the same as in Fig. 2, except that Lake Erie wetlands in which the (now excluded) gizzard shad had been dominant were not positioned nearly as far left. There was some more pronounced shifting of wetland positions along the vertical axis, reflecting the exclusion of taxa such as bowfin and redfin pickerel, whose vectors were oriented vertically to the ordination in Fig. 3c, but this did not appreciably affect the geographic grouping of sites. The effect of gizzard shad is also illustrated by the large change in position of one wetland between the year in which gizzard shad made up >90% versus the year they made up only 4% of the catch (Fig. 2). The other three wetlands at which we conducted repeat sampling ordinated essentially in the same location in both years.

Fig. 3. Ordinations of all 62 wetlands (point locations as in Fig. 2) overlain with vectors showing related anthropogenic stressor metrics and physical habitat variables (a), vegetation metrics (b), and fish taxa and traits (c). In panel (b), wetland points are coded by the identity of the dominant emergent taxa (symbol shape) and whether there was any substantial floating-leaf cover (symbol fill). Variables (defined in Tables 1 and 2 and Appendix A, Table A1) shown as vector overlays had either a substantial monotonic relationship to the ordination (solid vectors) or a nonmonotonic relationship identified by BEST analyses (broken vectors); for visual clarity, some closely overlapping vectors have been replaced by a single vector with multiple labels. Nonmonotonic relationships include Turb (high in wetlands on the left side but also in a few wetlands on the right situated in red-clay soils); SWdiv (lower in wetlands ordinating to the far left than in all the others); and %Large (higher in left than right half of ordination).



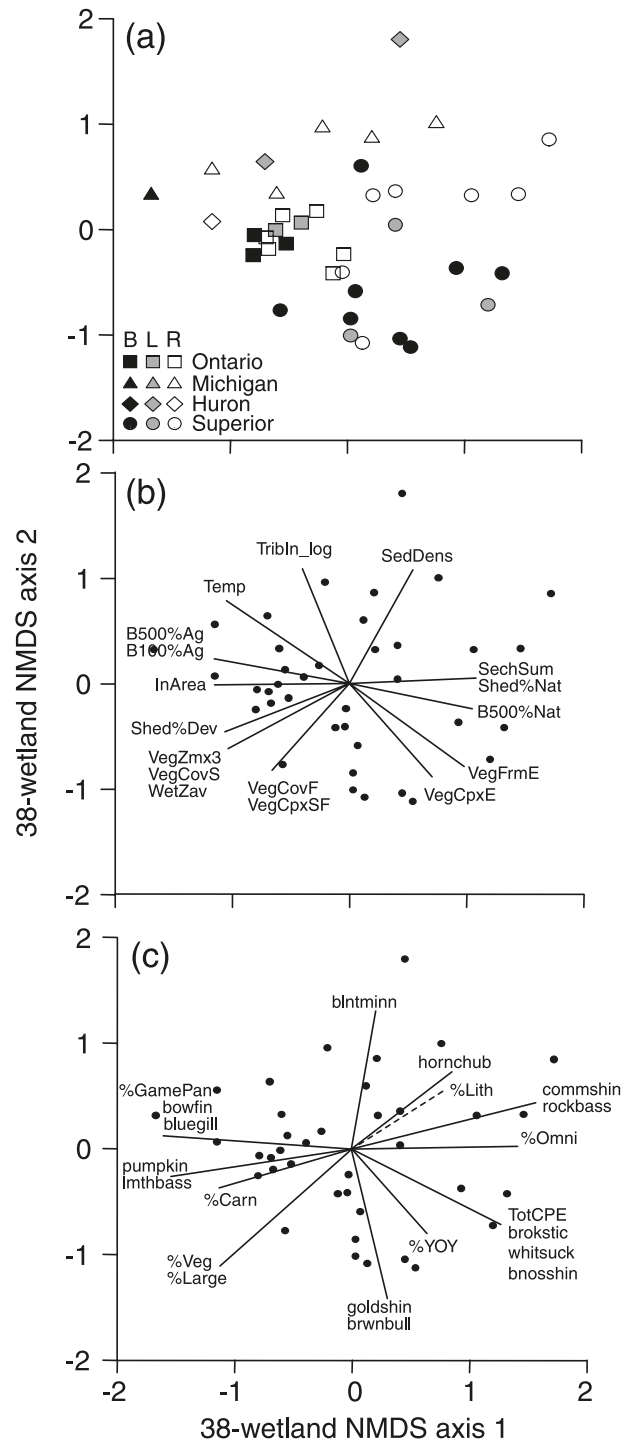
Fish–habitat patterns in low- versus high-disturbance wetlands

To focus more closely on natural factors structuring fish composition, we conducted separate ordinations on wetlands falling in the right half versus the left half of the disturbance gradient from the full 62-site ordination. The low-disturbance wetlands (axis 1 scores > 0 in Fig. 2) excluded all sites from Lake Erie and many from Lakes Michigan and Huron while retaining all sites from Lake Superior and most from Lake Ontario; conversely, the high-disturbance wetlands (axis 1 scores < 0 in Fig. 2) came primarily from Lakes Erie and Michigan. Of the 76 fish species caught across the basin, eight were not found in the low-disturbance wetlands (of which only white bass had been prominent in the full ordination), while 24 were absent from the high-disturbance wetlands (none of which had been prominent in the full ordination).

The ordination of the 38 low-disturbance wetlands revealed some fish–habitat associations that had not been apparent in the ordination of all 62 sites together. In addition to differences by lake, ecoprovince, and ecosection, there was now also a significant (ANOSIM $p = 0.04$) difference between riverine and protected wetlands in Lake Superior (Fig. 4), although not between lacustrine and barrier-beach lagoon protected types. An anthropogenic land use gradient was still present but seemed to have little influence on water clarity or fish, as Secchi, turbidity, TSS, and the percentage of fish that were exotic or turbidity-tolerant and -intolerant were no longer substantial vectors (Tables 1 and 2). Several variables describing hydrology and physical habitat (wetland area, sediment density, tributary inputs, seiche inputs) were prominent in the ordination of low-disturbance wetlands that had not been significant in the ordination of all 62 sites (Fig. 4). Wetlands ordinating high on the y axis were shallower, sandier, less vegetated, and characterized by small-bodied lithophilic or benthic fishes, while wetlands ordinating low on the y axis were deeper and more vegetated and characterized by larger-bodied, phytophilic species (Fig. 4). Riverine wetlands generally ordinated in the upper half of the y axis, while protected wetlands ordinated in the lower half; however, a few particularly lake-exposed lacustrine wetlands also ordinated high on the y axis, suggesting that strong lake exposure and river flow have similar implications for wetland substrate and vegetation. Among the more vegetated wetlands, there was a contrast between sites with complex emergent structure versus complex submerged and floating vegetation structure (vectors angled to the right versus the left in Fig. 4b).

The ordination of the 24 high-disturbance wetlands yielded no additional habitat associations, but did highlight additional details of the anthropogenic stressor regime. At the watershed scale, percent agriculture and developed land differed little across these wetlands and consequently were not correlated with the ordination, but the condition of the immediate shoreline (shoreline armoring, percent natural land within 100 or 500 m) mattered to fish composition (Fig. 5b). Total CPE and percentages of young-of-the-year (YOY), omnivore, large-bodied, and turbidity-tolerant fish such as gizzard shad and freshwater drum increased in concert with increasing shoreline armoring and loss of natural land in the buffer, while Shannon–Wiener diversity and per-

Fig. 4. Patterns in fish composition across the 38 low-disturbance wetlands, as expressed in a two-dimensional nonmetric multidimensional scaling (NMDS) ordination of catch-per-effort data (stress = 0.19, variation explained = 72%). In panel (a), wetlands are coded to indicate parent lake (symbol shape) and wetland type (symbol fill; B = barrier-beach lagoon, L = lacustrine-protected, R = riverine). Wetland type and lake coding is omitted in the other two panels, which instead overlay vectors showing related environmental variables (b) and fish species and traits (c). Conventions for depicting vectors are as in Fig. 3. %Lith is high along the right margin but also to the far left.



centages of intolerant, top carnivore, game and panfish and nest-guarding or lithophilic spawners such as northern pike decreased (Fig. 5). Out of all the vegetation variables measured, only maximum plant depth and floating plant cover were significantly associated with fish composition across the more disturbed sites. There was some separation between Lake Erie and Lake Michigan (ANOSIM $p < 0.01$, Fig. 5), but neither wetland type nor ecoprovince significantly structured fish composition across the 24 high-disturbance wetlands.

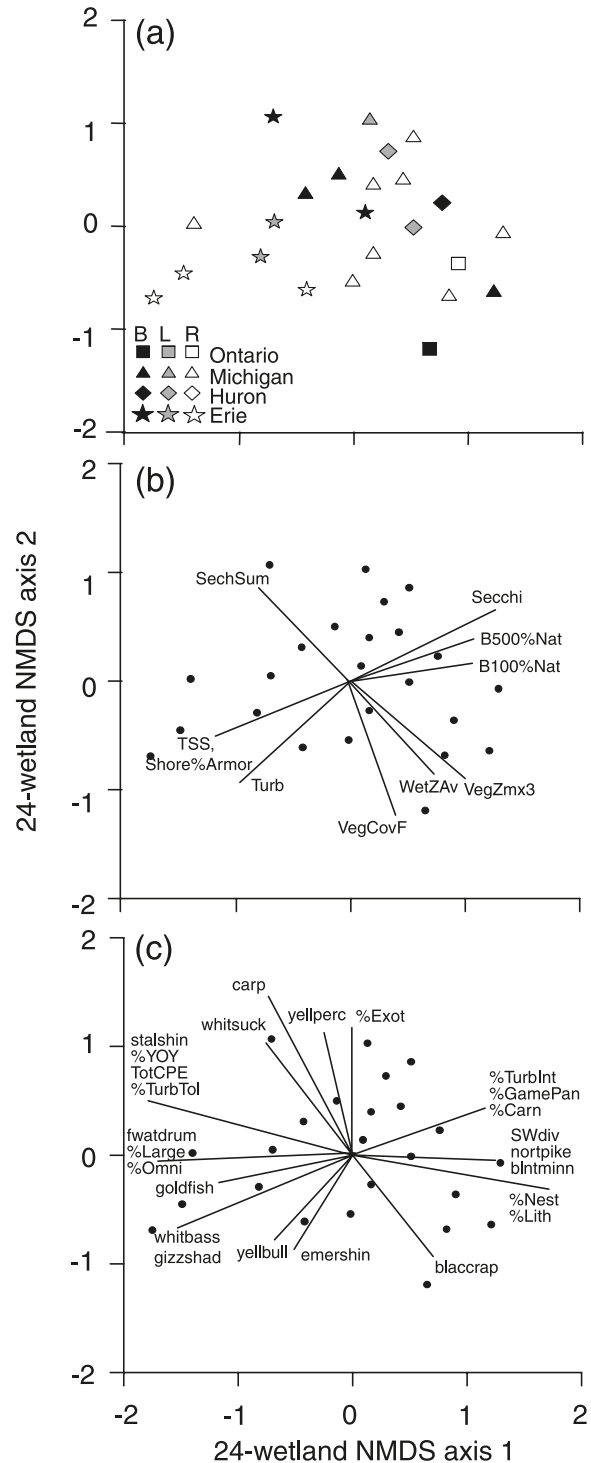
Discussion

Geographic patterning of fish composition and anthropogenic stressors

Our finding of significant lake, ecosection, and ecoprovince groupings in fish assemblages is consistent with previous studies showing geographic patterning of a variety of Great Lakes coastal wetland biota including algae, plants, macroinvertebrates, and fish (Lougheed et al. 2001; Brazner et al. 2007a). Both proximity and connectivity are no doubt important, as the two hydrologically contiguous lakes (Michigan and Huron) were also the only two between which fish composition was not significantly different. It is not clear, however, to what extent geography per se is responsible for these fish assemblage patterns, because anthropogenic activities are also geographically patterned in the Great Lakes basin (Detenbeck et al. 1999; Danz et al. 2007; Morrice et al. 2008), as confirmed here by the close alignment among vectors for anthropogenic stressors and latitude and water temperature. We saw the largest ordination spread across wetlands in Lake Michigan, which covers both the largest latitudinal gradient and the largest disturbance gradient (Niemi et al. 2007). Lake Ontario wetlands, however, were more closely clustered in ordination space than sites from any other lake, even though its latitudinal and disturbance gradient lengths are comparable to those in Lakes Erie and Superior (Niemi et al. 2007). The similarity in fish composition among Lake Ontario wetlands may be due to the relatively homogeneous habitat structure (characterized by dense, *Typha*-dominated emergent zones), which in turn may be an effect of tight water level regulation that has eliminated normal hydrologic variability (Wilcox et al. 2005).

Previous studies on fish composition in streams, lakes, and inland wetlands have found that land use measured over larger spatial scales is more generally predictive of fish patterns (e.g., Mensing et al. 1998; Strayer et al. 2003; Townsend et al. 2003), but that urbanization effects may be most evident in the immediate riparian zone (e.g., Wang et al. 2001). Results from our study are consistent with this duality in scales of influence. Across all 62 wetlands, we found little difference between the 500 m buffer and watershed-scale characterizations of land use — both were strongly correlated to fish composition — while land use in the 100 m buffer was less predictive of fish composition. Among the more disturbed wetlands, however, the amount of agriculture and urbanization in the watershed no longer distinguished sites, while the condition of the riparian buffer did. Fish composition was more degraded in these wetlands when the 100 m buffer was also quite disturbed (shoreline armoring, etc.) than when the 100 m buffer retained largely natural land cover.

Fig. 5. Patterns in fish composition across the 24 high-disturbance wetlands, as expressed in a two-dimensional nonmetric multidimensional scaling (NMDS) ordination of catch-per-effort data (stress = 0.17, variation explained = 42%). In panel (a), wetlands are coded to indicate parent lake (symbol shape) and wetland type (symbol fill; B = barrier-beach lagoon, L = lacustrine-protected, R = riverine). Wetland type and lake coding is omitted in the other two panels, which instead overlay vectors showing related environmental variables (b) or fish species and traits (c). Conventions for depicting vectors are as in Fig. 3.



Our approach of evaluating individual species by reference to their relationships with overall fish assemblage patterns gave results generally consistent with studies that directly correlated species abundances with measures of anthropogenic stress. Like Uzarski et al. (2005), Brazner et al. (2007a), and Seilheimer and Chow-Fraser (2007), we found species whose abundance most strongly increased with increasing anthropogenic disturbance to include gizzard shad, common carp, and freshwater drum. However, we found a strong negative association with anthropogenic disturbance for some taxa like golden shiner that others have described as tolerant of degradation (e.g., Simon et al. 2007).

Results in this paper are based on electrofishing CPE, ordinated with NMDS and without transformation or removal of any species. Trial ordinations with other data formats (e.g., log-transformed CPE, relative abundance) did not produce substantially different arrangements of wetlands from those reported here. Extreme dominance by gizzard shad clearly influenced details of the ordination, but the general position of wetlands was robust to the removal of this and other species having limited spatial distributions. Our experience is in distinct contrast with Uzarski et al.'s (2005) correspondence analysis-based ordination of fyke net data, in which it was necessary to remove rare and schooling species by an iterative process, after which a wetland type or lake effect was no longer evident. We are unsure whether differences in necessary data handling and results between that study and ours are due to the gear used or the ordination approach. Fyke nets catch a somewhat different fish assemblage than electrofishing, are more prone to all-or-none catches of schooling species, and give a somewhat different picture of responses to anthropogenic stressors (Brazner et al. 2007a; Chow-Fraser et al. 2007; Reutz et al. 2007). Since small and benthic fish species are more difficult to see and net when electrofishing in turbid water, it is possible that some of the apparent composition changes across the disturbance gradient are due to changes in fish detectability rather than distribution. Chow-Fraser et al. (2007) reported that electrofishing CPE declined in more eutrophic wetlands while fyke net CPE increased, but we found that electrofishing CPE increased with increasingly agricultural watersheds.

Fish-habitat relationships

Vegetation structure is recognized as a central habitat element for littoral fishes in both freshwater (reviewed in Smokorowski and Pratt 2007) and marine (e.g., Wyda et al. 2002; Saintilan 2004) environments. At a basin-wide scale, we found the strongest fish-habitat associations were with the cover and structural complexity of submerged and floating-leaf vegetation and with the water clarity needed to support that vegetation. This is consistent with earlier studies of Great Lakes wetland fishes (Brazner and Beals 1997; Höök et al. 2001; Seilheimer and Chow-Fraser 2007). Like Uzarski et al. (2005), we also found fish composition to be associated with emergent vegetation, as evidenced by contrasts between wetlands dominated by taxa that grow in very dense stands (*Typha*, *Phragmites*) versus wetlands dominated by taxa with more widely spaced stand architecture (e.g., *Schoenoplectus*, *Carex*, or *Sagittaria*). However, our metrics for emergent structure only weakly captured this

composition effect because the cover index was not a significant vector in any ordinations, and emergent growth form and structural complexity were associated with fish composition only in the low-disturbance wetlands. Emergent and submerged-floating vegetation appear to support different life stages of fish, since vectors for these two zones were aligned in different directions and with different fish attributes (young of year versus vegetation spawners) in the low-disturbance ordination.

We also found associations among fish composition and aspects of physical habitat such as sediment density, size of seiche and tributary inputs, and mean wetland depth, but with the exception of depth, these were evident only in ordinations of the low-disturbance wetlands. We had also expected to find difference in fish composition between riverine and protected wetland types, since these tend to differ in hydromorphic factors (e.g., water source, residence time, fetch; Keough et al. 1999) known to influence biota (Randall et al. 1996; Cardinale et al. 1998; Burton et al. 2004), but again we were able to resolve such differences only in low-disturbance wetlands. Hydromorphology also differs between the barrier-beach lagoon and the lacustrine-protected wetlands, but we did not find differences between these in whole-wetland fish composition. The two types of protected wetland types do, however, differ in internal variability in fish composition; at the within-wetland spatial scale, lacustrine-protected wetlands generally had more homogeneous fish composition than did barrier-beach lagoons (Treibitz et al. 2009).

Several habitat variables turned out not to be related to fish composition in any ordinations, although we had anticipated that they would be. We had thought that fetch and mouth size might be surrogates for exposure, that higher shoreline complexity might equate to higher diversity of habitat and fish, and that nearshore bottom slope and emergent zone width might affect fish composition because of earlier studies reporting such findings (Randall et al. 1996; Cardinale et al. 1998; MacKenzie et al. 2004). McNair and Chow-Fraser (2003) reported increasing benthic algal biomass with disturbance, leading us to expect a relationship of periphyton to fish composition via a common stressor gradient, if not also via a role in sheltering small fish and invertebrate food organisms. Watershed area has been found a predictor for wetland fish trait metrics in another study (Brazner et al. 2007b) and is generally correlated with tributary flow, which was a substantial vector in our ordination of the less-disturbed wetlands.

Natural disturbance can alter wetland habitat in ways that are superficially similar to anthropogenic disturbance, but our ordinations show that fish composition effectively distinguished among these cases. For example, both strong river flows and poor water clarity tend to eliminate submerged and floating vegetation, but wetland backbays and side channels remain well vegetated in the former case but not the latter. Likewise, elevated turbidity due to red-clay soils in some Lake Superior wetlands with largely natural watersheds resulted in a detectable association with fish composition, but these sites nevertheless had fish assemblages distinct from sites where poor water clarity was due to anthropogenic impacts.

Landscape–habitat linkages and effects of anthropogenic stressors

We believe that some fish–habitat relationships being evident basin-wide versus some being apparent only in low-disturbance wetlands is a consequence of how different habitat elements are affected by geography and anthropogenic stressors, rather than evidence that some factors are more important to fish than others. Studies in streams suggest that fish composition responds primarily to local habitat, but that regional setting and stressors strongly influence that local habitat (e.g., Townsend et al. 2003; Wang et al. 2003; Brazner et al. 2005). Benthic macroinvertebrates have similar habitat response scales as fish (Allen et al. 1999), and studies on them likewise highlight the importance of local habitat factors structured at larger spatial scales (e.g., Richards et al. 1997; Johnson et al. 2004; Cooper et al. 2006). Across the coastal wetlands we sampled, patterns in water quality and vegetation structure are strongly influenced by basin-wide gradients in geographic setting (climate, soils) and anthropogenic activities, while morphology and hydrology, although equally variable, are not similarly patterned. Certainly there is considerable potential for human activities to alter wetland hydromorphology, but with the exception of Metzger Marsh (which retains a connection with Lake Erie), we did not sample diked wetlands in which such alterations would be most pronounced.

Anthropogenic disturbance decouples the connections among fish composition and local habitat (Wang et al. 2003) by two distinct mechanisms. Fish composition tends to become homogenized among sites because of conditions that favor tolerant and non-native species at the expense of more sensitive indigenous fauna (Rahel 2002). Anthropogenic disturbance also disproportionately affects particular habitat elements such that these become limiting when a more diverse set of habitat elements structured fish composition beforehand. Evidence for this is provided in our study by the lack of vertical dispersion in fish composition among wetlands on the disturbed end of the ordination gradient and by the way in which a few strongly anthropogenically influenced habitat elements (water clarity, submerged vegetation) masked our ability to resolve other fish–habitat associations except in the low-disturbance wetlands.

Across the Great Lakes basin, coastal wetlands are substantially affected by a general disturbance syndrome in which increasing intensity of anthropogenic activities in watersheds (e.g., agriculture), along shorelines (e.g., urban development), and within wetlands themselves (e.g., recreational boating) lead via a variety of causal pathways (sedimentation, eutrophication, dredging, diking, shoreline hardening) to altered physical habitat (Wilcox 1995), poorer water clarity (Crosbie and Chow-Fraser 1999; Morrice et al. 2008), and degraded vegetation structure (Lougheed et al. 2001; Albert and Minc 2004; Trebitz and Taylor 2007). While this paints a powerful and coherent picture of how human activities impact coastal wetland fish assemblages (Whillans 1992; Jude et al. 2005), it also makes it difficult to disentangle proximate from ultimate causes of fish composition changes. Causative relationships between fish and habitat are difficult to establish, since factors that might not have direct importance to fish nevertheless respond to the same general anthropogenic stressor gradient. Wetland habi-

tat and fish composition no doubt always differed somewhat among the five Great Lakes because of natural differences in climate and productivity, but such patterns are at present heavily confounded with anthropogenic impacts.

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Appendix A

Table A1. List of fish species caught, name codes, and designations relative to the fish trait metrics analyzed.

Species	Code	Pattern	Angling	Size	Tolerance	Spawning	Benthic	Diet
Agnatha								
Chestnut lamprey (<i>Ichthyomyzon castaneus</i>)	cheslamp	R, L				Lyth		Carn
Lepisosteidae								
Spotted gar (<i>Lepisosteus oculatus</i>)	spotgar	R, L						Carn
Longnose gar (<i>Lepisosteus osseus</i>)	lnosegar	L		Large	T	Veg		Carn
Amiidae								
Bowfin (<i>Amia calva</i>)	bowfin	L		Large	T	Veg, guard		Carn
Clupeidae								
Alewife (<i>Alosa pseudoharengus</i>)	alewife	E			T			
Gizzard shad (<i>Dorosoma cepedianum</i>)	gizzshad	L		Large	T			Omni
Salmonidae								
Rainbow trout (<i>Oncorhynchus mykiss</i>)	raintrou	E	Game	Large		Lyth		Carn
Brown trout (<i>Salmo trutta</i>)	browtrou	E, R	Game	Large		Lyth		Carn
Brook trout (<i>Salvelinus fontinalis</i>)	brootrout		Game			Lyth		Carn
Umbridae								
Central mudminnow (<i>Umbra limi</i>)	mudminn				MI	Veg	Benth	Omni
Esocidae								
Redfin pickerel (<i>Esox americanus</i>)	redpick	L	Game	Large	MI	Veg		Carn
Northern pike (<i>Esox lucius</i>)	nortpike		Game	Large		Veg		Carn
Muskellunge (<i>Esox masquinongy</i>)	muskie		Game	Large		Veg		Carn
Cyprinidae								
Goldfish (<i>Carassius auratus</i>)	goldfish	E, L		Large	T	Veg	Benth	Omni
Spotfin shiner (<i>Cyprinella spiloptera</i>)	sfinshin	L			T			
Common carp (<i>Cyprinus carpio</i>)	carp	E		Large	T	Veg	Benth	Omni
Brassy minnow (<i>Hybognathus hankinsoni</i>)	brasminn	R				Veg	Benth	Omni
Common shiner (<i>Luxilus cornutus</i>)	commshin				T	Lyth, guard		Omni
Hornyhead chub (<i>Nocomis biguttatus</i>)	hornchub				MI	Lyth	Benth	Omni
Golden shiner (<i>Notemigonus crysoleucas</i>)	goldshin					Veg		Omni
Emerald shiner (<i>Notropis atherinoides</i>)	emershin				T	Lyth		
Blackchin shiner (<i>Notropis heterodon</i>)	bchishin				I			
Blacknose shiner (<i>Notropis heterolepis</i>)	bnosshin				MI	Lyth		Omni
Spottail shiner (<i>Notropis hudsonius</i>)	stalshin				T	Lyth		Omni
Sand shiner (<i>Notropis stramineus</i>)	sandshin					Lyth		Omni
Mimic shiner (<i>Notropis volucellus</i>)	mimishin				MI			Omni
Northern redbelly dace (<i>Phoxinus eos</i>)	nreddace					Veg		Omni
Bluntnose minnow (<i>Pimephales notatus</i>)	blntminn					Guard	Benth	Omni
Fathead minnow (<i>Pimephales promelas</i>)	fathminn					Guard	Benth	Omni
Eastern blacknose dace (<i>Rhinichthys atratulus</i>)	bnosdace	R				Lyth	Benth	Omni
Creek chub (<i>Semotilus atromaculatus</i>)	crekchub				MI	Lyth		
Catostomidae								
Quillback (<i>Carpionodes cyprinus</i>)	quillback			Large	T	Lyth	Benth	
White sucker (<i>Catostomus commersonii</i>)	whitsuck			Large		Lyth	Benth	Omni
Creek chubsucker (<i>Erimyzon oblongus</i>)	cchusuck	R, L					Benth	Omni
Bigmouth buffalo (<i>Ictiobus cyprinellus</i>)	bigbuff	L		Large			Benth	Omni
Spotted sucker (<i>Minytrema melanops</i>)	spotsuck	L		Large		Lyth	Benth	Omni
Silver redhorse (<i>Moxostoma anisurum</i>)	silvredh			Large	MI	Lyth	Benth	Omni
Golden redhorse (<i>Moxostoma erythrurum</i>)	goldredh			Large	T	Lyth	Benth	Omni
Shorthead redhorse (<i>Moxostoma macrolepidotum</i>)	shedredh			Large	MI	Lyth	Benth	Omni
Greater redhorse (<i>Moxostoma valenciennesi</i>)	gretredh	R		Large		Lyth	Benth	Omni
Ictaluridae								
Black bullhead (<i>Ameiurus melas</i>)	blacbull	R		Large		Guard	Benth	Carn
Yellow bullhead (<i>Ameiurus natalis</i>)	yellbull			Large	T	Veg, guard	Benth	Carn
Brown bullhead (<i>Ameiurus nebulosus</i>)	brwnbull			Large		Guard	Benth	Carn
Channel catfish (<i>Ictalurus punctatus</i>)	chancat		Game	Large	T	Guard	Benth	Carn
Tadpole madtom (<i>Noturus gyrinus</i>)	tadpmadt				MI	Veg, guard	Benth	

Table A1 (concluded).

Species	Code	Pattern	Angling	Size	Tolerance	Spawning	Benthic	Diet
Percopsidae								
Trout-perch (<i>Percopsis omiscomaycus</i>)	trouperc	R			MI			Carn
Aphredoderidae								
Pirate perch (<i>Aphredoderus sayanus</i>)	piraperc	R, L				Guard		
Fundulidae								
Banded killifish (<i>Fundulus diaphanus</i>)	bandkill	L				Veg		
Atherinopsidae								
Brook silverside (<i>Labidesthes sicculus</i>)	broksilv	L			T			
Gasterosteidae								
Brook stickleback (<i>Culaea inconstans</i>)	brokstic				I	Veg, guard		
Threespine stickleback (<i>Gasterosteus aculeatus</i>)	threstick	E, L			MI	Veg, guard		
Moronidae								
White perch (<i>Morone americana</i>)	whitperc	E		Large	T			Carn
White bass (<i>Morone chrysops</i>)	whitbass			Large	T			Carn
Centrarchidae								
Rock bass (<i>Ambloplites rupestris</i>)	rockbass		Pan			Lyth, guard		Carn
Unidentified sunfish (<i>Lepomis</i> sp.)	unidsunf		Pan			Guard		
Green sunfish (<i>Lepomis cyanellus</i>)	greesunf		Pan		T	Lyth, guard		Carn
Pumpkinseed (<i>Lepomis gibbosus</i>)	pumpkin		Pan			Veg, guard		
Warmouth (<i>Lepomis gulosus</i>)	warmouth	L	Pan		MI	Guard		Carn
Orangespotted sunfish (<i>Lepomis humilis</i>)	oransunf	L	Pan			Lyth, guard		
Bluegill (<i>Lepomis macrochirus</i>)	bluegill		Pan			Lyth, guard		Carn
Longear sunfish (<i>Lepomis megalotis</i>)	learsunf	R, L	Pan			Lyth, guard		
Redear sunfish (<i>Lepomis microlophus</i>)	redesunf	E, L	Pan			Guard		
Smallmouth bass (<i>Micropterus dolomieu</i>)	smthbass		Game	Large		Lyth, guard		Carn
Largemouth bass (<i>Micropterus salmoides</i>)	lmthbass		Game	Large		Veg, guard		Carn
Black crappie (<i>Pomoxis nigromaculatus</i>)	blaccrap		Pan	Large		Veg, guard		Carn
Percidae								
Iowa darter (<i>Etheostoma exile</i>)	iowadart						Benth	
Least darter (<i>Etheostoma microperca</i>)	leasdart						Benth	
Johnny darter (<i>Etheostoma nigrum</i>)	johndart					Guard	Benth	
Ruffe (<i>Gymnocephalus cernuus</i>)	ruffe	E, L			MI		Benth	
Yellow perch (<i>Perca flavescens</i>)	yellperc		Pan		T			Carn
Logperch (<i>Percina caprodes</i>)	logperch					Lyth	Benth	
Blackside darter (<i>Percina maculata</i>)	bsiddart					Lyth	Benth	
Walleye (<i>Sander vitreus</i>)	walleye		Game	Large		Lyth		Carn
Sciaenidae								
Freshwater drum (<i>Aplodinotus grunniens</i>)	fwatdrum			Large	T		Benth	Carn
Cottidae								
Mottled sculpin (<i>Cottus bairdi</i>)	mottscul					Guard	Benth	
Slimy sculpin (<i>Cottus cognatus</i>)	slimscul	R					Benth	
Gobiidae								
Round goby (<i>Neogobius melanostomus</i>)	routgoby	E				Guard	Benth	Carn

Note: Trait categories are as follows: origin–distribution pattern (E = exotic; R = rare — less than three wetlands and <1% maximum relative abundance; L = limited — not in all five lakes), desirability to anglers (game or panfish), body size (large), turbidity tolerance (T = tolerant; MI = moderately intolerant or I = intolerant (combined as a metric)), spawning behavior (nest guarding, vegetation spawning, lythophilic spawning), orientation (benthic), and diet (omnivore, top carnivore).