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Fish Assemblages and Environmental Conditions in the Lower Reaches of Northeastern Lake Erie Tributaries

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ABSTRACT. *Lake Erie and its tributaries have experienced extensive changes in environmental conditions and community structure during recent decades. To assess the relative importance of environmental conditions in determining fish community composition, fish communities and their associated environmental conditions were sampled from the lower reaches and mouths of the tributaries flowing into the northeastern basin of Lake Erie. These data were used to assess relationships between habitat and fish community composition on spatial and temporal scales using correspondence analysis and canonical correspondence analysis. Multivariate analyses revealed that the fish assemblage was size structured and related to water chemistry but also showed influences due to temperature, sampling date and aquatic macrophytes. The community composition showed the effects of biotic interactions, predominantly negative predator-prey associations, but there were also assemblage differences specific to particular tributaries and sampling methodologies.*

INDEX WORDS: *Fish community, environmental conditions, multivariate analyses, spatial and temporal variability.*

INTRODUCTION

The fish community in Lake Erie is one of the most diverse, dynamic and profitable freshwater fisheries in the world (Nepszy 1999, Johannsson *et al.* 2000). The fish community has shifted from a community with many well-represented species towards one dominated by fewer species, such as cyprinids and centrarchids (Ryan *et al.* 1999). This has been attributed to eutrophication and subsequent oligotrophication of the lake, overexploitation of fishery resources, changes in the focus of fisheries management, extensive habitat modification, and pollution (Koonce *et al.* 1996, Ryan *et al.* 1999). During the 1960s, the fish community of Lake Erie was extensively degraded, but as a result of fishery management strategies and pollution control programs (such as the Great Lakes Water Quality Agreement) beginning in the 1970s, the fish community began to flourish once again. The invasion of the Great Lakes by zebra mussels *(Dreissena polymorpha)* and quagga mussels *(D. bugensis)* has also changed the water quality and community structure of Lake Erie. Water clarity has increased, nutrient cycles have been altered, water-column chlorophyll *a* levels have declined, phytoplankton biomass has decreased, the abundance of small zooplankton has decreased, the densities of benthic invertebrates associated with mussel beds have increased, and the growth rates in benthivorous fishes have increased (Howell *et al.* 1996, Johannsson *et al.* 2000, Makarewicz *et al.* 2000). These changes in water quality and invertebrate and fish community structure have been associated with changes in fish species composition in Lake Erie, for example, declining abundances of walleye (Koonce *et al.* 1996, Kershner *et al.* 1999, Ryan *et al.* 1999).

Biological and environmental conditions in the lower reaches of tributaries and the lake confluence are important to examine as this region is heavily impacted by anthropogenic activities. Alterations to these lower reaches and stream/river mouths can have disproportionately large effects on the fish community (Christie *et al.* 1987) because they are spawning and larval retention areas for many sport and commercial fish species (Ryan *et al.* 1999). Plumes arise from spatial and temporal variability in environmental conditions (i.e., temperature, tur-

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bidity) between the river and lake, particularly in the mouths of large rivers when river flow is high (Ullman *et al.* 1998). Highly dynamic and biologically significant plume fronts from the river can affect the environmental conditions and the fish community in the nearshore (Mayer and Manning 1989, Ullman *et al.* 1998). The nearshore area of a lake is a region of high biological productivity, is heavily impacted by anthropogenic activities, and is greatly influenced by the environmental conditions in the tributaries, such as relatively higher nutrient concentrations (Nepszy 1999, Ryan *et al.* 1999). Changes in environmental conditions in the lower reaches of the tributaries and lake confluence can lead to changes in suitable fish habitat and distribution, abundance and fish community composition in the nearshore area (Koonce *et al.* 1996).

The objectives of our study are to describe the composition of the fish community and to determine the relative importance of environmental conditions structuring the fish assemblage in the lower reaches of the tributaries flowing into northeastern Lake Erie. This region is highly vulnerable to environmental changes and this study could be used as a good baseline for future comparisons.

METHODS

Study Site

Our study focused on the lower reaches and the mouths of the tributaries flowing into the northeastern basin of Lake Erie, specifically the Grand River, Nanticoke, Sandusk, and Big creeks, and Inner Long Point Bay. The Grand River is the largest tributary flowing into the northeastern basin of Lake Erie and is a highly diverse river system. The lower river is characterized by turbid conditions with high levels of suspended solids (Rott *et al.* 1998, Sharma 2004), slow to intermediate flow, and rich macrophyte coverage (Rott *et al.* 1998). Sandusk and Nanticoke creeks are smaller tributaries within large agricultural watersheds and have high suspended solid concentrations. Big Creek is the major source of nutrients and suspended solids to Inner Long Point Bay (Petrie and Knapton 1999) and the most westerly location in the northeastern Lake Erie basin.

Data Acquisition

Fish community data were collected in the lower reaches of the tributaries at the confluence of northeastern Lake Erie using boat and backpack electrofishing and seine netting between May and September 2001. Sampling was conducted by the Ontario Ministry of Natural Resources. Thirty-five sites in the lower reaches and lake confluence adjacent to Grand River, Sandusk Creek, Nanticoke Creek, Big Creek, and Inner Long Point Bay were sampled between 2230 and midnight (Fig. 1). A gradient of shorelines was sampled including sandy beach, bedrock shelf, and cobble at a variety of slopes. Each area was visited at least twice between May and September, resulting in more than 19 hours of electrofishing expenditure throughout the season and over 10,900 specimens sampled. Physical limitations to accessing sites prevented the use of a single sampling method across all areas. Boat and backpack electrofishing were used at 19 and 20 sites encompassing approximately 9.5 and 10 hours of electrofishing effort respectively. Backpack and boat electrofishing effort was defined as the number of seconds that the current was put into the water. Boat electrofishing sampling covered 500 m of shoreline per sample. Seine netting was used at two sites in the Grand River. Seine effort was defined as one sweep with a 22 m seine (0.65 cm mesh) along 25 m of shoreline. All fish within "pole-reach" were netted and transferred into a live-well. Fish were counted, identified to species level, the first twenty fish per species were measured (total and fork length), and then returned to the vicinity of capture. Unknown species were taken back to the laboratory or to the Royal Ontario Museum for positive identification. Data describing the morphology and physical habitat of the tributaries were also collected by the Ontario Ministry of Natural Resources. Variables included in data analyses were maximum water depth, minimum and maximum depths of fish sampling area and sampling date. Abundance of submergent and emergent plants, proportion of substrate comprising soft bottom, sand, or rock, bottom slope, and shoreline land use were visually assessed and categorized.

Water-chemistry surveys coincided as closely as possible, both spatially and temporally, with the fish community sampling. Five water-quality surveys were conducted by the Ontario Ministry of the Environment—Water Quality Monitoring and Reporting Branch over the nearshore and lower reaches of the tributaries in the northeastern basin of Lake Erie between April and November 2001. Both near-continuous (on a spatial scale) and discrete water samples were collected. Near-continuous field data were collected at depths of 1.5 m below the surface with readings logged at intervals

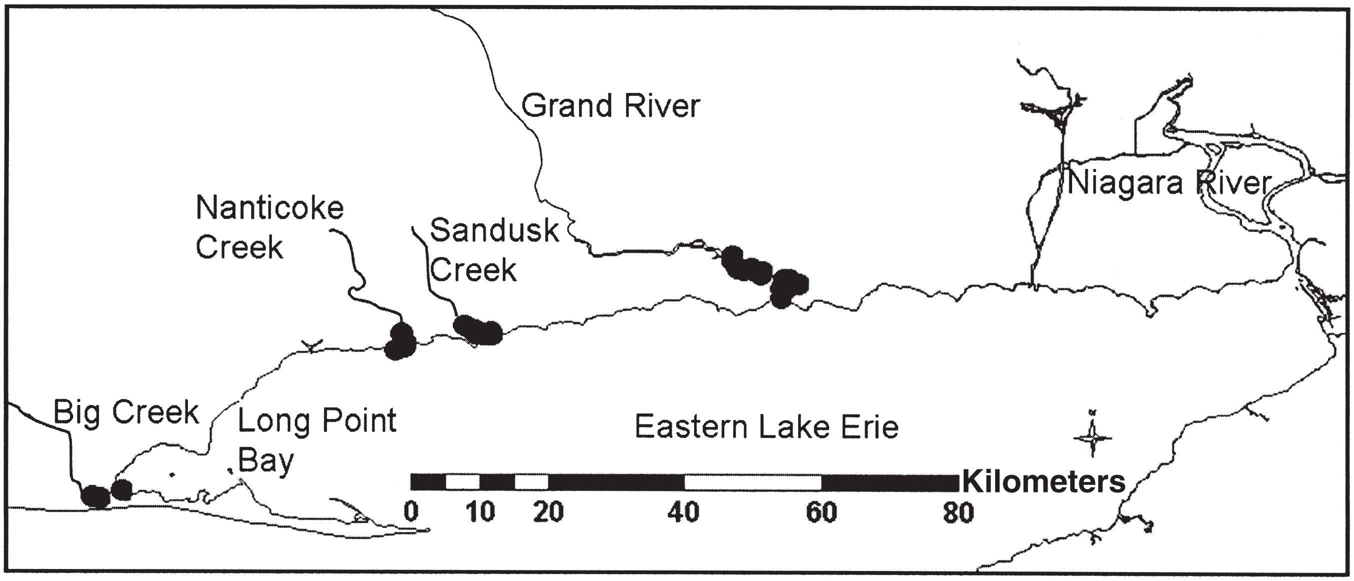

FIG. 1. Fish sampling sites in the lower reaches of Grand River, Sandusk Creek, Nanticoke Creek, and Big Creek flowing into eastern Lake Erie.

of approximately five to ten meters along a survey track. Variables measured included: latitude and longitude, bottom depth, temperature, and conductivity. Water samples (whole sub-surface grabs) were also collected along the survey track and upstream in the tributaries. Samples were taken back to the laboratory and analyzed for chloride, dissolved organic carbon, nitrates, phosphates, suspended solids, alkalinity, conductivity, pH, and chlorophyll *a*. In conjunction with the water samples, field probes were used to determine depth, conductivity, temperature, oxygen, pH, and turbidity. Water-quality parameters included in the statistical analysis were temperature, pH, alkalinity, chloride, conductivity, turbidity, dissolved organic carbon, total phosphorus, and total nitrogen. We used the mean values of the environmental variables coinciding spatially and temporally with the fish sampling area in our analyses (Sharma 2004).

Data Analysis

Fish community data were summarized as binary (presence-absence) data in order to combine collections made with all sampling techniques (Jackson and Harvey 1997) and minimize differences due to sampling by different gears. Presence-absence data provide a better representation of the fish community than species abundance data (Jackson and Harvey 1997). A standardized catch per unit effort (CPUE) could not be calculated for abundance data because different types of gears were used to sample the fish community (Jackson and Harvey 1993). The use of presence-absence data provided a dataset that contained a greater number of observations and a larger number of sampled sites than a dataset comprised of abundance data (Jackson and Harvey 1997). A total of 51 species (Table 1) from 58 sampling locations/times were included in the analyses. Nine species found in only one sample were removed prior to the analyses as rare species have a disproportionate effect on multivariate analyses (Jackson and Harvey 1989) and contribute little or nothing to understanding general community relationships. Environmental variables used in the analyses were water quality and physical habitat variables. Multicollinearity between environmental variables was tested. Variables were retained if they were deemed biologically significant and important to understanding the aquatic habitat used by the fish species.

Detrended Correspondence Analysis (DCA) was used to calculate the gradient length to determine the best ordination method to use with the data. Gradient length is a measure of unimodal species responses along an ordination axis. DCA revealed a gradient length of 2.829 and supported the use of Correspondence Analysis (CA) and Canonical Correspondence Analysis (CCA) (ter Braak and Smilauer 1998). Furthermore, the use of binary data

TABLE 1. Fish species names, code and frequency of occurrence included in the analyses. Fish codes refer to codes used in Figures 2 and 4. P/A represents presence/absence and S.U. represents sampling units for fishes sampled in the Grand River, Nanticoke Creek, Sandusk Creek, and Big Creek/Inner Long Point Bay. Rare species defined as fish that were found in only one sample were removed prior to the analyses. Rare species not included in the analyses were: alewife **(Alosa pseudoharengus)*****, grass pickerel*** **(Esox americanus)*****, pearl dace*** **(Semotilus margarita)*****, central stoneroller*** **(Campostoma anomalum)*****, Ameiurus sp., banded killifish*** **(Fundulus diaphanous)*****, black crappie*** **(Pomoxis nigromaculatus)*****, rainbow darter*** **(Etheostoma caerculeum)*****, and goldfish x carp.***

Fish code	Fish species	Scientific name	P/A: Grand R. (of 20 S.U.)	P/A: Nanticoke Cr. (of 15 S.U.)	P/A: Sandusk Cr. (of 16 S.U.)	P/A: Big Cr. (of 7 S.U.)	Abundance # of fish
	AMIIDAE—Bowfins						
bow	bowfin	*Amia calva*	4	0	2	2	10
	LEPISOSTEIDAE—Gars						
lg	longnose gar	*Lepisosteus osseus*	2	1	0	1	14
gs	gizzard shad	*Dorosoma cepedianum*	17	6	7	3	2,880
	HIODONTIDAE—Mooneyes						
me	mooneye	*Hiodon tergisus*	3	0	0	0	3
	SALMONINAE—Salmon, Trout						
rt	rainbow trout	*Oncorhynchus mykiss*	0	0	0	2	3
	OSMERIDAE—Smelts						
rs	rainbow smelt	*Osmerus mordax*	0	2	2	0	28
	ESOCIDAE—Pikes						
np	northern pike	*Esox lucius*	3	0	0	4	18
	UMBRIDAE—Mudminnows						
cmm	central mudminnow	*Umbra limi*	1	1	0	0	4
	CYPRINIDAE—Carps and Minnows						
gld	goldfish	*Carassius auratus*	15	4	10	0	411
sfsr	spotfin shiner	*Cyprinella spiloptera*	1	1	5	1	71
carp	common carp	*Cyprinus carpio*	15	7	11	5	522
mrcp	mirror carp	*Cyprinus carpio*	2	1	0	0	4
csr	common shiner	*Luxilus cornutus*	9	1	4	5	282
gsr	golden shiner	*Notemigonus crysoleucas*	0	2	0	3	35
esr	emerald shiner	*Notropis atherinoides*	16	6	2	7	2,198
bnsr	blacknose shiner	*Notropis heterolepis*	0	0	0	4	4
bnm	bluntnose minnow	*Pimephalus notatus*	3	9	12	3	1,424
fhm	fathead minnow	*Pimephalas promelas*	0	1	3	0	9
lndc	longnose dace	*Rhinichthys cataractae*	0	3	0	0	19
cc	creek chub	*Semotilius atromaculatus*	0	2	1	0	61
cyp	unidentified cyprinidae	*Cyprinidae*	2	0	1	0	56
	CATOSTOMIDAE—Suckers						
ws	white sucker	*Catostomus commersoni*	9	10	10	4	657
qbk	quillback	*Carpiodes cyprinus*	13	1	8	0	100
nhs	northern hog sucker	*Hypentelium nigricans*	2	0	0	0	2
srh	silver redhorse	*Moxostoma anisurum*	3	0	0	0	6
gdrh	golden redhorse	*Moxostoma erythrurum*	16	0	0	0	189
shrh	shorthead redhorse	*Moxostoma macrolepidotum*	16	1	1	0	113
grh	greater redhorse	*Moxostoma valenciennesi*	2	0	0	0	2

(Continued)

TABLE 1. Continued.

Fish code	Fish species	Scientific name	P/A: Grand R. (of 20 S.U.)	P/A: Nanticoke Cr. (of 15 S.U.)	P/A: Sandusk Cr. (of 16 S.U.)	P/A: Big Cr. (of 7 S.U.)	Abundance # of fish
	ICTALURIDAE—Bullhead Catfishes						
blbd	black bullhead	*Ameiurus melas*	2	1	0	0	4
bnbd	brown bullhead	*Ameiurus nebulosus*	15	5	11	4	273
ccf	channel catfish	*Ictalurus punctatus*	5	1	2	0	13
tpm	tadpole madtom	*Noturus gyrinus*	1	4	4	0	19
	PERCOPSIDAE—Trout-perches						
tp	trout-perch	*Percopsis omiscomaycus*	5	0	0	0	30
	ATHERINIDAE—Silversides						
bks	brook silverside	*Labidesthes sicculus*	3	0	0	4	10
	MORONIDAE—Temperate basses						
wp	white perch	*Morone americana*	2	0	3	0	10
wtbs	white bass	*Morone chrysops*	7	1	0	1	20
	CENTRARCHIDAE—Sunfishes						
rbs	rock bass	*Ambloplites rupestris*	5	7	2	6	67
grsf	green sunfish	*Lepomis cyanellus*	2	0	0	0	2
pksd	pumpkinseed	*Lepomis gibbosus*	5	6	6	6	115
bgl	bluegill	*Lepomis macrochirus*	4	6	3	5	223
lep	Lepomis sp.	*Lepomis*	1	6	7	1	157
smbs	smallmouth bass	*Micropterus dolomieu*	6	4	2	0	29
lgbs	largemouth bass	*Micropterus salmoides*	6	5	3	3	57
wcr	white crappie	*Pomoxis annularis*	3	0	0	0	14
	PERCIDAE—Perches						
jdt	johnny darter	*Etheostoma nigrum*	2	5	8	0	90
yp	yellow perch	*Perca flavescens*	4	5	4	7	268
lgp	logperch	*Percina caprodes*	8	2	4	1	45
bsdt	blackside darter	*Percina maculata*	0	2	0	0	3
wal	walleye	*Sander vitreus*	13	0	0	0	67
	SCIAENIDAE—Drums						
fd	freshwater drum	*Aplodinotus grunniens*	15	5	6	4	197
	GOBIIDAE—Gobies						
rg	round goby	*Neogobius melanostomus*	0	4	3	0	49

(presence-absence) is not suitable for linear-based ordination methods, these data are best analysed with unimodal methods, such as CA and CCA.

Correspondence analysis is an indirect gradient analysis approach which summarizes axes of variation from species data (ter Braak 1986). CA is not adversely affected by many zero values and can be used to summarize which sites are more similar to one another based on species composition (Jackson and Harvey 1989, Jackson 1997).

Canonical correspondence analysis is a direct gradient analysis approach in which community variation can be related directly to environmental variation. Patterns of variation in community composition that can be best explained by specific environmental variables are identified and modeled (ter Braak 1986, Borcard *et al.* 1992). CCA extracts the "best" synthetic gradients of biological communities and environmental conditions and forms a linear combination of environmental conditions that maximally separates the occurrence or abundance of particular species (ter Braak 1986, Jackson and Harvey 1993). CA and CCA were completed using Canoco 4.0 (ter Braak and Smilauer 1998).

Discernable fish community assemblages (as described by the CA scores from the first CA axis) were plotted on maps of the study regions (Grand River; Sandusk and Nanticoke creeks; Big Creek and Inner Long Point Bay) using ArcGIS 8.l. This was completed to visually assess the spatial associations of the fish community assemblages that could be related to environmental conditions *a posteriori*.

Decomposition of the various components of variation in the fish community allowed us to assess the relative importance of water quality and physical habitat variables. Partial canonical correspondence analyses were used to estimate how much of the variation in the composition of the fish community could be exclusively attributed to one set of variables, once the effect of the other set of variables (co-variables) had been taken into account. This study used the method proposed by Borcard *et al.* (1992) to decompose the sources of variation.

Five CCAs were completed in total: three CCAs and two partial CCAs, each one being constrained by varying sets of explanatory variables in order to determine the sum of canonical eigenvalues and thereby to decompose species variation. The first CCA (qp) was constrained by all of the *water quality* and *physical habitat* variables. CCA (qp) is designated by "q" representing water quality and "p" representing physical habitat. Such subscript designations hold for the remaining analyses. The second CCA (q) was constrained by the set of ten *water quality* variables. The third CCA (p) was constrained by the eleven *physical habitat* variables. The first partial CCA (q-p) was constrained by the *water quality* variables, and the variables describing physical habitat were used as co-variates in the analysis. This analysis quantified the amount of variation explained solely by water quality data and removed the influence/effect of the physical habitat of the tributaries. The final partial CCA (p-q) was constrained by *physical habitat*, and the water quality variables were used as co-variates, thereby removing the influence of water quality and only determining the amount of variation explained by physical habitat conditions in the composition of the fish community of the eastern Lake Erie basin (e.g., Borcard *et al.* 1992, Sharma 2004). Monte Carlo tests of significance were conducted on the first canonical eigenvalues and all canonical eigenvalues based on 1,000 permutations to determine the statistical significance of the first and all canonical eigenvalues.

RESULTS

Fish Community Composition

Species near the center of the CA ordination (e.g., carp (*Cyprinus carpio*), gizzard shad (*Dorosoma cepedianum*), brown bullhead (*Ameiurus nebulosus*) and white sucker (*Catostomus commersoni*)) were common and found ubiquitously (Fig. 2). Small-bodied fish species, such as several cyprinids (dace and shiners) and darters, were grouped together on the positive end of the first CA axis. Conversely, larger species like the redhorses and predatory species such as walleye (*Sander vitreus*) were positioned at the negative end of the first CA axis. Species such as the green sunfish (*Lepomis cyanellus*), rainbow smelt (*Osmerus mordax*), and rainbow trout (*Oncorhynchus mykiss*) were found at the edge of the biplot and were typically absent at most sites (Fig. 2).

Several environmental variables were associated with the fish community summarized by CA axis one (Table 2). Differences in community composition also showed distinct spatial patterns. Sites dominated by small-bodied fish species caught later in the sampling season (late summer to early fall) were characterized by higher water temperatures and DOC levels, and low alkalinity, chloride and conductivity levels. Sites dominated by larger and/or more predatory species caught earlier in the sampling season, were associated with low surface-water temperatures, low DOC levels, high alkalinity, conductivity and chloride concentrations (Table 2, Fig. 3). The Grand River was the largest and deepest tributary and contained many large-bodied fishes (e.g., walleye and redhorses), particularly near the Dunnville Dam and the mouth of the Grand River (Fig. 3a). In both Nanticoke and Sandusk creeks there were assemblages of small-bodied fish species (e.g., bluntnose minnow (*Pimephalus* notatus) and Johnny darter *(Etheostoma nigrum*)) upstream and larger-bodied species (e.g., carp and brown bullhead) near the tributary confluences with the lake (Fig. 3b). In Big Creek and Inner Long Point Bay, fishes present (e.g., brown bullhead, yellow perch (*Perca flavescens*), bluegill (*Lepomis macrochirus*), and pumpkinseed (*Lepomis gibbosus*)) were those commonly found in all tributaries (Fig. 3c).

The first CCA axis based on all environmental variables (water quality and physical habitat data) explained 21% of the species-environmental relationship and was significant ($p = 0.001$) indicating that the first and all canonical axes (also $p = 0.001$)

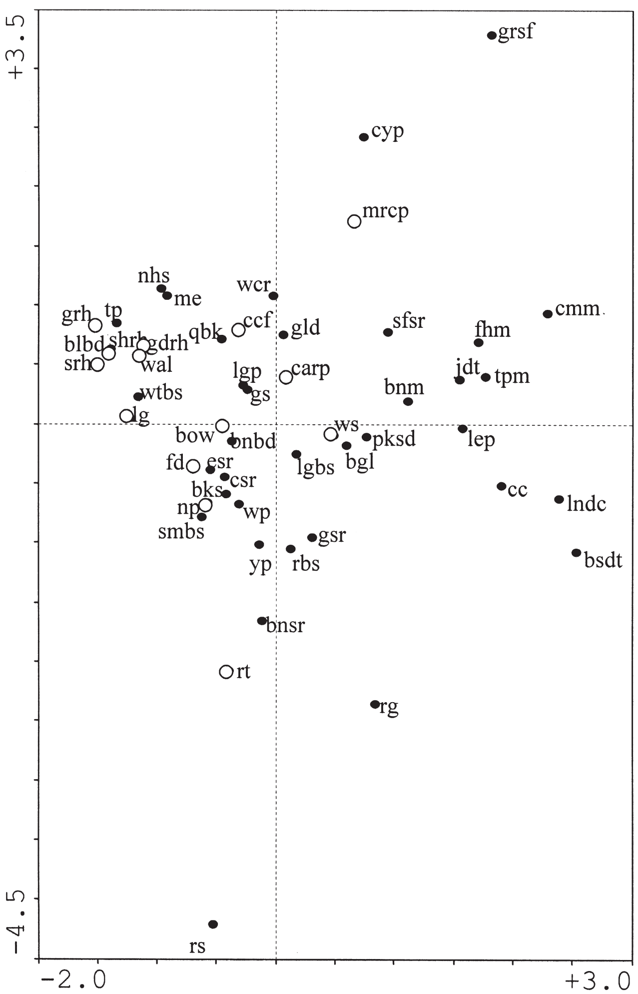

FIG. 2. Association of species based on a correspondence analysis of fish species presence-absence in the northeastern Lake Erie basin in 2001. Species located on the same end or close together on the CA axis are associated with each other whereas species found at opposite ends on the CA axis are very unlikely to be found together. Open circles represent fishes that are at least 30 centimeters long as adults (Scott and Crossman 1998). The first and second CA axes summarized approximately 12% and 7.8% of the variation respectively in species composition. (See Table 2 for codes of fish species).

significantly summarized relationships between the fish species and the environmental variables associated with those axes. As in the CA plot, small-bodied fish species were grouped on the positive end of the first canonical axis and larger and/or more predatory species were positioned on the negative end of the first two canonical axes (Fig. 4). This indicates that the community structure was similar regardless of whether the ordination of the fishes was constrained by the environmental conditions or not. Larger and more predatory species were positively correlated with conductivity and chloride levels and negatively correlated with sampling date and high abundances of submergent plants. Small-bodied fish species were positively correlated with sampling date, DOC, gradual slopes and high abundances of emergent plants and negatively with sampling depth. A temperature gradient was expressed on the second CCA axis with warmwater species together on the negative end of the second CCA axis, and cool or coldwater species more positively associated with the second CCA axis.

The results of each CCA or partial CCA and their corresponding significance tests are summarized in Table 3. For each of the analyses, the Monte Carlo test of significance based on the first canonical eigenvalue was significant ($p = 0.001$) with the exception of CCA (q-p) which was constrained by water quality and used physical habitat as co-variables, and attained a $p = 0.27$. Both the physical habitat and the water chemistry predictors explained similar amounts of variability of the fish (respectively over 34% and 30% of the fish-environment explained by the first axis). However, including the physical variables as covariates in the analysis reduced the information explained by the water chemistry to approximately 18% on axis 1 (Table 3). Approximately 52% of all variation in

TABLE 2. Correlations (and significance) of environmental variables and the fish community as described by the 1st CA axis.

Environmental variable	CA score 1
Sampling date	0.4746 ($p < 0.0001$)
Conductivity (µS/cm)	–0.4663 ($p < 0.0001$)
Alkalinity ($mg \cdot L^{-1}$)	–0.4758 ($p < 0.0001$)
Chloride concentrations ($\mu g \cdot L^{-1}$)	–0.3594 ($p < 0.01$)
Dissolved Organic Carbon ($mg \cdot L^{-1}$)	0.2836 ($p < 0.05$)
Temperature (°C)	0.2331 ($p = 0.08$)
Total phosphorus concentration ($mg \cdot L^{-1}$)	0.2053 ($p = 0.126$)
Total nitrogen concentration ($mg \cdot L^{-1}$)	0.1964 ($p = 0.143$)
Turbidity (FTU)	0.1694 ($p = 0.208$)
Suspended solids concentration ($mg \cdot L^{-1}$)	0.0877 ($p = 0.516$)
pH	–0.0848 ($p = 0.531$)
Depth (m)	–0.0809 ($p = 0.55$)

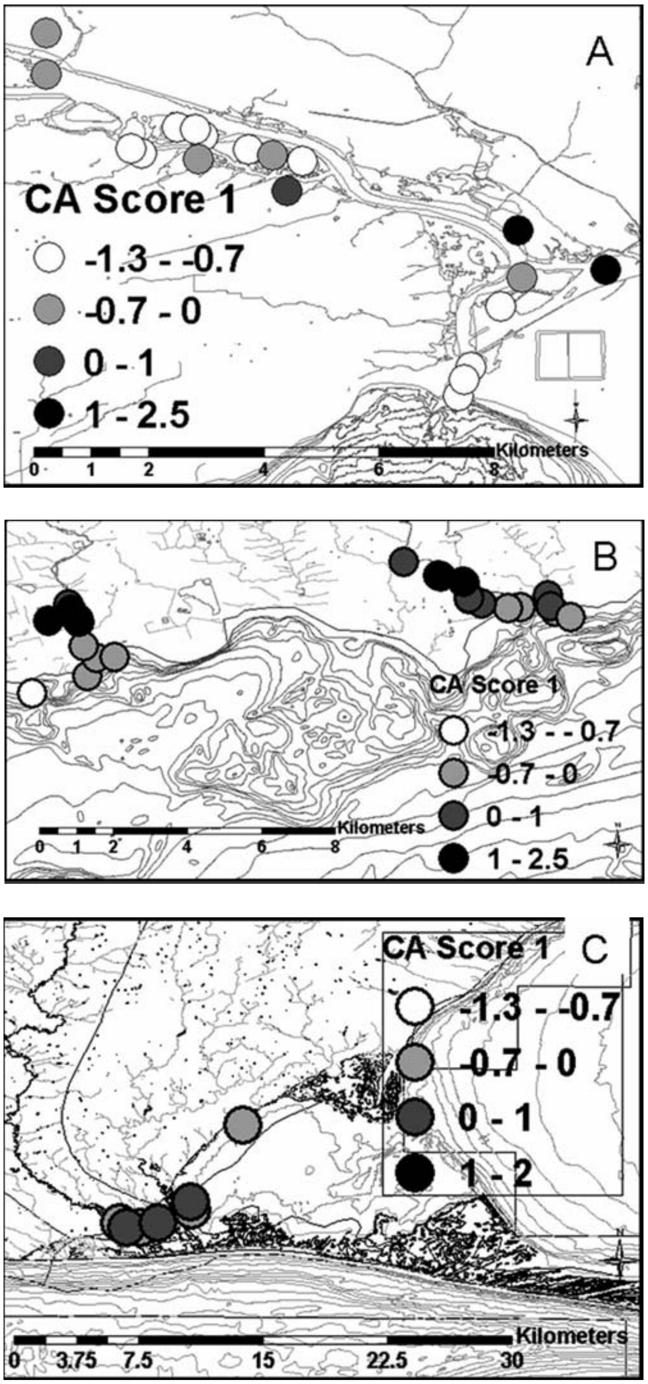

FIG. 3. (a) Similarity of sites based on fish species presence-absence in the lower Grand River. (b) Similarity of sites based on presence-absence of fish species from west Nanticoke Creek to east Sandusk Creek. (c) Similarity of sites based on presence-absence of fish species in Big Creek and Inner Long Point Bay. Black circles represent CA scores from the far positive end of the first CA axis (e.g., smaller-bodied fishes). White circles represent CA scores from the far negative end of the first CA axis (e.g., larger-bodied fishes).

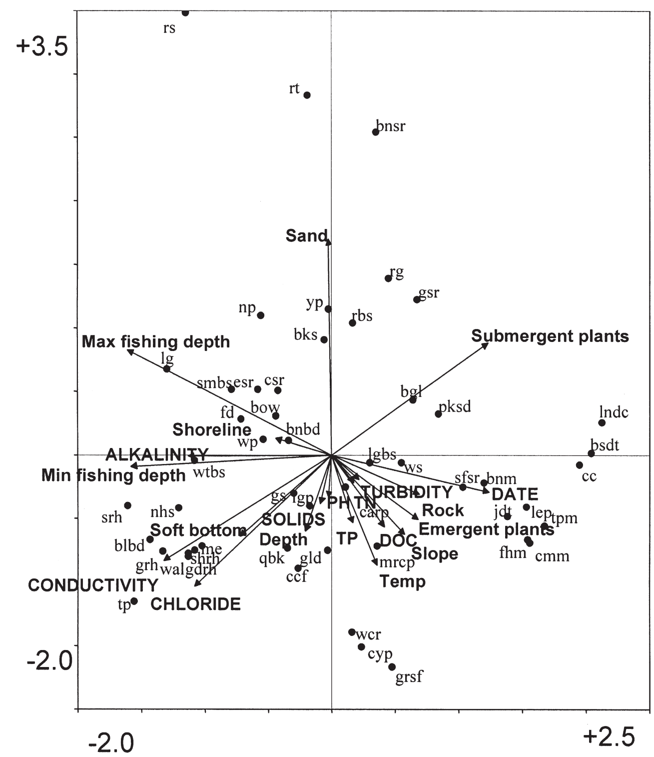

FIG. 4. Canonical correspondence analysis axes one and two, showing the association of fish species and all environmental variables based on the presence-absence of fish species. Points represent fish species and environmental variables are represented by arrows. Environmental variables that are capitalized represent water quality variables while the uncapitalized variables represent physical habitat variables. The length of an arrow reflects the importance of the environmental variable, a longer arrow represents a more important environmental variable; the direction of the arrow indicates how well species composition axes correlate with the environment; and the angle between arrows signifies the correlation between variables. Specific environmental preferences and distributions of species with respect to environmental variables are indicated by the location of species scores relative to the environmental arrows. The first and second CCA axes summarized approximately 10.9% and 6.6% of the variation respectively in species composition. (See Table 2 for fish codes).

TABLE 3. Eigenvalues and percentages of variation from canonical correspondence analysis of species presence-absence in the northeastern basin of Lake Erie in 2001 based on sets of environmental variables. Total inertia from the CA and CCA is 3.576.

CCA model evaluated	Axis eigenvalue and % variation explained		Sum of all canonical eigenvalues
	Axis 1	Axis 2	
Water quality and physical habitat	0.391* (21%)	0.234 (12.6%)	1.861* (52.4%)
Water quality	0.331* (32.5%)	0.166 (16.3%)	1.109* (28.5%)
Physical habitat	0.348* (30.2%)	0.217 (18.8%)	1.153* (32.4%)
Strictly water quality (physical habitat covariates)	0.117 (18.6%)	0.108 (17.2%)	0.629* (17.6%)
Strictly physical habitat (water quality covariates	0.209* (27.4%)	0.124 (16.3%)	0.763* (21.3%)
Variation shared between physical habitat and water quality	NA	NA	(8.7%)
Unexplained variation	NA	NA	(48%)

* $p < 0.01$

the nearshore fish community in the northeastern Lake Erie basin in 2001 could be explained by the water quality and physical habitat variables used in the analyses.

DISCUSSION

Habitat provides a good predictor of species distribution. Species will choose habitat based on both favorable abiotic and biotic factors (Henderson and Nepszy 1990, Jackson *et al.* 2001, Hampton 2004). We found physical habitat and water quality descriptors explained similar amounts of the total variation in the fish community, suggesting that a combination of water chemistry and physical habitat is structuring the fish community in the lower reaches of tributaries flowing into Lake Erie. Environmental conditions across broad spatial scales may reflect stream fish community composition (Kilgour and Barton 1999). For example, southern Ontario streams consisting of poor habitat and water quality were dominated by fish species that were more tolerant of degraded conditions (Kilgour and Barton 1999). Biotic interactions, such as competition and predation may also affect community composition (Jackson *et al.* 2001) and contribute to the size-structured patterns of composition noted.

Size-structured interactions between fish can be influenced by changes in thermal conditions along tributary-lake gradients (Magnuson *et al.* 1979, Schlosser *et al.* 2000). This is due to a combination of factors including physiology and development of fish species, in addition to predator-prey relationships (Schlosser *et al.* 2000). At a local scale, competition for resources and space between and within species may contribute to changes in fish distribution and community structure (Resetarits 1997, Jackson *et al.* 2001). Through direct and indirect mechanisms, predation can have a very strong effect on fish community composition. Size-selective predation can lead to changes in the size and structure of the fish community (Knight and Vondracek 1993). Predatory activity may alter fish distribution because fishes may move to structurally more complex habitats to decrease their risk of predation (Jackson *et al.* 2001, Pratt and Fox 2001). Scheuerell (2004) found that predators and prey were negatively associated at night and at large spatial scales. This was attributed to foraging by predators and predator avoidance by prey. In our study we found a predominance of negative predator-prey associations.

There also appeared to be species associations based on physical habitat preferences, such as depth and macrophyte coverage. The Lake Erie fish community composition has been associated with availability of suitable habitat (Nash 1950, Henderson and Nepszy 1990). Lake morphology and habitat heterogeneity largely contributed to the structure of the fish community of Lake Erie (Henderson and Nepszy 1990). Composition of fish communities in southern Ontario streams have been significantly correlated to natural environmental gradients, including water temperature and percent forest cover (Kilgour and Barton 1999). Emergent plants in the water column could be beneficial to small-bodied fish species to escape predation. Intermediate amounts of diverse and patchy macrophyte coverage are optimal to promote high fish species diversity because fish are attracted to the increased habitat heterogeneity provided by macrophyte coverage (Brazner and Beals 1997). However, very high abundances of macrophytes can yield suboptimal conditions for fish since these regions can often be characterised by reduced foraging efficiencies, and are areas with higher water temperatures and lower dissolved oxygen levels (Brazner and Beals 1997, Olson *et al.* 1998).

Differences in tributary characteristics were strongly associated with fish community composition. A study in the Mississippi River basin demonstrated that fish community function was different based on tributary size, suggesting that large rivers are composed of different fishes than small streams and rivers (Goldstein and Meador 2004). In lower Michigan streams, fish composition was related to tributary size (Zorn *et al.* 2002). In our study, walleye, redhorses, and bowfin are all larger or predatory species found in larger rivers or lakes and were only found in the Grand River, the largest tributary in northeastern Lake Erie. The mouth of the Grand River is deep, turbid, and has a very high abundance of cattails (*Typha* spp.) and the conditions in the region may account for the presence of large-bodied species being found in the Grand River. Small-bodied fishes, such as the cyprinids and darters, were associated together in shallower regions, for example, upstream in Sandusk and Nanticoke creeks, whereas larger species were found at the creek mouths. Upstream, the substrate was composed of hard riffle. The mouths of the creeks were composed of hardened muddy substrates and had a large prominence of cattails. The change in fish community composition from small-bodied fish species to larger, predatory fishes in the Nanticoke and Sandusk creek region may be due to predator-prey relationships and changes in habitat characteristics. Differences in water depth and substrate likely led to the difference in large-bodied species being found downstream relative to the small-bodied fishes upstream. Small-bodied species may reside in areas affording greater protection through shallow depth or complex substrate (Jackson *et al.* 2001).

In our study, there were fish assemblages of warmwater (e.g., smallmouth bass and freshwater drum), coolwater (e.g., northern pike and yellow perch), and coldwater species (e.g., rainbow smelt and rainbow trout found in the Grand River to spawn in the spring). Water temperature appear to be an important factor structuring fish communities in these tributaries and this is consistent with results of Kilgour and Barton (1999) who found the distribution of stream fishes in Southern Ontario was primarily associated with water temperature and forest cover. In the tributaries flowing into western Lake Superior, water temperature strongly influenced the association of fish species (Brazner *et al.* 2005). Thermal preferences and stream size determined fish community composition in lower Michigan streams (Zorn *et al.* 2002).

Historical reductions in riparian vegetation along the Grand River, Sandusk Creek, Nanticoke Creek, and Big Creek watersheds have likely contributed to increased water temperatures and may have changed the dynamic of the fish community by favoring more warmwater species in the region (Kilgour and Barton 1999). Considerable demand for water exists within the basin due to withdrawls for municipal and irrigation use, which have led to reductions in groundwater levels (de Loe *et al.* 2001). Increasing the relative amounts of groundwater flowing into tributaries and reducing the amount of damming and impounding would decrease summer water temperatures, thereby providing coolwater fish refuge in the summer and potentially supporting a more diverse fish community (e.g., Colby *et al.* 1994, Koonce *et al.* 1996, Bunt *et al.* 2000). Warmer temperatures and declining water levels as a result of climate change may result in drying of tributaries, reduced access to spawning sites, and increased turbidity levels (Meisner *et al.* 1987). It is most likely that Sandusk Creek and Nanticoke Creek will experience the greatest change from reductions in base flow or increased hydrologic "flashiness" and therefore their fish communities being most affected.

Although fish occurrence (presence-absence) data were used in the analyses, sampling methodologies (i.e., sampling gear and sampling time) may influence the fishes sampled, and thereby the observed fish community associations (Lester *et al.* 1996, Jackson and Harvey 1997). Biases may be incurred toward catching larger fishes rather than smaller ones, as well as decreased efficiency of catching fish in structurally complex habitats (Meador *et al.* 2003). Electrofishing methods are size selective and tend to select larger fish, both intraspecifically and interspecifically (King and Crook 2002, Meador *et al.* 2003, Tate *et al.* 2003) thereby biasing catches of different species of fishes (Kelso and Minns 1996).

In deeper areas of tributaries (for example, in the lower reaches of the Grand River and the mouths of Nanticoke, Sandusk, and Big creeks), boat electrofishing methods were employed. In these regions, there were greater abundances of large-bodied fish sampled and it is possible that the small-bodied species were underrepresented relative to the larger ones simply due to the differences in the way fish are affected by shocking and their visibility to netters. Backpack electrofishing was used upstream in Nanticoke, Sandusk, and Big creeks where conditions were shallower and precluded the use of boat electrofishing. During these sampling efforts, smaller-bodied fishes were caught later in the sampling season, most likely because they were too small to be caught earlier in the sampling season or by boat electrofishing methods. Later in the sampling season, the majority of sampling was done using backpack electrofishing methods mainly focused in Nanticoke and Sandusk creeks. This may have contributed to the increased presence of smaller-bodied fish species later in the sampling season. Size within fish species was generally not different over time and therefore patterns of species distribution cannot be directly attributed to patterns of recruitment of young-of-year fish. The difference in large-bodied species being found downstream relative to the small-bodied fishes upstream may be attributed to the differences in water depth and sampling protocol. Our treatment of the data as simply species presence-absence data reduces the potential for bias to be introduced due to different sampling methodologies. Different sampling protocols may lead to bias in the relative numbers captured, and hence differences in the perceived catch-per-unit-effort, which would contribute to differences had we used species relative abundance data in our analyses. However, as we used species presence-absence data, these among gear biases are either eliminated or reduced substantially.

Improving water quality is one of the most-proven methods of restoring fish habitat for native species (Colby *et al.* 1994). In the lower reaches of the tributaries flowing into Lake Erie, water quality improvements will be due to both nutrient and sediment reductions, in addition to maintaining suitable base-flow within the tributaries (e.g., increasing groundwater input). Future changes in environmental conditions, either natural or anthropogenic, may lead to changes in the fish community (Colby *et al.* 1994, Kershner *et al.* 1999). The continued establishment of exotic species is likely and their interaction with potential land-use changes and climate change is unpredictable. Clearly, change in Lake Erie is a given, but the trajectory of such change is unknown.

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