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Source: Freshwater Science, 33(4) : 1159-1173

Published By: Society for Freshwater Science

URL: https://doi.org/10.1086/678228

Linking the land and the lake: a fish habitat classification for the nearshore zone of Lake Ontario

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Abstract: The nearshore zones of the Great Lakes provide essential habitat for biota and are perhaps the region of the lakes most susceptible to human impacts. The objective of our study was to develop a fish habitat classification for the nearshore zone of Lake Ontario based on physical characteristics of that zone, land cover in the surrounding watershed, and fish community patterns. Nearly 80% of the spatial variation in fish community data was described by 2 physical variables (average fetch and bathymetric slope of the nearshore zone) and 2 land-cover variables (urban/industrial development and mixed forest cover) in adjacent watersheds. These variables are likely to be surrogates for other conditions in the nearshore, such as wave action, circulation, vegetation, and water quality. A 12-group fish habitat classification was developed from those variables. Validation and significance tests identified similarities and differences among the fish communities in the classes and indicated that the number of classes should be collapsed to 3: exposed, sheltered, and developed/urbanized. In general, the western basin of the lake was developed, the central region was exposed, and the eastern region of the lake was a mix of exposed and sheltered classes. These results highlight that even in lakes as large as Lake Ontario, the nearshore fish community is influenced by watershed land cover, and emphasize that management or restoration of the nearshore ecosystem in lakes will require integration of aquatic, watershed, and land-cover management.

Key words: Lake Ontario, fish habitat classification, nearshore, fish communities, land cover, Great Lakes

The nearshore zone of a lake provides essential habitat for biota and is the link between the terrestrial watershed and open water. It is the region of the lake that is most affected by human stressors, such as polluted runoff, altered stream discharge, regulated water-level fluctuations, dredging, shoreline hardening, and infilling in adjacent watersheds and in coastal areas (Goforth and Carman 2005, IJC 2009). The health and productivity of the nearshore zone strongly affect the quality of life for Great Lakes human communities and economies. Despite the importance of the nearshore zone, research and management actions in the Great Lakes have been focused on offshore or terrestrial programs (IJC 2009). The International Joint Commission (IJC) recently identified the nearshore zones of the Great Lakes as priority areas under the recently ratified Canada–United States Great Lakes Water Quality Agreement (IJC 2009, IJC 2012).

In Lake Ontario, significant physical, chemical, and biological changes have occurred and continue to occur in the nearshore zone. The physiochemical changes include shoreline hardening, water-level regulation, and increased water clarity. Thirty to 40% of the shoreline has been hardened with sheet piling, riprap, and steel and concrete walls (Lake Ontario Biodiversity Strategy Working Group 2009). Water-level fluctuations are dampened from their natural regimes to prevent flooding, provide dependable flow for hydropower, and offer adequate depths for navigation (IJC 2006). Since 1968, water clarity has increased with average Secchi depths rising by 3.1 m (Dobiesz and Lester 2009). This change has been facilitated by implementation of P controls as part of the 1972 Great Lakes Water Quality Agreement (GLWQA) and establishment of zebra mussels, *Dreissena* spp., in the 1990s (Mills et al. 2003). Point-source and nonpoint-source (e.g., diffuse runoff from urban or agricultural areas) discharges of suspended solids, bacteria, nutrients, metals, trace organic contaminants, and chemical by-products also degrade nearshore water quality (OMOE 1999).

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DOI: 10.1086/678228. Received 1 December 2012; Accepted 12 March 2014; Published online 14 August 2014.
Freshwater Science. 2014. 33(4):1159–1173. © 2014 by The Society for Freshwater Science.

These physiochemical changes have had biological consequences. Dampening of water level fluctuations has inadvertently reduced the area, quality, and functioning of coastal wetlands, and some wetlands have become monocultures of *Typha* spp. and *Phragmites australis* (Keddy and Reznicek 1986, Wilcox et al. 2003). The degradation of water quality at river outlets has facilitated blooms of nuisance alga, such as *Cladophora*, and toxic species, such as the bacterium *Clostridium botulinum*, recently linked to increases in fish and bird mortality in lakes Ontario and Erie (Hecky et al. 2004). Human communities around the lake are projected to increase from 7.8 million in 2001 to 11.5 million by 2031 (OMOI 2012), so these types of physiochemical and biological changes will continue to affect the nearshore ecosystem.

Authors of past studies have classified the nearshore zone of Lake Ontario to highlight regional similarities and differences and to provide a common language for management (Gregor and Rast 1982, Busch and Lary 1996, Rutherford and Geddes 2007). Gregor and Rast (1982) subdivided the nearshore zone into 27 regions based on physical conditions and amalgamated those 27 subdivisions into 3 trophic classes based on chlorophyll *a* (Chl*a*), and total P (TP) concentrations, and Secchi depth (Table 1). They classified most of the nearshore zone as mesotrophic but more eutrophic near the outlets of rivers and urban areas, specifically near the Niagara River and urban centers (Gregor and Rast 1982). Busch and Lary (1996) classified the nearshore zone into 4 main classes: shoreline and littoral zone, wetlands, tributaries and embayments, and special features. These classes were further subdivided based on physical features and characteristics of the vegetation (Table 1). Rutherford and Geddes (2007) clustered sites based on bathymetry, slope, mean summer daily temperature, substrate, and proximity to major river mouths into 2 groups (Table 1). Most of the north shore was clas-

Table 1. Classifications developed for the nearshore of Lake Ontario.

Source	Nearshore boundaries	Class	Subclass
Gregor and Rast (1982)	0–30 m	27 classes	Delineations based on presence of urban area on shoreline, areas of serious erosion on shoreline, extractive areas of mining industries on shoreline, inlets or embayments, and general nearshore circulation patterns, depth of thermocline, and homogeneous water quality in nearshore area
Busch and Lary (1996)	0–25 m	Shoreline and littoral zone	Active sand dune
			Erodible bluff
			Erodible plain
			Nonerodible bluff
			Nonerodible plain
			Relict sand dune
			Upland
		Wetlands	Open water, connected
			Not connected
		Tributary and embayments	Embayment, restricted
			Embayment, tributary dominated
			Tributary reach
		Special features	Artificial fill/break wall
			Artificial island
			Artificial shoal <25 m
			Artificial spit/jetty
			Barrier structures
			Offshore bar/lagoon
			Pond
			Rocky outcrop
			Shoal/reef <25 m
Rutherford and Geddes (2007)	0–15 m	1	Not close to river, deep, highly sloped, cool
		2	Close to river, shallow, gently sloped, warm

sified as "not close to river, deep, highly sloped, cool", whereas the south shore was classified in the same class or in a 2^{nd} class, "close to river, shallow, gently sloped, warm". To date, no classification for Lake Ontario has included characteristics of the surrounding watershed that could influence physical, chemical, and biological properties of the nearshore zone or has included fish.

Given the importance of the nearshore environment in Lake Ontario and the increased emphasis on this environment in the 2012 revised GLWQA (IJC 2012), our objective was to develop a fish habitat classification for the nearshore zone based on physical characteristics, land cover in the surrounding watershed, and fish community patterns. Physical and land-cover data were available for the entire (US and Canadian) nearshore zone of the lake, but fish community data from only the Canadian side of the lake were used to identify the characteristics associated with fish community composition. Results were used to develop the fish habitat classification, and fish community data from some regions on the American side of the lake were used to validate the classification.

METHODS

Study area

Lake Ontario is the smallest of the Great Lakes and has a surface area of 18,960 km^2 and a volume of 1640 km^3. The mean depth is 86 m with a maximum depth of 244 m. Approximately 79% of the water flowing into Lake Ontario comes from Lake Erie through the Niagara River. The remaining flow comes from the basin's tributaries (14%) and precipitation (7%) (Lake Ontario Biodiversity Strategy Working Group 2009). Land cover in the basin is dominated by agriculture and forest lands with several urban centers. The lake provides drinking water to almost 8 million residents and supports commercial, aboriginal, and recreational fisheries (Lake Ontario Biodiversity Strategy Working Group 2009).

Spatial units

Our study was based on data from 4 different spatial units: the nearshore zone, nearshore reaches, sites, and watersheds. The nearshore zone has been defined in different ways to account for differences in physical processes affecting nearshore ecosystems, e.g., wave action, circulation, and temperature (see Mackey 2009, McKenna and Castiglione 2010). In our study, the nearshore zone was defined as the region of the lake beginning at the shoreline (74.2 m asl based on the International Great Lakes Datum 1985; USACE 1991, Minns et al. 2005) and extending to the depth of the thermocline in late summer (~20 m deep; Edsall and Charlton 1997). The physical characteristics of the nearshore were obtained from the Lake Ontario Habitat Supply Analysis database (LOHDb; unpublished data), in which the nearshore zone of the whole lake (including islands) is divided into ~2500 1-km reaches (Stewart 2003, Minns et al. 2005). Each reach has a length equal to 1 km of shoreline and width equal to the distance from the shoreline to the 20-m depth contour. Fish communities were sampled at the site level, and some reaches had multiple sites. Land-cover data were summarized for the quaternary (Canadian) and equivalently sized Hydrological Unit Code (HUC 8; American) watersheds draining directly into the lake. The quaternary and HUC-8 watersheds are part of a hierarchy of major drainages and watersheds in North America (OMNR 2002, USGS 2011), and each typically encompasses 1 major tributary of the lake.

Data layers

Data describing the physical characteristics, watershed land cover, and fish communities in the nearshore zone were used to develop the fish habitat classification. Physical data (average fetch, water temperature zone, slope, and presence/absence of wetlands) were obtained from the LOHDb for 2454 1-km reaches (Minns et al. 2005; Table 2). Geology of the shoreline (0 m) and nearshore (0–20 m deep) were available for each reach (Stewart 2003; Table 2).

The Ontario Provincial Land Cover 2000 (OMNR 2000) was crosswalked with the US National Land Cover Dataset (NLCD; Homer et al. 2007) to produce a raster with consistent land-cover types surrounding the lake. Canadian quaternary and American HUC-8 watershed boundaries were overlaid onto the land-cover raster using ArcGIS® (version 9.0; Environmental Systems Research Institute, Redlands, California). Zonal statistics were used to calculate the proportions of different land-cover types within each watershed (Table 2).

Each 1-km reach was spatially joined to the overlapping watershed boundary to produce an estimate of land-cover conditions upstream. In cases where a reach spanned 2 watersheds, attributes of the dominant watershed were assigned to that reach. In no case was 1 reach shared equally by 2 watersheds. Twenty physical and land-cover variables were used to describe nearshore reaches (Table 2). Proportions of sparse forest, mine tailings, quarries, bedrock outcrop, and settlement and developed land were arcsin(x)-transformed to attain normality (Zar 1996). A Pearson correlation of the continuous variables (average fetch, slope, and land cover) identified highly correlated variables ($r \geq 0.7$). Variables correlated with ≥2 other variables were retained and the correlates were removed. When only 2 variables were correlated, 1 of the pair was randomly removed. Contingency tables were used to evaluate the associations among the categorical variables (temperature zone, shoreline geology, nearshore geology, wetland presence). Temperature zone was associated with shoreline geology and nearshore geology. Therefore, tem-

Table 2. Definitions of physical and land-cover variables used to describe the nearshore zone (0–20 m) of Lake Ontario (OMNR 2000, Stewart 2003, Minns et al. 2005). Land cover in the draining watershed for each reach was calculated as the proportion of the total watershed area with each land-cover type.

Physical or land-cover variable	Abbreviation	Description
Physical		
Average fetch (km)	AVGFTCH	Average unobstructed distance to the furthest point of land for each reach
Water temperature zone	TEMP	Five-group description of the deviation of each reach from the mean lake surface temperature (codes: 1, 2, 3, 4, and 5, which equal deviations of −1.0, −0.5, 0, +0.5 and +0.75, respectively)
Slope (m asl)	SLOPE	Shallow reaches with gradual slopes had average depths close to 74 m asl, whereas reaches with values close to 52 m asl had steep profiles; 52 m asl corresponds to the 20-m depth contour or lower extent of the nearshore zone
Presence of wetlands	WET	Wetland present (1) or not present (0)
Nearshore geology	NGEOL	Geological conditions (codes represent till, clay, leda clay, cobble/boulder, sand, bedrock, creek/river/harbor sediments) between 0–20 m depth (Stewart 2003)
Shoreline geology	SGEOL	Geological conditions at the shoreline (codes represent sand/bluffs, marine/leda clay, low, bank, barrier complex, sandy beach, coarse beach, bedrock, open shoreline wetlands and artificial) (Stewart 2003)
Land cover		
Water	WAT	Rivers and lakes
Freshwater marsh	MARSH	Marshes occurring on lakeshore
Swamp	SWAMP	Hardwood swamps and swamps with dense coniferous tree or shrub cover
Fen	FEN	Grassy or treed fen
Bog	BOG	Nontreed or treed bog
Dense forest	DENSEF	Continuous forest with 80% deciduous or coniferous species cover and coniferous plantations
Mixed forest	MIXEDF	50% of canopy is deciduous or coniferous species
Sparse forest	SPARSEF	Patchy or sparse forest canopy with 30–40% deciduous or coniferous species
Recent cutovers and burns	RCUT	Forest clear-cuts <10 y old
Old cuts and burns	OCB	Cuts and burns >10 y old
Mine tailings, quarries, and bedrock outcrop	MINE	Clearings for mining, quarries, and bedrock outcrops
Settlement and developed land	DEVE	Clearings for human settlement
Pasture and abandoned fields	PAST	Open grassland
Cropland	CROP	Agriculture

perature zone and wetland presence/absence were retained for subsequent analyses. Analysis of variance was used to test for differences among categorical and continuous data. Temperature zone was correlated strongly with slope and was removed. This process resulted in 9 variables for subsequent analyses (Table 3).

Physical, land cover, and fish community data for the Canadian side of the lake were used to develop the fish habitat classification. Data from the American side of the lake were used to validate the classification. Fish catch data (presence/absence) were compiled from several agencies conducting research in the Canadian nearshore zone. In total, 1136 sites were sampled (Fig. 1), and 74 fish species were caught using a variety of gear from May to October 2000–2010 (Appendices S1, S2). Species distributions vary seasonally, but the assumption was made that if a species was caught at a site, that site offered suitable habitat. Sites were sampled in different years from 2000–2010, so it was not possible to determine if species captured at any specific site varied temporally in a predictable manner.

Fish community data came from several agencies and were collected for different purposes, so multiple gear

Table 3. Descriptive statistics and results of canonical correspondence analysis for the 9 physical and land-cover variables used to develop a fish habitat classification of the nearshore zone of Lake Ontario. Bold indicates variables used to develop classification. See Table 2 for abbreviation definitions.

Variable	Minimum	Mean	Maximum	Axis 1	Axis 2
AVGFTCH	0.01	13.60	52.00	**0.98**	–0.12
SLOPE	52.00	63.24	79.58	**–0.54**	–0.05
WET		Categorical		0: –0.1	0: –0.05
		(0 = absent, 1 = present)		1: 0.1	1: 0.05
MARSH	0.00	0.01	0.09	–0.35	–0.39
DENSEF	0.01	0.11	0.26	0.13	–0.42
MIXEDF	0.01	0.07	0.28	–0.22	**–0.71**
MINE	0.0	0.01	0.06	–0.13	–0.34
DEVE	0.01	0.13	0.94	0.23	**0.83**
CROP	0.02	0.35	0.77	0.23	–0.02
Eigenvalue				0.41	0.1
Cumulative percentage				65.1	80.8

types were used at different sites and were used in different proportions among agencies. Each gear type may bias for collection of certain species, but the assumption was made that pooling all gear types within a site would provide a more robust estimate of fish community richness than limiting data analysis to any particular gear type.

In addition to the multiagency effect on fish gear types, the possibility existed that similar locations had been sampled repeatedly. The potential spatial autocorrelation was addressed by delineating 150-m buffers (approximate length of gillnet and electrofishing transects) around each site in ArcGIS. Sites that overlapped were merged into a single site and species caught at those sites were pooled to make a single species list for that site. Combining overlapping sites reduced the original 1136 sites to 958 sites. Sites were each associated with the nearest 1-km-long nearshore reach in ArcGIS.

Only 420 of the 1600 1-km reaches (26%) on the Canadian side of Lake Ontario had fish sampling sites. The number of sites sampled per reach was plotted against

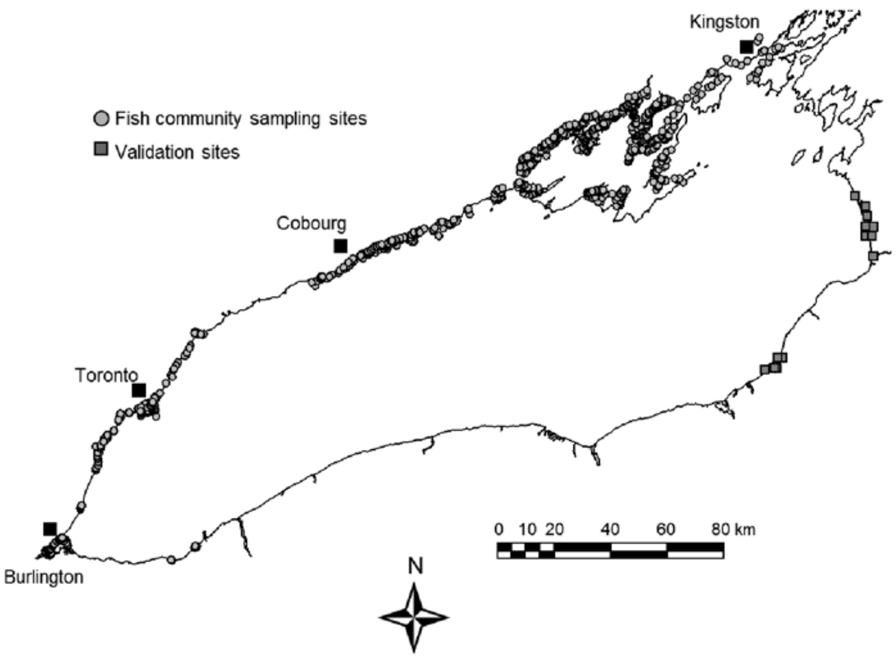

Figure 1. Sampled and validation sites used to examine the relationships among fish community composition and physical and land-cover characteristics of the nearshore zone and its watershed and to develop a nearshore fish habitat classification for Lake Ontario.

species richness to test for a sample–richness relationship (Fig. 2A, B). Results indicated that species richness in each reach increased with the number of sites sampled. Therefore, reaches with ≥2 sampled sites were used in the analyses (Fig. 2B). Two sites were selected at random when a reach had >2 sampled sites. This procedure further reduced the data set to 177 reaches (11%) retained for analysis. Species lists for the 2 sampled sites were combined into 1 list of species present in each reach.

Reaches represented 1-km delineations of the nearshore zone and fish may inhabit areas >1-km segments, so φ coefficient values based on species presence/absence were calculated for all pairwise combinations of reaches ≤50 km apart. φ coefficients were used to decide whether the 1-km reaches should be grouped into larger segments. The φ coefficient measures the strength of the association between dichotomous variables, such as species present at different sites (Jackson et al. 1989), and is calculated as:

$$\varphi = \frac{ad - bc}{\sqrt{(a+b)(a+c)(b+d)(c+d)}} \qquad \text{(Eq. 1)}$$

from a presence–absence matrix where presence = 1, absence = 0, and a = 1,1, b = 1,0, c = 0,1 and d = 0,0. Values typically range from −1 to +1. φ coefficients are less sensitive to the frequency of species occurrences than are other community similarity indices, such as Jaccard or

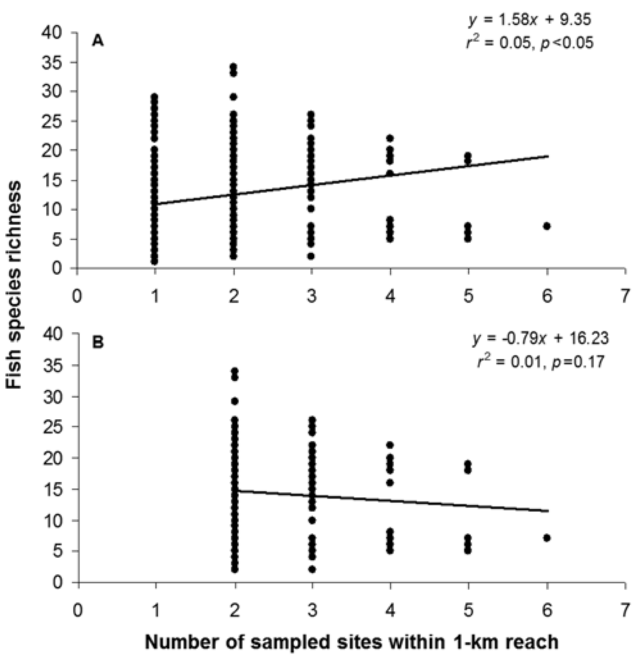

Figure 2. Fish species richness in relation to the number of sites sampled within 1-km reaches of the Lake Ontario nearshore zone at all reaches (A) and at reaches sampled >1 time (B).

Sørensen–Dice indices (Jackson et al. 1989). φ values decreased slightly as distance between reaches increased, but a clear threshold distance that could be used to cluster the reaches was not detected ($y = 0.0002x + 0.3001$, $r^2 = 0.01$). Therefore, data at the 1-km reach scale were used for analysis. φ values were calculated in XLSTAT (version 2012.06.04; AddinSoft, New York).

Classification

Detrended Correspondence Analysis (DCA) of the species presence–absence data was used to assess whether linear or unimodal ordination techniques should be used to relate the fish communities to their environment. DCA commonly uses reciprocal averaging to maximize the correlation between species and sample sites (Hill and Gauch 1980). The scores are detrended and rescaled to produce estimates of species diversity along the DCA axis. Ordination results can be used to identify species commonly found together or to visualize how species composition differs among sites (Hill and Gauch 1980, Lepš and Šmilauer 2003). The axes (gradient length), can be used to determine whether linear or unimodal ordination techniques are appropriate. Values >4 SD (species turnover) units indicate that unimodal ordination techniques should be used to relate species composition to the environmental data (Lepš and Šmilauer 2003).

Gradient lengths for the fish community data were >6 SD. Therefore, canonical correspondence analysis (CCA) was used to identify the environmental variables that described the variance in the fish community data. CCA is a direct gradient technique that uses species occurrences or abundances (e.g., counts of individuals) and data on environmental variables at sites to extract from the measured environmental variables synthetic gradients (ordination axes) that maximize the niche separation among species (ter Braak and Verdonschot 1995). The method is based on the assumption that species have unimodal distributions along those environmental gradients. CCA links variation in environmental data to variation in biological data via reciprocal averaging (eigenanalysis) and linear regression (ter Braak 1986, Palmer 1993). Ordination biplots produced with CCA project relationships among biological and environmental data in 2-dimensional space. Species at the center of the biplot are common among sampled sites, whereas species on the periphery of the biplot are less common and more site specific. Species locations on the biplots reflect their habitat preferences along an environmental gradient. The environmental gradient is shown as arrows with direction and length from the biplot origin indicating the magnitude and association of those variables with fish species. In CCA, eigenvalues represent variance in community data that is attributed to a particular axis (McCune and Grace 2002). Environmental variables most strongly describing fish community composition were used to develop a fish habitat classification of the nearshore zone of the Canadian portion of Lake Ontario. Species that were found in only 1 reach were removed from the analysis because rare species can distort CCA results (Sharma and Jackson 2007). Removal of rare species resulted in retention of 59 of the 74 species analyzed (Appendix S2). The DCA and CCA were done in Multivariate Statistical Package (version 3 for Windows; Kovach Computing Services, Anglesey, UK).

The 4 variables most strongly correlated (positively and negatively) with the 1st and 2nd axes of the CCA were used to develop the fish habitat classification. Mean values of those variables were used to define 2 categories for each variable. Values less than or greater than the mean refer to low and high categories, respectively. This process resulted in a 16-group classification of the nearshore zone based on combinations of the variables and the low and high categories for each.

Validation

Fish community data from the southern nearshore of the lake (American side) were used to validate the classification. Species presence data were available for 27 reaches (Goodyear 1982, Seilheimer and Chow-Fraser 2006, Arend and Bain 2008). φ coefficients were calculated to assess the similarities in species composition among the classes. χ^2 values were calculated from the φ coefficients:

$$\varphi^2 = \frac{\chi^2}{N} \quad \text{(Eq. 2)}$$

where N is the total number of observations (Chedzoy 2006). The χ^2 critical value at 1 df (3.841) was used to decide which fish communities were similar. Significant differences supported the alternative hypothesis that fish communities were related. The validation and χ^2 results were used to refine the 16-group classification. Classes with similar fish communities were combined.

RESULTS

Species richness (prior to removal of rare taxa) ranged from 5 to 34 species per reach. Species at the center of the CCA biplot, such as White Sucker (WhSuc), Brown Bullhead (BrBull), and Pumpkinseed (PMK), were ubiquitous (Fig. 3). White Suckers were found in 143, Brown Bullheads in 149, and Pumpkinseeds in 144 of the 177 reaches (Appendix S2). Cold-water species such as Lake Trout (LT), Lake Whitefish (LWF), and Round Whitefish (RWF), were grouped together (Fig. 3, lower right region).

The first 2 axes of the CCA described 80.8% of the variation in the community data (Table 3, Fig. 3). The 1st axis was associated with the physical variables of the nearshore reaches: average fetch (AVGFTCH, r = 0.98) and slope (SLOPE, r = –0.54). The 2nd axis was correlated with land-cover variables: development (DEVE, r = 0.83) and mixed forest (MIXEDF, r = –0.71) (Table 3, Fig. 3). Most species were associated with a mix of physical and land-cover variables, except cold-water species, which were positively associated with average fetch and negatively associated with slope, i.e., reaches that were exposed and had steep slopes (Fig. 3).

These 4 variables were used to develop the fish habitat classification. Mean values for average fetch, slope, and proportions of development and mixed forest were used to split the data sets for each variable into low and high categories (Table 4). Reaches with low average fetch were considered sheltered habitat, whereas reaches with high average fetch were considered exposed. Reaches with slope values of 52 m asl had steeper profiles than reaches with values near 70 m asl, which represented shallower reaches. The average fetch and slope were combined into 4 descriptive categories: beach, embayment, exposed bluff, and sheltered bluff (Table 4). Low and high values of development and mixed forest were categorized as developed, forested, mixed, and other. Mixed indicated that both development and mixed-forest land cover were abundant in the watershed in proportions greater than the mean. Other indicated that developed and mixed forest were not abundant (proportions less than the mean) in the watershed. No reach was classified as beach-mixed, sheltered bluff-mixed, or embayment-mixed, and only 1 reach was classified as exposed bluff-mixed. Therefore, the mixed classes were not included in the classification. Thus, the classification had 12 classes.

The number of reaches with fish community data varied from 1 to 69 in each class (Table 4). A dendogram of the φ coefficients indicated that the fish communities in the beach and exposed bluff classes grouped together as did the communities in the embayment and sheltered bluff classes (Fig. 4). χ^2 tests showed that, in general, fish communities in embayments and sheltered bluffs were significantly different from communities in beach and exposed bluff classes (Table 5). Within those 2 groups, developed classes grouped together (beach-developed with exposed bluff-developed and embayment-developed with sheltered bluff-developed) (Fig. 4). However, χ^2 results indicated that fish communities in developed classes were similar regardless of whether they were embayment, beach, sheltered bluff, or exposed bluff (Table 5). Forested and other classes clustered together within the exposed bluff, sheltered-bluff, and embayment classes (Fig. 4, Table 5). Beach-forested, beach-other, and beach-developed were all similar (Fig. 4, Table 5). Beach-forested and exposed bluff-forested were different from all of the embayment and sheltered bluff classes (Fig. 4, Table 5).

Species presence data from the American side of the lake were available for 27 reaches and represented 4 habi-

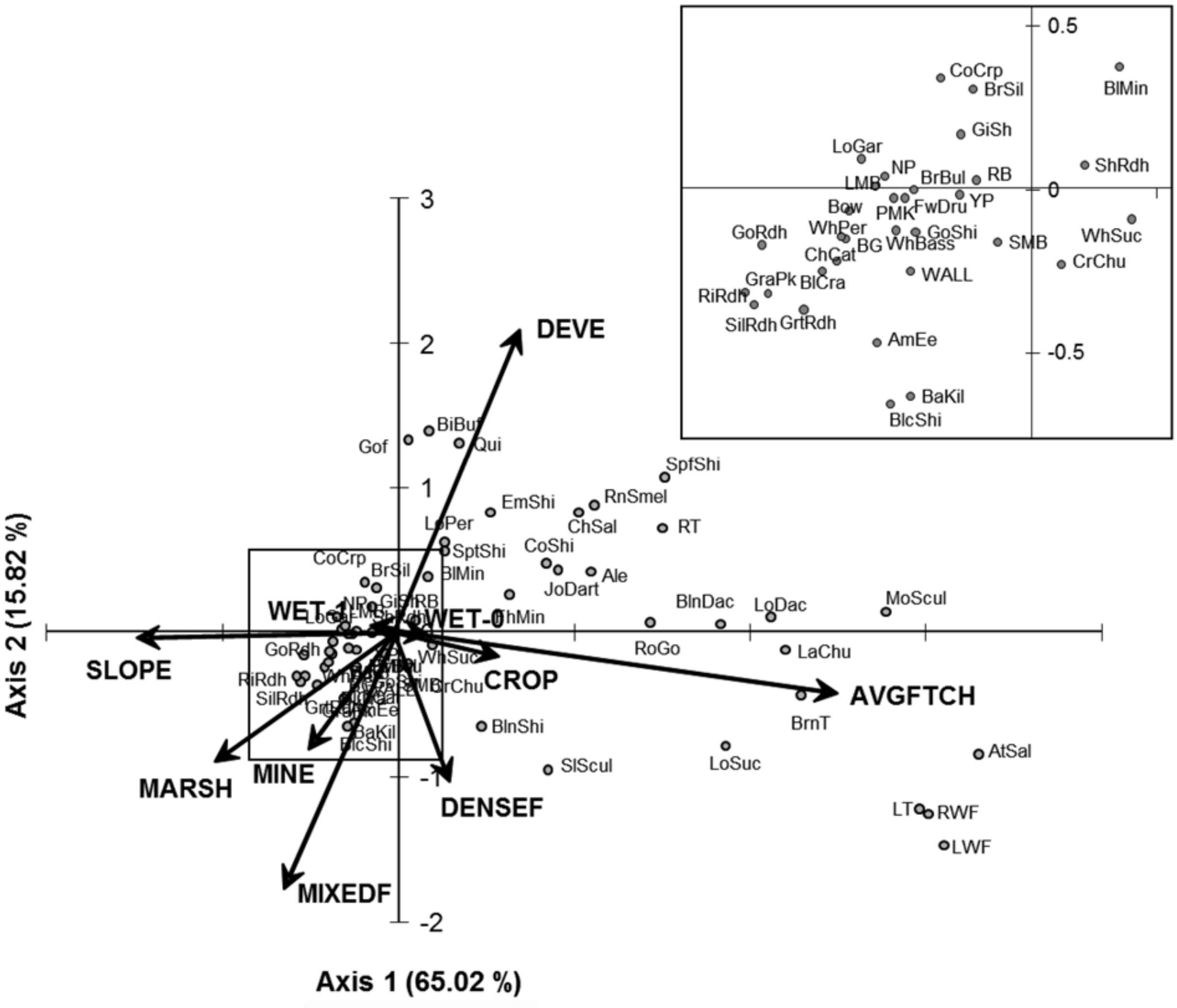

Figure 3. Results of canonical correspondence analysis to assess the relationship between fish community composition and physical and land-cover characteristics of the nearshore of Lake Ontario and its watershed. Inset box is an expansion of the center of the biplot (see Table 2 for variable abbreviations, Appendix S2 for abbreviations of species names, and text for explanation of figure).

tat classes: embayment-forested (number of reaches = 21), exposed bluff-forested (n = 3), exposed bluff-other (n = 1), and sheltered bluff-developed (n = 2). The exposed bluff-forested (ebf-val) and exposed bluff-other (ebo-val) validation reaches clustered with the exposed bluff and beach classes, whereas the sheltered bluff-developed (sbd-val) and embayment-forested validation (ef-val) reaches clustered with the sheltered bluff and embayment classes (Fig. 4). The ebf-val and ebo-val classes were more similar to the same classes on the Canadian side than to adjacent classes on the American side of the lake. The ebf-val class was significantly different only from embayment-forested, whereas ebo-val was significantly different from all of the classes except beach-other, exposed bluff-developed, exposed bluff-other, and embayment-forested (ef-val) (Table 5). The sbd-val class was most similar to sheltered bluff-other and significantly different from beach-developed, beach-forested, and exposed bluff-forested. The ef-val class was most similar to sheltered bluff-forested and was significantly different from all of the beach classes, exposed bluff-forested, and exposed bluff-other (Fig. 4, Table 5).

Validation and χ^2 significance results were used to refine the classification. Those results led to the collapse of all of the developed classes into 1 class regardless of whether they were bluffs, beach, or embayment. Validation and χ^2 test results also led to grouping of beach-forested, beach-other, exposed bluff-forested, and exposed bluff-other into 1 class, whereas embayment-forested, embayment-other, sheltered bluff-forested, and sheltered bluff-other were grouped into another class. Therefore, the species lists and reaches of the 12-group classification were condensed to 3 classes representing 'exposed', 'sheltered', and 'developed'

Table 4. Sixteen habitat classes, the number of reaches in each class, and number of reaches with fish community data used to develop a nearshore classification for Lake Ontario based on the relationships among fish communities and physical and land-cover characteristics of the nearshore zone and its watershed. N/A = not applicable.

Fish habitat class (abbreviations)	Average fetch (km)	Slope (m)	Proportion of watershed mixed forest	Proportion of watershed developed	Number of reaches in class	Number of reaches with fish community data
Beach-developed (bd)	13.6–52.0	63.3–79.6	0.01–0.07	0.13–0.94	41	2
Beach-forested (bf)	13.6–52.0	63.3–79.6	0.07–0.28	0.01–0.12	61	1
Beach-mixed (bm)	13.6–52.0	63.3–79.6	0.07–0.28	0.13–0.94	0	N/A
Beach-other (bo)	13.6–52.0	63.3–79.6	0.01–0.07	0.01–0.12	134	1
Exposed bluff-developed (ebd)	13.6–52.0	52.0–63.2	0.01–0.07	0.13–0.94	153	7
Exposed bluff-forested (ebf)	13.6–52.0	52.0–63.2	0.07–0.28	0.01–0.12	290	17
Exposed bluff-mixed (ebm)	13.6–52.0	52.0–63.2	0.07–0.28	0.13–0.94	1	N/A
Exposed bluff-other (ebo)	13.6–52.0	52.0–63.2	0.01–0.07	0.01–0.12	389	4
Embayment-developed (ed)	0.01–13.5	63.3–79.6	0.01–0.07	0.13–0.94	176	18
Embayment-forested (ef)	0.01–13.5	63.3–79.6	0.07–0.28	0.01–0.12	573	69
Embayment-mixed (em)	0.01–13.5	63.3–79.6	0.07–0.28	0.13–0.94	0	N/A
Embayment-other (eo)	0.01–13.5	63.3–79.6	0.01–0.07	0.01–0.12	377	24
Sheltered bluff-developed (sbd)	0.01–13.5	52.0–63.2	0.01–0.07	0.13–0.94	115	14
Sheltered bluff-forested (sdf)	0.01–13.5	52.0–63.2	0.07–0.28	0.01–0.12	65	11
Sheltered bluff-mixed (sbm)	0.01–13.5	52.0–63.2	0.07–0.28	0.13–0.94	0	N/A
Sheltered bluff-other (sbo)	0.01–13.5	52.0–63.2	0.01–0.07	0.01–0.12	79	9

environments. Species richness was 37 in the exposed class based on data from 23 reaches, 47 in the sheltered class based on data from 113 sampled reaches, and 55 in the developed class based on data from 41 sampled reaches (Appendix S2). φ coefficients and χ^2 analyses showed no relationships among the fish communities in these 3 classes (Table 6). Each reach in Lake Ontario was then classified into 1 of the 3 classes (Fig. 5). Species accumulation curves were calculated to determine whether the number of sampled reaches were sufficient to identify all species within each class. Chao and 1st-order jackknife estimators, which perform better than other estimators, were used

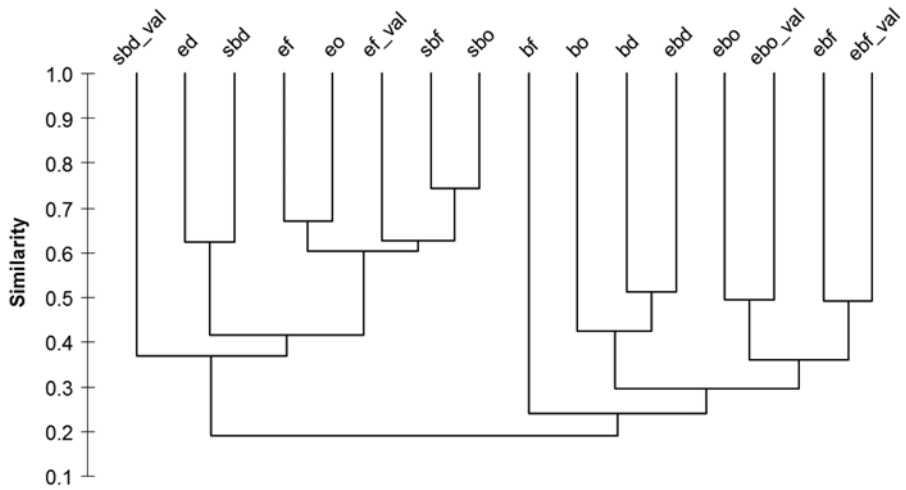

Figure 4. φ coefficient similarity values for the fish communities in 12 fish-habitat classes defined for the nearshore zone of Lake Ontario. b = beach, eb = exposed bluff, e = embayment, sb = sheltered bluff, d = development, f = forested and o = other. Ebo_val, ebf_val, ef_val, and sbd_val correspond to the validation data set for the exposed bluff-other, exposed bluff-forested, embayment forested, and sheltered bluff-developed habitat classes.

Table 5. χ^2 values calculated from φ coefficients to test the similarities among fish communities in 12 habitat classes and 4 validation classes of the nearshore of Lake Ontario. Values > 3.841 indicate similar fish communities (bold). See Table 4 for habitat classes.

Habitat class	Beach			Exposed bluff			Embayment			Sheltered bluff			Validation data set		
	bd	bf	bo	ebd	ebf	ebo	ed	ef	eo	sbd	sbf	sbo	ef_val	sbd_val	ebo_val
bf	**4.3**														
bo	**16.0**	**10.2**													
ebd	**19.3**	2.0	**11.0**												
ebf	**8.0**	**9.0**	**7.4**	1.9											
ebo	**8.8**	**5.7**	**16.5**	**6.1**	**13.4**										
ed	**5.6**	0.6	**7.0**	**16.1**	0.0	**6.1**									
ef	0.5	0.4	1.8	**5.4**	0.5	2.3	**3.9**								
eo	3.3	0.0	**4.5**	**9.2**	0.2	**7.6**	**13.4**	**33.3**							
sbd	**13.0**	**1.6**	**9.8**	**19.5**	2.0	**10.6**	**28.7**	**5.0**	**24.2**						
sbf	0.0	0.0	0.0	**7.3**	0.2	**5.7**	**14.1**	**29.0**	**29.8**	**18.2**					
sbo	1.0	0.4	2.1	**5.9**	0.5	**7.7**	**11.7**	**25.6**	**26.9**	**15.8**	**40.9**				
ef_val	1.4	0.1	3.4	**9.5**	0.2	3.1	**11.8**	**21.0**	**28.8**	**16.8**	**33.1**	**25.3**			
sbd_val	1.1	0.1	**5.5**	**7.3**	0.0	**5.5**	**8.7**	**6.1**	**8.7**	**13.0**	**12.0**	**15.2**	**8.4**		
ebo_val	2.4	0.1	**5.7**	**4.7**	3.3	**18.1**	1.1	1.4	0.2	1.9	2.6	0.2	**4.2**	2.4	
ebf_val	**5.4**	**7.2**	**6.4**	**9.5**	**17.8**	**15.1**	**11.8**	0.1	**4.3**	**13.2**	**8.1**	**4.6**	**6.0**	**12.0**	**9.5**

generate the curves in EstimateS software (Colwell 2005, Walther and Moore 2005). Species accumulation curves for all 3 classes reached asymptotes with the Chao estimator but increased for the exposed and developed classes with the 1st-order jackknife estimator (Fig. 6A–C).

Thirty-six percent of the nearshore was classified as exposed, 44% was classified as sheltered, and 20% was classified as developed. The Canadian nearshore is more heterogeneous than the American nearshore, which is dominated by the exposed class (Fig. 5). In general, the central region of the lake was classified as exposed. Many of the western reaches were classified as developed, and the bays along the eastern region were classified as sheltered (Fig. 5).

DISCUSSION

Our study highlights that even in lakes as large as Lake Ontario, the nearshore fish community is influenced by watershed land cover, and emphasizes the importance of terrestrial and aquatic linkages for nearshore ecosystems. Physical-habitat variables, average fetch, and slope, which influenced fish community composition and were correlated with richness, may be analogs for more complex nearshore conditions, particularly hydrodynamics, thermal conditions, and macrophyte cover. Reaches with high average fetch are exposed to more wave action than reaches with low average fetch, and the bathymetry of the reach can affect how that wave energy is dissipated within the

Table 6. φ coefficient of similarity for fish communities found in exposed, sheltered, and developed habitat classes. Asterisks indicate that fish communities were significantly different, which was determined after calculating χ^2 values from the φ coefficients and a χ^2 critical value of 3.841 at 1 df.

Habitat class	Exposed	Sheltered	Developed
Exposed	1		
Sheltered	−0.083*	1	
Developed	0.031*	0.098*	1

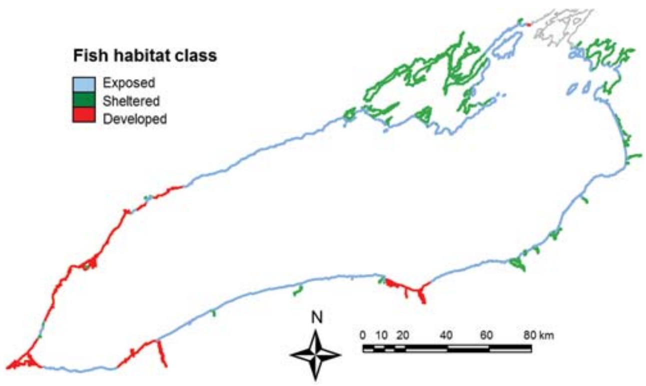

Figure 5. Fish-habitat classification of the nearshore of Lake Ontario derived from the relationships among fish community composition and physical and land-cover characteristics of the nearshore of Lake Ontario and its watershed. Grey unclassified area is part of the St. Lawrence River.

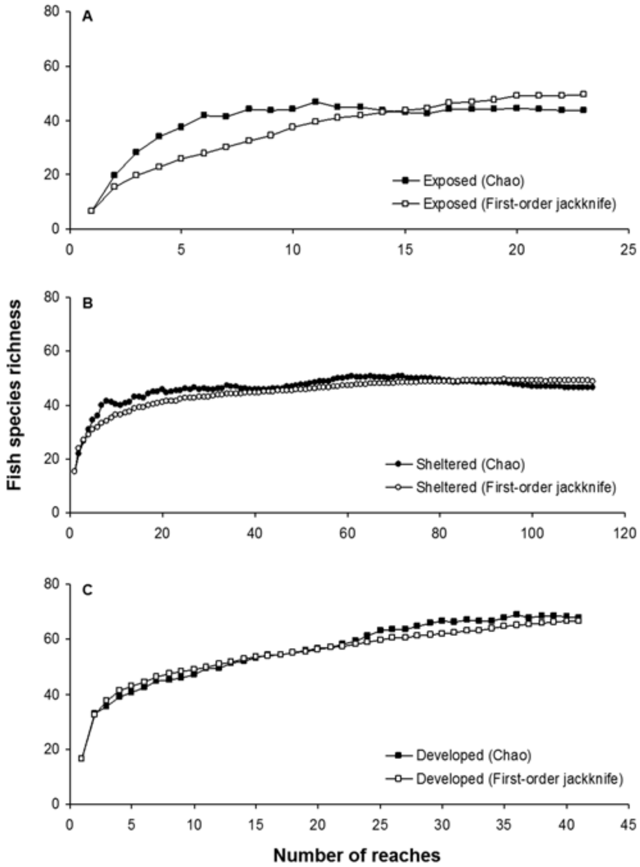

Figure 6. Species accumulation curves for the exposed (A), sheltered (B), and developed (C) fish habitat classes of the nearshore of Lake Ontario estimated using the Chao and 1st -order jackknife estimators.

nearshore zone (Goldman and Horne 1983, Rao and Schwab 2007, McKenna and Castiglione 2010). In Lake Ontario, prevailing winds are from the southwest–west. Currents run from west to east along the south shore with an additional clockwise gyre that spans from Toronto east to Prince Edward County along the north shore (Beletsky et al. 1999, Rao and Schwab 2007). Therefore, reaches along the northeast shore have different wave action and circulation patterns than reaches along the west and northwest shore. These differences have implications for the distribution of nutrients, tributary discharge plumes, substrate composition, sediment dynamics, and plankton transport that affect nearshore fish communities.

Cold-water species were positively associated with average fetch and steep slopes, which is indicative of habitats with cool thermal conditions or close proximity to cold-water refugia. In Lake Ontario and other lakes, surface water temperatures are influenced by solar radiation, air temperature, precipitation, evaporation, and tributary inflows. In spring, solar radiation and air temperature increase and heat energy is mixed downward through the water column (Edsall and Charlton 1997). In shallow sheltered areas, more heat energy is absorbed by the water and leads to faster rates of warming and warmer temperatures in general compared to exposed, steep reaches (Edsall and Charlton 1997, Hall et al. 2003). Therefore, the steeper and deeper reaches have cooler temperatures and provide more thermally suitable habitat for cold-water species than the shallow, sheltered reaches.

The land-cover variables, development and mixed forest, are likely to be indicative of water quality in the nearshore zone. Water from tributaries draining urban and industrial areas may contain suspended solids, bacteria, nutrients, metals, and trace organic contaminants, which limit suitability of the receiving nearshore reaches for some fish species (OMOE 1999, Sharma and Jackson 2007). In our study, development was positively associated with species that are moderately tolerant or tolerant of pollution, such as the Bigmouth Buffalo and Quillback (USEPA 2011). Fish species, such as Grass Pickerel and Greater Redhorse (USEPA 2011), that are moderately intolerant or intolerant of pollution were not found in the developed class.

Separation of fish community data on physical and land-cover axes is consistent with results of other studies in which the relationship between nearshore features and fish communities in the Great Lakes was examined (e.g., Randall and Minns 2002, Wei et al. 2004, Trebitz et al. 2009). In lakes Erie and Ontario, different fish communities were found at coastal wetlands, harbors, and exposed nearshore sites (Randall and Minns 2002). Wei et al. (2004) found that cold-water species used bedrock and sandy beach–dune habitats. Cool–cold-, cool-, and warm-water species used wetlands, and cool–warm-water species favored bedrock habitats. Most of the cold-water species in our study were found in exposed reaches. Cool–cold-, cool-, and cool–warm-water species were found in all 3 habitat classes. Trebitz et al. (2009) examined the relationship between fish communities and watershed, wetland, and water-quality conditions in all of the Great Lakes. Wetlands surrounded by agricultural watersheds had tolerant fish species, whereas wetlands surrounded by mostly natural watersheds had a higher diversity of tolerant and intolerant species.

Eighty percent of the variation in fish community structure among reaches was described by the physical and land-cover characteristics, which is consistent with other studies linking fish communities to physical and land-cover variables in the Great Lakes (e.g., Trebitz et al. 2009, Strecker et al. 2011). Trebitz et al. (2009) used nonmetric multidimensional scaling to show that 72 and 42% of the variation in fish composition was described by watershed, wetland, and water-quality variables in high- and low-disturbance wetlands, respectively. Strecker et al. (2011) used redundancy analysis to relate 28 to 53% of the variation in coastal fish assemblages in Lake Huron to climate, watershed, and site-level (e.g., substrate) conditions. In western Lake Erie, >70% of the spatial variation in fish community structure was attributed to variation in environmental variables, which included fetch, substrate, wetland type, water temperature, and macrophyte cover (McKenna and Castiglione 2010).

Similarities among fish communities draining developed watersheds, regardless of whether they were bluffs, beach, or embayment, suggests that habitat changes associated with developed watersheds result in homogenized nearshore fish communities. Rahel (2002) and Scott (2006) posited that anthropogenic changes to habitat and human-facilitated introductions of species to aquatic systems homogenize biotic communities. Throughout North America, human development has led to altered habitats, such as irrigation ditches, reservoirs, and canals, that have similar habitat characteristics and fish communities dominated by widespread species instead of endemic species (Rahel 2002, Clavero and Hermoso 2011). For this reason, and because receiving waters of developed watersheds often have poor water quality and lower biodiversity (OMOE 1999, Scott 2006, Stendera et al. 2012), our finding of higher species richness in the developed nearshore class is counterintuitive. Possible explanations of this pattern are: 1) development has occurred along the more productive areas of the lake, which may mean that these areas had higher predevelopment fish diversity, or 2) the developed class is associated with more nonnative or pollution tolerant fishes, which will increase diversity. Four of the 10 species that were unique to the developed class were nonnative or pollution tolerant. Further research is needed to determine the ecological processes governing this pattern in Lake Ontario.

Our classification has commonalities with those by Gregor and Rast (1982), Busch and Lary (1996), and Rutherford and Geddes (2007). All of these classifications included variable(s) that described morphometry, exposure, and circulation of the nearshore zone. In essence, hydrodynamics, thermal conditions, and probably benthic substrate and macrophyte cover influence fish distribution. As with our classification, Gregor and Rast (1982) found that the northern nearshore zone was divided into more classes than the southern nearshore zone (based on physical conditions). In their study, this separation translated into differences in Secchi depth, total P, and chlorophyll *a* concentrations. Our 3-group classification may seem oversimplified, but is consistent with the classification by Rutherford and Geddes (2007). Their habitat classifications of Lake Michigan into 2 nearshore and 4 offshore classes and of Lake Erie into 2 nearshore and 4 offshore classes were related to the spatial variability in recreational catch rates for Coho Salmon and catch rates for Walleye for Lake Michigan and Erie, respectively.

Limitations and future research

Sampling methods and the validation data set used in our study do have limitations. First, fish data were compiled from several agencies with potentially different goals for monitoring and studying nearshore fish communities along Lake Ontario. These data carry biases that reflect collection methods (sampling locations, sampling periodicity, and gear types) used to meet the differing objectives of those studies. We assumed that compiling data from multiple studies and gear types would provide an inclusive and robust description of these fish communities. Limiting our analyses to one gear type would have significantly under-represented community richness because gear type is selective for certain species and size classes (e.g., Hansen et al. 1997). By including all gear type, systematic bias among reaches was removed.

Second, our analysis of species accumulation curves derived from the 1st-order jackknife estimator suggested that more reaches should be sampled for exposed and developed habitat classes to quantify richness. However, jackknife estimates were not consistent with the Chao estimator, which suggested that enough reaches were sampled. Future investigators should apply the same sampling protocol to an equal number of randomly selected reaches in our 3 habitat classes to determine if these classes persist under more regimented sampling effort.

Last, our validation data set was only a partial representation of the fish communities in the initial 12-group habitat classification. It was compiled from 2 studies: Seilheimer and Chow-Fraser (2006) and Arend and Bain (2008). The data set for the Canadian side of the lake was a compilation from several studies conducted over several years in Ontario. Fish communities in the validation reaches were similar to the communities in their corresponding habitat classes on the Canadian side of the lake, but more sampling is needed in the under-represented classes to further support or refute collapsing the 12-group classification to 3 classes.

Our results align with other classification frameworks, particularly for the Great Lakes, that consider variables at multiple scales (e.g., McKenna and Castiglione 2010, Strecker et al. 2011). Average fetch and slope represent large-scale variables, such as wind and geomorphology, and small-scale variables, such as thermal conditions and hydrodynamics, that discriminate biological communities among reaches. Land-cover variables incorporated another layer of influence because terrestrial conditions generate runoff that also may alter fish community structure and richness in nearshore zones. Future work is needed to evaluate whether this 3-group classification can explain spatial heterogeneity in other response variables, such as water quality and macrophyte and invertebrate communities.

Research priorities for the nearshore zone outlined by IJC (2012) and documented in the newly ratified GLWQA include "A comprehensive and ecosystematic scientific assessment of condition of the nearshore waters and habitats of the Great Lakes" to inform an adaptive management approach. The classification presented here is directly related to this priority because it identifies nearshore areas with different fish habitat characteristics. The strong influence of development in the watershed suggests that activities, such as deforestation and expansion of urban and industrial areas, significantly affect fish communities and possibly other nearshore biota. As such, this classification can inform management decisions that can affect nearshore fishes, and it emphasizes that maintenance or rehabilitation of nearshore ecosystem health in the Great Lakes will require integration of aquatic and watershed planning and management.

ACKNOWLEDGEMENTS

This research would not have been possible without the collection and generous donations of data by several individuals and agencies: Jim Bowlby, Jim Hoyle, and Marc Desjardins of the Ontario Ministry of Natural Resources; Jon Clayton and Loveleen Clayton of Credit Valley Conservation; Christine Tu, Mike Correa, and Mike Portiss of Toronto Regional Conservation Authority; Carolyn Bakelaar, Christine Brousseau, and Erin Gertzen of Fisheries and Oceans. The validation data set was provided by Titus Seilheimer and Pat Chow-Fraser of McMaster University and Kristi Arend and Mark Bain of Cornell University. Comments and edits from Associate Editor Dave Arscott, A. S. Trebitz, and another anonymous referee greatly improved this manuscript. Funding was provided by Fisheries and Oceans Canada through the Lake Ontario Ecosystem Research Initiative. Additional support for CC was provided by Nature Conservancy of Canada and the Weston Foundation.

LITERATURE CITED

Arend, K. K., and M. B. Bain. 2008. Fish communities in coastal freshwater ecosystems: the role of the physical and chemical setting. BMC Ecology 8:23.

Beletsky, D., J. H. Saylor, and D. J. Schwab. 1999. Mean circulation in the Great Lakes. Journal of Great Lakes Research 25: 78–93.

Busch, W.-D. N., and S. J. Lary. 1996. Assessment of habitat impairments impacting the aquatic resources of Lake Ontario. Canadian Journal of Fisheries and Aquatic Sciences 53 (Supplement 1):113–120.

Chedzoy, O. B. 2006. Phi-coefficient. Page 367 *in* S. Kotz, C. Read, N. Balakrishnan, and B. Vidakovic (editors). Encyclopedia of statistical sciences. 2nd edition. John Wiley and Sons, New York.

Clavero, M., and V. Hermoso. 2011. Reservoirs promote the taxonomic homogenization of fish communities within river basins. Biodiversity and Conservation 20:41–57.

Colwell, R. K. 2005. EstimateS: statistical estimation of species richness and shared species for samples. Version 7.5. User's guide and application. (Available from: www.purl.oclc.org/estimates)

Dobiesz, N. E., and N. P. Lester. 2009. Changes in mid-summer water temperature and clarity across the Great Lakes between 1968 and 2002. Journal of Great Lakes Research 35:371–384.

Edsall, T. A., and M. N. Charlton. 1997. Nearshore waters of the Great Lakes. State of the Great Lakes Ecosystem Conference, 1996 Background Paper. US EPA 905-R-97-015a Cat. No. En40-11/35-1-1997E. Environment Canada and US Environmental Protection Agency, Windsor, Ontario.

Goforth, R. R., and S. M. Carman. 2005. Nearshore community characteristics related to shoreline properties in the Great Lakes. Journal of Great Lakes Research 31(Supplement 1):113–128.

Goldman, C. R., and A. J. Horne. 1983. Limnology. McGraw–Hill Publishing Company, Toronto, Ontario.

Goodyear, C. S., T. A. Edsall, D. M. Ormsby Dempsey, G. D. Moss, and P. E. Polanski. 1982. Atlas of the spawning and nursery areas of Great Lakes fishes. Volume XI: Lake Ontario. FWS/OBS-82/52. US Fish and Wildlife Service, Washington, DC.

Gregor, D. J., and W. Rast. 1982. Simple trophic state classification of the Canadian nearshore waters of the Great Lakes. Water Research Bulletin 18:565–573.

Hall, S. R., N. K. Pauliukonis, E. L. Mills, L. G. Rudstam, C. P. Schneider, S. J. Lary, and F. Arrhenius. 2003. A comparison of total phosphorus, chlorophyll *a*, and zooplankton in embayment, nearshore, and offshore habitats of Lake Ontario. Journal of Great Lakes Research 29:54–69.

Hansen, M. J., C. P. Madenjian, J. H. Selgeby, and T. E. Helser. 1997. Gillnet selectivity for lake trout (*Salvelinus namaycush*) in Lake Superior. Canadian Journal of Fisheries and Aquatic Sciences 54:2483–2490.

Hecky, R. E., R. E. H. Smith, D. R. Barton, S. J. Guildford, W. D. Taylor, M. N. Charlton, and T. Howell. 2004. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 61:1285–1293.

Hill, M. O., and H. G. Gauch. 1980. Detrended correspondence analysis, an improved ordination technique. Vegetatio 42:47–58.

Homer, C., J. Dewitz, J. Fry, M. Coan, N. Hossain, C. Larson, N. Herold, A. McKerrow, J. N. VanDriel, and J. Wickham. 2007. Completion of the 2001 National Land Cover Database for the conterminous United States. Photogrammetric Engineering and Remote Sensing 73:337–341.

IJC (International Joint Commission). 2006. International Lake Ontario–St. Lawrence River Study. Final Report. International Joint Commission, Ottawa, Ontario, and Washington, DC. (Available from: http://www.losl.org/reports/finalreport-e.html)

IJC (International Joint Commission). 2009. Nearshore Framework Advisory Workgroup to the International Joint Commission (IJC), Great Lakes Water Quality Agreement Priorities 2007-09 Series. Workgroup Report on the Nearshore Framework, 2009. Special Publication 2009-10. International Joint Commission, Windsor, Ontario. (Available from: http://www.ijc.org/files/publications/C224.pdf)

IJC (International Joint Commission). 2012. Great Lakes Water Quality Protocol of 2012 signed September 7 2012. International Joint Commission, Ottawa, Ontario, and Washington, DC. (Available from: http://www.epa.gov/greatlakes/glwqa/)

Jackson, D. A., K. M. Somers, and H. H. Harvey. 1989. Similarity coefficients: measures of co-occurrence and association or simply measures of occurrence? American Naturalist 133: 436–453.

Keddy, P. A., and A. A. Reznicek. 1986. Great Lakes vegetation dynamics: the role of fluctuating water levels and buried seeds. Journal of Great Lakes Research 12:25–36.

Lake Ontario Biodiversity Strategy Working Group. 2009. The beautiful lake: a binational biodiversity conservation strategy for Lake Ontario. US Environmental Protection Agency, Buffalo, New York. (Available from: http://www.epa.gov/greatlakes/lakeont/reports/lo_biodiversity.pdf)

Lepš, J., and P. Šmilauer. 2003. Multivariate analysis of ecological data using CANOCO. University Press, Cambridge, UK.

Mackey, S. D. 2009. Nearshore habitats of the Great Lakes. Pages 104–107 *in* State of the Lakes Ecosystem Conference 2008 Background Paper. E. K. Hinchey and R. Cestaric (editors). Nearshore Areas of the Great Lakes 2009. EPA 905-R-09-013 or Cat. No. En164-19/2009E-PDF. Environment Canada and US Environmental Protection Agency, Windsor, Ontario. (Available from: http://binational.net/solec/sogl2009/SOGL_2009_nearshore_en.pdf)

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.

McKenna, J. E., and C. Castiglione. 2010. Hierarchical multiscale classification of nearshore aquatic habitats of the Great Lakes: western Lake Erie. Journal of Great Lakes Research 36:757–771.

Mills, E. L., J. M. Casselman, R. Dermott, J. D. Fitzsimons, G. Gal, K. T. Holeck, J. A. Hoyle, O. E. Johannsson, B. F. Lantry, J. C. Makarewicz, E. S. Millard, I. F. Munawar, M. Munawar, R. O'Gorman, R. W. Owens, L. G. Rudstam, T. Schaner, and T. J. Stewart. 2003. Lake Ontario: food web dynamics in a changing ecosystem (1970–2000). Canadian Journal of Fisheries and Aquatic Sciences 60:471–490.

Minns, C. K., S. E. Doka, C. N. Bakelaar, C. Chu, and K. E. Seifried. 2005. Final report from the Burlington fish habitat group. IJC Lake Ontario–St. Lawrence water regulation study. International Joint Commission, Windsor, Ontario. (Available from: http://www.ijc.org/loslr/en/library/Environmental/02a%20IERM_report_draft-042905%20REDUCED.pdf)

OMNR (Ontario Ministry of Natural Resources). 2000. Provincial Land Cover 2000-27 Classes (PLC2000). Ontario Land Information Warehouse, Land Information Distribution System (LIDS), Peterborough, Ontario. (Available from: http://www.mnr.gov.on.ca/en/Business/LIO/index.html)

OMNR (Ontario Ministry of Natural Resources). 2002. A guide to the provincial watershed project. Water Resources Information Project. Provincial Geomatics Service Centre, Peterborough, Ontario. (Available from: http://www.mnr.gov.on.ca/en/Business/LIO/index.html)

OMOE (Ontario Ministry of the Environment). 1999. Surface Water Monitoring and Assessment 1997 Lake Ontario Report featuring a summary of tributary and nearshore conditions and trends for the Lake Ontario basin. Ontario Ministry of the Environment, Toronto, Ontario. (Available from: http://www.ontario.ca/environment-and-energy/provincial-stream-water-quality-monitoring-network-pwqmn-data)

OMOI (Ontario Ministry of Infrastructure). 2012. Growth plan for the Greater Golden Horseshoe. Ontario Ministry of Infrastructure, Toronto, Ontario. (Available from: https://www.placestogrow.ca/index.php?option=com_content&task=view&id=9&Itemid=14)

Palmer, M. W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. Ecology 74: 2215–2230.

Rahel, F. J. 2002. Homogenization of freshwater faunas. Annual Review of Ecology and Systematics 33:291–315.

Randall, R. G., and C. K. Minns. 2002. Comparison of a Habitat Productivity Index (HPI) and an Index of Biotic Integrity (IBI) for measuring the productive capacity of fish habitat in nearshore areas of the Great Lakes. Journal of Great Lakes Research 28:240–255.

Rao, Y. R., and D. J. Schwab. 2007. Transport and mixing between the coastal and offshore waters in the Great Lakes: a review. Journal of Great Lakes Research 33:202–218.

Rutherford, E., and C. Geddes. 2007. Ecological classification of nearshore and open-water fish habitats in the Great Lakes. Institute for Fisheries Research, University of Michigan School of Natural Resources and Environment, Ann Arbor, Michigan. (Available from: http://ifrgis.snre.umich.edu/projects/GLGIS/support_docs/html/classifications/gl_classification_report.pdf)

Scott, M. C. 2006. Winners and losers among stream fishes in relation to land use legacies and urban development in the southeastern US. Biological Conservation 127:301–309.

Seilheimer, T. S., and P. Chow-Fraser. 2006. Development and use of the Wetland Fish Index to assess the quality of coastal wetlands in the Laurentian Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 63:354–366.

Sharma, S., and D. A. Jackson. 2007. Fish assemblages and environmental conditions in the lower reaches of northeastern Lake Erie tributaries. Journal of Great Lakes Research 33:15–27.

Stendera, S., R. Adrian, N. Bonada, M. Cañedo-Argüelles, B. Hugueny, K. Januschke, F. Pletterbauer, and D. Hering. 2012. Drivers and stressors of freshwater biodiversity patterns across different ecosystems and scales: a review. Hydrobiologia 696: 1–28.

Stewart, C. J. 2003. A revised geomorphic, shore protection and nearshore classification of the Canadian and United States shorelines of Lake Ontario and the St. Lawrence River. Canadian Coastal Conference 2003. C. J. Stewart Consulting, Victoria, British Columbia. (Available from: http://www.cjscons.com/corporate/pubs.html)

Strecker, A. L., J. M. Casselman, M. Fortin, D. A. Jackson, M. S. Ridgway, P. A. Abrams, and B. J. Shuter. 2011. A multi-scale comparison of trait linkages to environmental and spatial variables in fish communities across a large freshwater lake. Oecologia (Berlin) 166:819–831.

ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167–1179.

ter Braak, C. J. F., and P. E. M. Verdonschot. 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquatic Sciences 57:255–289.

Trebitz, A. S., J. C. Brazner, N. P. Danz, M. S. Pearson, G. S. Peterson, D. K. Tanner, D. L. Taylor, C. W. West, and T. P. Hollenhorst. 2009. Geographic, anthropogenic, and habitat influences on Great Lakes coastal wetland fish assemblages. Canadian Journal of Fisheries and Aquatic Sciences 66:1328–1342.

USACE (US Army Corps of Engineers). 1991. Great Lakes levels. Update Letter No. 76. North Central Division, US Army Corps of Engineers, Cincinnati, Ohio. (Available from: http://www.lre.usace.army.mil/Portals/69/docs/GreatLakesInfo/docs/UpdateArticles/Update076.pdf)

USEPA (US Environmental Protection Agency). 2011. Biological indicators of watershed health. US Environmental Protections Agency, Washington, DC. (Available from: http://water.epa.gov/scitech/monitoring/rsl/bioassessment/app_c-2.cfm)

USGS (US Geological Survey). 2011. Hydrologic Unit Maps. US Geological Survey, Reston, Virginia. (Available from: http://water.usgs.gov/GIS/huc.html)

Walther, B. A., and J. L. Moore. 2005. The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. Ecography 28:815–829.

Wei, A., P. Chow-Fraser, and D. Albert. 2004. Influence of shoreline features on fish distribution in the Laurentian Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 61:1113–1123.

Wilcox, K. L., S. A. Petrie, L. A. Maynard, and S. W. Meyer. 2003. Historical distribution and abundance of *Phragmites australis* at Long Point, Lake Erie, Ontario. Journal of Great Lakes Research 29:664–680.

Zar, J. H. 1996. Biostatistical analysis. 3rd edition. Prentice Hall, Upper Saddle River, New Jersey.