Influence of shoreline features on fish distribution in the Laurentian Great Lakes

A. Wei, P. Chow-Fraser, and D. Albert

Abstract: In this paper, we used assembled fish distributions (over 9500 field observations) and correlated them with 11 categories of the Great Lakes shoreline (i.e., bedrock, bluff, coarse beach, sandy beach – dune, sandy–silty bank, clay bank, low riverine – coastal plain, composite, wetland, artificial, and unclassified) to validate the appropriateness of classifying Great Lakes fishes into three species complexes (taxocenes) that account for differences in their dependence on shoreline features. A χ^2 goodness-of-fit test with Bonferroni correction indicated a significant positive association between the presence of fish and three shoreline classes: wetland, sandy beach – dune, and bluff. The Dutilleul modified *t* test was used to quantify the correlation between wetlands and distribution of the 25 most abundant species and those of different functional groupings. Our results confirm that (*i*) the Great Lakes fish community utilizes certain shoreline features (especially wetlands) disproportionately to their availability, (*ii*) the distribution of wetland-associated taxa is influenced by wetland type (i.e., protected embayment versus open-shoreline wetland), and (*iii*) the preferred utilization of coastal wetlands by a majority of the fish community is consistent across geographical scales, from the local site to the entire Great Lakes shoreline.

Résumé : Nous utilisons dans notre étude des données accumulées sur la répartition des poissons (plus de 9500 observations de terrain) et les mettons en corrélation avec 11 catégories de rivage des Grands Lacs (i.e., roche mère, escarpement, plage grossière, plage – dune de sable, banc sablonneux–vaseux, banc glaiseux, plaine côtière riveraine basse, milieu mixte, terre humide, milieu artificiel et milieu non classifié). Nous cherchons à valider la pertinence de classifier les poissons des Grands Lacs en trois complexes d'espèces (taxocènes) d'après les différences dans leur dépendance des caractéristiques du rivage. Un test d'ajustement de χ^2 avec la correction de Bonferroni indique une association positive significative entre la présence des poissons et trois classes de rivages, soit les terres humides, les plages – dunes sablonneuses et les escarpements. Le test de *t* avec la modification de Dutilleul a servi à quantifier la corrélation entre les terres humides et la répartition des 25 espèces les plus abondantes, de même que de celle des différents groupes fonctionnels. Nos résultats confirment que (*i*) la communauté de poissons des Grands Lacs utilise certains milieux de rivage, particulièrement les terres humides, de façon disproportionnée à leur disponibilité, (*ii*) la répartition des taxons associés aux terres humides est influencée par le type de terres humides, soit les baies protégées par rapport aux terres humides des rivages ouverts et (*iii*) l'utilisation préférée des terres humides côtières par la majorité de la communauté de poissons est uniforme, quelle que soit l'échelle géographique, du site local à l'ensemble du rivage des Grands Lacs.

[Traduit par la Rédaction]

Introduction

Coastal wetlands of the Great Lakes provide important spawning and nursery habitat for wetland-dependent species that include a number of commercially and recreationally important taxa (Chubb and Liston 1986; Stephenson 1990; Jude and Pappas 1992). The US Nature Conservancy estimated that about 80% of the approximately 200 fish species found in the Great Lakes use the nearshore areas for at least part of the year and directly depend on coastal wetlands for some part of their life cycles (Chow-Fraser and Albert 1999). Jude and Pappas (1992) have suggested that there are three species complexes that vary according to their dependence on coastal wetland habitat. The "Great Lakes" taxocene, which is primarily associated with open water and only come into tributaries to spawn, does not depend on wetlands; the "transitional" taxocene, which utilizes open water and nearshore, will depend on wetlands for spawning and (or) nursery habitat; and the true "wetlands" taxocene, which includes species that are either permanent residents of wetlands or those that only migrate into wetlands for nursery, spawning, or shelter, is heavily dependent on wetlands. The importance of this proposed classification scheme is that it provides an ecological rather than strictly taxonomic basis for organizing and studying

Received 29 May 2003. Accepted 24 January 2004. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 14 August 2004.
J17550

A. Wei and P. Chow-Fraser.[1] Department of Biology, McMaster University, 1280 Main Street West, Hamilton, ON L8S 4K1, Canada.
D. Albert. Michigan Natural Features Inventory, Ecology Program, Stevens T. Mason Building, P.O. Box 30444, Lansing, MI 48909-7944, USA.

[1] Corresponding author (e-mail: chowfras@mcmaster.ca).

Can. J. Fish. Aquat. Sci. **61**: 1113–1123 (2004) doi: 10.1139/F04-061

the fish community. Once it has been properly validated, managers should be able to make inferences about availability of wetland fish habitat based on the relative abundance of fish that belong to the transitional and wetland taxocenes.

In this paper, we validate the appropriateness of the proposed classification scheme of Jude and Pappas (1992). We used an independent data set that includes information from all five Great Lakes and assigned them to one of three taxocenes and then related their distribution to 11 different habitat types. We determined whether or not fish of different species or taxocenes use wetlands in proportion to their availability or to the availability of other shoreline features. Finally, we examined the influence of wetland type (i.e., open shoreline versus protected embayment) on the distribution of wetland-dependent fish. By revealing the association between certain species or species complexes and particular shoreline features within the Great Lakes, we attempt to provide a scientifically defensible method for managers and policy makers to target the appropriate shoreline reaches for restoration, preservation, or conservation.

Methods

Data from various published and unpublished sources have been assembled for this study. Chow-Fraser and Albert (1999) used information from the “Atlas of spawning and nursery areas of Great Lakes fishes” (Goodyear et al. 1982) to determine the “biodiversity value” of different stretches of Great Lakes shoreline. This atlas remains the most comprehensive binational survey undertaken to date, containing information on all of the commercially and recreationally important species in the Great Lakes fishery. The 14-volume atlas documents the spawning and nursery location of 139 fish taxa along the entire shoreline of all five Great Lakes. A record in our fish database consisted of geographic coordinates of the site, fish taxonomic information, and other classification information such as taxocene or thermal preferences. Fish occurrences were collected and imported into ArcView Geographical Information System. Close to 9500 of the georeferenced records covering all five Great Lakes and connecting channels from the atlas were imported into the WIRE Net database (Wetland Inventory for Research and Education Network, McMaster University; http://www.wirenet.info). In this study, fish occurrence means spawning and (or) nursery use by a fish species at a particular site because we consider both spawning and nursery to be equally important.

Because of differences in gear type used, and the time of year when surveys were conducted, some species may have been missed, but we feel that this bias will affect a relatively small number of species because of the large number of records in the database. A more serious drawback is that common species may be overrepresented because of multiple entries, since more than one data source (scientific surveys and published studies) may be included for any site. We filtered out this type of sample bias by only including one record for a given species per site (e.g., a marsh), regardless of how many times the given species had been reported at the given site. Goodyear et al. (1982) also admitted to a bias in their database in favour of major recreational or commercial fishes or fish that were major components of the forage base.

The 96 of 139 fish taxa reported in the Goodyear et al. (1982) atlas were first grouped by taxocenes (Table 1). Jude and Pappas (1992) named their taxocenes“Great Lakes”, “transitional”, and “wetlands”. In this study, we have renamed the three taxocenes as “open water”, “intermediate”, and “coastal”, respectively, because we felt that the Great Lakes taxocene could cause confusion. For comparison, we have also used Coker et al.’s (2001) classification system based on temperature preferences to group fish into five categories: “cold” “cold–cool”, “cool”, “cool–warm”, and “warm” water species. The thermal criteria for cold, cool, and warm species are <19.0, 19–25, and >25 °C, respectively, while cold–cool species are those straddling the boundaries between cold and cool and cool–warm species are those straddling the boundaries between cool and warm. Coker et al. (2001) indicated that thermal preference was assigned in accordance with the published or reported preferred summer water temperature for a particular species. When data were available, thermal preferences were indicated by preference of adults for certain temperatures in laboratory experiments. If these were not available, then field temperatures at the time of capture reported by investigators were used. When more than one value or a range of values was available, Coker et al. (2001) used the midpoint.

Substrate type of shoreline

For substrate composite, we used medium resolution vector shoreline data provided by the National Oceanic and Atmospheric Administration (1999) for the Great Lakes – St. Lawrence River. The original 19 categories were regrouped into 11 to make the analysis more ecologically meaningful and manageable (see Table 2). Categories included bedrock, bluff, coarse beach, sandy beach – dune, sandy–silty bank, clay bank, low riverine – coastal plain, composite, wetland, artificial, and unclassified. We also classified wetlands into two subclasses according to geomorphology, “open shoreline” and “protected embayments”, in a manner similar to that used by Keough et al. (1996).

Statistical analysis

The classical statistical techniques (e.g., analysis of variance, χ^2, correlation analysis) assume independence of observations, but many ecological data are spatially autocorrelated and violation of assumption of independence may increase Type I error. One can remove spatial dependency among observations using prewhitening transformation, trend-surface analysis, or spatial variate differencing or by correcting the number of degrees of freedom (Dutilleul 1993).

Ease of calculation and interpretation has made categorical analysis (e.g., χ^2-based methods) a popular choice in habitat utilization studies (Brewer and McCann 1982; Alldredge and Ratti 1986, 1992; Thomas and Taylor 1990). For categorical analysis in the present study, the χ^2 test is appropriate because of the large number of observations in the database (Jongman et al. 1995). To deal with the problem of nonindependence, we followed the advice of Dale and Fortin (2002) who pointed out that a simple approach to the problem would be to acknowledge the existence of positive spatial autocorrelation in the data and then apply a conservative method, the Bonferroni adjustment (Boots 2002; Fortin et al. 2002), to reduce the Type I error rate (α) to a more conservative but

Table 1. Species in this study sorted by taxocene (after Jude and Pappas 1992) and temperature preference (after Coker et al. 2001).

Coastal taxocene		Intermediate taxocene		Open-water taxocene	
Species	Thermal group	Species	Thermal group	Species	Thermal group
Banded killifish (*Fundulus diaphanus*) (5)	Cool	Alewife (*Alosa pseudoharengus*) (228)	Cold	Atlantic salmon (*Salmo salar*) (68)	Cold
Blacknose dace (*Rhinichthys atratulus*) (3)	Cool	Rainbow smelt (*Osmerus mordax*) (519)	Cold	Blackfin cisco (*Coregonus nigripinnis*) (15)	Cold
Brook stickleback (*Culaea inconstans*) (7)	Cool	Trout-perch (*Percopsis omiscomaycus*) (93)	Cold	Bloater (*Coregonus hoyi*) (27)	Cold
Common shiner (*Luxilus cornutus*) (31)	Cool	Spottail shiner (*Notropis hudsonius*) (125)	Cold–cool	Brook trout (*Salvelinus fontinalis*) (73)	Cold
Fantail darter (*Etheostoma flabellare*) (4)	Cool	American eel (*Anguilla rostrata*) (1)	Cool	Chinook salmon (*Oncorhynchus tshawytscha*) (193)	Cold
Gizzard shad (*Dorosoma cepedianum*) (105)	Cool	Black crappie (*Pomoxis nigromaculatus*) (62)	Cool	Coho salmon (*Oncorhynchus kisutch*) (300)	Cold
Golden shiner (*Notemigonus crysoleucas*) (16)	Cool	Creek chub (*Semotilus atromaculatus*) (17)	Cool	Kiyi (*Coregonus kiyi*) (19)	Cold
Iowa darter (*Etheostoma exile*) (6)	Cool	Emerald shiner (*Notropis atherinoides*) (113)	Cool	Lake chub (*Couesius plumbeus*) (31)	Cold
Pugnose shiner (*Notropis anogenus*) (2)	Cool	Johnny darter (*Etheostoma nigrum*) (47)	Cool	Lake herring (*Coregonus artedi*) (320)	Cold
Quillback (*Carpiodes cyprinus*) (23)	Cool	Longnose dace (*Rhinichthys cataractae*) (40)	Cool	Lake trout (*Salvelinus namaycush*) (1150)	Cold
Rock bass (*Ambloplites rupestris*) (83)	Cool	Northern pike (*Esox lucius*) (321)	Cool	Lake whitefish (*Coregonus clupeaformis*) (675)	Cold
White crappie (*Pomoxis annularis*) (32)	Cool	Walleye (*Stizostedion vitreum*) (427)	Cool	Longnose sucker (*Catostomus catostomus*) (70)	Cold
Blacknose shiner (*Notropis heterolepis*) (2)	Cool–warm	White sucker (*Catostomus commersoni*) (229)	Cool	Mottled sculpin (*Cottus bairdi*) (15)	Cold
Central mudminnow (*Umbra limi*) (20)	Cool–warm	Yellow perch (*Perca flavescens*) (410)	Cool	Ninespine stickleback (*Pungitius pungitius*) (25)	Cold
Logperch (*Percina caprodes*) (74)	Cool–warm	Black redhorse (*Moxostoma duquesnei*) (3)	Cool–warm	Pink salmon (*Oncorhynchus gorbuscha*) (107)	Cold
Pugnose minnow (*Opsopoeodus emiliae*) (2)	Cool–warm	Brook silverside (*Labidesthes sicculus*) (25)	Cool–warm	Pygmy whitefish (*Prosopium coulteri*) (5)	Cold
Bigmouth buffalo (*Ictiobus cyprinellus*) (14)	Warm	Mooneye (*Hiodon tergisus*) (7)	Cool–warm	Rainbow trout (*Oncorhynchus mykiss*) (519)	Cold
Black bullhead (*Ameiurus melas*) (12)	Warm	Common carp (*Cyprinus carpio*) (247)	Warm	Round whitefish (*Prosopium cylindraceum*) (130)	Cold
Bluegill (*Lepomis macrochirus*) (44)	Warm	Channel catfish (*Ictalurus punctatus*) (97)	Warm	Sea lamprey (*Petromyzon marinus*) (448)	Cold
Bluntnose minnow (*Pimephales notatus*) (17)	Warm	Flathead catfish (*Pylodictis olivaris*) (2)	Warm	Slimy sculpin (*Cottus cognatus*) (40)	Cold
Bowfin (*Amia calva*) (41)	Warm	Golden redhorse (*Moxostoma erythrurum*) (13)	Warm	Spoonhead sculpin (*Cottus ricei*) (2)	Cold
Brindled madtom (*Noturus miurus*) (3)	Warm	Mimic shiner (*Notropis volucellus*) (6)	Warm	Threespine stickleback (*Gasterosteus aculeatus*) (12)	Cold
Brown bullhead (*Ameiurus nebulosus*) (72)	Warm	Muskellunge (*Esox masquinongy*) (79)	Warm	Brown trout (*Salmo trutta*) (138)	Cold–cool

Table 1 (*concluded*).

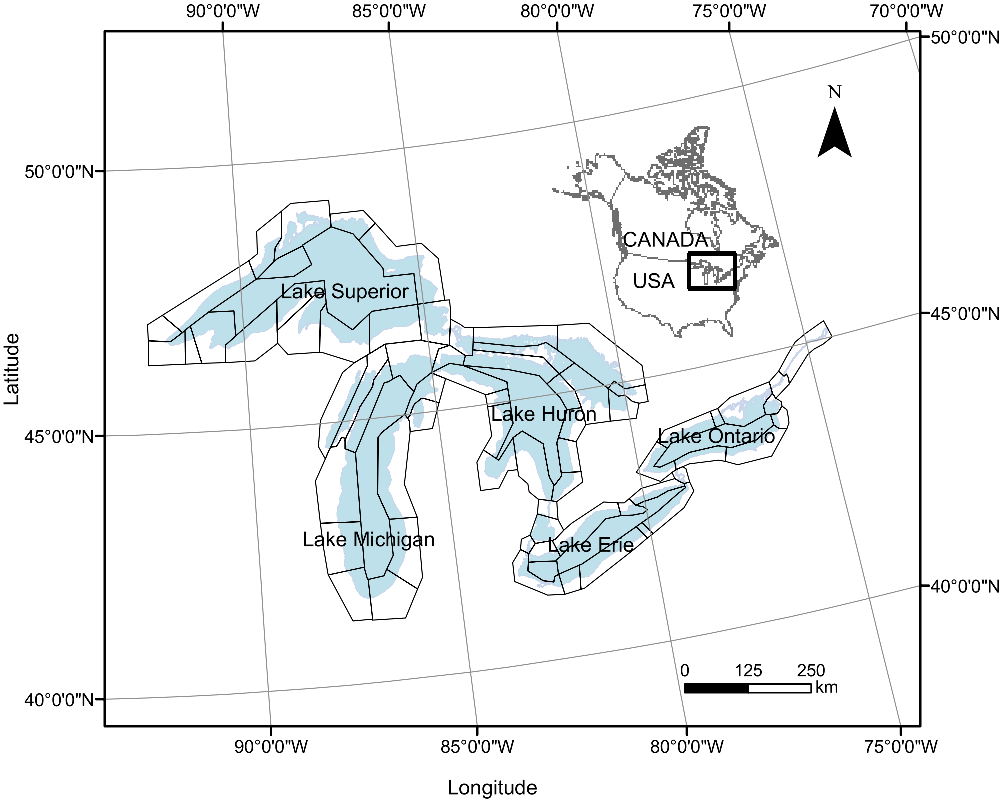
Coastal taxocene		Intermediate taxocene		Open-water taxocene	
Species	Thermal group	Species	Thermal group	Species	Thermal group
Fathead minnow (*Pimephales promelas*) (7)	Warm	Northern hog sucker (*Hypentelium nigricans*) (2)	Warm	Burbot (*Lota lota*) (125)	Cold–cool
Freshwater drum (*Aplodinotus grunniens*) (89)	Warm	Orangespotted sunfish (*Lepomis humilis*) (1)	Warm	Bridle shiner (*Notropis bifrenatus*) (3)	Cool
Goldfish (*Carassius auratus*) (53)	Warm	Shorthead redhorse (*Moxostoma macrolepidotum*) (30)	Warm	Sauger (*Stizostedion canadense*) (18)	Cool
Grass pickerel (*Esox americanus vermiculatus*) (7)	Warm	Smallmouth bass (*Micropterus dolomieu*) (308)	Warm	Silver redhorse (*Moxostoma anisurum*) (17)	Cool
Green sunfish (*Lepomis cyanellus*) (8)	Warm	Stonecat (*Noturus flavus*) (9)	Warm	Lake sturgeon (*Acipenser fulvescens*) (125)	Cool–cold
Lake chubsucker (*Erimyzon sucetta*) (6)	Warm			Channel darter (*Percina copelandi*) (33)	Cool–cold
Largemouth bass (*Micropterus salmoides*) (149)	Warm				
Longnose gar (*Lepisosteus osseus*) (37)	Warm				
Pumpkinseed (*Lepomis gibbosus*) (52)	Warm				
Sand shiner (*Notropis stramineus*) (11)	Warm				
Spotfin shiner (*Cyprinella spiloptera*) (12)	Warm				
Spotted gar (*Lepisosteus oculatus*) (2)	Warm				
Tadpole madtom (*Noturus gyrinus*) (4)	Warm				
White bass (*Morone chrysops*) (123)	Warm				
White perch (*Morone americana*) (32)	Warm				
Yellow bullhead (*Ameiurus natalis*) (7)	Warm				

Note: Numbers in parentheses indicate the total number of occurrences for each species in the database.

arbitrarily chosen value (e.g., $\alpha' = \alpha/5$). In addition, we also used a correction that prevents inflated Type I error related to the number of multiple tests conducted. Thus, the adjusted α was recalculated as $\alpha_{\text{Bonforroni}} = \alpha/(5 \times k)$, where α is 0.05, *k* is the number of tests, and 5 is an arbitrarily chosen value. Therefore, although use of χ^2 may not have been optimal in this study, the comparison of differences between expected and observed use of shoreline features was very useful in revealing the nature of the various associations.

We also wanted to carry out detailed correlation analyses to determine the relationships between different species of fish and their use of wetlands. To correct the effect of spatial autocorrelation, we applied Dutilleul's (1993) correction when carrying out the analyses (Fortin and Payette 2002; Legendre et al. 2002). We divided the shoreline into small segments and counted the number of fish that occurred in each and measured the length of shoreline associated with wetlands within each segment. In this way, we were able to obtain an independent data set of fish and wetland information for each segment. This procedure is referred to as "resampling". Size of sections used for resampling must be appropriate and ecologically meaningful; too small a size would require too much computation and make this approach impractical, whereas too large a size would mask any substantial relationships. We used two methods to divide the shoreline segments for resampling. First, we used Chow-Fraser and Albert's (1999) ecoreach (Fig. 1) delineations to divide the shoreline segments into 44 segments (the development of the ecoreach concept is provided below) and 77 subsegments (P. Chow-Fraser, unpublished data). Second, we superimposed 40 km × 50 km grids over the entire Great Lakes shoreline (total of 198 grid units). Dimensions of the

Fig. 1. Map of 77 ecoreaches for the Great Lakes (modified from Chow-Fraser and Albert 1999).



grid unit were chosen to encompass the maximum length of shoreline feature in the database. For each ecoreach and grid, we calculated fish occurrences and the length of shoreline features. We then used a FORTRAN program, "modtest" (P. Legendre, Program Mod_t_test, Département de sciences biologiques, Université de Montreal, Montréal, QC H3C 3J7, Canada; http://www.fas.umontreal.ca/BIOL/ legendre/) to perform the Dutilleul modified *t* test and to calculate a Pearson correlation coefficient corrected for spatial autocorrelation.

Description of "ecoreach"

In this study, we adopted the use of "ecoreaches" to represent stretches of the Great Lakes shoreline that support important concentrations of coastal wetlands and that are characterized by distinctive conditions for coastal wetland development based on differences in climate, bedrock, geology, glacial geomorphology, shoreline configuration, and sills as well as land use and disturbance factors (Minc 1997). Delineations of many of these ecoreaches do not match existing natural division maps of the Great Lakes area (Albert 1995) based on upland characteristics because coastline conditions reflect a combination of upland and nearshore characteristics. That is, the location of a reach relative to prevailing winds and persistent littoral currents and to areas of erosion (sources of sediment moved along the coast) is of equal importance to the shoreline configuration as are topography and substrates of immediately adjacent uplands. Detailed descriptions of landform and shoreline characteristics, dominant site types, soil substrates, and names of wetlands that are characteristic of each ecoreach are documented in Chow-Fraser and Albert (1999), which includes a detailed list of sources that were consulted to determine the boundaries of ecoreaches.

Results

Categorical analysis between fish and shoreline classes

The three most common shoreline classes where Great Lakes fish occurred were bedrock (includes both resistant and nonresistant, 21.9%), wetlands (includes open-shoreline, semiprotected, and bay-mouth barrier beaches, 21.8%), and sandy beaches – dunes (18.4%) (Table 2). Infrequently used classes included a composite class of unknown composition (0.7%), clay bank (0.8%), sandy–silty bank (2.4%), coastal plain (1.7%), coarse beach (3.7%), and artificial substrate (3.8%). Classes that had intermediate use included bluffs (11.2%) and an unclassified category (13.7%). The fish community used wetlands, sandy beaches – dunes, and bluffs more frequently than expected and bedrock less frequently than expected (χ^2 goodness-of-fit test, $P < 0.0001$, $\alpha_{\mathrm{Bonferroni}} = 0.05/(11 \times 5) = 0.0009$).

Analysis by taxocene

We found that 26.1% of the open-water taxocene was associated with bedrock. Use of this type of shoreline feature by the open-water taxocene was significantly greater than that for the other two taxocenes (17.3% and 17.7% for coastal and intermediate taxocenes, respectively; χ^2 test, $P < 0.0001$, $\alpha_{\mathrm{Bonferroni}} = 0.05/(33 \times 5) = 0.0003$). Sandy beaches – dunes (24.7%), wetlands (17.1%), and bluffs (10.8%) were also

Table 2. Occurrence of fish in different shoreline classes.

Shoreline class	Expected percentage	Expected counts	Observed percentage	Observed counts
Bedrock	**38.9**	3667.2	**21.9**	2062
Bluff	**8.4**	789.4	**11.2**	1057
Coarse beach	5.6	524.5	3.7	345
Sandy beach – dune	**15.0**	1415.4	**18.4**	1734
Sandy – silty bank	1.4	128.6	2.4	228
Clay bank	0.7	67.1	0.8	75
Low riverine – coastal plain	5.3	497.5	1.7	162
Composite	0.4	36.1	0.7	63
Wetland	**16.1**	1520.1	**21.8**	2056
Artificial	2.6	242.4	3.8	359
Unclassified	5.7	541.7	13.7	1289
Total	100.0	9430.0	100.0	9430

Note: Expected percentage = (length of shoreline class / length in total) × 100. Expected counts = (numbers of occurrences of fish × percentage). Observed percentage = (observed counts / total occurrence of fish) × 100. Observed counts = numbers of occurrences of fish associated with a shoreline class. Numbers in bold indicate that there is a significant difference between expected and observed after Bonferroni adjustment has been applied at $\alpha = 0.05/(11 \times 5)$.

Table 3. Number of fish associated with shoreline classes within three taxocenes.

		Taxocene			
Shoreline class	Expected percentage	Coastal	Intermediate	Open water	All taxocenes
Bedrock	38.9	211 (17.3)	613 (17.7)	1238 (**26.1**)	2062 (21.9)
Bluff	8.4	138 (11.3)	407 (11.8)	512 (10.8)	1057 (11.2)
Coarse beach	5.6	18 (1.5)	71 (2.1)	256 (5.4)	345 (3.7)
Sandy beach – dune	15.0	66 (5.4)	495 (14.3)	1173 (24.7)	1734 (18.4)
Sandy–silty banks	1.4	38 (3.1)	119 (3.4)	71 (1.5)	228 (2.4)
Clay bank	0.7	15 (1.2)	41 (1.2)	19 (0.4)	75 (0.8)
Low riverine – coastal plain	5.3	37 (3.0)	97 (2.8)	28 (0.6)	162 (1.7)
Composite	0.4	0 (0)	10 (0.3)	53 (1.1)	63 (0.7)
Wetland	16.1	378 (**31.1**)	865 (**25.0**)	813 (17.1)	2056 (**21.8**)
Artificial	2.6	61 (5.0)	143 (4.1)	155 (3.3)	359 (3.8)
Unclassified	5.7	255 (21.0)	600 (17.3)	434 (9.1)	1289 (13.7)
Total	100.0	1217	3461	4752	9430

Note: Numbers in parentheses are percentages. Numbers in bold indicate that they are the highest for the taxocene.

Table 4. Number of fish associated with shoreline classes within thermal preference groups.

	Thermal preference					
Shoreline class	Cold	Cold–cool	Cool	Cool–warm	Warm	Total
Bedrock	1303 (**25.4**)	71 (13.8)	351 (17.4)	38 (**22.9**)	299 (18.7)	2062 (21.9)
Bluff	562 (10.9)	73 (14.2)	227 (11.2)	30 (18.1)	165 (10.3)	1057 (11.2)
Coarse beach	262 (5.1)	12 (2.3)	38 (1.9)	3 (1.8)	30 (1.9)	345 (3.7)
Sandy beach – dune	1279 (24.9)	83 (16.2)	253 (12.5)	7 (4.2)	112 (7.0)	1734 (18.4)
Sandy–silty bank	81 (1.6)	18 (3.5)	72 (3.6)	9 (5.4)	48 (3.0)	228 (2.4)
Clay bank	21 (0.4)	6 (1.2)	25 (1.2)	2 (1.2)	21 (1.3)	75 (0.8)
Low riverine – coastal plain	36 (0.7)	7 (1.4)	68 (3.4)	2 (1.2)	49 (3.1)	162 (1.7)
Composite	52 (1.0)	5 (1.0)	6 (0.3)	0 (0)	0 (0)	63 (0.7)
Wetland	868 (16.9)	120 (**23.4**)	542 (**26.8**)	31 (18.7)	495 (**31.0**)	2056 (21.8)
Artificial	169 (3.3)	23 (4.5)	87 (4.3)	11 (6.6)	69 (4.3)	359 (3.8)
Unclassified	500 (9.7)	95 (18.5)	353 (17.5)	33 (19.9)	308 (19.3)	1289 (13.7)
Total	5133	513	2022	166	1596	9430

Note: Numbers in parentheses are percentages. Numbers in bold indicate that they are the highest for the group.

Table 5. Summary of correlation analyses for 25 fishes of the most abundant study species, which accounted for 80% of the fish occurrences.

Species	Pearson r by ecoreach resampling	P	Pearson r by grid resampling	P
Largemouth bass (C)	0.62653	**0.00263**	0.48418	**0.00404**
Gizzard shad (C)	0.30925	0.17835	0.25355	0.26007
Common carp (I)	0.40187	**0.00903**	0.33029	**0.02294**
Emerald shiner (I)	0.63841	**0.00764**	0.39918	**0.05702**
Northern pike (I)	0.57417	**0.00001**	0.43713	**0.00014**
Smallmouth bass (I)	0.43833	**0.01225**	0.32917	**0.01589**
Walleye (I)	0.52120	**0.00003**	0.40030	**0.00319**
Yellow perch (I)	0.55336	**0.00003**	0.46045	**0.00020**
Rainbow smelt (I)	0.13365	0.29795	0.25732	**0.01407**
Alewife (I)	0.19428	0.22837	0.20325	0.07421
Spottail shiner (I)	0.30467	0.12953	0.43135	**0.00591**
White bass (I)	0.23201	0.35469	0.22884	0.23583
White sucker (I)	0.05236	0.75798	0.21220	0.09707
Brown trout (O)	0.04420	0.79251	0.18301	0.20457
Burbot (O)	0.13034	0.46117	0.16825	0.28619
Chinook salmon (O)	–0.12042	0.42289	–0.01826	0.88384
Coho salmon (O)	–0.04538	0.75159	0.05423	0.62398
Lake trout (O)	0.08646	0.51231	–0.06632	0.54090
Pink salmon (O)	–0.09863	0.61812	–0.03304	0.86894
Rainbow trout (O)	–0.01937	0.88205	0.09872	0.31573
Sea lamprey (O)	0.12172	0.37750	0.19758	0.07251
Lake sturgeon (O)	0.61444	**0.00025**	0.56425	**0.00010**
Lake herring (O)	0.33458	**0.01496**	0.23469	**0.04857**
Lake whitefish (O)	0.33190	**0.01272**	0.30342	**0.00480**
Round whitefish (O)	0.36807	**0.05337**	0.07561	0.64704

Note: C, coastal; I, intermediate; O, open water. $P < 0.05$ indicated in bold.

widely used by the open-water taxocene (Table 3). These four shoreline classes together accounted for about 80% of the observed occurrences of the open-water taxa along the Great Lakes shoreline. Given that 16% of all shoreline classes were wetlands (Table 2) and 17% of the open-water taxocene was associated with wetlands, these fish were probably using wetlands in proportion to their availability. By comparison, 25% of all occurrences corresponding to the intermediate taxocene were associated with wetlands, indicating that fish in the intermediate taxocene significantly preferred coastal wetland habitat. Other shoreline habitats that were relatively well used by this taxocene included bedrock (17.7%), sandy beaches – dunes (14.3%), and bluffs (11.8%) (Table 3). These four shoreline classes together accounted for almost 70% of the observed distribution of the intermediate taxocene in the nearshore zone of the Great Lakes. Almost a third of the fish in the coastal taxocene were associated with coastal wetlands (31.1%) (Table 3), indicating a very high preference for wetland habitat. Other shoreline habitats that were spatially associated with this group included bedrock (17.3%) and bluffs (11.3%).

Analysis by thermal preference

A breakdown of fish occurrence among the 11 shoreline classes for the five thermal groups (i.e., cold, cold–cool, cool–cold, cool–warm, and warm) (Table 4) ($P < 0.0001$, $\alpha_{\text{Bonferroni}} = 0.05/(55 \times 5) = 0.00018$) showed that all five groups made extensive use of the four shoreline classes: bedrock, wetlands, sandy beach – dunes, and bluffs. However, when all shoreline classes were considered, bedrock was used most frequently by the cold-water (25.4%) and cool–warm (22.9%) taxa, indicating that these fish were using this habitat type in excess of its availability (21.9%). Wetlands, which co-occurred with 21.8% of the fish, were overutilized by the warm (31.0%), cool (26.8%), and cold–cool (23.4%) taxa. By comparison, sandy beach – dunes, which accounted for 18.4% of the used habitat, were used more than expected by the cold-water group (24.9%) but were underutilized by the cold–cool (16.2%), cool (12.5%), cool–warm (4.2%), and warm (7.0%) taxa.

Dutilleul modified *t* test of correlation between wetland and fish

Up to this point, we analyzed data using a χ^2 test on categorical data. We wanted to perform a more rigorous test to directly examine the correlation between wetland and fish. We pooled the data and found a highly significant correlation between wetlands and the presence of all species, regardless of taxocene or temperature preferences, and this was true when we resampled by ecoreach (Pearson $r = 0.60279$, $P < 0.00001$) or by shoreline grids (Pearson $r = 0.53534$, $P < 0.00001$).

Correlation by taxocene

When we sorted fish data by taxocene and performed the correlation analysis separately for each species complex, using

Table 6. Summary of correlation analyses for the 13 most abundant wetland-dependent fish species.

Species	Wetland type	Pearson r by ecoreach resampling	P	Pearson r by grid resampling	P
Largemouth bass (C)	PE	0.21498	0.39617	0.47089	**0.01595**
	OS	0.58273	**0.01984**	0.32502	0.16782
Gizzard shad (C)	PE	0.54499	**0.00783**	0.58024	**0.01065**
	OS	0.01273	0.97569	–0.07291	0.78411
Common carp (I)	PE	0.45868	**0.00239**	0.50280	**0.00015**
	OS	0.23486	0.34589	0.10343	0.59224
Emerald shiner (I)	PE	0.62559	**0.00254**	0.75615	**0.00016**
	OS	0.45634	0.18628	–0.03600	0.91231
Northern pike (I)	PE	0.60117	**0.00002**	0.43288	**0.00043**
	OS	0.26089	0.15036	0.27104	0.07507
Smallmouth bass (I)	PE	0.28233	0.13964	0.31385	**0.03122**
	OS	0.35034	0.09861	0.40666	**0.01414**
Walleye (I)	PE	0.52120	**0.00003**	0.61774	**0.00001**
	OS	0.39677	**0.05199**	0.12777	0.44339
Yellow perch (I)	PE	0.61386	**0.00001**	0.61546	**0.00001**
	OS	0.35468	0.06911	0.25465	0.10136
Rainbow smelt (I)	PE	0.23156	**0.05551**	0.36948	**0.00027**
	OS	0.10261	0.62064	0.14140	0.35058
Alewife (I)	PE	0.12035	0.42636	0.20946	0.09161
	OS	0.31244	0.13544	0.21207	0.21644
Spottail shiner (I)	PE	0.02532	0.88934	0.43148	**0.00896**
	OS	0.50803	0.12736	0.38045	**0.03239**
White bass (I)	PE	0.62533	**0.00215**	0.59268	**0.00930**
	OS	–0.27044	0.50746	–0.16921	0.48257
White sucker (I)	PE	0.02590	0.87767	0.17044	0.21383
	OS	0.08644	0.70362	0.29662	0.11370

Note: C, coastal; I, intermediate; O, open water; PE, protected embayment; OS, open shoreline. $P < 0.05$ indicated in bold.

the ecoreach to resample, both the coastal and intermediate taxocenes exhibited a highly significant positive correlation with wetlands (Pearson $r = 0.49553$, $P = 0.00154$ and Pearson $r = 0.62993$, $P < 0.00001$, respectively). By comparison, when we used shoreline grids to resample, we still obtained a significant positive correlation for these two taxocenes, even though the correlation coefficients were lower (Pearson $r = 0.38185$, $P = 0.01657$ and Pearson $r = 0.53568$, $P < 0.00001$ for coastal and intermediate taxocenes, respectively). In contrast, the open-water species complex was not significantly correlated with wetlands when we used ecoreaches to resample (Pearson $r = 0.15955$, $P = 0.20691$) and was only weakly correlated with wetlands when we used shoreline grids to resample (Pearson $r = 0.21921$, $P = 0.01686$).

Correlation by thermal group

We then sorted the data by thermal group and performed correlation analysis for each of the five groupings. Regardless of the units we used to resample, the warm (ecoreaches: Pearson $r = 0.62715$, $P < 0.00001$; grids: Pearson $r = 0.48708$, $P = 0.00034$), cool (ecoreaches: Pearson $r = 0.62260$, $P < 0.00001$; grids: Pearson $r = 0.51405$, $P < 0.00001$), and cold–cool groups (ecoreaches: Pearson $r = 0.45147$, $P = 0.00072$; grids: Pearson $r = 0.46065$, $P = 0.00002$) were significantly and positively correlated with wetlands. By comparison, there was either no significant correlation or only a weak correlation between wetlands and cold (ecoreaches: Pearson $r = 0.14441$, $P = 0.25412$; grids: Pearson $r = 0.20960$, $P = 0.02234$) and cool–warm taxa (ecoreaches: Pearson $r = 0.20244$, $P = 0.43364$; grids: Pearson $r = 0.20903$, $P = 0.26760$).

Correlation by species

We also calculated correlation coefficients for the top 25 species (by occurrence), which accounted for 80% of the data (Table 5). With ecoreach resampling, we found the distribution of 11 taxa to be significantly correlated with wetlands. Seven of these were consistent with the classification of Jude and Pappas (1992) as either coastal or intermediate (common carp (*Cyprinus carpio*), emerald shiner (*Notropis atherinoides*), largemouth bass (*Micropterus salmoides*), northern pike (*Esox lucius*), smallmouth bass (*Micropterus dolomieu*), walleye (*Stizostedion vitreum*), and yellow perch (*Perca flavescens*) (Table 1). Unexpectedly, there were four open-water taxa (lake herring (*Coregonus artedi*), lake whitefish (*Coregonus clupeaformis*), round whitefish (*Prosopium cylindraceum*), and lake sturgeon (*Acipenser fulvescens*) (Table 1) that were also significantly correlated with wetlands. Consistent with expectations, there were eight open-water species that were not significantly correlated with wetlands (brook trout (*Salvelinus fontinalis*), chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch*), lake trout (*Salvelinus namaycush*), pink salmon (*Oncorhynchus gorbuscha*), rainbow trout (*Oncorhynchus mykiss*), sea lamprey (*Petromyzon marinus*), and burbot (*Lota lota*) (Table 5). Nevertheless, six species that were classified as being either coastal or intermediate were not significantly correlated with wetlands (alewife (*Alosa pseudoharengus*), gizzard shad (*Dorosoma cepedianum*), white bass (*Morone chrysops*), rainbow smelt (*Osmerus mordax*), spottail shiner (*Notropis hudsonius*), and white sucker *Catostomus commersoni*).

Resampling the shoreline with the grid increased the number of significant positive associations from seven to nine species within the coastal and intermediate designations (Table 5) and reduced the positive associations in the open-water taxocene by one. Therefore, the correlation revealed by the grid resampling appeared to be more consistent with the classification of Jude and Pappas (1992). Regardless of resampling strategies, however, we found some wetland-dependent taxa identified by Jude and Pappas (1992) to be distributed independently of wetlands. We speculated that these anomalies might be due to confounding effects of lumping wetland types together in the analysis, since some fish are known to prefer quiescent environments within protected embayments, while others can tolerate or even prefer exposed habitats of open-shoreline wetlands. Therefore, we recalculated correlation coefficients for the 13 coastal and intermediate taxa after accounting for differences in site type (Table 6). This procedure increased the number of significant associations from seven to nine species when we used the ecoreaches to resample and from nine to 11 when we used the shoreline grid to resample. Accounting for wetland type revealed that gizzard shad, rainbow smelt, and white bass were associated with protected embayments, even though we were unable to determine such a significant association when wetland types were lumped.

Discussion

Coastal wetlands are important to fish because of the presence of emergent and submergent plants that provide shelter and a food source for benthic invertebrates (Chow-Fraser et al. 1998; Lougheed and Chow-Fraser 1998) and epiphytic algae on which larval and juvenile fish feed during their first few months of life (McNair and Chow-Fraser 2003). In turn, these fish become prey for both resident and migratory piscivores. Another reason for the preferred utilization of coastal wetlands by fishes is that coastal wetlands are warm and sheltered from the often-harsh wave conditions of the open water. It is therefore desirable to have a means to accurately predict which of the Great Lakes fishes depend on wetlands for nursery and spawning habitat so that managers can estimate the impact on the Great Lakes fishery when wetland habitats are lost or restored.

For the most part, we have validated that Jude and Pappas' (1992) classification can be applied to Great Lakes fishes to predict their dependence on wetland versus nonwetland habitat. Of the 25 most abundant species examined, we accurately predicted their preference for or against wetland habitat for 19 and 20 taxa with ecoreach and grid resampling, respectively, once we accounted for wetland site type (either as open shoreline or protected embayment). Furthermore, our results indicate that the fish community, as a whole or when classified according to taxocene or temperature preferences, used wetlands in excess of their availability. The highly significant positive association between warm- and cool-water fish and wetlands was not surprising, since most of these also belonged to the coastal and intermediate taxocenes. We also found a significant positive correlation between cold–cool species and wetlands, and this was somewhat unexpected for burbot and brown trout (*Salmo trutta*) but not for the spottail shiner, which is a common species in coastal wetlands of the lower Great Lakes (T. Seilheimer and P. Chow-Fraser, personal observation). The lack of a significant correlation between cool–warm taxa and wetlands may have been due to their relatively small sample size (six of the seven species having observations <25). By comparison, we expected the distribution of cold-water taxa to vary independently with wetlands, since these species correspond primarily to the open-water taxocene that associated more strongly with bedrock, coarse beaches, and sandy beach – dunes than with wetlands.

We also found that wetland type (i.e., open-shoreline wetland versus protected embayment) influenced the distribution of certain wetland-dependent taxa. The results from the correlation analysis with ecoreach resampling suggested that common carp, emerald shiner, gizzard shad, northern pike, rainbow smelt, walleye, white bass, and yellow perch favour protected embayments for spawning and (or) nurseries. In contrast, alewife, largemouth bass, smallmouth bass, and spottail shiner appeared to favour open-shoreline wetlands. The results from correlation analysis with grid resampling were consistent with those resampled by ecoreach except for largemouth bass and spottail shiner.

There were several departures from expected based on Jude and Pappas' (1992) classification and knowledge of the temperature preferences of the fish in question. The lack of a significant correlation between the distribution of white sucker and alewife with either wetland type could have been due to sampling bias related to the timing of surveys. These intermediate taxa are migratory species that swim into wetlands to spawn during early spring (Scott and Crossman 1998) and may have been undersampled if surveys had been conducted only in midsummer and fall. The positive association between lake sturgeon and wetlands is not surprising because of their presence in deeper areas of Lake St. Clair and the connecting channels (M. Thomas, Michigan Department of Natural Resources, Mt. Clemens, 33135 South River Road, Mt. Clemens, MI 48045, USA, personal communication); hence, even though it is classified as a cold-water species and an open-water taxocene, it is probably dependent on deeper areas of wetlands. We also found a significant positive association between wetlands and two other open-water, cold-water species, lake herring and lake whitefish. Mitsch and Gosselink (2000) have indicated that lake herring utilize coastal marshes or protected embayments for at least parts of their life cycle, and several investigators have observed a number of larval lake whitefish and lake herring in shallow areas along the St. Marys River (<2 m) (Clady 1976; Liston et al. 1986; Jude et al. 1998) and in Grand Traverse Bay (<3 m) (Freeberg et al. 1990). Therefore, wetlands are probably very important habitat for at least these open-water taxa, and the extent to which others may depend on wetlands should be verified with future field surveys.

In addition to coastal wetlands, our study also indicated that nearshore waters associated with bedrock, sandy beach – dunes, and bluffs are widely used as reproductive habitats by the Great Lakes fish community. These three shoreline features are well represented along the Great Lakes shoreline and account for 62% of the total shoreline length. Frequent occurrence of fish in these nearshore areas probably reflects use by both permanent residents as well as migratory fish (e.g., anadromous fishes) that use these for temporary feeding or nursery grounds (Edsall and Charlton 1997).

To our knowledge, this study is one of the most extensive examinations of fish distribution patterns at the scale of the Great Lakes basin. We have confirmed that the Great Lakes fish community, especially species identified as wetland dependent by Jude and Pappas (1992) (transitional and wetlands taxocenes), preferentially use coastal wetlands for spawning and nursery habitat. We also confirmed that the distribution of wetland-associated taxa is influenced by wetland type (i.e., protected embayment versus open-shoreline wetland) and that the Great Lakes fish community utilize certain shoreline features (especially wetlands) disproportionately to their availability. Future studies should determine the specific environmental attributes (water or substrate quality, food web components, etc.) in wetlands that make these habitats important for the particular species complexes.

Acknowledgements

Funding for this study was provided as a research grant from the Great Lakes Fishery Commission to P.C.-F. We thank Drs. C.K. Minns, D.J. Jude, and an anonymous referee for constructive comments on an earlier draft and the exceptionally helpful advice of Drs. M.-J. Fortin and P. Peres-Neto on using appropriate spatial statistics.

References

Albert, D.A. 1995. Regional landscape ecosystems of Michigan, Minnesota, and Wisconsin: a working map and classification. US For. Serv. Gen. Tech. Rep. NC-178.

Alldredge, J.R., and Ratti, J.T. 1986. Comparision of some statistical techniques for analysis of resource selection. J. Wildl. Manag. **50**: 157–165.

Alldredge, J.R., and Ratti, J.T. 1992. Further comparision of some statistical techniques for analysis of resource selection. J. Wildl. Manag. **56**: 1–9.

Boots, B. 2002. Local measures of spatial association. Ecoscience, **9**: 168–176.

Brewer, E., and McCann, M.T. 1982. Laboratory and field manual of ecology. Saunders College Publishing, Fort Worth, Tex.

Chow-Fraser, P., and Albert, D. 1999. Biodiversity Investment Areas for coastal wetlands ecosystems. *In* State of the Great Lakes Ecosystem Conference, 1998. US Environmental Protection Agency and Environment Canada, Buffalo, N.Y.

Chow-Fraser, P., Lougheed, V.L., Crosbie, B., LeThiec, V., Simser, L., and Lord, J. 1998. Long-term response of the biotic community to fluctuating water levels and changes in water quality in Cootes Paradise Marsh, a degraded coastal wetland of L. Ontario. Wetlands Ecol. Manag. **6**: 19–42.

Chubb, S.L., and Liston, C.R. 1986. Density and distribution of larval fishes in Pentwater Marsh, a coastal wetland on Lake Michigan. J. Gt. Lakes Res. **12**: 332–343.

Clady, M.D. 1976. Distribution and abundance of larval ciscoes, *Coregonus artedii*, and burbot, *Lota lota*, in Oneida Lake. J. Gt. Lakes Res. **2**: 234–247.

Coker, G.A., Portt, C.B., and Minns, C.K. 2001. Morphological and ecological characteristics of Canadian freshwater fishes. Can. Manuscr. Rep. Fish. Aquat. Sci. No. 2554.

Dale, M.R.T., and Fortin, M.-J. 2002. Spatial autocorrelation and statistical tests in ecology. Ecoscience, **9**: 162–167.

Dutilleul, P. 1993. Modifying the *t* test for assessing the correlation between two spatial processes. Biometrics, **49**: 305–314.

Edsall, T.A., and Charlton, M.N. 1997. Near-shore waters of the Great Lakes. *In* State of the Great Lakes Ecosystem Conference, 1996. US Environmental Protection Agency and Environment Canada, Windsor, Ont.

Fortin, M.-J., and Paytte, S. 2002. How to test the significance of the relation between spatially autocorrelated data at the landscape scale: a case study using fire and forest map. EcoScience, **9**: 213–218.

Fortin, M.-J., Dale, M.R.T., and Hoef J.V. 2002. Spatial analysis in ecology. *In* Encyclopedia of environmetrics. Vol. 4. *Edited by* A.H. El-Shaarawi and W.W. Piegorsch. John Wiley & Sons, Ltd., Chichester, UK. pp. 2051–2058.

Freeberg, M.H., Taylor, W.W., and Brown, R.W. 1990. Effect of egg and larval survival on year-class strength of lake whitefish in Grand Traverse Bay, Lake Michigan. Trans. Am. Fish. Soc. **119**: 92–100.

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

Jongman, R.H.G., ter Braak, C.J.F., and Van Tongeren, O.F.R. 1995. Data analysis in community and landscape ecology. Cambridge University Press, Cambridge, UK.

Jude, D.J., and Pappas, J. 1992. Fish utilization of Great Lakes coastal wetlands. J. Gt. Lakes Res. **18**: 651–672.

Jude, D.J., Tesar, F.J., and Tin, H.T. 1998. Spring distribution and abundance of larval fishes in the St. Marys River, with a note on potential effects of freighter traffic on survival of eggs and larvae. J. Gt. Lakes Res. **24**: 569–581.

Keough, J.R., Thompson, T.A., Guntenspergen, G.R., and Wilcox, D.A. 1996. Hydrogeomorphic factors and ecosystem responses in coastal wetlands of the Great Lakes. Wetlands, **19**: 821–834.

Legendre, P., Dale, M.R.T., Fortin, M.-J., Gurevitch, J., Hohn, M., and Myers, D. 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. Ecography, **25**: 601–615.

Liston, C.R., McNabb, C.D., Brazo, D., Bohr, J., Craig, J., Duffy, W., Fleischer, G., Knoeckleuin, G., Koehler, F., Ligman, R., O'Neal, R., Siami, M., and Roettger, P. 1986. Environmental baseline studies of the St. Marys River during 1982 and 1983 prior to proposed extension of the navigation season. Biol. Rep. 85(2). Office of Biological Services, Fish and Wildlife Service, US Department of the Interior, Twin Cities, Minn.

Lougheed, V.L., and Chow-Fraser, P. 1998. Factors that regulate the community structure of a turbid, hypereutrophic Great Lakes wetland. Can. J. Fish. Aquat. Sci. **55**: 150–161.

McNair, S., and Chow-Fraser, P. 2003. Change in biomass of benthic and planktonic algae along a disturbance gradient for 24 Great Lakes coastal wetlands. Can. J. Fish. Aquat. Sci. **60**: 676–689.

Minc, L.D. 1997. Great Lakes coastal wetlands: an overview of controlling abiotic factors, regional distribution, and species composition. A report submitted to Michigan Natural Features Inventory, December 1997. Funded by EPA Great Lakes National Program Office (Federal Grant GL9 95810-02) through the Nature Conservancy's Great Lakes Program Office. Michigan Natural Features Inventory, Lansing, Mich.

Mitsch, W.J., and Gosselink, J.G. 2000. Wetlands. 3rd ed. John Wiley & Sons, Inc., New York.

National Oceanic and Atmospheric Administration. 1999. Metadata for the Great Lakes and St. Lawrence River medium resolution vector shoreline data. Great Lakes Environmental Research Laboratory, Ann Arbor, Mich. Available from http://www.glerl.noaa.gov/data/char/glshoreline.html.

Scott, W.B., and Crossman, E.J. 1998. Freshwater fishes of Canada. Galt House Publications Ltd., Oakville, Ont.

Stephenson, T.D. 1990. Fish reproductive utilization of coastal marshes of Lake Ontario near Toronto. J. Gt. Lakes Res. **16**: 71–81.

Thomas, D.L., and Taylor, E.J. 1990. Study designs and tests for comparing resource use and availability. J. Wildl. Manag. **54**: 322–330.