A SPATIAL ANALYSIS OF FISH HABITATS IN COASTAL WETLANDS

A SPATIAL ANALYSIS OF FISH HABITATS IN COASTAL WETLANDS OF THE LAURENTIAN GREAT LAKES

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GENERAL ABSTRACT

The overall objective of this study was to provide a spatial pattern analysis of fish distribution in the Great Lakes and to relate these patterns to shoreline features such as coastal wetlands, tributaries and substrate type. Very little is known regarding the distribution patterns of fish in the Great Lakes at the geographical scale of each lake basin.

I first explored whether there were systematic patterns in distribution of fish and coastal wetlands by looking at density maps of each and calculating nearest neighbor distances. I used three different classification schemes to sort the 139 fish taxa into functional categories to produce ecologically meaningful distribution maps. There were striking differences in the overall distribution pattern of nursery and spawning habitat in the five Great Lakes when data were compared for Jude and Pappas' classification taxocenes: open-water, intermediate and coastal. Overall, open-water species were the most abundant, and were also widely distributed throughout all five lakes. Coastal species were the least abundant and appeared to be restricted to the two lower lakes. The distribution pattern of coastal and intermediate taxa overlapped a great deal; both taxocenes made extensive use of the two lower lakes for spawning and nursery habitat during this synoptic survey, especially in western Lake Erie and eastern Lake Ontario. Fish distribution patterns sorted by thermal preference and by reproductive guild were compared with those sorted by taxocene. Results from a chi-square analysis indicated a high degree of overlap between thermal classes and taxocenes. There were also positive

associations between many reproductive guilds and the three taxocenes, although these were not as strong as the previous comparison.

I then examined spatial association between distributions of fish and coastal wetlands and other geomorphic features by testing the distribution of fish along the shore of the Great Lakes and calculating the correlation between fish and coastal wetlands of Lake Ontario.

A chi-square goodness-of-fit test indicated strong associations between the distribution of fish and three shoreline classes: (wetland, sandy beach/dunes and bluff) and fish used coastal wetlands preferentially for spawning and nursery habitat at a basin-wide scale. Bivariate pattern analysis indicated that occurrences of fish in L. Ontario were positively associated with both coastal wetlands and tributaries, although the relationship was considerably weaker for tributaries than for wetlands.

Results from this study indicated that 1) Fish have an aggregated distribution pattern along the shores of Great Lakes and L. Ontario; 2) Coastal wetlands have an aggregated distribution pattern along the shores of Great Lakes and L. Ontario; 3) Spatial distribution of fish and wetlands is positively associated; 4) The preferred utilization of coastal wetlands by majority of the Great Lakes fishes is consistent across geographic scales, from the site level to that of the entire Great Lakes basin.

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GENERAL INTRODUCTION

Fisheries resources of the Great Lakes have been changing since European settlement in the early 19th century. The greatest commercial fishing harvests were recorded in 1889 and 1899 at about 147 million pounds. Over the following century, however, harvests declined, and in 1996, only about 63 million pounds of fish were caught commercially in the basin. Three major factors that currently limit fish production in the Great Lakes are: 1) deterioration in water quality (resulting from inputs of both nutrients and toxic contaminants), 2) spread of aquatic nuisance species, and 3) habitat degradation and loss (Environment Canada and EPA 1995). Government programs implemented in the 1970s and 1980s to improve water quality have to a large extent, achieved their objectives. Since the 1950s, sea-lamprey control and fishing quotas have greatly helped to restore the health of the fisheries. In response to the series of Ponto-Caspian species invasions in the late 1980s, individual Great Lakes Sea Grant programs initiated major research programs to study the ecological impacts of these exotic invaders and to develop control techniques. Relatively little research has been devoted to measure the quality and quantity of fish habitat, and to implement programs to conserve and protect them (Goodyear et al. 1982).

Dodge and Kavetsky (1995) divided habitats of the Great Lakes into the following types: open-lake, coastal wetland, shoreline, tributaries, connecting channels and inland habitats. Of these, coastal wetlands have received more attention recently because these habitats are among the most productive ecosystems in the world, comparable to tropical rain forests and coral reefs according to the National Oceanographic and Atmospheric Agency (NOAA) (http://www.nmfs.noaa.gov/habitat/habitatprotection/wetlands.htm), and have disappeared at an alarming rate throughout settled regions of the Laurentian Great Lakes (Herdendorf, 1981; Whillans, 1982; Dahl, 1990 from Brazner, 1997; Jude and Pappas, 1992). Environmental agencies in many federal and state/provincial jurisdictions have initiated programs in the last decade to restore and protect the remaining wetlands, and to conduct research to better understand the relationship between habitat quality and the Great Lakes fish community.

Formation and classification of coastal wetlands

In general, a wetland can be operationally defined as "land where the water table is at, near, or above the land surface long enough to promote the formation of hydric soils or to support the growth of hydrophytes (Cowardin et al. 1977). In their extensive inventory of coastal Great Lakes wetlands, Herdendorf and Hartley (1981) identified "coastal" wetlands as those located entirely or partially within 1000 feet of the shoreline of the Great Lakes and their connecting channels. Chow-Fraser and Albert (1999) modified this definition further to include only those wetlands that are hydrologically linked with the Great Lakes or connecting channels, and it is this definition that is adopted in the present study.

Many of the coastal marshes were formed behind coastal barriers, in deltas and behind natural levees deposited by the Pleistocene ice sheets, and their ecology and geomorphology continue to be affected by large-lake processes such as wave and wind action, ice-scour and especially long- and short-term water-level fluctuations (Herdendorf and Hartley 1981; Dodge and Kavetsky 1995). Accordingly, Great Lakes wetlands can be classified as the following seven wetland types based on how they are influenced by Great Lakes processes (International Lake Erie Regulation Study Board, 1981; from Dodge and Kavetsky, 1995).

- Open shoreline wetlands
- Unrestricted bays
- Shallow sloping beach wetlands
- River deltas
- Restricted riverine wetlands
- Lake-connected inland wetlands
- Protected (or Barrier beach) wetlands

Various other classification schemes have been developed based on other criteria. For instance, the Ontario Ministry of Natural Resources (OMNR; 1993) first classifies all wetlands into four basic types: "marshes", "swamps", "bogs" and "fens"; OMNR also independently sorts wetlands (regardless of types) into four *site types*: "riverine", "lacustrine", "palustrine", and "isolated", which describes their association with other geographic features such as rivers (riverine) and lakes (lacustrine). Hence, coastal wetlands could be a riverine or lacustrine marsh, swamp, bog or fen. By comparison, in the Environmental Sensitivity Atlases, Environment Canada separates Great Lakes coastal wetlands into only two classes: "fringing" and "broad" wetlands and disregards site types. The Michigan Natural Features Inventories (MNFI) classifies coastal wetlands into *aquatic system* and *site types* (Chow-Fraser and Albert 1999). The aquatic system includes lacustrine, connecting channel, riverine, and lacustrine or freshwater estuary. Further division of the aquatic systems into site types includes:

- Open embayment
- Protected embayment
- Barrier beach lagoon
- Sand-spit embayment and sand-spit swale
- Dune and swale complex
- Tombolo
- Channel-side wetland
- Channel embayment
- Delta
- Open estuary
- Barred estuary

Maynard and Wilcox (1997) used "geomorphological settings" to describe wetland site types while others have used a combination form, "glacial landforms (site types)", to describe *site types*. In their review, Chow-Fraser and Albert (1999) recognized there were different uses of "site type" by Canadian and U.S. researchers and developed a single classification scheme with 17 site types that incorporated elements from both the OMNR and MNFI classification system in an effort to encourage data integration from different sources. In 2001, the Great Lakes Coastal Wetlands Consortium (http://www.glc.org/monitoring/wetlands/) proposed yet another classification scheme that avoids the use of "site types" but includes three specific *systems* based on their dominant hydrologic source and current hydrologic connectivity to each lake, and ten wetland *types* based on their geomorphic features and shoreline processes. Despite the clear need for the scientific community to endorse a standardized classification scheme, there is not yet widespread adoption of any of these schemes, and choice of using one scheme over another remains arbitrary.

Distribution and origin of coastal wetlands in the Great Lakes

Much of the Great Lakes Basin was covered by ice during the Wisconsin glaciation of the Pleistocene Epoch. The five Great Lakes, with their outlets and approximate lake levels as they are today, probably date back less than 5,000 years (U.S. Army Corps of Engineers 1971; from Herdendorf and Hartley 1981). The processes of stream and shoreline erosion have only made moderate changes in the original topography, but these slight changes are significant in the origin and development of coastal wetlands. Although the gross configuration of the Great Lakes has been little altered since their glacial development, formation of deltas, estuaries and creation of sand dunes and lagoons have created many favorable conditions for development of coastal wetlands that we see today (Herdendorf 1992).

Glacial landforms, in combination with recent long-shore transport processes, create the prevalent physiographic features along much of the Great Lakes shorelines. Their characteristic differences in substrate, soils, slope, and drainage conditions largely determine both natural shoreline configuration and sediment composition. These, in turn, generate distinctive contexts for wetland development that vary in their exposure and resilience to lake stresses, and in their floristic composition (Minc 1997). Despite the large size of the Great Lakes and the diversity of wetland types, these geomorphic and geological processes have created conditions for wetland development that characterizes large shoreline segments of each Great Lake. For instance, the Canadian shoreline of the upper lakes (Superior and Huron) and the St. Lawrence are underlain by the Canadian Shield, consisting of Precambrian igneous and metamorphic rocks that are difficult to weather. By comparison, the shoreline of the lower lakes (Erie and Ontario) and L. Michigan tend to be composed of sedimentary rocks such as shale, limestone, sandstone and dolomite, that are easily eroded.

In Lakes Ontario and Erie, wetlands on the U.S. shoreline tend to be barrier beaches, whereas in Lake Huron, there are a greater number of dune and swales. Many wetlands in Lake Michigan and Saginaw Bay of Lake Huron tend to be large exposed embayments, while Canadian wetlands in Lakes Ontario, Erie and Huron are largely protected embayments and drowned rivermouth marshes. The wetland types in the U.S. shore of Lake Superior are largely barrier beaches and dune and swale wetlands, while coastal wetlands on the Canadian shore are scarce and tend to be exposed, fringe wetlands, with only a small percentage that are protected embayments (Chow-Fraser and Albert 1999).

Importance of Coastal wetlands to fish production

Coastal wetlands are among the most productive ecosystems in the world, comparable to tropical rain forests and coral reefs (http://www.nmfs.noaa.gov/habitat/habitatprotection/wetlands.htm). An immense variety of microbes, plants, insects, amphibians, reptiles, birds, fish, and mammals can be part of such a natural wetland ecosystem. Most of our knowledge on the use of wetlands by the fish community stems from studies of inland wetlands rather than coastal wetlands (Brazner 1997). In inland wetlands, the dominant fish community appears to consist of non-salmonid, warm-water or cool-water species such as carp (*Cyprinus carpio*), northern pike (*Esox lucius*), bullheads (*Ameiurus melas, A. natalis, A. nebulosus*), and buffalo (*Ictiobus cyprinellus*). The prevalence of bottom feeders such as bullheads, channel catfish (*Ictalurus punctatus*), carp and buffalos in wetland habitats is attributed to the predominance of clayey and organic-rich substrates (Herdendorf et al., 1981).

Even though the significance of coastal wetlands to the Great Lakes fish community fish has not yet been properly studied on either a regional or a basin-wide scale, there is general acceptance that wetlands are important to fish production because they provide spawning habitats for wetland-dependent species. The spawning substrates of important freshwater fish species in the Great Lakes have been summarized by Lane et al. (1996). Typically wetland-dependent species such as northern pike broadcast their eggs in shallow sedge marshes or in flooded fields, over vegetation and debris. Since these fish species spawn only on specific substrate types, modification of wetland substrate through anthropogenic activities (dredging, draining, erosion, and flow alteration) may result in the elimination or degradation of wetland spawning grounds.

Besides providing spawning habitat, wetlands also provide important nursery habitat for a host of fish species. Presence of emergent and submergent plants provide shelter and a food-source for benthic invertebrates and epiphytic algae on which larval and juvenile fish feed during their first few months of life. In turn, these fish become prey for both resident and migratory piscivores. About 80% of the approximately 200 fish species found in the Great Lakes use the near-shore 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).

Wetland-associated fish taxa

Wetlands provide critical spawning and nursery habitats for many Great Lakes fish species, and several authors have reported high species richness of young fishes from wetland habitats. Chubb and Liston (1986) identified larvae of 18 fish species in Pentwater Marsh, a coastal wetland on Lake Michigan. Stephenson (1990) found juveniles of 31 fish species in one or more of five coastal marshes in the Toronto area of Lake Ontario, with the number of species at individual sites ranging from 12 to 25. Young-of-the-year of 19 species were present in Second Marsh, Lake Ontario (OMNR 1980). Brazner (1997) examined wetland and beach fish assemblages in Green Bay, Lake Michigan. He reported that 47 of total 54 species were observed at wetland sites. These results indicate that coastal wetlands are important to fish production.

Although the values of the coastal wetlands have now been generally recognized, no comprehensive studies have ever been undertaken to examine the spatial distribution patterns of fish and their associations with coastal wetlands and characteristics of shoreline habitats at a large geographical scale. To address this deficiency, we propose the following three objectives:

1) We will determine the regional distribution pattern of fish along the shores of the Great Lakes
2) We will determine the regional distribution pattern of fish in relation to geographic features of the shoreline habitats, and
3) We will determine the degree of spatial overlap between fish distribution and wetland occurrences

GENERAL APPROACH

Databases

Fish distribution

To undertake this study, data from two different sources was required. 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 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. One major limitation to any regional-scale coarse survey such as this is that use of specific habitat by any species is subject to sampling error and we cannot interpret absence of a species from a site to mean that the habitat is unavailable for that species. Nevertheless, the atlas provides the most extensive historical coverage of spawning and nursery habitat of the Great Lakes fishery. This dataset was deemed acceptable because our study focuses on mapping the occurrences of fish and identifying regional-scale spatial patterns of fish habitat rather than documenting distribution at the site level.

Wetland and geographic features

The other data source required was a comprehensive coastal wetland inventory for the Great Lakes, along with shoreline classification that would identify basic geographic features and substrate type (i.e. wetlands, beaches, hardened shoreline, etc.). Unfortunately, no relevant wetland inventory is available for all of the Great Lakes, but an inventory exists in the WIRE Net (Wetland Inventory for Research and Education Network, McMaster University, http://www.wirenet.info) database that is complete for Lake Ontario (both Canada and U.S. shorelines). We also use medium-resolution vector shoreline data for the entire coastline of the Great Lakes (GLERL, 1997) and tributary data for Lake Ontario (OMNR, 2002), which had been imported into the WIRE Net database. For the purpose of this study, near 9500 of the geo-referenced data records (occurrences of fish species) covering all five Great Lakes and connecting channels from the Goodyear et al. (1982) atlas were imported into the WIRE Net database. This study also adopts the use of " **eco-reaches**" (Chow-Fraser and Albert 1999) to represent stretches of the Great Lakes shoreline that support significant concentrations of coastal wetlands, and which 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). Chow-Fraser and Albert (1999) have already pointed out that many of these delineations do not match existing natural division maps of the Great Lakes area (Carpenter et al. 1995, Albert 1995) based on upland characteristics because coastline conditions reflect a combination of upland and near-shore characteristics.

GIS and spatial analysis

The basic assumption of studies of spatial distribution is that individuals of a species (or other entities) will be spaced randomly unless something is biasing the distribution. Non-random distribution is a clue to physical or biotic factors important in the ecology of the organism. Organisms may be clumped (aggregated) because of patchiness in the physical environment or for biotic reasons (Brewer and McCam 1982). A typical analysis of spatial point data such as this one involves estimating the intensity of distributed points and calculating nearest neighbor distances.

Density mapping

A density map shows where the highest concentration of points is located and is useful for looking at patterns rather than for locating individual features. Because of the large volume of information and the computational requirements, a geographic information system (GIS) is generally required to generate density maps. The GIS creates a density map by first defining a neighborhood around each cell center (based on the radius "*h*" which we specify). It then calculates the total number of features that fall within that neighborhood and assigns a value to the cell. The GIS then moves on to the next cell and repeats the process (Mitchell 1999).

Kernel estimate

Kernel estimate is an alternative to produce a density map. It was originally developed to obtain a smooth estimate of a univariate or multivariate probability density from an observed sample of observations (Bailey and Gatrell 1995). A kernel estimate can be defined as:

$$\hat{f}_h(x) = \frac{1}{nh^2} \sum_{i=1}^{n} K\left[\frac{x - X_i}{h}\right],$$

where the kernel K is a probability density function, and h is the smoothing parameter that can be varied by the user.

The following is an intuitive interpretation of the kernel method. A probability density function, namely the kernel, is placed over each data point and the estimator is constructed by adding the n components. Thus, where there is a concentration of points, the kernel estimate has a higher density than where there are few points (Worton 1989). If a small value of smoothing parameter "h" is used, the fine detail of the data can be observed.

Nearest neighbor distances

Several methods are available for studying the distribution patterns of plants or animals. The Clark-Evans (1954) nearest neighbor method consists of obtaining a ratio, R, between the actual mean distance from each individual to its nearest neighbor and the expected mean distance between neighbors in a random population of the same density. When R =1, the distribution is random. If it is much smaller than 1, the population is aggregated; if it is much larger than 1, the population is evenly distributed (Brewer and McCam, 1982; Bailey and Gatrell 1995).

Another simple approach to summarizing pattern using nearest neighbour distances is to estimate the empirical cumulative probability distribution or distribution function (Bailey and Gatrell 1995; Kaluzny et al. 1998; Mathsoft, Inc. 2000):

$$G_{hat}(w) = \#\,(w_i \leq w)\,/\,n$$

where # refers to 'number of', n is the number of events in the study area and w is nearest neighbor distances. The resulting empirical cumulative distribution function G_{hat} can then be plotted against w. The distribution function which climbs very steeply in the early part of its range before flattening out would suggest clustering. Alternatively, if it climbs very steeply in the latter part of its range, then the suggestion might be one of repulsion or regularity.

Analysis of multiple types of events

The above methods enable us to analyze whether the occurrences of any one type of event exhibit clustering or regularity; however, in this study we are also interested in a knowing if the occurrence pattern of fish is related to occurrences of particular landscape features or shoreline characteristics such as coastal wetlands. A number of approaches to test independence of a bivariate pattern have been suggested. A simple one to implement is to take a random sample of points in the study area and measure the distance between nearest-neighbor-point-events, i (i.e. location of. fish), and the distance between the nearest-neighbor-point-events, j (i.e. coastal wetlands), corresponding to this sample of random points. Distances in each of these samples are then replaced by their rank within their respective sample. As a result, one is left with a set of pairs of point-event distance ranks. These may then be tested for independence using a standard procedure such as that based on Spearman's or Kendall's rank correlation coefficient (Upton and Fingleton 1985; Bailey and Gatrell 1995).

ORGANIZATION OF THESIS

The thesis has been organized into two chapters, each designed to address one topic. The first chapter is devoted to describing the spatial distribution pattern of a subset of Great Lakes fishes reported in the Goodyear et al. (1982) database. The second chapter investigates the relationships between spatial distribution of fish occurrences, shoreline habitat characteristics, and coastal wetlands of Lake Ontario.

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CHAPTER 1:

Spatial-pattern analysis of fish distribution in the near-shore environment of the Laurentian Great Lakes

By

Anhua Wei and Patricia Chow-Fraser

ABSTRACT: Data from a binational field survey that included the locations of spawning and nursery habitat for Great Lakes fishes were used to determine if there are systematic regional distribution patterns along the Great Lakes shoreline. We used three differentclassification schemes to sort the 139 fish taxa into functional categories to produce ecologically meaningful distribution maps. The three classification schemes were: 1) Jude and Pappas' (1992) taxocene classification based on the dependence of fish on wetland, transitional and open-water habitats; 2) Coker et al.'s (2001) classification based on fish thermal preferences; and 3) Balon's (1975) classification based on reproductive requirements and behaviours of fish. There were striking differences in the overall distribution pattern of nursery and spawning habitat in the five Great Lakes when data were compared for the three taxocenes: open-water, intermediate and coastal. Overall, open-water species were the most abundant, and were also widely distributed throughout all five lakes. Coastal species were the least abundant and were mainly restricted to the two lower lakes. The distribution pattern of coastal and intermediate taxa overlapped a great deal; both taxocenes made extensive use of the two lower lakes for spawning and nursery habitat during this synoptic survey, especially in western Lake Erie and eastern Lake Ontario. Fish distribution patterns sorted by thermal preference and by reproductive guild were compared with those sorted by taxocene. Results from a chi-square analysis indicated a high degree of overlap between thermal classes and taxocenes. There were also positive associations between many reproductive guilds and the three taxocenes, although these were not as strong as the previous comparison.

INTRODUCTION

Explicit consideration of spatial structure in ecological studies has become increasingly more important in our attempt to better understand and manage ecological processes, and spatial analysis has emerged as an important tool in this rapidly growing sub-discipline of ecology (Fortin 2002). Levin (1992) provides an insightful exhortation of the problem of pattern and scale in ecology. He pointed out that there was no single natural scale at which ecological phenomena should be studied. In some cases, patterns emerge from the collective behaviors of large ensembles of smaller-scale units; in other cases, patterns are imposed by lager-scale constraints. An example of this can be found in the fisheries literature, where geographic scale has recently become a key consideration in developing plans to conserve and restore fish habitat (Sly, P. G. et al., 1992; Cunjak 1996; Crowder et al., 1996; Imhof et al., 1996; Kelso et al., 1996; Lewis et al., 1996; Minns et al., 1996; Richards et al., 1996; Armstrong et al., 1998; Folt et al., 1998; Mather et al., 1998).

Although fisheries ecologists have realized that cross-scale studies are critical to complement more traditional studies carried out on narrowly-defined spatial and temporal scales, large-scale analyses of fish distribution in systems as large as the Laurentian Great Lakes has never been attempted. This is probably directly related to two main factors: 1) lack of appropriate computational tools and 2) lack of comprehensive and basin- wide geo-referenced data. Recent advances in the integration of Geographic Information

Systems (GIS) and readily available spatial statistics, however, has moved us closer to achieving the goal of analyzing fish distribution at the scale of all five Great Lakes.

Even without the benefit of spatial analysis, GIS has been useful for tracking organisms and habitat features, which are important first steps in development of effective environmental management plans. By superimposing results of biotic surveys over geographic features, managers have been able to target critical habitats for protection and conservation (Miller 1994). Maps also provide spatial information that can be easily interpreted by a wide variety of experts, as well as by the general public. Therefore, maps are used routinely to display distribution of natural resources (e.g. fish habitats) in environmental impact assessment studies and environmental management plans alike. They help integrate interdisciplinary information and identify information gaps that are important in habitat and species conservation (Miller and Allen 1994).

Although there is a long tradition of publishing species distribution maps in ecology (Buttefield et al. 1994), most of these maps only show the locations of species with their associated habitat features, and rarely indicate intensity of use by the species. Any association between species distribution and particular habitat features is gleaned by eye without the benefit of spatial statistics. In a GIS environment, however, distribution maps can assess information regarding intensity of use and relative densities of habitat features, thus making them more ecologically relevant. Another advantage to using GIS to produce these maps is the ease with which organisms can be plotted according to traditional phylogenetic classification schemes or replotted according to a number of other functional categories such as Balon's (1975) fish guilds, Jude and Pappas' (1992) taxocenes, or Coker et al.'s (2001) temperature preferenda that more appropriately reflect the complex ecological interactions among species and their abiotic environment.

In this study, the underlying intent in analyzing spatial distribution patterns of fish at the scale of each of the Great Lakes is to determine if there are systematic regional patterns that are associated with landscape features such as thermal zone, bedrock or coastal wetlands. General knowledge of fish distribution in a heterogeneous environment such as the Great Lakes shoreline is essential when identifying important fish habitats for preservation and conservation. Our overall objective is to detect spatial distribution patterns of fish along the shoreline of the Great Lakes, and to determine if broad groupings of fish (i.e. taxocenes , reproductive or thermal guilds) have a clumped, regular or random distribution. This study represents the first broad-scale examination of fish distribution patterns of the Great Lakes fish community, and permits inferences about the relationship between fish species and their near-shore spawning and nursery habitats.

METHODS

Fish occurrence information

Species occurrence data for this study were obtained from the Atlas of Spawning and Nursery Areas of Great Lakes Fishes (Goodyear et al. 1982). The atlas is the most comprehensive binational geo-referenced database that could have been used for our purpose. It contains information on all of the commercially and recreationally important species that use the tributaries, littoral and open-water areas of the Great Lakes as spawning and nursery habitats. To our knowledge, information in this database which is reported in 13 volumes has never been imported into GIS and analyzed in the fashion that we have proposed. Therefore, near 9500 geo-referenced data records (occurrences of fish species) were imported into an existing Great-Lakes–based GIS (WIRE Net; Wetland Inventory for Research and Education Network; see description in Chow-Fraser and Albert 1999).

The 139 fish taxa reported in the Atlas had to be grouped into fewer broad categories to produce meaningful distribution maps. We deliberately avoided the use of traditional taxonomic groupings because data sorted by an ecological classification scheme permit ecosystem analyses (Balon, 1975) and produce ecologically meaningful maps. Instead, we chose three functional classification schemes. Jude and Pappas (1992) used Correspondence Analysis to partition fish species associated with the open water of each of the five Great Lakes and nine coastal wetlands. Three species complexes were suggested: a Great Lakes taxocene; a transitional taxocene, which utilized open water, near-shore, and wetlands; and a wetland taxocene. We chose this as one of the classification schemes because we are particularly interested in identifying the distribution pattern of fish with coastal wetlands; for clarity sake, we have renamed these taxocenes *coastal*, *intermediate* and *open-water*, respectively. For comparison, we also used Coker et al.'s (2001) classification based on temperature preferenda (see Table 1.1) and Balon's (1975) reproductive guild classification (see Table 1.2)

Data analysis

Spatial analyses in this study involved two spatial techniques: *kernel estimate* and *nearest-neighbor distance*. Density maps produced by a GIS are useful for looking at distribution patterns of target organisms, and for identifying areas that require action, or for monitoring changes in environmental condition. Kernel estimate is an alternative to producing a density map. It was originally developed to obtain a smooth estimate of a univariate or multivariate probability density from an observed sample of observations (Bailey and Gatrell, 1995). The intuitive interpretation of the kernel method is that where there is a concentration of points the kernel estimate has a higher density than where there are few points (Worton, 1988).

Several methods are available for calculating nearest-neighbor distances (Brewer and McCam 1982; Bailey and Gatrell 1995). A simple approach to summarize distribution patterns using nearest-neighbor distances is to estimate the empirical cumulative probability distribution or the distribution function (Bailey and Gatrell 1995; Kaluzny et al. 1998; Mathsoft, Inc., 2000):

$$G_{hat}(w) = \#\ (w_i \leq w)\ /\ n$$

where # refers to 'number of ', n is the number of events in the study area and w is nearest neighbor distances. The resulting empirical cumulative distribution function G_{hat} can then be plotted against w. The distribution function that climbs very steeply in the early part of its range before flattening out suggests a clustered distribution. On the other hand, one that climbs very steeply in the latter part of its range suggests a regular distribution (Bailey and Gatrell, 1995; MathSoft 2000).

Both the "mapping approach" (e.g. kernel estimate) and "nearest-neighbor distance" approach have been widely used in ecological studies (Rice 1993; Tothmeresz 1994, Haase, 1995; Bertrand 1996; Comport 1996; Manly 1996; Seaman and Powell 1996; Mateu, 1998; Sauer et al. 1999; Tarumi and Blamey 1999; Wood et al. 2000; Lundquist et al., 2001; Liu 2001; Kenward et al., 2001; Havlicek and Carpenter, 2001; Kie et al. 2002; Monchot and Lhelle 2002; Taulman and Seaman 2002). The major difficulty with all the nearest-neighbor techniques is the influence of the boundary of the study region. The expected nearest-neighbor distance for a point near the boundary will be greater than that for a point well inside the region, because the former is denied the possibility of neighbors outside the boundary (Upton and Fingleton, 1985), and this is referred to as the "edge effect". We do not need to consider the edge effect in this study because the fish distribution is bounded by the Great Lakes shoreline, which is a natural rather than an arbitrarily imposed boundary.

All density maps were created in ArcView with Spatial Analyst extension. The calculation of G_{hat} was done by using S-plus for windows 2000 with SpatialStats module.

RESULTS

Fish distribution pattern by taxocene

There were striking differences in the overall distribution pattern of nursery and spawning habitat in the five Great Lakes when data were compared for the three taxocenes: open-water, intermediate and coastal (Fig. 1.1a to c, respectively). Overall, open-water species were the most abundant, and were also widely distributed throughout all five lakes. The coastal species were the least abundant and appeared to be restricted to the two lower lakes. Even though the intermediate species were most strongly represented in western Lake Erie and Lake St. Clair, they were also widely distributed throughout the remaining four lakes and connecting channels. The distribution pattern of coastal and intermediate taxa overlapped a great deal (Fig. 1.1b and c); both taxocenes made extensive use of the two lower lakes for spawning and nursery habitat during this synoptic survey, especially in western Lake Erie and eastern Lake Ontario.

Open-water taxocene

The relative importance of the near-shore areas as spawning and nursery habitat for open-water species was more obvious when data were examined on a lake-by-lake basis. For L. Superior, the western segment on the Canadian shoreline near the city of Thunder Bay, Ontario, and almost the entire western half of the U.S. shoreline from the city of Duluth, Minnesota to the Apostle Islands to the Keewenaw Peninsula were important habitat (Fig. 1.2a). For L. Huron, the more important habitat were located on the U.S. portion of the shoreline, especially near Saginaw Bay, although extensive near-shore areas of Georgian Bay and Manitoulin Island experienced low to moderate use (Fig. 1.3a). For L. Michigan, the entire shoreline had low to moderate use by open-water taxa, especially in Green Bay, while the area near Algoma, Wisconsin was associated with exceptionally high use (Fig. 1.4a). For Lake Erie, the western shoreline, especially the islands located on the U.S. portion (Catawba, Kelleys and the Bass Islands), the area near Long Point Marsh Complex in Ontario, and Presque Isle in Pennsylvania were areas that were well used (Fig. 1.5a). Most of the Canadian shoreline of Lake Ontario west of the town of Cobourg, Ontario and south to the Niagara River appeared to be good spawning and nursery habitat for open-water taxa, as were the near-shore area in eastern New York from Sodus Point north to Sackets Harbor (Fig. 1.6a).

Intermediate taxocene

Compared with that for open-water taxa, spawning and nursery habitat for the intermediate taxocene in L. Superior were generally scarce on the Canadian shoreline, and only well represented on the western tip of the U.S. shoreline at the mouth of the St. Louis River in Duluth, Minnesota (Fig. 1.2b). The distribution pattern for the intermediate taxa in L. Huron was similar to that for open-water taxa, with a concentration near Saginaw Bay and Upper Michigan Peninsula along the U.S. shoreline and in lower Georgian Bay, Ontario along the Canadian shoreline (Fig. 1.3b). By comparison, habitat was distributed throughout the shoreline of L. Michigan, with locally important areas in Green Bay and the southern portion of the lake from Kenosha, Wisconsin on the western shore to Muskegon, Michigan on the eastern shore (Fig. 1.4b). As was the case for the open-water taxa, western L. Erie and the associated U.S. islands were important habitat to the intermediate taxocene (Fig. 1.5b). There was a concentration of spawning and nursery habitat for the intermediate taxocene in eastern Lake Ontario, near the city of Kingston and the Bay of Quinte, Ontario; there were other important areas near the cities of Toronto and Hamilton in Ontario, and in eastern New York near the town of Oswego (Fig. 1.6b).

Coastal taxocene

There was almost no spawning and nursery habitat for coastal taxa in L. Superior except in Duluth, Minnesota (Fig. 1.2c). Likewise, habitat for the coastal taxocene in L. Huron was primarily located in Saginaw Bay (Fig. 1.3c), and that for L. Michigan were localized around only a few areas (e.g. city of Chicago, Illinois, and the city of Muskegon, Michigan; Fig. 1.4c). The distribution pattern in L. Erie showed a concentration in the western U.S. islands and near the Long Point Marsh complex in Ontario (Fig. 1.5c). The most important coastal habitats in L. Ontario appeared to be located both at the west end near Hamilton, Ontario, and at the east end, near Kingston, Ontario and Sacket Harbor, New York (Fig. 1.6c).

Fish distribution pattern by thermal preference

We also sorted the fish according to Coker et al. (2001)'s five thermal preferences: cold, cold-cool, cool, cool-warm and warm, and mapped their distributions throughout the Great Lakes (Fig.1.7). The thermal criteria that we use in this study were first described by Coker et al. (1992) and are presented in Table 1.1. The distribution pattern of habitat for the "cold" (Fig. 1.7a) was remarkably similar to that of the " open-water" taxocene (Fig. 1.1a); habitat for these fish were widely distributed and were most common in L. Superior. Patterns of the "cold-cool", and "cool" (Fig. 1.7b and c) were similar to that of the intermediate taxocene (Fig. 1.1b), while that of "cool-warm" and "warm" (Fig. 1.7 e and f) were very similar to that of the coastal taxocene (Fig. 1.1c).

Fish distribution pattern by reproductive guilds

Balon (1975) classified fish into thirty-two reproductive guilds, of which we found 13 to be applicable to this study (see Table 1.2). We organized the maps according to degree of similarity in distribution patterns. The first set of maps correspond to guilds that favor the lower lakes and these include maps for A.1.1 (Nonguarders: Open substratum spawners: Pelagophils), A.1.6 (Nonguarders: Open substratum spawners: Psammophils), B1.4 (Guarders: Substratum choosers: Phytophils), B.2.2 (Guarders: Nest Spawners: Polyphils), B.2.3 (Guarders: Nest Spawners: Lithophils), B.2.4 (Guarders: Nest Spawners: Ariadnophils), B.2.5 (Guarders: Nest Spawners: Phytophils), and B.2.7 (Guarders: Nest Spawners: Speleophils) (Fig. 1.8a-h, respectively). These guilds appeared to have very similar distribution patterns to that of the coastal taxocene (Fig. 1.1c). A group of guilds that included A.1.2 (Nonguarders: Open substratum spawners: Litho-pelagophils), A.1.3 (Nonguarders: Open substratum spawners: Lithophils), A.1.4 (Nonguarders: Open substratum spawners: Phyto-lithophils) and A.1.5 (Nonguarders: Open substratum spawners: Phytophils) (Fig. 1.9a-d) had distribution patterns that appeared similar to that of the intermediate taxocene (Fig. 1.1b). Finally, A.2.3

(Nonguarders: Brook hiders: Lithophils) (Fig. 1.10) could be singled out as the guild that was most similar to the open-water taxocene (Fig. 1.1a) by favoring the upper lakes and was also very widely distributed.

Association between functional classification schemes

Results from a chi-square analysis indicated a high degree of overlap between thermal classes and taxocenes (Pearson chi-square; P<0.001; symmetric lambda = .46; Table 1.3). 84 % of occurrences of cold water species were associated with open-water taxa, while only 16 % of these were associated with intermediate and none with coastal taxa. More than two-thirds of the cold-cool class were classified as open-water taxa, with the remainder classified as intermediate. Most of the cool-water species were associated with intermediate taxa, By comparison, over half of those in the cool/warm and warm classes were also classified into the coastal taxocene. Thus, fish that generally prefer cold water (includes cold and cold-cool categories) correspond well with open-water taxa that migrate inshore to spawn and then return to the open-water for most of the year. The intermediate taxa include almost all of the cool-water species as well as substantial numbers of the warm-water species. By contrast, the coastal taxa are those fish that prefer warm and cool-warm environments, which tend to characterize the coastal habitat of the Great Lakes.

There were positive associations between reproductive guilds and the three taxocenes (Pearson chi-square; P<0.001; symmetric lambda = .303; Table 1.4), although these were not as strong as the previous comparison between thermal classes and the taxocenes. When data were sorted according to reproductive guilds within the three taxocenes, the open-water taxocene was strongly associated with **A.1.2** (Nonguarders: Open substratum spawners: Litho-pelagophils), **A.1.5** (Nonguarders: Open substratum spawners: Phytophils), **A.2.3** (Nonguarders: Brook hiders: Lithophils) and **B.2.4** (Guarders: Nest Spawners: Ariadnophils), the intermediate taxocene was strongly associated with **A.1.1** (Nonguarders: Open substratum spawners: Pelagophils), **A.1.3** (Nonguarders: Open substratum spawners: Lithophils), **A.1.4** (Nonguarders: Open substratum spawners: Phyto-lithophils), **B.2.3** (Guarders: Nest Spawners: Lithophils), and **B.2.7** (Guarders: Nest Spawners: Speleophils), while the Coastal taxocene was associated with **B.1.4** (Guarders: Substratum choosers: Phytophils), **B.2.2** (Guarders: Nest Spawners: Polyphils), and **B.2.5** (Guarders: Nest Spawners: Phytophils).

Positive associations were also found between reproductive guilds and the five thermal classes (Pearson chi-square; $P<0.001$; symmetric lambda = .235; Table 1.5). When data were sorted according to reproductive guilds within the five thermal classes, **A.2.3** (Nonguarders: Brook hiders: Lithophils), **A.1.3** (Nonguarders: Open substratum spawners: Lithophils), **A.1.5** (Nonguarders: Open substratum spawners: Phytophils), and **B.2.4** (Guarders: Nest Spawners: Ariadnophils), were associated with the cold-water species. **A.1.2** (Nonguarders: Open substratum spawners: Litho-pelagophils), **A.1.4** (Nonguarders: Open substratum spawners: Phyto-lithophils), **A.1.1**(Nonguarders: Open substratum spawners: Pelagophils), and **B.1.4** (Guarders: Substratum choosers: Phytophils) were associated with the cool-water species, while **B.2.3** (Guarders: Nest

Spawners: Lithophils), **B.2.7** (Guarders: Nest Spawners: Speleophils), **B.2.5** (Guarders: Nest Spawners: Phytophils) and **B.2.2** (Guarders: Nest Spawners: Polyphils) were associated with the warm-water species.

Nearest-neighbor distance

An appropriate interpretation of the results of the nearest-neighbor analysis is that if objects have a clustered distribution, we would expect to see disproportionately high frequency of short distances between nearest neighbors, whereas if objects are distributed regularly, we would expect to see disproportionately high frequency of long distances between neighbors (MathSoft, 2000). Results of our nearest-neighbor analysis indicate that there is a high probability of short distances between nearest neighbors for all three taxocenes (Fig. 1.11 a to c). Therefore, we conclude that the distribution pattern of all three taxocenes have clumped distributions.

DISCUSSION

The basic assumption of studies involving spatial distribution is that individuals of a species will be spaced randomly unless some factor is biasing the distribution. Hence, a non-random distribution may be interpreted as a clue that some associated abiotic or biotic factor is important to the ecology of the organism (Brewer and McCann 1982). However, the relative importance of these factors, as well as interpretation of the dispersion pattern may change with the scale of the study. For instance, small-scale studies (e.g. involving only one site) may reveal the importance of biotic factors such as interspecific competition, whereas large-scale studies (e.g. involving many sites over a large geographic region) may emphasize abiotic factors (Jackson et al. 1992). This study is one of the first to look at the distribution pattern of fish habitat for the entire Great Lakes fish community, and is expected to reveal insights into abiotic factors that influence their distribution.

Fish communities can be classified in various ways that reflect the goals of the study. Jackson et al. (2000) summarized three approaches to classify fish communities. The first approach is based on numerical dominance or economic value of a particular species or group of species. This classification is convenient for fish resource managers. Another approach uses the concept of guilds, which groups organisms according to similarities in their feeding, reproductive behaviours or thermal preferences (Balon 1975; Coker et al. 2001). Although this approach can be useful to ecologists because it emphasizes similarities in the functional roles of organisms, it can also be problematic to apply. For example, classifications based on feeding guilds are dependent on life stages and size of the fish, and hence, a single species can be classified into several guilds. Balon's (1975) classification scheme is based mainly on preference for spawning substrate and reproductive behaviours and does not rely on the life stage of the fish; however, it is a much more elaborate and complex system to apply, requiring a great deal of knowledge about the biology of the fish. A third approach is to classify fish through the use of multivariate statistical methods (e.g. Jude and Pappas' classification). This multivariate approach objectively identifies patterns in species assemblages through statistical relationships between species distributions and environmental conditions. This classification system will be limited by the degree to which the field survey represents the larger community in terms of the fish species and range of environmental variables.

In this study, we have classified the Great Lakes fishes in three different ways, including Jude and Pappas's (1992) taxocenes, Coker et al.'s (2001) thermal preferences, and Balon's (1975) reproductive guilds. Some authors have argued that a community is really just an arbitrary subdivision of a continuous gradation of local species assemblages (Whittaker, 1975; from Levin, 1992) and that communities are not well integrated units. Our study, however, indicate that instead of being distributed in a random fashion, the fish have a predictably clumped distribution pattern, regardless of the classification system used.

Determinants of spatial pattern

The physical environment is the basic template for all life processes where organisms evolve and persist (or not) through time. Ectothermic organisms such as fish are particularly dependent on the thermal environments because they have limited physiological means to control and regulate body temperatures (Welsh et al. 2001). Therefore, the thermal niche is an important ecological parameter that defines the distribution pattern of fish. Hence, in the upper lakes, where the mean water temperature is colder, the lakes are dominated by cold-water species, whereas in the lower lakes, warm-water species dominate. These spatial patterns by thermal preference are consistent with differences in climatic regimes between the upper and the lower lakes.

Some studies suggested that coastal wetlands were important to fish production. Several authors have reported high species richness of young fishes from wetland habitats. Chubb and Liston (1986) identified larvae of 18 fish species in Pentwater Marsh, a coastal wetland on Lake Michigan. Stephenson (1990) found juveniles of 31 fish species in one or more of five coastal marshes in the Toronto area of Lake Ontario, with the number of species at individual sites ranging from 12 to 25. Young-of-the-year of 19 species were present in Second Marsh, Lake Ontario Braner (1997) examined wetland and beach fish assemblages in Green Bay, Lake Michigan. He reported that 47 of total 54 species were observed at wetland sites.

Our study indicated that the wetland-associated taxocene appeared to be closely related to bedrock types that overlap well with the distribution of coastal wetlands along shorelines of the Great Lakes (Figure 1.12). For instance, about two-thirds of coastal wetlands in the Great Lakes have developed in shale, limestone and dolomite shoreline, while only about a third have developed in sandstone, igneous and metamorphic shoreline. By comparison, about 78 % of wetland-associated fish occurrences are located within shale, limestone and dolomite areas, such as that found in the lower Great Lakes shoreline, while only 12 % of fish surveyed have been found on sandstone, igneous and metamorphic surfaces such as the Pre-Cambrian Shield that underlies much of the Canadian shoreline of the Upper Lakes and the St. Lawrence River. This implied that the distribution of fish distribution along shorelines of the Great Lakes was to some extent constrained by the distribution of coastal wetlands in the Great Lakes. This will be tested in future study.

Coastal wetlands are important to fish is because they provide critical spawning and nursery habitats for many Great Lakes fish species The reproductive characteristics of a wetland-associated species such as largemouth bass usually requires unique environments similar to those of coastal wetlands. Goodyear et al. (1982) summarized that before spawning adult largemouth bass moves short distances inshore or into marshes, bays, harbors, sloughs, lagoons, and creek mouths when water temperature reaches at 58-70°F. Nest is usually among vegetation or near structures and male guards nest. After hatching, young spend the first summer of life in sheltered, littoral, weedy areas near spawning grounds and move offshore in fall. The nursery grounds may include vegetation, sand, mud, detritus; occasionally stone or rubble. Our analysis indicated that the distribution of wetland-associated taxocenes (e.g. intermediate and coastal) overlapped well with that of cool-warm water and warm water groups, as well as that of guilds **A.1.1** (Nonguarders: Open substratum spawners: Pelagophils), **A.1.3** (Nonguarders: Open substratum spawners: Lithophils), **A.1.4** (Nonguarders: Open substratum spawners: Phyto-lithophils), **A.1.6** (Nonguarders: Open substratum spawners: Psammophils), **B.1.4** (Guarders: Substratum choosers: Phytophils), **B.2.2** (Guarders: Nest Spawners: Polyphils), **B.2.3** (Guarders: Nest Spawners: Lithophils), **B.2.5** (Guarders: Nest Spawners: Phytophils), and **B.2.7** (Guarders: Nest Spawners: Speleophils). This probably indicates that cool-warm and warm water species and the above guilds require similar habitats to wetland-associated taxocenes. This hypothesis will be tested in further study.

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Table 1.1 Thermal criteria used by Coker et al. (2001) to classify fish

Thermal category	**Thermal Criteria (°C)**
Cold	<19.0
Cold-cool	straddling the boundaries between "cold" and "cool"
Cool	19 - 25
Cool-warm	straddling the boundaries between "cool" and "warm"
Warm	>25.0

Table 1.2 Brief description of the reproductive guilds used by Balon (1975) that are relevant to this study.

Reproductive guild	Description
A.1.1 Pelagophils	Non-guarders and open-substratum spawners. Non-adhesive eggs are released and scattered in open waters. Strong phototropism keeps embryos and larvae of pelagophils in the open and away from shaded areas. Adapted to highly oxygenated waters.
A.1.2 Litho-pelagophils	Non-guarders and open-substratum spawners. Eggs are deposited on rocks and gravels or semi-buoyant. Eleutheroembryos and larva become buoyant. Display no photophobia.
A.1.3 Lithophils	Non-guarders and open-substratum spawners. Deposit eggs on a rock, rubble, or gravel bottom where their embryos and larvae develop. Embryos hatch early and are highly photophobic which helps them to scatter and hide under stones.
A.1.4 Phyto-lithophils	Non-guarders and open-substratum spawners. Deposit eggs in relatively clear-water habitats on submerged plants, or on other submerged items such as logs, gravel, and rocks. Photophobia.
A.1.5 Phytophils	Non-guarders and open substratum spawners. Scatter or deposit eggs with an adhesive membrane that sticks to plants. Do not deposit eggs on the bottom. Are adapted to survive in habitats with dense plant and muddy bottom and with very low oxygen concentration.
A.1.6 Psammophils	Non-guarders and open-substratum spawners. Eggs with an adhesive membrane are scattered on sandy bottom or near fine roots of plants that hang over the sandy bottom. Embryos are phototropic. Adapted to highly oxygenated waters.

A.2.3 Ostracophils.	Non-guarders and brood hiders. Eggs are hidden in the gill chambers of live mussels, crabs, ascidians, or in specially constructed places (called redds in salmonids).
B.1.4 Pelagophils	Guarders and substratum choosers. Spawning sites with low oxygen content can be used because the guarding parents clean the eggs and produce flow of water around them by fin-fanning and oral ventilation. Eggs are non-adhesive and positively buoyant.
B.2.2 Phytophils	Guarders and nest spawners. Are adapted to nesting above or on a soft muddy bottom amid algae and vascular plants. Eggs are guarded by males.
B.2.3 Psammophils	Guarders and nest spawners. Eggs are covered with sand grains. Female does some fanning of eggs. Eleutheroembryos and larvae remain in the nest.
B.2.4 Aphrophils	Guarders and nest spawners. Froth nests usually are built in grass or reeds.
B.2.5 Spelephils	Guarders and nest spawners. The majority deposit eggs on a cleaned area of the undersurface of flat stones, natural holes, cavities, or in specially constructed burrows.
B.2.7 Ariadnophils	Guarder and nest spawners. Eggs are constantly ventilated by the guarding male.

Table 1.3 The number of fish classified into respective thermal categories within the three taxocenes. Numbers below in brackets are percents. Numbers in bold indicate that they are the highest for the three taxocenes.

Thermal category	Jude and Pappas' taxocene			All Taxocenes
	Open-water	**Intermediate**	**Coastal**	
Cold	**4293** (83.6)	840 (16.4)	---	5133 (54.4)
Cold-cool	**388** (75.6)	125 (24.4)	---	513 (5.4)
Cool	38 (1.9)	**1667** (82.4)	317 (15.7)	2022 (21.4)
Cool-warm	33 (19.9)	35 (21.1)	**98** (59.0)	166 (1.8)
Warm	---	794 (49.7)	**802** (50.3)	1596 (16.9)
Total	4752 (50.4)	3461 (36.7)	1217 (12.9)	9430

Table 1.4 The number of fish classified into reproductive guilds within the three taxocenes. Numbers below in brackets are percents. Numbers in bold indicate that they are the highest for the three taxocenes.

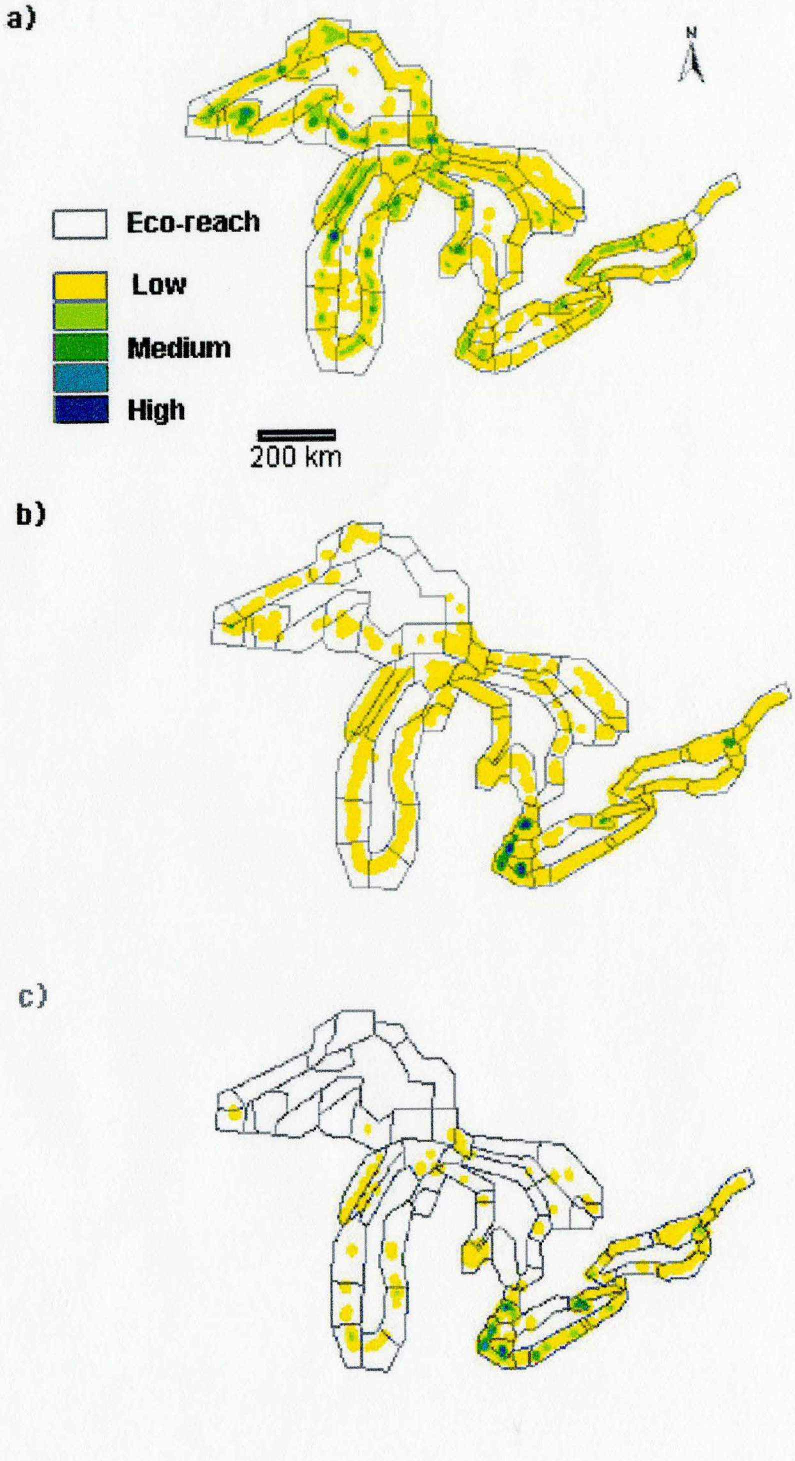
Reproductive guild	Taxocene			All Taxocenes
	Open-water	Intermediate	Coastal	
A.1.1	15 (6.9)	**114** (52.3)	89 (40.8)	218 (2.3)
A.1.2	**616** (53.3)	434 (37.6)	105 (9.1)	1155 (12.2)
A.1.3	271 (22.5)	**929** (77.1)	5 (0.4)	1205 (12.8)
A.1.4	---	**669** (79.5)	173 (20.5)	842 (8.9)
A.1.5	**678** (45.6)	647 (43.5)	162 (10.9)	1487 (15.8)
A.1.6	---	**125** (53.2)	110 (46.8)	235 (2.5)
A.2.3	**3078** (99.5)	17 (0.5)	---	3095 (32.8)
B.1.4	---	---	**32** (100)	32 (0.3)
B.2.2	---	---	**53** (100)	52 (0.6)
B.2.3	---	**311** (63.6)	178 (36.4)	489 (5.2)
B.2.4	**37** (84.1)	---	7 (15.9)	44 (0.5)
B.2.5	---	62 (24.6)	**190** (75.4)	252 (2.7)

B.2.7	57 (17.6)	**153** (47.2)	114 (35.2)	324 (3.4)
Total	4752 (50.4)	3461 (36.7)	1217 (12.9)	9430

Table 1.5 The number of fish classified into reproductive guilds within thermal classes. Numbers below in brackets are percents. Numbers in bold indicate that they are the highest for the thermal classes

Guild	Thermal class					Total
	cold	cold/cool	cool	cool/warm	warm	
A.1.1	15	---	**114**	---	89	218
	(6.9)		(52.3)	---	(40.8)	(100)
A.1.2	366	250	**532**	7	---	1155
	(31.7)	(21.6)	(46.1)	(0.6)	---	(100)
A.1.3	**848**	---	309	3	45	1205
	(70.4)	---	(25.6)	(0.2)	(3.7)	(100)
A.1.4	228	---	**416**	25	173	842
	(27.1)	---	(49.4)	(3.0)	(20.5)	(100)
A.1.5	**675**	---	345	22	445	1487
	(45.4)	---	(23.2)	(1.5)	(29.9)	(100)
A.1.6	---	**125**	23	76	11	235
	---	(53.2)	(9.8)	(32.3)	(4.7)	(100)
A.2.3	**2907**	138	17	33	---	3095
	(93.9)	(4.5)	(0.5)	(1.1)	---	(100)
B.1.4	---	---	**32**	---	---	32
	---	---	(100)	---	---	(100)
B.2.2	---	---	---	---	**52**	52
	---	---	---	---	(100)	(100)
B.2.3	---	---	114	---	**375**	489
	---	---	(23.3)	---	(76.7)	(100)
B.2.4	**37**	---	7	---	---	44
	(84.1)	---	(15.9)	---	---	(100)
B.2.5	---	---	62	---	**190**	252
	---	---	(24.6)	---	(75.4)	(100)
B.2.7	57	---	51	---	**216**	324
	(17.6)		(15.7)		(66.7)	(100)
Total	5133	513	2022	166	1596	9430
	(54.4)	(5.4)	(21.4)	(1.8)	(16.9)	(100)

Figure 1.1 Distribution patterns of spawning and nursery habitat for Great Lakes fishes sorted by a) open-water, b) intermediate, and c) coastal taxocenes



a)
Eco-reach
Low
Medium
High
200 km
N
b)
c)

Figure 1.2 Distribution patterns of spawning and nursery habitat for L. Superior fishes sorted by a) open-water, b) intermediate, and c) coastal taxocenes.

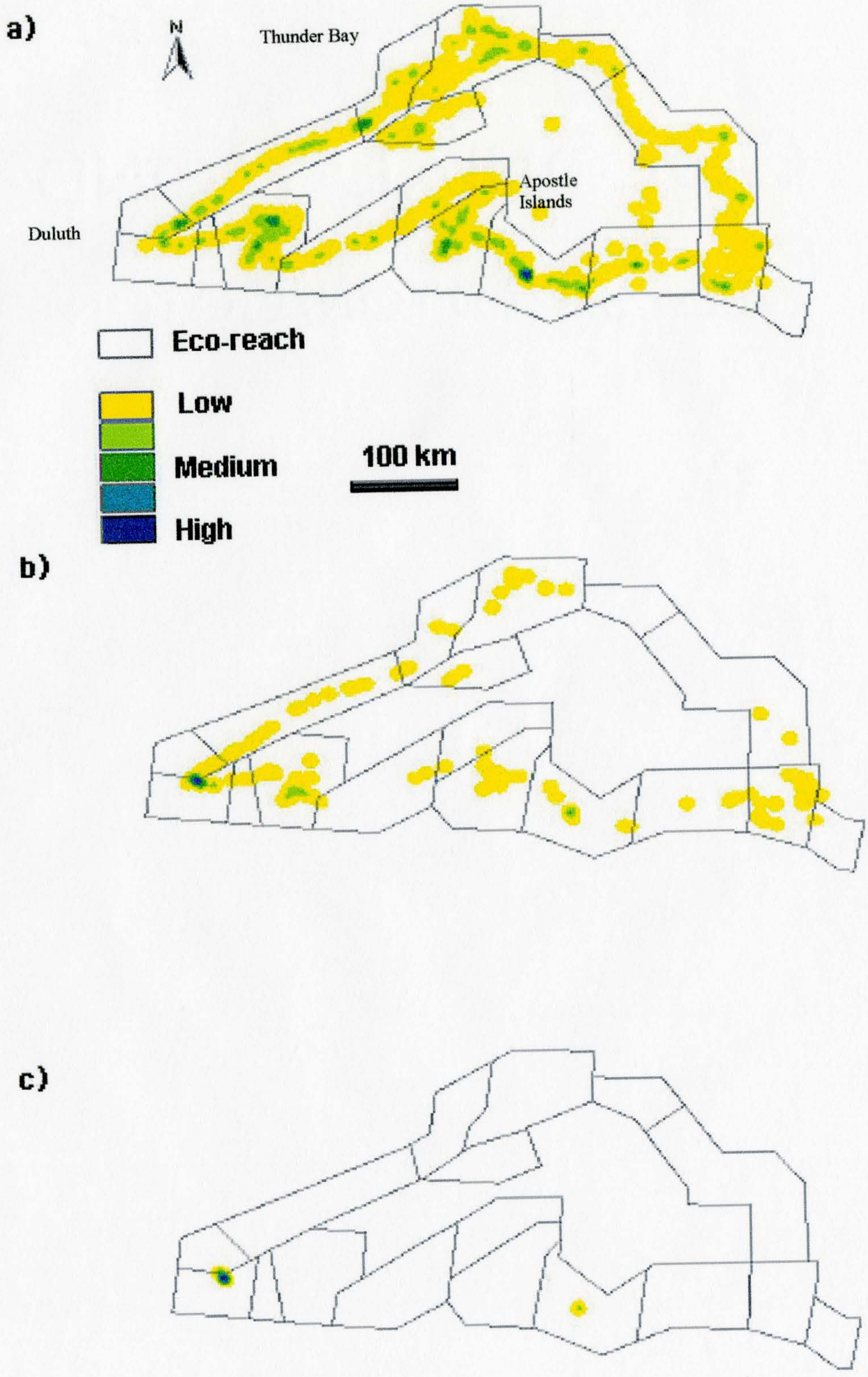

a)
N
Thunder Bay
Duluth
Apostle
Islands
Eco-reach
Low
Medium
High
100 km
b)
c)

Figure 1.3 Distribution patterns of spawning and nursery habitat for L. Huron fishes sorted by a) open-water, b) intermediate, and c) coastal taxocenes.

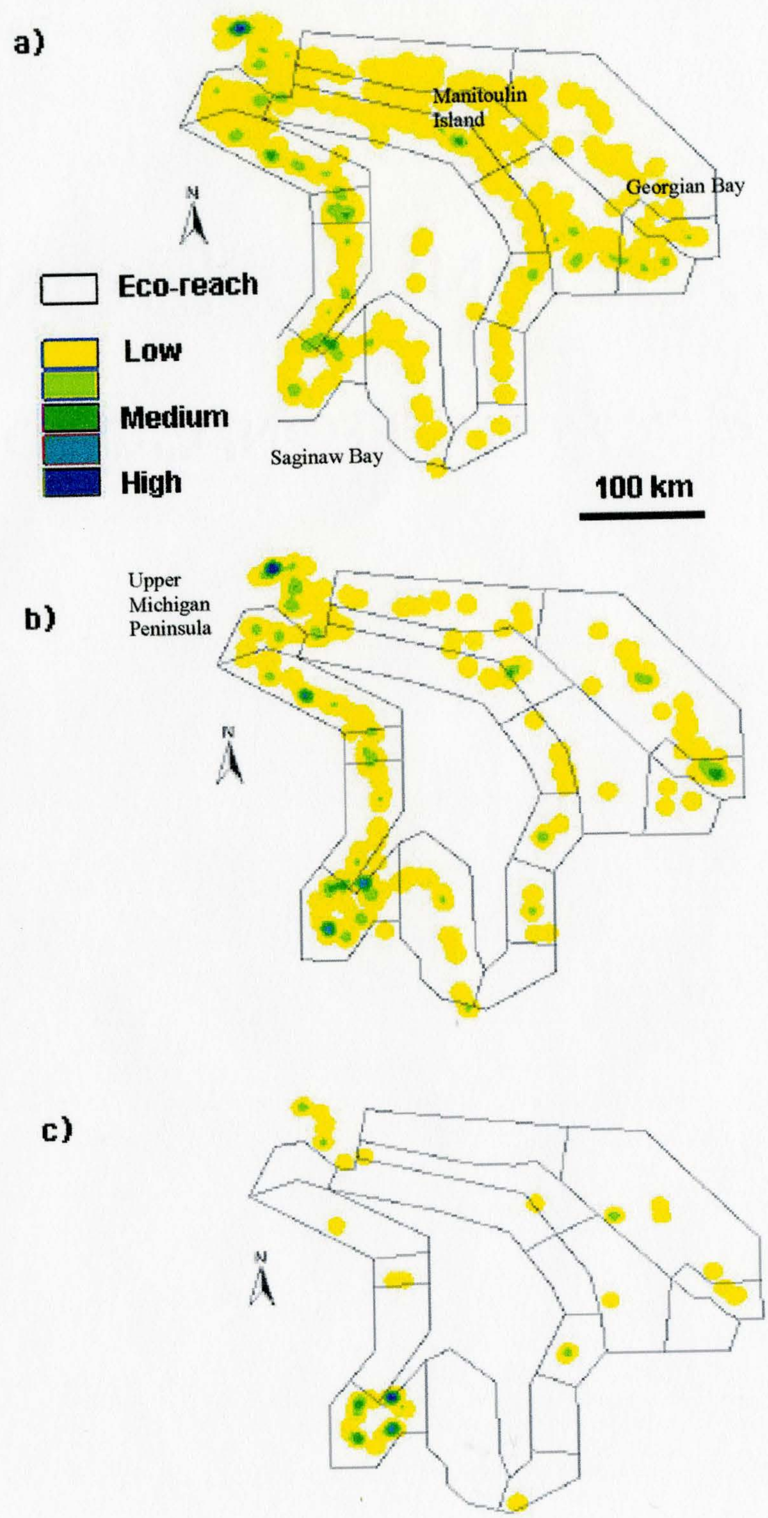

a)
Manitoulin
Island
Georgian Bay
N
Eco-reach
Low
Medium
High
Saginaw Bay
100 km
Upper
Michigan
Peninsula
b)
N
c)
N

Figure 1.4 Distribution patterns of spawning and nursery habitat for L. Michigan fishes sorted by a) open-water, b) intermediate, and c) coastal taxocenes.

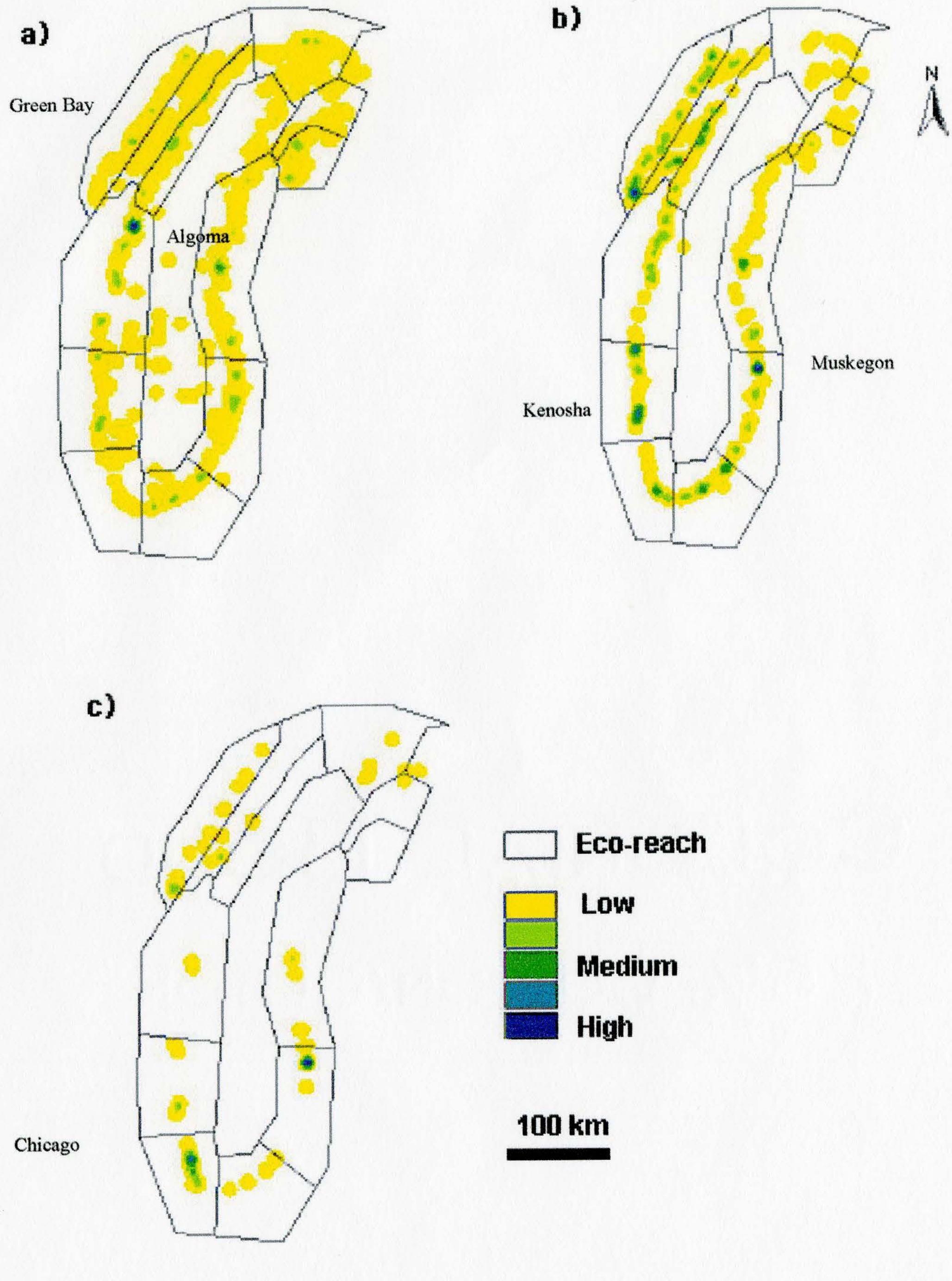
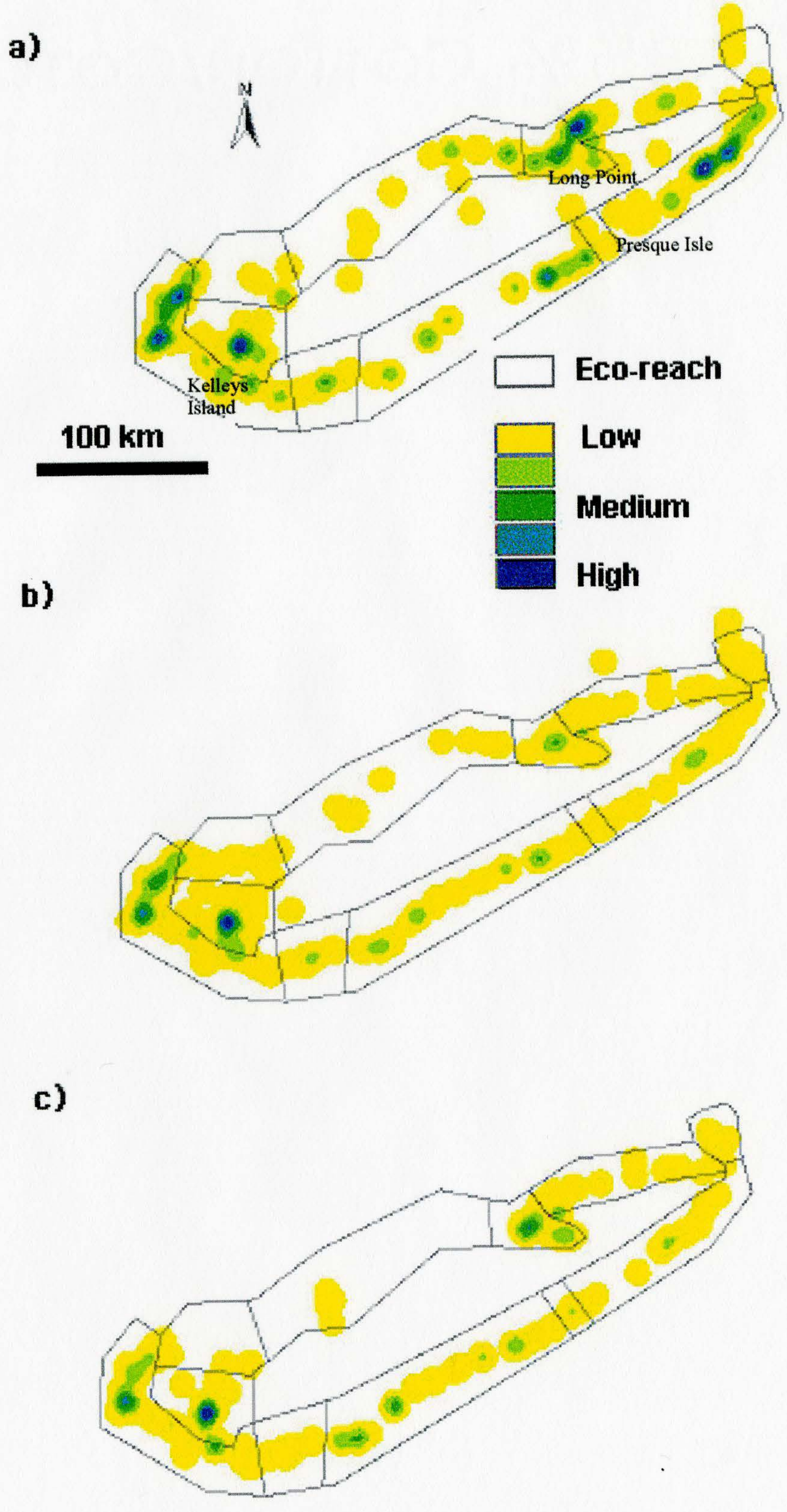

a)
Green Bay
Algoma
b)
Kenosha
Muskegon
N
c)
Chicago
Eco-reach
Low
Medium
High
100 km

Figure 1.5 Distribution patterns of spawning and nursery habitat for L. Erie fishes sorted by a) open-water, b) intermediate, and c) coastal taxocenes.



a)
N
Long Point
Presque Isle
Kelleys
Island
100 km
Eco-reach
Low
Medium
High
b)
c)

Figure 1.6 Distribution patterns of spawning and nursery habitat for L. Ontario fishes sorted by a) open-water, b) intermediate, and c) coastal taxocenes.

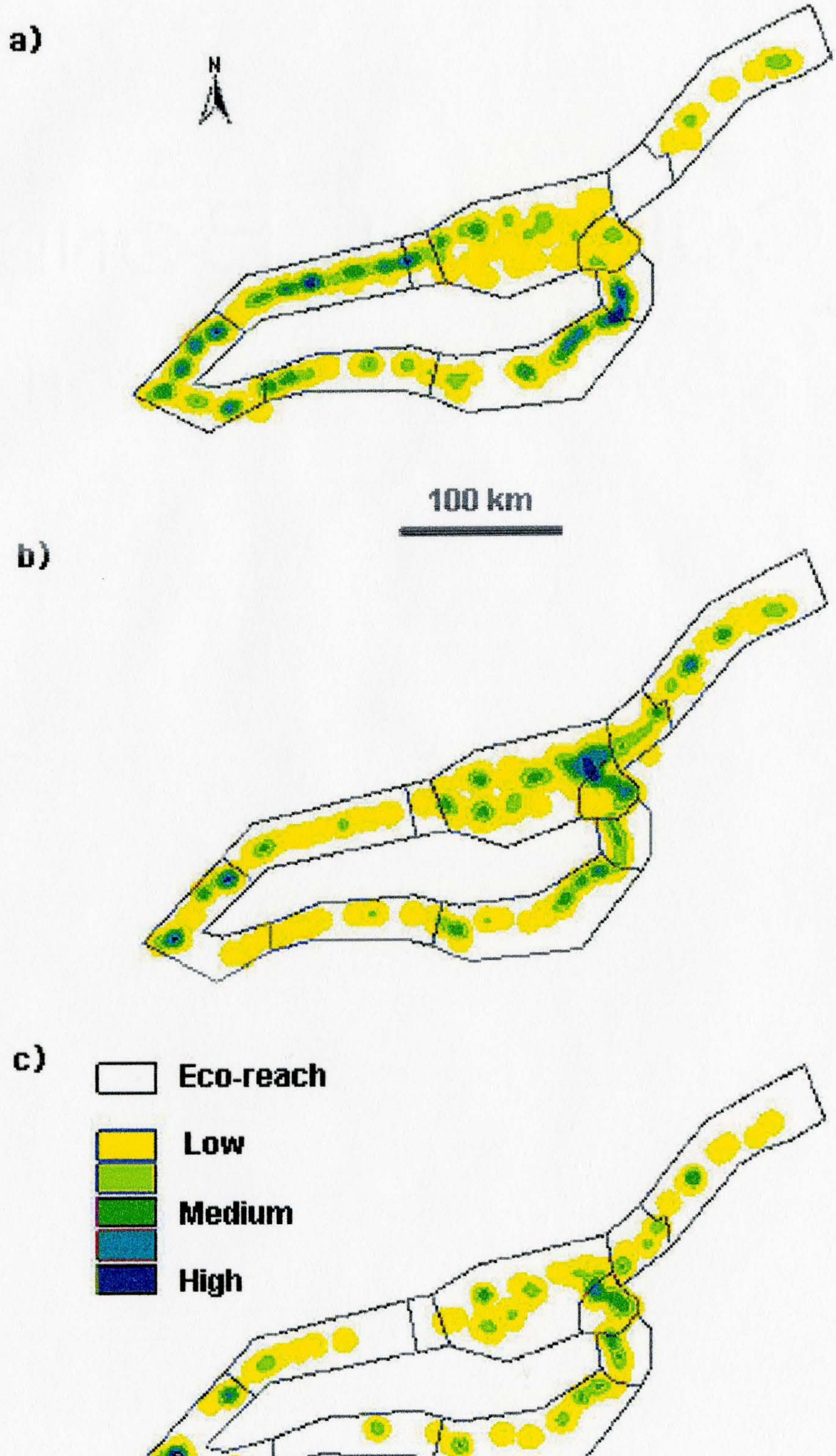
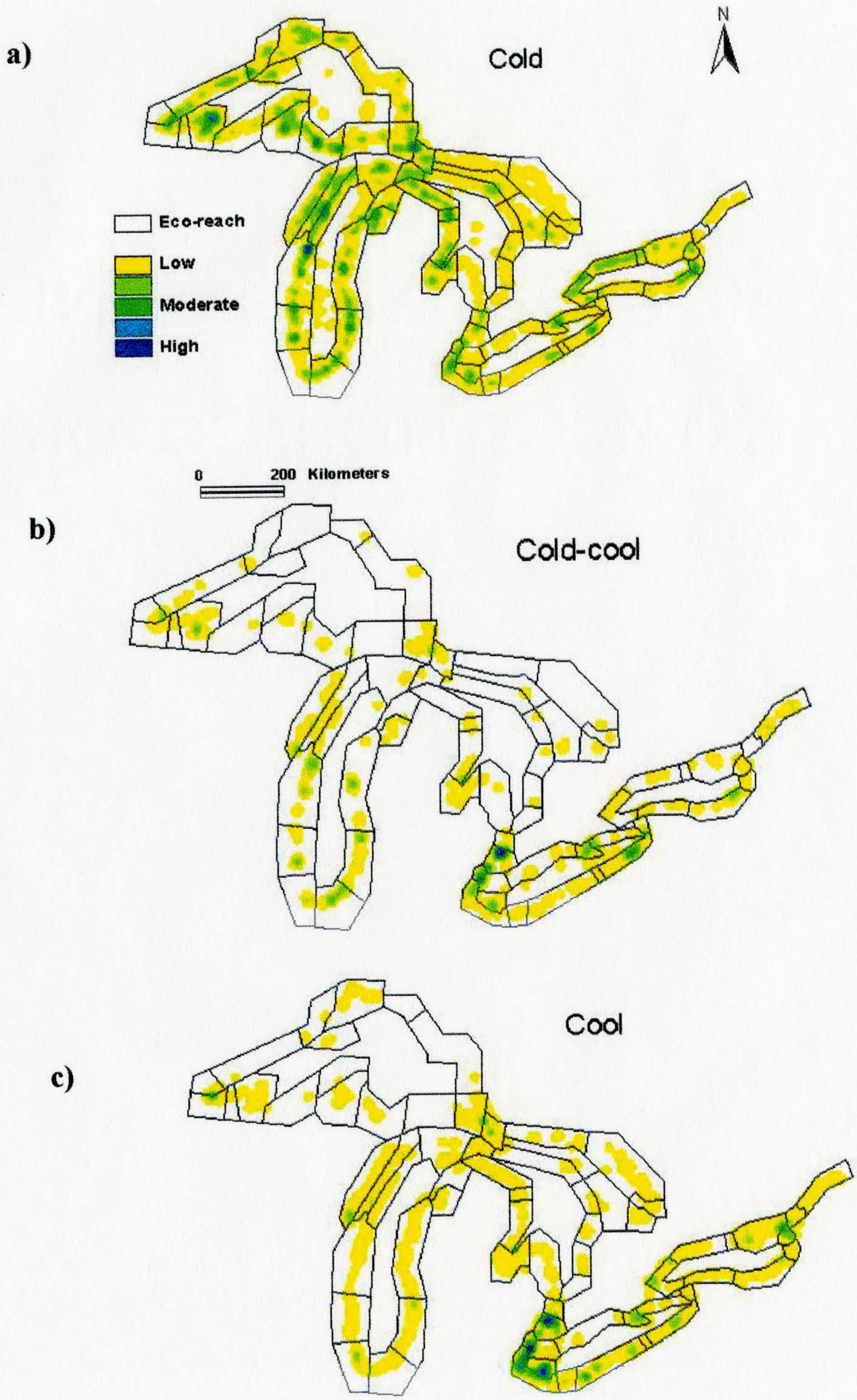
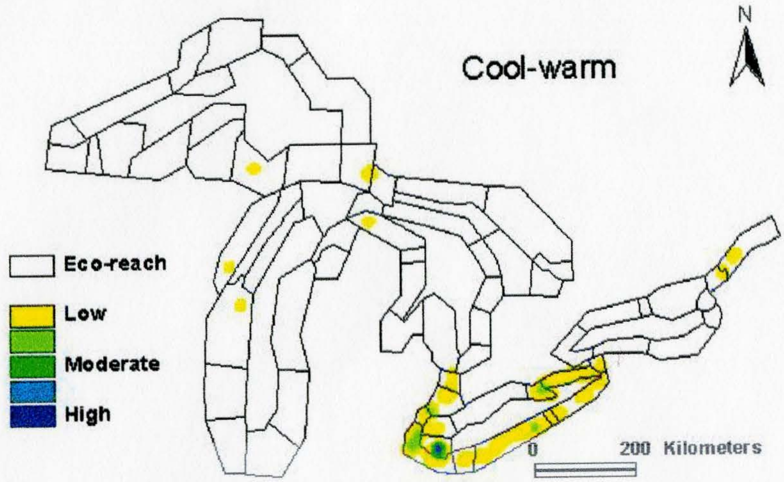

a)
N
100 km
b)
c)
Eco-reach
Low
Medium
High
0
100 Kilometers

Figure 1.7 Distribution patterns of spawning and nursery habitat for Great Lakes fishes sorted by thermal preferences a) cold, b) cold-cool, c) cool d) cool-warm and e) warm.



a)
Cold
N
Eco-reach
Low
Moderate
High
0 200 Kilometers
b)
Cold-cool
Cool
c)

d)


Cool-warm
N
Eco-reach
Low
Moderate
High
0
200 Kilometers

e)

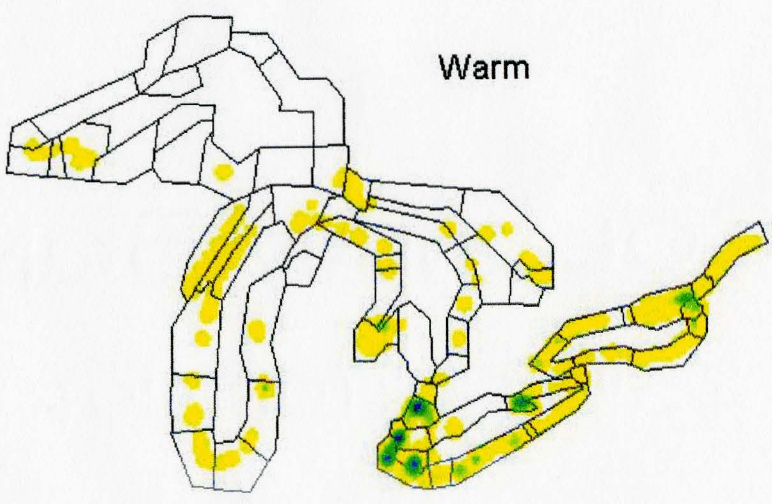

Warm

Figure 1.8 Distribution patterns of spawning and nursery habitat for Great Lakes fishes sorted by reproductive guilds that favor the lower lakes: a) A.1.1, b) A.1.6, c) B.1.4, d) B.2.2, e) B.2.3, f) B.2.4, g) B.2.5, and h) B.2.7

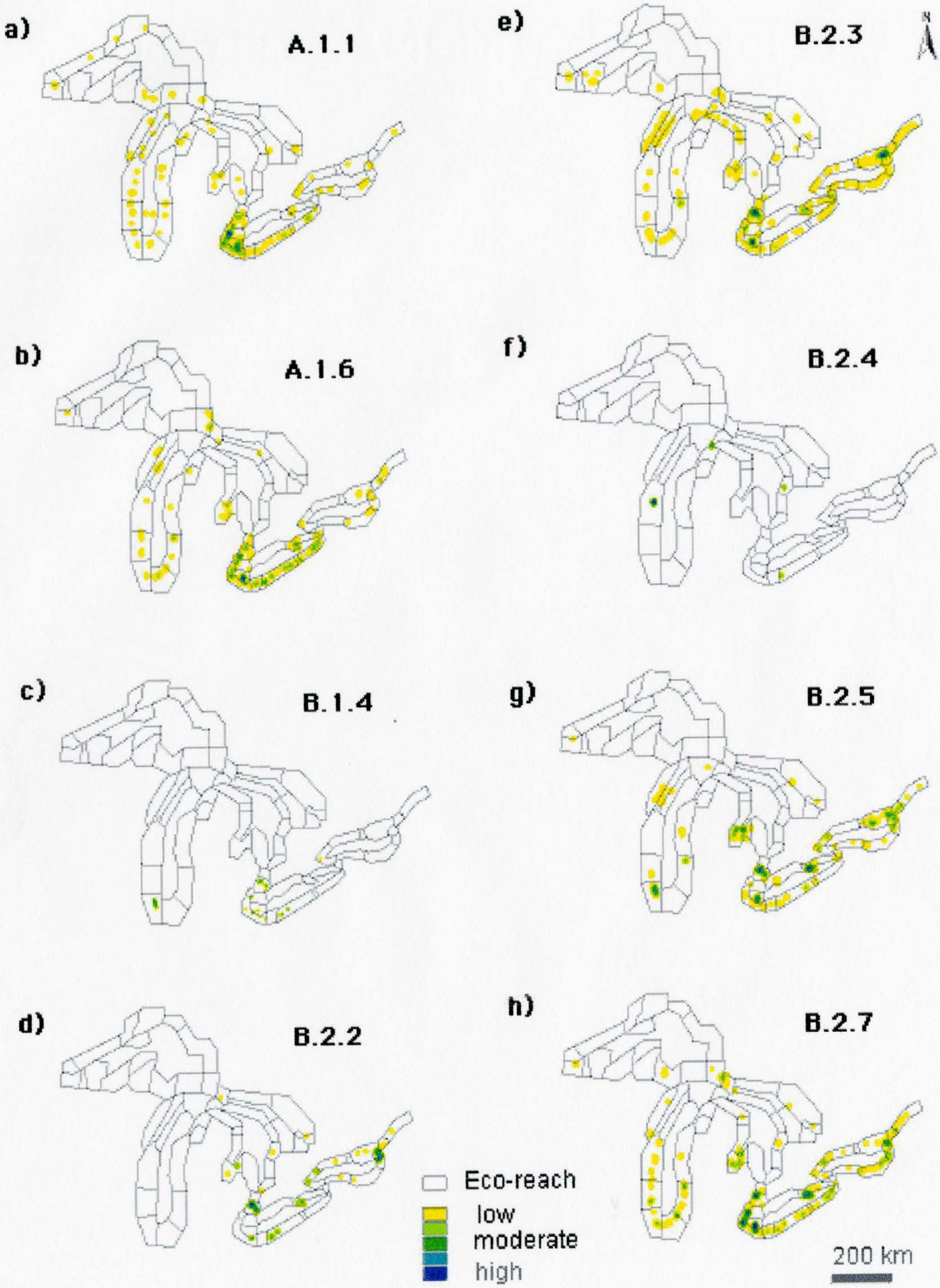
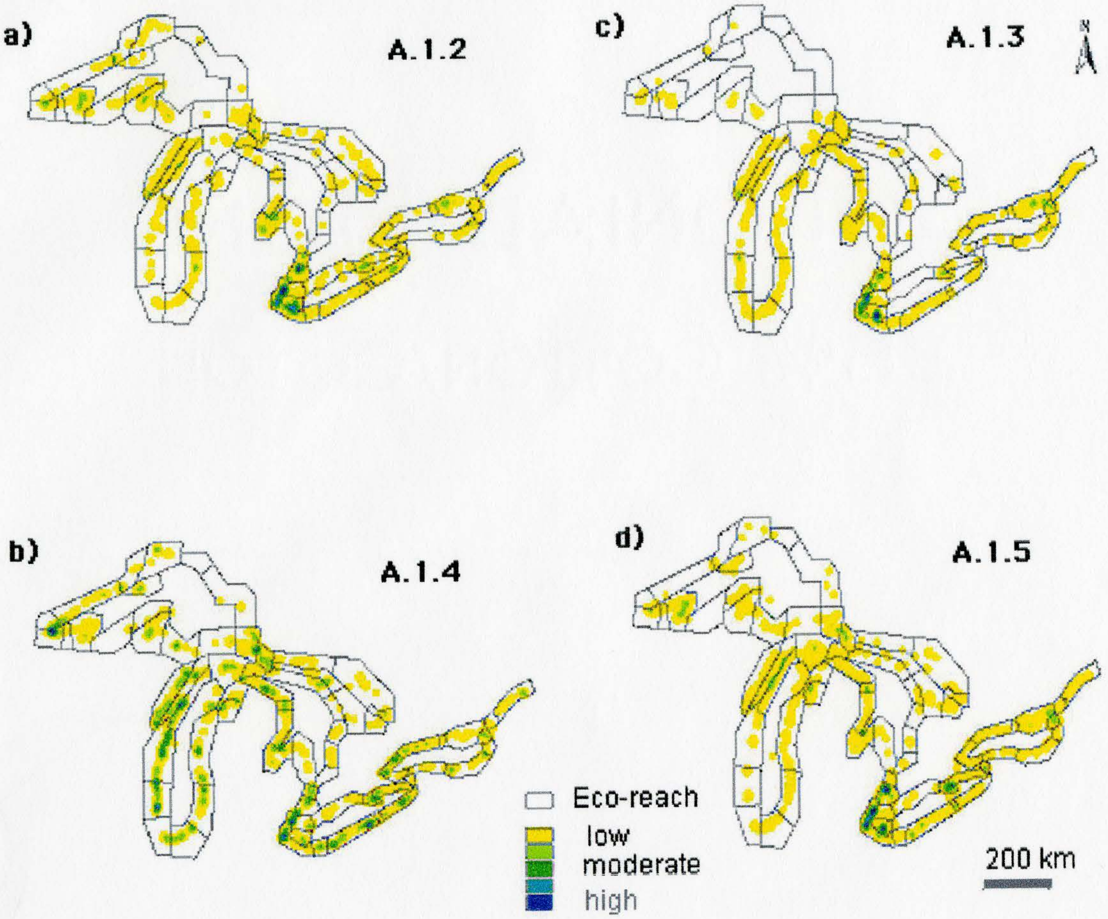

a)
A.1.1
e)
B.2.3
N
b)
A.1.6
f)
B.2.4
c)
B.1.4
g)
B.2.5
d)
B.2.2
h)
B.2.7
Eco-reach
low
moderate
high
200 km

Figure 1.9 Distribution patterns of spawning and nursery habitat for Great Lakes fishes sorted by reproductive guilds that correspond to intermediate taxocene: a) A.1.2, b) A.1.4, c) A.1.3, and d) A.1.5



a)
A.1.2
c)
A.1.3
N
b)
A.1.4
d)
A.1.5
Eco-reach
low
moderate
high
200 km

Fig. 1.10 Distribution patterns of spawning and nursery habitat for Great Lakes fishes sorted by reproductive guilds that correspond to open-water taxocene

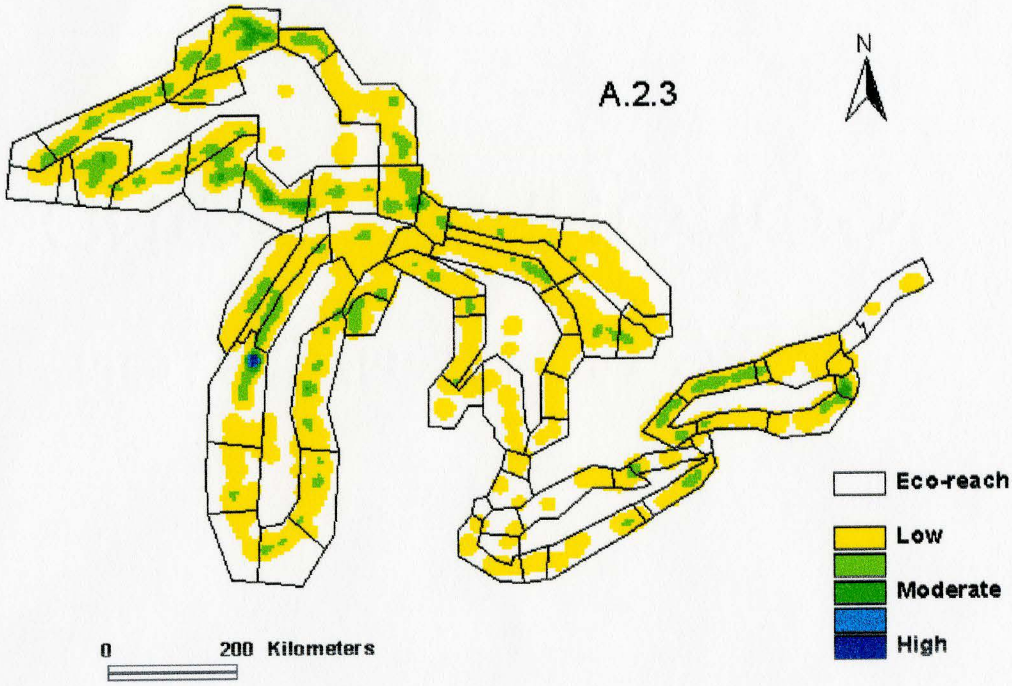
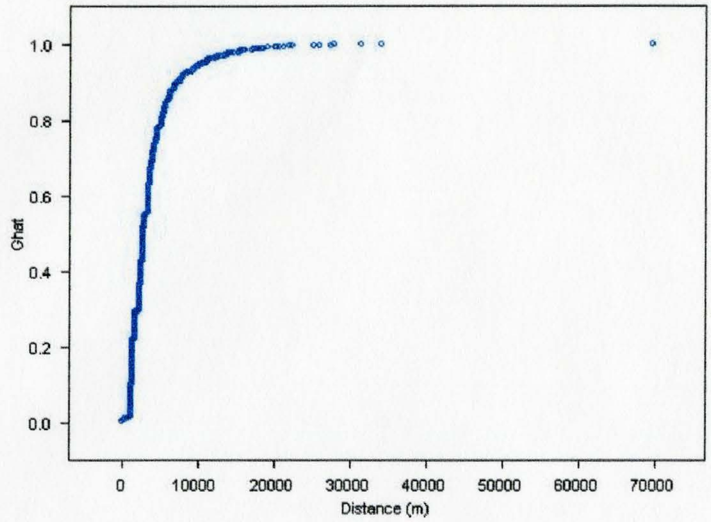

A.2.3
N
Eco-reach
Low
Moderate
High
0
200 Kilometers

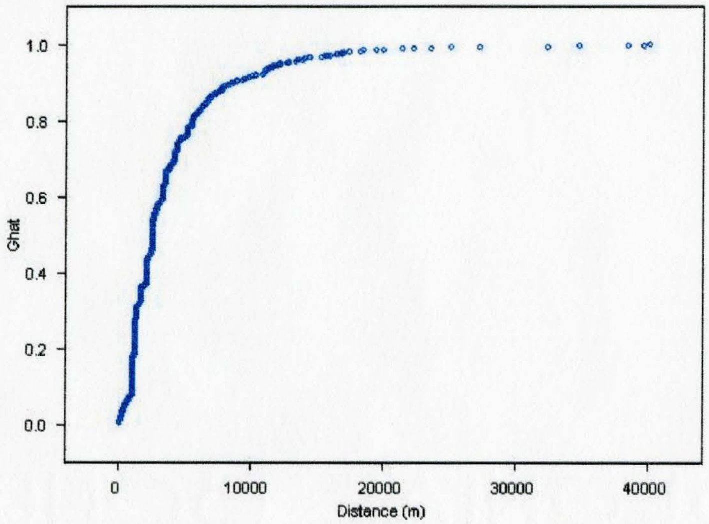
Figure 1.11 Plot of cumulative probability distribution (G_{hat}) for a) open-water b) intermediate and c) coastal taxocenes

a)



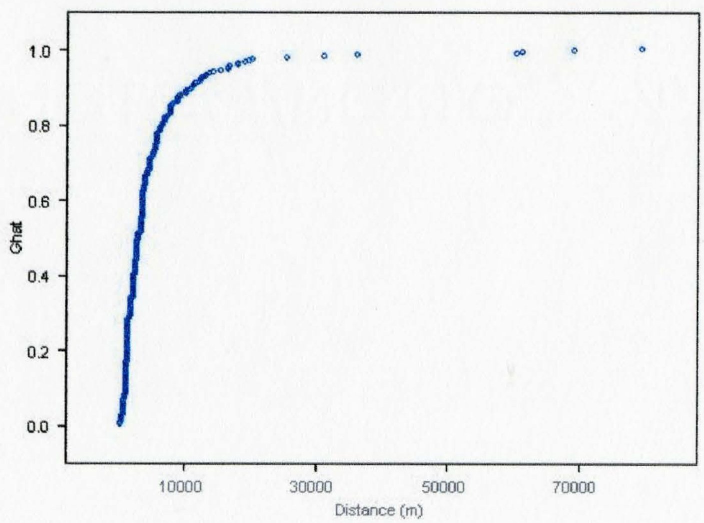
1.0
0.8
0.6
0.4
0.2
0.0
Ghat
0
10000
20000
30000
40000
50000
60000
70000
Distance (m)

b)



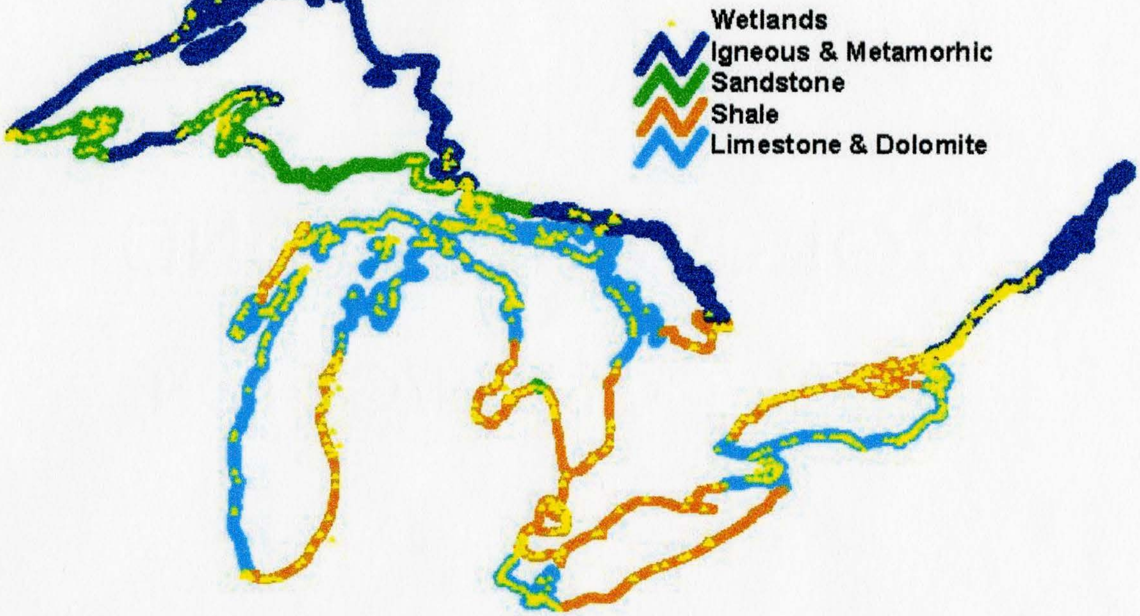
1.0
0.8
0.6
0.4
0.2
0.0
Ghat
0
10000
20000
30000
40000
Distance (m)

c)



1.0
0.8
0.6
0.4
0.2
0.0
Ghat
10000
30000
50000
70000
Distance (m)

Figure 1.12 Primary bedrock types and coastal wetlands along shorelines of the Great Lakes


Wetlands
Igneous & Metamorhic
Sandstone
Shale
Limestone & Dolomite

CHAPTER 2:

Spatial relationship between wetland-associated fish and shoreline features of the Laurentian Great Lakes

By

Anhua Wei and Patricia Chow-Fraser

ABSTRACT: The objective of this study was to examine the correlation between the spatial distribution patterns of fish and shoreline substrate classes at the geographical scale of the Great Lakes basin. A chi-square goodness-of-fit test indicated strong association between the distribution of fish and three shoreline classes: (wetland, sandy beach/dunes and bluff). The fish community did not use the shoreline classes in proportion to their availability, but used wetlands, sandy beaches/dunes, and bluffs more frequently than expected and bedrock less frequently than expected. A bivariate pattern analysis was applied to test if the occurrence pattern of fish is related to occurrences of tributaries and coastal wetlands in Lake Ontario. The bivariate pattern analysis indicated that occurrences of fish in L. Ontario were positively associated with both coastal wetlands and tributaries, although the relationship was considerably weaker for tributaries than for wetlands. These results confirm that the preferred utilization of coastal wetlands by majority of the Great Lakes fishes is consistent across geographic scales, from the site level to that of the entire Great Lakes basin.

INTRODUCTION

Coastal wetlands are known to be very important to the fisheries of the Laurentian Great Lakes because they provide spawning and nursery habitat for wetland-dependent species that include a large number of commercially and recreationally important taxa (Herdendorf and Hartley, 1981; Chubb and Liston, 1986; Stephenson, 1990; Jude and Pappas, 1992; Brazner, 1997). The U.S. Nature Conservancy estimated that about 80% of the approximately 200 fish species found in the Great Lakes use the near-shore 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).

Despite this widespread acceptance of the importance of coastal wetlands as habitat, direct field evidence has been limited to a few studies which are geographically restricted to shoreline segments of only one or two of the five Great Lakes (Chubb and Liston 1986; Stephenson 1990; Brazner 1997). Although Jude and Pappas' (1992) study included sites from all five Great Lakes, only nine coastal wetlands were examined in total. Thus, even though the value of coastal wetlands is generally recognized, no comprehensive studies has ever been undertaken to statistically examine the association between fish and coastal wetlands, as well as other features of the shoreline at the geographical scale of all five Great Lakes. Interpretation of the relative importance of abiotic and biotic factors may depend on the scale of the study. For instance, small-scale studies (e.g. involving only one site) may reveal the importance of biotic factors such as interspecific competition, whereas large-scale studies (e.g. involving many sites over a large geographic region) may emphasize abiotic factors (Jackson et al. 1992). Therefore, proper examination of the association between fish and wetlands (or any other shoreline feature) for the Great Lakes community should be conducted at the scale of the entire basin. This study is one of the first to look at the distribution pattern of fish habitat for the entire Great Lakes fish community, and is expected to reveal insights into abiotic factors that influence their distribution.

Results of Chapter 1 indicate an aggregated distribution pattern of fish in the near-shore of the five Great Lakes that appears to be associated with location of coastal wetlands. Based on these observations, we formally test the hypothesis that there is a positive association between fish distribution and wetland location. We will accomplish this by conducting spatial-pattern analysis to detect associations between spatial distribution of fish and shoreline features that are not known to be associated with wetland-dependent taxa (e.g. bluffs, boulders, hardened surfaces, etc.), as well as those that are (e.g. tributaries, coastal wetlands)

METHODS

Databases

Fish distribution data

To undertake this study, data from two different sources were assembled. 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 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. One major limitation to any regional-scale coarse survey such as this is that use of specific habitat by any species is subject to sampling error and we cannot interpret absence of a species from a site to mean that the habitat is unavailable for that species. Nevertheless, the atlas provides the most extensive historical coverage of spawning and nursery habitat of the Great Lakes fishery. This dataset was deemed acceptable because our study focuses on mapping the occurrences of fish and identifying regional-scale spatial patterns of fish habitat rather than documenting distribution at the site level. Close to 9,500 of the geo-referenced data records (occurrences of fish species) covering all five Great Lakes and connecting channels from the Goodyear et al. (1982) atlas were imported into the WIRE Net database (see below).

Wetland and geographic features

Another data source required was a comprehensive coastal habitat inventory for the Great Lakes, along with shoreline classification that would identify basic geographic features and substrate type (i.e. wetlands, beaches, hardened shoreline, etc.). The shoreline data were obtained from the U.S. Corps of Army Engineers (GLERL 1997) for the U.S. shoreline. The data were first re-classified and reduced to a smaller number of eleven classes (Tables 2.1 and 2.2).

This study also adopts the use of " **eco-reaches**" (Chow-Fraser and Albert 1999) to represent stretches of the Great Lakes shoreline that support significant concentrations of coastal wetlands, and which 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). Chow-Fraser and Albert (1999) have already pointed out that many of these delineations do not match existing natural division maps of the Great Lakes area (Carpenter et al. 1995, Albert 1995) based on upland characteristics because coastline conditions reflect a combination of upland and near-shore characteristics. Superimposition of these "eco-reach" delineations on the Great Lakes shoreline provides an easier way to interpret the results of the spatial-pattern analyses.

For spatial pattern analysis between fish distribution and those of coastal wetlands and tributaries, we required access to a high-resolution dataset that contains a complete inventory of Great Lakes wetlands and tributary information. Unfortunately, no relevant wetland inventory is available for all of the Great Lakes, but we had access to the WIRE

Net (Wetland Inventory for Research and Education Network, McMaster University, http://www.wirenet.info) inventory that is complete for Lake Ontario (both Canada and U.S. shorelines). The WIRE Net database also contained the location of the major streams for Lake Ontario (OMNR 2002).

Data analysis

A chi-square test was used to test association between fish occurrences and the Great Lakes shoreline habitat characteristics. Spatial analysis in this study includes the following: Kernel estimate and bivariate pattern analysis. Kernel estimate was used to produce density maps of coastal wetlands and fish occurrences of Lake Ontario. A bivariate pattern analysis was used to determine if the occurrence pattern of fish was related to occurrences of tributaries and coastal wetlands in Lake Ontario.

A number of approaches to test independence of a bivariate spatial pattern have been suggested. The approach taken in this study is to take a random sample of points in the study area and measure the distance between nearest-neighbor-point-events, *i* (i.e. location of fish), and the distance between the nearest-neighbor-point-events, *j* (i.e. coastal wetlands), corresponding to this sample of random points. Distances in each of these samples are then replaced by their rank within their respective sample. As a result, one is left with pairs of point-event distance ranks. These can then be tested for independence using a standard procedure such as that based on Spearman's or Kendall's rank correlation coefficient (Upton and Fingleton 1985; Bailey and Gatrell 1995). If the two types of point patterns are located in an independent fashion, then there should be no correlation between i and j. If they exhibit attraction, the pair of values (i, j) will be positively correlated. On the other hand, if they exhibit repulsion, the pairs of observations will display negative correlation (Diggle and Cox, 1983; Upton and Fingleton, 1985).

RESULTS

The three most common shoreline classes where Great Lakes fish occurred were bedrock (includes both resistant and non-resistant; 21.9%), wetlands (includes open-shoreline, semi-protected and bay-mouth barrier beaches; 21.8%), and sandy beaches/dunes (18.4%) (Table 2.3). Infrequently used classes included a composite class of unknown composition (0.7%), clay banks (0.8%), sand-silty banks (2.4%), coastal plains (1.7%), coarse beaches (3.7%) and artificial substrates (3.8%). Classes that had intermediate use included bluffs (11.2%) and unclassified (13.7%). A chi-square goodness-of-fit test (Chi-square = 43.152, df = 10, $P<0.0001$) indicated that the fish community did not use the shoreline classes in proportion to their availability, but used wetlands, sandy beaches/dunes, and bluffs more frequently than expected and bedrock less frequently than expected.

Analysis by taxocene

When the data were sorted according to Jude and Pappas' taxocenes (see description in Chapter 1), we found that 26.1 % of the open-water taxocene were spatially associated with bedrock. A chi-square test indicated that 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%, respectively for coastal and intermediate taxocenes). Sandy beaches/dunes (24.7%), wetlands (17.1%), and bluffs (10.8%) were also found widely associated with the open-water taxocene (Table 2.4). These four shorelines classes together accounted for close to 80% of the observed occurrences of open-water taxa along the Great Lakes shoreline.

By comparison, 25% of the occurrences of the intermediate taxocene was associated with wetlands (Table 2.4). Given that only 16% of all shoreline classes in this study were wetlands (Table 2.3), this relatively high value indicates a significant preference by the intermediate taxocene for coastal wetland habitat (chi-square test; $P<0.0001$). The 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 2.4). These four shoreline classes together accounted for almost 70 % of the observed distribution of intermediate taxocene in the near-shore zone of the Great Lakes.

The highest proportion of fish classified into the coastal taxocene were associated with coastal wetlands (31.1 %; Table 2.4). Other shoreline habitats that were spatially associated with this taxocene included bedrock (17.3%) and bluffs (11.3%). Given the availability of shoreline habitats (Table 2.3), the coastal taxocene showed the highest preference for wetlands, and the least for bedrock.

Analysis by Thermal Preference

A breakdown of how fish occurrence for the five thermal groups (i.e. cold, cold-cool, cool, cool-warm and warm) were distributed among the eleven shoreline classes are shown in Table 2.5. All five groups made extensive use of 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-water** taxa (22.9%), a frequency that exceeded that based on availability (21.9%). Wetlands, which co-occurred with 21.8% of the fish, were over-utilized by the **warm-** (31.0%), **cool-** (26.8%) and **cold/cool-water** (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 was underutilized by the the **cold/cool-** (16.2%), **cool-** (12.5%), **cool/warm-** (4.2%), and **warm-water** (7.0%) taxa.

Analysis by Reproductive Guild

The association between fish occurrences and shoreline characteristics were also analyzed for each of the thirteen relevant reproductive guilds (Balon 1975; see Chapter 1, Table 1.3 for description). In most instances, wetlands were associated with the highest frequency of occurrence, ranging from 20% for **A.1.6** (psammophils that deposit egg masses that stick to sandy bottom or plant roots) to 42.1% for **B.2.5** (spelephils that deposit eggs on cleared areas of the under-surface of flat stones, natural holes, cavities, or in specially constructed burrows). The only guild that under-utilized wetlands were **A.2.3** (15.9%), which are ostracophils that hide their brood in gill chambers of live mussels, crabs, ascidians, or in specially constructed places such as redds). Although only 1.7% of all fish occurred in riverine-coastal plains, all except **A.1.3** (lithophils that deposit eggs on rock, rubble, or gravel) and **A.2.3** (i.e. brood hiders) made use of these habitats in excess of their availability (frequency ranging from 2.0 to 5.8%). Both **A.2.3** and **B.2.3** (psammophils whose eggs are covered with sand grains and fanned by females preferred bedrock (27.0 and 25.8%, respectively), while **A.1.3** (lithophils) and **B.2.4** (nest guarders and spawners that build their nests in grass or reeds) were found positively associated with sandy beach-dunes (22.9 and 22.7%, respectively) and with wetlands (21.8 and 20.5%, respectively).

Location of coastal wetlands in the Great Lakes shoreline

Since wetlands were one of the four most commonly used habitats in the above analysis, we will show how the three classes of wetlands included in the GLERL (1997) shoreline classification scheme (Table 2.1) are distributed throughout the Great Lakes shoreline (Fig. 2.1). Open-shoreline wetlands are the least abundant of the three types, occurring primarily in the north shore of Lake Superior, the St. Marys River, Saginaw Bay, Lake St. Clair, and Bay of Quinte and the St. Lawrence River (Fig. 2.1a). Semi-protected wetlands are located primarily along the south shore of Lake Superior, the St. Marys River, lower Green Bay, western Lake Erie and eastern Lake Ontario (Fig. 2.1b). Bay-mouth barrier-beach wetlands occur abundantly in the southwestern shoreline of Lake Superior, throughout Lake Michigan, and in the two lower lakes, but were extremely rare in Lake Huron, the north shore of Lake Superior, and the St. Lawrence River (Fig. 2.1c). Because these data are only medium-resolution vector data, they are not suitable for detailed spatial pattern analysis, although they are useful for indicating broad regional distribution patterns, and may be helpful for generating hypotheses regarding the distribution of certain wetland type and fish categories.

Association between fish occurrence and coastal wetlands of Lake Ontario

For this analysis, Goodyear et al.'s (1982) fish occurrence data for Lake Ontario were first plotted (Fig. 2.2a) and then a density map of these occurrences were generated (Fig. 2.2b). The density map confirms the extensive use by all fish in the eastern and western ends of the lake. When the fish distributions were examined by taxocene, it was clear that both the coastal (Fig. 2.3a) and intermediate (Fig. 2.3b) taxocenes made extensive use of the three types of wetlands that occur abundantly in eastern Lake Ontario (Fig. 2.1). By contrast, the open-water taxocene were distributed widely along the entire shore of L. Ontario, but the highest concentration did not occur at the eastern end of the lake (Fig. 2.3c).

The distribution pattern and density map of coastal wetlands in Lake Ontario are shown in Fig. 2.4a and b, respectively. There is clearly a high concentration of wetlands at the eastern end that coincides with the high density of coastal and intermediate taxocenes (Fig. 2.3a and b, respectively). On the other hand, the concentration of open-water taxocene (Fig. 2 3c) did not appear to be located near this wetland cluster.

We performed a bivariate pattern analysis (Diggle and Cox, 1983; Upton and Fingleton, 1985; Baily and Gatrell 1995) to determine the association between each of the three taxocenes with the coastal wetlands. In all three cases, the taxocenes were positively associated with the wetlands, as indicated by significant positive Spearman's rank correlation coefficients of + 0.7211 for the intermediate taxocene (normal - z = 0.71746; $P < 0.0001$), +0.5799 for the coastal taxocene (normal – z = 5.7694; P< 0.0001) and +0.3639 for the open-water taxocene (normal – z = 3.6208; P<0.0001).

Association between fish occurrence and major streams of Lake Ontario

Since the prevalent use of streams by the open-water taxa for spawning habitat is well documented, we decided to conduct a bivariate pattern analysis to determine the association between the distribution pattern of the three taxocenes with the occurrence of major streams in Lake Ontario. The distribution pattern of the open-water taxocene, along with the major streams of L. Ontario are presented in Fig. 2.5. We found that all three taxocenes were significantly associated with streams, although the value of the correlation coefficients were substantially lower than that for the previous analysis; the Spearman's rank correlation coefficients was + 0.3323 (normal – z =3.3062; P= 0.0009) for the intermediate taxocene; +0.3002 (normal – z = 2.9872; P = 0.0028) for the coastal taxocene; and + 0.1958 (normal – z = 1.9485; P = 0.0514) for the open-water taxocene. When we used the same procedure to determine the spatial association between coastal wetlands and streams in L. Ontario, we found a significant positive association; the Spearman's rank correlation coefficient was + 0.3483 (normal – z = 3.4659; P = 0.0005).

DISCUSSION

There were significant positive associations between the distribution pattern of fish and several of the shoreline classes. First, regardless of classification scheme used (i.e. taxocene, thermal preference or reproductive guild), the observed fish distribution associated with the wetland class were almost always greater than expected (16.1 %). Secondly, clay banks and coarse beaches were rarely used as spawning and nursery habitat. Thirdly, near-shore areas characterized by bedrock, sandy beach/dunes and bluffs were widely used as reproductive habitat by the Great Lakes fish community (Tables 2.3 - 2.5).

Stephenson (1990) pointed out that the significance of local coastal marshes should be assessed in a regional context. Kelso and Minns (1996) indicated that fish species measurements at a location in the Great Lakes are primarily related to a response to regional factors. They also pointed out that at the community level especially in the Great Lakes, patchiness in habitat and resources critical to different life stages will be particularly important. To our knowledge, this study is the first attempt at determining the importance of coastal wetlands to fish at the scale of the lake basins. Our study confirmed that the regional distribution pattern of fish along the shores of the Great Lakes is positively correlated with that of coastal wetland and other important geographic features at both large (e.g. Great Lakes) and intermediate (e.g. L. Ontario) scales. It also confirms the findings of previous studies conducted at a much reduced scale (e.g. Chubb and Liston 1986, Stephenson 1990; Brazner 1997) which suggested that coastal wetlands provide critical spawning and nursery habitat for Great Lakes fishes. This means that the preferred utilization of coastal wetlands by fishes is a consistent phenomenon that can be upheld across geographical scales.

What is perhaps a surprising finding is that coastal wetlands are not only important to the coastal taxocene that are defined as wetland-dependent (Jude and Pappas 1992), but are also important to the intermediate and open-water taxocenes.. One reason for the importance of coastal wetlands to fish in general is that the presence of emergent and submergent plant provide shelter and a food-source for benthic invertebrates and epiphytic algae on which larval and juvenile fish feed during their first few months of life. 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 in a larger water body (Jude and Pappas, 1992).

Our study also indicated that near-shore waters that are spatially associated with bedrock, sandy beaches/dunes, and bluffs are widely used as reproductive habitat by the Great Lakes fishes (Table 2.3). These three classes are well-represented in the Great Lakes shoreline, together accounting for 62% of the total shoreline length. Frequent occurrence of fish in these near-shore areas probably reflect 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).

Fish have a narrow and relatively unique range of summer temperatures at which they grow best. They are highly mobile and actively seek their "preferred" range in summer. As a result, species with similar preferred range in temperatures generally have similar spatial distributions in summer. Since coastal wetlands are shallow and warm, they provide ideal habitats for both warm water and cool-water species (Table 2.5). Our analysis further indicated that warm-water species were positively associated with coastal wetlands, and displayed the strongest association with this shoreline class among all thermal categories.

In Chapter 1, we found that the distribution of wetland-associated taxocenes (e.g. intermediate and coastal) overlapped extensively with that of the cool-warm- and warm-water groups, as well as that of nine reproductive guilds (A.1.1, A.1.3, A.1.4, A.1.6, B.1.4, B.2.2, B.2.3, B.2.5, and B.2.7). In this study, we found a spatial preference for wetlands by almost all thirteen guilds (A.1.1, A.1.2, A.1.4, A.1.5, A.1.6, B.1.4, B.2.2, B.2.3, B.2.5, and B.2.7), thus confirming the association between the distribution pattern of wetland-associated taxa and wetland occurrence, and allows us to conclude that the three classification schemes can be used interchangeably for the purpose of identifying coarse habitat type.

Coastal wetlands as a unique habitat type integrate many important habitat requirements for fish. They not only provide necessary spawning and nursery grounds, but also provide other important habitat requirements such as food source, shelter and thermal niche etc. for wetland-dependent fish. That coastal wetlands provide shelter is an important requirement for "non-guarders" such as A.1.4, A.1.5, and A.1.6, which deposit eggs on submerged plants or fine roots, and do not guard their embryos. On the other hand "guarders" such as B.1.4, B.2.2, B.2.3, B.2.5, and B.2.7 benefit from the presence of emergent and submergent plants in coastal wetlands that provide protection from larval predation. The pelagophils (A.1.1 and A.1.2) however, do not require wetland habitat since they release their eggs in open water or on rocks and gravel.

According to Goodyear et al. (1982), more than 90 species of fish have been recorded as residents in L. Ontario and 55 were native to the lake. Most of these native species and 12 exotic species spawn in tributaries or in shallow, protected waters of the lake. The authors have suggested that both tributaries and coastal wetlands are important spawning and nursery areas, even though the relative importance of each had not been determined. According to our analysis, all three taxocenes were positively associated with streams along the shoreline of L. Ontario although the strength of the associations was weaker than that between the occurrence of fish and coastal wetlands. As expected, the open-water taxocene displayed the weakest spatial association with coastal wetland; however, it also displayed a relatively weak spatial association with tributaries and this was unexpected. The reason for this weak association may be attributed to the fact that species in this taxocene do not solely spawn in tributaries but may also use offshore habatitats.

This study is one of the most extensive examinations of fish distribution patterns at the scale of the Great Lake basin. We have confirmed that majority of the fish preferentially use coastal wetlands for spawning and nursery habitat. Future studies on the other Great Lakes should be undertaken to confirm the positive association established here for Lake Ontario between fish distribution, and the occurrence of coastal wetlands and tributaries.

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Table 2.1 Classification of shoreline features used by GLERL (1997).

01	High (>15m) Bluff
02	High (>15m) Bluff with Beach
03	Low (<15m) Bluff
04	Low (<15m) Bluff with Beach
05	Sandy/Silty Banks
06	Clay Banks
07	Sandy Beach/Dunes
08	Coarse Beaches
09	Bay-mouth-Barrier Beaches
10	Bedrock (Resistant)
11	Bedrock (Non-resistant)
12	Low Riverine/Coastal Plain
13	Open Shoreline Wetlands
14	Semi-Protected Wetlands
15	Composite
16	U.S. Shore: Unclassified
16	Canadian Shore: Unclassified
17	U.S. Shore: Artificial
17	Canadian Shore: Artificial
99	Unclassified (coded by the compiler)

Table 2.2 Classification scheme of shoreline habitat characteristics used in this study

Code	Shoreline class	Abbreviation
01	Bedrock	BR
02	Bluff	BL
03	Coarse Beaches	CB
04	Sandy Beaches-Dunes	SB
05	Sandy-Silty Banks	SS
06	Clay Banks	CL
07	Low Riverine-Coastal Plain	RP
08	Composite	CP
09	Wetlands	WL
10	Artificial	AR
99	Unclassified	UN

Table 2.3 Occurrence of fish in different shoreline classes. Expected percent = [Length of a shoreline habitat type / Length in total]*100. Observed counts = numbers of occurrences of fish associated with a shoreline habitat type. Expected counts = [numbers of occurrences of fish * percent].

Code	**Shoreline class**	**Abbr.**	**Length (m)**	**Expected Percent (%)**	**Expected counts**	**Observed Percent (%)**	**Observed counts**
01	Bedrock	BR	8392126	38.9	3667.2	21.9	2062
02	Bluff	BL	1806448	8.4	789.4	11.2	1057
03	Coarse Beaches	CB	1200374	5.6	524.5	3.7	345
04	Sandy Beaches/Dunes	SB	3239041	15.0	1415.4	18.4	1734
05	Sandy-Silty Banks	SS	294274	1.4	128.6	2.4	228
06	Clay Banks	CL	153471	0.7	67.1	0.8	75
07	Low Riverine-Coastal Plain	RP	1138461	5.3	497.5	1.7	162
08	Composite	CP	82696	0.4	36.1	0.7	63
09	Wetlands	WL	3478559	16.1	1520.1	21.8	2056
10	Artificial	AR	554651	2.6	242.4	3.8	359
99	Unclassified	UN	1239514	5.7	541.7	13.7	1289
Total			21579615	100.0	9430.0	100.0	9430

Table 2.4 The number of fish associated with shoreline classes within three taxocenes. Numbers below in brackets are percents. Numbers in bold indicate that they are the highest for the taxocene

Shoreline class	Expected Percent (%)	Taxocene			
		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 Beaches	5.6	18 (1.5)	71 (2.1)	256 (5.4)	345 (3.7)
Sandy Beaches-Dunes	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 Banks	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	--- ---	10 (0.3)	53 (1.1)	63 (0.7)
Wetlands	16.4	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	1217	3461	4752	9430

Table 2.5 The number of fish associated with shoreline classes within thermal preference groups. Numbers below in brackets are percents. Numbers in bold indicate that they are the highest for the group.

Shoreline class	Thermal preference					Total
	Cold	Cold/cool	Cool	Cool/warm	Warm	
Bedrock	1303	71	351	38	299	2062
	(25.4)	(13.8)	(17.4)	**(22.9)**	(18.7)	(21.9)
Bluff	562	73	227	30	165	1057
	(10.9)	(14.2)	(11.2)	(18.1)	(10.3)	(11.2)
Coarse Beaches	262	12	38	3	30	345
	(5.1)	(2.3)	(1.9)	(1.8)	(1.9)	(3.7)
Sandy Beach-Dunes	1279	83	253	7	112	1734
	(24.9)	(16.2)	(12.5)	(4.2)	(7.0)	(18.4)
Sandy-Silty Banks	81	18	72	9	48	228
	(1.6)	(3.5)	(3.6)	(5.4)	(3.0)	(2.4)
Clay Banks	21	6	25	2	21	75
	(0.4)	(1.2)	(1.2)	(1.2)	(1.3)	(0.8)
Low Riverine-Coastal Plain	36	7	68	2	49	162
	(0.7)	(1.4)	(3.4)	(1.2)	(3.1)	(1.7)
Composite	52	5	6	---	---	63
	(1.0)	(1.0)	(0.3)	---	---	(0.7)
Wetland	868	120	542	31	495	2056
	(15.9)	**(23.4)**	**(26.8)**	(18.7)	**(31.0)**	(21.8)
Artificial	169	23	87	11	69	359
	(3.3)	(4.5)	(4.3)	(6.6)	(4.3)	(3.8)
Unclassified	500	95	353	33	308	1289
	(9.7)	(18.5)	(17.5)	(19.9)	(19.3)	(13.7)
Total	5133	513	2022	166	1596	9430

Table 2.6 The number of fish associated with shoreline classes within guilds. Numbers below in brackets are percents. Numbers in bold indicate that they are the highest for the guild

Abbr. Guild	A.1.1	A.1.2	A.1.3	A.1.4	A.1.5	A.1.6	A.2.3	B.1.4	B.2.2	B.2.3	B.2.4	B.2.5	B.2.7	Total
BR	38	252	176	171	322	41	836	4	11	126	5	34	46	2062
	(17.4)	(21.8)	(14.6)	(20.3)	(21.7)	(17.4)	**(27.0)**	(12.5)	(21.2)	**(25.8)**	(11.4)	(13.5)	(14.2)	(21.9)
BL	33	104	156	102	147	33	365	1	5	49	5	15	42	1057
	(15.1)	(9.0)	(12.9)	(12.1)	(9.9)	(14.0)	(11.8)	(3.1)	(9.6)	(10.0)	(11.4)	(6.0)	(13.0)	(11.2)
CB	6	25	39	12	45	4	188	–	–	20	1	1	4	345
	(2.8)	(2.2)	(3.2)	(1.4)	(3.0)	(1.7)	(6.1)	–	–	(4.1)	(2.3)	(0.4)	(1.2)	(3.7)
SB	11	145	276	131	242	20	787	–	2	45	10	24	41	1734
	(5.0)	(12.6)	**(22.9)**	(15.6)	(16.3)	(8.5)	(25.4)	–	(3.8)	(9.2)	**(22.7)**	(9.5)	(12.7)	(18.4)
SS	17	41	35	24	39	10	34	1	1	8	3	5	10	228
	(7.8)	(3.5)	(2.9)	(2.9)	(2.6)	(4.3)	(1.1)	(3.1)	(1.9)	(1.6)	(6.8)	(2.0)	(3.1)	(2.4)
CL	6	12	8	5	20	5	8	–	–	8	–	1	2	75
	(2.8)	(1.0)	(0.7)	(0.6)	(1.3)	(2.1)	(0.3)	–	–	(1.6)	–	(0.4)	(.6)	(0.8)
RP	5	26	17	25	29	6	13	1	3	21	1	8	7	162
	(2.3)	(2.3)	(1.4)	(3.0)	(2.0)	(2.6)	(0.4)	(3.1)	(5.8)	(4.3)	(2.3)	(3.2)	(2.2)	(1.7)
CP	–	8	11	2	3	–	39	–	–	–	–	–	–	63
	–	(0.7)	(0.9)	(0.2)	(0.2)	–	(1.3)	–	–	–	–	–	–	(0.7)
WL	46	291	263	187	368	47	493	8	19	126	9	106	93	2056
	(21.1)	**(25.2)**	(21.8)	**(22.2)**	**(24.7)**	**(20.0)**	(15.9)	**(25.0)**	**(36.5)**	**(25.8)**	(20.5)	**(42.1)**	**(28.7)**	(21.8)
AR	6	50	55	33	51	11	105	2	4	17	2	13	10	359
	(2.8)	(4.3)	(4.6)	(3.9)	(3.4)	(4.7)	(3.4)	(6.3)	(7.7)	(3.5)	(4.5)	(5.2)	(3.1)	(3.8)
UN	50	201	169	150	221	58	227	15	7	69	8	45	69	1289
	(22.9)	(17.4)	(14.0)	(17.8)	(14.9)	(24.7)	(7.3)	(46.9)	(13.5)	(14.1)	(18.2)	(17.9)	(21.3)	(13.7)
Total	218	1155	1205	842	1487	235	3095	32	52	489	44	252	324	9430

Figure 2.1 Great Lakes shoreline showing the location of a) open shoreline wetlands, b) semi-protected wetlands, and c) bay-mouth-barrier beaches (data from Great Lakes Environmental Research Laboratory, 1997)

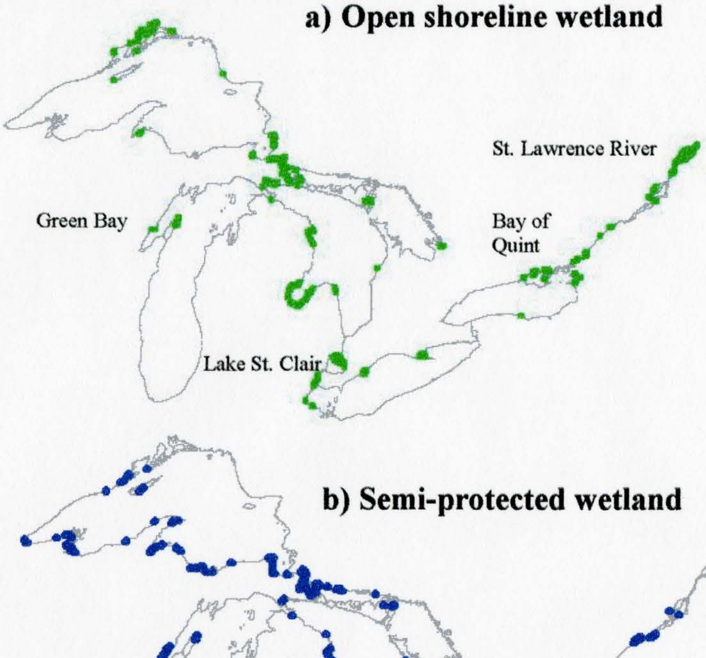
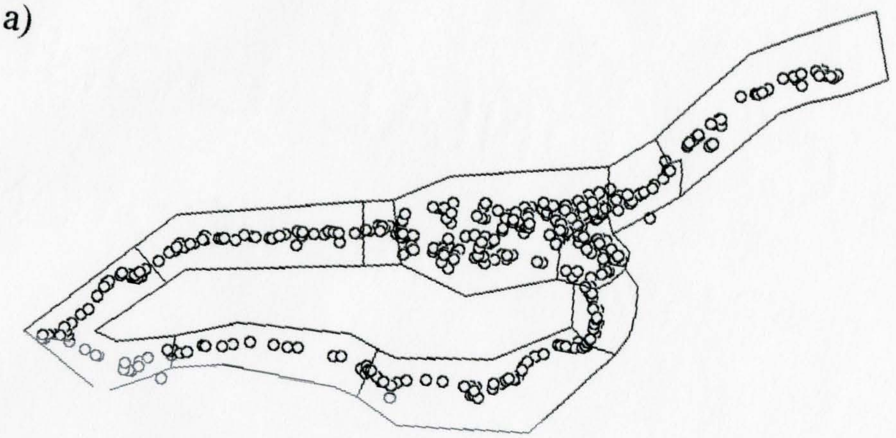

a) Open shoreline wetland
St. Lawrence River
Green Bay
Bay of
Quint
Lake St. Clair
b) Semi-protected wetland
c) Bay mouth barrier beach

Figure 2.2 Occurrence of fish along Lake Ontario shoreline a) location of occurrence of fish, b) density map of occurrence of fish (data from Goodyear et al. 1982)

a)



b)

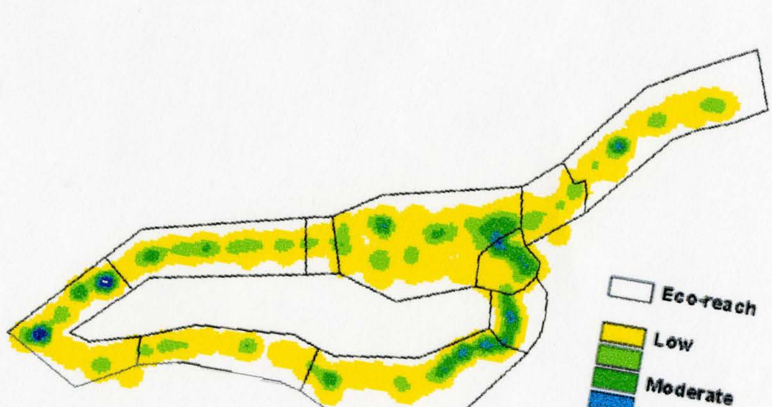


Figure 2.3 Distribution pattern of occurrences of fish in Lake Ontario for the a) coastal, b) intermediate, and c) open-water taxocene

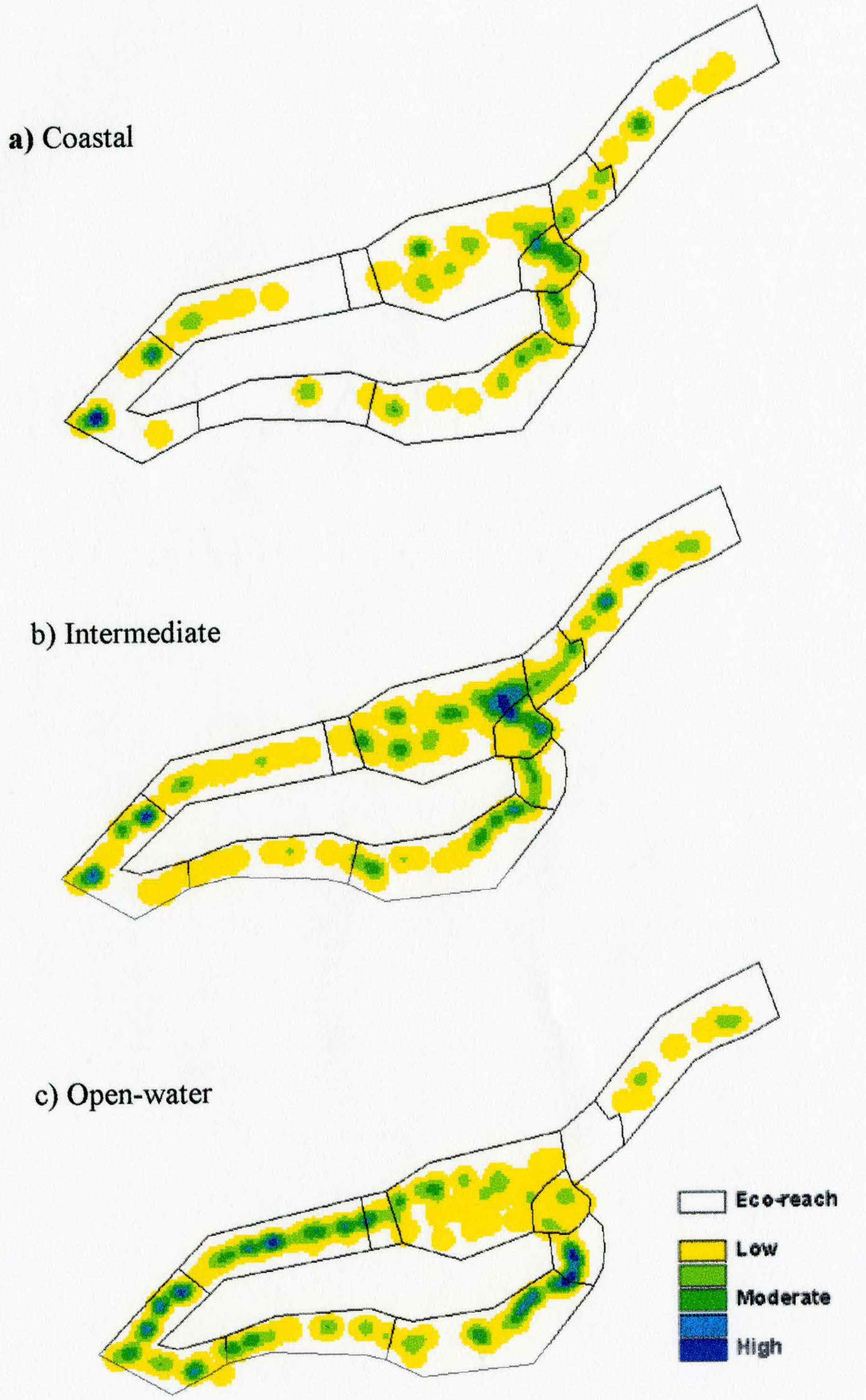
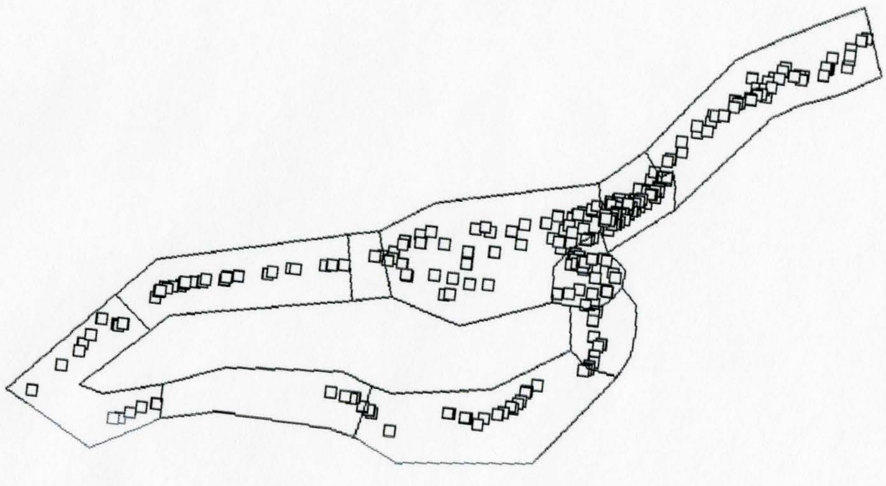

a) Coastal
b) Intermediate
c) Open-water
Eco-reach
Low
Moderate
High

Figure 2.4 a) Location of coastal wetlands along the shoreline of Lake Ontario and b) Density map of coastal wetlands

a)



b)

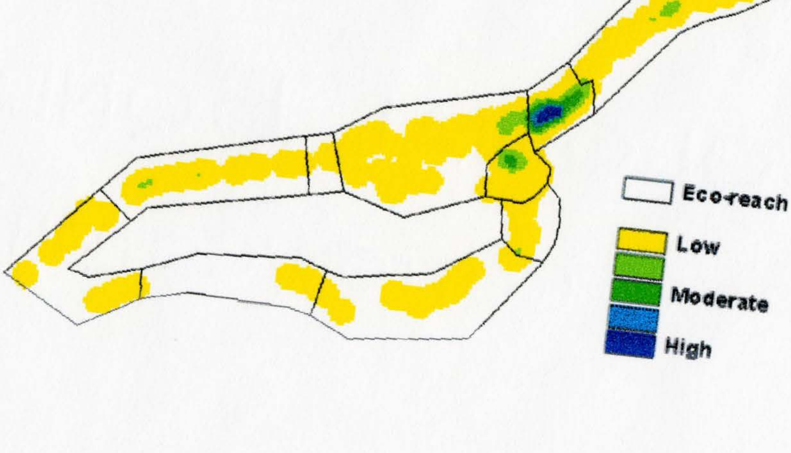
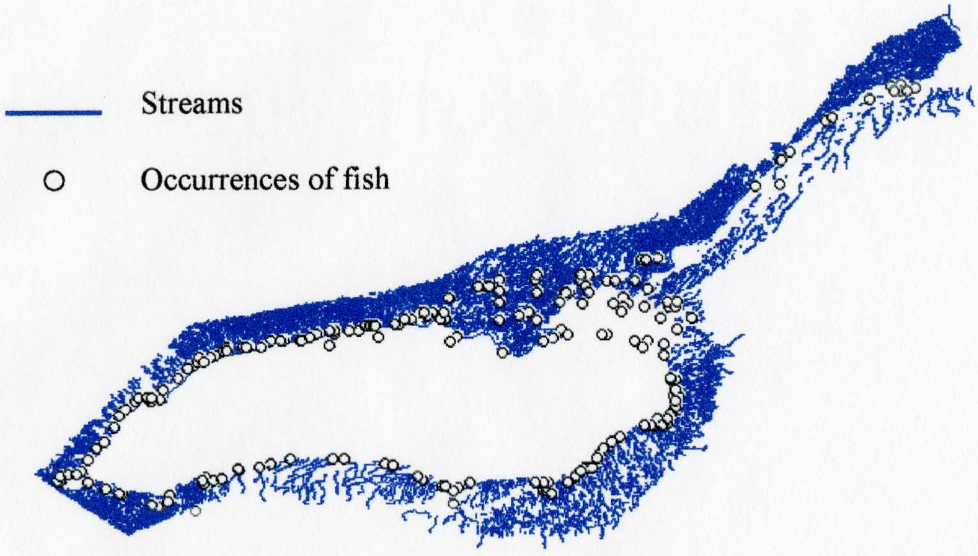


Figure 2.5 Distribution of open-water taxocene and major tributaries of Lake Ontario.


Streams
Occurrences of fish