J. Great Lakes Res. 18(4):651–672
Internat. Assoc. Great Lakes Res., 1992

FISH UTLIZATION OF GREAT LAKES COASTAL WETLANDS

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ABSTRACT. Correspondence analysis was used to partition fish species associated with the open water of each of the five Great Lakes and nine coastal wetlands for which data were available. Included in the analysis were 113 species in 25 families. Three species complexes were suggested: a Great Lakes taxocene (31 species); a transitional community which utilized open water, nearshore, and wetlands (35 species); and a wetlands taxocene, comprised of 47 species found to be closely associated with coastal wetlands. The wetland species split into two main groups: permanent residents (e.g., brown bullhead Ictalurus nebulosus, *mudminnow* Umbra lima, *longnose gar* Lepisosteus osseus) *and migratory species. Migratory species included three subgroups: (1) those that spawned in the wetlands and then left (e.g., northern pike* Esox lucius, *common carp* Cyprinus carpio, *white sucker* Catostomus commersoni, *walleye* Stizostedion vitreum), *(2) those that used the wetlands as a nursery area (e.g., northern pike, gizzard shad* Dorosoma cepedianum, *spottail shiner* Notropis hudsonius), *and (3) those that migrated into the wetland from other wetlands or a Great Lake for shelter, spawning sites, or food; as part of the sustaining process of dispersal of young; or as part of wandering behavior (e.g., burbot* Lota lota, *rainbow smelt* Osmerus mordax, *rainbow trout* Oncorhynchus mykiss). *It was found that most remaining coastal wetlands are degraded or altered to some degree, and are dominated by a characteristic silt- and turbidity-tolerant fish fauna (e.g., common carp, gizzard shad, goldfish* Carassius auratus, *and brown bullhead). Nevertheless, even degraded wetlands still functioned as important fish habitat by exporting large quantities of fish, first to avian, piscine, and mammalian food chains through predation, and second to the Great Lakes as young-of-the-year sport and forage fish. The research implies that a wetland must maintain a connection with a Great Lake to promote and enhance efficient fish utilization of the high productivity of marshes; that additional resilience is provided to species which spawn in wetlands since they can produce two cohorts (one in wetlands and one in the Great Lakes), and that fluctuating water levels are important in sustaining habitat diversity and productivity.*
INDEX WORDS: Wetlands, Great Lakes, correspondence analysis, spawning, nursery areas, rehabilitation, marshes, fish species complexes.

INTRODUCTION

Within the United States a total of 1,370 distinct coastal wetlands fringe the Great Lakes and their connecting channels, for a combined wetland area of 1,209 km^2 (Herdendorf *et al.* 1981a). Lake Erie has the best developed estuaries, with its abundance of drowned river mouths and wetland systems (Herdendorf 1990). The surface areas of U.S. wetlands for each Great Lake are as follows: Lake Superior 267 km^2, Lake Michigan 490 km^2, Lake Huron 285 km^2, Lake Erie 83 km^2, and Lake Ontario 84 km^2. General characteristics and an inventory of Canadian coastal wetlands in the St. Lawrence River, Lake Ontario, Lake Erie, Lake St. Clair, Lake Huron, and Georgian Bay are given in Smith *et al.* (1991). Wetland losses have been considerable in all the Great Lakes; over 14,000 km^2 (61%) of original wetlands in southern Ontario have been converted since settlement times. Leach (1991) noted that Lake St. Clair coastal wetlands have declined by 41% in the past century and only about half of the remaining wetlands are now connected to the lake. Herdendorf (1987) stated only 10% of the original coastal marshes remain along Lake Erie. Whillans (1982) showed that from early times (1789–1962) to the 1970s the Canadian shoreline of Lake Ontario west of the Bay of Quinte had a net loss of about 16 km^2 of marsh area or a 57% reduction. The net loss of wetlands has been dramatic and has been attributed to agriculture, land filling, and port development. About 75% of the baseline wetland areas has been lost in heavily settled Great Lakes areas. Losses of marsh area have often been compounded by a decline of quality in surviving marshes. Despite losses of wetlands throughout the Great Lakes, remaining wetlands are still threatened with destruction to serve burgeoning human interests.

Extensive utilization of wetlands by fish and wildlife is related to the high primary productivity and diversity of structural habitat. Both are maintained in coastal marshes by periodical rejuvenating natural fluctuations in Great Lakes water levels (Geis 1979). Aquatic plant diversity in Lake Erie coastal wetlands is among the highest in the Great Lakes area and is maintained by the dynamic and fluctuating water levels creating alternating exposed and flooded substrate for native species (Stuckey 1989). Herdendorf (1990) noted that because of these fluctuating water levels, Great Lakes coastal wetlands do not senesce; constant change occurs among wetland communities. Because of changing water levels, landforms such as barrier bars, deltas, beaches, spits, lagoons, and natural levees have been deposited or formed. This has resulted in a great diversity of wetland habitats along the Great Lakes.

Freshwater wetlands are highly productive systems, serving as an important connecting link between land and water systems (Clark 1979, Wetzel 1990). They have been exploited and managed over long periods of time to promote the proliferation of waterfowl (Weller 1978) with little consideration given to fishery values. Wetlands serve many functions, including water retention, sediment removal, wildlife nursery areas, and high productivity of invertebrate prey, which enhances growth of juvenile and adult fish. Clark (1979) pointed out that wetlands create a diverse and complicated food chain that reaches from benthos to herons and forage fish to diving ducks. A number of studies have focused on determining the importance of wetlands to fish in each of the Great Lakes. Wetlands, like the Great Lakes, have undergone substantial changes and alterations, mostly to the detriment of the quality and quantity of remaining habitat (Steedman and Regier 1987). Because of the loss of many of these important ecosystems, pollution inputs, and nutrient enrichment, there has been a decline in the quality and diversity of species using wetlands and a concomitant degradation of the integrity of the health of these ecosystems. Those wetlands that are not altered or destroyed outright are degraded by urbanization and watershed changes which detrimentally affect water quality and water regime (Steedman and Regier 1987).

Many authors (Herdendorf *et al.* 1986, Busch and Lewis 1982, Liston and Chubb 1986, Smith *et al.* 1991) have called for more research on the community structure, spawning and nursery function, and migratory patterns and feeding of fish in Great Lakes coastal wetlands. These data are needed to evaluate environmental changes, document current conditions, and rehabilitate degraded wetlands. This paper attempts to summarize some of the available data and establish a foundation for determining whether there are characteristic fish species associated with various wetland types in the Great Lakes coastal zone and how they change when these habitats are degraded.

STUDY AREAS

Lake Superior

Data for fish diversity in Lake Superior were obtained from Goodyear *et al.* (1982a).

St. Louis River\Duluth Harbor, Western Lake Superior

Data on abundance of fish in the St. Louis estuary, a 4,700-ha Lake Superior harbor complex (see Fig. 1), were provided by Jim Selgeby, USFWS, Ashland, Wisconsin. Fish samples were collected at several stations using trawls during 1988–1991.

Northern Lake Michigan

Data for northern Lake Michigan were taken from Brazo and Liston (1979). Adult and juvenile fish were sampled from around the Ludington Pumped Storage Project, a large power plant south of Ludington, Michigan, on the central-east Lake Michigan shoreline. Various gear types (gill nets, beach seines, trawls, trap nets) were deployed during spring to fall, 1971–1977, at stations within the reservoir and in nearby and offshore Lake Michigan from the beach zone to 24 m of water.

Pentwater Marsh, Northern Lake Michigan

The Pentwater Marsh is a drowned river mouth estuary along the eastern shore of Lake Michigan.

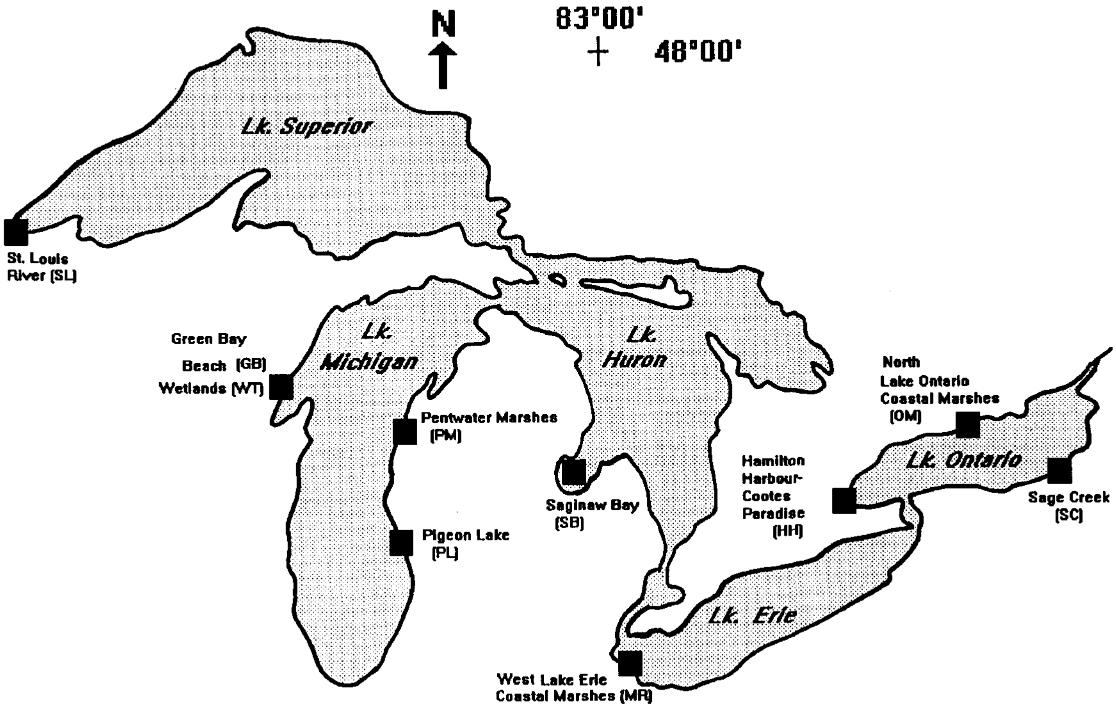

FIG. 1. Map of the Great Lakes showing approximate locations of the nine wetlands used for fish species association analyses. Two-letter abbreviation for each site is also given.

It is at the point where the Pentwater River enters Lake Michigan through a partially diked, 30-m wide channel (Chubb and Liston 1986). It is approximately 50 ha in size and has a 425-km^2 watershed. There are river channels, bayous, and heavily vegetated areas of emergent bur reeds *Sparganium eurycarpum,* water lilies *Nuphar* spp. and *Nymphea* spp., and submerged coontail *Certophyllum demersum* and pondweeds *Potamogeton* spp. Over 1,000 larval fish samples were collected from the marsh in 1983–1984 with push nets and drop nets. The species diversity was somewhat reduced for this sample set because only larval fish were collected and because of the inherent difficulty in identifying fish to species.

Eastern Lake Michigan

These data are taken from Jude *et al.* (1980, 1981b); they conducted studies in Lake Michigan near the J. H. Campbell Power Plant, south of Grand Haven, Michigan, along the sandy, open water stretch of eastern Lake Michigan shoreline in 1977–1980. Samples were collected approximately monthly, April-November, using seines, trawls, gill nets, and plankton nets. The latter sampled larval fish. Station depths ranged from the beach zone to 15 m.

Pigeon Lake Drowned River Mouth, Eastern Lake Michigan

The Pigeon Lake drowned river mouth is probably the site with the most diverse habitat and was sampled the most extensively of all the sites reported. The Pigeon River runs into Pigeon Lake (9 m deep in the center), and then into Lake Michigan. Habitat ranges from shallow macrophyte-dominated areas where the river enters, to sandy, less vegetated shorelines adjacent to high sand dunes near Lake Michigan. It is well developed with shoreline houses on the south shore, but not developed on the north shore; however, the J. H. Campbell Power Plant is located just north of this shoreline. Data for abundance and species composition were collected from 1977 to 1979 and included at least monthly sampling with seines, gill nets, electroshocking, and plankton nets for larval, juvenile, and adult fish (Jude *et al.* 1981a,b).

Green Bay Beach Habitats, Northwestern Lake Michigan

Data for the beach habitats of Green Bay, Lake Michigan, were obtained from John Brazner, University of Wisconsin-Madison, Madison, Wisconsin. He conducted a 2-year study of fish utilization of wetlands and other nearshore areas at 24 sites along the entire 180-km length of Green Bay from the city of Green Bay, Wisconsin to Little Bay de Noc. Twelve sites were beaches (the Green Bay beach habitat Lake Michigan dataset) and the other 12 were various wetland types. The lower Green Bay sites were turbid, while upper Green Bay sites were clear. Within each type, he further split sites between developed sites and undeveloped. He sampled these sites once during spring, summer, and fall, 1990–1991. Fish were sampled with a 10-m bag seine, small trap nets, and minnow traps. Beach habitats sampled were unprotected sites along the bay, with bottom types composed mostly of sand with little or no vegetation.

Green Bay Wetlands, Northwestern Lake Michigan

See above for details. Wetlands sampled were dominated by marshes that are peripheral to and contiguous with the main body of Green Bay. Bulrushes *Scirpus* spp., cattails *Typha* spp., arrowheads *Sagittaria,* and sedges *Carex* spp. were dominant emergents; *Potomageton* spp. were common submergents, while water lilies *Nymphaea* spp. were common floating macrophytes. Wetlands there are protected from heavy wave action, but conterminous with the bay.

Lake Huron

Data for fish diversity in Lake Huron were obtained from Goodyear *et al.* (1982b).

Saginaw Bay, Western Lake Huron

Data on abundance and diversity of fish were compiled from trawling in the bay at a number of stations from 1987 to 1991 (personal communication, Robert Haas, Michigan Department of Natural Resources, Mount Clemens, Michigan; Mrozinski *et al.* 1991) and from O'Gorman's (1983) larval fish study in the bay during 1973–1975. Saginaw Bay is a highly eutrophic embayment of Lake Huron with conditions in the western sector strongly affected by inputs from the silt- and nutrient-laden Saginaw River. Water quality gradually improves toward Lake Huron, where depths up to 15 m are recorded. A great diversity of habitats exists from the large and extensive wetlands and bulrush-fringed shores, to extensive gravel, sandy, and highly sedimented areas offshore, to the rocky Charity Islands in the middle of the bay.

Lake Ontario

Data for fish diversity in Lake Ontario were obtained from Goodyear *et al.* (1982d).

Toronto Area Coastal Marshes, Northern Lake Ontario

Stephenson (1988, 1990) provides detailed information on juvenile and adult fish sampling at five marshes (Humber, Rouge, Duffins, Carruthers, and Frenchmans Bay) adjacent to Toronto, Ontario, on Lake Ontario. The marshes ranged in size from 8 to 41 ha, while the watersheds ranged from 15 to 860 ha. Fish were collected in 1985–1986 using hoop nets, baited traps, seines, and a backpack electroshocker. The marshes were identified as environmentally sensitive areas, differed in size and physical characteristics, and presented a range from degraded to healthy ecosystems. They all are at or near the lake shore or near the mouths of rivers or streams. Their closeness to Toronto has subjected them to varying degrees of degradation. Data from all five marshes were pooled for this analysis.

Sage Creek Marsh, Southeastern Lake Ontario

Sage Creek Marsh is located in Mexico, New York, which is northeast of Oswego, New York (USFWS 1982). It is a flood pond system which developed at the mouth of Sage Creek where it empties into Lake Ontario. It is 12.2 ha in size and has an intermittent barrier beach. The area contains narrow-leaved, non-persistent emergents and many submerged macrophytes. The surrounding area is mostly developed for seasonal and occasional permanent residences. Gill nets, trap nets, seines, plankton nets, and electroshocking gear were utilized during spring and summer 1981 to sample the fish population.

Hamilton Harbour-Cootes Paradise, Western Lake Ontario

The Hamilton Harbour-Cootes Paradise complex is the largest harbor-wetland ecosystem on Lake Ontario and it is one of the most severely degraded (Holmes 1988). The harbor is located at the western end of Lake Ontario, is 22 km^2 in area, and is connected to Lake Ontario via the Burlington Ship Canal. Cootes Paradise is a wetland to the west of the harbor with a surface area of 1.2 km^2, and a mean depth of 0.5 m; it is connected to the harbor via the Desjardins Canal. Almost 60% of a largely rural 500-km^2 watershed drains into the wetland. It also receives input of industrial wastes and sewage. Records from Ontario Ministry of Natural Resources, commercial fishermen, and other sources were used to construct a table of abundance of all species found in the harbor-wetland complex (Holmes 1988). These data and data from a larval fish survey conducted using boat-mounted push nets and larval fish seines in 1985 and 1987 (Leslie and Timmins in press) were used to provide a current species ranking.

Lake Erie

Data for fish diversity in Lake Erie were obtained from Goodyear *et al.* (1982c).

Lake Erie Coastal Marshes

Extensive data were compiled by Johnson (1989) on the diversity and abundance of fish species in western Lake Erie's coastal wetlands. These wetlands are large in size, diverse, and extensive along the western coast. They are usually heavily vegetated, often with cattails, American lotus *Nelumbo*, and submerged macrophytes. Besides the usual losses suffered by these wetlands, many of the remaining wetlands have been diked for waterfowl management. Because of its southern location, diversity of habitats, and extensive study, Lake Erie and its associated wetlands have one of the highest species diversities among sites reported on here.

METHODS

Data on abundance of fish in wetlands were obtained from the published literature and through contact with investigators who graciously provided data. An attempt was made to obtain data on species abundance for each of the Great Lakes and wetlands within each lake. Based on the system of Cowardin *et al.* (1979), a wide range of different habitat types can qualify as wetlands, provided there are sufficient hydrated soils, shallowness, and periodically flooded terrestrial habitat. The wetlands selected for this analysis ranged from small marshes with connections to a Great Lake to Saginaw Bay, a large Lake Huron embayment.

Correspondence analysis (Hill 1974) is a multivariate statistical technique used to partition species along an environmental gradient among the sixteen sites chosen for analysis. These sites included each of the Great Lakes (three open water sites were available for Lake Michigan which corresponded with the companion wetland dataset) and nine wetlands, all connected with a Great Lake (some had barrier beaches which periodically closed the system). The catch data for fish species (mostly juvenile and adult fish) were assigned a rating of 3 for abundant, 2 for common, or 1 for rare based on catch totals or reported abundance data. In the case of Lakes Ontario, Huron, Erie, and Superior, a judgement was made on species abundances based on known species distributions and current status in each of these lakes. Correspondence analysis was accomplished by utilizing CANOCO, a multivariate statistical package developed by C. J. F. ter Braak, Agricultural Mathematics Group, Box 100, 6700 AC Wageningen, Netherlands.

RESULTS

There were 113 species from 25 families tabulated from the Great Lakes and wetland datasets assessed for this analysis (Table 1). Fish collected near and within wetlands in the Great Lakes ranged from species which have rarely or never been collected in a wetland (deepwater sculpin *Myxocephalus thompsoni*) to species which have only been collected in wetlands (mudminnow *Umbra lima*); the rest are somewhere in between. From correspondence analysis, the first ordination axis extracted depicts an environmental gradient of fish species with species associated with the Great Lakes on the right, a transitional group in the middle, and a wetlands group on the left (Fig. 2). The species scores represent optima with respect to the environmental gradient. The rank of these species is given in ascending order starting from right (Great Lakes species) to left (wetland species) (Table 1). Correspondence analysis also placed each site at the centroid of those species associated with it. That is, those species nearest the lake sites occur most often in lakes, and those species nearest wetlands occur most often in wetlands. Those species which were rarest or uncommon are farthest from the first ordination axis; their scores are approximately equal to their site's score (Fig. 2). The species depicted in Figure 2 were arbitrarily divided into three major species associations or taxocenes: an upper Great Lakes and Lake Ontario open wa-

*TABLE 1. Alphabetical listing by family and species within family of fish species collected as juveniles or adults from the open waters of the Great Lakes and adjacent wetlands. The rank of species is given (see number next to common name) in ascending order starting with Great Lakes species and proceeding to wetland species. A = abundant, C = common, R = rare, * = collected as larvae. # = introduced species. LO = Lake Ontario (Goodyear* et al. *1982d); OM = Ontario marshes near Toronto (Stevenson 1988, 1990); SC = Sage Creek, a Lake Ontario marsh/creek system (USFWS 1982); HH = Hamilton Harbour/Cootes Paradise (Holmes 1988, Leslie and Timmins, in press); LE = Lake Erie open water (Goodyear* et al. *1982c); MR = marshes of Lake Erie (Johnson 1989); LH = Lake Huron (Goodyear* et al. *1982b); SB = Saginaw Bay (Mrozinski* et al. *1991, O'Gorman 1983); LM = SE Lake Michigan open water (Jude* et al. *1981a); PL = Pigeon Lake, a drowned river mouth/lake (Jude* et al. *1981b); NM = northern Lake Michigan open water (Brazo and Liston 1979); PM = Pentwater marshes, Ludington, MI (Chubb and Liston 1986); GB = Green Bay, Lake Michigan nearshore area, WT = wetlands adjacent to Green Bay (John Brazner, personal communication, University of Wisconsin, Madison); LS = Lake Superior (Goodyear* et al. *1982a); SL = St. Louis River, Duluth, MN (personal communication, J. Selgeby, U.S. Fish and Wildlife Service, Ashland, WI). Common names according to Robins* et al. *(1991).*

	Lake Ontario				Lake Erie		Lake Huron		Lake Michigan						Lake Superior	
Species	LO	OM	SC	HH	LE	MR	LH	SB	LM	PL	NM	PM	GB	WT	LS	SL
Acipenseridae																
Lake sturgeon **14**	R				R		R				R				R	R
Amiidae																
Bowfin **81**	R	R	C	R	R	R				C	R	R		R		
Anguilidae																
American eel **53**	R	R	R	R							R					
Aphredoderidae																
Pirate perch **60**										R						
Atherinidae																
Brook silversides **38**		R		R					R	C	R	C			R	
Catostomidae																
Black redhorse **54**					R											
Bigmouth buffalo **108**					R	C										
Golden redhorse **33**					R		R		R	R	R			R		
Lake chubsucker **89**			R		R	R				C						
Large scale sucker **105**			R													
Longnose sucker **16**	C	R			R		R		C	R	C				C	R
Northern hog sucker **49**			R							R	R					
Quillback **76**					R	C		R	R	R	R		R	C		
River redhorse **106**			R													
Shorthead redhorse **42**	R		R	R	R	C		R	R	R	R				R	R
Silver redhorse **17**	R				R										R	R
Spotted sucker **113**						R										
White sucker **44**	C	C	C	A	C	A	C	C	C	C	C	R	C	C	C	C
Centrarchidae																
Black crappie **64**	R	R	R	R	R	C	R	R		C	R	A		R		C
Bluegill **69**	R		R	C	R	C		R	R	A	R		R	C		R
Green sunfish **92**					R	C			R	R			A	C		
Largemouth bass **86**	R	C	R	R	R	C		R		C	R		R	C		
Orangespotted sunfish **55**					R											
Pumpkinseed **83**	R	A	A	C	R	C		R	R	R	R		R	C		R
Rock bass **82**	R	C	A	R	R	C	R	R		C	R	R	C	A		R
Smallmouth bass **48**	C	R	C	C	C	C	R		R	R	R		C	R	R	R
Warmouth **58**					R					R						
White crappie **99**	R					A				R						
Clupeidae																
Alewife# **41**	A	A	R	A	C		A	A	A	A	A	C	A	A	R	R
Gizzard shad **71**	C	C	C	C	A	A	R	A	R	R	C	C	A	A		
Cottidae																
Deepwater sculpin **4**							A	R*	C*						A	
Mottled sculpin **29**	R				R				C	R	C	R		R	R	
Slimy sculpin **13**	A				R		C		C	R	C				C	R
Spoonhead sculpin **5**														R	R	
Cyprinidae																
Bigmouth shiner **61**										R						

Continued

TABLE 1. Continued

	Lake Ontario				Lake Erie		Lake Huron		Lake Michigan						Lake Superior	
Species	LO	OM	SC	HH	LE	MR	LH	SB	LM	PL	NM	PM	GB	WT	LS	SL
Blackchin shiner **110**				R		R										
Blacknose dace **68**	R	R		R												
Blacknose shiner **102**			R	R		R				R				R		
Bluntnose minnow **96**	R	A	A	R	R	A		R	R	A			A	A		
Bridle shiner **22**	R															
Common carp# **65**	R	C	C	A	C	A	R	C	R	R	C	A	C	C	R	R
Common shiner **95**	R	A	A	R						R			C	A		R
Creek chub **66**	R	C		R						R						R
Emerald shiner **59**	R	C	A	R	A	A	R	C	R	A	R		A	A	R	A
Fallfish# **51**	R		R													
Fathead minnow **78**	R	A	R	R		C			R	C	R		R	R		R
Golden shiner **85**	R	A	C	R	R	C		R		C	R		R	C		R
Goldfish# **67**	R	R		A	C	C		R	R	R	R					
Lake chub **15**	R						R				R					R
Longnose dace **36**	R	R			R				R	R	C					
Mimic shiner **52**				R	R											R
Pugnose minnow **112**						R										
Pugnose shiner **111**			R			R										
Sand shiner **70**					R					C	R		C	R		
Spotfin shiner **75**	R	R			R		R						A	A		
Spottail shiner **50**	C	C	C	R	C	A		A	A	A	A		A	A	R	A
Stoneroller **103**		R														
Striped shiner **97**				R												
Cyprinodontidae																
Banded killifish **100**			R	R	R	R				R		R	C	C		
Esocidae																
Grass pickerel **109**			R			C				R						
Muskellunge **40**	R				R	R				R				R	R	R
Northern pike **43**	R	R	C	R	R	R	R		R	R	R	C		R	R	R
Gadidae																
Burbot **20**	C				C		C	R*	R	R	C			R	C	R
Gasterosteidae																
Brook stickleback **74**				R		C	R					R		R		R
Threespine stickleback# **10**	R						R									
Ninespine stickleback **18**							R		R	R	R		R	R	C	R
Hiodontidae																
Mooneye **56**					R											
Ictaluridae																
Black bullhead **72**				R	R	A	R			R	R		R	C		C
Brindled madtom **87**					R	R		R								
Brown bullhead **93**	R	A	A	A	R	C				R	R	C	R	R		
Channel catfish **57**	R			R	A	C		C	R	R	R		C	R		C
Flathead catfish **39**					R					R	R					
Stonecat **46**					R			R		R						R
Tadpole madtom **77**		R	R	R	R					C						R
Yellow bullhead **88**	R			R	R	C				R				R		
Lepisosteidae																
Spotted gar **90**					R	R				R						
Longnose gar **79**	R		R	R	R	C		R		R	R		R			
Osmeridae																
Rainbow smelt# **35**	A	R	C	A	A		A	A	A	C	A		C		C	A
Percicthyidae																
White perch# **84**	C	C	C	A	A	A		A					C	C		C
White bass **98**	R	R	C	C	A	A		C					A	A		
Percidae																
Blackside darter **62**										R						
Channel darter **21**					R		R									
Fantail darter **107**			R													
Iowa darter **101**						R				R						
Johnny darter **45**	C	R	A	R	R		R	R	A	A	C	C	C	C		C
River darter **104**														R		

Continued

TABLE 1. Continued

	Lake Ontario				Lake Erie		Lake Huron		Lake Michigan						Lake Superior	
Species	LO	OM	SC	HH	LE	MR	LH	SB	LM	PL	NM	PM	GB	WT	LS	SL
Logperch **91**		R	C	R	C	A		R		R			C			C
Rainbow darter **80**				R	R											
Ruffe# **37**																A
Sauger **23**	R															
Walleye **32**	C			R	C		R	C	R	R	R				R	C
Yellow perch **47**	C	A	C	C	A	A	C	A	A	A	A	C	A	A	R	C
Percopsidae																
Trout-perch **34**	C			R	C		R	A	A	C	C	R	R		R	A
Petromyzontidae																
Chestnut lamprey **63**										R						
Sea lamprey# **30**	R				R		R			R	R		R		R	A
Salmonidae																
Coregoninae																
Bloater **8**							C		A	R	C				C	
Kiyi **1**															R	
Lake herring **7**	R						R			R	R				A	R
Lake whitefish **12**	C				R		C	R	C	R*	R				C	
Pygmy whitefish **2**															R	
Round whitefish **9**	R						R	R	C		C				C	
Shortjaw cisco **3**															R	
Salmoninae																
Atlantic salmon **24**	R															
Brook trout **31**				R							R		R		R	
Brown trout# **27**	R		R		R		R	R		R	C				R	
Chinook salmon# **26**	C		C		R		R		C	R	C				R	R
Coho salmon# **19**	C			R	R		R		C	R	C				R	
Kokanee# **25**	R															
Lake trout **11**	C				R		C		C	R	C				C	R
Pink salmon# **6**	R			R			R								C	
Rainbow trout# **28**	R	R	R	R	R		R			R	C				C	
Sciaenidae																
Freshwater drum **73**	C			R	A	A		C		R			C	R		C
Umbridae																
Central mudminnow **94**		R		C		C				R		C				R
Total No. Families	19	14	14	19	20	14	15	13	14	21	19	14	15	14	15	18
Total No. Species	62	36	41	51	68	46	38	34	37	71	52	17	35	40	38	45

ter species complex (species no. 1 to 31 in Table 1); an intermediate complex associated with large bays, river estuaries, and Lake Erie, containing species which utilize habitats of both the Great Lakes and wetlands during some stage of their life cycle (35 species, nos. 32–66); and a coastal marshes complex (47 species, nos. 67–113).

The Great Lakes complex is comprised of 31 species in nine families and is dominated by families associated with oligotrophic water bodies, Salmonidae (16 species) and Cottidae (four species) (Table 1). The transitional species complex contains 35 species in 14 families. Dominants included Cyprinidae (eight species), Catostomidae (six species), Percidae (five species), and Centrarchidae (four species). The coastal marshes complex is the largest and includes 47 species in 14 families (Table 1) with Cyprinidae (15 species), Centrarchidae (six species), Percidae (four species), Catostomidae (four species), and Ictaluridae (four species) the dominant families, all warmwater species.

Of the seven Great Lakes open water sites, five of them (Lakes Superior, Huron, eastern Michigan, northern Michigan, and Ontario) are clustered along the first part of the environmental gradient (Fig. 2). Interestingly, Lake Superior, with the most depauperate and unique ichthyofauna among all the Great Lakes, was the farthest separated from all the other lakes, followed by Lake Huron, Lake Michigan, and then Lake Ontario. The two anomalies, Lake Erie and northwestern Lake Michigan (beach habitat Green Bay), both

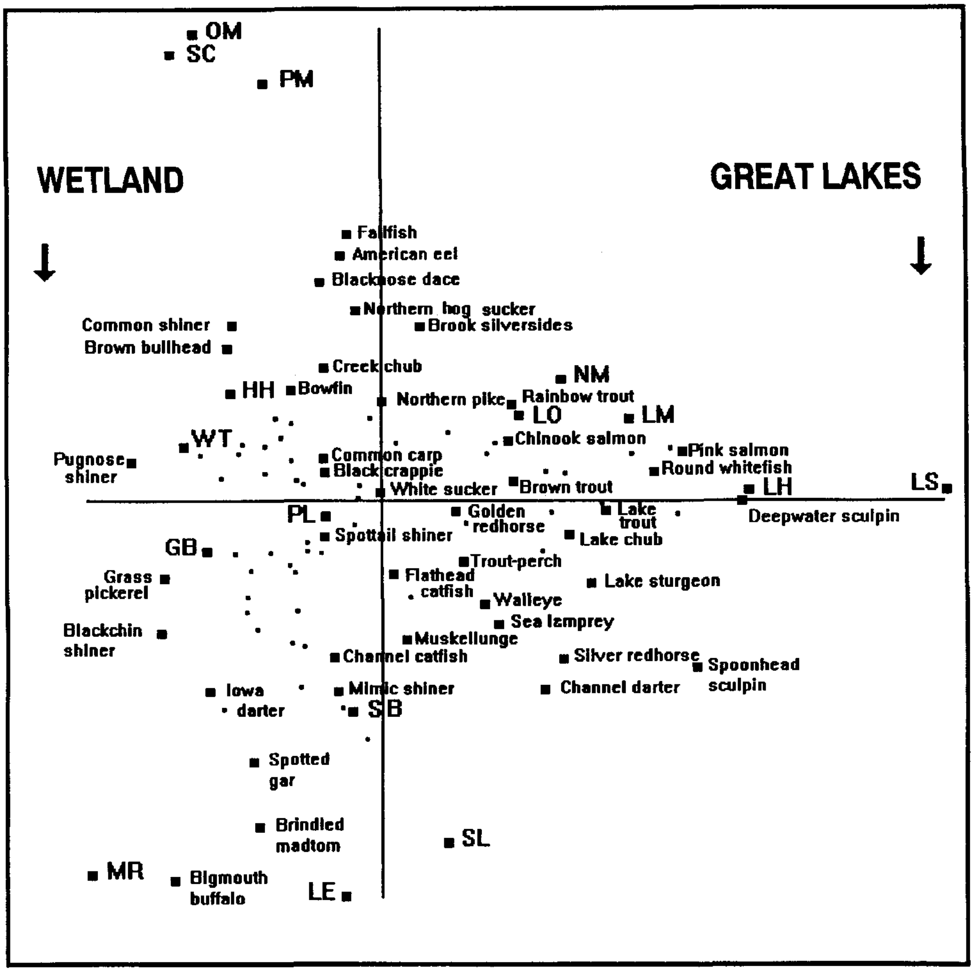

FIG. 2. Correspondence analysis of fish abundance and diversity data from 16 Great Lakes sites (large squares). There are 113 species (small squares and dots) partitioned along the horizontal axis in a pattern ranging from Great Lakes "characteristic" species on the right (species nos. 1–31) to wetland species on the left (nos. 67–113). See Table 1 for definition of abbreviations and the ranking of species, starting from no. 1 (kiyi) to no. 113 (pugnose minnow). Selected species locations are identified for orientation (small squares); some co-occurred with the site designator and so are obscured.

fell in the transitional and wetland grouping on the far left of the axis. However, Lake Erie species diversity, which is highest of all the Great Lakes, placed the lake near the open water Great Lakes groupings, but considerably displaced downward. This is a reflection of its large number of rare species. The other anomaly, nearshore Green Bay in northwestern Lake Michigan, strongly suggests these nearshore areas provide habitat containing species more similar to those found in wetlands than other open water Lake Michigan datasets recorded here. The northwestern Lake Michigan dataset came from areas within Green Bay, the data were gathered by sampling wadable water only, and the position of this area on Figure 2 is very close in species associations to that found in adjacent marshes and wetlands of Green Bay.

Three other sites (Saginaw Bay, Pigeon Lake on Lake Michigan, and the St. Louis estuary in Lake Superior), along with Lake Erie, lined up in positions between the open water Great Lakes and coastal wetlands suggesting intermediate species associations comprised of Great Lakes and wetlands-specific fish species. These three sites also shared similar physical characteristics and differed substantially from the smaller and much more heavily vegetated marshes and drowned river mouths represented by the other wetland sites. These three sites are all terminal sites of river entry into a Great Lake, are productive, large (except for Pigeon Lake), and because of their size and diversity of habitats, contain a concomitant large suite of fish species. Saginaw Bay species associations are most like the St. Louis estuary on Lake Superior, while Pigeon Lake is clearly separated from these two sites. This separation of Pigeon Lake from the other two sites is probably due to (1) the large number of rare species sampled during the relatively intensive sampling in the Pigeon Lake estuary, and (2) the diversity of habitats, including the Pigeon River and Pigeon Lake. The access provided by Pigeon Lake to fish migrating from Lake Michigan further increased the species documented in this system.

Hamilton Harbour-Cootes Paradise on western Lake Ontario shares physical characteristics with the above three sites discussed and one would predict they would contain species complexes similar to these sites. However, Hamilton Harbour-Cootes Paradise is a degraded harbor-wetland system which has lost many species due to various chemical, physical, and biological insults (Holmes 1988, Whillans 1979). Therefore, Hamilton Harbour-Cootes Paradise fell into the same grouping as the seven wetland sites depicted on the far left of the axis (Fig. 2).

Among the seven wetland sites found on the far left of the ordination (Fig. 2), two sites (both large in area) have already been treated. They include the Green Bay open water site, which was concluded to be more like the wetlands adjacent to Green Bay than to open water Lake Michigan species associations, and Hamilton Harbour-Cootes Paradise in Lake Ontario which apparently also mimics wetland species associations because of its degraded nature, despite its large size and diversity of habitats. The remaining five sites also share many common attributes, including that they are relatively small in surface area, they are marshes or drowned river mouths usually with heavy vegetation, and they are shallow. Two of the three Lake Ontario wetlands were very close to each other on the ordination (Fig. 2), despite their being on the northern and southeastern sides of the lake. Species associations at these Lake Ontario sites were similar to those found at the Pere Marquette Marsh on Lake Michigan even though species diversity was modest at the Lake Michigan site. The lower-than-expected diversity at Pere Marquette was partially due to sampling gear which was limited to larval fish. There are many accompanying difficulties identifying many species of larval fish (e.g., *Lepomis* spp.), even though it is known that more than one species of centrachrid was present at the Lake Michigan site. Hamilton Harbour-Cootes Paradise, wetlands of Green Bay, and the beach habitat of Green Bay all occurred in a similar location in the ordination (Fig. 2) implying similar species diversities and abundances among their fish habitats. Turbidity and harsh environmental conditions (low dissolved oxygen, high temperature, ammonia production, etc.) may limit the species found in some of these areas to tolerant species, thus making species associations among these sites more similar than one would expect.

The last site (the marshes of western Lake Erie), which is somewhat of an outlier, shows a high diversity with many rare species; this deflects the location of the site downward on the ordination (Fig. 2). This same high diversity of rare species was also a characteristic of Lake Erie among the Great Lakes. This characteristic sets the western Lake Erie marshes apart from the other marshes of the Great Lakes included within this dataset. Part of the high diversity recorded is due to the inclusion of many marshes along Western Lake Erie, increasing the probability of recording more species. It should also be noted that the two Lake Erie sites (marshes of western Lake Erie and Lake Erie open water) are deflected downward on the ordination reflecting the close proximity of these two sites in the same watersheds, shared species, and the high diversity of fish species found in both areas. Also the eutrophic Lake Erie is the shallowest of the Great Lakes, the most productive, and, except for the eastern basin, contains a warmwater species complex. Therefore wetland species complexes in Lake Erie more closely resemble species complexes found in the adjacent wetlands than complexes found in the upper Great Lakes, where wetlands tend toward eutrophy, while the adjacent Great Lake is typically meso- or oligotrophic.

DISCUSSION

Fish Species Composition in Wetlands

Studies cited here reported many of the same fish species from a variety of wetlands throughout the Great Lakes region. Species recorded most often and in the highest abundance in the nine wetlands included: yellow perch, spottail shiner, white sucker, alewife, gizzard shad, common carp, emerald shiner, white perch, bluntnose minnow, and brown bullhead. Chubb and Liston (1986) found that crappies *Pomoxis* spp., gizzard shad *Dorosoma cepedianum,* common carp *Cyprinus carpio,* and sunfish were dominants in Pentwater Marsh on Lake Michigan. Hoffman (1985) found that gizzard shad were the most abundant fish in Old Woman Creek Estuary, western Lake Erie. Leslie and Timmins (1990) identified 44 species of fishes utilizing drainage ditches in southwestern Ontario. Greater than 90% of the species spawned in the ditches. Cyprinids led all families in representation (10 species), followed by centrarchids (8), and ictalurids (5); gizzard shad was the most common and abundant larval fish. These are examples of degraded habitats which still have high species diversity.

Derksen and Gillies (1985) in their study of the Saskeram marshes of the Saskatchewan River Delta, found that there was a spring movement into the marsh of common carp, northern pike *Esox lucius*, white sucker *Catostomus commersoni*, and walleye *Stizostedion vitreum*. Stephenson (1988) found 36 species in 14 families in her northern Lake Ontario marshes, where brown bullhead *Ictalurus nebulosus*, pumpkinseed *Lepomis gibbosus*, yellow perch *Perca flavescens*, alewife *Alosa pseudoharengus*, golden shiner *Notemigonus crysoleucas*, bluntnose minnow *Pimephales notatus*, common shiner *Notropis cornutus*, and fathead minnow *Pimephales promelas* composed 83% of the total number of fish caught. Northern pike and largemouth bass *Micropterus salmoides* were caught frequently. Toronto (Stephenson 1988, 1990) and Sage Creek marshes (USFWS 1982), Lake Ontario, were partially dominated by brown bullheads. Alewife, brown bullhead, and pumpkinseed were the most abundant species in Cootes Paradise, Lake Ontario, in the late 1940s (Holmes 1988). Yellow perch, white sucker, and northern pike were also shared common species in Pentwater Marsh, Lake Michigan (Chubb and Liston 1986), Sage Creek, New York (USFWS 1982), and Jefferson County, New York wetlands (Marean 1976, Phillips 1982). These species, along with a suite of minnows, white perch *Morone americana,* gizzard shad, and white bass, made up 90% of all the fish caught in the Toronto marshes. Thus there is high correspondence with what can be regarded as the "characteristic" assemblage of fish species in Great Lakes coastal wetlands. All of these species were either in the transitional group or designated wetland species by the correspondence analysis.

Wetland Productivity

Fish productivity in wetlands is closely linked to the high primary production in these ecosystems. Diversity of habitat promotes a diverse fish population (Emery 1978, Eadie and Keast 1984), and wetland properties enhance fish production. The concept of the nearshore zone acting as a center of organization (Steedman and Regier 1987) certainly applies to wetlands, since they have such a diversity of habitats, high productivity, and serve as important nurturing areas for young-of-the-year keystone predators. These diverse habitats reduce the predation risk for larval and juvenile fish and provide excellent conditions for good growth (Turner 1988b), since wetland ecosystems are among the most productive ecosystems known (Wetzel 1990), approaching that observed in tropical forests and marine estuaries (Whittaker 1975). Reasons for the preferred utilization of marshes by fishes include the high primary productivity which translates into a rich zooplankton and benthos food source. Also, marshes are warm and sheltered from the often harsh wave conditions in a larger water body. Much energy produced in wetlands is transferred outside the wetland through predation on young fish by piscine, avian, and mammalian predators. Another component of this energy transfer is through common carp, gizzard shad, and channel catfish *Ictalurus punctatus,* which consume benthos and detritus, then leave the wetland for open water (Petering and Johnson 1991).

Compared with terrestrial ecosystems, aquatic ecosystems tend to have a higher percentage of consumption of primary productivity by secondary consumers, a higher efficiency of conversion, and possibly higher standing biomass (Turner 1988a). Riparian wetlands have high primary production that is available to consumers, a fluctuating environment, and an aquatic-terrestrial food web or chain resulting in concentrated secondary production. Riparian wetlands also have more species per number of trophic links than do non-wetland ecosystems. Extensive utilization by fish species is related to the high primary productivity and diversity of structural habitat maintained in coastal marshes by periodical rejuvenating natural fluctuations in Great Lakes water levels (Geis 1979). Aquatic macrophytes are the most important primary producers in freshwater marshes (Wetzel 1983). The living plants harbor large populations of invertebrate prey species (Herdendorf 1987), but macrophyte production enters the trophic system mainly through the detritus and benthos pathway (Tilton and Schwegler 1978). MacCrimmon (1980) studied Wye marsh, a coastal Great Lakes marsh in the Georgian Bay watershed of Lake Huron. There were several large fish species (common carp, longnose gar *Lepisosteus osseus*) which were suspected to be noteworthy accumulators of available nutrients. Ducks, preying birds, and aquatic emerging insects transported nutrients from the marsh ecosystem.

Connectedness

A key component of maximal utilization of wetlands by fish is their connection with a Great Lake. These connections between a wetland and bodies of open water serve valuable functions as migratory routes for predatory fishes and as conduits of materials both into and out of the wetlands (Clark 1979). Wetlands with surface water connections generally had a more diverse and abundant fauna than those with no connections. Fish communities were composed of small forage fishes, which are joined by larger fishes with other trophic roles. Bottom feeders such as bullheads *Ictalurus* spp., channel catfish, and common carp occur in many wetlands. Stephenson (1988, 1990) found that alewives, yellow perch, and white suckers moved in and out of the marshes in large numbers, whereas species such as common carp and northern pike stayed in the marsh through most of the summer, but moved in and out in the spring and fall. Thus it is important that fish access to the marshes not be blocked because of diking, dams, or other manmade obstacles. Fish of various guilds using wetlands varied by season and time of day (Johnson 1989). Ready egress and ingress were important to provide fish access to abundant prey species and spawning grounds, but also as a means of escape from adverse environmental conditions, such as low dissolved oxygen, floods, siltation, or extreme water temperatures. The continuum was also important to maintain genetic flow among fish along the shoreline as well as a path for invading species (Johnson 1989), a concept also discussed for aquatic plants (Stuckey 1989). Many of the coastal marshes of Lake Erie (over half in Ohio waters) have been diked to provide controlled water levels to promote and protect waterfowl habitat. This has had an adverse effect on fish, especially northern pike, since the varied seasonal and diel movements by larger fish for spawning and foraging activities have been substantially reduced. Common predator species are pickerel *Esox* spp., northern pike, warmouth *Lepomis gulosus*, and various species of bass (*Micropterus, Morone*). Most larger fishes are temporary residents of wetlands, entering them to feed or spawn. The young of these fish often spend their first summer using these habitats as nurseries. Wetlands adjacent to river mouths also provide feeding and spawning sites for anadromous fish. Lastly, the nursery function for fish is just being documented in coastal Great Lakes wetlands; clearly, wetlands must be connected to a larger water body so young-of-the-year fish can move from these nursery areas.

Diked vs. Undiked Wetlands

Diked wetlands, which are common in Lake Erie marshes for waterfowl production, change wetland functions dramatically. McLaughlin and Harris (1990) found that aquatic insect biomass, diversity, and abundance were higher in a diked wetland than in an undiked one in a eutrophic area of Green Bay. They attributed this increased production to sheltering from the depressing effects of the increased turbidity, nutrient enrichment, and common carp invasions from Green Bay waters. Petering and Johnson (1991) found that gizzard shad, crappie, sunfish, common carp, and goldfish *Carassius auratus* were the most abundant taxa in samples (94% of total) collected from West Marsh, a diked marsh in Lake Erie, in 1984–85. Diking may also prevent important nutrient exchange (Sager *et al.* 1985) and interfere with naturally fluctuating water levels which can act to rejuvenate productivity and maintain coastal vegetation (Harris *et al.* 1977, Keddy and Reznicek 1985).

Fish Recruitment in Wetlands

Despite losses of wetlands throughout the Great Lakes, remaining wetlands are still under considerable pressure to be "developed" for human uses or habitation. There is extensive use of coastal marshes for spawning and nursery habitat by several Great Lakes fish species, including yellow perch and alewife, which is fostered by warmer temperature, relief from waves and currents, and higher productivity and more food for young fish in the marsh setting.

Wetlands contribute large numbers of sport, forage, and commercial species to Great Lakes fisheries (Herdendorf 1987, Herdendorf *et al.* 1986). Stephenson (1988, 1990) maintains from her study and those of Chubb and Liston (1986) and Mansfield (1984) that coastal marshes produce large numbers of forage fish, provide food for larger predatory species, and furnish spawning and nursery areas for many species of important fishes. Norcross and Shaw (1984) noted that most coastal oceanic species increased their reproductive potential with high fecundities, protracted spawning seasons, or multiple spawning sites to counteract the mortalities associated with "unpredictable" environments. In the Great Lakes, yellow perch, spottail shiners *Notropis hudsonius*, and alewives (Jude *et al.* 1980, Perrone *et al.* 1983, Mansfield 1984, and Stephenson 1990) increase their reproductive output by spawning in wetlands and tributaries early, then produce another cohort in the Great Lakes at a later time, sometimes a month later, when temperatures there increase to optimal levels.

Fish Production: Value and Numbers

The value of fish produced in wetlands has seldom been documented, except by Jaworski and Raphael (1978). Derksen and Gillies (1985), in their study of the Sakeram marshes of the Saskatchewan River Delta, found that this marsh produced 150,000 northern pike young of the year each year at a replacement value of 0.5 million dollars. Young-of-the-year northern pike density varied between 9 and 11 per ha, while productivity ranged from 0.5 to 2.3 kg per ha. Chubb and Liston (1986) estimated that each ha of shallow-water wetland in the Pentwater Marsh during 1982–1984 produced (in thousands) 294–708 common carp, 56–317 minnows, 86–283 sunfish, 1.9–5.7 northern pike, and 1.4–2.6 yellow perch each year. Mansfield (1984) documented that over 100,000 larvae per day were transported to Lake Michigan over a 12-day period from a stream-wetland tributary. Panek (1979), in discussing the cumulative effects of small modifications to marine estuarine habitat, stated that about 6.8% of these areas have already been lost to dredging and filling. It was estimated that for each ha of estuary already lost due to dredging and filling, there is a 388-kg loss of biological production.

Fish as Bioindicators

Fish diversity in wetlands should be useable as a bioindicator of ecosystem quality. Degradation of wetlands ultimately results in narrowed habitat dimensions, which reduce the survival ability of species which cannot adapt. Hamilton Harbour, a degraded area, and Pentwater Marsh, for different reasons, have reduced fish species diversity, since they were dominated by common carp and other silt-tolerant species. The Ohio Environmental Protection Agency (OEPA 1987) defined water quality tolerances for 82 fish species as an attempt to characterize mostly stream habitats. This and other similar approaches to assess water quality using fish or benthos as indicators of ecosystem health (e.g., Berkman *et al.* 1986) suggest it should be possible to establish species complexes derived from this analysis as indicative of unimpaired and degraded habitat. Fish data from more degraded habitats could be analyzed to provide needed quantification of relationships. These species diversities could then be used in a comparison with other habitats to assess ecosystem quality using the fish as biological indicators. For example, Leslie and Timmins (1991) found that there were distinct differences between fish diversity in the St. Clair River Delta, Lake St. Clair, and Pentwater Marsh, Lake Michigan. Fish larvae in Pentwater Marsh were dominated by common carp, which formed 80% of the catch (Chubb and Liston 1986); whereas, in the St. Clair River Delta, common carp formed less than 1% of the total catch. Alewife and gizzard shad composed 73%-89% of the St. Clair River Delta totals, while in the Pentwater Marsh they made up 0.6%.

Tolerant Fish

Wetlands provide strident environments for fish, especially during summer, when temperatures are maximal. Whole fish communities and species within families show a differential physiological adaptation to a given set of harsh environmental conditions. The pattern of changes and extinctions in the complex of fish species in the Great Lakes has shown a consistent trend, with the more intolerant species succumbing first, followed by increases in populations of more resilient species (Smith 1968, 1972). For example, the bloater is the only surviving, and smallest member of the deepwater chub complex in Lake Michigan (Smith 1964). The deepwater sculpin is a common, albeit sensitive species, inhabiting the deepwater abyss of the upper Great Lakes, but it has inexplicably disappeared from Lake Ontario where it once was abundant (Christie 1974). Interestingly, deepwater sculpin appears fourth in the correspondence analysis, confirming its close association with the unique, and presumably more sensitive Lake Superior ichthyofauna. There is a similar replacement pattern of fish in wetlands which suggests this correspondence analysis or future research efforts might profitably document so that habitat quality might be defined in terms of species-specific complexes, a recent request of fish managers (Eshenroder *et al.* 1991).

In Lake Erie wetlands, Johnson (1989) noted that fish using wetlands later in summer were the more tolerant species able to function in dense vegetation, higher water temperatures, and periodic low dissolved oxygen. Ready egress and ingress to wetlands were important to provide fish a means of escape from adverse environmental conditions, such as low dissolved oxygen, floods, siltation, or extreme water temperatures. With wetlands becoming generally more hostile environments, Johnson (1989) predicted that in much the same way as the lake fish community in general has reacted, the wetland fish community will be reduced in diversity and dominated by more tolerant species, a phenomenon also noted by Stuckey (1989) for wetland plants. Because many of the most abundant fish in both the undiked and diked wetlands studied by Johnson (1989) are tolerant species, he concluded that both habitats, but especially the diked ones, were not providing the full range of diversity and quality of habitat, since they lacked many intolerant species. He also noted that turbidity reduced the number of sight feeders (piscivores) and has been shown to reduce growth of white crappies. Benthivores, not sight feeders, dominated fish communities.

Studies conducted on Old Woman Creek (D. Jude, unpublished data), a Lake Erie estuary once renowned for its northern pike populations, showed none were caught in this turbid wetland during 1990 and only a few largemouth bass were collected despite extensive fish collections. Derksen and Gillies (1985), in their study of the Sakeram marshes of the Saskatchewan River Delta, found that some winterkills of fish were observed near control structures developed by Ducks Unlimited Canada to manage the marshes for waterfowl and muskrat production. The system is subject to winterkill and summerkill on occasion. Two species found in the Sakeram marshes, brook stickleback *Culaea inconstans* and fathead minnow, were also found by Klinger *et al.* (1982) to survive in a winterkill lake where dissolved oxygen levels throughout the lake were generally less than 0.3 mg/L. These species were also "marsh" species in the correspondence analysis performed for this study. MacCrimmon (1980) studied Wye Marsh, a coastal Great Lakes marsh in the Georgian Bay watershed of Lake Huron. He found that high summer water temperatures in the marsh (up to 36°C) limited permanent aquatic marsh biota to species with a high thermal tolerance. Holmes (1988) noted that degradation of the Hamilton Harbour environment led to dominance by exotics. These fish are all tolerant of the enriched environments, higher water levels, and vegetation increases, that have occurred in Cootes Paradise. Fish larvae collected from West Marsh (Petering and Johnson 1991) were best characterized as warmwater, silt, and turbidity-tolerant species. Only the brook silverside *Labidesthes sicculus* and tadpole madtom *Noturus gyrinus* are turbidity intolerant (Herdendorf *et al.* 1981b). There were no visual predators collected.

Common Carp

Holmes (1988) stressed the theme of degradation of the environment of Hamilton Harbour leading to dominance by exotic fish. The wetland there, Cootes Paradise, was adversely affected by sediment inputs from Spencer creek, nutrients from the Dundas sewage treatment plant, and a large common carp population. White perch and common carp have extended spawning periods which may enhance their success in Great Lakes ecosystems. Swee and McCrimmon (1966) studied common carp in marsh areas of Lake St. Lawrence, along the central area of the St. Lawrence River. Common carp spawned during high water temperatures and high water levels. There was substantial survival of YOY common carp produced in May, June, and July. Common carp were observed to spawn more than one time, sometimes a month later after an initial spawning, which partially accounts for their success in marsh environments. Common carp have also had a detrimental effect on wetland habitat (Crivelli 1983). There was a strong inverse relationship between biomass of common carp and amount of aquatic vegetation present in study enclosures. He found in literature reviews that all studies showed that common carp negatively affected vegetation, but no significant differences in turbidity were documented. Common carp stomachs he examined contained no green vegetation. Also, northern pike does not seem to regulate the common carp population in the U.S. as it does in most natural European waters. This may be due to rapid growth rate of common carp, to more turbid waters in North America (preventing predation), and to absence of northern pike in the southern and western U.S. Common carp can dominate fish communities (70% of total catch), as was found by Chubb and Liston (1986). McLaughlin and Harris (1990) studied aquatic insect emergence from two Great Lakes marshes and found that the community was enhanced in diked wetlands as opposed to undiked ones in Green Bay, Lake Michigan, which they attributed to the diked marshes being physically separated from the eutrophic lower Green Bay and from the influx of common carp, which can have a major impact on aquatic vegetation (King and Hunt 1967, Threinin and Helm 1954).

Degraded Wetlands and Habitat

Many wetlands reported on here were degraded or altered (Farney and Bookout 1982) to one degree or another. Panek (1979), in discussing the cumulative effects of small modifications to habitat, stated that aquatic communities are resilient and have evolved adaptive mechanisms for maintaining stability and productivity under environmentally stressful conditions. Each community has a unique adaptive capacity for change, which is a direct result of the evolutionary processes operating on the range of environmental and biotic conditions characteristic of the ecosystem (Regier and Loftus 1972). Small habitat modifications produce additional and potentially adverse stress on those mechanisms that maintain the integrity and stability of these systems (Panek 1979, Jaworski and Raphael 1976). In Hamilton Harbour-Cootes Paradise, western Lake Ontario, white perch, common carp, goldfish, suckers, and gizzard shad have gained dominance over a richer and more coolwater ichthyofauna (Holmes 1988). These species are tolerant of degraded water quality. A similar decrease in plant diversity has occurred because of the drastic modifications to wetland environments, resulting in loss of species with narrow ecological tolerances (Stuckey 1989).

Whillans (1979) examined fish transformations in two Lake Ontario bays, Toronto and Burlington, and Inner Long Point Bay, Lake Erie. Differences between responses of pelagic migrants and nearshore residents to stress appeared to vary according to pre-adaptation of the species and flexibility of its life pathways. Transformations were indicated by altered growth rates in taxa, year classes of unusual size, shifts in behavior by taxa, local extinction of various taxa, and entry of non-endemic taxa. With few exceptions, the species that exhibited stress were endemic residents, whereas those that prospered were the exotics. Responses to stressors are consequently more predictable. Loosely structured associations were composed of more facultative species which responded more haphazardly to perturbation, except for opportunistic species such as white bass.

Degradation of the Hamilton Harbour environment in western Lake Ontario has resulted in the large white perch, brown bullhead, and common carp exceeding consumption guidelines for fish and there is high incidence of tumors in benthic species (Holmes 1988). For example, white suckers >40 cm have up to 40% incidence of papillomas.

Rehabilitation

Francis *et al.* (1979, 1985) discussed rehabilitation of ecosystems, which they maintain must be considered for degraded wetlands on a per watershed basis. Rehabilitation of Hamilton Harbour has already begun with improvements in water quality and the macroinvertebrate and fish communities. MacCrimmon (1980) suggested Wye marsh could be rehabilitated by removal of accumulated biomass of plants and animals, thereby reducing the standing nutrient load. No loss of ecological stability would occur, eutrophication would be retarded, and the capability of the marsh as a nutrient and sediment sump for materials entering it from the Wye River watershed would be preserved.

In other wetlands, turbidity is a detrimental factor, decreasing macrophyte abundance and algal productivity. Rehabilitation efforts to reduce turbidity will promote a high diversity and abundance of macrophtyes, which has been shown to foster a greater abundance and diversity of fish species because of the many ecological functions (e.g, spawning substrate, cover, diverse benthos) that plants serve in these ecosystems.

Turbidity

Turbidity is an important variable in determining the composition of fish in wetlands, especially those degraded by agricultural and non-point source inputs. Grandall and Swenson (1982) found that with increased turbidity fish reduced their reliance on cover. However, turbidity may reduce plankton production and could increase foraging time of larval fish, allowing only those species adapted to low light conditions to flourish in turbid wetland systems. Blaber and Blaber (1980) investigated 25 species of teleosts in subtropical Moreton Bay, Queensland, to examine the factors influencing the distribution of juveniles in estuaries. Turbidity was the single most important factor. They also concluded that juveniles of many species are probably not attracted to estuaries per se but to shallow turbid areas. Many juvenile fish were only observed in highly turbid waters. The effects of turbidity on fish have not been widely investigated. Swenson (1978) showed that in the Great Lakes, high turbidities stimulate high zooplankton densities in surface waters, in turn promoting an increase in numbers of filter-feeding fish. The primary mechanism through which turbidity affects fish is through reduced light intensity which in turn affects feeding and predation. Petering and Johnson (1991) noted that the larval fish found in their wetland studies in Lake Erie were warmwater, silt- and turbidity-tolerant species.

Turbidity is very important in reducing the effectiveness of a predator, thus increasing survival of prey. High turbidity may also inhibit or decrease diversity of submersed macrophytes (Stuckey 1989) and decrease algal productivity, causing important forage fish prey, zooplankton, to decrease. Only fish adapted to feeding under highly turbid conditions can thus flourish.

Importance of Vegetation to Fish

Shallow littoral zones with dense stands of aquatic vegetation are important ecologically for the production of fish and invertebrates (Guillory *et al.* 1979) as Petering and Johnson (1991) found for sunfish, common carp, and goldfish (cyprinids), which were abundant and most often collected from vegetation in a diked Lake Erie marsh. Aquatic macrophytes create microhabitats, renew detritus, screen fishes, store and release nutrients, intercept sunlight, and buffer water movements (Engel 1988). Conrow *et al.* (1990) found that larval and juvenile fishes were found in highest densities in areas of mixed floating and emergent vegetation in a Florida lake. McLaughlin and Harris (1990) found that the greatest insect biomass emerged from the sparse emergent vegetation zone, which was consistent with other studies which found the vegetation zone an important component of productive wetland habitat (Kaminski and Prince 1981, Voigts 1976).

A diverse habitat, especially one with different types of plants, promotes a diverse fish population (Emery 1978, Eadie and Keast 1984). Wetlands and shallow littoral areas usually have vegetation of many different types (submersed, emergent, terrestrial that can become flooded), including a heterogeneous environment of submerged trees, mud flats, shallow sandy areas, rocks, and open water. Keast *et al.* (1978) found that in Lake Opinicon (Ontario, Canada) most fish biomass was concentrated in the physically diverse inshore habitat. Different habitat types (weedy inlets, sandy shallows, etc.) supported a characteristic species assemblage. Macrophyte beds supported the highest biomass and diversity of fish. They concluded that some habitats provide conditions for cover-dependent species and others a spawning substrate. Macrophyte beds generally supported high fish densities and diversity; other habitats, which were less diverse, supported fewer species. A few fish species were confined to specific habitats, while other species were more ubiquitous in distribution, a finding similar to that of Kilgore *et al.* (1989). The importance of vegetation for nursery habitat for northern pike is well documented (Derksen and Gillies 1985, Holland and Huston 1984, Marean 1976).

The sequence of changes that occurs when a marsh becomes degraded or altered is usually related to degraded water quality, promoted by increased nutrients and sediment loads, which cause massive shifts in plant diversity and abundance (Stuckey 1989) and change macrophyte-algae dominance patterns. Grimm and Backx (1990) in the Netherlands found that in the 1950s eutrophication led to a decline in fish communities associated with lush stands of aquatic vegetation. Cyprinids, mainly bream *Abramis brama* and roach *Rutilus rutilus*, replaced these productive fish communities. In addition, there was a decline in water transparency and waters are now extremely turbid. Common carp were found to be a dominant benthivore that exploited food resources so efficiently that it outcompeted other benthivorous species such as bream. The sequence of events was: increased eutrophication caused increased turbidity, species composition shifted toward cyprinids, vegetation declined with increased turbidity, fewer plants resulted in fewer pike to prey on the cyprinids, and as the production of young cyprinids became too large to be eaten by the resident pike, large-bodied zooplankton declined, and phytoplankton increased, causing reduced abundance and species composition of macrophytes.

Timms and Moss (1984) reported on the sequence of nutrient-induced changes in the Norfolk Broads in England. These lakes were flooded in the 14th century, are shallow, small, and until the last 30 years were dominated by submersed and floating-leafed plant communities. Eutrophication via sewage effluent and agricultural land drainage caused a shift to a phytoplankton-dominated system with complete elimination of the macrophytes. Loss of submerged plants has meant loss of habitat for rare invertebrates, reduced populations of herbivorous birds, reduced stock size and diversity of the fish community through loss of spawning habitat, and loss of the large, macrophyte-associated invertebrates used by cyprinids for food. There have been increased sedimentation rates, probably caused by loss of the weed bed along the shore. Now currents and waves on the rivers cause more erosional damage to the system's banks. In addition, these banks must be stabilized artificially at great cost.

Successful nutrient competition with phytoplankton by an established plant biomass able to achieve luxury uptake is one mechanism which may stabilize the dominance of an aquatic plant community, the secretion of phytoplankton-inhibiting metabolites is another (Phillips *et al.* 1978), and lack of adequate cover (refuges) for phytoplankton-grazing zooplankton (Cladocera) to avoid fish predation may be a third (Timms and Moss 1984). Therefore plants may be necessary to tilt the balance between fish predators and their most vulnerable prey in favor of the latter. Larger Cladocera are more likely to be eaten by fish than are smaller ones, causing a buildup of algae in sites where refuges are not available. The switch from macrophyte dominance to algae may have occurred through nutrient loading alone, but it undoubtedly was accelerated by some disturbance of the balance between Cladocera and their fish predators.

Najas responded to increased nutrient loading with decreased growth because of increased epiphyte growth on its walls and proliferation of filamentous algae (Phillips *et al.* 1978). After this scenario transpired, algal populations developed and dominance shifted. These observations suggest that a two-stage combination of the effects of nutrient loading with disturbance of the phytoplankton-grazing mechanism (and perhaps also mechanisms concerning the grazers of epiphytes and filamentous algae) might have underlain first the change from low-growing aquatic plants to taller, more profuse, macrophytes and filamentous algae, and then the often precipitous disappearance of macrophytes altogether at total phosphorus concentrations around 100 μg/L. Therefore the relative abundance of small zooplanktivorous fish may reflect the loss of plants rather than have been a precursor to this loss. Phillips *et al.* (1978) suggested recovery in this system might be spurred on with bundles of twigs submerged in place of plants to provide refuge for cladocerans.

RESEARCH RECOMMENDATIONS

There have been a number of wetland studies done which have given us a basic understanding of the importance of these habitats for fish spawning, use as nurseries, and as a source of forage for piscivorous fish. However, we still lack information on what are the important physical and chemical characteristics that promote a diversity of fish species which utilize these wetlands and how these attributes change with perturbations, both human-induced (e.g., nutrient and sediment loading) and environmental (e.g., flooding, water level changes). This suggests several recommendations for research which would further our comprehension of wetland form and function, aid in the current efforts to preserve the wetlands we have, provide direction in the creation of new ones, and assist in the rehabilitation of those that have been altered or degraded, especially in Areas of Concern. Additional research needs to be done in the following areas:

1) A better classification system for Great Lakes coastal wetlands, especially species-specific habitat requirements for fish (see Eshenroder *et al.* 1991, p. 6) is required. At present the system of Cowardin *et al.* (1979) provides an excellent basis from which to work, but the special characteristics of Great Lakes wetlands need better definitions. Currently, any shallow area in a Great Lake proper or connected to a Great Lake can be considered a wetland. Such a system would go a long way toward providing a basic template on which additional research on other aspects can be synthesized. A larger work focusing on inventory and classifica-

tion of Great Lakes aquatic habitat (Busch and Sly 1992) addresses some of these needs.

2) More lower food chain research on the characteristic vegetation (see Stuckey 1989, Smith *et al.* 1991), microorganisms (Tilton and Schwegler 1978), algae, zooplankton, and benthos to be expected in various wetland habitats is required to aid the unraveling of the complex interactions among biological communities in wetland systems. The benthos and zooplankton are important food items of fish as is detritus (Tilton and Schwegler 1978), and we need to understand how they change with various perturbations, such as rain events (Krieger and Klarer 1991), water level changes, harsh chemical conditions, and fish predation.

3) The use of aquatic plant diversity (Stuckey 1989), fish, and benthos (Berkman *et al.* 1986) as bioindicators of habitat quality is an important concept applied in other habitats, and should be developed for Great Lakes coastal wetlands. Johnson (1989) has begun initial work on fish for Lake Erie. He has listed the fish species known from wetlands along with their tolerances, current distribution, and status. A matrix of fish species should be compiled from each type of wetland. Data from correspondence analyses provided here, along with tolerances of fish to degraded water quality, and comparisons among perturbed and less perturbed habitats would provide the basis for evaluating wetlands for which no data have been collected. It would also provide goals for remedial action programs and a measure of success when new wetlands are created.

4) More studies are needed on the mechanisms of how wetlands become degraded and how the chemical, physical, and biological characteristics are altered due to these changes. This information would be very useful in restoring wetlands that have lost some of their diversity and productivity, and now have nuisance levels of aquatic organisms, especially exotic species such as common carp, Eurasian watermilfoil *Myriophyllum spicatum*, and purple loosestrife *Lythrum salicaria*.

5) Vegetation plays a strong role in determining the quality and quantity of secondary production in wetlands (Turner 1988a). Development of an organic matrix, such as a bed of macrophytes, has been shown to increase fish diversity (Emery 1978). Aquatic plants have been shown to be very important in wetlands, serving as primary producers, taking up nutrients, reducing current flow, thereby promoting sediment removal. They are important as benthos habitat and provide spawning substrate and nursery areas for fish. Therefore, the role of aquatic plants in wetland ecosystems needs to be better documented (see Smith *et al.* 1991 for an example) to provide understanding of their importance to fish and their role in wetland rehabilitation (Stuckey 1989).

6) Turbidity plays a critical role in many wetlands, changing ecosystem functioning, especially for fish-zooplankton interactions. More information on how turbidity affects predator-prey interactions and the impacted biological communities is required to determine if controls of sediment input to wetlands would improve fish species production and diversity.

7) The wetland environment provides harsh chemical and physical conditions at certain times for biological organisms, especially fish. Therefore, seasonal documentation of critical limnological parameters limiting to fish, e.g., water temperature, prolonged ice cover or freezing to the bottom, dissolved oxygen (see Mitsch and Reeder 1989), ammonia, hydrogen sulfide, and carbon dioxide are imperative to enhance our understanding of the need of fish to have an outlet to a less severe environment, while still having access to the protected nursery areas and high productivity of wetlands.

8) Studies on fish utilization of a diversity of wetlands, incorporating some orthogonal comparisons (e.g., clear vs. turbid, non-vegetated vs. vegetated, degraded water quality vs. good water quality, physically altered vs. unimpaired) and relating the habitat types to specific fish species use for spawning, nurseries, and food (see Keast *et al.* 1978) would help isolate these factors and their importance in promoting fish utilization of Great Lakes wetlands.

ACKNOWLEDGMENTS

We want to acknowledge the encouragement from Ken Krieger, and datasets provided by John Brazner, Robert Haas, James Selgeby, Robert Werner, and Dieter Busch. We wish to especially thank John Brazner, who provided insights and a review, and preliminary findings from his wetlands work on Green Bay. Reviews were provided by Eugene Stoermer, Donna Francis, Stephen Schneider, and Dieter Busch. Beverly McClellan produced the figures and entered all text. This is contribution no. 551 of the Center for Great Lakes and Aquatic Sciences.

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Submitted: 4 June 1992
Accepted: 21 October 1992