Restoration of Lake Erie: contribution of water quality and natural resource management

Joseph F. Koonce, W.-Dieter N. Busch, and Thomas Czapla

Abstract: Since the 1960s, the open-water fish community of Lake Erie recovered dramatically, partly as a result of water-quality and natural-resource management initiatives (including reduction in loadings of phosphorus and toxic contaminants, promotion of wetland protection, restriction of commercial fishing, and implementation of quota management for walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*)). Reviews of historical changes reveal complex interactions of overexploitation of fishery resources, invasion of non-indigenous species, eutrophication, extensive habitat modification, and toxic contamination. Native fish species that required tributary or neashore habitat for spawning and nursery areas have declined markedly. Among surviving native species, such as walleye, stock diversity declined with the loss of tributary spawning stocks and lake spawning stocks became dominant. With the rarefaction of native species, abundance of formerly subdominant species or opportunistic, non-indigenous species increased. Species such as smelt (*Osmerus mordax*), gizzard shad (*Dorosoma cepedianum*), and white perch (*Morone americana*) have less dependence on critical tributary and nearshore habitat. In this paper, we evaluate whether the shifts in fish community structure in Lake Erie reflect the elimination of tributary and wetland habitat. Major unresolved issues are the extent to which habitat loss inhibits recovery of native species associations and the sufficiency of management coordination to identify and restore critical habitat.

Résumé : Depuis les années 1960, la communauté ichtyenne des eaux libres du lac Érié s'est rétablie de façon exceptionnelle, en partie à cause des mesures prises pour améliorer la qualité de l'eau et la gestion des ressources naturelles (notamment une réduction du phosphore et des contaminants toxiques, la promotion de la protection des milieux humides, les restrictions en matière de pêche commerciale et la mise en oeuvre de contingents pour le doré et la perchaude). Les études qui ont porté sur les changements survenus dans le passé ont révélé des interactions complexes entre la surexploitation des ressources halieutiques, l'invasion d'espèces non indigènes, l'eutrophisation, la modification considérable de l'habitat et la contamination par des matières toxiques. Parmi les espèces de poissons indigènes, celles qui ont besoin d'habitats dans des affluents ou près du rivage pour la fraye et l'alevinage ont considérablement diminué. Chez celles qui ont survécu, tel le doré, la diversité des stocks a diminué avec la perte des stocks de géniteurs provenant des affluents, au profit de ceux du lac. Avec la raréfaction des espèces indigènes, on a observé une augmentation des espèces non indigènes, jadis subdominantes et opportunistes. Des espèces comme l'éperlan, l'alose à gésier et le baret n'ont pas un besoin vital des habitats situés dans les affluents et près du rivage. Dans le présent article, nous examinons si les changements intervenus dans la structure de la communauté ichtyenne du lac Érié peuvent être corrélés à l'élimination des habitats des affluents et des milieux humides. Parmi les principaux points qui restent à résoudre, signalons l'absence de données permettant de déterminer à quel point la perte d'habitats empêche le rétablissement des associations d'espèces indigènes, et le manque de coordination au niveau de la gestion pour déterminer quels sont les habitats vitaux et de quelle façon on pourrait les remettre en état.
[Traduit par la Rédaction]

Introduction

Lake Erie is a recovering ecosystem. According to Hartman (1973), the degradation of the fish community of Lake Erie reached its most extreme level in the 1960s. The combined effects of eutrophication, overexploitation of fishery resources, extensive habitat modification, and pollution had severely changed the entire Lake Erie ecosystem. Commercial fisheries experienced declines in preferred species and harvests reflected a progressive decline in lake trout (*Salvelinus namaycush*), lake herring (*Coregonus artedii*), lake whitefish (*Coregonus clupeaformis*), sauger (*Stizostedion canadense*), and blue pike (*Stizostedion vitreum glaucum*) and increasing reliance on less preferred species (Leach and Nepszy 1977). By the late 1960s, the last remaining native predator, the walleye (*Stizostedion vitreum vitreum*), had fallen to a low level. Beginning in the 1970s, fishery management strategies and pollution abatement programs contributed to a dramatic reversal. Lake Erie walleye fisheries rebounded to world-class status (Hatch et al. 1987), and point-source phosphorus loading has declined to target levels in the 1972 Great Lake Water Quality Agreement (Dolan 1993). Associated with these reductions in phosphorus loading were a dramatic decrease in the abundance of nuisance and eutrophic species of phytoplankton (Makarewicz 1993*a*) and an decline in zooplankton biomass (Makarewicz 1993*b*). Surveys of the benthic macroinvertebrate communities further illustrate the improvement in the most degraded sediment areas of western Lake

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Erie. Compared with surveys conducted in 1969 and 1979, Farara and Burt (1993) found that there was a marked decline in the abundance of pollution tolerant oligochaetes and that overall the macroinvertebrate community of western Lake Erie shifted to more pollution intolerant and facultative taxa.

The invasion of zebra mussels (*Dreissena polymorpha*) into Lake Erie has affected this recovery trend. Leach (1993) reported that, associated with zebra mussel increases between 1988 and 1991, water transparency increased 77%, chlorophyll *a* decreased 60%, and number of zooplankters declined 65%. Although Leach (1993) observed an increase in *Gammarus* in nearshore benthic communities dominated by zebra mussels, Dermott (1993) has observed an inverse relation to abundance of *Diporeia* and the quagga mussel (*Dreissena bugensis*). These changes in water quality and associated plankton and benthic communities make predictions about future status of the Lake Erie ecosystem highly uncertain. Recent trends show declines in abundance of smelt (*Osmerus mordax)*, white perch (*Morone americana*), yellow perch (*Perca flavescens*), and walleye with increase in abundance of lake whitefish. Understanding these changes requires separation of cause-effect linkages among pollution reduction, exploitation, and habitat modification.

This paper evaluates the effects of these ecosystem changes and associated water-quality and fish-management initiatives on changes in the structure of the fish community in Lake Erie. Specifically, we formulate and explore a hypothesis that habitat degradation is the primary organizing factor underlying changes in fish community structure. In habitat degradation, we consider chemical loadings, which lead to changes in water quality, and nearshore and tributary habitat alterations, which lead to changes in the physical structure of critical spawning and nursery habitat.

Methods

We obtained data for this paper primarily through historical sources. Catch records from commercial fisheries were the main source of information about changes in the fish community of Lake Erie (Baldwin et al. 1979) from 1900 through the 1970s. The Great Lakes Fishery Commission (M. Dochoda, personal communication) maintains these summaries by distributing reports of Lake Committees for each of the Great Lakes. The Lake Committee reports also include reports of harvest by sports fisheries as well as results of various, ongoing assessment studies. We also relied on reports of walleye and yellow perch task groups of the Lake Erie Committee for virtual population reconstructions from catch data (Knight et al. 1994; Dietz et al. 1993). To develop profiles of habitat preferences of selected fish species, we drew upon a report by Hartley and Herdendorf (1977), an expansion on this report in Herdendorf et al. (1992), and narrative summaries of Trautman (1981) and Scott and Crossman (1973).

The documentation of the history of nutrient and toxic contaminant loadings is widely available. In addition to many literature sources, we relied extensively on recent reports of the governments of the United States and Canada that were distributed for the 1994 State of the Lakes Ecosystem Conference, SOLEC (Environment Canada and U.S. Environmental Protection Agency 1995). We found the history of habitat modification more difficult to reconstruct and relied on another of the SOLEC reports (Dodge and Kavetsky 1994) and other literature sources to generate a profile of habitat changes.

Results and analysis

In examining changes in commercial fish production between 1900 and 1965, Beeton (1969) noted the nearly simultaneous demise of the fisheries for sauger, whitefish, blue pike, and walleye from 1955 to 1960. This period also included the first reported extensive oxygen depletion and changes in the benthos of Lake Erie. Concern with the deteriorating condition of Lake Erie, in fact, had led the governments of Canada and the United States in 1964 to refer the matter to the International Joint Commission (IJC) under the provisions of Article IX of the Boundary Waters Treaty of 1909. The governments were convinced that these changes were caused by pollution from sewage and industrial wastes. In the popular press, this was the time of the “death” of Lake Erie.

In 1969, an IJC report (Campbell et al. 1969) found that all major sources of pollution contributed directly or indirectly to the degraded condition of Lake Erie, Lake Ontario, and the international section of the St. Lawrence River. Of the problem areas identified, eutrophication emerged as the dominant threat to the Lake Erie ecosystem. The role of phosphorus in stimulating excess algal growth had been well established (Campbell et al. 1969), and the effect of the excess production on oxygen demand in the sediments of the lake was cause for concern. Hartman (1973) reported that periods of low dissolved oxygen were a major problem in Lake Erie, with the elimination of mayflies (*Hexagenia*) being an indication of the severity of the problem. The rate of oxygen depletion had apparently increased by the early 1950s. In 1953, a period of calm, hot weather caused sufficient stratification for the bottom waters of the western basin of Lake Erie to fall below 1 $mg \cdot L^{-1}$. This level proved fatal for mayfly nymphs. Mayflies did not recover and by the early 1960s were absent from the benthos that they once dominated.

With the 1972 Great Lakes Water Quality Agreement, Canada and the United States sought to lower phosphorus loading. The agreement had three main objectives: (*i*) eliminate nuisance algal growth in Lake Erie, Lake Ontario, and the International Section of the St. Lawrence River; (*ii*) restore year-round aerobic conditions to the hypolimnion of the central basin of Lake Erie; and (*iii*) maintain the oligotrophic condition of the upper Great Lakes.

Fish biologists were also concerned about patterns of anoxia in the central basin hypolimnion. Regier and Hartman (1973) argued that the central basin hypolimnion may have gone anoxic for the first time in the mid-1950s. Anoxia in the hypolimnion, therefore, was associated prominently with the demise of blue pike, which reached greatest abundance in the deep waters of the central and eastern basins of Lake Erie. The goal of restoring year-round aerobic conditions to the central basin became a necessary condition to restore the habitat for fish, and the governments of Canada and the United States set a target phosphorus load of 11 000 $t\ yr^{-1}$ to achieve this goal (Vallentyne and Thomas 1978). Bertram (1993) found evidence that that total phosphorus concentrations and oxygen depletion rates in the central basin of Lake Erie are decreasing in response to these loading reductions, but Charlton et al. (1993) also showed that resilience of the offshore of the central basin seems to make it less responsive to nutrient reductions than nearshore areas or the western basin.

Understanding of the relation between phosphorus loading and incidence of anoxia in the hypolimnion of the central basin has changed since the setting of targets for phosphorus loading. Charlton (1980) first noted that, when oxygen depletion

Fig. 1. Mean monthly water levels for Lake Erie from 1900 to 1990. Data are courtesy of the Great Lakes Environmental Research Laboratory.

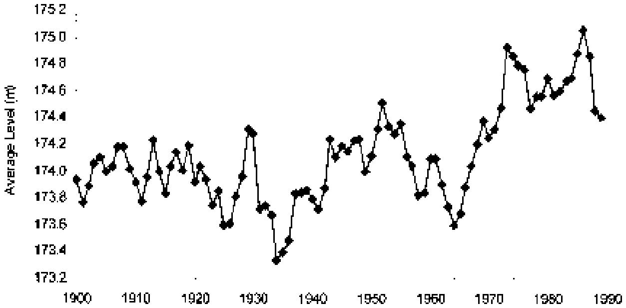
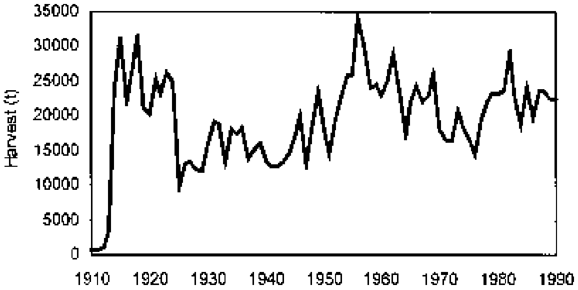


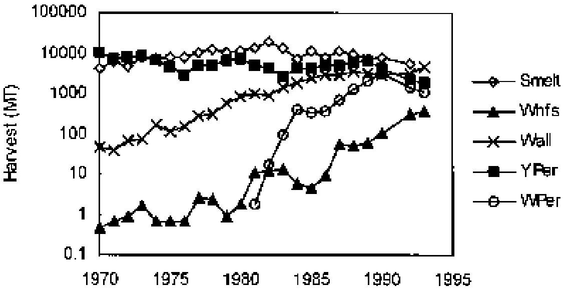
Fig. 2. Trends in commercial harvest, 1910–1990 (after Baldwin et al. (1979) and data from the Great Lakes Fishery Commission).



rates are corrected for hypolimnion thickness and temperature, there appears to be no historical trend in the rate of oxygen depletion (hence probability of anoxia) from the 1930s to the 1970s. Reynoldson and Hamilton (1993) further reported that, from profiles of mayfly tusks in sediment cores of Lake Erie, periods of anoxia occurred prior to European colonization. El-Shaarawi (1987) related the probability of anoxia in the central basin to the joint effect of climate and phosphorus loading. Climatic factors affect the temperature of the hypolimnion and the mean water level of the lake. As Charlton (1980) noted, hypolimnion temperature is a function of weather conditions during the spring, but water level fluctuations have long-term periodicities (Fig. 1). From this vantage point, it is not surprising that the 1960s was a period of poor water quality in Lake Erie. Water levels in 1962 were among the lowest on record (Fig. 1), and through much of the 1960s low water levels were characteristic of Lake Erie. Thus, even without elevated phosphorus loading, there would have been a higher probability of anoxia in the central basin hypolimnion.

Eutrophication was not the only concern of fish biologists. Analyses of the changes of the fish community (Hartman 1973; Regier and Hartman 1973; Leach and Nepszy 1977) revealed a number of possible causes: overexploitation, watershed and shore erosion, nutrient loading, introduction of toxic materials, invasion of new species, and stream and wetland destruction. Leach and Nepszy (1977) argued that the commercial fishery through overexploitation was the dominant stress leading to the declines of lake trout, lake herring, sauger, blue pike, walleye, and yellow perch and that the major concern for the immediate future was the regulation of exploitation.

Fig. 3. Total harvests of selected species: smelt, lake whitefish (Whfs), walleye (Wall), yellow perch (Yper), and white perch (WPer) (after Baldwin et al. 1979 and data from the Great Lakes Fishery Commission).



The decline and recovery of walleye was the prime example of the importance of overexploitation. After the extinction of blue pike, walleye harvests also began to decline (Hartman 1973). Through the 1960s, walleye abundance fluctuated about low levels until the discovery of mercury contamination, which resulted in closure of the walleye fishery (Leach and Nepszy 1977). With the closure of the walleye fishery, fish management agencies began to limit exploitation. The walleye recovery in Lake Erie most certainly results from the aggressive regulation of fishing mortality imposed by a quota management strategy (Hatch et al. 1987). Prior to the closure of the fishery, J.H. Kutkuhn (unpublished data, available from the Great Lakes Fishery Commission, Ann Arbor, Mich., Scientific Protocol Committee Report on western Lake Erie walleye, submitted to the Lake Erie Committee June 1976) estimated that walleye older than 1.5 yr had annual mortality rates of 90%. Under quota management, mortality rates dropped to 30% (Hatch et al. 1987). The walleye recovery was dramatic. Hatch et al. (1987) report that angling catch rates rarely exceeded 0.1 walleye per angler hour during the 1950s and 1960s. By 1975, these catch rates had risen to 0.61 walleye per angler hour, and there followed a dramatic increase in sports harvests and sports fishing effort.

Although the historical variation of walleye abundance is consistent with changes in exploitation, other changes in fish community structure in Lake Erie are difficult to reconcile primarily with either effects of pollution or commercial fisheries. As Leach and Nepszy (1977) noted, commercial fisheries have fluctuated about a long-term average of 20 000 t from 1915 to 1993 (Fig. 2). Since 1970, smelt and yellow perch have been major components of the commercial harvest. The contribution of these two species, however, has declined while other species have increased (e.g., walleye, white perch, and lake whitefish; Fig. 3).

The response of these five species is not as expected if pollution (particularly eutrophication) and overexploitation were the dominant and controlling stresses on the fish community. Fish managers lowered fishing mortality on walleye and then yellow perch through implementation of quota management. Water-quality management produced declining phosphorus loading. The effects of these management actions are in conflict. Lowered fishing mortality should result in higher abundance of yellow perch and walleye. Lowered nutrient loading should decrease primary production, which limits growth and reproduction of walleye, yellow perch, and other

Fig. 4. Abundance estimates of walleye and yellow perch in Lake Erie from 1978 to 1994. Virtual population estimates for yellow perch are after Dietz et al. (1993) and for walleye, after Knight et al. (1994).

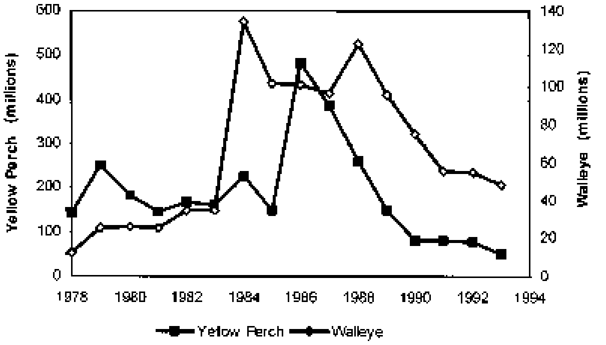
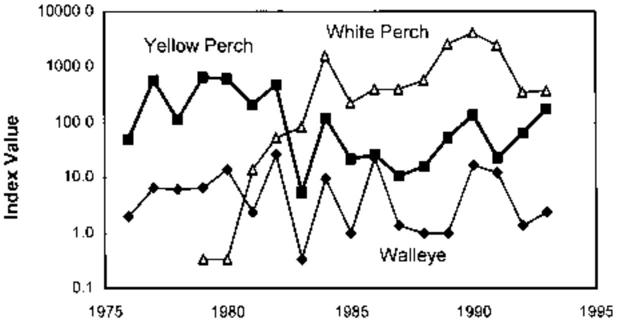


Fig. 5. Trends in relative abundance of age-0 walleye, yellow perch, and white perch in Ohio waters of Lake Erie, 1976-1993. Data are averages of index values for Districts 1, 2, and 3. Index values are based on fall trawl surveys conducted by Ohio Department of Natural Resources.



species. In concert, therefore, these actions should result in greater abundance of adult fish, having lower growth rates, and a decrease in recruitment, caused both by decreased productivity and by increased predation on juveniles.

Fish species did not respond to these changes in management actions as expected. Lake whitefish increased in reported harvests by commercial fishing while smelt yields decreased in recent years (Fig. 3). Both walleye and yellow perch populations increased dramatically in the early 1980s (Fig. 4), but both populations later declined. Trawl surveys of young-of-the-year reveal that walleye and yellow perch had variable recruitment from 1976 to 1993 with a slight downward trend (Fig. 5). In contrast, white perch recruitment increased from the early 1980s to 1990 until it began declining through 1993 in parallel with declining harvests in the commercial fishery. Because these five species function quite differently in the Lake Erie fish community, ecological interactions may explain these varied responses to reduction in nutrient loading and quota management of the fisheries. Nevertheless, it is difficult to reconcile these varied responses with simple cause-effect hypotheses involving the direct effects of quota management on yellow perch and walleye and of reduction of phosphorus loading.

A more general review of changes in diversity of Lake Erie fish indicates that other factors may have caused the instability of the fish community. Van Meter and Trautman (1970) document observations of 138 fish species in Lake Erie and its tributaries. Commercial fishing records are available for 35 of these species and 19 species have contributed significant harvests (Hartman 1973). In Table 1, we present a summary of information on 35 species for which sufficient evidence exists to compare their origins, spawning habitat requirements, and changes in abundance. This summary draws upon a report by Hartley and Herdendorf (1977), an expansion on this report in Herdendorf et al. (1992), and work by Trautman (1981) and Scott and Crossman (1973). Six of the 35 species in Table 1 are non-indigenous, including goldfish (*Carassius auratus*), carp (*Cyprinus carpio)*, gizzard shad (*Dorosoma cepedianum*), smelt, alewife (*Alosa pseudoharengus)*, and white perch. Using these sources, we assigned a relative abundance rank for both the period prior to 1800 and current conditions: abundant, common, rare, extinct (or extirpated), and not present. We also summarized spawning habitat preference for tributary or nearshore habitat and the specificity of habitat preference. We assigned a low habitat specificity (L) to those species that spawn in a variety of habitat types and high specificity (H) to species with a narrow preference range for physical features of spawning habitat.

The change in the species composition of Lake Erie is associated with a decline in abundance of species that have narrow preferences for spawning habitat (Table 1). Of the 11 species that we now judge to be common or abundant, 5 are non-indigenous with low specificity for spawning habitat. We judged that 16 of the species had low specificity for spawning habitat. Native species included in this list were quillback (*Carpiodes cyprinus*), largemouth bass (*Micropterus salmoides*), emerald shiner (*Notropis atherinoides*), northern pike (*Esox lucius*), muskellunge (*Esox masquinongy*), black bullhead (*Ameiurus melas*), yellow bullhead (*Ameiurus natalis*), brown bullhead (*Ameiurus nebulosus*), sauger (*Stizostedion canadense*), walleye, and lake whitefish. Of these, three have recently increased (walleye, lake whitefish, and black bullheads). As discussed by Trautman (1981), the inverse abundance relationship between black and both brown and yellow bullheads is related to habitat degradation. Of the remaining species, esocids (muskellunge and northern pike) and centrachids depend as adults upon nearshore habitat with submerged aquatic vegetation. Quillback remained stable and the decline of emerald shiner seems unrelated to spawning habitat. Therefore, we propose that degradation of spawning and nursery habitat in tributaries and the nearshore environment of Lake Erie has contributed to the decline of many native species (lake sturgeon (*Acipenser fulvescens*), several cyprinids, white sucker (*Catostomus commersoni*), and lake herring) and remains an obstacle to their recovery.

Habitat degradation does not always limit production of species with high specificity for spawning habitat. The critical determinant of limitation is not the absolute amount of habitat, but amount of habitat relative to habitat requirements of all life-history stages of a species (cf. Minns 1995). Although we lack the level of detail necessary to characterize fully the spawning and nursery habitat requirements of Lake Erie fish species, we found ample reason to pursue an expansion of Table 1. Fish community structure of Lake Erie depends upon the biological diversity of its fish species, and variability of life-history expression reflects the biological diversity of each

Table 1. Summary of characteristics of selected species of Lake Erie fish.

			Spawning		Abundance	+
Species name	Common name	Origin[a]	Location[b]	Specificity[c]	Pre-1800	Now
Carassius auratus	Goldfish	NI	T,N	L	NP	C
Cyprinus carpio	Common carp	NI	T,N	L	NP	A
Dorosoma cepedianum	Gizzard shad	NI	T,N	L	NP	A
Osmerus mordax	Rainbow smelt	NI	T,N	L	NP	C
Alosa pseudoharengus	Alewife	NI	T,N	L	NP	C
Morone americana	White perch	NI	T	H	NP	A
Acipenser fulvescens	Lake sturgeon	N	T	H	C	R
Carpiodes cyprinus	Quillback	N	T,N	L	R	R
Catostomus commersoni	White sucker	N	T	H	C	R
Lepomis gibbosus	Pumpkinseed	N	N	H	C	R
Lepomis macrochirus	Bluegill	N	N	H	C	R
Micropterus dolomieui	Smallmouth bass	N	N	H	C	R
Micropterus salmoides	Largemouth bass	N	T,N	L	C	R
Pomoxis annularis	White crappie	N	N	H	C	C
Pomoxis nigromaculatus	Black crappie	N	N	H	R	R
Notemigonus crysoleucas	Golden shiner	N	T	H	C	R
Notropis atherinoides	Emerald shiner	N	N,O	L	C	R
Notropis hudsonius	Spottail shiner	N	N	H	C	R
Pimephales notatus	Bluntnose minnow	N	T	H	C	R
Pimephales promelus	Fathead minnow	N	T	H	R	R
Esox lucius	Northern pike	N	T,N	L	C	R
Esox masquinongy	Muskellunge	N	T,N	L	C	R
Ameiurus melas	Black bullhead	N	T,N	L	R	C
Ameiurus natalis	Yellow bullhead	N	T,N	L	C	R
Ameiurus nebulosus	Brown bullhead	N	T,N	L	C	R
Ictalurus punctatus	Channel catfish	N	T	H	C	R
Morone chrysops	White bass	N	N	H	A	R
Perca flavescens	Yellow perch	N	N	H	A	C
Stizostedion canadense	Sauger	N	T,N	L	C	E
Stizostedion vitreum glaucum	Blue pike	N	?	?	A	E
Stizostedion vitreum vitreum	Walleye	N	T,N	L	C	C
Coregonus artedii	Lake herring or cisco	N	N	H	A	R
Coregonus clupeaformis	Lake whitefish	N	T,N	L	C	R
Salvelinus namaycush	Lake trout	N	N	H	C	R
Aplodinotus grunniens	Freshwater drum	N	N	H	A	A

[a] N, native species; NI, non-indigenous species.

[b] T, tributary; N, nearshore; O, open lake.

[c] L, low; H, high.

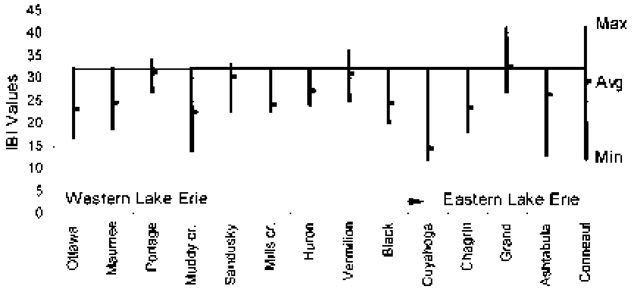
[d] A, Abundant; C, common; R, rare; E, extinct or extirpated; NP, not present.

species. Walleye, for example, spawn in rivers and spawning reefs, and these spawning preferences are the basis of walleye subpopulation structure in Lake Erie. This biological diversity of walleye provides the means of escaping limitation due to degradation of tributary spawning habitat by dams, siltation, and other tributary modifications. Nevertheless, the relative absence of reef habitat in the central basin limits the productivity of central basin walleye more than in the western basin. In losing nearshore and tributary habitat, the structure of the Lake Erie fish community continues to be driven by the most opportunistic species. The dominance of non-indigenous species in Lake Erie thus could be due more to habitat degradation than to overexploitation and nutrient enrichment.

Because habitat degradation and alteration is the least understood of the major stresses acting on the Lake Erie ecosystem, rigorous testing of this hypothesis is not possible. Although the importance of physical and chemical habitat to lake productivity has long been recognized (e.g., Rawson 1939), the complexity of these interactions and their effects on community structure and function remains a barrier to developing a workable system for inventory and classification of Great Lakes habitat (Herdendorf et al. 1992). Nevertheless, the losses of nearshore and tributary habitat of Lake Erie due to human activities has been major:

(*i*) Loss of coastal wetlands. Through drainage and infilling, the extensive wetlands of the western basin have been reduced. The Black Swamp in the Maumee River drainage basin, for example, has been reduced from 4000 to 100 km^2 (Dodge and Kavetsky 1994). Of the remaining coastal wetlands, nearly all are diked to provide protection from wave

Fig. 6. Minimum, maximum, and mean index of biotic integrity (IBI) for 14 estuaries. For comparison the Warm Water Habitat aquatic life use criterion value of 32 is plotted as a solid line (WWH Criterion). Figure is from R.F. Thoma (Ohio Environmental Protection Agency).



action (Bookhout et al. 1989). The remaining undiked wetlands are often degraded by erosion and siltation (Prince et al. 1992).

(*ii*) Loss of tributary habitat. The 21 tributaries have been subjected to extensive modification, including dams, channelization, dredging to maintain navigation channels, hardening of the shorelines of the estuarine reaches with rip-rap and bulkheads, and erosion and sedimentation due to bank destabilization in upper reaches.

(*iii*) Loss of rocky shorelines. The nearshore of Lake Erie has been extensively modified with groins, jetties, and breakwaters, which have altered natural shore processes of erosion and deposition (Carter 1973). The shifting of unstable substrates creates barrier beaches and zones of erosion where more resistant substrates become exposed. Much of the Lake Erie shoreline is composed of beach. Exposed rocky substrates are thus threatened by altered patterns of erosion and deposition as well as by the spread of zebra mussels (Dodge and Kavetsky 1994).

The significance of this loss of habitat is suggested by the loss of fish species diversity (Table 1). R.F. Thoma (Ohio Environmental Protection Agency, Columbus, Ohio, unpublished data) found that the degradation of the biological integrity of the estauarine portions of Ohio's tributaries to Lake Erie was severe (Fig. 6). Using an Index of Biotic Integrity, Thoma found that only one of the 14 estuaries met minimal integrity standards. Factors responsible for the degraded conditions included extensive habitat modification, loss of wetlands, point source discharges, and non-point-source pollutants. The remaining habitats are critically imperiled. Despite government commitments to "no net loss of aquatic habitat," conversion of natural habitats for agricultural, urban, or industrial uses continues (Dodge and Kavetsky 1994). Protection of remaining coastal wetlands through diking preserves wetland habitat for wildlife and migrating waterfowl, but not for fish. Furthermore, diked wetlands become extremely vulnerable to long-term changes in water level. The present system of dikes and distribution of coastal wetlands arose in a period of high water levels. Koonce and Hobbs (1994) reasoned that the patchwork pattern of preserved wetland areas may be insufficient for adaptation to changing regimes of water levels that will be associated with future climate change. The coastal development of Lake Erie thus limits the capacity of natural shorelines to adapt to changing flow and water level regimes in a way that minimizes additional damage to fish and wildlife populations.

Discussion

On a lakewide basis, regulation of pollution and regulation of fisheries have been the basis of Lake Erie management. There is no doubt that sewage effluents, industrial discharges, and excessive fishing have contributed to the degradation of the fish community of Lake Erie. However, invasion of non-indigenous species and habitat degradation severely limit its biological recovery (Koonce 1994). In fact, we find sufficient evidence to hypothesize that habitat alteration fundamentally entrained the extent of change in the structure and function of the Lake Erie fish community.

The current fish community of Lake Erie represents a balance of stresses and recovery transients. Summarizing the effects of management activities on trends in fish community structure, we find the following:

(*i*) Exploitation is now regulated. The value of the fisheries may fluctuate with the abundance of desired species, but targeted species remain vulnerable. Fishery landings, while variable, continue to provide harvests commensurate with historical averages. Commercial fishery is now focused on small-bodied animals and non-indigenous species are a major component of the harvest. Angling is similarly opportunistic with the result that fishery management adapts to constraints imposed by invasions of non-indigenous species and habitat loss.

(*ii*) Eutrophication is now less of a threat. Phosphorus loadings have declined to target levels, and there is new concern that Lake Erie's central and western basins are in transition from mesotrophy to oligotrophy and eutrophy to mesotrophy, raising the question whether fish species are limited now more by productivity or habitat. A transition in ecosystem function is taking place, but fish community may lack the species diversity to respond to benthic-based food webs that are being created by the invasion of zebra mussels.

(*iii*) Contaminants remain a problem in that they seem to have stabilized at a level sufficient to warrant concern. Given the growing significance of atmospheric sources, there seems to be little expectation of change. In fact, there may follow a slight increase in body burdens of some organochlorine compounds with additional complication of food webs.

Invasion of non-indigenous species and habitat loss are largely unregulated. Prevention measures taken by governments (such as adopting balast discharge regulations) reduce these stresses, but these efforts have neither the scale of effort nor resources that have been devoted to regulation of exploitation and chemical pollution. This imbalance of approach seems curious in retrospect. Invasion of exotic species and habitat disturbance are linked, and we believe that a new framework is needed to manage habitat protection and restoration.

Herdendorf et al. (1992) reviewed the physical and chemical basis for classification and inventory of Great Lakes habitat. Their approach to habitat classification linked morphometry to community structure and function. We suspect that the key to understanding changes in the fish community of Lake Erie requires understanding the effects of habitat alteration on the success of individual fish species. Diversity of a fish community, its structure, and its function depend first on the availability of species that are capable of completing their life cycle within the lake ecosystem. Species vary, however, in their attributes and contribution to community structure and function. Current declines in smelt and white perch populations may represent a shift in the food web of Lake Erie resulting from the invasion of zebra mussels. Energy flow seems to be channeled more to the benthos, and planktivory as a feeding niche will become less productive. Historically, macroinvertebrates such as mayflies were an important component of the food web, and though species characteristics are quite different, we see a return to a benthic-based food webs in Lake Erie. Many of the historically important fish species in Lake Erie, however, are now limited by availability of spawning and nursery habitat, and non-native species such as white perch and smelt do not seem sufficiently adaptable to fill this benthic feeding niche.

We suggest that understanding the historical changes in the fish community of Lake Erie and its future restoration will depend upon a clearer perspective on styles of use of habitat by fish. For example, there is new concern over the limitation of phosphorus loading for Lake Erie with the invasion of zebra mussels (Neilson et al. 1994). The basic question is whether phosphorus reduction now imperils the productivity of the Lake Erie fish community. Addressing this issue requires determining whether productivity is limited by habitat or by nutrient loading. If managers accept the premise that, due to habitat constraints, a planktivory-based fish community is the choice of fishery managers, then the system may indeed be limited by nutrient loading. Should the habitat constraints be removed from fish populations, which can utilize benthic-based food webs more effectively, then managers might find fish production less dependent on nutrient loading. We believe that the loss of so many native species and their failure to recover is a manifestation of habitat limitation.

Water quality and fishery management have approached restoration of Lake Erie from different perspectives. Obvious problems have been corrected, but Lake Erie remains a highly stressed ecosystem. It seems time to ask fundamental questions about why Lake Erie is so vulnerable to disruption by the invasion of exotic species. The zebra mussel invasion has radically altered energy flow and nutrient cycling dynamics in Lake Erie. Ruffe (*Gymnocephalus cernuus*) invasion and expansion in Lake Superior threatens yet another major challenge to the Lake Erie ecosystem (Dodge and Kavetsky 1994). Existing independence of management of water quality, fishery resources, and even water quantity seems no longer productive or sufficient to deal with emerging challenges of ecosystem management. Lakewide management plans (LaMP) offer an opportunity for unification of approaches.

Within the framework of the Joint Plan for the Strategic Management of Great Lakes fisheries (SGLFMP), Lake Erie fish managers are attempting to develop a set of Fish Community Objectives (FCO) that will guide future management actions. They are also required to develop a set of complementary Environmental Objectives that specify the environmental characteristics necessary to achieve the FCOs. As set forth in the 1987 Protocol for the Great Lakes Water Quality Agreement, water-quality managers are committed to developing Ecosystem Objectives for each of the Great Lakes and to restoring their beneficial uses. Environmental Objectives of the fish managers could be useful benchmarks for the water-quality managers in their determination of restoration of beneficial uses. This overlap of common interests, however, depends upon reconciling FCOs and Ecosystem Objectives. Clearly, this reconciliation must involve an integration of plans for the development of nearshore environments. The Lake Erie LaMP offers the opportunity for discussion of these issues, but the technical foundations of these discussions will require a more careful consideration of the linkage between physical habitat and stable life-history patterns among fish species. Derivation of something like a habitat guild concept would be an important step in completing the kind of classification and inventory system propose by Herdendorf et al. (1992). With such a system in place, derivation of specific Environmental Objectives for Lake Erie will be placed on a firmer scientific foundation.

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References

Baldwin, N.S., Saalfeld, R.W., Ross, M.A., and Buettner, H.J. 1979. Commercial fish production in the Great Lakes 1867-1977. Great Lakes Fish. Comm. Tech. Rep. 3.

Beeton, A.M. 1969. Changes in the environment and biota of the Great Lakes. *In* Eutrophication: causes, consequences, and corrections. National Academy of Sciences, Washington, D.C. pp. 150-187.

Bertram, P.E. 1993. Total phosphorus and dissolved oxygen trends in the central basin of Lake Erie, 1970–1991. J. Great Lakes Res. **19**: 224–236

Bookhout, T.A., Bednarik, K.E., and Kroll, R.W. 1989. The Great Lakes marshes. *In* Habitat management for migrating and wintering waterfowl in North America. *Edited by* L.M. Smith, R.L. Pederson, and R.M. Kaminski. Texas Tech University Press, Lubbock, Texas. pp. 131-156.

Campbell, N.J., Bruce, J.P., Hendrickson, J.F., Higgins, P.M., Pemberton, C., Steggles, W.A., and Vallentyne, J.R. 1969. Pollution of Lake Erie, Lake Ontario, and the international section of the St. Lawrence River. Report to the IJC by the International Lake Erie Water Pollution Board and the International Lake Ontario - St. Lawrence River Water Pollution Board. Vol 1. International Joint Committee, Windsor, Ont.

Carter, C.H. 1973. Natural and manmade features affecting the Ohio shore of Lake Erie. Guidebook 1. Ohio Department of Natural Resources, Division of Geological Survey, Columbus, Ohio.

Charlton, M.N. 1980. Oxygen depletion in Lake Erie: has there been any change? Can. J. Fish. Aquat. Sci. **37**: 72-81.

Charlton, M.N., Milne, J.E., Booth, W.G., and Chiocchio, F. 1993. Lake Erie offshore in 1990: restoraton and resilience in the central basin. J. Great Lakes Res. **19**: 291–309

Dermott, R.M. 1993. Distribution and ecological impact of Quagga mussels in the lower Great Lakes. *In* Proceedings of the 3rd International Zebra Mussel Conference, February 1993, Toronto, Ont. Electric Power Res. Inst. Rep. No. TR-102077.

Dietz, P., Freeman, M., Kenyon, R., Knight, C., Muth, K., and Thomas, M. 1993. Report of the Lake Erie Yellow Perch Task Group. Standing Technical Committee, Lake Erie Committee, Great Lakes Fishery Commission, Ann Arbor, Mich.

Dodge, D., and Kavetsky, R. 1994. Aquatic habitat and wetlands of the Great Lakes. State of the Lakes Ecosystem Conference. U.S.

Environmental Protection Agency, Great Lakes National Program Office, Chicago, Ill.

Dolan, D.M. 1993. Point source loadings of phosphorus to Lake Erie: 1986-1990. J. Great Lakes Res. **19**: 212-223.

El-Shaarawi, A.H. 1987. Water quality changes in Lake Erie, 1968-1980. J. Great Lakes Res. **13**: 674-683.

Environment Canada and U. S. Environmental Protection Agency. 1995. State of the Great Lakes. EPA 905-R–95–010. U.S. Environmental Protection Agency, Great Lakes National Program Office, Chicago, Ill.

Farara, D.G., and Burt, A.J. 1993. Environmental assessment of Western Lake Erie Sediments and Benthic Communities—1991. Report prepared for the Ontario Ministry of Environment and Energy, Water Research Branch, Great Lakes Section by Beak Consultants Ltd., Brampton, Ont. Available from Ontario Ministry of Energy and Environment, Toronto, Ont.

Hartley, S.M., and Herdendorf, C.E. 1977. Spawning ecology of Lake Erie fishes. Tech. Rep. No. 62. Center for Lake Erie Area Research, Ohio State University, Columbus, Ohio.

Hartman, W.L. 1973. Effects of exploitation, environmental changes, and new species on the fish habitats and resources of Lake Erie. Great Lakes Fish. Comm. Tech. Rep. No. 22.

Hatch, R.W., Nepszy, S.J., Muth, K.M., and Baker, C.T. 1987. Dynamics of the recovery of the Western Lake Erie walleye (*Stizostedion vitreum vitreum*) stock. Can. J. Fish. Aquat. Sci. **44**: 15-22.

Herdendorf, C.E., Hakanson, L., Jude, D.J., and Sly, P.G. 1992. A review of the physical and chemical components of the Great lakes: a basis for classification and inventory of aquatic habitats. *In* The development of an aquatic habitat classification system for lakes. *Edited by* D. Busch and P.G. Sly. CRC Press, Ann Arbor, Mich. pp. 109-160.

Knight, R., Einhouse, D., Haas, B., Henderson, B., Kenyon, R., MacLennan, D., Muth, K., Nepszy,S., Thomas, M., Turner, M., and Wolfert, D. 1994. Report of the Lake Erie Walleye Task Group. Standing Technical Committee, Lake Erie Committee, Great Lakes Fishery Commission, Ann Arbor, Mich.

Koonce, J.F. 1994. Aquatic community health of the Great Lakes. State of the Lakes Ecosystem Conference. U.S. Environmental Protection Agency, Great Lakes National Program Office, Chicago, Ill.

Koonce, J.F., and Hobbs, B.F. 1994. Climate change and the health of the Great Lakes ecosystem. *In* Great Lakes climate change, research priorities for assessing the impacts of climate change in the Great Lakes Basin. *Edited* by C.M. Ryan et al. NOAA Workshop, Ypsilanti, MI, March 1994. pp. 36–53

Leach, J.H. 1993. Population dynamics and ecological impacts of zebra mussels in Western Lake Erie. Abstract. Third International Zebra Mussel Conference, Toronto, Ont., 23-26 Feb. 1993.

Leach, J.H., and Nepszy, S.J. 1977. The fish community in Lake Erie. J. Fish. Res. Board Can. **33**: 622-638.

Makarewicz, J.C. 1993*a*. Phytoplankton biomass and species composition in Lake Erie, 1970 to 1987. J. Great Lakes Res. **19**: 258-274.

Makarewicz, J.C. 1993*b*. A lakewide comparison of zooplankton biomass and its species composition in Lake Erie, 1983-87. J. Great Lakes Res. **19**: 275-290.

Minns, C.K. 1995. Calculating net change of productivity of fish habitats. Can. MS Rep. Fish. Aquat. Sci. 2282.

Neilson, M., Italien, S. L.', Glumac, V., Williams, D., and Bertram, P. 1994. Nutrients: trends and system response. State of the Lakes Ecosystem Conference. U.S. Environmental Protection Agency, Great Lakes National Program Office, Chicago, Ill.

Prince, H.H., Padding, P.I., and Knapton, R.W. 1992. Water fowl use of the Laurentian Great Lakes. J. Great Lakes Res. **18**: 673-699.

Rawson, D.S. 1939. Some physical and chemical factors in the metabolism of lakes. Sci. Publ. No. 10. American Association for the Advancement of Science, Washington, D.C. pp. 9-26.

Regier, H.A., and Hartman, W.L. 1973. Lake Erie's fish community: 150 years of cultural stresses. Science (Washington, D.C.), **180**: 1248-1255.

Reynoldson, T.B., and Hamilton, A.L. 1993. Historic changes in populations of burrowing mayflies (*Hexagenia limbata*) from Lake Erie based on sediment tusk profiles. J. Great Lakes Res. **19**: 250-257.

Scott, W.B., and Crossman, E.J. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184.

Trautman, M.B. 1981. The fishes of Ohio. Ohio State University Press, Columbus, Ohio.

Vallentyne, J.R., and Thomas, N.A. 1978. Fifth year review of Canada - United States Great Lakes Water Quality Agreement. Report of Task Group III, A Technical Group to Report Phosphorus Loadings, to the Parties of the Great Lakes Water Quality Agreement of 1972. International Joint Commission, Windsor, Ont.

Van Meter, H.D., and Trautman, M.B. 1970. An annotated list of the fishes of Lake Erie and its tributary waters exclusive of the Detroit River. Ohio J. Sci. **70**: 65-78.