J. Great Lakes Res. 34:755–769
Internat. Assoc. Great Lakes Res., 2008

Ichthyoplankton Assemblages of Coastal West-Central Lake Erie and Associated Habitat Characteristics

James E. McKenna, Jr.[1,*], Bruce M. Davis[2], Mary C. Fabrizio[3], Jacqueline F. Savino[2], Thomas N. Todd[2], and Michael Bur[4]

[1]*Tunison Laboratory of Aquatic Science*
USGS, Great Lakes Science Center
3075 Gracie Road
Cortland, New York 13045

[2]*USGS, Great Lakes Science Center*
1451 Green Road
Ann Arbor, Michigan 48105-2807

[3]*Virginia Institute of Marine Science*
Department of Fisheries Science
P.O. Box 1346
Gloucester Point, Virginia 23062

[4]*Lake Erie Biological Station, USGS, Great Lakes Science Center*
6100 Columbus Ave.
Sandusky, Ohio 44870

ABSTRACT. *Early life stage survival often determines fish cohort strength and that survival is affected by habitat conditions. The structure and dynamics of ichthyoplankton assemblages can tell us much about biodiversity and fish population dynamics, but are poorly understood in nearshore areas of the Great Lakes, where most spawning and nursery habitats exist. Ichthyoplankton samples were collected with a neuston net in waters 2–13 m deep weekly or biweekly from mid-April through August, during 3 years (2000–2002) as part of a study of fish assemblages in west-central Lake Erie. A suite of abiotic variables was simultaneously measured to characterize habitat. Cluster and ordination analyses revealed several distinct ichthyoplankton assemblages that changed seasonally. A lake whitefish* (Coregonus clupeaformis) *dominated assemblage appeared first in April. In May, assemblages were dominated by several percid species. Summer assemblages were overwhelmingly dominated by emerald shiner* (Notropis atherinoides), *with large gizzard shad* (Dorosoma cepedianum) *and alewife* (Alosa pseudoharengus) *components. This seasonal trend in species assemblages was also associated with increasing temperature and water clarity. Water depth and drift processes may also play a role in structuring these assemblages. The most common and widely distributed assemblages were not associated with substratum type, which we characterized as either hard or soft. The timing of hatch and larval growth separated the major groups in time and may have adaptive significance for the members of each major assemblage. The quality and locations (with reference to lake circulation) of spawning and nursery grounds may determine larval success and affect year class strength.*

INDEX WORDS: *Larval fish, freshwater fish, Great Lakes, community structure, lentic environment.*

INTRODUCTION

The success of larval fish often determines cohort strength for a population (Hjort 1926) and is affected by a number of environmental factors (Freeberg *et al.* 1990, Matthews 1998, for example). Habitat conditions change both spatially and temporally (seasonally and on longer time scales) and larval fishes are planktonic, drifting with the current.

*Corresponding author. E-mail: jemckenna@usgs.gov

Orientation of spawning grounds to appropriate juvenile habitats is important to successful recruitment of larvae to the juvenile stage (Huret *et al.* 2007). Survival during the larval period and effective transport to nursery grounds can depend on how well spawning time (and subsequent hatch) coincides with optimal environmental conditions (Sinclare 1988). Food availability and avoidance of predators are critical to larval growth and survival (Matthews 1998). These biotic factors interact with temperature, turbidity, and other abiotic conditions in the water mass to influence larvae (Höök *et al.* 2006). For example, temperature affects physiological rates, which determines larval respiratory needs, growth, and other critical functions (Kleiber 1961, Letcher and Bengston 1993). High turbidity in Lake Superior has been associated with rainbow smelt (*Osmerus mordax*) moving into shallow water and increasing predation on larval fish (Swenson 1978). Study of the response of ichthyoplankton to benthic substratum is rare, but findings show correlations of fish larvae with particular habitat types (Baily *et al.* 2003, Maynou *et al.* 2006) and indicate that larvae can alter their behavior to arrive at appropriate nursery habitat (Grioche *et al.* 1997).

Rivers are major external influences on nearshore habitats that can affect lake circulation and the quality of both pelagic and benthic environments via seasonally varying discharges of material loads, particularly plant nutrients and suspended matter (Swenson 1978, Rukavina and Zeman 1987). Many species of larvae depend on abundant food associated with the spring plankton bloom, high river discharge, and lake mixing, especially at the first feeding stage (Hjort 1926, Lasker 1975).

In the Laurentian Great Lakes, nearshore habitats (approximately $\leq$ 10 m depth) are critical to fishes because many of the important feeding, spawning, and nursery grounds are found in these areas (Goodyear *et al.* 1982). Nearly all Great Lakes fishes (> 95%) are known to spawn in waters < 1 m or rely on shallow water for some component of the life cycle, or both (Goodyear *et al.* 1982; Lane *et al.* 1996a,b). Thus, multispecies sympatric assemblages of ichthyoplankton exist in nearshore waters. However, with a few exceptions (e.g., walleye *Sander vitreum*), the distributions, abundances of, and optimal conditions for larval and juvenile fishes in coastal Great Lakes habitats are poorly understood. This is partly because nearshore zones of Great Lakes coasts are dynamic areas where conditions can be harsh and sampling is difficult.

The west-central basin of Lake Erie (USA) is one such nearshore area that contains many important fish habitats (Ludsin and Stein 2001). We would expect to find the larvae, and possibly juveniles, of many nearshore-dependent species in this coastal area (Goodyear *et al.* 1982). However, it is unclear which nearshore habitats are most important for support of the early life stages of fishes in this portion of Lake Erie. Better information on the factors affecting the occurrence and relative abundance of larval fishes would greatly enhance our ability to predict the response of Lake Erie fish populations to perturbations and identify those areas most in need of protection, restoration, or other management action. This requires an understanding of the structure of the fish community and distribution of biodiversity in this region.

We examined ichthyoplankton composition, abundances, and distributions in the vicinity of major river mouths within the west-central basin of Lake Erie, to 1) determine whether spatial or temporal structure exists, 2) describe any observed structure using ecological community attributes, and 3) quantify the relationship of that structure to habitat conditions. The first objective is important because if there is no detectable structure, then there is also no significant habitat influence on those assemblages (McKenna 1993). The second objective provides standard measures of species assemblage status that can be compared in space and time and with results of other studies. The third objective provides the most powerful application of our findings by highlighting which habitat conditions are most strongly associated with particular fish assemblages and which might be managed for some desirable objective.

METHODS

Study Area

The west-central Lake Erie basin (on the U.S. side) extends from roughly Sandusky Bay on the west to Avon Point on the east—a distance of approximately 75 km (Fig. 1). The three largest rivers draining into this section of Lake Erie are the Huron River, Vermilion River, and Black River. Mean annual discharges for the Huron River and Black River are nearly the same (9.2–9.8 m^3/s), while the Vermilion River supplies about 80% of that discharge (7.7 m^3/s) (USGS 2008). The nearshore lake bottom consists of large areas of mud, with some exposed bedrock, making it a transition zone between the western basin (muddy) and central basin (rocky).

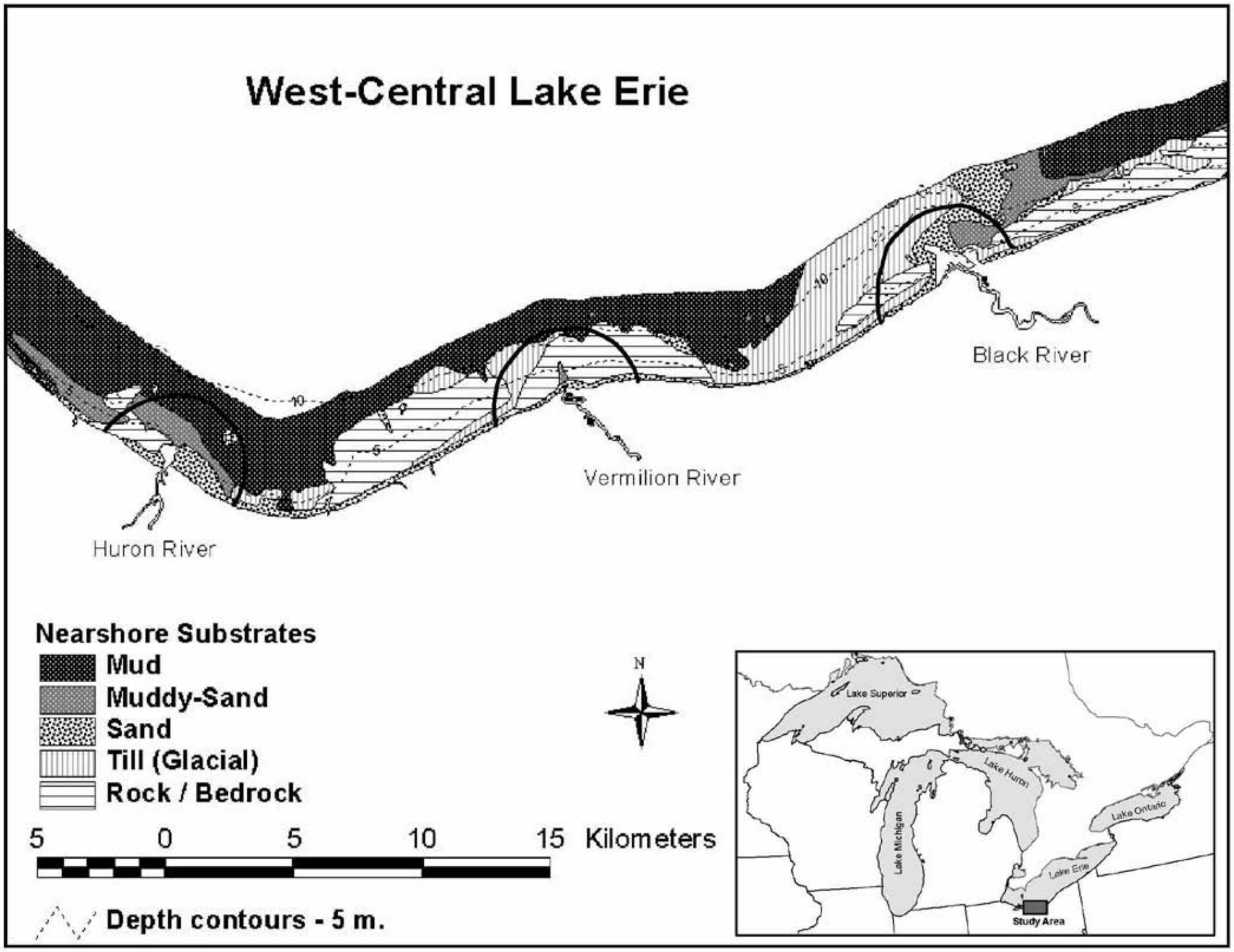

FIG. 1. Map of west-central Lake Erie study area. Bottom type as soft [mud ( ), muddy sand ( ), or sand ( ); or hard [till ( ) or rock ( )] is indicated by the background shading. Sampling areas were centered on each major river mouth (circles).

Field Collections

A series of grid cells (30 seconds longitude × 30 seconds latitude) was laid out within an arc centered on each river mouth and having a radius of 4 km. These sampling zones encompass nearshore areas adjacent to approximately 32% of the basin coastline. Ichthyoplankton samples were collected biweekly, in randomly selected map grid cells from April–September in 2000, 2001, and 2002. The Ohio Division of Geological Survey (ODGS) and the U.S. Geological Survey conducted side-scan sonar surveys to describe substrate type of the entire coastal area of the Ohio waters of Lake Erie within ~ 3.4 km of the shore (Fuller 1998). Hence, each cell grid could be described as containing soft or hard substrate or a combination of both (Fig. 1). On each sampling date, a total of six randomly selected grid cells, stratified by substrate (three soft substrate and three hard substrate), were sampled near each river mouth. Huron River and Vermilion River sites were sampled routinely each year. The Black River site was sampled during every other sampling trip in 2001 and routinely with the other two sites in 2002. Bottom depths ranged from 2–13 m.

Spatial and temporal sampling was designed to characterize and compare fish and invertebrate assemblages associated with a variety of aquatic habitats, including contrasts between soft- or hard-bottom areas in each major river-dominated zone. This study was designed for a broad assessment of nearshore communities and habitat associations. Although this paper focuses only on ichthyoplankon, the broad design allowed us to test for benthic habitat correlations, as well as relations to pelagic conditions. Other aspects of this study, which include zooplankton, benthic, and juvenile fish assemblages, will be discussed in subsequent publications.

Ichthyoplankton were collected at each site with a neuston net (500-µm mesh, 2 × 1 m frame) equipped with a Rigosha 5571-B flowmeter, and towed for 5 min at the water surface. Flow meter measurements were then used to standardize ichthyoplankton catches to abundance per 1,000 m^3 filtered. Samples were preserved in 80% ethanol in the field, after excess water was removed. Individuals were sorted under a dissecting microscope, identified to species (using Auer 1982), enumerated, and measured to the nearest mm in the laboratory.

A suite of abiotic variables (including benthic substratum characterized as hard or soft) was measured along with several biological components to characterize the habitat. At each sampling station we recorded GPS coordinates (Garmin GPS 125 Sounder with GBR 21 differential beacon receiver) and water depth to the nearest m (sounding line of Ray Jefferson Model 202, depth computer). Water samples were taken within 1 m of the water surface and 1 m above the bottom with a Kemmerer bottle. In situ water quality was assessed by measuring temperature (°C) and dissolved oxygen concentrations (mg/L; Yellow Springs Instruments Model 54 Oxygen Meter), clarity (m; Secchi disk), and conductivity (µS/cm^2; Oakton TDSTestr3) at each site. Water samples were taken for chlorophyll *a* (µg/L) and phosphorus (mg/L) seasonally in 2001 and analyzed by standard colorometric methods (USEPA 1982). In 2002, an Aquaflor 8000 flourometer was used to obtain chlorophyll *a* at each sampling station. Substratum was surveyed with side-scan sonar (ODGS) and areal extent of hard or soft bottom was determined within each study area (Fuller 1998).

Data Analysis

Exploratory data analysis included examination of sample species assemblages by Bootstrapping Cluster Analysis (BCA) (McKenna 2003a) and Canonical Correspondence Analysis (CCA; ter Braak 1986) to identify distinct assemblages and ecological patterns. Sample species assemblages consisted of the unit abundance (number /1,000 m^3) of each species collected during a given sampling event. The BCA used the Bray-Curtis similarity measure, the UPGMA linkage method (Boesch 1977), and 100 bootstrap samples to test each linkage (McKenna 2003a, b); significance of each linkage and all other statistical tests was determined at the $\alpha = 0.05$ level. CCA provides a direct gradient analysis, revealing gradients in both biotic and abiotic variables and identifying significant species-habitat relationships (ter Braak 1986). This analysis was performed with the CANOCO program (ter Braak 1987), using a Monte Carlo permutation procedure (499 permutations) to identify abiotic variables that significantly affected the ichthyoplankton assemblages. Only variables of significant influence that contributed > 10% to explained variation were retained in the analysis. Overlay of distinct cluster groups on the ordination triplot (samples, species optima, and abiotic vectors [gradients]) was used to help characterize optimal environmental conditions and relationships among different assemblages (McKenna 2003b). Species richness and the Shannon-Weaver index (Shannon and Weaver 1949) were used as measures of biodiversity.

A χ^2 test for goodness of fit was used to test the correspondence of ichthyoplankton assemblage occurrence and bottom substratum. Kolmogorov-Smirnov tests were used to determine the significance of differences in spatial distributions of major ichthyoplankton assemblages. Long-shore distributional differences examined frequency of occurrence of major cluster types within 0.05° longitude (~4.2 km) classes. Onshore-offshore distributional differences examined frequency of occurrence of major cluster types within 0.01° latitude (~1.1 km) classes. One-way Analysis of Variance (ANOVA) was used to test significance of differences in optimum values (means within clusters) of abiotic variables among distinct species assemblages (cluster groups). Tukey's multiple comparison test was applied to identify significantly different groups, when ANOVA detected overall significant differences among groups (Zar 1999). Simple linear regression was used to test species-specific responses of fish abundances to Secchi depth.

RESULTS

Ichthyoplankton Community Structure

Larval fish were captured from April through September; total abundance peaked in June or July

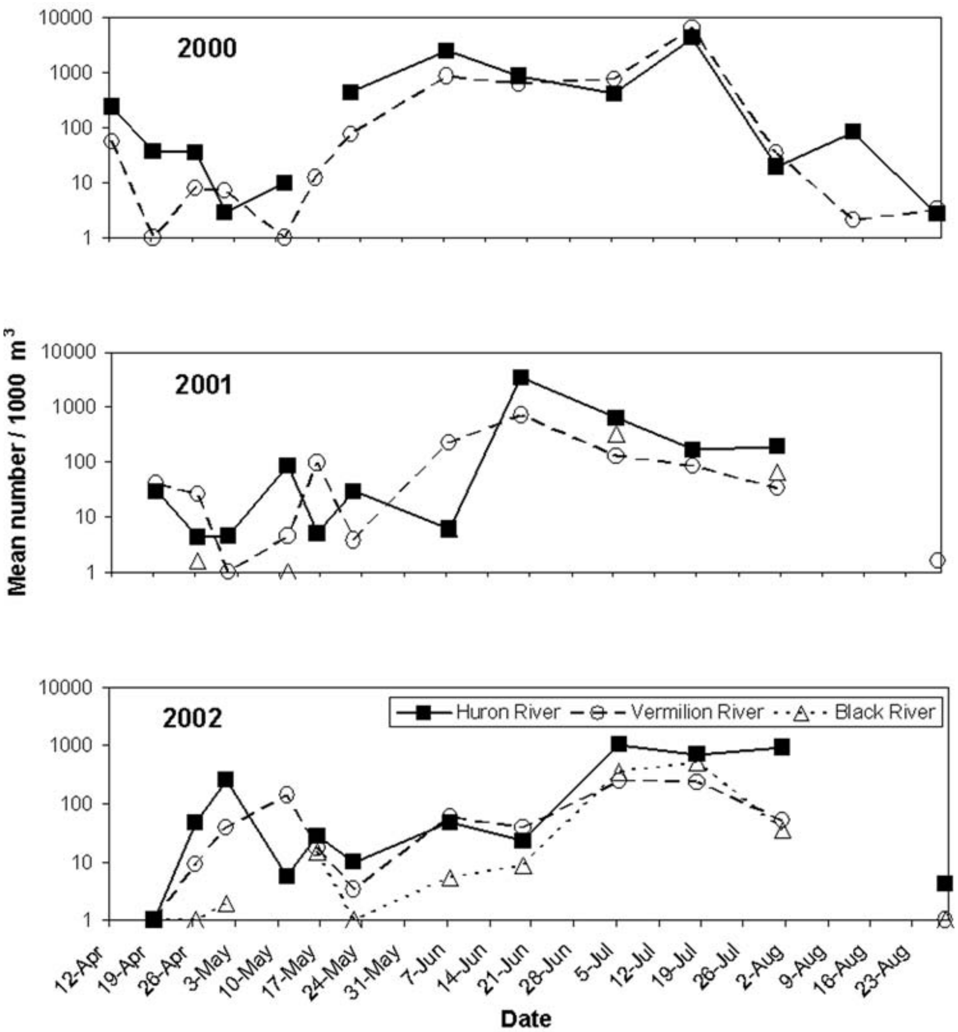

***FIG. 2.** Larval fish abundance (mean number/1,000 m^3) during the Lake Erie Nearshore Study 2000–2002.*

each year (Fig. 2). Seasonal patterns of fish density were similar among sites, but densities were usually higher at the Huron River. Generally, spring fish abundance at the Vermilion River lagged 1 to 2 weeks behind that at the Huron River. Fish densities varied greatly at some sites among years, but were generally highest in 2000 and lowest in 2002. Fish densities were not recorded at the Black River site in 2000 and only intermittently in 2001; however, fish abundance in 2001 at that site was similar to that observed in 2002.

Twenty-six fish species were collected during the 3 years of study (Table 1). Fourteen species were found in each year of the study and several species were consistently prominent. Lake whitefish were the primary species collected in April each year (Fig. 3). Percids (yellow perch, *Perca flavescens*; walleye; and logperch, *Percina caprodes*, primarily) were most abundant in May or June of 2000 and 2001. A large number of cyprinids (dominated by emerald shiners, *Notropis atherinoides*) were abundant each summer. Centrarchids (*Lepomis*, *Micropterus*, and *Pomoxis* spp.) and temperate basses (*Morone* spp., white perch and white bass) were also well represented in summer. Rainbow smelt, *Osmerus mordax*, were most numerous in 2000, while clupeids (alewife, *Alosa pseudoharengus*, and gizzard shad, *Dorosoma cepedianum*) were numerous in 2000 and 2002.

Initial cluster analysis results identified 14 distinct ichthyoplankton species assemblages. However, emerald shiners, a ubiquitous and abundant

TABLE 1. Fish species recorded in neuston tows during 2000–2002 in west-central Lake Erie. The locations at which each ichthyoplankton species was present are indicated by B (Black River), H (Huron River), or V (Vermilion River).

Species	Common name	Group	Years Collected	Locations Present
Coregonus clupeaformis	Lake Whitefish	Whitefish	All	B, H, V
Osmerus mordax	Rainbow smelt	Smelt	All	B, H, V
Alosa pseudoharengus	Alewife	Clupeid	2002	B, H, V
Dorosoma cepedianum	Gizzard shad	Clupeid	All	B, H, V
Carassius auratus	Goldfish	Cyprinid	2000, 2002	H, V
Cyprinus carpio	Carp	Cyprinid	2000	V
Luxilus cornutus	Common shiner	Cyprinid	All	B, H, V
Notemigonus crysoleucas	Golden shiner	Cyprinid	2000	H
Notropis atherinoides	Emerald shiner	Cyprinid	All	B, H, V
Notropis hudsonius	Spottail shiner	Cyprinid	All	B, H
Morone americana	White perch	Morone	All	B, H, V
Morone chrysops	White bass	Morone	All	H, V
Etheostoma nigrum	Johnny darter	Percid	2001	V
Percina caprodes	Logperch	Percid	All	B, H, V
Perca flavescens	Yellow perch	Percid	All	B, H, V
Sander vitreum	Walleye	Percid	All	B, H, V
Lepomis spp.	Sunfish	Centrarchid	All	B, H, V
Lepomis macrochirus	Bluegill	Centrarchid	2000, 2001	H, V
Micropterus salmoides	Largemouth bass	Centrarchid	2000	H
Pomoxis spp.	Crappie	Centrarchid	All	B, H, V
Pomoxis nigromaculatus	Black crappie	Centrarchid	2000	H
Aplodinotus grunniens	Freshwater drum	Misc.	All	B, H, V
Carpiodes cyprinus	Quillback carpsucker	Misc.	2001	H
Erimyzon sucetta	Lake chubsucker	Misc.	2000, 2001	H, V
Ictiobus spp.	Buffalo	Misc.	2000	H
Neogobius melanostomus	Round goby	Misc.	2001	H, V

species, obscured the pattern of other ichthyoplankton assemblage components. Species assemblages were more distinct and the seasonal pattern clearer when emerald shiners were treated as a co-variable, by removing them from the cluster analysis and replacing them as a component of each distinct cluster posteriori. Controlling for the influence of emerald shiner, BCA revealed nine distinct species assemblages labeled A through I (Fig. 4). However, > 95% of sample assemblages were members of only three clusters (A, C, and E; Table 2). These clusters represent three common assemblages corresponding to an early spring lake whitefish-dominated assemblage (A), a mid-spring percid-dominated assemblage (E), and a late-spring to summer emerald shiner-dominated assemblage (C). Minor assemblages F and G (dominated by darters and walleye) joined the mid-spring cluster (E) and added to the general "percid" character of prevalent assemblages at that time (Fig. 4). The other minor assemblages (mostly dominated by emerald shiner) were rare and generally occurred in conjunction with the summer assemblage (C).

Although some overlap of the hyperspaces (CCA) occupied by the three major assemblages (clusters) occurred in the ordination space, assemblage boundaries were clear (Fig. 5). Assemblage changes were evident with increasing temperature and assemblages moved inshore as the seasons progressed. Most species optima (ordination location of maximum species abundance) were located within the bounds (ordination) of the summer shiner assemblage (C). However, johnny darter, *Etheostoma nigrum*, yellow perch, walleye, and logperch optima were associated with the mid-spring percid (E) assemblage and the lake whitefish (A) optimum was unique to the early spring assemblage. Monte Carlo tests of ordination results showed that month was the strongest factor affecting species assemblage structure and was closely

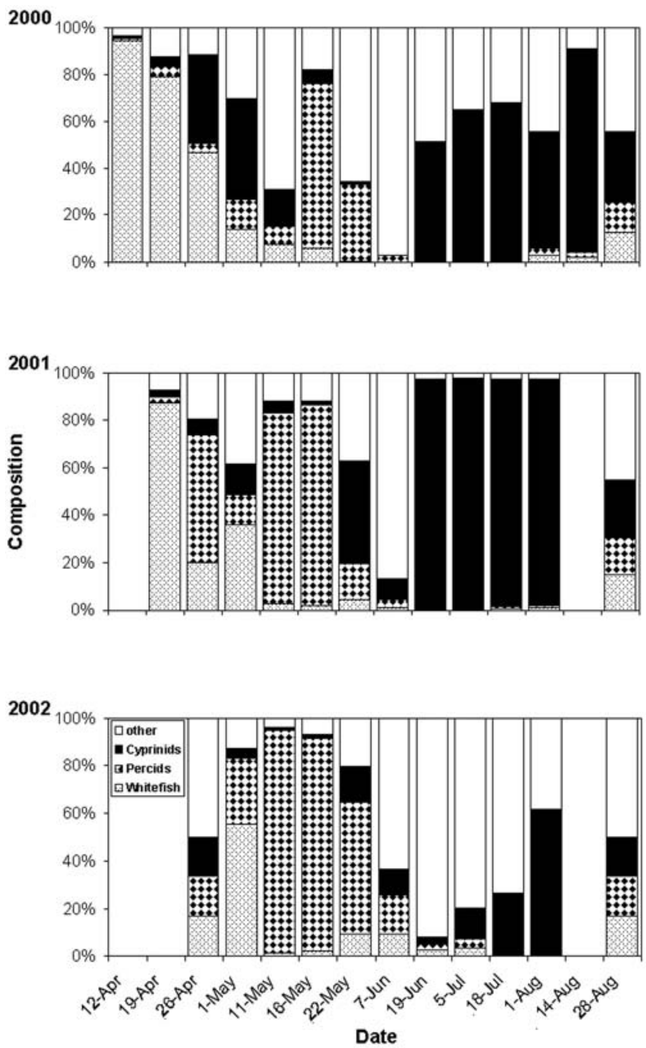

FIG. 3. Taxonomic composition as percent of total abundance for each group of larval fish caught during Lake Erie Nearshore Study during 2000, 2001, and 2002. The "other" group consisted primarily of clupeids and smelt, but also may include the other species listed in Table 1 as Centrarchid or Misc.

associated with surface water temperature and decreasing depth (Fig. 5). The CCA also identified important associations (environmental gradient vectors) of assemblages with Secchi depth and substrate, and to a lesser extent surface conductivity. However, we found no significant association between occurrence of the major species assemblages and substrate type (Whitefish-$\chi^2_{0.05(2),43} = 0.00$, Percid-$\chi^2_{0.05(2),66} = 1.23$, Shiner-$\chi^2_{0.05(2),178} = 0.68$).

Superclusters were formed by joining similar assemblages to aid in statistical tests of the broadest species assemblage patterns. The three superclusters consisted of the whitefish assemblage (cluster A only), the percid assemblage (Clusters E, F, and G), and all other clusters (the shiner assemblage); minor clusters B, D, H, and I were grouped with the shiner assemblage, because of their dominant cyprinid composition or summer occurrence (or both). Hereafter, discussion will focus on these three superclusters (which will be referred to as major assemblages), except where noted otherwise.

Relative abundances and biodiversity were clearly different among the major assemblages (Table 2). Overall ichthyoplankton abundance of the shiner assemblage was significantly greater than that of either the whitefish or percid assemblages ($F_{0.05(1),2,285} = 6.7$, $P < 0.001$). Species richness significantly increased as assemblage dominance shifted over time ($F_{0.05(1),2,285} = 43.0$, $P < 0.001$) and diversity of the whitefish assemblage was significantly less than that of the two subsequent assemblages ($F_{0.05(1),2,285} = 25.8$, $P < 0.001$).

Environmental Conditions and Larval-habitat Relationships

The seasonal river discharge patterns were nearly identical among the three rivers in the sampling area, with nearly linear decreases from high April values (13–18 m^3/s) to low July and August values (< 1–3 m^3/s). Water temperature did not differ noticeably among the three study years and did not account for the differences in overall abundances of the assemblages (Fig. 6). Dissolved oxygen (D.O.) varied somewhat with year, but correlations with changing species abundance were not apparent (Fig. 6). Water temperatures increased ($F_{0.05(1),2,232} = 411.38$, $P < 0.001$) and D.O. ($F_{0.05(1),2,232} = 74.55$, $P < 0.001$) and conductivity ($F_{0.05(1),2,232} = 41.92$, $P < 0.001$) decreased as spring progressed to summer. Water clarity (Secchi depth) also increased ($F_{0.05(1),2,232} = 14.50$, $P < 0.001$) with season (Fig. 6).

ANOVA results indicated that month and eight habitat variables differed significantly among ichthyoplankton assemblages (Table 3), corroborating most multivariate patterns. The summer shiner assemblage occurred significantly later than did the whitefish or percid assemblage. The whitefish assemblage occurred earlier than any other assemblage (except minor assemblage F, walleye only). Secchi depth increased after the peak of the percid assemblage. Of the dominant species in each as-

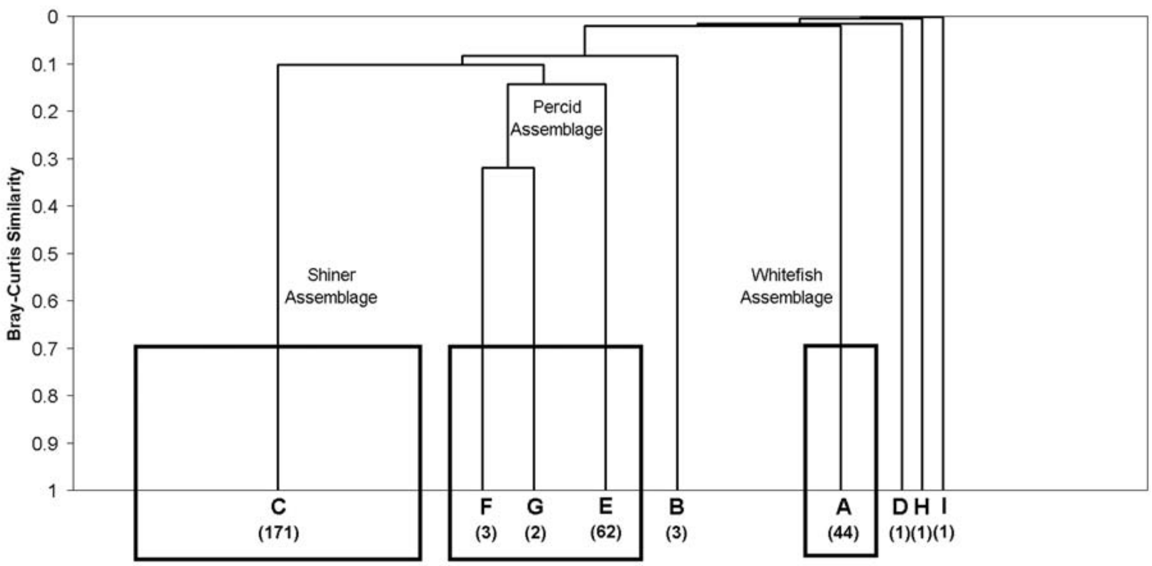

FIG. 4. Dendrogram of bootstrapping cluster analysis results. Values along the ordinate indicate Bray-Curtis Similarity. Letters along the abscissa identify significantly distinct clusters of sample assemblages; lettering follows order of cluster formation. Only linkages between significantly different groups are shown; the number of sample assemblages comprising each distinct cluster is given below each Letter. Large boxes enclose samples comprising superclusters; minor clusters B, D, H, and I were grouped with cluster C to form the shiner supercluster, because of their dominant cyprinid composition or summer occurrence (or both).

semblage, only lake whitefish displayed a significant (negative) response (log-linear) to water clarity (Secchi depth, $F_{0.05(1),1,367} = 42.1$, $P < 0.001$, $R^2 = 0.10$). Surface and bottom water temperatures increased significantly as the peak of each major assemblage occurred (Table 3). Surface conductivity was significantly greater when the early (whitefish) and mid-spring (percid) assemblages were dominant, than later in the year. Surface and bottom D.O. remained high while the early and mid-spring assemblages (whitefish and percid) were dominant, but decreased significantly during the time of the summer shiner assemblage.

We found significant differences among spatial distributions of the major ichthyoplankton assemblages. Latitudinal distributions of the whitefish and percid assemblages did not differ significantly from that of the shiner assemblage, but the whitefish assemblage was more offshore (higher latitude) than the percid assemblage ($D = 0.34$, $df = 14$, $P = 0.05$). Longitudinal distributions of the whitefish and percid assemblages did not differ significantly from that of the shiner assemblage, but tended to be found in more westerly waters ($D = 0.431$, $df = 8$, $P < 0.06$). The whitefish assemblage was distributed more easterly than the percid assemblage ($D = 0.619$, $df = 8$, $P < 0.001$).

DISCUSSION

Ichthyoplankton Community Structure

West-central Lake Erie is known to be a valuable production area for larval and juvenile stages of nearshore-dependent sport, commercial, and forage fishes (Ludsin and Stein 2001). Yellow perch was a dominant component of one major ichthyoplankton assemblage and is an important sport and commercial species in central Lake Erie. Commercial and recreational catches of yellow perch in central Lake Erie accounted for 68% and 32% of the statewide Ohio landings (ODNR 2007). Forage fishes, especially dominant members of the shiner assemblage (e.g., emerald shiners and gizzard shad) are major prey items for valuable Lake Erie piscivores such as walleye, smallmouth bass, and yellow perch (Knight *et al.* 1984). However, the Great Lakes are more like oceans than inland lakes (Meadows *et al.* 2005) and difficulty of working in the nearshore zone means that relatively few studies have been conducted there (Uzarski *et al.* 2005). Previous

TABLE 2. Distinct Ichthyoplankton assemblages in nearshore habitats of west-central Lake Erie. Superclusters are a combination of similar, but distinct assemblages. Mean values are averages of all sample assemblages within each supercluster.

Supercluster	Cluster	Cluster	Mean Fish Abundance	Species Richness	Species Diversity	Species Composition	Mean Species Abundance
Whitefish	A	44	36	4	0.06	Lake Whitefish	35.5
						other	0.3
Percid	E	62	65	14	1.24	Logperch	38.8
						Yellow Perch	14.5
						Walleye	5.2
						Lake Whitefish	3.2
						White Perch	1.1
						other	2.4
	F	3	44	1	0.00	Walleye	43.7
	G	2	3	2	0.69	Walleye	1.4
						Johnny Darter	1.2
	Mean	67	63	2.22	0.48		
Shiner	B	3	57	2	0.19	Emerald Shiner	53.9
						White Perch	2.7
	C	171	904	24	1.19	Emerald Shiner	490.5
						Gizzard Shad	272.8
						Rainbow Smelt	90.1
						Alewife	19.6
						other	31.2
	D	3	242	3	0.06	Emerald Shiner	239.1
						other	2.6
	H	1	3	1	0.00	Bluegill	2.6
	I	1	22	2	0.45	Emerald Shiner	18.3
						Round Goby	3.7
	Mean	179	787	3.04	0.49		

work provides only a few scattered accounts of the presence of young fish in the west-central basin of Lake Erie (e.g., Goodyear *et al.* 1982) and some indications of habitat associations (Goforth and Carman 2005). This study provides a more systematic investigation of larval fish communities in this region of the lake. The open-water nearshore area in our study consistently supported a dynamic and diverse larval fish assemblage, with at least 26 species contributing to the ichthyoplankton. Similar ichthyoplankton species richness has been observed in western Lake Erie (Mizera *et al.* 1981) and this value is higher than that reported for other Great Lakes areas (Klumb *et al.* 2003; Oyadomari and Auer 2004; D. Crabtree, The Nature Conservancy, June 2008, pers. comm.). We identified significant ichthyoplankton community structure associated with both taxonomic groups and temporal changes. That structure was characterized by three main assemblages that overlapped somewhat in time, but followed each other sequentially through the seasons—whitefish, percid, and then shiner. The same general timing of peak larval abundances was also observed by Mizera *et al.* (1981) in western Lake Erie. These common assemblages provide the best information about the broad general patterns of fish assemblage structure and habitat associations that are likely to most strongly influence the west-central Lake Erie ecosystem.

Lake whitefish comprised a monospecific unique assemblage that occurred in early spring, when temperatures were coldest and clarity was lowest. This historically important native species is a cold water coregonid and benthic feeder (Trautman 1981), well known for wide, environmentally-driven population fluctuations (Freeburg *et al.* 1990). These fish have adapted to spawn in late fall-winter (often under ice), broadcasting their eggs over rocky substrate in nearshore areas. Their larvae are some of the first to hatch and start feeding each spring.

In mid-spring, the percid assemblage became prominent, as temperature increased. This group in-

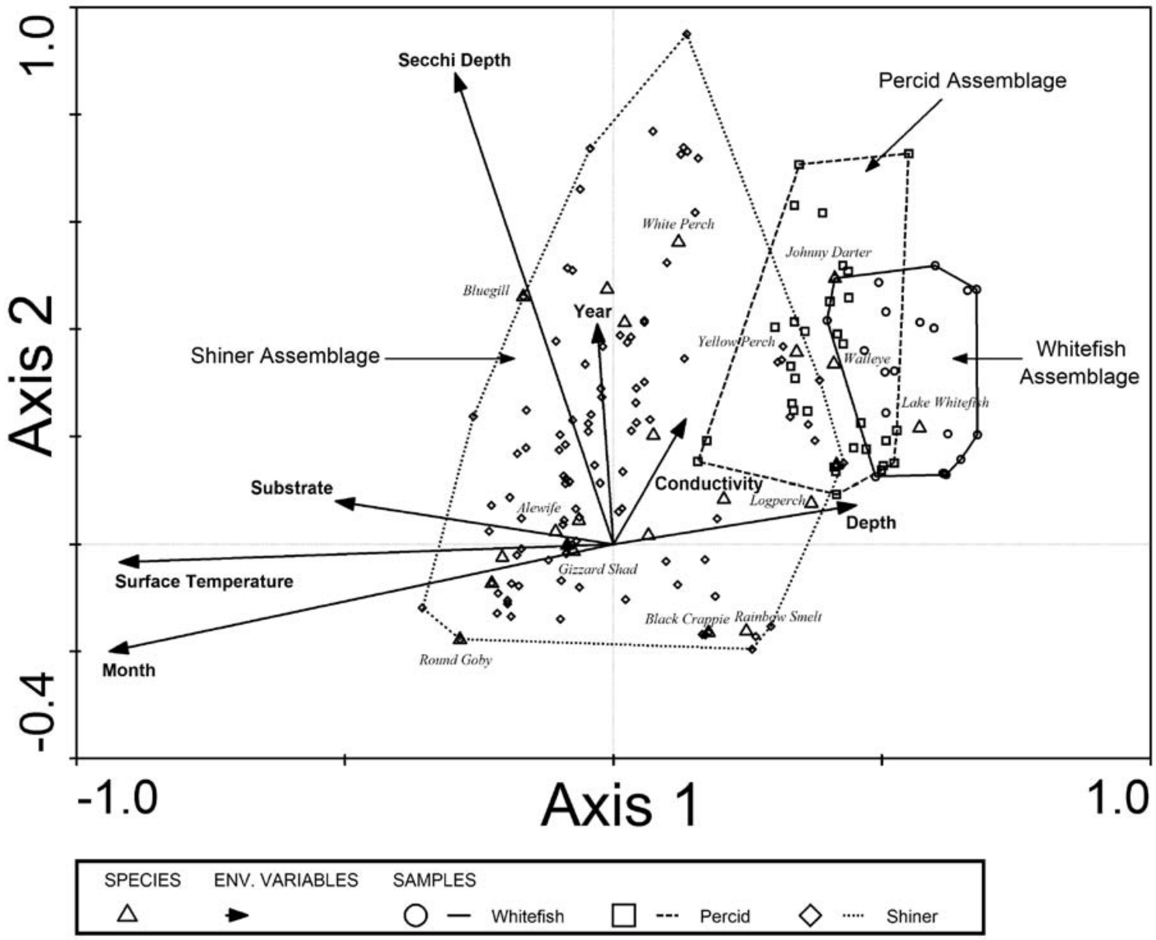

FIG. 5. Canonical correspondence analysis triplot of species optima, sample locations, and significant temporal and environmental gradients within the first two axes of the ordination space. Species optima are indicated by open triangles (Δ); only species mentioned in the text are labeled in the figure. Sample assemblages of each superclusters are enclosed within polygons. Whitefish sample assemblages are indicated by circles, percid assemblages by squares, and shiner assemblages by diamonds. Each environmental gradient increases in the direction the vector points and strength of the influence on the fish assemblage is indicated by the length of each vector.

cluded yellow perch, logperch, johnny darter, and walleye. The observed overlap in time and space of these species' optima (CCA) indicates similar resource requirements of the percids at this larval stage. Ontogenetic and habitat shifts at other stages likely minimize competition as fish grow and food availability becomes limiting (Craig 2000). These Percidae species deposit eggs on a variety of substrate and invest different amounts of parental protection in the young, from none in walleye, to territorial guarding by johnny darter. As adults, darters are benthic insectivores. Walleye and yellow perch are demersal and raptorial; walleye begin eating fish at a young age. Juveniles of these species are often associated with submerged aquatic vegetation and other benthic structures (Trautman 1981).

The shiner assemblage was most diverse, abundant, and widespread, but dominated by emerald shiner, gizzard shad, rainbow smelt, and alewife. These species are generally r-selected, broadcast spawners that deposit many eggs in nearshore waters or tributaries. Parental care of young varies widely within this assemblage, but the dominant species do not invest in protection of larvae, which drift with the plankton. As adults, they are typically pelagic planktivores. This assemblage includes sev-

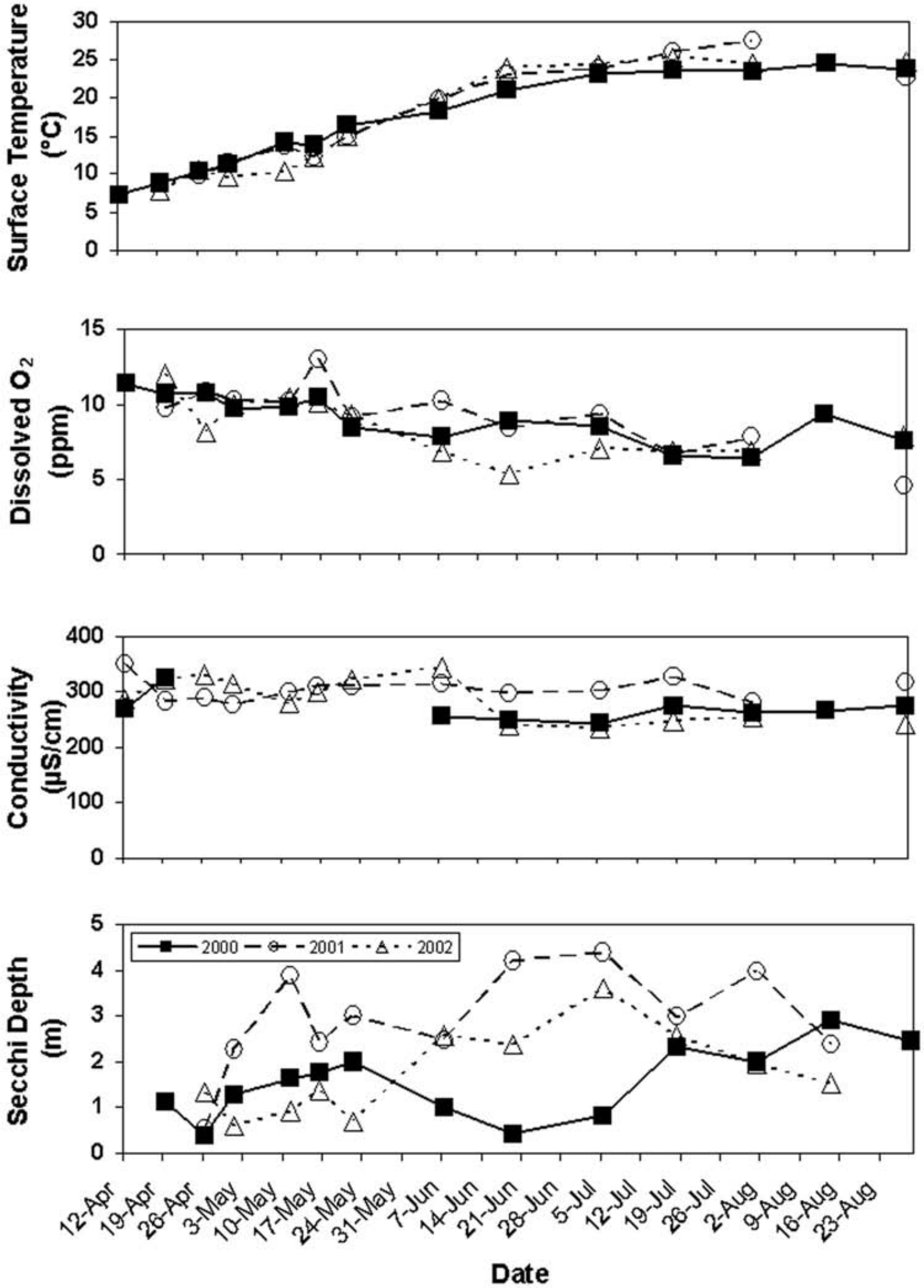

FIG. 6. Mean surface temperature (°C), mean surface dissolved oxygen (ppm), mean surface conductivity (µS/cm), and Secchi depth (m) for all sites during the Lake Erie Nearshore Study 2000–2002. Values for 2000 are represented by squares (■), those for 2001 by triangles (△), and those for 2002 by circles (○).

TABLE 3. Mean habitat variable values by major ichthyoplankton assemblage (supercluster). Results of one-way ANOVA testing ($\alpha = 0.05$) for differences among supercluster means are provided by F and P, where model d.f. = 2 and error d.f. = 232. Multiple comparison test results indicate significant differences among specific assemblages. The depth associated with the shiner supercluster was not significantly different from that of the whitefish or percid clusters.

	Mean by Super Cluster					
Habitat Variable	Whitefish	Percid	Shiner	F	P	Multiple Comparisons
Conductivity (surface)	323.6	313.0	272.0	41.92	< 0.0001	Shiner < Whitefish = Percid
Depth	8.8	6.50	7.52	4.60	0.0109	Whitefish > Percid
D.O. (bottom)	9.77	10.21	6.58	127.58	< 0.0001	Shiner < Whitefish = Percid
D.O. (surface)	9.78	10.38	7.62	74.55	< 0.0001	Shiner < Whitefish = Percid
Month	4.04	4.92	6.66	223.73	< 0.0001	Shiner > Percid > Whitefish.
Secchi depth	1.05	1.46	2.31	14.50	< 0.0001	Shiner < Whitefish = Percid
Substrate	1.56	1.58	1.53	0.28	0.7565	no significance
Temperature (bottom)	9.05	12.19	20.68	228.77	< 0.0001	Shiner > Percid > Whitefish
Temperature (surface)	9.92	12.60	22.40	411.38	< 0.0001	Shiner > Percid > Whitefish

eral non-native species (e.g., rainbow smelt and alewife). Members of this assemblage were most numerous in late summer when water temperatures were high and were found in shallow waters throughout west-central Lake Erie.

Environmental Conditions

Environmental variables generally followed the normal seasonal progression of increasing water temperature and clarity. Water temperature was one of the strongest correlates with ichthyoplankton assemblage structure and represented a general index of seasonal change. Temperature affects physiological rates, including respiratory and feeding rates, and possibly growth efficiency (Klieber 1961). There was little difference in water temperature trends during this study, but in longer-term studies (> 30 years), fish growth has been positively correlated with increasing temperature (Hall and Rudstam 1999). Water clarity also was a strong correlate with assemblage structure and lake whitefish abundance was negatively correlated with Secchi depth. Turbid conditions may be an indication of suspended sediment or abundant food for the more pelagic groups. Ichthyoplankton densities (e.g., walleye) have also been correlated with decreasing water clarity in other Great Lakes areas (Roseman *et al.* 2005).

The absence of a significant relationship between larvae and any particular bottom location is not surprising given that, by definition, planktonic larvae cannot effectively swim against a current (though they may adjust their depth to take advantage of different food environments and flow regimes). Thus, they are at the whim of lake circulation. However, suitable spawning locations (relative to that circulation) are critical to larval survival and for fish populations to persist, the larvae must successfully reach the nursery areas. Our results indicate that even as coastal conditions change and sediment input to the lake changes in quality and volume (Rukavina and Zeman 1987), the nearshore zone remains a viable and important habitat for Lake Erie fishes, many of which spawn on rocky substrate. Future diet and benthic invertebrate analyses associated with this research should provide additional insights into the value of these habitats for older fish.

Ecological Implications

The annual cycle of primary production is well known in temperate aquatic systems (Wetzel 1975, Haffner *et al.* 1984). The location of spawning grounds and timing of spawning and hatching for the major ichthyoplankton groups is likely to have adaptive significance for this fish community because of coordination with this annual cycle (Lasker 1975). The large, high-quality lake whitefish eggs hatch at a time when there is abundant larval food available from the spring phytoplankton bloom and associated zooplankton increase. Competition for this resource is weak, because few other species hatch at that time. Increased zooplankton production provides abundant food for the emerging Percid larvae at the tail end of the planktonic bloom (Wetzel 1975, Patalas 1972, Haffner *et al.* 1984, Gardner *et al.* 1989). Benthic invertebrate production may be stimulated a short time later as much of the spring bloom production is transferred to the bottom (Dermott and Corning 1988). The warm late spring-summer season provides a sustained period of pelagic production and a diverse assemblage of ichthyoplankton species is supported. The older, more mobile juveniles of species hatched earlier in the year may also take advantage of the summer productivity.

It is unclear why the Whitefish assemblage was distributed more easterly than the Percid assemblage. Both lake whitefish and walleye (dominant species of each assemblage) have major spawning grounds in Lake Erie's west-central basin (Goodyear *et al.* 1982). Perhaps downlake circulation was more intense in the early spring when the whitefish assemblage was most prominent. We are not aware of local circulation studies in the area, but the general downlake transport and complexity of nearshore circulation is known (Saylor and Miller 1987). Wind and currents are also important in concentrating larvae (e.g., walleye) in nearshore areas of western Lake Erie, where ichthyoplankton prey and warm waters are most prevalent (Roseman *et al.* 2005). This spatial difference may also be evidence of river-specific effects. The three major study rivers have flows (18 m^3/s in spring to 1–2 m^3/s in summer) within the range that can affect lake conditions (Bedford 1992). Ludsin and Stein (2001) found that enhanced river discharge during April, May, and summer from central Lake Erie streams was positively correlated with improved fish production, especially yellow perch. Although phosphorus loading does not appear to be directly related to fish year class formation (Ludsin and Stein 2001), increased river flow is often related to enhanced system productivity through increased lower trophic level production (Makarewicz 1993, Livinston 1997). This often corresponds with increased fish biomass (Nakashima and Leggett 1975, Ney 1996).

The ichthyoplankton community structure elucidated by this work highlights the relationships of valuable fisheries to habitat conditions and ecosystem processes. Understanding habitat changes and their effects on the early life history stages of fishes is critical to formulation of effective measures that ensure the sustainability of offshore fisheries and continued production of nearshore areas. This study identifies the distinct groups of ichthyoplankton in west-central Lake Erie and highlights their temporal succession and associated habitat conditions. We hope this information will help managers identify critical areas or processes in need of protection.

ACKNOWLEDGMENTS

Numerous individuals helped us in all aspects of this study. We would especially like to thank S. Mackey for his initial involvement and for providing us with substrate maps. M. Chriscinske and J. Hovis oversaw field operations and provided laboratory assistance. L. Ogilvie, M. Kostich, J.R.P. French, C. Muzinic, M. Stapanian, S. Tinnirello, J. Amberg, and M. Haack also provided laboratory and field assistance. P. Hudson provided laboratory assistance in invertebrate identification. M. Chriscinske and L. Zhang oversaw our data management. Other staff, students, and volunteers from the Great Lakes Science Center in Ann Arbor, Michigan and the Lake Erie Biological Station in Sandusky, OH provided welcome help in obtaining or processing samples. This article is contribution #1499 of the USGS Great Lakes Science Center. This paper is Contribution No. 2965 of the Virginia Institute of Marine Science, The College of William and Mary.

REFERENCES

Auer, N.A. 1982. *Identification of larval fishes of the Great Lakes basin with emphasis on the Lake Michigan drainage.* Great Lakes Fish. Comm. Special Publication 82-3, Ann Arbor, MI.

Bailey, K.M., Brown, E.S., and Duffy-Anderson, J.T. 2003. Aspects of distribution, transport and recruitment of Alaska plaice (*Pleuronectes quadrituberculatus*) in the Gulf of Alaska and eastern Bering Sea: comparison of marginal and central populations. *J. Sea Res.* 50:87–95.

Bedford, K.W. 1992. The physical effects of the Great Lakes on tributaries and wetlands. *J. Great Lakes Res.* 18:571–589.

Boesch, D.F. 1977. *Application of numerical classification in ecological investigations of water pollution.* Special Scientific Report No 77, Virginia Institute of Marine Science. EPA-006/3-77-033, March 1977.

Craig, J.F. 2000. *Percid Fishes: Systematics, Ecology, and Exploitation*. Fish and Aquatic Resources Series 3, Oxford: Blackwell Science.

Dermott, R., and Corning, K. 1988. Seasonal ingestion rates of *Pontoporeia hoyi* (Amphipoda) in Lake Ontario. *Can. J. Fish. Aquat. Sci.* 45:1886–1895.

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

Fuller, J. 1998. *Distribution of surficial sediments in Ohio's nearshore (Lake Erie) as interpreted from sidescan sonar and 35 kHz subbottom data*. Report of the Ohio Geological Survey Division.

Gardner, W.S., Eadie, B.J., Chandler, J.F., Parrish, C.C., and Malczyk, J.M. 1989. Mass Flux and "Nutritional Composition" of settling Epilimnetic Particles in Lake Michigan. *Can. J. Fish. Aquat. Sci.* 46:1118–1124.

Goforth, R.R., and Carman, S.M. 2005. Nearshore community characteristics related to shoreline properties in the Great Lakes. *J. Great Lakes Res.* 31 (Suppl. 1):113–128.

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

Grioche, A., Koubbi, P., and Sautour, B. 1997. Ontogenic migration of *Pleuronectes flesus* larvae in the eastern English Channel. *J. Fish. Biol.* 51:385–396.

Haffner, G.D., Griffith, M., and Hebert, P.D.N. 1984. Phytoplankton community structure and distribution in the nearshore zone of Lake Ontario. *Hydrobio*. 114:51–66.

Hall, S.R., and Rudstam, L.G. 1999. Habitat use and recruitment: a comparison of long-term recruitment patterns among fish species in a shallow eutrophic lake, Oneida Lake, NY, USA. *Hydrobio*. 408/409:101–113.

Hjort, J. 1926. Fluctuations in the year classes of important food fishes. *Int. Counc. Explor. Sea* 1:5–38.

Höök,T.O., McCormick, M.J., Rutherford, E.S., Mason, D.M., and Carter, G.S. 2006. Short-term Water Mass Movements in Lake Michigan: Implications for Larval Fish Transport. *J. Great Lakes Res*. 32:728–737.

Huret, M., Runge, J.A., Chen, C.S., Cowles, G., Xu, Q.C., and Pringle, J.M. 2007. Dispersal modeling of fish early life stages: sensitivity with application to Atlantic cod in the western Gulf of Maine. *Mar. Eco.-Prog. Ser.* 347:261–274.

Kleiber, M. 1961.*The fire of life*. New York:John Wiley & Sons, Inc.

Klumb, R.A., Rudstam, L.G., Mills, E.L., Schneider, C.P., and Sawyko, P.M. 2003. Importance of Lake Ontario empayments and nearshore habitats as nurseries of larval fishes with emphasis on alewife (*Alosa pseudoharengus*). *J. Great Lakes Res*. 29:181–198.

Knight, R.L., Margraf, F.J., and Carline, R.F. 1984. Piscivory by walleyes and yellow perch in western Lake Erie. *Trans. Am. Fish. Soc.* 113:677–693.

Lane, J.A., Portt, C.B., and Minns, C.K. 1996a. *Spawning habitat characteristics of Great Lakes fishes.* Canadian Manuscript Report of Fisheries and Aquatic Sciences 2368.

_____, Portt, C.B., and Minns, C.K. 1996b. *Nursery habitat characteristics of Great Lakes fishes.* Canadian Manuscript Report of Fisheries and Aquatic Sciences. 2338.

Lasker, R. 1975. Field criteria for survival of anchovy larvae: The relation between inshore chlorophyll maximum layers and successful first feeding. *Fish. Bull. (U.S.)* 73:435–462.

Letcher B.H., and Bengston, D.A. 1993. Effects of food density and temperature on feeding and growth of young inland silversides (*Menidia beryllina*). *J. Fish Biol.* 43:671–686.

Livinston, R.J. 1997. Trophic response of estuarine fishes to long-term changes in river runoff. *Bull. Mar. Sci.* 60:984–1004.

Ludsin, S.A., and Stein, R.A. 2001. *Species interactions among young-of-year fishes in lake Erie*. Federal Aid in Sport Fish Restoration, Project F-69-9, Final Performance Report, Columbus, Ohio. Ohio Department of Natural Resources-division of Wildlife.

Makarewicz, J.C. 1993. A lakewide comparison of zooplankton biomass and its species composition in Lake Erie, 1983–1987. *J. Great Lakes Res.* 19:275–290.

Matthews, W.J. 1998. *Patterns in freshwater fish ecology.* New York:Chapman & Hall.

Maynou, F,. Olivar, M.P., and Emelianov, M. 2006. Patchiness of eggs, larvae and juveniles of European hake *Merluccius merluccius* from the NW Mediterranean. Fish. Ocean. 15:390–341.

McKenna, J.E.Jr. 1993 Spatial structure and temporal continuity of the South Georgian Antarctic fish community. *Fish. Bull. (U.S.)* 91:475–490.

_____. 2003a. An enhanced cluster analysis program with bootstrap significance testing for ecological community analysis. *Environ. Model. Soft.* 18:205–220.

_____. 2003b. Biological Structure and Dynamics of Fish Assemblages in Tributaries of Eastern Lake Ontario. In *State of Lake Ontario (SOLO)—Past, Present and Future,* Ecovision World Monograph Series, Aquatic Ecosystem Health and Management Society. M. Munawar, ed., pp. 443–474. New Delhi: Goodword Books Pvt. Ltd.

Meadows, G.A., and 10 authors. 2005. Cumulative habitat impacts of nearshore engineering. *J. Great Lakes Res.* 31 (Suppl. 1):90–112.

Mizera, J.J, Cooper, C.L., and Herdendorf, C.E. 1981. Limnetic larval fish in the nearshore zone of the western basin of Lake Erie. *J. Great Lakes Res.* 7:62–64.

Nakashima, B.S., and Leggett, W.C. 1975. Yellow perch (*Perca flavescens*) biomasses responses to different levels of phytoplankton and benthic biomasses in Lake Memphremagog, Quebec-Vermont. *J.Fish. Res. Board Can.* 32:1785–1797.

Ney, J.J. 1996. Oligotrophication and its discontents: effects of reduced nutrient loading on reservoir fishes. *American Fisheries Symposium* 16:661–671.

ODNR (Ohio Department of Natural Resources). 2007. *Ohio's Lake Erie Fisheries*. Federal Aid in Sport Fish Restoration, Project F69-P, 2006 Annual Report, Columbus, Ohio. Ohio Department of Natural Resources.

Oyadomari, J.K., and Auer, N.A. 2004. Inshore-offshore distribution of larval fidhes in Lake Superior off the western coast of the Keweenaw Peninsula, Michigan. *J. Great Lakes Res.* 30 (Suppl. 1):369–384.

Patalas, K. 1972. Crustacean plankton and eutrophication of St. Lawrence Great Lakes. *J. Fish. Res. Bd. Can.* 26:1451–1462.

Roseman, E.F., Taylor, W.W., Hayes, D.B., Tyson, J.T., and Haas, R.C. 2005. Spatial patterns emphasize the importance of coastal zones as nursery areas for larval walleye in western Lake Erie. *J. Great Lakes Res.* 31 (Suppl. 1):28–44.

Rukavina, N.A., and Zeman, A.J. 1987. Erosion and sedimentation along a cohesive shoreline-the north-central shore of Lake Erie. *J. Great Lakes Res.* 13:202–217.

Saylor, J.H., and Miller, G.S. 1987. Studies of large-scale currents in Lake Erie, 1979–80. *J. Great Lakes Res.* 13:487–514.

Shannon, C.E., and Weaver, W. 1949. *The mathematical theory of communication*. Urbana, Illinois: University of Illinois Press.

Sinclare, M. 1988. *Marine populations, an essay on population regulation and speciation*. Seattle, WA:University of Washington Press.

Swenson, W.A. 1978. Influence of turbidity on fish abundance in western Lake Superior. *U.S. EPA Technical Report*, EPA-600/3-78-067.

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

______. 1987. *CANOCO—a FORTRAN program for canonical Community Ordination.* Available from: Microcomputer Power, Ithaca, NY, USA.

Trautman, M.B. 1981. *The fishes of Ohio: with illustrated keys*. Columbus, Ohio:Ohio State University Press.

U.S. Environmental Protection Agency [USEPA]. 1982. Methods for chemical analysis of water and wastes. *EPA 600/4-79-020.* US Government Print Office, Washington, DC.

U.S. Geological Survey [USGS]. 2008. Mean monthly river discharge data for the Black River at Elyria, OH (Station 04200500); the Huron River at Milan, OH (Station 04199000); and the Vermilion River near Vermilion, OH (Station 04199500). *U.S. Geological Survey, Water Resources Data.* Available from: http://waterdata.usgs.gov/oh/nwis/. Accessed on 2 June 2008.

Uzarski, D.G., Burton, T.M., Cooper, M.J., Ingram, J.W., and Timmermans, S.T.A. 2005. Fish habitat use within and across wetland classes in coastal wetlands of the five Great Lakes: development of a fish-based index of biotic integrity. *J. Great Lakes Res.* 31 (Suppl. 1):171–187.

Wetzel, R.G. 1975. *Limnology*. Philadelphia:W. B. Sanders Company.

Zar, J.H. 1999. *Biostatistical Analysis*. Fourth Edition. Upper Saddle River, New Jersey: Prentice Hall.

Submitted: 28 February 2008
Accepted: 28 July 2008
Editorial handling: Geoffrey Steinhart