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[Article]

The Interplay of Morphology, Habitat, Resource Use, and Genetic Relationships in Young Yellow Perch

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Abstract.—Morphological divergence resulting from differences in resource and habitat use is common in many fishes inhabiting postglacial ecosystems. We tested whether young yellow perch *Perca flavescens* differ in morphology, genetic composition, or diet in the nearshore (deep open-water) versus wetland and littoral habitats (shallow zones) of Lake Michigan and Saginaw Bay, Lake Huron. Twenty-one morphological measurements and six meristic counts were compared for 132 age-1 yellow perch, and the genetic variation at 12 nuclear DNA microsatellite loci was assessed for a subset of age-1 individuals across habitats and adults from nearshore zones. The results showed morphological and genetic divergence in yellow perch between Lake Michigan and Lake Huron and among those in nearshore versus wetland habitats in Lake Michigan (but not Lake Huron). Lake Huron yellow perch had deeper, longer bodies and larger dorsal fins than those from Lake Michigan. Those in nearshore habitats from both lakes had deeper, longer bodies and larger dorsal fins than did those occupying wetlands, which may reflect an adaptive response to predators and open-water cruising. In Lake Michigan, these differences may have a genetic basis that is not apparent in Lake Huron, suggesting a role for phenotypic plasticity. Piscivorous and zooplanktivorous individuals had similar morphologies, with larger body depths than insectivores, which may be useful for fast-starts during prey capture and provide protection from predation in open water. Comparisons of morphology, population structure, and diet thus reveal that the morphological diversity of yellow perch between habitats and lake basins reflects an interplay between phenotypic plasticity and genetic divergence.

Natural environments vary spatially and temporally (Levins 1968). Phenotypic plasticity is one mechanism by which populations respond to environmental heterogeneity (Bradshaw 1965; West-Eberhard 1989) that has been well studied in fishes (Robinson and Wilson 1994). Such plasticity may facilitate their occupation of new environments and enhance genetic diversity (Schlichting 2004), leading to adaptive radiations and speciation through ecological contexts in some taxa (Schluter 1993; Robinson and Parsons 2002; Langerhans et al. 2004).

Studies of northern postglacial-lake fishes have demonstrated morphological divergence between populations in pelagic and littoral environments, attributed to phenotypic plasticity (Day et al. 1994; Robinson and Wilson 1994; Svanbäck and Eklöv 2006). Typically, individuals inhabiting pelagic lake habitats have a more streamlined morphology that is better suited for a planktivorous feeding mode (Keast and Webb 1966; Webb 1984). In lake littoral zones, fish usually have a deeper body morphology with larger paired fins, which enhances three-dimensional (3-D) movement and feeding on benthos in structurally complex vegetated zones (Robinson and Wilson 1994; Robinson and Parsons 2002).

Most studies of fish phenotypic plasticity have focused on the adult stages of ontogeny; however, a growing body of literature is examining morphological

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TABLE 1.—Descriptions and characteristics of yellow perch habitats sampled.

Lake basin	Habitat type	Habitat structure	Habitat description
Lake Michigan	Nearshore	Open water, no emergent vegetation	Open water pelagic
	Wetland–littoral	Structurally complex vegetation, woody debris, or both	Drowned river mouth lake littoral zones and associated wetlands
Saginaw Bay, Lake Huron	Nearshore	Open water, no emergent vegetation	Open water pelagic
	Wetland–littoral	Structurally complex vegetation, woody debris, or both	Coastal fringing wetlands

diversification throughout ontogeny (Snorrason et al. 1994; Robinson et al. 1996; Svanbäck and Eklöv 2002). For fish to maximize growth throughout ontogeny, they generally switch habitats and food types (Werner and Gilliam 1984; Sebens 1987). Ontogenetic changes in ecological niche may reflect different selection pressures, with morphological adjustment to enhance exploitation of the new environment (e.g., Svanbäck and Eklöv 2002).

The natural geographic distribution of yellow perch *Perca flavescens* ranges from mid-Canada through the northeastern United States (Billington 1996); however, introductions have led to their presence in 46 U.S. states and western Canada (Crossman 1991; Rahel 2000). Yellow perch exploit a wide variety of environments throughout this expanse, including nearshore habitats of the Laurentian Great Lakes, small inland lakes, slow moving rivers, and wetlands (Becker 1983). Whether yellow perch exhibit adaptive morphological variation across Great Lakes habitats using a combination of genetic and morphological analyses has not previously been tested. Hubbs (1961) proposed that yellow perch in open water habitats morphologically differed from those occupying the wetlands along Douglas Lake, Michigan. Lippert et al. (2007) contended that yellow perch living in lakes in the Sudbury, Ontario, region exhibited phenotypic plasticity in response to predators. Yellow perch in lakes with predators had deeper body morphologies than those in habitats devoid of predators, with variation hypothesized to help thwart predation (gape-limitation) or to enhance foraging (Lippert et al. 2007).

Until recently, discerning the population genetic structure of Great Lakes yellow perch has been problematic due to low polymorphism in mitochondrial DNA (Billington 1996, 1998; Stepien and Faber 1998; Ford and Stepien 2004; Sepulveda-Villet et al. 2009) and allozyme loci (Leary and Booke 1982; Todd and Hatcher 1993). However, a study by Miller (2003) of nuclear microsatellite DNA loci provided new information on the population structure of Lake Michigan yellow perch, resolving separate spawning stocks in Green Bay and Lake Michigan proper, with those in Lake Michigan being homogenous. In this study we examine population genetic and morphological variation of yellow perch over a larger spatial scale, including both Lake Michigan and Saginaw Bay, Lake Huron, and test for differences in nearshore habitats versus adjacent wetlands and drowned river mouth systems.

Yellow perch occupying Great Lakes nearshore habitats and wetlands exhibit different early life history strategies. In the Great Lakes nearshore environments, adult yellow perch spawn on cobble and sand substrates (Robillard and Marsden 2001) and larvae are then advected offshore, where they remain for as long as 75 d (Dettmers et al. 2005) before settling on nearshore benthic habitat (Beletsky et al. 2007). In more structurally complex wetland and lake littoral zones, yellow perch spawn on plants and woody debris (Nelson and Walburg 1977; Becker 1983), and after hatching the larvae are transported to the pelagic region before migrating to the littoral zone after about 40 d (Whiteside et al. 1985). Most yellow perch spawned in Great Lakes coastal wetlands appear to stay within the wetland complexes as young-of-the-year (age-0) and age-1 juveniles before dispersing to open water habitats (Stephenson 1990; Brazner et al. 1998, 2001).

The primary objectives of this research were to assess whether young Great Lakes yellow perch morphologically differed according to habitat and dietary type, and determine whether this was associated with population genetic variation. Adult (age 2 and older) yellow perch from nearshore habitats were included in the genetic analyses to indirectly assess whether those from wetland and littoral areas were the progeny of nearshore adults.

Methods

Study areas.—Nearshore habitats in Lakes Michigan and Huron (Table 1) include shallow open-water areas between the shoreline and the 10-m depth contour (Mackey and Goforth 2005). Saginaw Bay is a large shallow embayment of western Lake Huron (Figure 1) covering 277,000 ha (Nalepa et al. 1995) and reaches a depth of 15 m (Jude and Pappas 1992). The bottom substrates of the inner bay mainly consist of sand, gravel, and cobble, with large sand–gravel bars

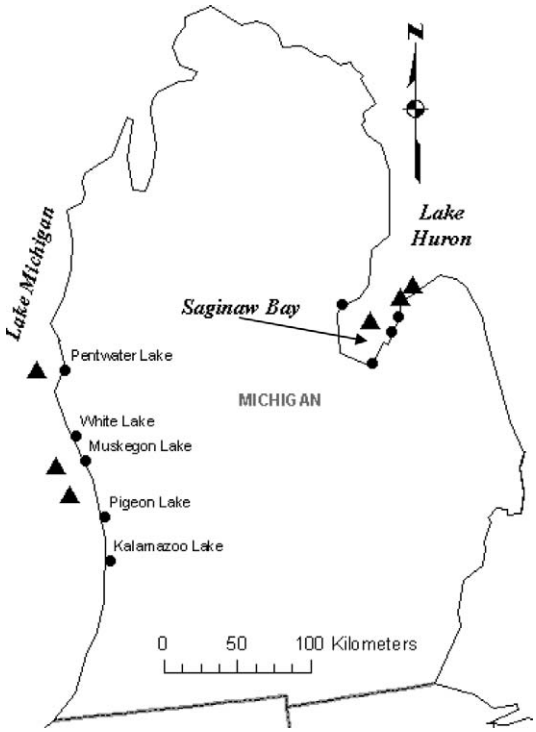

FIGURE 1.—Collection locations of yellow perch. Triangles denote nearshore locations in Lake Michigan and Saginaw Bay (Lake Huron), circles show locations in Lake Michigan drowned river mouth complexes and Saginaw Bay wetlands.

extending along the shorelines (Nalepa et al. 1995). Most shallow littoral areas of the bay are occupied by open lacustrine fringing marshes with large stands of bulrush *Schoenoplectus* spp. (Jude and Pappas 1992; Albert 2003) and are strongly influenced by lake water-level oscillations (Keough et al. 1999). Fish readily use these wetlands as spawning grounds, feeding areas, and resting sites (Jude and Pappas 1992; Albert 2003).

The present study sampled yellow perch from Lake Michigan wetland and littoral habitats in five drowned river mouth ecosystems: Kalamazoo Lake (130 ha), Pigeon Lake (31 ha), Muskegon Lake (1,680 ha), White Lake (1,040 ha), and Pentwater Lake (176 ha) along the eastern shoreline (Figure 1; Table 1), which are characterized by flooded confluences that form lakes with wetlands in their upper reaches (Wilcox et al. 2002). The drowned river mouth systems have direct surface water connections via channels to Lake Michigan, and are hydrologically influenced by Lake Michigan levels and riverine inputs (Keough et al. 1999; Wilcox et al. 2002; Jude et al. 2005). Yellow perch from the different drowned river mouth systems were not compared for morphological or genetic differences. The eastern nearshore region of Lake Michigan consists mainly of silt and sand substrate, with few natural cobble areas (Powers and Robertson 1968; Janssen et al. 2005).

Fish sampling.—Wetland and littoral yellow perch were collected using fyke nets during the summers of 2004 and 2005 (Uzarski et al. 2005; Breen and Ruetz 2006; Cooper et al. 2007). Some yellow perch also were captured in the Muskegon Lake littoral zone using boat electrofishing in 2004 and 2005 (reported by Ruetz et al. 2007). Those captured in wetland and littoral zones were euthanized in the field with tricaine methanesulfonate (MS-222) and their stomachs were manually compressed to remove the contents, which were then preserved in 95% ethanol. Manual stomach compression proved to be an efficient method as most stomachs were completely empty when the fish were later dissected. The fish then were stored on ice until placed in a freezer.

Nearshore yellow perch were captured using gill nets and bottom trawls by the Michigan Department of Natural Resources (MDNR) during September 2004 in Saginaw Bay. Lake Michigan nearshore samples were captured off the coast of Muskegon, Michigan, during May (gill nets) and August (trawling) in 2004 by the National Oceanic and Atmospheric Administration (NOAA). The MDNR also captured Lake Michigan yellow perch using trawl nets during May 2004 (from Grand Haven, Michigan) and August 2005 (Grand Haven and Pentwater, Michigan; Figure 1) (e.g., Fielder and Thomas 2006). Stomach contents from nearshore individuals were not removed in the field; instead, the fish were immediately frozen, and their stomach contents later were removed and analyzed in the laboratory. The MDNR and NOAA were not required to use MS-222.

Diet, age, and morphology.—After the stomach contents were subdivided based on whether they contained fish, macroinvertebrates, or zooplankton, they were weighed and each fish was classified as primarily zooplanktivorous, insectivorous, or piscivorous depending on which prey category constituted greater than 50% of the diet by weight. All yellow perch were aged from sagittal otoliths using a modified break-and-burn method from Robillard and Marsden (1996); before burning, the cut sides of the otoliths were sanded with 1500- and 2000-grit sand paper, and immersion oil was placed on the sanded otoliths before aging.

Data for each fish included 21 morphological distance measurements using a digital caliper and six meristic counts (Table 2) following Hubbs et al. (2004), except for measures of body girth and gill-raker length. In our study, body girth was determined

TABLE 2.—Mean (SE) morphological measurements (cm) and meristic counts for different yellow perch groups tested for the effects of habitat, diet, and basin, along with their standardized canonical coefficients. Values in bold italics indicate standardized canonical coefficients greater than one SD of the mean.

	Habitat			Diet			
Measurement or count	Standardized canonical coefficient	Nearshore	Wetland	Standardized canonical coefficient	Piscivores	Insectivores	Zooplanktivores
Body girth	***−1.1822***	***7.08 (0.07)***	***5.55 (0.13)***	0.6509	6.24 (0.17)	5.37 (0.21)	6.76 (0.12)
Body depth	***0.9680***	***2.44 (0.04)***	***2.06 (0.05)***	***−0.8962***	***2.28 (0.06)***	***2.01 (0.08)***	***2.32 (0.04)***
Caudal peduncle depth	−0.4036	0.94 (0.01)	0.75 (0.02)	0.5176	0.83 (0.02)	0.73 (0.03)	0.90 (0.02)
Caudal peduncle length	***1.0191***	***2.29 (0.03)***	***1.92 (0.04)***	0.1289	2.04 (0.06)	1.95 (0.07)	2.20 (0.03)
Head length	***−2.8458***	***3.10 (0.03)***	***2.58 (0.05)***	***−1.8705***	***2.87 (0.06)***	***2.52 (0.10)***	***2.95 (0.04)***
Head depth	***1.5584***	***1.52 (0.02)***	***1.28 (0.03)***	***−1.8416***	***1.43 (0.03)***	***1.24 (0.05)***	***1.45 (0.02)***
Maxillary length	0.9371	1.05 (0.02)	0.88 (0.02)	−0.2544	0.99 (0.03)	0.86 (0.04)	0.99 (0.02)
Maxillary width	0.0479	0.78 (0.01)	0.67 (0.02)	0.7091	0.75 (0.02)	0.64 (0.03)	0.75 (0.02)
Mandible length	0.6046	0.98 (0.02)	0.83 (0.02)	***−0.9113***	***0.94 (0.03)***	***0.82 (0.04)***	***0.93 (0.02)***
Preorbital length	−0.8185	0.70 (0.01)	0.58 (0.01)	0.0858	0.65 (0.02)	0.57 (0.03)	0.66 (0.01)
Orbital length	0.1556	0.86 (0.10)	0.66 (0.01)	0.0764	0.71 (0.01)	0.65 (0.02)	0.83 (0.11)
Post-orbital length	0.3891	1.66 (0.02)	1.37 (0.03)	***0.9230***	***1.53 (0.04)***	***1.33 (0.05)***	***1.58 (0.03)***
Trunk length	***1.5633***	***4.50 (0.08)***	***3.45 (0.07)***	0.1535	3.48 (0.11)	3.44 (0.16)	4.27 (0.10)
Dorsal fin 1 length	−0.2954	3.28 (0.04)	2.66 (0.06)	***−1.5750***	***2.95 (0.08)***	***2.64 (0.12)***	***3.11 (0.06)***
Dorsal fin 2 length	***−1.0763***	***1.85 (0.03)***	***1.49 (0.03)***	0.3130	1.64 (0.05)	1.50 (0.07)	1.76 (0.03)
Dorsal fin 1 height	***−1.4897***	***1.57 (0.02)***	***1.31 (0.03)***	0.6181	1.46 (0.04)	1.27 (0.06)	1.50 (0.02)
Dorsal fin 2 height	0.0032	1.35 (0.02)	1.08 (0.03)	−0.6288	1.22 (0.04)	1.06 (0.05)	1.27 (0.02)
Anal fin length	0.1511	1.09 (0.03)	0.89 (0.02)	0.0407	0.95 (0.02)	0.90 (0.03)	1.05 (0.03)
Pectoral fin length	0.4333	1.84 (0.02)	1.48 (0.03)	***1.3245***	***1.63 (0.04)***	***1.46 (0.06)***	***1.76 (0.03)***
Pelvic fin length	0.8637	1.99 (0.02)	1.61 (0.03)	0.1593	1.77 (0.04)	1.60 (0.06)	1.91 (0.03)
Gill raker length	0.2244	0.27 (0.03)	0.24 (0.03)	***1.0714***	***0.25 (0.04)***	***0.24 (0.07)***	***0.26 (0.03)***
Gill raker count	−0.1321	35.98 (0.26)	36.12 (0.26)	0.1622	35.77 (0.33)	36.78 (0.44)	35.97 (0.25)
Dorsal 1 ray count	−0.0183	14.08 (0.08)	14.06 (0.06)	0.1407	14.00 (0.08)	14.04 (0.10)	14.12 (0.08)
Dorsal 2 ray count	−0.2055	15.14 (0.09)	15.12 (0.09)	−0.0184	14.93 (0.10)	15.19 (0.15)	15.23 (0.09)
Anal ray count	−0.1827	10.29 (0.09)	9.65 (0.06)	−0.0813	9.68 (0.08)	9.59 (0.10)	10.31 (0.09)
Pectoral ray count	0.1744	14.0 (0.07)	14.11 (0.06)	−0.2820	14.08 (0.07)	14.19 (0.12)	13.98 (0.07)
Pelvic ray count	−0.0735	6.00 (0.00)	5.98 (0.02)	0.0394	5.98 (0.03)	6.00 (0.00)	6.00 (0.00)
Mean	0.0137			−0.0461			
SD	0.9445			0.8098			

by wrapping a piece of string around the fish in front of the first dorsal fin and then measuring its length (millimeters). Lengths of the four largest gill rakers on the first left brachial arch, from the base of the gill raker to the tip, were measured for all fish and averaged (Ruzzante et al. 1998).

Age-2 and older yellow perch morphologies, diets, and sizes were not assessed since few adult fish were captured in wetlands that could be compared with adult nearshore yellow perch. Also, juvenile and adult yellow perch size distributions were strongly bimodal, which did not fit the assumption of normality needed for statistical analysis. However, adult yellow perch from the nearshore habitats were used in the genetic analysis. Our approach combined all yellow perch based on diets rather than comparisons of their trophic-position morphologies within individual habitats because their morphological adaptations probably are the same since they undergo the same ontogenetic niche shifts regardless of habitat.

We tested for size differences using standard length (SL) as a dependent variable and examined effects of habitat (nearshore or wetland–littoral), diet (zooplanktivorous, insectivorous, or piscivorous), sex, date of capture (as a continuous variable), all interactions between main effects, and basin (Saginaw Bay and Lake Michigan), with the habitat × diet × sex interaction nested within. We used the same model in a multivariate analysis of covariance (MANCOVA) with morphological ($n = 21$) and log-transformed meristic data ($n = 6$) for age-1 yellow perch serving as dependent variables. Standard length served as the covariate to control for size variation (Ehlinger and Wilson 1988; Brönmark and Miner 1992). Interactions between main effects and the covariate were removed when not significant ($P > 0.05$). Only age-1 yellow perch with stomach contents present were included in the model.

We used the standardized canonical coefficient scores from MANCOVA to assess whether groups differed in morphological or meristic characters (McGarigal et al. 2000). Morphological and meristic characteristics with standardized canonical coefficient scores greater than the first mean SD of all coefficients were regarded as responsible for group differences.

TABLE 2.—Extended.

Measurement or count	Standardized canonical coefficient	Basin	
		Saginaw Bay	Lake Michigan
Body girth	***−1.8661***	***6.53 (0.09)***	***5.64 (0.28)***
Body depth	***1.2293***	***2.28 (0.03)***	***2.14 (0.11)***
Caudal peduncle depth	−0.1166	0.87 (0.01)	0.78 (0.04)
Caudal peduncle length	***1.5193***	***2.09 (0.03)***	***2.13 (0.09)***
Head length	***1.3035***	***2.89 (0.03)***	***2.69 (0.12)***
Head depth	0.6826	1.43 (0.02)	1.31 (0.06)
Maxillary length	***−1.7280***	***0.97 (0.01)***	***0.94 (0.05)***
Maxillary width	***−1.1535***	***0.74 (0.01)***	***0.67 (0.03)***
Mandible length	***1.7576***	***0.91 (0.01)***	***0.92 (0.05)***
Preorbital length	−0.4797	0.65 (0.01)	0.62 (0.03)
Orbital length	0.0441	0.79 (0.07)	0.67 (0.03)
Post-orbital length	***−1.0079***	***1.54 (0.02)***	***1.43 (0.07)***
Trunk length	0.0058	4.05 (0.07)	3.73 (0.19)
Dorsal fin 1 length	0.7591	3.01 (0.04)	2.82 (0.14)
Dorsal fin 2 length	0.0349	1.68 (0.02)	1.64 (0.08)
Dorsal fin 1 height	***1.5381***	***1.47 (0.02)***	***1.35 (0.07)***
Dorsal fin 2 height	−0.0913	1.24 (0.02)	1.14 (0.06)
Anal fin length	0.0478	1.00 (0.02)	0.96 (0.04)
Pectoral fin length	−0.1287	1.69 (0.02)	1.56 (0.07)
Pelvic fin length	0.1714	1.83 (0.02)	1.71 (0.08)
Gill raker length	−0.7413	0.25 (0.03)	2.60 (0.06)
Gill raker count	0.1415	35.52 (0.18)	37.72 (0.40)
Dorsal 1 ray count	−0.2738	14.09 (0.06)	14.00 (0.10)
Dorsal 2 ray count	−0.0619	15.08 (0.07)	15.28 (0.14)
Anal ray count	−0.1020	10.10 (0.07)	9.56 (0.10)
Pectoral ray count	0.0116	13.97 (0.05)	14.31 (0.11)
Pelvic ray count	−0.0147	5.99 (0.01)	6.00 (0.00)
Mean	0.0549		
SD	0.9138		

Population genetics.—Genetic analyses were performed on a subset of each group of yellow perch collected as follows: Lake Michigan nearshore (n = 31), Lake Michigan drowned river mouths (n = 29), Lake Huron's Saginaw Bay nearshore (n = 18), and Saginaw Bay wetlands (n = 42). The DNA was extracted from caudal or pectoral fin tissues using a DNeasy kit (Qiagen, Inc., Valencia, California).

A total of 12 nuclear microsatellite loci were used, including eight microsatellite loci, originally developed for walleye *Sander vitreus*: *Svi4*, *Svi6*, *Svi17*, *Svi18*, and *Svi33* from Borer et al. (1999) and *Svi2*, *Svi3*, and *Svi7* from Eldridge et al. (2002). Of these, *Svi2*, *Svi3*, *Svi4*, *Svi6*, and *Svi7* also were employed by Miller (2003) to assess Lake Michigan yellow perch population structure. In addition, we used two microsatellite loci, *YP6* and *YP16*, developed for yellow perch by Li et al. (2007), and two others from M. Grzybowski (University of Wisconsin, personal communication), *Mpf5* and *Mpf6*.

Microsatellites were amplified using the polymerase chain reaction (PCR) on a MJ Thermocycler PTC 200 (GeneTool, Inc., Silicon Valley, California) with no-DNA negative controls for each reaction series. Each forward primer was synthesized with a 5′ fluorescent label and four different dye labels were used, facilitating multiplexes and poolplexes. The PCRs contained 50 mM KCl, 1.5 mM $MgCl_2$, 10 mM tris-HCl, 50 μM of each deoxynucleotide, 0.5 μM of both forward and reverse primers, 5–30 ng DNA template, and 0.6–1.2 units of *Taq* polymerase per 10 μL reaction volume. A thermal cycle of 2 min at 94°C for initial denaturation was followed by 40 cycles of denaturation (92°C, 30 s), primer annealing (1 min) at 56°C (*Svi3*, *4*, *17*, *18*, and *33*, *YP6* and *16*, and *Mpf5* and *6*) or 58°C (*Svi2*, *6*, and *7*), and polymerase extension (72°C, 30 s). A final extension at 72°C for 5 min was included to minimize partial strands. Amplification products were diluted 1:50 with double-distilled H_2O, of which 1 μL was added to 13 μL of a solution containing formamide and ABI Gene Scan 500 size standard and then loaded onto a 96-well microtiter plate. Microsatellite products were denatured for 2 min at 95°C and analyzed on an ABI 3130XL Genetic Analyzer (Applied Biosystems, Inc., Fullerton, California) with GeneMapper version 3.7 software. We also manually checked all output profiles to confirm allelic size variants.

Genetic data analysis.—Samples were tested for conformance to Hardy–Weinberg (HW) equilibrium expectations at each locus, and the Markov chain Monte Carlo method and 10,000 randomization procedures were used to estimate significance following Guo and Thompson (1992), as implemented in GENEPOP (Raymond and Rousset 1995, 2004; available at wbiomed.curtin.edu.au/genepop). Deviations were tested for heterozygosity deficiency or excess, and each locus was tested for linkage disequilibrium (LD). Levels of significance for H-W and LD tests were adjusted using nonsequential Bonferroni corrections (Sokal and Rohlf 1995; e.g., $\alpha = 0.0016$ for 32 comparisons). Possible occurrence of null (nonamplified) alleles was assessed using the procedure of van Oosterhout et al. (2004, 2006) in the program Microchecker (available at: www.microchecker.hull.ac.uk).

Genetic variability of yellow perch subgroups was assessed as number of alleles per locus (N_A), mean number of alleles per sample, number of private alleles (N_{PA}), proportion of private alleles (P_{PA}), and observed (H_O) versus expected (H_E) heterozygosities. Unbiased θ estimates of F-statistics (Weir and Cockerham 1984) and their associated levels of significance were used to quantify genetic heterogeneity using the program *F*stat (Goudet 2002) in GENEPOP. There is ongoing debate as to which equivalents of F_{ST} are best suited for analyzing divergences based on microsatellite data (see Hedrick 1999; Balloux and Lugon-Moulin 2002).

TABLE 3.—Mean (SE) standard lengths (cm) of yellow perch according to habitat and diet.

Habitat	Diet (*n*)	Length
Lake Huron, Saginaw Bay nearshore	Piscivores (3)	11.6 (0.15)
	Zooplanktivores (55)	10.3 (0.11)
Lake Huron, Saginaw Bay wetlands	Piscivores (33)	9.1 (0.16)
	Insectivores (9)	8.4 (0.36)
Lake Michigan nearshore	Piscivores (2)	11.4 (1.21)
	Insectivores (3)	13.1 (0.22)
	Zooplanktivores (3)	12.4 (0.83)
Lake Michigan drowned river mouths	Piscivores (2)	13.0 (1.45)
	Insectivores (15)	7.9 (0.19)
	Zooplanktivores (7)	7.6 (0.45)

Since relationships among recently diverged populations, such as those tested here, are better resolved in models with θ_{ST} (the F_{ST} estimate of Weir and Cockerham 1984; see Balloux and Lugon-Moulin 2002) that method was adopted here. Values of θ_{ST} that differed significantly from zero were interpreted as evidence rejecting the null hypothesis of panmixia (i.e., gene flow) between sites. Probability values of pairwise tests employing multiple posthoc comparisons were adjusted using the sequential Bonferroni correction (Rice 1989) to minimize Type I errors (six pairwise comparisons).

Genetix version 4.05 (Belkhir et al. 2004; available at: www.genetix.univ-montp2.fr/genetix/intro.htm) was used to explore population divisions and clustering with three-dimensional factorial correspondence analysis (3D-FCA; Benzecri 1973), which evaluated variation within and among sites, clustering them according to similarities without a priori assumptions about relationships. We analyzed population structure among sampling sites and among dietary groups separately. Analysis of molecular variance (AMOVA) (Excoffier et al. 1992) in Arlequin was used to test hypotheses of hierarchical population structure among geographic groups for several different scenarios by site location, habitat (wetland versus nearshore), or diet (piscivorous, insectivorous, or planktivorous).

Bayesian-based clustering further evaluated population structure in the program Structure (version 2.2.3, Pritchard et al. 2000; Pritchard and Wen 2004; available at: pritch.bsd.uchicago.edu/software.html), which assigned individual fish to one or more population groups, disregarding a priori classification of origin. We tested for number of true population groups in independent runs, ranging from the null hypothesis of $K = 1$ (panmixia) to $K = 4$ (each sampling location as an independent population group), with 10 independent runs for each K, 100,000 burn-ins, and 200,000 replicates. Optimal K scenarios were determined with ΔK evaluations (Evanno et al. 2005). Results from Structure analyses then were compared with those from the genetic divergence and AMOVA analyses.

Results

After aging and diet analyses, 132 yellow perch were included in the MANCOVA model for morphometric analysis: Saginaw Bay nearshore, $n = 58$ (SL = 8.9–12.4 cm); Saginaw Bay wetlands, $n = 42$ (SL = 6.4–11.9 cm), Lake Michigan nearshore, $n = 8$ (SL = 10.2–13.4 cm); and Lake Michigan drowned river mouth wetland and littoral zones, $n = 24$ (SL = 5.6–14.5 cm) (Figure 1; Table 3). Seventy-nine percent of the individuals included in the model contained a single prey type in their stomachs; 17% contained two prey types, in which the higher trophic group made up a larger dietary percentage than the next lower group (e.g., a greater percentage of fish than macroinvertebrates or a larger percentage of macroinvertebrates than zooplankton). The remaining individuals sampled also consumed two food types, but had larger percentages in the lower trophic group than in a higher one (e.g., a larger amount of macroinvertebrates than fish).

Nearshore yellow perch were larger in size than those in wetland and littoral habitats ($F_{1, 115} = 120.25$, $P < 0.0001$), and piscivores and insectivores were larger than zooplanktivores ($F_{2, 115} = 10.77$, $P < 0.0001$). There was no size difference between males and females ($F_{1, 115} = 0.65$, $P = 0.4233$). When testing for a habitat × diet interaction, nearshore yellow perch representing all trophic niches (piscivores, insectivores, and zooplanktivores) were larger than those occupying wetland–littoral habitat ($F_{2, 115} = 9.78$, $P < 0.0001$). There was no habitat × sex interaction ($F_{1, 115} = 1.64$, $P = 0.2032$). When testing for a diet × sex interaction, female piscivores and insectivores were larger than respective males, and male zooplanktivores were larger than the females ($F_{2, 115} = 8.87$, $P = 0.0003$). There was no habitat × diet × sex interaction ($F_{2, 115} = 1.80$, $P = 0.1707$). When testing for a habitat × diet × sex interaction nested within basin, Lake Michigan yellow perch were larger than those in Saginaw Bay, Lake Huron ($F_{5, 115} = 11.57$, $P < 0.0001$). Standard length was used as a covariate in all subsequent morphological analyses.

Morphology

Habitat × SL was the only significant interaction in the MANCOVA model, which is most likely because nearshore yellow perch were larger than those in the wetland and littoral areas. All other factors that had nonsignificant ($P > 0.05$) interactions with SL were removed from the final model (Table 4). Between lakes, yellow perch from Saginaw Bay in Lake Huron

TABLE 4.—Multivariate analysis of variance results for effects of different variables on yellow perch morphology. Effect sizes are given as partial η^2.

Effect	*F*	df	*P*	Partial η^2
Habitat	2.33	27, 87	0.0016	0.42
Diet	1.52[a]	54, 174	0.0227	0.23
Sex	0.62	27, 87	0.9184	0.16
Habitat × diet	0.94[a]	54, 174	0.5989	0.16
Habitat × sex	1.06	27, 87	0.4100	0.09
Diet × sex	1.36[a]	54, 174	0.0689	0.21
Habitat × diet × sex	1.34[a]	54, 174	0.0819	0.21
Basin (habitat × diet × sex)	1.98[a]	135, 434.12	<0.0001	0.55
Standard length	63.47	27, 87	<0.0001	0.95
Standard length × habitat	2.56	27, 87	0.0005	0.18

[a] *F* was approximated using Wilks' λ.

had larger mean body girths and body depths, greater head lengths, larger mouths, and higher first dorsal fins than did those in Lake Michigan. The latter had longer caudal peduncles than those in Lake Huron (Table 2). Age-1 yellow perch were morphologically distinct between habitats and diets, but there was no interaction between the variables (Table 4; Figure 2A) indicating that, regardless of habitat, individuals consuming a particular prey developed similar morphologies for resource exploitation (Table 4; Figure 2B). Nearshore yellow perch had larger mean body girths and body depths, longer caudal peduncles and trunks, higher dorsal fins, longer heads, larger head depths, and longer second dorsal fins than did those in wetland and littoral habitats (Table 2).

Piscivorous individuals had larger body depths, greater head lengths, greater postorbital lengths, larger head depths, longer first dorsal rays, and longer mandibles than did insectivores (Table 2). Zooplanktivorous individuals had longer gill rakers and pectoral fins (Table 2). We did not detect any morphological differences between sexes (Table 4).

Genetics

All 12 loci were polymorphic in each lake habitat site, except for *YP16* in Lake Huron's Saginaw Bay (both habitats) and *Svi18* in Saginaw Bay wetlands (Table 5). Yellow perch from Lake Huron nearshore systems had the highest proportion of private alleles ($P_{PA} = 0.135$), and those from Lake Michigan nearshore and Saginaw Bay wetland habitats had the lowest proportion ($P_{PA} = 0.051$ and 0.056 respectively; Table 5). Samples from Lake Michigan (nearshore and drowned river mouth systems combined) had 28 private alleles and those from Lake Huron (nearshore and wetlands) were distinguished by 34 private alleles. All loci conformed to expectations of linkage equilibrium. Genetic results include age-1 and adult yellow perch.

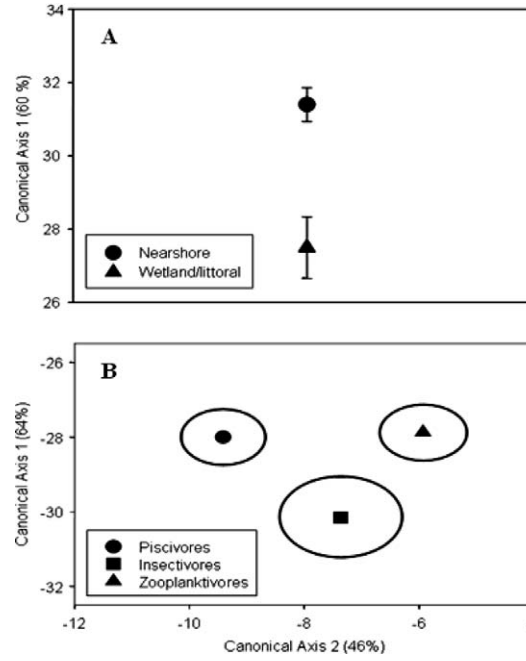

FIGURE 2.—Canonical biplot centroids ±95% confidence intervals for **(A)** yellow perch habitat and **(B)** yellow perch diet.

Four loci in three habitat sites (*Svi4* in Lake Huron nearshore and wetlands, *Svi7* in nearshore Lake Michigan, and *YP6* and *Mpf6* in Saginaw Bay wetlands) had higher observed (H_O) than expected heterozygosities (H_E) deviating from Hardy–Weinberg (HW) equilibrium expectations after Bonferroni correction (Table 5). The *Svi33* locus deviated in three of the four samples, whereas *Svi6* and *Svi18* deviated in two samples, which the program Microchecker attributed to null alleles (Table 5). We therefore ran the analyses without those loci except for the 3-D factorial correspondence analysis, which is independent of all assumptions. The fourth locus (*YP6*) deviated in two samples, but showed no evidence of null alleles, and so was retained in analyses. Thus, we based our analyses on nine loci.

Results of all analyses revealed marked genetic divergence between yellow perch populations in Saginaw Bay, Lake Huron, versus Lake Michigan, including pairwise F_{ST} analog tests (Table 6), AMOVA tests (Table 7), Bayesian structure (Figure 3; $K = 2$ population groups, posterior probability = 0.901), and 3-D factorial correspondence (Figure 4) analyses. The 3-D factorial correspondence analysis (Figure 3), pairwise F_{ST} analog tests (Table 6) and AMOVA tests (Table 7) distinguished between the wetland versus nearshore locations (Figure 3) for Lake Michigan. We

TABLE 5.—Genetic variation (allelic richness [F_{IS} statistic]) of yellow perch subgroups at 12 microsatellite loci. Also shown are the observed heterozygosity (H_O), expected heterozygosity (H_E), mean number of alleles per individual sampled (N_A), number of private alleles (N_{PA}), and proportion of private alleles (P_{PA}).

	Lake Michigan		Saginaw Bay	
Locus	Nearshore	Drowned river mouths	Nearshore	Wetlands
Svi2	3 (0.282)	5 (0.425)	4 (0.258)	5 (0.290)
H_O	0.419[a]	0.310	0.389	0.429
H_E	0.581	0.539	0.575	0.598
Svi3	3 (0.663)	6 (0.333)	5 (0.501)	6 (0.280)
H_O	0.032	0.172	0.222	0.214[b]
H_E	0.126	0.259	0.354	0.445
Svi4	12 (0.234)	13 (0.110)	12 (−0.019)	16 (−0.119)
H_O	0.677[b]	0.759	1.000	0.881
H_E	0.882	0.852	0.897	0.866
Svi6	17 (0.089)	14 (0.042)	16 (0.188)	23 (0.181)
H_O	0.806	0.862	0.778[b]	0.762[b]
H_E	0.894	0.900	0.956	0.941
Svi7	3 (−0.075)	6 (0.304)	5 (0.188)	6 (0.202)
H_O	0.194	0.138	0.278	0.214
H_E	0.180	0.198	0.395	0.284
Svi17	9 (0.509)	2 (0.368)	12 (0.169)	8 (0.017)
H_O	0.323	0.414	0.619	0.667
H_E	0.657	0.655	0.745	0.678
Svi18	2 (1.000)	3 (1.000)	2 (0.000)	1 (0.000)
H_O	0.000[b]	0.000[b]	0.056	0.000
H_E	0.154	0.197	0.056	0.000
Svi33	21 (0.291)	27 (0.167)	16 (0.304)	26 (0.294)
H_O	0.677[b]	0.793	0.667[b]	0.667[b]
H_E	0.956	0.958	0.951	0.962
YP6	2 (0.277)	2 (0.802)	3 (0.309)	2 (−0.063)
H_O	0.129	0.103	0.333	0.167
H_E	0.179	0.522	0.483	0.157
YP16	2 (0.000)	4 (0.000)	1 (0.000)	1 (0.000)
H_O	0.032	0.035	0.000	0.000
H_E	0.032	0.035	0.000	0.000
Mpf5	8 (0.272)	8 (0.126)	15 (0.204)	5 (0.487)
H_O	0.548	0.448	0.619	0.333
H_E	0.754	0.513	0.778	0.650
Mpf6	9 (0.246)	12 (0.073)	13 (0.160)	8 (0.372)
H_O	0.613	0.724	0.595	0.500
H_E	0.813	0.781	0.709	0.372
Number of subgroups	31	29	18	42
Mean N_A	7.58	8.50	8.67	8.92
Mean H_O	0.371[a]	0.397[a]	0.463[a]	0.403[a]
Mean H_E	0.517	0.534	0.576	0.575
N_{PA}	9	19	24	10
P_{PA}	0.051	0.107	0.135	0.056

[a] Sample not in Hardy–Weinberg equilibrium after Bonferroni correction. Overall, samples were in equilibrium for nine loci.

[b] Sample not in Hardy–Weinberg equilibrium and null alleles present as indicated by Microchecker (Van Oosterhout 2004).

TABLE 6.—Pairwise θ_{ST} values (Weir and Cockerham 1984) and associated *P*-values (parentheses) for yellow perch subgroups using nine microsatellite loci with equilibrium proportions for habitats in Lake Michigan and Lake Huron. Single asterisks denote significant differences before sequential Bonferroni correction, double asterisks significant differences after correction (Rice 1989).

Habitat	Lake Michigan nearshore	Lake Michigan drowned river mouths	Lake Huron wetlands
Lake Michigan drowned river mouths	0.206 (0.002)**		
Lake Huron wetlands	0.411 (0.0001)**	0.295 (0.0001)**	
Lake Huron nearshore	0.290 (0.0001)**	0.440 (0.0001)**	0.139 (0.027)*

TABLE 7.—Partitioning of genetic variability among yellow perch samples using analysis of molecular variance (Excoffier 1989) between two main population groups (Lake Michigan versus Lake Huron's Saginaw Bay) and their four component habitats (Lake Michigan nearshore and Lake Michigan drowned river mouth lake–river complexes, Lake Huron's Saginaw Bay nearshore, and Saginaw Bay wetlands).

Source of variation	% Variation	Fixation index	*P*-value
Between Lake Michigan and Lake Huron	13.03	0.130	<0.001
Between sampling habitats within lakes	1.27	0.015	<0.001
Within habitats	85.70	0.143	<0.001

found no genetic differences between habitats in Lake Huron (Tables 6, 7), which may be due to the lower sample size for the nearshore group. Samples were not distinguishable according to diet composition in 3-D FCA analysis (Figure A.1), but differed in pairwise F_{ST} analog and AMOVA analyses for insectivores versus piscivores in Lake Michigan ($\theta_{ST} = 0.070$, $P < 0.0001$) after sequential Bonferroni correction (Rice 1989). However, the genetic differences between the two diet groups are probably a result of them occupying different habitats and are not indicative of dietary specialization. Most of the insectivorous yellow perch were in the drowned river mouth systems, whereas the piscivores were mainly in the Lake Michigan nearshore habitat. All other genetic comparisons of yellow perch based on diets within lake basins were nonsignificant ($P > 0.05$).

Discussion

We combined analyses of morphology, genetic variation at neutral loci, and stomach contents to assess the mechanisms regulating phenotypic differences among yellow perch collected in different habitats and basins. Observed morphological variation matched existing functional paradigms describing feeding and predator-induced morphologies and was consistent between habitats and diet categories for populations in Lake Michigan and Saginaw Bay, Lake Huron. However, there was evidence for pronounced genetic separation between yellow perch populations in Lakes Michigan and Huron using these selectively neutral microsatellite loci. Our results also indicated genetic differences between fish collected in wetland–littoral and nearshore habitats in Lake Michigan, but not in Lake Huron, suggesting an interplay between genetic divergence and phenotypic plasticity in generating observed morphological variation. This merits further study.

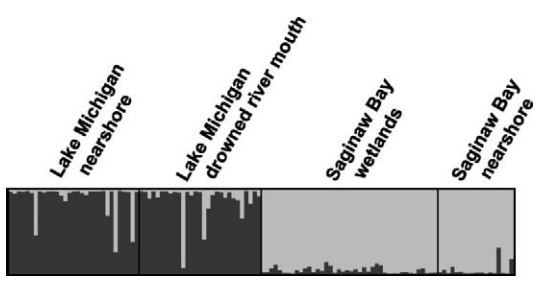

FIGURE 3.—Estimated population structure of yellow perch from Bayesian structure analysis (Pritchard et al. 2000, 2004) for $K = 2$ groups (posterior probability = 0.901), which was the optimum number determined using ΔK evaluations (Evanno et al. 2005). Individuals are represented by thin vertical lines, which are partitioned into K shaded segments representing the individuals' estimated membership fractions. The black lines separate sampling sites.

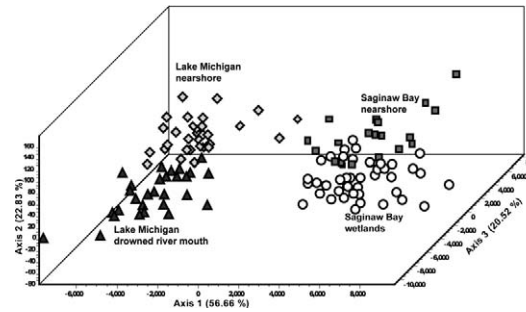

FIGURE 4.—Three-dimensional factorial correspondence analysis (Benzecri 1973; Belkhir et al. 2004) of yellow perch microsatellite data showing the clusters of Lake Michigan and Lake Huron individuals by sampling habitat location.

Phenotypic plasticity also has been demonstrated in Eurasian perch *P. fluviatilis* (e.g., Hjelm et al. 2001; Svanbäck and Eklöv 2003, 2004). Eurasian perch and yellow perch are genetically separable species, having similar life histories and behaviors (Marsden et al. 1995), with their primary apparent morphological difference being the position of the predorsal bone (Collette and Bănărescu 1977). Eurasian perch phenotypic plasticity is influenced by habitat structure and feeding mode (Olsson and Eklöv 2005), as well as growth rate (Olsson et al. 2006, 2007).

Olsson and Eklöv (2005) found that when young Eurasian perch were placed in aquaria with artificial vegetation and fed benthic prey, they developed deeper bodies and more downward-oriented snouts than did those that were placed in open-water aquaria and fed suspended prey. However, when fish were transferred from the vegetated aquaria to open water, their bodies became more slender and their snouts less downward-oriented after just 4 weeks (Olsson and Eklöv 2005).

Svanbäck and Eklöv (2006) tested the importance of phenotypic plasticity and genetic variation in explaining the morphologies of Eurasian perch by placing the offspring of littoral and pelagic fish in either vegetated or open-water pond enclosures. Despite their parentage, fish raised in vegetated enclosures had deep bodies and downward-pointing snouts and those raised in open-water had more slender bodies with upturned snouts. The offspring of littoral perch did have deeper bodies than the pelagic offspring raised in the same environments; however, most of the morphological variation was explained by environmental factors rather than parental type (Svanbäck and Eklöv 2006).

Genetics

We found that yellow perch populations in Lakes Michigan and Huron exhibited low to moderate levels of genetic variation, averaging an observed heterozygosity of 0.41 per habitat sampling site, with significant differentiation between the lake populations and some habitats. The number of alleles per locus and heterozygosity levels per sampling site in our study were similar to those obtained by Miller (2003) using five of the same loci. Low to moderate genetic diversity is common among some freshwater fishes inhabiting postglacial environments, despite their relatively high phenotypic diversity (Bernatchez and Wilson 1998). By comparison, Strange and Stepien (2007) found that heterozygosity of walleye in Lake Erie averaged 0.71 among spawning locations, based on 10 loci (including six of those tested here), and Stepien et al. (2007) found that heterozygosity values for smallmouth bass *Micropterus dolomieu* averaged 0.52 within Great Lakes populations, based on eight loci. Both of those species showed patterns of significant population genetic differences among spawning groups within lakes, and greater divergences among lakes (Strange and Stepien 2007; Stepien et al. 2007).

Our results and those of other studies indicate that adult yellow perch groups mix within the nearshore lake system, but exhibit divergent spawning site fidelity (see recent summary by Sepulveda-Villet et al. 2009). Yellow perch frequently reproduce in wetlands (Albert 2003; Gyekis 2006), and adults that live in the nearshore environment of Lake Huron's Saginaw Bay probably return to those habitats to spawn. Large (sexually mature) yellow perch were rarely found in wetlands and littoral zones, indicating that this life history stage may primarily occupy these areas for reproduction alone. Thus, the young yellow perch that we sampled in the wetlands of Saginaw Bay were probably the progeny of adult yellow perch originating from the nearshore areas. Even in small lake systems, cohort-splitting can homogenize populations when some larvae remain in the pelagic zone (Post et al. 1997) instead of returning to the littoral zone (Whiteside et al. 1985; Urho 1996).

Our study indicates appreciable genetic separation between yellow perch in Lake Michigan's drowned river mouth systems and nearshore habitats. The drowned river mouth systems that we sampled had deep lake bodies, which were the likely locations where adult yellow perch could be found after leaving the wetland–littoral areas, rather than migrating to Lake Michigan. Bogan (2004) also found that yellow perch in two drowned river mouth systems were genetically different from those in Lake Michigan proper.

The occurrence of some lower-than-expected observed heterozygosities (Table 5) suggests mixing of two or more spawning sites within the population, possibly indicating a Wahlund effect (Smith 1998). Notably, in our study multiple spawning populations of yellow perch were sampled together during the nonspawning season. Aalto and Newsome (1989, 1990) proposed that yellow perch populations in a Canadian lake exhibited spawning-site fidelity, and evidence has shown that walleye, which are closely related to yellow perch, exhibit spawning-site fidelity as well (Stepien and Faber 1998; Strange and Stepien 2007). Ford and Stepien (2004) and Sepulveda-Villet et al. (2009) evoked natal homing and spawning-site philopatry to explain significant differences among some yellow perch spawning locations in Lake Erie. Gerlach et al. (2001) showed that Eurasian perch can recognize kin (probably due to olfactory cues), which may provide a homing mechanism; this finding merits testing in yellow perch and other percids.

Morphology

Morphological and genetic differences were found between yellow perch from Lake Michigan and Lake Huron's Saginaw Bay. Our study discerned no sexual dimorphism in age-1 yellow perch, probably because they were immature according to visual inspection of gonads (Treasurer and Holliday 1981). Lippert et al. (2007) found that yellow perch display sexual dimorphism by age 2, when most are mature (Craig 2000).

Although many studies of fish morphological plasticity focus on the end stages of ontogeny (Svanbäck and Eklöv 2002), a growing amount of literature has examined resource polymorphism throughout ontogeny as individuals shift their resource use (Skúlason et al. 1989; Wainwright et al. 1991; Snorrason et al. 1994; Claessen and Dieckmann 2002; Hjelm et al. 2003), including studies of Eurasian perch (Hjelm et al. 2001; Svanbäck and Eklöv 2002).

Yellow perch undergo two major ontogenetic niche shifts during development (Keast 1977): as larvae and age-0 fish they feed on zooplankton (Bremigan et al. 2003; Dettmers et al. 2003) before switching to insectivory, and then ultimately make a final switch to piscivory (Keast 1977; Tonn and Paszkowski 1987; Harvey and Brown 2004).

We examined age-1 yellow perch in this study to examine evidence of resource polymorphism because individuals undergo the transition between zooplanktivory, insectivory, and piscivory during this ontogenetic period. Piscivorous and zooplanktivorous yellow perch had deep bodies and long dorsal fins compared with the insectivores. Svanbäck and Eklöv (2002) likewise found that piscivory in Eurasian perch was correlated with deeper bodies. Notably, large body depths function in allowing fast-starts and powered turns when capturing prey (Webb 1984). Lundvall et al. (1999) hypothesized that maneuverability may be more important than speed for prey capture success by piscivorous Eurasian perch.

We found that yellow perch consuming zooplankton had longer pectoral fins than did the piscivores (Table 2), which may increase the former's braking efficiency (Alexander 1967) and thereby aid them in picking zooplankton out of the water column. Zooplanktivorous yellow perch also had slightly longer gill rakers (Table 2), which are associated with planktivory (Lindsey 1981; Schluter and McPhail 1992; Schluter 1998). Zooplanktivory is positively correlated with slender body morphology in yellow perch (Lippert et al. 2007), thereby reducing drag to facilitate open-water foraging (e.g., Webb 1984). Most zooplanktivorous individuals were collected in nearshore habitats where predatory fishes occur, and predation threat may therefore override selection for foraging efficiency, thereby explaining the morphological (and genetic) similarity between piscivores and zooplanktivores. There was no evidence of genetic divergence in these neutral markers for individuals consuming different diets, suggesting that these morphological differences develop from phenotypic plasticity. Experiments directly testing for phenotypic plasticity have revealed that fish display morphological diversification as a result of type (Ruehl and DeWitt 2007) and position of food resources (Ruehl and DeWitt 2005).

Nearshore yellow perch had deeper bodies than those found in wetland and littoral habitats (Table 2). Deep-bodied fish are more difficult for predators, such as northern pike *Esox lucius*, to capture and handle (Brönmark and Miner 1992; Nilsson et al. 1995). Young Eurasian perch developed deep bodies in the presence of northern pike (Magnhagen and Heibo 2004; Eklöv and Jonsson 2007) and had longer dorsal fins in lakes with dense pike populations (Magnhagen and Heibo 2004). In a recent study, Lippert et al. (2007) found that yellow perch had deeper bodies and more anteriorly positioned dorsal fins compared with those in predator-free lakes. Our study found that nearshore yellow perch had deeper and longer body profiles, and taller and longer dorsal fins than those living in wetland habitats. A common behavioral response for perch in the presence of predators is to erect their dorsal spines, making them appear larger and less palatable (Vainikka et al. 2005). Moreover, large body depths are useful for fast-starts to avoid predators (Webb 1984; Langerhans et al. 2004; Ruehl and DeWitt 2005).

Large piscivorous species, including adult yellow perch and lake trout *Salvelinus namaycush*, occupy nearshore environments of Lake Michigan (Miller and Holey 1992; Madenjian et al. 2002), and Lake Huron's Saginaw Bay contains piscivorous adult yellow perch, walleye, and channel catfish *Ictalurus punctatus* (Fielder and Thomas 2006). In contrast, large predatory fishes are largely absent in Great Lakes coastal wetlands (Brazner et al. 1998, 2001; Uzarski et al. 2005). Vegetated littoral zones are often used as refuge from predators by small fish (Savino and Stein 1982; Werner et al. 1983; Rozas and Odum 1988), including young Eurasian perch (Diehl and Eklöv 1995).

Conclusions

Yellow perch occupy diverse habitats throughout the Great Lakes region where they are both economically and ecologically important. Those spawned in nearshore habitats and wetlands experience very different early life histories during their critical first year, and studies to date indicate some genetic differences occur among spawning groups within the lakes (Miller 2003; Bogan 2004; Sepulveda-Villet et al. 2009). Our results contribute to previous research by discerning that age-1 yellow perch develop habitat and diet specific morphologies that fit functional paradigms established for avoiding predators and capturing food items. As yellow perch change habitats during their first year, their morphology alters with their ontogenetic niche shift to piscivory. By the time yellow perch reach age 2, the groups converge to live in deep-water habitats with adults probably returning to their natal wetland–littoral areas to spawn. We found that morphological variation in yellow perch has both a genetic component and a phenotypic plasticity component. The relative contribution of genetic and plastic processes in generating observed phenotypic variation in yellow perch warrants further study.

Acknowledgments

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Appendix 1: Yellow Perch Microsatellite Data Analysis

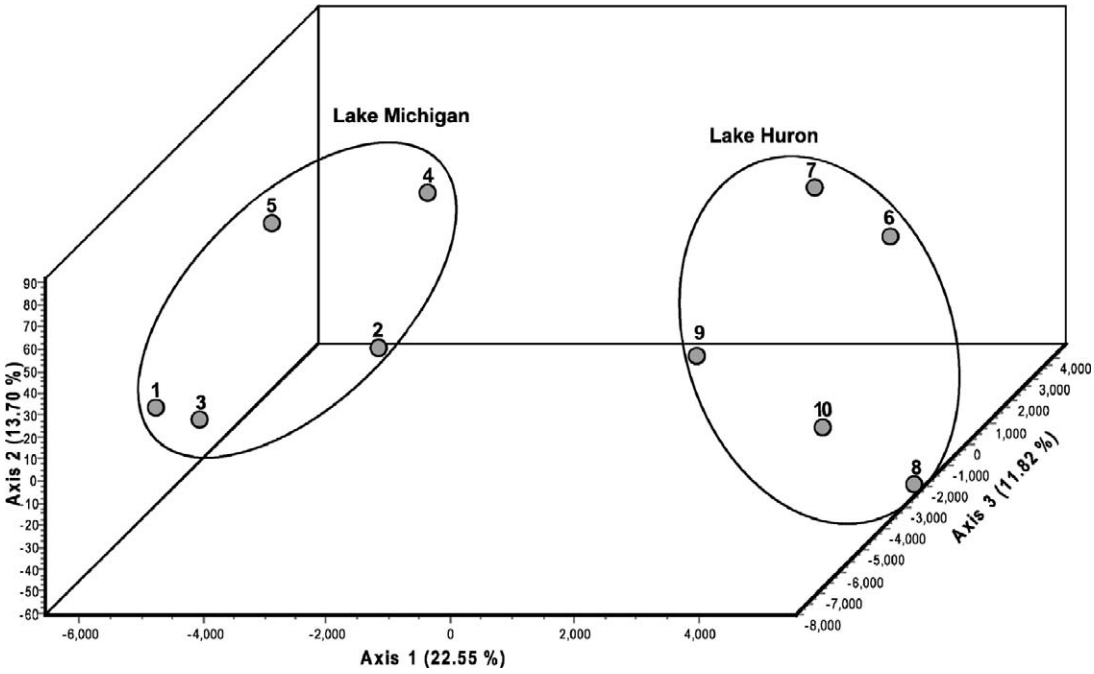

FIGURE A.1.—Three-dimensional factorial correspondence analysis (Benzecri 1973; Belkhir et al. 2004) of yellow perch microsatellite data from 12 loci showing clusters from Lake Michigan and Lake Huron, grouped by diet types. Code numbers are as follows: Lake Michigan nearshore: 1, piscivores; 2, insectivores; and 3, zooplanktivores. Lake Michigan drowned river mouths: 4, insectivores; and 5, zooplanktivores. Lake Huron wetlands: 6, piscivores; and 7, insectivores. Lake Huron nearshore: 8, piscivores; 9, insectivores; and 10, zooplanktivores.