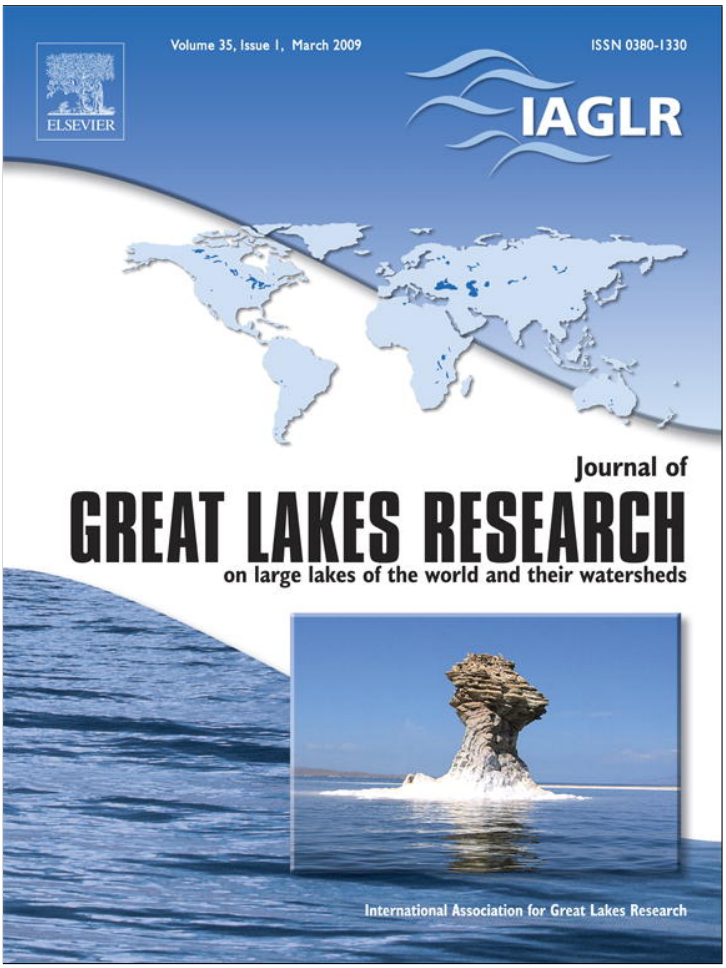

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# Population genetic diversity and phylogeographic divergence patterns of the yellow perch (*Perca flavescens*)

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ABSTRACT

Great Lakes populations of yellow perch have fluctuated throughout past decades to the present due to unstable recruitment patterns and exploitation. Our study analyzes genetic diversity and structure across the native range in order to interpret phylogeographic history and contemporary patterns. We compare complete mitochondrial DNA control region sequences (912 bp) from 568 spawning individuals at 32 sites, encompassing all 5 Great Lakes and outlying watersheds from the upper Mississippi River, Lake Winnipeg, Lake Champlain, and Atlantic and Gulf coastal relict populations. These broad-scale divergences additionally are compared with fine-scale patterns from 334 individuals at 16 spawning sites across Lake Erie's 4 fishery management units. We identify 21 mtDNA haplotypes, including a widespread type that totals 87% of individuals across the Great Lakes. Overall genetic diversity is relatively low in comparison with other Great Lakes fishes, congruent with prior allozyme and microsatellite studies. The largest genetic demarcation separates 2 primary population groups: one in the Great Lakes, Lake Winnipeg, and upper Mississippi River watersheds and the other along the Atlantic and Gulf coasts, together with Lake Champlain; which diverged ~365,000 years ago. In addition, the watersheds house genetically separable groups, whose patterns reflect broad-scale isolation by geographic distance. A few spawning groups show some fine-scale differentiation within Lake Erie, which do not reflect fishery management units and need further study with higher-resolution markers.



## Introduction

The yellow perch *Perca flavescens* (Percidae: Teleostei) is a key North American sport and commercial fish whose populations have fluctuated over the past several decades due to unstable recruitment patterns and exploitation (Marsden and Robillard, 2004; Bronte et al., 1993). Its abundance and native distribution center in the lower Great Lakes region (Scott and Crossman, 1973), whose populations originated ~13,000 years ago (ya) from 2 primary glacial refugia (Bailey and Smith, 1981; Crossman and McAllister, 1986; Todd and Hatcher, 1993). The objective of our study is to test for broad versus fine-scale population genetic divergence among yellow perch spawning groups across the Great Lakes in comparison with other areas of the native range (Fig. 1). We use mitochondrial (mt) DNA control region sequences to compare genetic diversity and divergence levels, test the hypothesis of genetic isolation by geographic distance, and evaluate postglacial colonization and present day patterns.

Maintenance of population genetic diversity is regarded as important to an organism's ability to withstand environmental changes (Moritz and Faith, 1998; Avise, 2004), which may include climate alterations, pollution, habitat loss, biological invasions, and exploitation; all of which likely have negatively affected yellow perch in the Great Lakes (Henderson and Nepszy, 1989; Tyson and Knight, 2001). Notably, Great Lakes yellow perch populations have withstood exploitation dating to the early 1900s, severe pollution in the 1950–60s, and biological invasions from the 1970s–present. Invasive species believed to have affected yellow perch populations include white perch *Morone americana* introduced in 1977 (Parrish and Margraf, 1990; Munawar et al., 2005), ruffe *Gymnocephalus cernuus* dating to 1985 (Pratt et al., 1992; Fullerton and Lamberti, 2006), and round goby *Neogobius melanostomus* since 1990 (Jude et al., 1992; Gonzalez, 2006).

Although sometimes regarded as a "second rate pan fish", the yellow perch has been economically important to the Great Lakes

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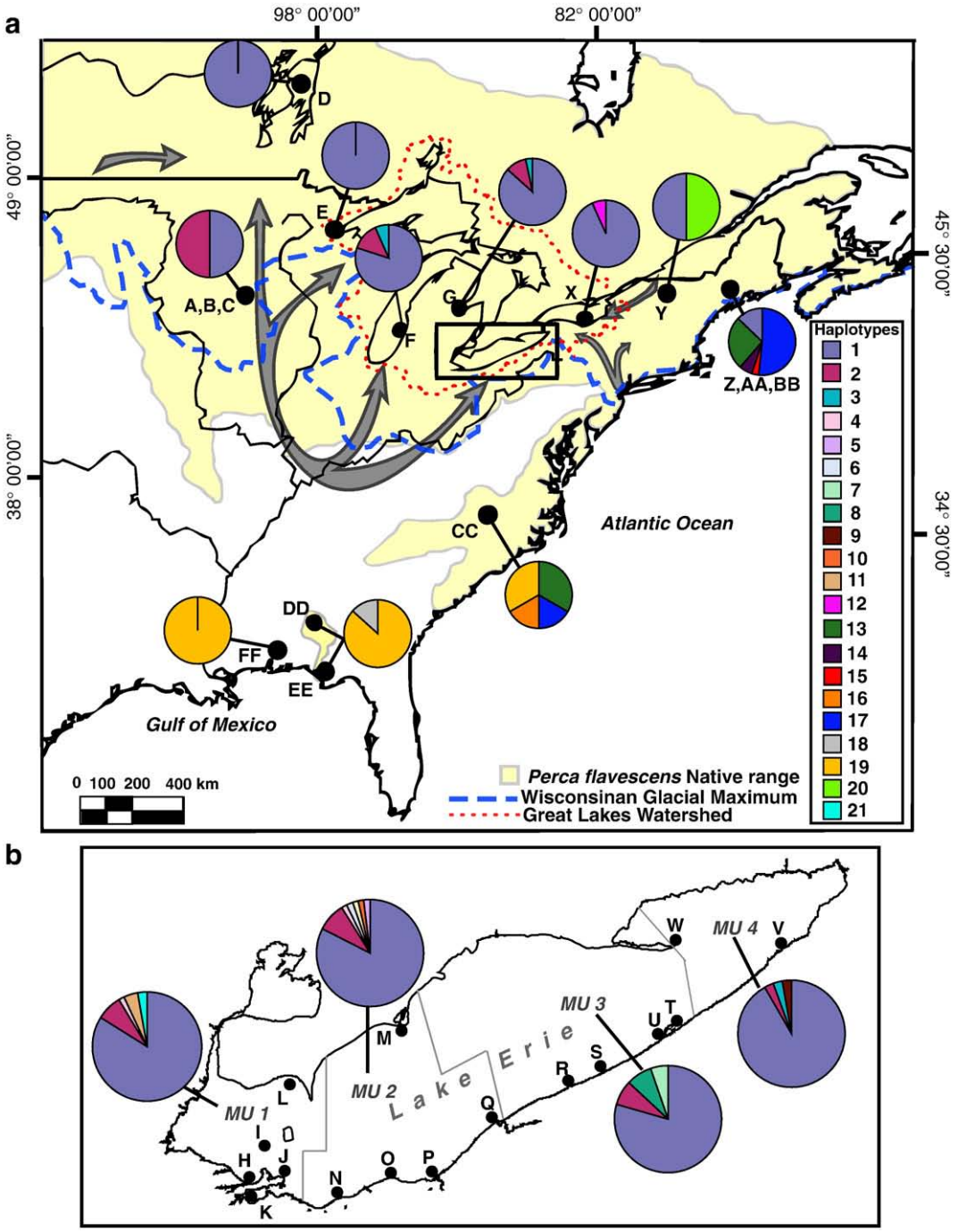


**Fig. 1.** Maps showing (a) the native distribution of yellow perch *Perca flavescens* (shaded; adapted from Lee et al., 1980), our sampling sites (lettered according to Table 1), distribution of yellow perch mtDNA control region haplotypes (numbered per Table 2) among the sites, and hypothesized colonization pathways from glacial refugia (arrows, adapted from Mandrak and Crossman, 1992), (b) sampling sites in Lake Erie, with boundaries of Lake Erie management units (MUs 1–4 per GLFC, 2006).

for more than a century (Clapp and Dettmers, 2004), with its most significant fishery in Lake Erie (Trautman, 1981). Yellow perch survival and recruitment are highly stochastic (Trautman, 1981), with Great Lakes populations undergoing many fluctuations in recruitment and population sizes (Kenyon and Murray, 2001; GLFC, 2004). Peak fishery harvests occurred from 1928–35 and the mid-1950s to the early 1970s, mostly in years coinciding with low numbers of walleye *Sander vitreus* (Craig, 2000). During the early 1930s, Lake Erie yellow perch commercial landings increased to 5700 metric tons, fueled by the collapse of the cisco *Coregonus artedi* fishery and a switch of fishing efforts to the more abundant yellow perch (Craig, 2000). Decline in water quality, caused by organic compounds and phosphorous-bearing detergent wastewater, as well as continued fishing pressure reduced the Lake Erie yellow perch catch below 3175 metric tons by 1976 (Hartman et al., 1980).

Yellow perch became more abundant during the 1980s and then markedly declined during the 1990s through the early 2000s, variously attributed to fluctuating phosphorous levels, recruitment failures, overexploitation, and influence of exotic species —

including the white perch and alewife *Alosa pseudoharengus* (Shroyer and McComish, 2000; Ryan et al., 2003; Lauer et al., 2008). The Lake Michigan yellow perch fishery collapsed in 1990 (Fulford et al., 2006) and has not yet fully recovered (Marsden and Robillard, 2004; GLFC, 2008a). Wilberg et al. (2005) estimated the remaining number of yellow perch in Lake Michigan waters in 2005 as 10% of those found in 1986. Interagency cooperation across the Great Lakes reduced exploitation and sought to protect spawning groups, increasing stocks and harvests (Ryan et al., 2003). Recent surveys point to an increase in mean fish length and a higher proportion of reproductive-age females as indicators of further improvement of yellow perch populations in Lake Michigan, but recruitment remains erratic (Lauer et al., 2008). Fishery recovery in Lake Erie has been gradual, with a total allowable 2006 catch of 7475 metric tons and profit exceeding $42 million wholesale, largely due to the success of the 2003 year class (GLFC, 2006). However, the 2007 total allowable catch was only 5165 metric tons, due to weaker year classes in 2002, 2004, and 2006 (GLFC, 2007a). The total allowable catch for 2008 further was decreased to 4386 metric tons, due to declining numbers of perch remaining in the 2003 year class and lower recruitment in subsequent years (GLFC, 2008b).

Our study was requested by the Great Lakes Fishery Commission's Lake Erie Yellow Perch Task Group, who sought the genetic basis for stock structure in order to facilitate management decisions and stabilize populations. We expanded our study's scope to relate the population structure of yellow perch across the Great Lakes to its broad-scale phylogeography, thereby increasing understanding of relative genetic diversity and divergence patterns. We evaluate (1) the hypothesis of genetic isolation by geographic distance, (2) divergence patterns stemming from prior isolation in glacial refugia, and (3) historic versus present-day barriers and dispersal pathways. Lastly, we relate our findings to known historic and present-day yellow perch population abundances, stock structure, and anthropogenic stresses; as well as to patterns in other fishes.

## Materials and methods

### *Sample and DNA data collection*

A total of 568 yellow perch were sampled by fishery agency collectors from 32 native sites that are believed not to have been stocked, including all Great Lakes (Superior, Michigan, Huron, Lake Erie, and Ontario) and outlying populations from the upper Mississippi River, Lake Winnipeg, Lake Champlain, and relict areas along the Atlantic and Gulf coasts (Table 1, Fig. 1). Fine-scale concentration in Lake Erie includes 334 samples from 16 spawning sites, and its 4 management units designated by the Great Lakes Fishery Commission (GLFC, 2006, 2007b). Tissue samples from fin clips were either preserved in 95% ethanol (EtOH) in the field or frozen after collection. In some cases, fish were tagged and released as part of regular monitoring activities by the collecting agencies, and in others they were sacrificed, and used for age and diet studies by agencies. Geographic coordinates were recorded, as well as available length and sex data.

The entire mtDNA control region, a non-coding portion of the mtDNA genome comprising 912 bp and containing the D-loop, was used to analyze the population structure of yellow perch following Faber and Stepien (1997). DNA was extracted from 25 mg of fin clip tissue using a Qiagen DNeasy Tissue Kit (#69506, Qiagen Sciences, Inc., Germantown, MD). MtDNA primers used for the polymerase chain reaction (PCR) were: LW1-f (Gatt et al., 2000), 12Sar-h (Martin et al., 1992), Tl-f (Kocher et al., 1989) and HW1-r (Gatt et al., 2000). PCR reactions contained 50 mM KCl, 1.5 mM $MgCl_2$, 10 mM Tris–HCl, 200 μM dNTPs, 0.5 μM each of the paired primers, 30 ng DNA template, and 1 U of *Taq* polymerase in a 25 μl volume. Amplification on a MJ Research Tetrad thermalcycler (Bio-Rad, Hercules, CA) included 40 cycles of 45 s denaturation at 92 °C, 45 s annealing at 53 °C, and 1.5 min polymerization at 72 °C; followed by a 5 min extension step at 72 °C.

DNA strands were sequenced separately in both directions for independent verification using the PCR primers LW1-f, HW1-r, and HN20-r (Bernatchez et al., 1992) and Big Dye terminator chemistry sequencing (Applied Biosystems, Inc. (ABI); Fullerton, CA). Sequencing was performed by the Life Sciences Core Laboratory Center at Cornell University (http://cores.lifesciences.cornell.edu/brcinfo/), which used ABI Automated 3730 DNA Analyzers. We collected sequence data in both directions in overlapping sections, in order to lower the possibility of polymerization-induced mutation and to corroborate substitutions. MtDNA sequences then were aligned by us

**Table 1**
Location and mtDNA control region genetic diversity of yellow perch *Perca flavescens* sampling sites

| Locality | Lat °N | Long °W | N | $N_h$ | $H_d$ | $N_{ph}$ |
|---|---|---|---|---|---|---|
| Upper Mississippi R. watershed | | | 18 | 2 | 0.529 ±0.040 | 0 |
| A. Green Lake, MN | 45.23694 | −94.93750 | 8 | 2 | 0.529 ±0.040 | 0 |
| B. Florida Lake, MN | 45.2486 1 | −95.04583 | 7 | 2 | 0.517 ±0.040 | 0 |
| C. Scandina via Lake, MN | 45.590 00 | −95.97028 | 3 | 1 | 0.000 ±0.000 | 0 |
| Lake Winnipeg | | | 30 | 1 | 0.000 ±0.000 | 0 |
| D. Lake Winnipeg, MB | 52.08753 | −97.68875 | 30 | 1 | 0.000 ±0.000 | 0 |
| Lake Superior | | | 25 | 1 | 0.000 ±0.000 | 0 |
| E. St. Louis Bay, MN | 46.659 72 | −92.20694 | 25 | 1 | 0.000 ±0.000 | 0 |
| Lake Michigan | | | 30 | 3 | 0.349 ±0.102 | 0 |
| F. Grand Haven, MI | 43.065 83 | −86.34500 | 30 | 3 | 0.349 ±0.102 | 0 |
| Lake Huron | | | 30 | 3 | 0.356 ±0.106 | 0 |
| G. Saginaw Bay, MI | 43.429 17 | −83.75361 | 30 | 3 | 0.356 ±0.106 | 0 |
| Lake Erie | | | 334 | 12 | 0.231 ±0.030 | 9 |
| MU 1 | | | 115 | 4 | 0.253 ±0.052 | 2 |
| H. Port Clinton, OH | 41.51944 | −82.92083 | 15 | 3 | 0.647 ±0.088 | 1 |
| I. South Bass Island, OH | 41.65750 | −82.82222 | 15 | 3 | 0.447 ±0.134 | 1 |
| J. Cedar Point, OH | 41.47222 | −82.65833 | 40 | 3 | 0.098 ±0.064 | 0 |
| K. Sandusky , OH | 41.45139 | −83.04833 | 15 | 3 | 0.133 ±0.112 | 0 |
| L. Sturgeon Creek, ON | 42.0 0833 | −82.58750 | 30 | 2 | 0.129 ±0.079 | 1 |
| MU 2 | | | 110 | 6 | 0.247 ±0.052 | 3 |
| M. Erieau, ON | 42.25 152 | −81.91667 | 30 | 1 | 0.000 ±0.000 | 0 |
| N. Vermilion, OH | 41.49667 | −82.36722 | 15 | 3 | 0.343 ±0.012 | 1 |
| O. Lorain, OH | 41.5380 6 | −82.08611 | 15 | 3 | 0.257 ±0.014 | 0 |
| P. Cleveland, OH | 41.50056 | −81.82806 | 40 | 5 | 0.315 ±0.091 | 1 |
| Q. Fairport, OH | 41.80583 | −81.41778 | 10 | 3 | 0.511 ±0.164 | 1 |
| MU 3 | | | 39 | 5 | 0.363 ±0.094 | 2 |
| R. Geneva, OH | 41.95056 | −80.83861 | 8 | 1 | 0.000 ±0.000 | 0 |
| S. Ashtabula, OH | 41.997 50 | −80.58972 | 10 | 2 | 0.200 ±0.154 | 1 |
| T. Presque Isle, PA | 42.17528 | −80.11222 | 6 | 1 | 0.333 ±0.215 | 1 |
| U. Erie, PA | 42.12778 | −80.26944 | 15 | 4 | 0.619 ±0.119 | 0 |
| MU 4 | | | 70 | 4 | 0.084 ±0.046 | 2 |
| V. Dunkirk, NY | 42.504 72 | −79.33389 | 40 | 4 | 0.146 ±0.075 | 2 |
| W. Long Point Bay, ON | 42.64 444 | −80.22250 | 30 | 1 | 0.000 ±0.000 | 0 |
| Lake Ontario | | | 15 | 2 | 0.133 ±0.112 | 1 |
| X. Rochester , NY | 43.2880 1 | −77.14111 | 15 | 2 | 0.133 ±0.112 | 1 |
| Lake Champlain | | | 30 | 2 | 0.517 ±0.024 | 1 |
| Y. Burlington, VT | 44.46 806 | −73.50250 | 30 | 2 | 0.517 ±0.024 | 1 |
| North Atlantic coastal region | | | 31 | 5 | 0.667 ±0.066 | 3 |
| Z. Sebasticook River, ME | 44.78722 | −69.38139 | 9 | 2 | 0.556 ±0.090 | 0 |
| AA. Quantabacook Lake, ME | 44.39556 | −69.18472 | 12 | 3 | 0.439 ±0.158 | 2 |
| BB. St. Johns River, ME | 47.31923 | −68.20152 | 10 | 2 | 0.467 ±0.132 | 0 |
| South Atlantic coastal region | | | 6 | 4 | 0.822 ±0.129 | 1 |
| CC. Morgan Creek, NC | 35.42 722 | −78.97472 | 6 | 4 | 0.822 ±0.129 | 1 |
| Gulf region | | | 19 | 2 | 0.198 ±0.112 | 1 |
| DD. Chattahoochee River, GA | 31.43222 | −85.06083 | 12 | 2 | 0.303 ±0.147 | 1 |
| EE. Apalachicola River , FL | 31.352 11 | −87.01147 | 3 | 1 | 0.000 ±0.000 | 0 |
| FF. Mobile River, AL | 30.79 166 | −88.08888 | 4 | 1 | 0.000 ±0.000 | 0 |
| Total | | | 568 | 21 | 0.395 ±0.026 | |

$N$ = number of individuals, $N_h$ = number of haplotypes; $H_d$ = haplotype diversity, $N_{ph}$ = number of private (unique to that location) haplotypes. MU 1–4 = Lake Erie management units (GLFC, 2006). Vertical bars denote adjacent sites combined during analysis, which were not significantly different in individual pairwise tests.

using the software BioEdit v. 7.05 (Hall, 1999; http://bioedit.software.informer.com/). Haplotypes were determined and compared to previous results obtained by our laboratory (i.e., Faber and Stepien, 1997; Ford and Stepien, 2004).

*Data analyses*

Population genetic data were analyzed using Arlequin 3.11 (Excoffier et al., 2005; http://cmpg.unibe.ch/software/arlequin3/) and Genepop 4.0 (Rousset, 2007; http://kimura.univ-montp2.fr/~rousset/Genepop.htm) software packages in order to compare patterns of genetic divergence and diversity within and among sampling locations. Genetic variability measures included haplotypic diversity ($h$) and nucleotide diversity ($\pi$), along with their standard errors (following Nei, 1987). Pairwise comparisons among spawning sites and population groups were conducted using the $F$-statistic analog $\theta_{ST}$ (Weir and Cockerham, 1984; see Balloux and Lugon-Moulin, 2002) and $\chi^2$ contingency tests (Raymond and Rousset, 1995). Samples in adjacent areas were combined when pairwise tests indicated they were not significantly different (i.e., the upper Mississippi River watershed, Gulf coastal region, 2 sites from Maine in the North Atlantic coastal region — excluding the Sebasticook River, and some adjacent areas within a single MU in Lake Erie; see Table 1). Resultant probability values were adjusted using sequential Bonferroni correction (Rice, 1989).

Analysis of MOlecular Variance (AMOVA; Excoffier, 1994) in Arlequin was used to evaluate comparative hierarchical population genetic structure, with sampling sites grouped to test hypotheses of their genetic and geographic relationships. Relationships among haplotypes were evaluated using neighbor-joining trees (Saitou and Nei, 1987) with Kimura (1980) 2-parameter genetic distances, which corrected for unequal rates of transitions and transversions characteristic of mtDNA, in Mega 4.0 (Tamura et al., 2007; http://www.megasoftware.net/). Trees were rooted to the mtDNA control region sequence of the Eurasian perch *P. fluviatilis* (GenBank # Y14724; Nesbo et al., 1999; http://www.ncbi.nlm.nih.gov/Genbank). Bootstrap support for nodes of the tree was evaluated with 1000 pseudoreplications (Felsenstein, 1985). We used a genetic distance estimate of 2% nucleotide divergence per million years for the mtDNA control region, determined from Faber and Stepien (1997 and 1998) for yellow perch and walleye. This estimate matched that determined by Near and Benard (2004) for cytochrome *b* mtDNA of the related logperch darters *Percina spp*.

The program Isolde (in Genepop) was employed to test the hypothesis of whether genetic distance $\theta_{ST}/(1-\theta_{ST})$ corresponded to geographic distance using the natural logarithm measured as the shortest distances between pairs of spawning sites (Rousset, 1997). Regression significance was tested using Mantel's (1967) procedure with 1000 permutations in Genepop. Fine-scale structure was tested among individual and grouped locations in the 4 Lake Erie Management Units (MUs 1–4) designated for the yellow perch fishery (GLFC, 2006).

Phylogeographic patterns further were analyzed using a Nested Clade Analysis (NCA; Templeton et al., 1995) to delineate patterns of genetic aggregation and spatial dispersion, beginning with a statistical parsimony haplotype network created using TCS 1.21 (Clement et al., 2000; http://darwin.uvigo.es/software/tcs.html). The software Geodis v2.5 (Posada et al., 2000; http://darwin.uvigo.es/software/geodis.html) additionally was used to determine whether spatial distribution influenced haplotype distribution, by estimating 2 variables: 1) clade dispersion, which is the distance between the members of the clade and its geographic focus, and 2) clade displacement, which is the average distance of members of a given clade to the geographic focus of the next incremental nesting group (Posada et al., 2006).

## Results

*Haplotypes and their geographic distribution*

We identify 21 mtDNA control region yellow perch haplotypes (Tables 1–2 and Fig. 1; GenBank accession numbers FJ155931 – FJ155951) that differ at 24 nucleotide positions, including 17

**Table 2**
MtDNA control region sequence haplotypes (numbered 1–21) of yellow perch *Perca flavescens*, compared with sequence of the Eurasian perch *P. fluviatilis* (Nesbo et al., 1999)

| Haplotype number | GenBank # | 00 05 | 00 06 | 00 80 | 01 04 | 01 25 | 01 38 | 01 68 | 03 57 | 04 52 | 04 81 | 05 28 | 05 70 | 05 75 | 05 76 | 05 80 | 05 85 | 06 09 | 06 31 | 06 36 | 06 63 | 06 67 | 07 01 | 07 19 | 07 50 | *N* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | FJ155931 | A | A | C | T | C | T | C | A | A | G | C | A | T | T | C | T | A | ~ | C | A | G | G | G | T | 439 |
| 2 | FJ155932 | | | | | | | | ~ | G | | | | | | | | | | | | | | | | 39 |
| 21 | FJ155951 | | | | | | | | ~ | C | | | | | | | | | | | | | | | | 2 |
| 3 | FJ155933 | | | | C | | | | ~ | | | | | | | | | | | | | | | | | 1 |
| 4 | FJ155934 | | | T | | | | | ~ | G | | | | | | | | | | | | | | | | 2 |
| 5 | FJ155935 | | | | | | | | ~ | | | | T | | | | | | | | | | | | | 4 |
| 6 | FJ155936 | | | | | | | | ~ | | | | | | | | | | | G | | | | | | 1 |
| 7 | FJ155937 | | | | | | | | A | | | | | | | | | | | | | | | | | 3 |
| 8 | FJ155938 | | | | | | | | ~ | | | | | | | | | | | | | C | | | | 3 |
| 9 | FJ155939 | | G | | | | | | ~ | | | | | | | | | | | | | | | | | 1 |
| 10 | FJ155940 | | | | | | | | ~ | | | | | | | T | | | | | | | | | | 1 |
| 11 | FJ155941 | T | | | | | | | ~ | | | | | | | | | | | | | | | | | 4 |
| 12 | FJ155942 | | | | | | | | ~ | | A | | | | | | | | | | | | | | | 1 |
| 13 | FJ155943 | | | | C | | C | T | ~ | | | ~ | | | A | | C | G | A | | | ~ | ~ | C | | 10 |
| 14 | FJ155944 | | | | C | | C | T | ~ | | | | | A | A | | C | G | A | T | | ~ | ~ | C | | 2 |
| 15 | FJ155945 | | | | | | | | ~ | | | ~ | | A | A | | C | G | A | T | | ~ | ~ | C | | 1 |
| 16 | FJ155946 | | | | C | | C | | ~ | | | T | | A | | | C | G | | | | A | | A | C | 1 |
| 17 | FJ155947 | | | | | | C | T | ~ | | | | | A | | | C | G | | | | A | | A | C | 17 |
| 18 | FJ155948 | | | | C | T | C | T | ~ | | | | | A | | | C | G | | | | A | | A | C | 2 |
| 19 | FJ155949 | | | | C | | C | T | ~ | | | | | A | | | | | | | | | | A | C | 19 |
| 20 | FJ155950 | | | | C | | C | T | ~ | G | | | | A | | | | | | | | | | A | C | 15 |
| *P. fluviatilis* | Y14724 | A | A | C | C | C | C | T | A | A | G | C | A | T | ~ | C | C | A | ~ | ~ | G | G | | G | C | |

Numbers across the top are the nucleotide position of the substitution or indel (numbered from the beginning of the mtDNA control region; see Faber and Stepien, 1997). Blanks denote nucleotides identical to haplotype 1. ~ = indel.

**Table 3**
Number and relative frequency (in parentheses) of haplotypes (1–20) per sampling site lettered (A–FF per Table 1) across (a) North American sampling locations (note * indicates group without Sebasticook River location as that site differed somewhat) and (b) Lake Erie management units (MUs per Great Lakes Fishery Commission, 2006)

(a)

| Haplotype number | Upper Mississippi watershed | L. Winnipeg | L. Superior | L. Michigan | L. Huron | L. Erie | L. Ontario | L. Champlain | Sebasticook R. | N. Atlantic coastal* | S. Atlantic coastal | Gulf coastal | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | A–C | D | E | F | G | H–W | X | Y | Z | AA–BB | CC | DD–FF | |
| 1 | 9 (.50) | 30 (1) | 25 (1) | 24 (.80) | 26 (.86) | 292 (.874) | 14 (.93) | 15 (.50) | 4 (.444) | | – | – | 439 (.7729) |
| 2 | 9 (.50) | – | – | 4 (.133) | 3 (.10) | 23 (.069) | – | – | | – | – | – | 39 (.0687) |
| 3 | – | – | – | – | – | 1 (.003) | – | – | | – | – | – | 1 (.0018) |
| 4 | – | – | – | – | – | 2 (.006) | – | – | | – | – | – | 2 (.0035) |
| 5 | – | – | – | 2 (.067) | 1 (.03) | 1 (.004) | – | – | | – | – | – | 4 (.0070) |
| 6 | – | – | – | – | – | 1 (.003) | – | – | | – | – | – | 1 (.0018) |
| 7 | – | – | – | – | – | 3 (.009) | – | – | | – | – | – | 3 (.0053) |
| 8 | – | – | – | – | – | 3 (.009) | – | – | | – | – | – | 3 (.0053) |
| 9 | – | – | – | – | – | 1 (.003) | – | – | | – | – | – | 1 (.0018) |
| 10 | – | – | – | – | – | 1 (.003) | – | – | | – | – | – | 1 (.0018) |
| 11 | – | – | – | – | – | 4 (.012) | – | – | | – | – | – | 4 (.0070) |
| 12 | – | – | – | – | – | – | 1 (.067) | – | | – | – | – | 1 (.0018) |
| 13 | – | – | – | – | – | – | – | – | 5 (.556) | 3 (.136) | 2 (.333) | – | 10 (.0176) |
| 14 | – | – | – | – | – | – | – | – | | 2 (.091) | – | – | 2 (.0035) |
| 15 | – | – | – | – | – | – | – | – | | 1 (.046) | – | – | 1 (.0022) |
| 16 | – | – | – | – | – | – | – | – | | – | 1 (.167) | – | 1 (.0022) |
| 17 | – | – | – | – | – | – | – | – | | 16 (.727) | 1 (.167) | – | 17 (.0299) |
| 18 | – | – | – | – | – | – | – | – | | – | – | 2 (.105) | 2 (.0035) |
| 19 | – | – | – | – | – | – | – | – | | – | 2 (.333) | 17 (.895) | 19 (.0335) |
| 20 | – | – | – | – | – | – | – | 15 (.50) | | – | – | – | 15 (.0264) |
| 21 | – | – | – | – | – | 2 (.006) | – | – | | – | – | – | 2 (.0035) |
| Total | 18 | 30 | 25 | 30 | 30 | 334 | 15 | 30 | 9 | 22 | 6 | 19 | 568 |

(b)

| Haplotype number | MU 1 | MU 2 | MU 3 | MU 4 | Lake Erie Total |
|---|---|---|---|---|---|
| | H–L | M–Q | R–U | V–W | |
| | 99 (.861) | 95 (.864) | 31 (.795) | 67 (.958) | 292 (.8742) |
| 2 | 9 (.078) | 10 (.091) | 3 (.077) | 1 (.014) | 23 (.0688) |
| 3 | – | – | – | 1 (.014) | 1 (.0030) |
| 4 | 1 (.009) | 1 (.009) | – | – | 2 (.0060) |
| 5 | – | 1 (.009) | – | – | 1 (.0030) |
| 6 | – | 1 (.009) | – | – | 1 (.0030) |
| 7 | – | – | 3 (.077) | – | 3 (.0090) |
| 8 | – | 1 (.009) | 2 (.051) | – | 3 (.0090) |
| 9 | – | – | – | 1 (.014) | 1 (.0030) |
| 10 | – | 1 (.009) | – | – | 1 (.0030) |
| 11 | 4 (.035) | – | – | – | 4 (.0120) |
| 21 | 2 (.017) | – | – | – | 2 (.0060) |
| Total | 115 | 110 | 39 | 70 | 334 |

transitional substitutions, 7 transversions, and 5 indels (Table 2). Haplotype 1 is the most common and widespread; characterizing 87.8% of the individuals across the Great Lakes region (reaching 100% in Lake Superior), 100% in Lake Winnipeg, 50% in the upper Mississippi River watershed, 50% in Lake Champlain, and 44.4% in Maine's Sebasticook River site (Table 3a and Fig. 1). Haplotype 1 is absent from other sites to the east along the Atlantic coast, leading to a significant divergence of yellow perch spawning in the Sebasticook River from other locations (Table 4a). Haplotype 2 is the next most widely spread, found in the upper Mississippi River watershed (50%) and Lakes Michigan, Huron, and Erie (where it ranges from 13.3% to 10% to 6.9%). Type 5 is found only in Lakes Michigan, Huron, and Erie; types 13 and 17 occur in the north and south Atlantic coastal sites alone; and 19 is shared between the south Atlantic and Gulf coastal samples.

Other haplotypes are exclusively found in individual watersheds (Table 3). Notably, 10 rare haplotypes uniquely appear in Lake Erie sites (which may reflect larger sample sizes), each constituting 0.3–1.2%. Rare haplotypes elsewhere in the Great Lakes include haplotype 12, which is found only in a single individual from Lake Ontario. Haplotype 20 appears only in Lake Champlain and characterizes half of its sampled individuals. Two unique haplotypes occur in the Quantabacook Lake site in Maine (14 and 15, representing 16.7% and 8.3% of its respective individuals). Two other haplotypes (13 and 17) are found both in the north (Maine — in the Sebasticook and St. John's Rivers) and the south Atlantic coastal samples (North Carolina), respectively totaling 27% (combined Maine sites) and 48.6%. Haplotype 16 appears unique to the south Atlantic coastal yellow perch sample (totaling 16.7%) and type 19 is found both in the south Atlantic and Gulf coastal samples (33.3% versus 89.5%, respectively). Haplotype 18 uniquely characterizes 2 individuals from the Gulf coastal site in Georgia (10.5%). Haplotypes thus show a geographic pattern of closer relationship between those found in the Great Lakes (including Lake Winnipeg and the upper Mississippi River system), which then markedly diverge from those in the east and south (including Lake Champlain, and the Atlantic and Gulf coastal regions; Figs. 1 and 2).

Haplotype diversity levels in our yellow perch samples range from 0.000 (a single haplotype) in some locations, including Lake Winnipeg, Lake Superior, 3 locations in Lake Erie, and 2 sites in

**Table 4**
Pairwise genetic divergences between yellow perch samples (lettered per Table 1) using $\theta_{ST}$ (below diagonal; Weir and Cockerham, 1984) and $\chi^2$ contingency tests (above diagonal; Raymond and Rousset, 1995) across (a) North American watershed sites (note: Sebasticook River, Maine site was not included in the North Atlantic coastal group* in this Table due to some differences), (b) Lake Erie spawning sites (adjacent locations are combined that do not differ in some individual pairwise tests), and (c) Lake Erie management units (MUs)

(a)

| | Upper Mississippi watershed | Lake Winnipeg | Lake Superior | Lake Michigan | Lake Huron | Lake Erie | Lake Ontario | Lake Champlain | Sebasticook River | North Atlantic coastal* | South Atlantic coastal | Gulf coastal |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | A–C | D | E | F | G | H–W | X | Y | Z | AA–BB | CC | DD–FF |
| A–C | – | 21.27** | 18.68** | 8.89* | 10.99* | 12.32* | 13.05* | Inf** | 15.64** | Inf** | Inf** | Inf** |
| D | 0.552** | – | 0.00 | 6.43* | 3.51 | 1.29 | 2.15 | 22.66** | 16.65** | Inf** | Inf** | Inf** |
| E | 0.522** | 0.000 | – | 5.66 | 2.82 | 1.24 | 1.97 | 21.64** | 15.62** | Inf** | Inf** | Inf** |
| F | 0.219* | 0.080 | 0.069 | – | 0.00 | 2.98 | 4.58 | Inf** | 16.75** | Inf** | Inf** | Inf** |
| G | 0.290* | 0.052 | 0.042 | 0.000 | – | 0.82 | 2.99 | Inf** | 16.81** | Inf** | Inf** | Inf** |
| H–W | 0.409** | 0.011 | 0.008 | 0.012 | 0.000 | – | 3.37 | Inf** | Inf** | Inf** | Inf** | Inf** |
| X | 0.399** | 0.050 | 0.036 | 0.040 | 0.022 | 0.012 | – | 14.76** | 11.45* | Inf** | 20.58** | Inf** |
| Y | 0.359** | 0.483** | 0.458** | 0.441** | 0.452** | 0.768** | 0.396** | – | 20.70** | Inf** | Inf** | Inf** |
| Z | 0.587** | 0.714** | 0.682** | 0.650** | 0.669** | 0.870** | 0.575** | 0.316* | – | 23.03** | 7.17* | Inf** |
| AA–BB | 0.822** | 0.875** | 0.863** | 0.852** | 0.859** | 0.950** | 0.824** | 0.554** | 0.498** | – | 10.01* | Inf** |
| CC | 0.797** | 0.893** | 0.876** | 0.848** | 0.861** | 0.948** | 0.808** | 0.338* | 0.217 | 0.176* | – | 11.34* |
| DD–FF | 0.904** | 0.952** | 0.946** | 0.919** | 0.929** | 0.958** | 0.922** | 0.399** | 0.690** | 0.648** | 0.430* | – |

(b)

| | Port Clinton/ South Bass Isl. | Cedar Pt./ Sandusky | Sturgeon Creek | Erieau | Vermilion | Lorain/Cleveland/ Fairport | Geneva/Ashtabula/ Presque Isle/Erie | Dunkirk | Long Pt. Bay |
|---|---|---|---|---|---|---|---|---|---|
| | H–I | J–K | L | M | N | O–Q | R–U | V | W |
| H–I | – | 12.46** | 12.81** | 12.02** | 1.64 | 5.85 | 9.08* | 9.79** | 11.69** |
| J–K | 0.122** | – | 4.24 | 1.24 | 3.48 | 1.03 | 6.98* | 0.79 | 1.23 |
| L | 0.117* | 0.004 | – | 1.42 | 7.97* | 5.99* | 8.34* | 2.33 | 1.43 |
| M | 0.169** | 0.010 | 0.034 | – | 6.90* | 4.05 | 6.79* | 0.00 | 0.00 |
| N | 0.000 | 0.069 | 0.096 | 0.236* | – | 0.24 | 2.59 | 2.85 | 6.93** |
| O–Q | 0.009 | 0.156** | 0.143** | 0.199** | 0.000 | – | 3.12 | 2.81 | 4.05 |
| R–U | 0.076* | 0.000 | 0.010 | 0.031 | 0.019 | 0.094* | – | 4.96 | 6.77** |
| V | 0.131** | 0.000 | 0.004 | 0.000 | 0.101 | 0.165** | 0.008 | – | 0.00 |
| W | 0.169** | 0.010 | 0.034 | 0.000 | 0.236* | 0.199 | 0.031 | 0.000 | – |

(c)

| | MU 1 | MU 2 | MU 3 | MU 4 |
|---|---|---|---|---|
| | H–L | M–Q | R–U | V–W |
| MU 1 | – | 4.11 | 10.44** | 8.09** |
| MU 2 | 0.000 | – | 5.04 | 5.99* |
| MU 3 | 0.009 | 0.006 | – | 10.26** |
| MU 4 | 0.029** | 0.029** | 0.080** | – |

* = significant at 0.05 level.
** = significant following sequential Bonferroni correction (Rice, 1989). Inf = $\chi^2$ value indicated by Genepop as "infinite".

the Gulf coastal region (the latter may be an artifact of small sample size) to 0.822 in the south Atlantic coastal site; averaging $0.395 \pm 0.026$ across all of our samples (Tables 1 and 3a). In the Great Lakes, genetic diversity is greater in yellow perch samples from Lakes Huron and Michigan than in Lakes Erie and Ontario. Genetic diversity is higher in Lake Champlain, as well as along the Atlantic coastal sites. (Table 1).

Divergences among individual haplotypes reach a pairwise genetic distance of $P = 0.0073$, corresponding to ~365,000 estimated years of separation (Fig. 2). This greatest genetic divergence level separates haplotypes characteristic of the Great Lakes region (types 1–12 and 21; including Lake Winnipeg and the upper Mississippi River samples) from those in the east comprising the Lake Champlain/Atlantic/Gulf coastal population group (types 13–20). Maximal pairwise genetic divergence among Great Lakes haplotypes is $P = 0.0031$, corresponding to ~155,000 years of separation. Sequence divergence of $P = 0.0034$ separates haplotypes found only in the north Atlantic coastal sites, diverging up to ~170,000 years, whereas the single unique south Atlantic coastal haplotype (16) differs only by $P = 0.0007$ and ~34,000 years. The unique haplotype (18) in the Gulf coastal sites is separated from the Atlantic coastal types by $P = 0.0025$ and ~124,000 years. Haplotype 20 uniquely characterizes the Lake Champlain sample, diverging by $P = 0.001$ and ~50,000 years (Fig. 2).

*Broad-scale population relationships*

Genetic divergence between the Upper Mississippi River/Great Lakes/Lake Winnipeg samples versus the Lake Champlain/Atlantic/Gulf coastal regions explains 72% of the overall genetic variation in the AMOVA analysis ($p < 0.0019$) and has a fixation index value of 0.73 (Table 5a), indicating a great genetic divergence level (see Hartl, 1988). Further division into 3 groups (splitting the Gulf coast group from the Atlantic coastal/Lake Champlain group) accounts for 75% of the divergence, and a fixation index of 0.75. There also is significant partitioning of variation among spawning locations within the groups in both analyses; respectively totaling 14% and 11%, with fixation indices of 0.86 and 0.86 (Tables 5a, b). Thus, the hypothesis of 3 primary yellow perch population groups is best supported by our data in these analyses.

Many of the pairwise $\theta_{ST}$ (Weir and Cockerham, 1984) and $\chi^2$ contingency test comparisons (Raymond and Rousset, 1995) reveal significant divergences between individual spawning population sites, particularly those located in disparate geographic regions, ranging from $\theta_{ST} = 0.907$ between samples from the Gulf coastal region versus sites in the upper Mississippi River, Lake Winnipeg, and the Great Lakes (Table 4a). These sites also have the greatest geographic separation. Samples that

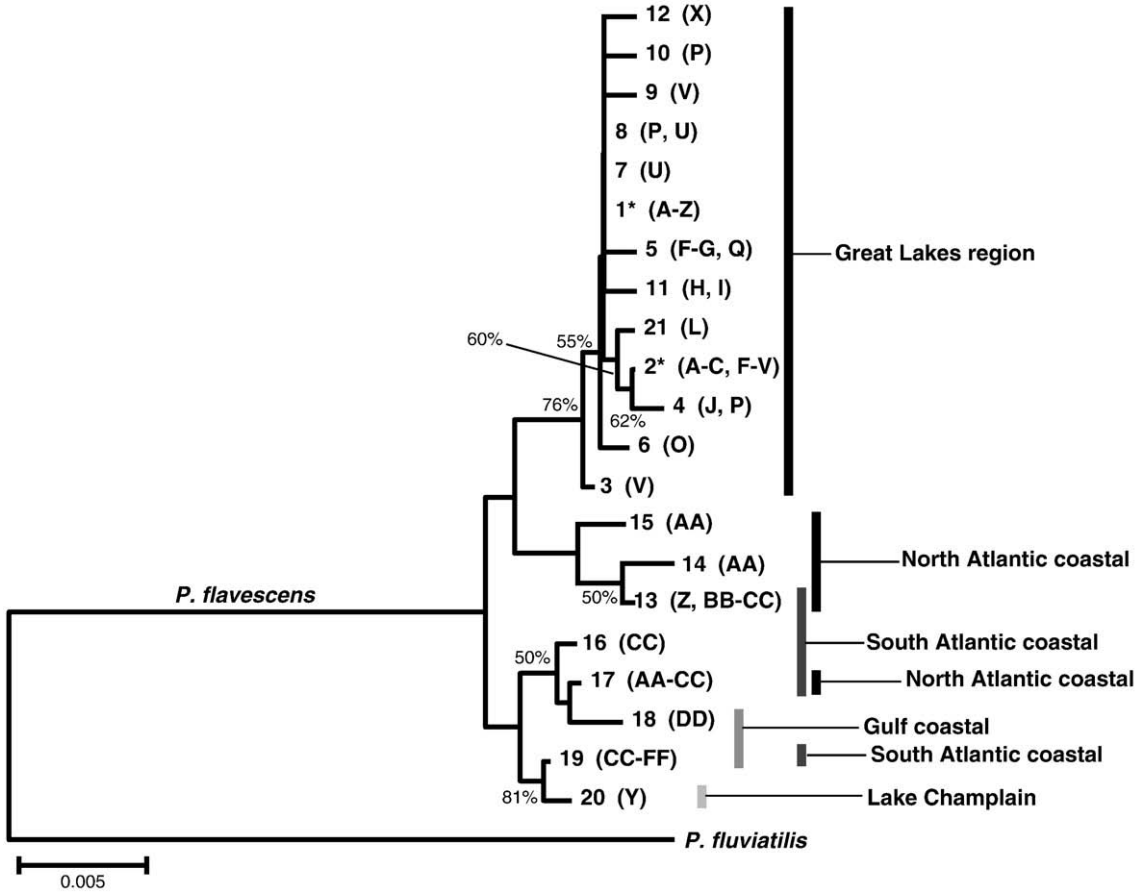


**Fig. 2.** Neighbor-joining tree (Saitou and Nei, 1987) of Kimura (1980) 2-parameter genetic distances showing relationships among yellow perch mtDNA haplotypes (numbered per Table 2), rooted to Eurasian perch and constructed in Mega (Tamura et al., 2007). Percentages denote nodal support from 1000 bootstrap pseudoreplicates (showing those greater than 50%). Horizontal bar in lower left denotes genetic distance calibration. * = most common haplotypes (1, 2) that are most widely distributed. Vertical bars denote primary geographical regions (with sites lettered as A-FF per Table 1).

significantly diverge from all other locations include those from the upper Mississippi River watershed, the north Atlantic coastal region, and the Gulf coastal region. A Mantel (1967) test of pairwise $\theta_{ST}/(\theta_{ST}-1)$ values versus geographical distance across all sampling locations reveals a positive association ($R^2=0.413$, $p=0.003$; Fig. 3a), supporting the hypothesis of broad-scale genetic isolation by geographic distance.

Nested Clade Analysis indicates 2 primary yellow perch population clades (one in the Great Lakes/Upper Mississippi River/Lake Winnipeg region and the other containing the Atlantic/Gulf coastal/ Lake Champlain sites; not shown), with each containing significantly defined component groups. Seven clades at various nesting levels are significant, with the majority supporting restricted gene flow due to genetic isolation by geographic distance. This result thus is congruent with the Mantel test. The Nested Clade Analysis indicates gradual range expansion followed by fragmentation for populations found in Lake Champlain and in the north Atlantic coastal region. A pattern of contiguous range expansion is supported for all Great Lakes populations except Lake Superior.

**Table 5**
Distribution of genetic variation among yellow perch samples using Analysis of MOlecular Variance (AMOVA) across (a) North America partitioned in 2 regions (Upper Mississippi River/Great Lakes/Lake Winnipeg, A–X versus the Atlantic/Gulf coastal region/Lake Champlain, Y–FF), (b) North America partitioned in 3 regions (additionally separating Atlantic coastal/Lake Champlain samples, X–CC from the Gulf coastal samples, DD–FF), (c) Lake Erie management units (MUs 1–4) (H–W).

| Source of variation | % Variation | Fixation index | Significance |
|---|---|---|---|
| *(a)* | | | |
| Between 2 North American regions | 72.31 | 0.723 | $p<0.0019$ |
| Among sampling sites within regions | 13.65 | 0.859 | $p<0.0001$ |
| Within sampling sites | 14.05 | 0.493 | $p<0.0001$ |
| *(b)* | | | |
| Among 3 North American regions | 75.42 | 0.754 | $p<0.0019$ |
| Among sampling sites within regions | 10.76 | 0.862 | $p<0.0001$ |
| Within sampling sites | 13.82 | 0.438 | $p<0.0001$ |
| *(c)* | | | |
| Among 4 Lake Erie Management Units | 0.36 | 0.000 | $p=0.4125$ |
| Among sampling sites within MUs | 4.31 | 0.036 | $p=0.0205$ |
| Within Lake Erie sampling sites | 95.33 | 0.043 | $p=0.0068$ |

### *Fine-scale haplotype patterns in Lake Erie*

Haplotypes 1 and 2 are common in yellow perch throughout Lake Erie, with type 1 more common and type 2 rarer in the east in MU4 (Fig. 1b and Table 3b). Unique haplotypes are found in all Lake Erie MUs, including types 11 and 21 in MU 1 (comprising 3.5% and 1.7% of the sample, respectively), types 6 and 10 in MU 2 (each singletons), type 7 in MU 3 (7.7%), and types 3 and 9 in MU 4 (singletons). Haplotype 4 is rare and found only in western Lake Erie (averaging

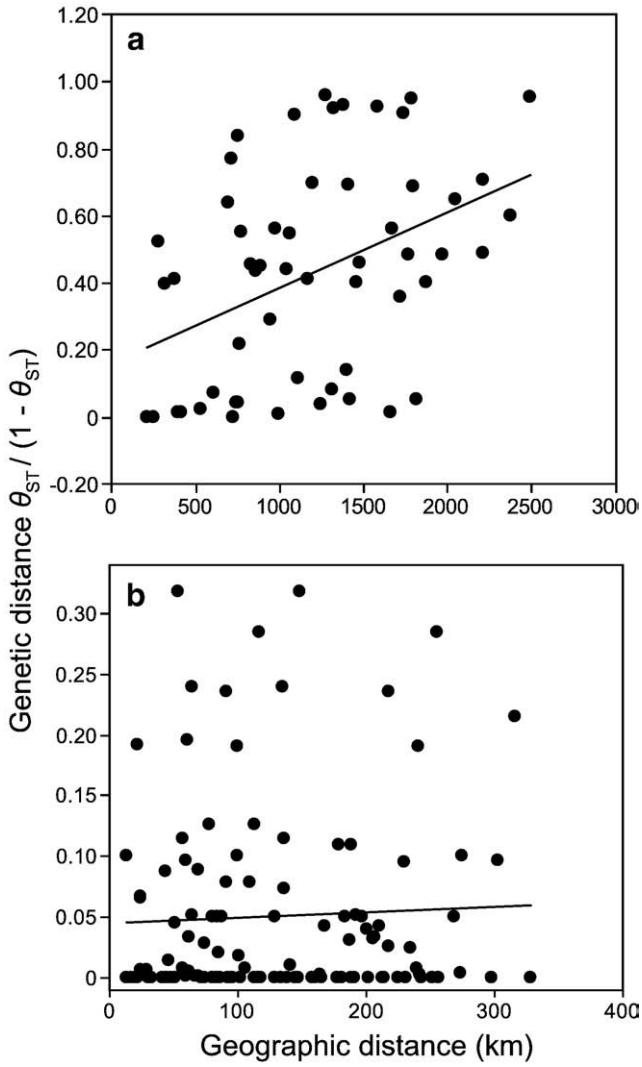


**Fig. 3.** Mantel (1967) pairwise test for relationship between genetic distance ($\theta_{ST}$/ 1 $-\theta_{ST}$) and geographical distance (km) among yellow perch sampling sites. (a) Across North American sites; $p = 0.003$**, $R^2 = 0.413$, $y = 0.0002$ (km) + 0.1609. (b) Across Lake Erie: $p = 0.604$ (NS), $R^2 = 0.046$. $y = 0.00005$ (km) + 0.0434.

0.9% in MUs 1 and 2) and type 8 characterizes only the central locations (averaging 3.1% in MUs 2 and 3).

Unlike broad-scale relationships across the range, fine-scale relationships among Lake Erie spawning groups of yellow perch do not correspond to an isolation by geographic distance pattern ($R^2 = 0.046$, $p = 0.604$, not significant; Fig. 3b). $\theta_{ST}$ analyses (Table 4b) show significant pairwise divergences for 8 of the comparisons between combined Lake Erie spawning sites, which involve sites in all MUs. Seven comparisons are significant using $\chi^2$ contingency tests. When spawning sites are grouped by MU, only $\theta_{ST}$ comparisons involving MU 4 appear significantly different (Table 4c). Comparisons using $\chi^2$ contingency tests yield similar results, with an additional significant difference between MU 1 versus MU 3.

However, AMOVA analyses show no significant partitioning of genetic variation among the 4 MUs (Table 5c). This also is true of a separate AMOVA analysis comparison of population variation among the 3 Lake Erie physiographic basins, and a comparison between the northern and southern shores (not shown). Thus, our data do not match the designation of MUs in Lake Erie.

## Discussion

### *Genetic diversity of yellow perch populations*

MtDNA control region sequence haplotypes in our study reveal greater genetic diversity in yellow perch than found in previous broad-scale studies using lower resolution genetic techniques, including allozymes (Leary and Booke, 1982; Todd and Hatcher, 1993; Moyer and Billington, 2004) and mtDNA restriction fragment length polymorphisms (RFLPs) (Billington, 1993; Moyer and Billington, 2004). Likewise, recent microsatellite DNA analysis of yellow perch in Lake Michigan revealed relatively low heterozygosity levels of $h = 0.210$ (Miller, 2003) and similar ranges were described in captive yellow perch broodstocks founded by parents from Lakes Huron and Erie (Brown et al., 2007). Despite the enhanced resolution of our study, mtDNA sequences of the entire control region likewise reveal that yellow perch have relatively low genetic variation in comparison with other fishes, which for several of our sampling sites also may reflect small sample sizes (Table 4b).

Overall mtDNA genetic diversity of yellow perch is lower than that of walleye *Sander vitreus* (Stepien and Faber, 1998; Stepien et al., 2004), and roughly equivalent to that determined for Eurasian perch *Perca fluviatilis* (Refseth et al., 1998; Nesbo et al., 1998, 1999). Similarly, *P. fluviatilis* had relatively low allozymic genetic diversity (Gyllensten et al., 1985; Bodaly et al., 1989). Relatively low genetic diversity in both mtDNA and nuclear DNA thus appears characteristic of the genus *Perca*. Moreover, mtDNA control region and nuclear LdhA6 intron sequences revealed little variation in the ruffe *Gymnocephalus cernuus* across Eurasia (Stepien et al., 1998, 2005), which is the sister genus to *Perca* (Faber and Stepien, 1997). This finding appears to indicate that generally low genetic diversity is characteristic of the *Perca-Gymnocephalus* lineage.

MtDNA control region haplotypes of yellow perch present in the Great Lakes region likely descended from the Mississippian glacial refugium and remain divergent from those descending from the Atlantic coastal region. Populations in the Mississippian refugium are hypothesized to have experienced more genetic bottlenecking, and their descendents consequently are less genetically variable than those originating from the Atlantic refugium (McPhail and Lindsey, 1970), which appears true for yellow perch in our study and others (see Todd and Hatcher, 1993). Likewise, Haponski and Stepien (2008) found greater haplotypic diversity in the greenside darter subspecies *Etheostoma blennioides blennioides* descendent from an easterly refugium, in comparison to *E. b. pholidotum* tracing to the Mississippian refugium in the Wabash River system. Exploitation and fluctuations of yellow perch populations in the Great Lakes since the early 1900s presumably further decreased genetic diversity, as suggested by Strittholt et al. (1988).

Our mtDNA control region data reveal higher haplotypic diversity in yellow perch from the Atlantic coastal region than found in the Great Lakes samples, appearing greatest in the North Carolina location. This finding of higher genetic variability along the south Atlantic coastal region is corroborated by allozyme results of Todd and Hatcher (1993). As that region was unglaciated during the Ice Ages and is one of the most southerly regions in our study (see Fig. 1), its populations likely accumulated and retained more historic genetic variation. This is a common trend in many freshwater fishes across North America, with areas that were unglaciated housing higher genetic variability and more genetic divergence today than are found in regions that were once glaciated (see Billington and Hebert, 1991; Bernatchez and Wilson, 1998). Less genetic diversity is found in the Gulf coastal sites, where yellow perch are rare.

*Broad-scale genetic divergence patterns*

Two primary clades of yellow perch haplotypes are resolved across North America, corresponding to a primary division between the descendents from the Mississippian refugium to the west versus the Atlantic coastal refugium and southern unglaciated regions to the east. Using the molecular clock calibration of 2% per million years (my) of Faber and Stepien (1998) and Near and Benard (2004), this separation of 0.73% dates to ~365,000 years ago (ya) and a mid-Pleistocene divergence. This time corresponds to the longest prolonged cold period during the Pleistocene ice age (Crespi et al., 2003), when there likely was little exchange between refugia.

A microsatellite study of smallmouth bass (Stepien et al., 2007) also found a marked divergence between the Great Lakes versus Atlantic coastal groups, which was the largest division among populations across North America. Other fishes show similar dichotomies between Mississippian and Atlantic ancestral distributions, including cisco *Coregonus artedi* (Turgeon and Bernatchez, 2001a,b), brook char *Salvelinus fontinalis* (Wilson and Hebert, 1996; Angers and Bernatchez, 1998; Danzmann et al., 1998), and northern hogsucker *Hypentelium nigricans* (Berendzen et al., 2003). Yellow perch haplotype 1 is widely distributed in the north to western Maine, likely indicating common ancestry, but does not occur in the Atlantic seaboard populations. Most haplotypes in the Mississippi refugium that later colonized the Great Lakes differ only slightly from haplotype 1, with maximal divergence time among them ranging to ~155,000 years.

Additional population division supports long-term separation of yellow perch in the Gulf coastal region from those in the Atlantic coastal samples. The Atlantic coastal haplotypes diverge from one another by up to ~170,000 years and from the unique Gulf coastal type by ~124,000 years. Billington et al. (1992) similarly found marked divergence in walleye from a relict population in the Gulf coast versus other North American locations analyzed.

The Lake Champlain population of yellow perch shows genetic isolation from populations in the Great Lakes drainage, as well as from those in the Atlantic/Gulf coasts. Notably, Lake Champlain houses unique haplotype 20 that is the sister type of 19 from the southern Atlantic and Gulf coastal sites, suggesting a divergent post-glacial dispersal pathway from the south that did not lead to Maine (see Fig. 1). Prevalence of haplotype 1 in Lake Champlain and western Maine also suggests common genetic contribution from the west, which apparently did not reach the sites in eastern Maine or locations to the south. The genetic divergence of endemic haplotype 20 dates to ~50,000 ya (*P*-distance = 0.001), indicating that it predated modern Lake Champlain.

*Fine-scale divergence in Lake Erie*

Stepien and Faber (1998) and Strange and Stepien (2007) postulated that genetic divergence patterns of walleye *Sander vitreus* spawning groups across Lake Erie were the result of historic recolonization patterns from western (Mississippian) and eastern (Atlantic) glacial refugia, maintained by spawning site philopatry and likely natal homing to spawning sites. We find less genetic divergence in yellow perch across Lake Erie than in walleye (Stepien and Faber, 1998; Strange and Stepien, 2007) or smallmouth bass (Stepien et al., 2007). Both walleye and smallmouth bass had greater genetic diversity in eastern Lake Erie. Our results suggest that yellow perch in Lake Erie received less genetic contribution from an eastern glacial refugium than occurred for either walleye or smallmouth bass.

Relatively low mtDNA genetic diversity and divergence levels in Lake Erie yellow perch may have resulted from bottlenecks due to population size fluctuations (Marsden and Robillard, 2004), which affect mtDNA more than nuclear DNA (see Avise, 2004). In contrast to our study, a fine-scale microsatellite analysis of yellow perch in Lake Michigan (Miller, 2003) described significant divergence between samples from Green Bay and surrounding inland lake sites, as well as groups in open waters of Lake Michigan. Microsatellite markers also resolved fine-scale differentiation in the St. Lawrence River system (LeClerc et al., 2008). Whereas we discern significant broad-scale correspondence between genetic divergence and geographic distance in yellow perch, this is not true for its fine-scale analysis in Lake Erie. Likewise, walleye samples across Lake Erie did not correspond to a genetic isolation by geographic distance pattern (Strange and Stepien, 2007).

Overall, our mtDNA results indicate relatively low genetic variability and population structure in Lake Erie. The distribution of this genetic variation in Lake Erie yellow perch does not appear to correspond to fishery management units (MUs). Our study reveals some genetic divergences among a few yellow perch spawning groups across Lake Erie, including differentiation of the eastern samples (MU 4), which should be further assessed with higher-resolution microsatellite data.

*Summary and conclusions*

The yellow perch displays considerable broad-scale population genetic structure across its range — reflecting vicariance among drainages, isolation by geographic distance, glacial refugium patterns, and post-glacial dispersion pathways. In comparison with other percids, the yellow perch has relatively low genetic diversity, likely due to population fluctuations as well as its phylogenetic history (since other *Perca* and *Gymnocephalus* species show similarly low values). Further fine-scale studies of yellow perch population genetic structure using higher-resolution nuclear microsatellites additionally will aid stock discrimination and help managers to conserve what genetic diversity remains.

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## Appendix A

Pairwise genetic divergences between yellow perch samples using $\theta_{ST}$ (below diagonal; Weir and Cockerham, 1984) and $\chi^2$ contingency tests (above diagonal; Raymond and Rousset, 1995) across (a) all North American sites (identified by letters as indicated in Table 1), and (b) Lake Erie spawning sites. * = significant at 0.05 level, ** = significant following sequential Bonferroni correction (Rice, 1989). Inf = $\chi^2$ value indicated by Genepop as "infinite".

(a1)

| | A | B | C | D | E | F | G | H | I | J | K | L | M | N | O | P | Q | R | S | T | U | V | W | X | Y | Z |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| A | – | 0.00 | 3.40 | 18.38** | 15.95* | 7.59* | 10.53* | 3.25 | 5.23 | 17.81** | 9.38* | 18.42** | 18.77** | 5.27 | 9.55* | 6.71* | 3.89 | 7.39* | 6.30* | 3.98 | 8.20* | 16.72** | 17.69** | 12.76* | 21.64** | 10.97* |
| B | 0.000 | – | 3.22 | 14.81* | 14.23* | 5.74 | 7.21* | 3.50 | 2.39 | 13.84* | 7.75* | 13.89* | 15.09* | 3.86 | 7.70* | 4.97 | 2.39 | 7.30* | 4.56 | 2.65 | 5.95 | 13.31* | 15.19* | 10.45* | 18.23** | 9.56* |
| C | 0.415 | 0.344 | – | 0.00 | 0.00 | 0.00 | 0.00 | 2.00 | 0.82 | 0.00 | 0.00 | 0.00 | 0.00 | 0.97 | 0.00 | 0.00 | 0.75 | 0.00 | 0.00 | 0.00 | 1.02 | 0.00 | 0.00 | 0.00 | 2.91 | 3.16 |
| D | 0.786** | 0.764** | 0.000 | – | 0.00 | 7.42* | 4.36 | 17.78** | 9.28 | 0.00 | 2.2 | 1.42 | 0.00 | 6.88* | 4.50 | 4.10 | 8.74* | 0.00 | 2.78 | 3.58 | 14.59* | 0.00 | 0.00 | 2.20 | 24.86** | 16.28** |
| E | 0.759* | 0.734* | 0.000 | 0.000 | – | 5.70 | 2.83 | 16.45** | 8.42* | 0.00 | 1.96 | 1.41 | 0.00 | 6.19* | 4.00 | 3.27 | 8.03* | 0.00 | 2.51 | 3.27 | 13.53* | 0.00 | 0.00 | 1.97 | 24.05** | 15.25* |
| F | 0.349* | 0.285* | 0.000 | 0.080 | 0.069 | – | 0.51 | 7.29* | 1.99* | 5.86 | 1.55 | 7.94* | 7.44* | 1.42 | 2.18 | 1.75 | 0.37 | 2.54 | 0.36 | 0.00 | 9.09* | 5.43 | 7.50* | 5.17 | Inf** | 17.34** |
| G | 0.450* | 0.390* | 0.000 | 0.052 | 0.042 | 0.000 | – | 8.50* | 2.12 | 2.81 | 0.00 | 4.95 | 4.37 | 0.54 | 0.76 | 0.06 | 1.00 | 0.81 | 0.00 | 0.00 | 8.99* | 2.40 | 4.39 | 2.99 | 26.24** | 16.60** |
| H | 0.130 | 0.077 | 0.000 | 0.285** | 0.255** | 0.07 | 0.103* | – | 2.83 | 15.59* | 5.54 | 17.69** | 17.90** | 3.14 | 5.56 | 7.95* | 2.99 | 5.97 | 3.49 | 1.67 | 7.45* | 11.30* | 17.69** | 10.17* | 22.35** | 13.40* |
| I | 0.217 | 0.151 | 0.000 | 0.191* | 0.167* | 0.000 | 0.000 | 0.000 | – | 7.28* | 2.22 | 9.90* | 9.33* | 0.00 | 1.57 | 1.32 | 0.28 | 2.05 | 0.52 | 0.00 | 4.36 | 4.62 | 9.39* | 3.73 | 20.36** | 11.97* |
| J | 0.605* | 0.556** | 0.000 | 0.008 | 0.002 | 0.020 | 0.000 | 0.192* | 0.067 | – | 0.00 | 2.83 | 0.00 | 4.01 | 1.33 | 1.17 | 5.36 | 0.00 | 0.00 | 2.09 | 12.55* | 0.00 | 0.00 | 0.94 | Inf** | 18.23** |
| K | 0.517* | 0.462* | 0.000 | 0.050 | 0.036 | 0.000 | 0.000 | 0.101 | 0.006 | 0.000 | – | 2.68 | 2.20 | 1.03 | 0.00 | 0.00 | 2.06 | 0.00 | 0.00 | 0.00 | 4.69 | 0.00 | 2.20 | 0.00 | 14.60* | 11.75* |
| L | 0.618** | 0.573* | 0.000 | 0.034 | 0.026 | 0.037 | 0.013 | 0.195** | 0.088* | 0.001 | 0.000 | – | 1.42 | 7.89* | 3.69 | 5.84 | 7.31* | 0.83 | 3.15 | 3.34 | 14.52* | 2.34 | 1.42 | 2.69 | Inf** | 16.33** |
| M | 0.786** | 0.764* | 0.000 | 0.000 | 0.000 | 0.080* | 0.052 | 0.285** | 0.191* | 0.008 | 0.050 | 0.034 | – | 6.86* | 4.47 | 4.11 | 8.77* | 0.00 | 2.78 | 3.58 | 14.22* | 0.00 | 0.00 | 2.20 | Inf** | 16.36** |
| N | 0.258 | 0.187 | 0.000 | 0.236* | 0.208* | 0.000 | 0.000 | 0.014 | 0.000 | 0.066 | 0.008 | 0.096 | 0.236* | – | 1.03 | 0.27 | 0.52 | 2.48 | 0.94 | 0.00 | 4.64 | 2.85 | 6.88* | 3.01 | 18.50** | 12.41* |
| O | 0.442* | 0.382* | 0.000 | 0.050 | 0.036 | 0.000 | 0.000 | 0.089 | 0.005 | 0.000 | 0.000 | 0.001 | 0.050 | 0.006 | – | 0.42 | 1.39 | 0.00 | 0.00 | 0.00 | 4.67 | 0.85 | 4.48 | 0.00 | 16.22** | 11.39* |
| P | 0.357* | 0.295* | 0.000 | 0.050 | 0.041 | 0.000 | 0.000 | 0.078 | 0.000 | 0.001 | 0.000 | 0.021 | 0.050 | 0.000 | 0.000 | – | 1.69 | 0.54 | 0.00 | 0.00 | 6.62 | 3.27 | 4.09 | 2.19 | Inf** | 17.45 |
| Q | 0.191 | 0.124 | 0.000 | 0.239* | 0.206* | 0.000 | 0.000 | 0.000 | 0.000 | 0.079 | 0.010 | 0.101 | 0.239* | 0.000 | 0.002 | 0.000 | – | 1.48 | 1.08 | 0.00 | 2.90 | 3.96 | 8.68 | 4.85 | 16.84** | 8.59*** |
| R | 0.571* | 0.525* | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.109 | 0.042 | 0.000 | 0.000 | 0.000 | 0.000 | 0.073 | 0.000 | 0.000 | 0.045 | – | 0.00 | 1.70 | 3.30 | 0.00 | 0.00 | 0.00 | 8.63* | 7.07* |
| S | 0.406* | 0.340 | 0.000 | 0.126 | 0.102 | 0.000 | 0.000 | 0.040 | 0.000 | 0.000 | 0.000 | 0.000 | 0.126 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | – | 0.00 | 2.85 | 0.00 | 2.78 | 0.86 | 12.84* | 7.92* |
| T | 0.242 | 0.166 | 0.000 | 0.318 | 0.275 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.032 | 0.318 | 0.000 | 0.000 | 0.000 | 0.000 | 0.051 | 0.000 | – | 1.67 | 1.64 | 3.58 | 1.40 | 8.86* | 5.88* |
| U | 0.400* | 0.341* | 0.000 | 0.114 | 0.095 | 0.021 | 0.018 | 0.095 | 0.026 | 0.042 | 0.002 | 0.052 | 0.114* | 0.031 | 0.002 | 0.000 | 0.018 | 0.000 | 0.000 | 0.000 | – | 11.24* | 14.80* | 7.23* | 24.05** | 11.47* |
| V | 0.623** | 0.578** | 0.000 | 0.000 | 0.000 | 0.041 | 0.012 | 0.215* | 0.097* | 0.000 | 0.000 | 0.004 | 0.000 | 0.101* | 0.000 | 0.024 | 0.109 | 0.000 | 0.000 | 0.028 | 0.050 | – | 0.00 | 0.64 | Inf** | 18.59** |
| W | 0.786** | 0.764** | 0.000 | 0.000 | 0.000 | 0.080 | 0.052 | 0.285** | 0.191* | 0.008 | 0.050 | 0.034 | 0.000 | 0.236* | 0.050 | 0.050 | 0.239* | 0.000 | 0.126 | 0.318 | 0.114* | 0.000 | – | 2.20 | Inf** | 16.83** |
| X | 0.580* | 0.534* | 0.000 | 0.050 | 0.036 | 0.040 | 0.022 | 0.161* | 0.086 | 0.007 | 0.000 | 0.018 | 0.050 | 0.107 | 0.000 | 0.024 | 0.090 | 0.000 | 0.007 | 0.054 | 0.036 | 0.000 | 0.050 | – | 14.91* | 11.82* |
| Y | 0.297* | 0.285* | 0.25 | 0.483** | 0.458** | 0.441** | 0.452** | 0.352* | 0.361* | 0.504** | 0.386* | 0.469** | 0.483** | 0.364* | 0.382* | 0.475** | 0.327* | 0.342* | 0.344* | 0.293 | 0.381* | 0.504** | 0.483* | 0.396* | – | 21.45** |
| Z | 0.495* | 0.468* | 0.321 | 0.714** | 0.682* | 0.650** | 0.669** | 0.525* | 0.544* | 0.729** | 0.575* | 0.690** | 0.714** | 0.557** | 0.562* | 0.683** | 0.483* | 0.480* | 0.504* | 0.422* | 0.542* | 0.726* | 0.714** | 0.575* | 0.316* | – |

(a2)

| | A | B | C | D | E | F | G | H | I | J | K | L | M | N | O | P | Q | R | S | T | U | V | W | X | Y | Z |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AA | 0.818** | 0.809** | 0.773* | 0.917** | 0.906** | 0.886** | 0.895** | 0.830** | 0.845** | 0.918** | 0.865** | 0.906** | 0.917** | 0.853** | 0.857** | 0.897** | 0.821** | 0.831** | 0.836** | 0.803* | 0.848** | 0.918** | 0.917** | 0.865** | 0.545** | 0.504** |
| BB | 0.816** | 0.806** | 0.766* | 0.923** | 0.912** | 0.888** | 0.899** | 0.828** | 0.846** | 0.922** | 0.869** | 0.910** | 0.923** | 0.855** | 0.859** | 0.899** | 0.819** | 0.832** | 0.838** | 0.800** | 0.849** | 0.922** | 0.923** | 0.869** | 0.523** | 0.425** |
| CC | 0.720* | 0.700** | 0.597* | 0.893** | 0.876** | 0.848** | 0.861** | 0.756** | 0.778** | 0.895** | 0.808** | 0.876** | 0.893** | 0.790** | 0.796** | 0.865** | 0.730** | 0.738** | 0.754** | 0.682* | 0.783** | 0.894** | 0.893** | 0.808** | 0.338* | 0.217* |
| DD | 0.871** | 0.865** | 0.852* | 0.948** | 0.941** | 0.910** | 0.922** | 0.865** | 0.884** | 0.941** | 0.909** | 0.935** | 0.948** | 0.894** | 0.899** | 0.916** | 0.869** | 0.891** | 0.889** | 0.865** | 0.890** | 0.940** | 0.948** | 0.909** | 0.363* | 0.612** |
| EE | 0.938* | 0.936* | 1.000 | 1.000** | 1.000** | 0.945** | 0.962* | 0.900* | 0.935* | 0.977** | 0.981** | 0.980** | 1.000** | 0.952** | 0.962** | 0.944** | 0.929** | 1.000** | 0.973** | 0.962** | 0.947** | 0.976** | 1.000** | 0.981** | 0.25 | 0.535* |
| FF | 0.944* | 0.943* | 1.000* | 1.000** | 1.000** | 0.947** | 0.963** | 0.905** | 0.938** | 0.978** | 0.982** | 0.981** | 1.000** | 0.955** | 0.965** | 0.945** | 0.935** | 1.000** | 0.976** | 0.966** | 0.950** | 0.977** | 1.000** | 0.982** | 0.281 | 0.571** |

(a3)

| | AA | BB | CC | DD | EE | FF |
|---|---|---|---|---|---|---|
| A | 23.03** | 20.36** | 11.90* | 22.66** | 8.85* | 12.25* |
| B | 22.66** | 16.90** | 10.83* | 20.70** | 8.16* | 10.23* |
| C | 10.88* | 10.05* | 5.65** | 12.26* | 4.61 | 7.14* |
| D | Inf** | Inf** | Inf** | Inf** | 16.86** | 22.66** |
| E | Inf** | Inf** | Inf** | Inf** | 16.60** | 20.70** |
| F | Inf** | Inf** | Inf** | Inf** | 18.27** | 23.47** |
| G | Inf** | Inf** | 22.66** | Inf** | 15.96* | 20.36** |
| H | Inf** | Inf** | 19.25** | Inf** | 11.66* | 15.21* |
| I | Inf** | Inf** | 17.53** | Inf** | 11.97* | 14.65* |
| J | Inf** | Inf** | Inf** | Inf** | 19.58** | 20.70** |
| K | Inf** | Inf** | 21.64** | Inf** | 13.53* | 16.96** |
| L | Inf** | Inf** | Inf** | Inf** | 17.38** | 23.47** |
| M | Inf** | Inf** | Inf** | Inf** | 16.70** | 21.64** |
| N | 24.85 | Inf** | 17.66** | Inf** | 11.90* | 16.38** |
| O | Inf** | Inf** | 17.99** | Inf** | 12.98* | 16.62** |
| P | Inf** | Inf** | Inf** | Inf** | 17.48** | 20.46** |
| Q | Inf** | 19.97** | 13.86* | 26.24** | 10.13* | 13.65* |
| R | Inf** | 24.05** | 15.23* | 23.03** | 10.28* | 12.68* |
| S | 26.24** | 23.47** | 16.42** | Inf** | 11.27* | 14.02* |
| T | 17.87** | 18.30** | 10.09* | 20.58** | 8.75* | 10.77* |
| U | Inf** | Inf** | 14.73* | Inf** | 11.18* | 15.67* |
| V | Inf** | Inf** | Inf** | Inf** | 17.64** | 24.05** |
| W | Inf** | Inf** | Inf** | Inf** | 17.16** | 23.03** |
| X | Inf** | Inf** | 17.96** | Inf** | 13.26* | 15.95* |
| Y | Inf** | Inf** | Inf** | Inf** | 17.12** | 22.66** |
| Z | 26.24** | 12.59* | 7.26* | Inf** | 10.94* | 11.51* |

(a4)

| | AA | BB | CC | DD | EE | FF |
|---|---|---|---|---|---|---|
| AA | – | 4.88 | 10.84* | 24.86** | 10.74* | 15.09* |
| BB | 0.000 | – | 5.79 | Inf** | 10.00* | 14.03* |
| CC | 0.198* | 0.086 | – | 8.51* | 1.29 | 2.57 |
| DD | 0.609** | 0.598** | 0.296* | – | 0.00 | 1.02 |
| EE | 0.632* | 0.622* | 0.229 | 0.000 | – | 0.00 |
| FF | 0.656** | 0.650** | 0.294 | 0.000 | 0.000 | – |

(a5)

| | Port Clinton | South Bass Is. | Cedar Point | Sandusky | Sturgeon Creek | Erieau | Vermilion | Lorain | Cleveland | Fairport | Geneva | Ashtabula | Presque Isle | Erie | Dunkirk | Long Pt. Bay |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | H | I | J | K | L | M | N | O | P | Q | R | S | T | U | V | W |
| H | – | 0.00 | 8.62* | 2.85 | 13.22** | 11.69** | 1.73 | 3.15 | 4.28 | 2.25 | 2.93 | 1.44 | 0.38 | 8.91* | 8.18* | 11.71** |
| I | 0.000 | – | 7.22* | 2.21 | 9.87* | 9.41* | 0.00 | 1.57 | 1.35 | 0.28 | 2.04 | 0.52 | 0.00 | 4.35 | 4.64 | 9.25* |
| J | 0.192** | 0.067 | – | 0.00 | 2.85 | 0.00 | 3.98 | 1.33 | 1.17 | 5.28 | 0.00 | 0.00 | 2.11 | 12.15** | 0.00 | 0.00 |
| K | 0.101 | 0.006 | 0.000 | – | 2.72 | 2.19 | 1.03 | 0.00 | 0.00 | 2.05 | 0.00 | 0.00 | 0.00 | 4.72 | 0.00 | 2.19 |
| L | 0.195** | 0.088* | 0.001 | 0.000 | – | 1.42 | 7.90* | 3.67 | 5.87 | 7.23* | 0.84 | 3.18 | 3.34 | 14.23** | 2.30 | 1.41 |
| M | 0.285** | 0.191** | 0.008 | 0.050 | 0.034 | – | 6.89* | 4.48 | 4.11 | 8.73* | 0.00 | 2.77 | 3.59 | 14.55** | 0.00 | 0.00 |
| N | 0.014 | 0.000 | 0.066 | 0.008 | 0.096 | 0.236* | – | 1.03 | 0.27 | 0.53 | 2.49 | 0.93 | 0.00 | 4.67 | 2.88 | 6.87* |
| O | 0.089 | 0.005 | 0.000 | 0.000 | 0.001 | 0.050 | 0.006 | – | 0.42 | 1.38 | 0.00 | 0.00 | 0.00 | 4.70 | 0.83 | 4.50 |
| P | 0.078 | 0.000 | 0.001 | 0.000 | 0.021 | 0.050 | 0.000 | 0.000 | – | 1.69 | 0.55 | 0.00 | 0.00 | 6.68* | 3.27 | 4.08 |
| Q | 0.000 | 0.000 | 0.079 | 0.010 | 0.101 | 0.239* | 0.000 | 0.002 | 0.000 | – | 1.49 | 1.08 | 0.00 | 2.92 | 3.96 | 8.79* |
| R | 0.109 | 0.042 | 0.000 | 0.000 | 0.000 | 0.000 | 0.073 | 0.000 | 0.000 | 0.045 | – | 0.00 | 1.69 | 3.29 | 0.00 | 0.00 |
| S | 0.040 | 0.000 | 0.000 | 0.000 | 0.000 | 0.126 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | – | 0.00 | 2.84 | 0.00 | 2.77 |
| T | 0.000 | 0.000 | 0.000 | 0.000 | 0.032 | 0.318 | 0.000 | 0.000 | 0.000 | 0.000 | 0.051 | 0.000 | – | 1.66 | 1.65 | 3.58 |
| U | 0.095 | 0.026 | 0.042 | 0.002 | 0.052 | 0.114* | 0.031 | 0.002 | 0.000 | 0.018 | 0.000 | 0.000 | 0.000 | – | 11.20** | 0.00 |
| V | 0.215** | 0.097* | 0.008 | 0.000 | 0.004 | 0.000 | 0.101 | 0.000 | 0.024 | 0.109* | 0.000 | 0.000 | 0.028 | 0.050 | – | 0.00 |
| W | 0.285** | 0.191* | 0.008 | 0.050 | 0.034 | 0.000 | 0.236* | 0.050 | 0.050 | 0.239* | 0.000 | 0.126 | 0.318 | 0.114* | 0.000 | – |

## References


Angers, B., Bernatchez, L., 1998. Combined use of SMM and non-SMM methods to infer fine structure and evolutionary history of closely related brook charr (*Salvelinus fontinalis*, Salmonidae) populations from microsatellites. Mol. Biol. Evol. 15, 143–159.

Avise, J.C., 2004. Molecular Markers, Natural History and Evolution. Chapman and Hall, New York.

Bailey, R.M., Smith, G.R., 1981. Origin and geography of the fish fauna of the Laurentian Great Lakes basin. Can. J. Fish Aquat. Sci. 38, 1539–1561.

Balloux, F., Lugon-Moulin, N., 2002. The estimation of population differentiation with microsatellite markers. Mol. Ecol. 11, 155–165.

Berendzen, P.B., Simons, A.M., Wood, R.M., 2003. Phylogeography of the northern hogsucker, *Hypentelium nigricans* (Teleostei: Cypriniformes): genetic evidence for the existence of the ancient Teays River. J. Biogeogr. 30, 1139–1152.

Bernatchez, L., Wilson, C.C., 1998. Comparative phylogeography of Nearctic and Palearctic fishes. Mol. Ecol. 7, 431–452.

Bernatchez, L., Gyuomark, R., Bonhomme, F., 1992. Sequence variation of the mitochondrial control region among geographically and morphologically remote European brown trout (*Salmo trutta*) populations. Mol. Ecol. 1, 161–173.

Billington, N., 1993. Genetic variation in Lake Erie yellow perch (*Perca flavescens*) demonstrated by mitochondrial DNA analysis. J. Fish Biol. 43, 941–943.

Billington, N., Hebert, P.D.N., 1991. Mitochondrial DNA diversity in fishes and its implications for introductions. Can. J. Fish Aquat. Sci. 48, 80–94.

Billington, N., Barrette, R.J., Hebert, P.D.N., 1992. Management implications of mitochondrial DNA variation in walleye stocks. North Am. J. Fish. Manage. 12, 276–284.

Bodaly, R.A., Ward, R.D., Mills, C.A., 1989. A genetic stock study of perch, *Perca fluviatilis*, in Windermere. J. Fish Biol. 34, 965–967.

Bronte, C.R., Selgeby, J.H., Swedberg, D.V., 1993. Dynamics of a yellow perch population in Lake Superior. North Am. J. Fish. Manage. 12, 511–523.

Brown, B., Wang, H.P., Givens, C., Wallet, G., 2007. Yellow perch strain evaluation I: genetic variance of six broodstock populations. Aquaculture 271, 142–151.

Clapp, D.F., Dettmers, J.M., 2004. Fisheries research and management in Lake Michigan: evaluating progress in a cooperative effort, 1997–2001. Fisheries 29, 11–20.

Clement, M., Posada, D., Crandall, K., 2000. TCS: a computer program to estimate gene genealogies. Mol. Ecol. 9, 1657–1660.

Craig, J.F., 2000. Percid Fishes: Systematics, Ecology and Exploitation. Blackwell Science, Ltd, Oxford, UK.

Crespi, E.J., Rissler, L.J., Browne, R.A., 2003. Testing Pleistocene refugia theory: phylogeographical analysis of *Desmognathus wrighti*, a high-elevation salamander in the southern Appalachians. Mol. Ecol. 12, 969–984.

Crossman, E.J., McAllister, D.E., 1986. Zoogeography of freshwater fishes of the Hudson Bay drainage, Ungava Bay and the Artic Archipelago. In: Hocutt, C.H., Wiley, E.O. (Eds.), The Zoogeography of North American Freshwater Fishes. John Wiley and Sons, New York, pp. 53–104.

Danzmann, R.G., Morgan II, R.P., Jones, M.W., Bernatchez, L., Ihssen, P.E., 1998. A major sextet of mitochondrial DNA phylogenetic assemblages extant in eastern North American brook trout (*Salvelinus fontinalis*): distribution and post-glacial dispersal patterns. Can. J. Zool. 76, 1300–1318.

Excoffier, L., 1994. The statistical analysis of molecular data for inferring population genetic structure: the Amova framework. In: Perrin, N., Keller, L., Goudet, J. (Eds.), Bull. Soc. Vaud. Sc. Nat. Evolution of Structured Populations, 83, pp. 159–160.

Excoffier, L., Laval, G., Schneider, S., 2005. Arlequin ver. 3.0: an integrated software package for population genetics data analysis. Evol. Bioinformatics Online 1, 47–50.

Faber, J.E., Stepien, C.A., 1997. The utility of mitochondrial DNA control region sequences for analyzing phylogenetic relationships among populations, species, and genera of the Percidae. In: Kocher, T.D., Stepien, C.A. (Eds.), Molecular Systematics of Fishes. Academic Press, San Diego, California, pp. 199–218.

Faber, J.E., Stepien, C.A., 1998. Tandemly repeated sequences in the mitochondrial DNA control region and phylogeography of the pike-perches *Stizostedion*. Mol. Phylogenet. Evol. 10, 310–323.

Felsenstein, J., 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39, 783–791.

Ford, A.M., Stepien, C.A., 2004. Genetic variation and spawning population structure in Lake Erie yellow perch, *Perca flavescens*: a comparison with a Maine population. In: Barry, T.P., Malison, J.A. (Eds.), Proceedings of Percis III, the 3rd International Symposium on Percid Fishes. University of Wisconsin Sea Grant Institute, Madison, Wisconsin, pp. 131–132.

Fulford, R.S., Rice, J.A., Miller, T.J., Binkowski, F.P., 2006. Elucidating patterns of size-dependent predation on larval yellow perch (*Perca flavescens*) in Lake Michigan: an experimental and modeling approach. Can. J. Fish Aquat. Sci. 63, 11–27.

Fullerton, A.H., Lamberti, G.A., 2006. A comparison of habitat use and habitat-specific feeding efficiency by Eurasian ruffe (*Gymnocephalus cernuus*) and yellow perch (*Perca flavescens*). Ecol. Freshw. Fish 15, 1–9.

Gatt, M.H., Ferguson, M.M., Liskauskas, A.P., 2000. Comparison of control region sequencing and fragment RFLP analysis for resolving mitochondrial DNA variation and phylogenetic relationships among Great Lakes walleyes. Trans. Am. Fish. Soc. 129, 1288–1299.

Gonzalez, M.J. 2006. Competitive interactions between yellow perch and round goby. Lake Erie Protection Fund project report. Toledo, Ohio: Ohio Lake Erie Commission (http://www.epa.state.oh.us/oleo/Grant/freports/smallfinals/2004/sg234-04.pdf).

Great Lakes Fishery Commission, 2004. Annual Report of the Lake Erie Yellow Perch Task Group. Lake Erie Commission, Great Lakes Fishery Commission, Windsor, Ontario.

Great Lakes Fishery Commission, 2006. Lake Erie Committee Executive Summary. Lake Erie Commission, Great Lakes Fishery Commission, Windsor, Ontario.

Great Lakes Fishery Commission, 2007a. Catch Limits Set for Walleye and Yellow Perch for 2007. Lake Erie Commission, Great Lakes Fishery Commission, Windsor, Ontario.

Great Lakes Fishery Commission, 2007b. Annual Report of the Lake Erie Yellow Perch Task Group. Lake Erie Commission, Great Lakes Fishery Commission, Windsor, Ontario.

Great Lakes Fishery Commission, 2008a. Status of Yellow Perch in Lake Michigan and Yellow Perch Task Group Progress Report. Report to the Lake Michigan Committee. Lake Michigan Committee, Great Lakes Fishery Commission, Niagara Falls, Ontario.

Great Lakes Fishery Commission, 2008b. Lake Erie Committee Executive Summary. Lake Erie Commission, Great Lakes Fishery Commission, Windsor, Ontario.

Gyllensten, U., Ryman, N., Stahl, G., 1985. Monomorphism of allozymes in perch (*Perca fluviatilis* L.). Hereditas 102, 57–61.

Hall, T.A., 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symp. Ser. 41, 95–99.

Haponski, A.E., and Stepien, C.A. 2008. Molecular, morphological, and biogeographic resolution of cryptic taxa in the greenside darter *Etheostoma blennioides* complex. Mol. Phyl. Evol. 49, 69–83.

Hartl, D.L., 1988. A Primer of Population Genetics. Sinauer Associates, Inc, Sunderland, Massachusetts.

Hartman, W.L., Nepszy, S.J., Scholl, R.L., 1980. Minimum size limits for yellow perch *Perca flavescens* in western Lake Erie, Canada, USA. Great Lakes Fishery Commission Tech. Report 39, 1–32.

Henderson, B.A., Nepszy, S.J., 1989. Recruitment of yellow perch *Perca flavescens* affected by stock size and water temperature in lakes Erie and St. Clair 1965–85. J. Great Lakes Res. 14, 205–215.

Jude, D.J., Reider, R.H., Smith, G.R., 1992. Establishment of Gobiidae in the Great Lakes basin. Can. J. Fish Aquat. Sci. 49, 416–421.

Kenyon, R., Murray, C., 2001. A Review of the Lake Erie and Presque Isle Bay Yellow Perch Sport Angling Fisheries, 1997–2001. Pennsylvania Fish and Boat Commission, Lake Erie Research Unit, Fairview, PA.

Kimura, M., 1980. A simple method for estimating evolutionary rate of base substitution through comparative studies of nucleotide sequences. J. Mol. Evol. 16, 111–120.

Kocher, T.D., Thomas, W.K., Meyer, A., Edwards, S.V., Paabo, S., Villablanca, F.X., Wilson, A.C., 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. Proc. Nat. Acad. Sci. U. S. A. 86, 6196–6200.

Lauer, T.E., Doll, J.C., Allen, P.J., Breidert, B., Palla, J., 2008. Changes in yellow perch length frequencies and sex ratios following closure of the commercial fishery and reduction in sport bag limits in southern Lake Michigan. Fish. Mgt. Ecol. 15, 39–47.

Leary, R., Booke, H.E., 1982. Genetic stock analysis of yellow perch from Green Bay and Lake Michigan. Trans. Am. Fish. Soc. 111, 52–57.

LeClerc, E., Mailhot, Y., Mingelbier, M., Bernatchez, L., 2008. The landscape genetics of yellow perch (*Perca flavescens*) in a large fluvial ecosystem. Mol. Ecol. 17, 1702–1717.

Lee, D.S., Gilbert, C.R., Hocutt, C.H., Jenkins, R.E., McAllister, D.E., and Stauffer, J.R., Jr. 1980. Atlas of North American Freshwater Fishes. North Carolina Biological Survey Publication 1980-12. Raleigh, North Carolina: North Carolina State Museum of Natural History. (with 1993 Supplement by Lee, D.S., Platania, S.P., and Burgess, G.H. North Carolina Biological Survey Contribution 1983-6).

Mandrak, N.E., Crossman, E.J., 1992. Postglacial dispersal of freshwater fishes into Ontario. Can. J. Zool. 70, 2247–2259.

Mantel, N., 1967. The detection of disease clustering and a generalized regression approach. Cancer Res. 27, 209–220.

Marsden, J.E., Robillard, S.R., 2004. Decline of yellow perch in southwestern Lake Michigan, 1987–1997. North Am. J. Fish. Manage. 24, 952–967.

Martin, A.P., Humphreys, R., Palumbi, S.R., 1992. Population genetic structure of the armorhead, *Psudopentaceros wheeleri*, in the North Pacific Ocean: application to fisheries problems. Can. J. Fish Aquat. Sci. 49, 2386–2391.

McPhail, J.D., Lindsey, C.C., 1970. Freshwater fishes of northwestern Canada and Alaska. Fish. Res. Board Can. Bull. 173, 1–381.

Miller, L.M., 2003. Microsatellite DNA loci reveal genetic structure of yellow perch in Lake Michigan. Trans. Am. Fish. Soc. 132, 503–513.

Moritz, C., Faith, D.P., 1998. Comparative phylogeography and the identification of genetically divergent areas for conservation. Mol. Ecol. 7, 419–429.

Moyer, G.R., Billington, N., 2004. A survey of genetic variation among yellow perch (*Perca flavescens*) populations determined from allozyme and mitochondrial DNA data. In: Barry, T.P., Malison, J.A. (Eds.), Proceedings of Percis III, the 3rd International Symposium on Percid Fishes. University of Wisconsin Sea Grant Institute, Madison, Wisconsin, pp. 93–94.

Munawar, M., Munawar, I.F., Mandrak, N.E., Fitzpatrick, M., Dermott, R., Leach, J., 2005. An overview of the impact of non-indigenous species on the food web integrity of North American Great Lakes: Lake Erie example. Aquat. Ecosyst. Health Manag. 8, 375–395.

Near, T.J., Benard, M.F., 2004. Rapid allopatric speciation in logperch darters (Percidae: *Percina*). Evolution 58, 2798–2808.

Nei, M., 1987. Molecular Evolutionary Genetics. Columbia University Press, New York.

Nesbo, C.L., Magnhagen, C., Jakobsen, K.S., 1998. Genetic differentiation among stationary and anadromous perch (*Perca fluviatilis*) in the Baltic Sea. Hereditas 129, 241–249.

Nesbo, C.L., Fossheim, T., Vollestad, L.A., Jakobsen, K.S., 1999. Genetic divergence and phylogeographic relationships among European perch (*Perca fluviatilis*) populations reflect glacial refugia and postglacial colonization. Mol. Ecol. 8, 1387–1404.

Parrish, D.L., Margraf, F.J., 1990. Interactions between white perch (*Morone americana*) and yellow perch (*Perca flavescens*) in Lake Erie as determined from feeding and growth. Can. J. Fish Aquat. Sci. 47, 1779–1787.

Posada, D., Crandall, K.A., Templeton, A.R., 2000. GeoDis: a program for the cladistic analysis of the geographical distribution of genetic haplotypes. Mol. Ecol. 9, 487–488.
Posada, D., Crandall, K.A., Templeton, A.R., 2006. Nested clade analysis statistics. Mol. Ecol. Notes 6, 590–593.
Pratt, D.M., Blust, W.H., Selgeby, J.H., 1992. Ruffe, *Gymnocephalus cernuus*: newly introduced in North America. Can. J. Fish Aquat. Sci. 49, 1616–1618.
Raymond, M., Rousset, F., 1995. Genepop (Version 1.2): population genetics software for exact tests and ecumenicism. J. Heredity 86, 248–249.
Refseth, U.H., Nesbo, C.L., Stacy, J.E., Vollestad, L.A., Fjeld, E., Jakobsen, K.S., 1998. Genetic evidence for different migration routes of freshwater fish into Norway revealed by analysis of current perch (*Perca fluviatilis*) populations in Scandinavia. Mol. Ecol. 7, 1015–1027.
Rice, W.R., 1989. Analyzing tables of statistical tests. Evolution 43, 223–225.
Rousset, F., 1997. Genetic differentiation and estimation of gene flow from *F*-statistics under isolation by distance. Genetics 145, 1219–1228.
Rousset, F., 2008. Genepop '007: a complete re-implementation of the Genepop software for Windows and Linux. Mol. Ecol. Res. 8, 103–106.
Ryan, P.A., Knight, R., MacGregor, R., Towns, G., Hoopes, R., Culligan, W., 2003. Fish-community goals and objectives for Lake Erie. Great Lakes Fish. Comm. Spec. Publ. 03-02, pp 1–56. Great Lakes Fishery Commission, Ann Arbor, Michigan.
Saitou, N., Nei, M., 1987. The neighbor-joining method: a new method for reconstructing phylogenetic trees. Mol. Biol. Evol. 4, 406–425.
Scott, W.B., Crossman, E.J., 1973. Freshwater Fishes of Canada. Canadian Government Publishing Centre, Ottawa, Canada.
Shroyer, S.M., McComish, T.S., 2000. Relationship between alewife abundance and yellow perch recruitment in southern Lake Michigan. North Am. J. Fish. Manage. 20, 220–225.
Stepien, C.A., Faber, J.E., 1998. Population genetic structure, phylogeography, and spawning philopatry in walleye (*Stizostedion vitreum*) from mtDNA control region sequences. Mol. Ecol. 7, 1757–1769.
Stepien, C.A., Dillon, A.K., Chandler, M.D., 1998. Genetic identity, phylogeography, and systematics of ruffe *Gymnocephalus* in the North American Great Lakes and Eurasia. J. Great Lakes Res. 24, 361–378.
Stepien, C.A., Brown, J.E., Neilson, M.E., Tumeo, M.A., 2005. Genetic diversity of invasive species in the Great Lakes versus their Eurasian source populations: insights for risk analysis. Risk Anal. 25, 1043–1060.
Stepien, C.A., Taylor, C.D., Einhouse, D.W., 2004. An analysis of genetic risk to a native spawning stock of walleye Sander vitreus (Stizostedion vitreum) due to stocking in Cattaraugus Creek. In: Barry, T.P., Malison, J.A. (Eds.), Proceedings of Percis III, the 3rd International Symposium on Percid Fishes. University of Wisconsin Sea Grant Institute, Madison, WI, pp. 93–94.
Stepien, C.A., Murphy, D., Strange, R.M., 2007. Broad- to fine-scale population genetic patterning in the smallmouth bass *Micropterus dolomieu* across the Laurentian Great Lakes and beyond: an interplay of behavior and geography. Mol. Ecol. 16, 1605–1624.
Strange, R.M., Stepien, C.A., 2007. Genetic divergence and connectivity among river and reef spawning populations of walleye (*Sander vitreus*) in Lake Erie. Can J. Fish Aquat. Sci. 64, 437–448.
Stritthol, J.R., Guttman, S.I., Wissing, T.E., 1988. Low levels of genetic variability of yellow perch (*Perca flavescens*) in Lake Erie and selected impoundments. In: Downhower, J.E. (Ed.), The Biogeography of the Island Region of Western Lake Erie. Ohio State University Press, Columbus, Ohio, pp. 246–257.
Tamura, K., Dudley, J., Nei, M., Kumar, S., 2007. Mega 4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0. Mol. Biol. Evol. 24, 1596–1599.
Templeton, A.R., Routman, E., Phillips, C.A., 1995. Separating population structure from population history: a cladistic analysis of the geographical distribution of mitochondrial DNA haplotypes in the tiger salamander, *Ambystoma tigrinum*. Genetics 140, 767–782.
Todd, N., Hatcher, C.O., 1993. Genetic variability and glacial origins of yellow perch (*Perca flavescens*) in North America. Can. J. Fish Aquat. Sci. 50, 1828–1834.
Trautman, M.B., 1981. The Fishes of Ohio. Ohio State University Press, Columbus, Ohio.
Turgeon, J., Bernatchez, L., 2001a. Mitochondrial DNA phylogeography of lake cisco (*Coregonus artedi*): evidence supporting extensive secondary contacts between two glacial races. Mol. Ecol. 10, 987–1001.
Turgeon, J., Bernatchez, L., 2001b. Clinal variation at microsatellite loci reveals historical secondary intergradation between glacial races of *Coregonus artedi* (Teleostei: Coregoninae). Evolution 55, 2274–2286.
Tyson, J.T., Knight, R.L., 2001. Response of yellow perch to changes in the benthic invertebrate community of western Lake Erie. Trans. Am. Fish. Soc. 130, 766–782.
Weir, B.S., Cockerham, C.C., 1984. Estimating *F*-statistics for the analysis of population structure. Evolution 38, 1358–1370.
Wilberg, M.J., Bence, J.R., Eggold, B.T., Makauskas, D., Clapp, D.F., 2005. Yellow perch dynamics in southwestern Lake Michigan during 1986–2002. North Am. J. Fish. Manage. 25, 1130–1152.
Wilson, C.C., Hebert, P.D.N., 1996. Phylogeographic origins of lake trout (*Salvelinus namaycush*) in eastern North America. Can. J. Fish Aquat. Sci. 53, 2764–2775.