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Waterscape genetics of the yellow perch (*Perca flavescens*): patterns across large connected ecosystems and isolated relict populations

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Abstract

Comparisons of a species' genetic diversity and divergence patterns across large connected populations vs. isolated relict areas provide important data for understanding potential response to global warming, habitat alterations and other perturbations. Aquatic taxa offer ideal case studies for interpreting these patterns, because their dispersal and gene flow often are constrained through narrow connectivity channels that have changed over geological time and/or from contemporary anthropogenic perturbations. Our research objective is to better understand the interplay between historic influences and modern-day factors (fishery exploitation, stocking supplementation and habitat loss) in shaping population genetic patterns of the yellow perch *Perca flavescens* (Percidae: Teleostei) across its native North American range. We employ a modified landscape genetics approach, analysing sequences from the entire mitochondrial DNA control region and 15 nuclear DNA microsatellite loci of 664 spawning adults from 24 populations. Results support that perch from primary glacial refugium areas (Missourian, Mississippian and Atlantic) founded contemporary northern populations. Genetic diversity today is highest in southern (never glaciated) populations and also is appreciable in northern areas that were founded from multiple refugia. Divergence is greater among isolated populations, both north and south; the southern Gulf Coast relict populations are the most divergent, reflecting their long history of isolation. Understanding the influence of past and current waterway connections on the genetic structure of yellow perch populations may help us to assess the roles of ongoing climate change and habitat disruptions towards conserving aquatic biodiversity.

Keywords: glacial refugia, landscape genetics, *Perca*, Percidae, relict populations, waterscape genetics, yellow perch

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Introduction

The genetic diversity of a species that has a wide geographic range is regulated by habitat connectivity, dispersal and distribution over the landscape (Petit *et al.* 2003; Stepien *et al.* 2009; Blum *et al.* 2012). Climate change may disproportionally increase or decrease genetic variability across a taxon's range due to shifts in physical conditions or biological resources (Hewitt 1999; Petit *et al.* 2003; Hampe & Jump 2011), as occurred during Pleistocene glaciations (Oberdorff *et al.* 1997; Davis & Shaw 2001; Soltis *et al.* 2006) and is ongoing today (Araújo & Rahbek 2006; Harris & Taylor 2010). Large connected ranges are believed to provide a variety of environmental resources that foster robust, diverse populations, reflecting interplay between migration opportunity and localized adaptation (Lindsay *et al.* 2008; Vandewoestijne *et al.* 2008; Kunin *et al.* 2009). In contrast,

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isolated relict populations with little connectivity probably possess relatively low genetic diversity due to genetic drift, bottlenecks and selection (Moran & Hopper 1983; Petit *et al.* 2003; Coulon *et al.* 2012). However, such relict and 'rear edge' populations (those found in fringe latitudinal portions of the native range) may house critical repositories of genetic diversity, serving as possible sources for future range expansion in the face of climate changes (Hampe & Petit 2005; Diekmann & Serrão 2012).

Aquatic ecosystems offer greater opportunity than most terrestrial systems to evaluate the respective roles of historic and contemporary connectivity patterns in shaping genetic variability due to the preponderance of narrow and relatively ephemeral connections that link populations (Boizard *et al.* 2009; Lamberti *et al.* 2010). Because most aquatic populations depend on these linkages among lakes, rivers, streams and channels to migrate and disperse, such physical 'landscape' components pose distinct biological challenges. For example, small connected channels may offer limited food and shelter and extensively differ in size and habitat complexity, which then influence the distribution of population variability.

Temperate fauna were shaped by climate change, habitat loss and geophysical modifications during the Pleistocene glaciations 2.6 million—10 000 years ago (ya), whose populations persisted by retreating to glacial refugia (Petit *et al.* 2003; Hewitt 2004; Provan & Bennett 2008). Migrants from three primary North American glacial refugia—Missourian, Mississippian and Atlantic—then founded the contemporary biodiversity of populations in the northeast and Midwest regions (Fig. 1). Notably, an estimated 90 fish species migrated northward from the Mississippian glacial refugium to found modern populations in the Laurentian Great Lakes, another 14 expanded up from the Atlantic coastal refugium and some from each met and mixed. To the west, colonists from the Missourian refugium primarily founded populations in the upper Great Plains and Canadian prairies—we term these the 'Northwest Lake Plains'—as well as the upper Mississippi River watershed and western Lake Superior (Mandrak & Crossman 1992; Billington 1996; Stepien *et al.* 2009; Backhouse-James & Docker 2012).

Our study evaluates the distribution of genetic diversity across the broad native geographic range of the yellow perch *Perca flavescens* (Percidae: Teleostei),

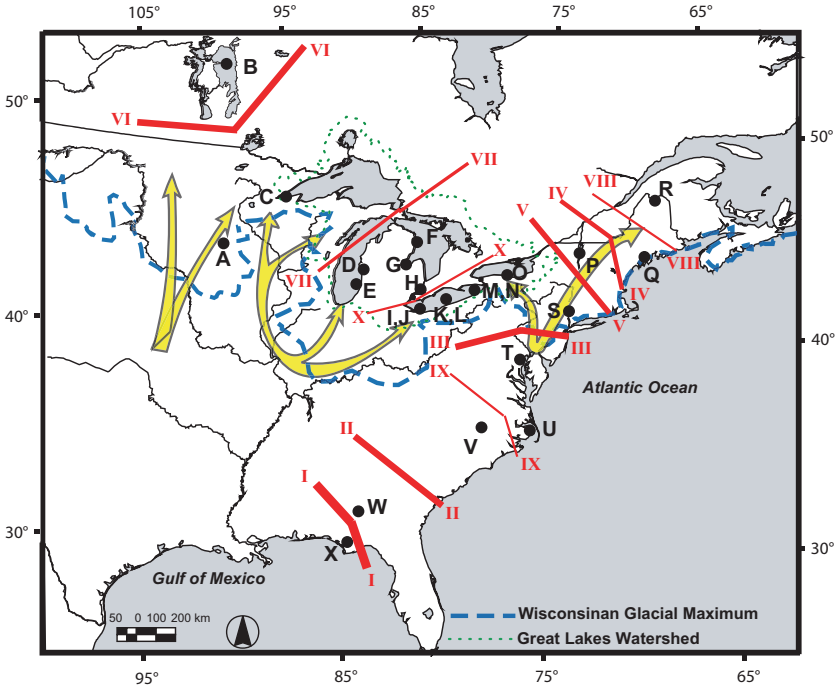


Fig. 1 Map of yellow perch sampling sites across North America (lettered according to Table 1). Dashed line indicates maximum extent of the Wisconsinan glaciations, dotted line delineates the boundaries of the Laurentian Great Lakes watershed. Arrows denote likely routes of postglacial population colonizations, adapted from Mandrak & Crossman (1992) to our findings. Solid lines indicate major barriers to gene flow based on 15 μsat loci (ranked I–X, in the order of decreasing magnitude) from the BARRIER analysis (Manni *et al.* 2004b). Thickness of barriers depict locus support. Loci support/mean F_{ST} are as follows: Barrier I, 13 loci/0.364; II, 11 loci/0.247; III, 11 loci/0.342; IV, 9 loci/0.282; V, 10 loci/0.239; VI, 9 loci/0.207; VII, 7 loci/0.177; VIII, 6 loci/0.173; IX, 5 loci/0.141; X, 6 loci/0.098.

comparing and contrasting genetic structure of northern postglacial vs. southern relict populations. Its native range spanned from Nova Scotia to southern Gulf of Mexico estuaries, with its greatest numbers in Lake Erie (Fig. 1; Scott & Crossman 1973; Boschung & Mayden 2004). Although largely a freshwater species, a few native yellow perch populations inhabit brackish estuarine systems, including deltas of the Chesapeake Bay (Hardy 1978) and coastal Atlantic seaboard lagoons (Wang & Kernehan 1979; Jenkins & Burkhead 1994), which are evaluated here (Fig. 1). We also analyse a rare relict native population from the Gulf Coast, documented from 1851 (Smith-Vaniz 1968) and archaeological bone evidence from native American settlements (Sheldon & Cottier 1983). The yellow perch was widely and intentionally introduced for fisheries throughout much of North America, for which Great Lakes stocks were prevalently used (Lee *et al.* 1980; Grzybowski *et al.* 2010). Here, we avoid sampling stocked areas to concentrate on native population patterns.

Yellow perch school throughout the year, with large schools of adults congregating in shallow areas of lakes or rivers during the late spring for spawning (Krieger *et al.* 1983; Jansen *et al.* 2009). Mark and recapture studies in Lake Michigan suggest loosely organized spawning complexes, with some straying among proximate spawning groups (Glover *et al.* 2008). Evidence for kin recognition and aggregative homing using olfactory cues has been reported in the European perch *Perca fluviatilis* (Gerlach *et al.* 2001; Behrmann-Godel & Gerlach 2008), which similarly might govern fidelity of yellow perch. Small groups of spawning yellow perch males fertilize the egg strands of a female (Mangan 2004), which are draped on submerged vegetation or other structures (Scott & Crossman 1973). Aalto & Newsome (1990) found that egg mass removals from given spawning sites led to fewer fish returning to that population in subsequent years than in control sites, suggesting that yellow perch return to the same spawning populations year after year. Movements of yellow perch after the spawning season largely are dictated by habitat complexity and foraging capacity, with highest seasonal movements during the fall and the lowest in summer (Radabaugh *et al.* 2010). Thus, habitat connectivity and the presence of discrete spawning groups may determine the overall genetic structure of yellow perch in a water body.

Earlier studies described selected yellow perch populations using various genetic markers, including allozymes (Todd & Hatcher 1993; Moyer & Billington 2004), mitochondrial (mt) DNA restriction enzyme fragment polymorphisms (Billington 1993), mtDNA control region (D-loop) sequences (Ford & Stepien 2004; Sepulveda-Villet *et al.* 2009) and nuclear DNA microsatellites (Brown *et al.* 2007; Leclerc *et al.* 2008; Parker *et al.* 2009; Grzybowski *et al.* 2010; Sepulveda-Villet & Stepien 2011). Sampling limitations and/or lack of genetic marker resolution precluded prior comprehensive understanding of their population relationships. Here, we evaluate contemporary and historic influences on yellow perch population genetic diversity and divergence across the native range using mtDNA control region sequences and 15 nuclear DNA microsatellite (μsat) loci. We believe that the combination of mitochondrial and nuclear microsatellite analyses, as well as additional sample sites, allows us to better evaluate the relationships among spawning groups, improving our understanding of population structure.

Objective, hypotheses and experimental framework

Our objective is to analyse population genetic variability of an ecologically important and commercially valuable fish species as a baseline in the face of ongoing climate and anthropogenic changes. We employ a 'waterscape' genetics approach that adapts landscape genetics (the interplay of physical and environmental features on population genetic structure; Manel *et al.* 2003; Sork & Waits 2010) to a system of isolated relict populations and geographically connected watersheds linked by small channels. Our study compares results from nuclear and mitochondrial DNA markers to evaluate possible evolutionary factors and contemporary influences that shaped diversity and divergence. Northerly populations were recolonized from glacial refugia and thus may have lower genetic diversity from founder effects. Large populations in the Great Lakes may be relatively genetically homogenous with high gene flow. Southerly populations resided a longer time in relatively stable environments, probably allowing them to differentiate in specialized habitats, but presumably experienced bottlenecks and drift due to small population sizes. The following hypotheses (alternative/null) are tested:

1 Genetic diversity and divergence patterns differ/are comparable in connected vs. isolated populations.
2 Relationships reflect/do not reflect a pattern of genetic isolation with geographic distance in connected vs. unconnected populations.
3 Relationships among northern populations show/do not show genetic patterns consistent with colonization from various hypothesized glacial refugia.
4 Genetic diversity and divergence are greater/comparable for populations found in formerly unglaciated regions than in those that were glaciated.

Materials and methods

Sampling, DNA extraction and amplification and sequencing

Spawning adult yellow perch ($N = 664$) were collected by agency scientists, colleagues and our laboratory from 24 native locations (Table 1). We avoided areas having known stocking supplementation from nonoriginal population sources (Lee *et al.* 1980; Fuller & Neilson 2012). Fin clip tissues were preserved in 95% ethanol in the field or frozen after collection, from which genomic DNA was extracted and purified with DNeasy Qiaquick kits (QIAGEN, Inc., Valencia, CA, USA) and aliquots were frozen at −80 °C, labelled and archived.

We analysed 15 nuclear μsat DNA loci: *Svi*4, 17 and 33 (Borer *et al.* 1999), *Svi*2, 3 and 7 (Eldridge *et al.* 2002), *YP*13 and 17 (Li *et al.* 2007) and *Mpf*1–7 (Grzybowski *et al.* 2010), multiplexing some loci and running others separately, following Sepulveda-Villet & Stepien (2011). Denatured amplification products were analysed on our ABI 3130XL Genetic Analyzer with GeneMapper v3.7 software (Applied Biosystems Inc., Foster size City, CA, USA). Output profiles were manually reviewed to confirm correct identification of allelic size variants.

The mtDNA control region (912 bp) was amplified and sequenced in both directions following Sepulveda-Villet *et al.* (2009) using the PCR primers Pro-L, HW1-r and 12sarH (Martin *et al.* 1992) and Applied Biosystems, Inc. (ABI; Fullerton, CA, USA) big dye terminator chemistry sequencing. Sequences were aligned by us with BIOEDIT v.7.05 (Hall 1999; http://www.mbio.ncsu.edu/bioedit/bioedit.html, and unique haplotypes were identified and compared with our laboratory databases and other percid sequences (Faber & Stepien 1997; Ford & Stepien 2004; Strange & Stepien 2007; Sepulveda-Villet *et al.* 2009). GenBank Accession numbers for the unique haplotype sequences are as follows: 1 = FJ155931, 2 = FJ155932, 3 = FJ155933, 4 = FJ155934, 5 = FJ155935, 6 = FJ155936, 7 = FJ155937, 8 = FJ155938, 9 = FJ155939, 10 = FJ155940, 11 = FJ155941, 12 = FJ155942, 13 = FJ155943, 14 = FJ155944, 15 = FJ155945, 16 = FJ155946, 17 = FJ155947, 18 = FJ155948, 19 = FJ155949, 20 = FJ155950, 21 = FJ155951, 22 = JX454954, 23 = JX454955, 24 = X454956, 25 = JX454957 and 26 = JX454958. Five haplotypes were newly described in this study (22–26); other numbers that are not included here were endemic to Lake Erie and not found in the present study's sampling regime (Sepulveda-Villet *et al.* 2009).

Microsatellite DNA data analyses

Population samples were tested for conformance to Hardy–Weinberg equilibrium (HWE) expectations at each locus, with significance estimated using the Markov Chain Monte Carlo (MCMC) method and 1000 randomization procedures (Guo & Thompson 1992) in GENEPOP v4.0 (Rousset 2008; http://kimura.univ-montp2.fr/~rousset/Genepop.htm). Deviations were tested for heterozygote deficiency and null (nonamplified) alleles (MICRO-CHECKER v2.2.3; van Oosterhout *et al.* 2004, 2006; http://www.microchecker.hull.ac.uk), and loci were analysed for linkage disequilibrium (LD). Significance levels for HWE and LD tests were adjusted using Bonferroni correction (Sokal & Rohlf 1995). Numbers of private (unique) alleles (N_{PA}; those occurring only in a single spawning group) were identified with CONVERT v1.31 (Glaubitz 2004; http://www.agriculture.purdue.edu/fnr/html/faculty/rhodes/students and staff/glaubitz/software.htm). Numbers of alleles (N_A) and allelic richness (A_R; the number of alleles per locus, adjusted for sample size using rarefaction per Mousadik & Petit (1996)) were calculated with FSTAT v2.9.3.2 (Goudet 2002; http://www2.unil.ch/popgen/softwares/fstat.htm).

To evaluate hypothesis 1 of whether spawning populations genetically differ, unbiased θ (Weir & Cockerham 1984) and ρ (Michalakis & Excoffier 1996) estimates of *F*-statistics and their associated levels of significance were compared with genetic heterogeneity at different scales in FSTAT. Pairwise tests for microsatellite and mtDNA data used θ_{ST} (the F_{ST} estimate of Weir & Cockerham 1984), shown to effectively evaluate recently diverged populations (Balloux & Lugon-Moulin 2002), and exact nonparametric comparisons with MCMC probability estimates; both were conducted in Genepop (Raymond & Rousset 1995; Goudet *et al.* 1996), with probabilities adjusted via sequential Bonferroni corrections to minimize type I errors (Rice 1989). Our use of θ_{ST} facilitated comparisons with our other studies on this species and other percids (Sepulveda-Villet *et al.* 2009; Stepien *et al.* 2009; Sepulveda-Villet & Stepien 2011).

We assessed demographic partitioning of genetic variation, testing for correspondence of genetic distance ($\theta_{ST}/1 - \theta_{ST}$) to the natural logarithm of geographic distance, measured as the shortest waterway distance; regression significance was interpreted from 1000 permutations in GENEPOP (Rousset 1997). Relative magnitude of genetic differences among populations was investigated with BARRIER v2.2 (Manni *et al.* 2004a,b; http://www.mnhn.fr/mnhn/ecoanthropologie/software/barrier.html) to identify genetically discontinuous assemblages, independent from a priori knowledge of their relationships. Barriers were ranked according to their relative number of supporting loci, and bootstrap support from 2000 iterations of the multilocus θ_{ST} matrix in GENELAND v3.1.4 (Guillot *et al.* 2005a,b, 2008;

Table 1 Sampling populations tested, sample size (*N*) and mean genetic variability values from 15 μsat loci and mtDNA control region sequences

			15 μsat loci								mtDNA haplotypes			
Locality	Lat °N	Long °W	*N*	H_O	H_E	F_{IS}	N_A	A_R	N_{PA}	P_{PA}	N_H	H_D	N_{PH}	P_{PH}
Northern formerly glaciated regions (A–S)			579	0.747	0.802	0.274	405	17.99	75	0.185	18	0.383	16	0.214
Northwest Lake Plains region (isolated, populations A–B)			30	0.505	0.634	0.205	136	8.84	5	0.037	2	0.311	0	0.000
Upper Mississippi R. watershed														
A. Green L./Florida L./Scandinavia L., MN	45.2369	−94.9370	18	0.515	0.617	0.165	112	7.47	4	0.036	2	0.529	0	0.000
Hudson Bay watershed														
B. L. Winnipeg, MB	52.0875	−97.6888	12	0.494	0.490	−0.010	68	4.53	1	0.015	1	0.000	0	0.000
Great Lakes region (connected; populations C-O)			459	0.551	0.695	0.206	363	9.97	51	0.140	14	0.224	12	0.066
L. Superior														
C. St. Louis Bay, MN	46.6597	−92.2069	25	0.635	0.690	0.080	119	7.93	1	0.008	1	0.000	0	0.000
L. Michigan			65	0.539	0.653	0.174	298	9.93	15	0.050	3	0.336	0	0.000
D. Muskegon L., MI	43.2363	−86.3123	40	0.553	0.691	0.200	163	10.87	9	0.055	3	0.349	0	0.000
E. Grand Haven, MI	43.0658	−86.3450	25	0.524	0.616	0.148	135	9.00	6	0.044	3	0.311	0	0.000
L. Huron			80	0.611	0.706	0.135	355	11.83	7	0.020	4	0.404	1	0.152
F. Thunder Bay, MI	44.9754	−83.3618	48	0.632	0.707	0.106	188	12.53	4	0.021	2	0.452	1	0.438
G. Saginaw Bay, MI	43.4292	−83.7536	32	0.590	0.705	0.163	167	11.13	3	0.018	3	0.356	0	0.000
L. St. Clair														
H. Anchor Bay, MI	42.6319	−82.7764	39	0.531	0.594	0.107	149	9.93	5	0.034	1	0.000	0	0.000
L. Erie			235	0.524	0.570	0.076	886	9.84	18	0.020	12	0.207	4	0.032
Western Basin			77	0.536	0.596	0.099	321	10.70	7	0.022	4	0.273	1	0.029
I. Monroe, MI	41.8683	−83.3178	48	0.559	0.630	0.113	183	12.20	3	0.016	3	0.098	0	0.000
J. South Bass Isl., OH	41.6575	−83.7536	29	0.514	0.562	0.085	138	9.20	4	0.029	3	0.447	1	0.067
Central Basin			68	0.516	0.544	0.047	264	8.80	8	0.030	3	0.256	1	0.040
K. Fairport, OH	41.8058	−81.4178	20	0.510	0.499	−0.022	92	6.13	4	0.043	3	0.511	1	0.050
L. Perry, OH	41.8077	−81.1452	48	0.521	0.589	0.116	172	11.47	4	0.023	1	0.000	0	0.000
Eastern Basin			88	0.520	0.570	0.083	301	10.03	3	0.010	4	0.073	2	0.029
M. Pt. Colborne/Pt. Albino, ON	42.8444	−79.1892	40	0.478	0.597	0.199	162	10.80	1	0.006	1	0.000	0	0.000
N. Dunkirk, NY	42.5047	−79.3339	48	0.562	0.544	−0.033	139	9.27	2	0.014	4	0.146	2	0.050
L. Ontario														
O. Rochester, NY	43.2880	−77.1411	15	0.514	0.620	0.170	100	9.93	5	0.034	2	0.133	1	0.067
L. Champlain														
P. Burlington, VT	44.4681	−73.5025	30	0.598	0.666	0.103	128	8.53	3	0.023	2	0.517	1	0.500
U.S. North Atlantic coastal region (isolated)			60	0.495	0.645	0.236	347	7.71	16	0.048	3	0.478	3	0.289
Q. Sebasticook R., ME	44.7872	−69.3814	17	0.502	0.633	0.207	93	6.20	7	0.075	3	0.439	2	0.143
R. St. Johns R., ME	47.3192	−68.2015	32	0.391	0.624	0.373	146	9.73	6	0.041	2	0.467	0	0.000
S. Hudson R., NY	43.2424	−73.7875	16	0.592	0.678	0.127	108	7.20	3	0.028	2	0.527	1	0.714
Southern unglaciated regions (T–X)			83	0.806	0.834	0.257	254	17.79	29	0.114	9	0.392	5	0.393
U.S. South Atlantic coastal region (isolated; T–V)			68	0.603	0.694	0.132	349	7.78	21	0.060	7	0.633	4	0.618

Continued

Locality	Lat °N	Long °W	15 μsat loci								mtDNA haplotypes			
			N	H_O	H_E	F_{IS}	N_A	A_R	N_{PA}	P_{PA}	N_H	H_D	N_{PH}	P_{PH}
T. Bush R., MD	39.4357	−76.2424	32	0.670	0.758	0.116	157	10.53	11	0.070	2	0.564	2	1.000
U. Scuppernong R., NC	35.9327	−76.2982	32	0.623	0.675	0.077	140	9.33	10	0.071	2	0.512	1	0.357
V. Morgan Ck., NC	35.4272	−78.9747	4	0.517	0.647	0.202	52	3.47	0	0.000	4	0.822	1	0.250
U.S. Gulf coastal region (connected; W–X)			15	0.387	0.595	0.346	108	3.60	8	0.074	2	0.151	1	0.133
W. Chattahoochee R., GA	31.4322	−85.0608	12	0.441	0.578	0.237	69	4.60	2	0.029	2	0.303	1	0.167
X. Apalachicola R., FL	31.3521	−87.0115	3	0.333	0.611	0.454	39	2.60	6	0.154	1	0.000	0	0.000
Total (A–X)			664	0.533	0.626	0.145	442	8.39	101	0.229	26	0.312	14	0.149

Microsatellite data include the following: observed (H_O) and expected (H_E) heterozygosity, inbreeding coefficient (F_{IS}), number of μsat alleles across all loci (N_A), allelic richness (A_R), number of private alleles (N_{PA}) and proportion of private alleles (P_{PA}). Values for mtDNA include number of haplotypes (N_H), haplotypic diversity (H_D), number of private haplotypes (N_{PH}) and proportion of private haplotypes (P_{PH}).

http://www2.imm.dtu.dk/~gigu/Geneland/) using R v2.13.1 (R Development Core Team 2008; http://www.r-project.org/). To further test for distinctive populations, Bayesian-based STRUCTURE v2.3.3 analyses (Pritchard *et al.* 2000; Pritchard & Wen 2004; http://pritch.bsd.uchicago.edu/structure.html) evaluated membership of individuals to groups, regardless of their population identity. We compared results from $K = 1$ to $K = 21$ (the total N of significantly divergent spawning groups) with 10 independent runs each, with burn-ins of 100 000 and 500 000 MCMC replicates, using an admixture model, an initial inferred alpha value of 1.0, a correlated allele assumption, a prior F_{ST} mean of 0.01 and a prior for standard deviation of 0.05. Optimal K was determined via the ΔK likelihood procedure from Evanno *et al.* (2005).

The Bayesian program GENECLASS2 (Piry *et al.* 2004; http://www1.montpellier.inra.fr/URLB/index.html) evaluated self-assignment of individuals to populations, using a simulated population size of 10 000 individuals per site, with a 0.01 rejection level (Cornuet *et al.* 1999). To more comprehensively test scenarios of demographic partitioning, we evaluated % genetic variance and its significance using Analysis of Molecular Variance (AMOVA; Excoffier *et al.* 1992) in ARLEQUIN v3.5.12 (Excoffier *et al.* 2005; Excoffier & Lischer 2010; http://cmpg.unibe.ch/software/arlequin35/), which compared relative levels of variation among and within population samples. To further examine relationships among sampling sites, Nei's (1972) pairwise genetic distances (Ds) and Cavalli-Sforza and Edwards' (1967) chord distances (Dc) were calculated using GENDIST in PHYLIP v3.69 (Felsenstein 2008) and used to construct a neighbor-joining (NJ) tree (Saitou and Nei 1987). Relative support values for the nodes were estimated using 1000 bootstrap pseudoreplicates (Felsenstein 1985) in PHYLIP. To test the relationship between environmental variation and genetic structure, we compared heterozygosity and water body area (km^2) using GESTE v2.0 (http://www-leca.ujf-grenoble.fr/logiciels.htm; Foll & Gaggiotti 2006), which utilizes F_{ST} values and relates them to the surface area values using a general linear model.

Mitochondrial DNA control region data analyses

Pairwise comparisons between sites were performed as previously described for microsatellite loci. Relationships among mtDNA control region haplotypes were evaluated using maximum likelihood (ML) in PHYML 3.0 (Guindon *et al.* 2010; http://www.atgc-montpellier.fr/phyml/). The tree was rooted to the European perch *Perca fluviatilis* (GenBank #Y14724; Nesbø *et al.* 1999; http://www.ncbi.nlm.nih.gov/Genbank). The corrected

Akaike information criterion (AIC_C) from JMODELTEST 0.1.1 (Posada 2008; http://darwin.uvigo.es/software/jmodeltest.html) was used to determine the most appropriate model of substitution; the Kimura (1981) six-parameter model, with unequal frequencies (A = 0.3106; C = 0.2061; G = 0.1601; T = 0.3231) and a gamma distribution ($\alpha = 0.100$), was selected. Support for nodes of the tree was evaluated with 2000 bootstrap pseudoreplications (Felsenstein 1985).

The ML tree was compared with a Bayesian analysis using a Metropolis-coupled MCMC (MC^3) approach in MRBAYES 3.10 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003). Analyses were run for 10 million generations, with sampling every 100. The MC^3 burn-in period was determined by plotting log-likelihood values for each generation to identify when stationarity was reached; 25% of the generations were discarded as burn-in, along with the trees and parameter values sampled prior to burn-in. A 50% majority rule consensus tree was based on the remaining generations, and branch support was obtained via the posterior probability distribution (Holder & Lewis 2003) in MRBAYES.

Divergence times among yellow perch haplotypes were evaluated using a penalized likelihood approach (Sanderson 2002) in R8S v1.71 (Sanderson 2003). Initially, the data set was tested for conformance to a molecular clock model, from which it was determined to vary significantly ($P < 0.0001$). A second analysis then was conducted with an optimal smoothing parameter (=1.00) determined via cross-validation. Divergence time estimates under the latter method need three or more fossil calibration points to estimate the dates of their respective nodes, for which other members of the family Percidae were used: *Gymnocephalus cernua* (GenBank #AF025355.1; Stepien *et al.* 1998; Stepien *et al.* 2005, *G. baloni* (AF025360.1), *G. schraetser* (AF025361.1), *P. fluviatilis* (Y14724), *Sander vitreus* (AF162272), *S. canadensis* (U90618.1) and *Percina maculata* (PMU90623). Fossil date estimates for origins of three percid genera included the early Pliocene epoch [*c.* 1.8 million years ago (Ma)] for *Gymnocephalus* (Holčík & Hensel 1974), Pliocene epoch (*c.* 8–10 Ma) for *Sander* (Murray *et al.* 2009), and Miocene epoch (*c.* 26 Ma) for *Perca* (Lebedev 1952; based on *P. fluviatilis* from the Crimean Peninsula in Ukraine). To determine localized mutation rates and 95% confidence intervals, we utilized the BEAST software suite (1.7.2, Drummond *et al.* 2012), as well as the software TRACER 1.4 (Rambaut & Drummond 2007), to visualize interval and rate data points. We additionally delineated patterns of genetic aggregation and spatial dispersion, using a statistical parsimony haplotype network in TCS 1.21 (Clement *et al.* 2000, http://darwin.uvigo.es/software/tcs.html).

Results

Genetic composition and diversity of connected and isolated populations (Question 1)

Population genetic parameters from 15 nuclear DNA μsat loci and mtDNA control region sequences for 24 spawning sites across much of the native range of yellow perch (Fig. 1) are compared in Table 1. All μsat loci were unlinked and conformed to HWE expectations after Bonferroni correction (Appendix I). Numbers of μsat alleles per locus ranged from 14 (*Svi*3 and 7) to 53 (*Mpf*1), totalling 442 throughout the sampling range. Populations from the Great Lakes, that is, Thunder Bay in Lake Michigan (site F; 188 alleles) and Monroe in western Lake Erie (site I; 183 alleles), possessed the most alleles (Table 1). In comparison, a total of 26 mtDNA control region haplotypes were recovered across the range (Appendix II) and haplotype diversity per sample was relatively low, ranging from a single haplotype (in three populations: Lake Winnipeg, site B; Anchor Bay of Lake St. Clair, site H; Apalachicola River in the U.S. Gulf coastal region, site X) to a maximum of four (two populations: Dunkirk in eastern Lake Erie, site N; Morgan Creek in the U.S. Atlantic coastal region, site V).

Nuclear DNA heterozygosity (H_O) per single sampling location was highest overall in the Bush River of the U.S. South Atlantic coastal region (site T; 0.670 mean H_O), and lowest in the Apalachicola River of the Gulf coastal region (site X; 0.333)—with the latter congruent with its low mtDNA diversity. All populations except for Morgan Creek in the South Atlantic coastal region (site V) contained private (i.e. unique) μsat alleles (Table 1); they numbered from one (Lake Winnipeg; site D) to 11 (Bush River; site U). Overall, there was a higher proportion of private alleles in the South Atlantic and Gulf coastal populations, with the Apalachicola River having the most (site X; 0.154) and Great Lakes populations having the least—lowest at Pt. Colborne/Pt. Albino in eastern Lake Erie (site M; 0.006; Table 1).

In contrast, few regions and individual populations were distinguished by unique mtDNA control region haplotypes, with the Great Lakes containing a total of 12 (of those, few were unique to a single Lake; i.e. Huron-1, Erie-4 and Ontario-1) and the U.S. North Atlantic coastal region containing three unique haplotypes, including one predominant in the Hudson River sample (site S; 0.714). The South Atlantic coastal region housed the largest proportions of private haplotypes (0.618), including the Bush River sample (site T; 1.000) that contained two unique endemic types, distinguishing all of its individuals (Table 1). Levels of private haplotypes in the other South Atlantic coastal populations also were high. Other appreciable private haplotype rep-

Table 2 Pairwise tests of yellow perch population sample heterogeneity. (a) Major geographic regions using the F_{ST} analogue θ_{ST} (Weir & Cockerham 1984) for 15 μsat loci (below diagonal) and mtDNA control region sequences (above diagonal); and (b) θ_{ST} values for selected hierarchical group scenarios (15 μsat loci/mtDNA control region sequences)

(a)

	Northwest Lake Plains	Great Lakes region	Lake Champlain	North Atlantic coastal	South Atlantic coastal	Gulf coastal
Northwest Lake Plains	—	0.007	*0.240*	*0.685*	*0.592*	*0.929*
Great Lakes region	*0.140*	—	*0.410*	*0.762*	*0.787*	*0.827*
Lake Champlain	*0.228*	*0.188*	—	*0.327*	*0.290*	*0.287*
U.S. North Atlantic coastal	*0.227*	*0.172*	*0.136*	—	*0.422*	*0.404*
U.S. South Atlantic coastal	*0.236*	*0.219*	*0.196*	*0.119*	—	*0.436*
U.S. Gulf coastal	*0.285*	*0.260*	*0.258*	*0.189*	*0.186*	—

(b)

	Comparison	θ_{ST} between groups	Mean θ_{ST} within a	Mean θ_{ST} within b
1.	a. Formerly glaciated groups (A–S) vs. b. Unglaciated groups (T–X)	*0.161/0.613*	*0.193/0.324*	*0.265/0.464*
2.	a. All connected groups (D–O, W–X) vs. b. All isolated groups (A–B, P–V)	*0.126/0.308*	*0.118/0.105*	*0.206/0.486*
3.	a. Connected groups in North (D–O) vs. b. Isolated groups in North (A–B, P–S)	*0.126/0.192*	*0.114/0.106*	*0.202/0.500*
4.	a. Connected groups in North (D–O) vs. b. Connected groups in South (W–X)	*0.271/0.827*	*0.114/0.106*	*0.393*/N.A.
5.	a. Isolated groups in North (A–B, P–S) vs. b. Isolated groups in South (T–V)	*0.094/0.441*	*0.202/0.500*	*0.206/0.483*

Regular text = not significant, underlined italics = remained significant following sequential Bonferroni correction (Rice 1989; 270 of 276 μsat comparisons).
N.A., not applicable.

resentation characterized populations from Lake Champlain (site P; 0.500) and Thunder Bay in Lake Huron (site F; 0.438). By comparison, overall representation of unique haplotypes in Lake Erie was much less (0.032).

Genetic structure and divergence among populations and regions (Question 1)

Pairwise comparison tests showed that most yellow perch populations were genetically distinctive, (270 of

276 μsat comparisons), revealing significant genetic structure (Appendix III). Results of θ_{ST} and ρ_{ST} tests were congruent, and thus, patterns were not influenced by sample size; we report the former to facilitate comparisons with other studies. The most pronounced differences were between the Northwest Lake Plains and Gulf coastal population regions (Table 2a). Isolated populations had greater among site divergences than characterized connected populations (Table 2b). This pattern was evident in the south as well as in the previously glaciated northern groups, with both having similar divergence levels. Significant differences among spawning groups within bodies of water further denoted local and regional genetic structure.

Relationship of geographic distance and population isolation to genetic divergence (Question 2)

Genetic differences among yellow perch populations reflected isolation by geographic distance, discerned from both genetic marker systems: μsat loci ($R^2 = 0.387$, $P < 0.001$; Appendix IVa) and mtDNA control region sequences ($R^2 = 0.041$, $P < 0.001$; Appendix IVb). Overall, geographically more distant populations were distinguished by higher divergences, yet some nearby groups also were very different [e.g. Anchor Bay in Lake St. Clair (site H) vs. western Lake Erie's South Bass Island (site D)], indicating localized genetic structure within connected waterways. Notably, genetic differences among Lake Erie yellow perch spawning groups appeared independent of geographic distance in our earlier fine-scale study using μsat data ($R^2 = 0.014$, N.S.; see Sepulveda-Villet & Stepien 2011). Likewise, among the connected populations of the Great Lakes region, genetic isolation did not follow geographic distance using our present μsat ($R^2 = 0.130$, N.S.) and mtDNA data ($R^2 < 0.001$, N.S.).

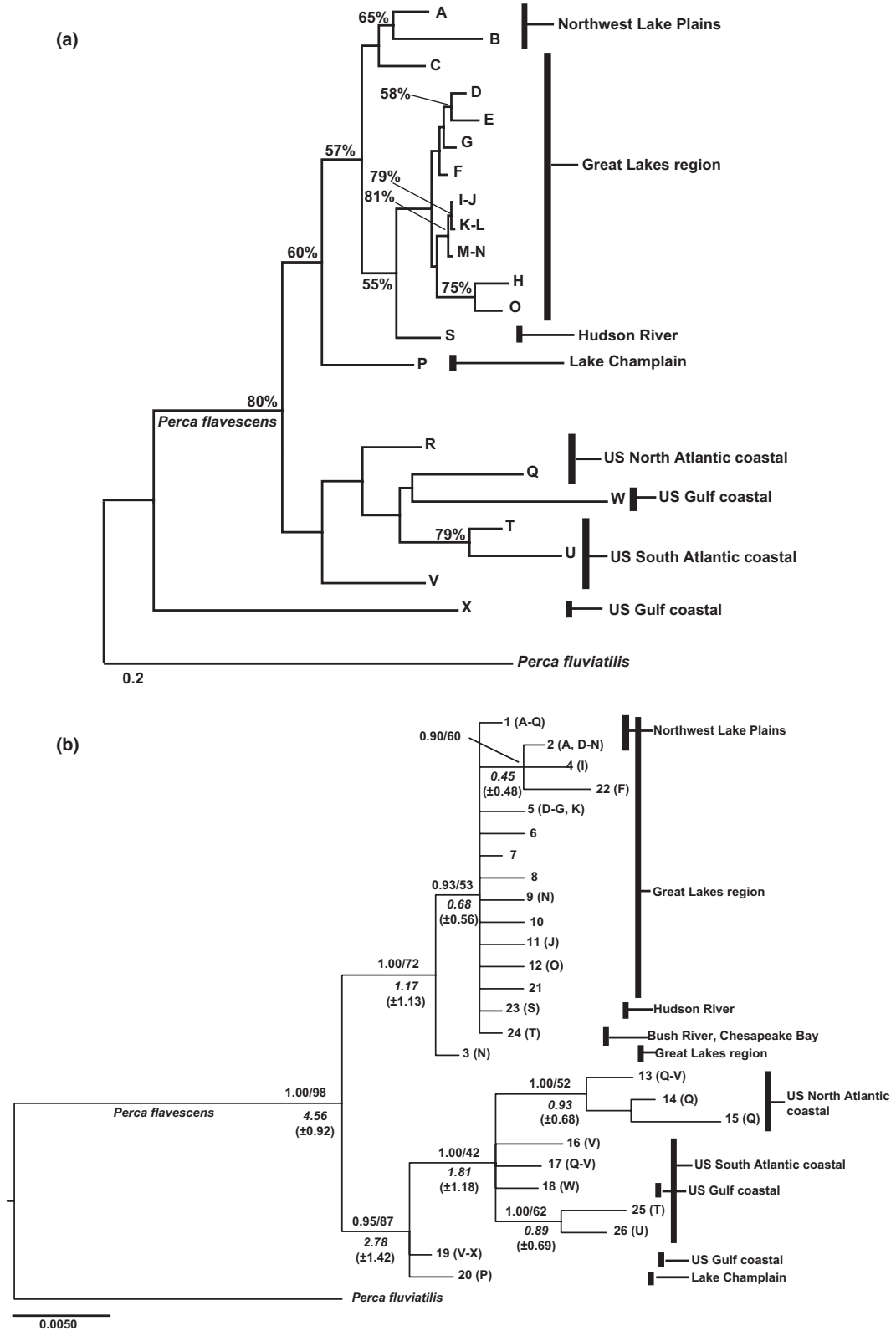
Patterns of genetic delineation and phylogenetic relationships (Question 3)

BARRIER analysis results identified probable genetic discontinuities across the native North American range of yellow perch. The two most significant barriers (Barrier I, 13 loci/0.364 mean F_{ST}; II, 11 loci/0.247) separated the Gulf coastal populations from the others, with the third (III, 11 loci/0.342) isolating unglaciated Atlantic Coast populations from those north of the maximum extent of the last glaciations. The next two barriers (IV, 9 loci/0.282; V, 10 loci/0.239) distinguished the North Atlantic coastal from the Great Lakes and Northwest populations, and barrier VI (9 loci/0.207) divided Lake Winnipeg from the rest. The remaining barriers isolated smaller populations, such as Lake Superior from the other upper Great Lakes (VII, 7 loci/0.177), the St. Johns River from other Atlantic coastal locations (VIII, 6 loci/0.173), Morgan Creek from nearby Chesapeake Bay and Albemarle Sound (IX, 5 loci/0.141) and finally a division between the upper and lower Great Lakes (X, 6 loci/0.098; Fig. 1).

Phylogenetic and genetic distance trees (Fig. 2) discerned similar population relationships using nuclear μsat loci (Fig. 2a) and mtDNA haplotypes (2b). The μsat neighbor-joining tree (Fig. 2a) depicted the Gulf coastal Apalachicola River population as basal to two clusters, one containing the other Gulf coast population (site W), along with populations from the South Atlantic (sites T-V) and North Atlantic coasts (Sebasticook and St. Johns rivers; sites Q-R). The other cluster contained spawning groups A-P, encompassing the Northwest Lake Plains (sites A-B), Great Lakes region (sites C-O), Lake Champlain (site P) and the Hudson River (site S). Populations from the Northwest Lake Plains (sites A-B) clustered together with those from Lake Superior (site C), whereas the residual populations from the Great Lakes region formed a single cluster.

The phylogenetic tree of mtDNA haplotypes (Fig. 2b) supported two primary clades, distinguished by relatively high posterior probability and bootstrap support. One primary clade (diverging *c*. 1.17 ± 1.13 Ma) comprised haplotypes from the Northwest Lake Plains and the Great Lakes (haplotypes 1–2, 4–12 and 21–22 from sites A-Q), along with the Hudson River (haplotype 23; site S) and the Bush River (24; site T). Within that first primary clade, haplotype 3 (unique to site N, the eastern basin of Lake Erie at Dunkirk, NY) was basal, diverging *c*. 0.45 (±0.48) Ma and forming the sister lineage to the others. The second primary mtDNA clade, which diverged *c*. 2.78 (±1.42) Ma, contained haplotypes from the Atlantic and Gulf coastal populations (with an individual clade of North Atlantic haplotypes 13–15, *c*. 1.81 ± 1.18 Ma; and 25–26 from the South Atlantic region, *c*. 0.89 ± 0.69 Ma), along with two haplotypes located basally: 20 from Lake Champlain (site P) and 19 widespread in the Gulf coastal region (sites V-X).

The statistical parsimony network in Fig. 3 identified a broadly distributed haplotype 1 from the Northwest Lake Plains (sites A–B), the Great Lakes region (sites C–O), Lake Champlain (site P) and the Sebasticook (site Q) and Hudson (site S) rivers, which was less prevalent in the east. The network depicted a large closely related haplotype group from the Great Lakes and Northwest Lake Plains (2–3, 5–12, and 21), along with haplotype 23 in the Hudson River (site S) and haplotype 26 of the Scuppernong River (site U); all differ by single nucleotides from predominant haplotype 1. From this Great Lakes cluster, five substitutions separated haplotype 19 of Morgan Creek (site V) and the Gulf Coast (sites W–X), with an additional substitution distinguishing



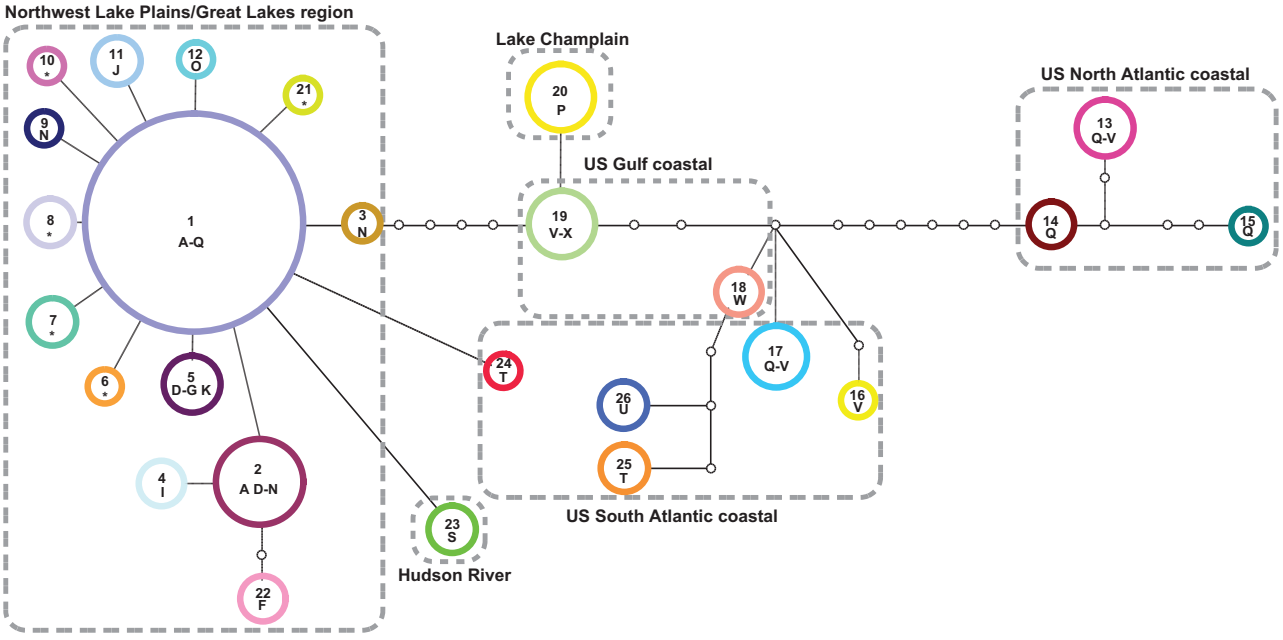


Fig. 3 Statistical parsimony network among yellow perch mtDNA control region haplotypes (numbered) constructed in TCS 1.21 (Clement *et al.* 2000). Circles are sized according to total observed frequency of the haplotype. Letters in circles denote sample sites where that haplotype was recovered. Asterisks in circles denote haplotypes recovered and identified in Sepulveda-Villet *et al.* (2009) but not recovered in this study. Lines indicate a single mutational step between the haplotypes. Small, unlabelled circles represent hypothesized unsampled haplotypes. Dashed lines enclosing haplotype groups denote major regional delineations used in this study. Circle colours also reflect haplotype identities as portrayed in Fig 4b.

haplotype 20 of Lake Champlain (site P). Finally, the North Atlantic coastal haplotypes appeared the most distant of all, with 10 mutational steps separating haplotype 14 of the Sebasticook River (site Q) from haplotype 19, three additional substitutions to haplotype 13 found in the St. Johns River (site R), Sebasticook River (site Q) and Morgan Creek (site V), and four steps to 15, found only in the Sebasticook River sample (site Q). Thus, the North Atlantic coastal haplotypes showed pronounced divergence.

Broad-scale population patterns (Questions 3 and 4)

Bayesian STRUCTURE analyses shown in Fig. 4a identified $K = 17$ population clusters (Appendix VI) (using the ΔK method of Evanno *et al.* 2005), which distinguished yellow perch spawning groups from the upper Mississippi River watershed (site A; coloured grey) as grouping with Lake Winnipeg (site B; grey), as well as among each of the Great Lakes: Lake Superior (site C; magenta), Lake Michigan (sites D–E; tan), Lake Huron (sites F–G; yellow), Lake St. Clair (site H; purple), Lake Erie (sites I–N; similar mixed colours) and Lake Ontario (site O; navy). Structure analyses also differentiated populations from Lake Champlain (site P; pink), the Sebasticook and St. Johns rivers (sites Q–R; blue), the Hudson River (site S; light blue), the South Atlantic coast (sites T–U; olive) and the Gulf coast (sites W–X; brown). Some individuals from Lake Ontario (site O) had relatively small assignment probabilities to eastern Lake Erie (sites M–N; orange and green), however, most self-assigned (navy). In the South Atlantic region, the sample from Morgan Creek (site V) showed some evidence of comprising two clusters (olive and violet).

Fig. 2 Trees showing yellow perch relationships: (a) neighbor-joining tree of populations from μsat data, based on Nei's (1972) distance in PHYLIP (Felsenstein 2008) and (b) Bayesian 50% majority rule consensus trees of 26 yellow perch mtDNA control region haplotypes, rooted to the Eurasian perch *Perca fluviatilis* and constructed in MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003). Tree is congruent with our maximum likelihood (ML) analyses (Appendix VII). Values above nodes = Bayesian posterior probability/percentage support from 1000 bootstrap pseudoreplications in ML. Values below nodes = estimated divergence times (given as millions of years) as determined in r8s 1.71 (Sanderson 2003) and 95% confidence intervals (in parentheses) as determined in BEAST 1.7.2 (Drummond *et al.* 2012) and TRACER 1.4 (Rambaut & Drummond 2007). Letters in parentheses denote sampling sites in which haplotypes were recovered. Vertical bars denote geographical regions.

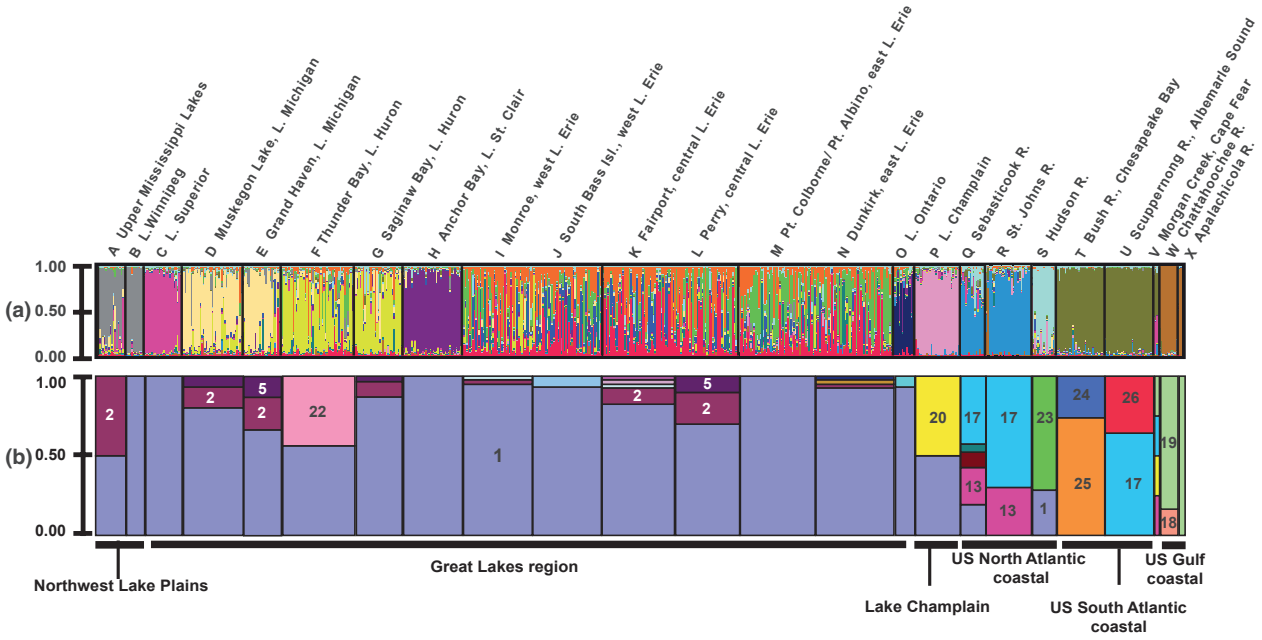


Fig. 4 Estimated yellow perch population structure from (a) Bayesian STRUCTURE analyses (Pritchard *et al*. 2000; Pritchard & Wen 2004) for $K = 17$ groups using 15 μsat loci. Optimal $K = 17$ (pp = 0.999) was determined from ΔK likelihood evaluations (Evanno *et al*. 2005). Individuals are represented by thin vertical lines, partitioned into K coloured segments that represent estimated membership fractions. (b) mtDNA control region frequencies of 26 haplotypes. Vertical black lines separate different spawning groups. Bar colours reflect haplotype identities as portrayed in Fig. 3.

A similar pattern was discerned with mtDNA control region haplotypes (Fig. 4b). Haplotype 1 (violet) was widespread among all Great Lakes populations, with types 2 (magenta) and 5 (purple) being the next most abundant. To the east, other haplotypes were more prevalent, with 20 (gold) unique to Lake Champlain (site P), 17 (blue) in the Sebasticook, St. John, and Scuppernong rivers (sites Q, R and U), 23 (chartreuse) only in the Hudson River (site S), 24 and 25 (navy, orange) composing the entire Bush River sample (site T) and 26 (red) endemic to the Scuppernong River (site U). Finally, haplotypes 18 and 19 (salmon, light green) solely occurred in the Gulf coastal populations (sites W–X).

Bayesian assignment tests in GENECLASS2 similarly detected significant self-assignment of individuals to their respective 'home' populations (Appendix Va). Only a single spawning group in central Lake Erie (site L; Perry) did not primarily self-assign, with most of its individuals instead assigning to western Lake Erie (site I; Monroe). Most individuals that misassigned to other samples retained affinity to their corresponding lake or watershed (Appendix Va). Assignment tests to major geographic regions also showed that most self-assigned to their 'home' region (Appendix Vb). However, the majority of upper Mississippi River individuals (site A) assigned to the Great Lakes watershed, rather than to the Northwest Lake Plains and those from the Hudson River (site S) were equally divided between the Great Lakes watershed and the North Atlantic coastal region. Similarly, assignment tests to putative glacial refugia or regions traced most individuals from Lake Winnipeg (site B) and western Lake Superior (site C) to a Missourian refugium origin; those from the Great Lakes and the upper Mississippi River strongly assigned to the Mississippian refugium (Appendix Vc). Individuals from Lake Champlain (site P) and the Atlantic coast (sites Q–V) ascribed to the Atlantic coastal group. A final group consisted of Gulf coastal relicts (sites W–X), which all self-assigned (Appendix Vc). No clear relationship was found between heterozygosity and water body area, with low posterior probability (pp = 0.217).

Hierarchical relationships tested using AMOVA (Table 3) showed highest support for metapopulation distinction between formerly glaciated (sites A–S) vs. unglaciated (sites T–X) regions, which explained the most overall variation (two groups = 14% μsat/58% mtDNA; among populations = 15%/24%; total = 29%/82%), with a greater proportion distinguishing among populations in the two groups. Analysis partitioning variation among six major geographic regions also accounted for higher levels the Northwest Lake Plains (sites A–B), Great Lakes (sites C–O), Lake Champlain (site P), North Atlantic coastal (sites Q–S), South Atlan-

Table 3 Relative distribution of genetic variation among and within yellow perch spawning populations using Analysis of Molecular Variance, based on: (a) 15 μsat loci and (b) mtDNA control region sequences

	Source of variation		% Variation	Fixation Index	Significance (*P*-value)
(a) μsat loci	1.	Among the six regions	18.04	0.180	*0.001*
		Among sampling sites within regions	7.56	0.092	*0.001*
		Within the sampling sites	74.40	0.256	*0.001*
	2.	Among four glacial refugia/relict groups	14.93	0.149	*0.001*
		Among the sampling sites within groups	9.84	0.111	*0.001*
		Within the sampling sites	75.59	0.244	*0.001*
	3.	Between glaciated vs. unglaciated regions	13.99	0.140	*0.001*
		Among populations within regions	14.93	0.174	*0.001*
		Within populations	71.08	0.289	*0.001*
	4.	Between isolated vs. connected groups	10.97	0.110	*0.001*
		Among populations within groups	12.30	0.138	*0.001*
		Within populations	76.73	0.233	*0.001*
	5.	Between connected groups in north vs. south	24.82	0.248	*0.013*
		Among populations within connected groups	7.97	0.106	*0.001*
		Within populations	67.22	0.328	*0.001*
	6.	Between isolated groups in north vs. south	4.20	0.042	*0.032*
		Among populations within isolated groups	21.54	0.225	*0.001*
		Within populations	74.26	0.257	*0.001*
(b) mtDNA	1.	Among the six regions	49.75	0.498	*0.002*
		Among sampling sites within regions	24.99	0.497	*0.001*
		Within the sampling sites	25.27	0.747	*0.001*
	2.	Among four glacial refugia/relicts	36.51	0.365	*0.018*
		Among the sampling sites within refugia	36.87	0.581	*0.001*
		Within the sampling sites	26.62	0.734	*0.001*
	3.	Between glaciated vs. unglaciated regions	58.30	0.583	*0.001*
		Among populations within regions	24.07	0.824	*0.001*
		Within populations	17.63	0.577	*0.001*
	4.	Between isolated vs. connected groups	13.97	0.140	*0.008*
		Among populations within groups	39.64	0.536	*0.001*
		Within populations	46.39	0.461	*0.001*
	5.	Between connected groups in north vs. south	79.69	0.797	*0.018*
		Among populations within connected groups	7.31	0.870	*0.001*
		Within populations	13.00	0.360	*0.001*
	6.	Between isolated groups in north vs. south	37.38	0.374	*0.003*
		Among populations within isolated groups	37.83	0.752	*0.001*
		Within populations	24.79	0.604	*0.001*

Scenario 1 tested significance for the regions sampled (Northwest Lake Plains, Great Lakes, Lake Champlain, U.S. North Atlantic coastal, U.S. South Atlantic coastal, U.S. Gulf coastal), scenario 2 tested for four putative glacial refugia/region origins (Missourian, Mississippian, Atlantic and Gulf relicts), scenario 3 tested formerly glaciated (sites A–S) vs. unglaciated (T–X) regions, scenario 4 tested isolated (sites A–C, P–R) vs. connected (D–N) regions, scenario 5 evaluated connected groups in the north (sites D–N) vs. connected groups in the south (W–X), and scenario 6 tested isolated groups in the north (sites A–C, P–R) vs. those in the south (T–X). Regular text = not significant, underlined italics = significant at 0.05 level.

tic coastal (sites T–V) and Gulf coastal populations (sites W–X; variation among the six groups = 18% μsat/50% mtDNA; among populations within them = 8%/25%; combined total = 26/75%). Tests for divisions among possible glacial refugia and historic regions (Missourian refugium, Mississippian refugium, Atlantic coastal region and Gulf coastal relict populations) explained slightly less of the variation (four groups = 15% μsat/37% mtDNA; among populations = 10%/37%; total = 25%/73%). The scenario that tested isolated (sites A–C, P–R) vs. connected (sites D–N) populations likewise showed less partitioning (two groups; 11%/14%; among populations = 13%/40%; total = 23%/54%).

Most populations significantly differed in the pairwise tests (Appendix III; Table 2). Greater among-population genetic divergences characterized unglaciated than previously glaciated regions (Table 2b; scenario 1). Isolated populations also were more divergent than connected ones, across the range (scenario 2). Likewise, isolated populations in the north were more divergent from each other than were connected ones (scenario 3), whereas connected groups in the south differed more than those

in the north (scenario 4). Isolated groups in the north and south had similar degrees of interpopulational divergence (scenario 5).

Discussion

Waterscape genetic patterns and relation to our hypotheses

Our results lend support to the following underlying questions and hypotheses:

1 Are genetic diversity and divergence patterns different or comparable in connected vs. isolated populations for yellow perch across its native range? We find that genetic diversity is highest in southern populations of moderate sizes (i.e. the U.S. South Atlantic coastal region) and also is relatively high in areas where colonists from more than a single glacial refugium probably met to found the populations (i.e. Lake Erie; a connected system). Genetic diversity also is higher in connected population systems, in comparison with isolated ones. Genetic divergence is greater among isolated populations, both in formerly glaciated and unglaciated regions.

2 Do population relationships reflect a pattern of genetic isolation with geographic distance in connected vs. unconnected sites? There is significant genetic isolation with geographic distance across the native North American range of yellow perch. However, this pattern often breaks down at fine-scales among sites within a single water body or connected watersheds. Specifically, genetic relationships among spawning groups in Lake Erie and across the Great Lakes system do not conform to an isolation-by-distance hypothesis, indicating that genetic structuring is mediated by other processes, such as natal homing and habitat specificity.

3 Are relationships among northern populations consistent with colonization from various hypothesized glacial refugia? Yes, our results indicate contribution from at least two primary glacial refugia to the analysed populations; yellow perch from the Missourian refugium may have founded present-day populations in the Northwest Lake Plains and western Lake Superior. Origins of most Great Lakes yellow perch trace to the Mississippian refugium, with some possible contribution from the Atlantic refugium in the east (eastern Lake Erie and Lake Ontario). Yellow perch from the Atlantic coastal refugium founded northern populations along the Atlantic seaboard, Lake Champlain, and west to the Appalachian Mountains.

4 Is genetic diversity and divergence greater in unglaciated vs. glaciated regions? Our AMOVA results show that genetic diversity overall is higher in unglaciated populations vs. previously glaciated ones, especially in the South Atlantic coastal region. U.S. Gulf coastal relict populations are markedly isolated and divergent from other samples, as well as from each other. These rare relict populations occupy restricted ranges and have relatively low diversity, which particularly affected their mtDNA diversity (as it has a smaller effective population size; see Avise 2004). Divergences among populations are greater in the south than in formerly glaciated populations; however, isolated groups of both have similarly high divergence levels. Thus, geographic and genetic isolation provided the strongest driver.

Genetic diversity and divergence trends

Our data show that genetic diversities of yellow perch populations appear relatively consistent across the native range, but are considerably lower in the small relict Gulf coastal populations (by 17%, $H = 0.387$). Greater diversity (by 13%) characterizes the southern Atlantic coastal sites ($H = 0.603$), which were unglaciated and have smaller population sizes than those in the Great Lakes (Muncy 1962). These South Atlantic coastal populations also contain more unique alleles and haplotypes than characterize other locations, indicating that they may constitute an important genetic 'reservoir' for the species. Higher genetic diversity often is characteristic of older, long-established populations, provided that they have not undergone bottlenecks (Tessier & Bernatchez 1999). The South Atlantic coastal yellow perch populations are adapted to mesohaline conditions and probably can readily migrate from fresh to brackish waters (Grzybowski *et al.* 2010). These coastal populations appear particularly diverse.

Overall, yellow perch populations from formerly glaciated regions have lower heterozygosities in both nuclear and mitochondrial markers and lower proportions of private alleles/haplotypes. In walleye, populations from unglaciated vs. formerly glaciated regions had similar μsat heterozygosity levels (mean $H_O = 0.698$, range = 0.612–0.778), except for a rare relict population in the Gulf coast, whose lower diversity ($H_O = 0.537$) was attributed to bottlenecks (Stepien *et al.* 2009). Yellow perch and walleye have different dispersal abilities, with walleye travelling greater distances during foraging seasons (Houde 1969). The two species occupy some different habitats, with walleye less common in smaller lakes and reservoirs (Nelson & Walburg 1977). They thus presumably responded differently to

geographic isolation, with greater divergences among yellow perch populations (θ_{ST} ranging to 0.018–0.472 in our study) vs. walleye (0.010–0.295; Stepien *et al.* 2009). Similarly, southerly populations of yellow perch are differentiated by greater divergences (0.226–0.300) than those in the north (0.011–0.276; Stepien *et al.* 2007).

Major population divisions

Our genetic divergence results delineate yellow perch population divisions among six major geographic regions: Northwest Lake Plains, Great Lakes watershed, Lake Champlain, U.S. North Atlantic coastal, South Atlantic coastal and Gulf coastal. A similar pattern was discerned by Stepien *et al.* (2009) for the genetic structure of walleye populations, which approximately corresponded to our divisions: Northwest Lake Plains (Lake Winnipeg, McKim Lake in Ontario, and the upper Mississippi River), the Great Lakes watershed (divided into six groups: Lake Superior, Lakes Michigan/Huron, Lake Huron's Georgian Bay, Lake St. Clair, Lake Erie and Lake Ontario), North Atlantic coastal, South Atlantic coastal and Gulf coastal groups. Yellow perch and walleye belong to the same family, occupy similar native ranges, co-occur in many habitats and are both exploited; they thus probably experienced similar historical and contemporary selective and population pressures. Both are believed to return to spawn in natal areas; however, the walleye has been much better studied (Craig 2000; Roseman *et al.* 2010; Barton 2011).

We discern genetic distinctiveness of most yellow perch spawning groups across broad and fine geographic scales, as evidenced by our barrier and F_{ST} analyses. Broadscale patterns for yellow perch fit a range-wide pattern of genetic isolation with geographic distance, as have been shown for walleye (Stepien *et al.* 2009), smallmouth bass *Micropterus dolomieu* (Stepien *et al.* 2007) and ninespine stickleback *Pungitius pungitius* (Aldenhoven *et al.* 2010).

Whereas geographic distance appears to significantly drive genetic divergence among distant yellow perch populations, site-to-site distance is not a significant determinant of genetic structure among closely located spawning populations within a single body of water (e.g. Lake Erie; Sepulveda-Villet & Stepien 2011) or among connected lakes (i.e., within the Great Lakes). Likewise, relationships among closely spaced spawning groups of walleye within lakes did not fit a genetic isolation by geographic distance pattern (Strange & Stepien 2007; Stepien *et al.* 2009, 2010), suggesting that spawning site specificity drives genetic structure. Similarly, smallmouth bass showed greater divergence than expected among closely spaced tributary populations (Stepien *et al.* 2007). Our present study found no significant correlation between genetic diversity and water area of the sampled locations (using the method of Foll & Gaggiotti 2006), suggesting that processes other than available habitat determine these patterns.

Many yellow perch spawning groups within a given body of water are genetically divergent despite the apparent potential for dispersal and gene flow among them (e.g. those within Lake Erie; also see Sepulveda-Villet & Stepien 2011). This may be due to homing behaviour and spawning group fidelity. A study by Bergek & Björklund (2007) based on eight microsatellite loci described divergent yet sympatric kin groups of European perch in a small lake that lacked physical barriers to gene flow. Barriers to gene flow for European perch probably resulted from reproductive isolation, either via kin recognition (Gerlach *et al.* 2001) or due to reduced hybrid fitness between sympatric but divergent cohorts (Behrmann-Godel & Gerlach 2008). These factors remain to be tested for yellow perch.

Evidence for discrete population groups within connected water bodies recently was determined for yellow perch in Lake Erie, from whole-body morphometric analyses (Kocovsky & Knight 2012). In that study, morphometric shape patterns distinguished among Lake Erie population samples. Our current results and previous work (Sepulveda-Villet & Stepien 2011) support similar fine-scale genetic patterns among yellow perch spawning populations, which may be maintained by reproductive isolation due to spawning group fidelity.

Relationships of contemporary northern populations to glacial refugia

Our divergence time estimates here used fossil records as calibration points, which may affect accuracy, given the vagaries in identifying and dating fossils and the likelihood of variation in mutation rates, as discussed by Ho *et al.* (2005, 2011). In contrast, our previous mtDNA control region divergence estimates in Sepulveda-Villet *et al.* (2009) were based on a molecular clock calibrated to logperch *Percina caprodes* by Near & Benard (2004) at 2%/my. However, our results here revealed lack of correspondence to a strict molecular clock. In the present analysis, localized branch mutation rates ranged from 0.15% to 0.29%/my (about an order of magnitude slower than the previous calibration). It thus is advisable to carefully select a combination of available calibration sources to better reconcile analytical variations in these estimates.

Our mtDNA phylogeny indicates that yellow perch populations are divided in two primary clades that may have diverged *c.* 4.56 Ma. Most of the southern population haplotypes appear to have differentiated *c.* 0.89–2.78 Ma, with the North Atlantic coastal haplotypes

separating from the South Atlantic and Gulf coastal haplotypes by *c.* 1.81 my. The South Atlantic and Gulf coastal haplotypes are more closely related to each other than to those from the North Atlantic. The second major clade shows that the northern haplotypes shared a more recent common ancestry, estimated as *c.* 0.45–1.17 Ma.

Yellow perch in the Northwest Lake Plains (Lake Winnipeg and upper Mississippi River) and western Lake Superior may have descended from Missourian refugium colonists, following similar phylogeographic patterns to those found in walleye (Stepien *et al.* 2009) and other fish. The Missourian refugium similarly founded populations of lake sturgeon *Acipenser fulvescens* in the Hudson Bay drainage (Ferguson & Duckworth 1997) and brown bullhead *Ameiurus nebulosus* in western Lake Superior (Murdoch & Hebert 1997). Glacial Lake Agassiz initially occupied much of the Hudson Bay watershed (including Lake Winnipeg), which probably had some southern drainage to Lake Superior (Mandrak & Crossman 1992; Rempel & Smith 1998), facilitating fish movements 13 000–8500 ya. Ice later blocked this passage, isolating the yellow perch populations in our Northwest Lake Plains sites (Saarnisto 1974; Teller & Mahnic 1988), as is shown by their high divergences. This pattern appears consistent with genetic and geographic isolation of walleye populations from Lake Winnipeg, southwest Ontario and the upper Mississippi River watersheds (Stepien *et al.* 2009). These northwestern fish populations always have been small in size and presumably occupy suboptimal habitats (Hoagstrom & Berry 2010). We note that our samples did not include sites from unglaciated portions of the Missouri River, and thus, our interpretation of that refugium is subject to further verification. However, the extensive history of yellow perch stocking in those regions (Lee *et al.* 1980; Fuller & Neilson 2012) probably obscured the ability to detect a native genetic profile.

The Mississippian glacial refugium is believed to have founded most of the Great Lakes fauna (Underhill 1986; Mandrak & Crossman 1992; Todd & Hatcher 1993), as indicated for yellow perch here, walleye (Stepien *et al.* 1998; Stepien *et al.* 2009, 2010), smallmouth bass (Stepien *et al.* 2007), rainbow darter (Haponski *et al.* 2009) and lake sturgeon (Ferguson & Duckworth 1997). Some mixed signal indicates genetic contributions from the Atlantic refugium into the lower Great Lakes for walleye (Stepien *et al.* 1998; Strange & Stepien 2007; Stepien *et al.* 2009, 2010), smallmouth bass (Stepien *et al.* 2007), brown bullhead (Murdoch & Hebert 1997), lake trout (Wilson & Hebert 1996) and ninespine stickleback (Aldenhoven *et al.* 2010).

It generally is thought that southerly unglaciated populations may harbour more genetic diversity, because they have experienced a longer undisturbed history for evolution and local adaptation (Petit *et al.* 2003). Greater diversity also is hypothesized for areas where descendants from two or more glacial refugia met (Petit *et al.* 2003). Thus, mixing of descendants from multiple refugia may account for the relatively high degree of genetic diversity in our Great Lakes populations, as found in eastern Lake Erie. Unconnected fringe populations that traced to a single refugium probably experienced bottlenecks and genetic drift, thereby reducing heterozygosity, as shown in our Lake Winnipeg and Maine samples. The southern Gulf relict population also has low heterozygosity, characteristic of its small population size, bottlenecks, and genetic drift.

Lake Champlain drains into the St. Lawrence River and its yellow perch appear to trace to mixed origins from the Atlantic and Mississippian refugia, but today have a very divergent genetic composition from our other samples. Lake Champlain received meltwaters from glacial Lake St. Lawrence (*c.* 11 600 ya), and then Lake Agassiz (*c.* 10 900–8000 ya) and glacial Lake Barlow-Ojibway (9500–8000 ya). This produced an extensive freshwater habitat that replaced the former saline Champlain Sea, which was a temporary inlet of the Atlantic Ocean formed by the retreating glaciers (Rodrigues & Vilks 1994). Regional flooding presumably led to colonization of Lake Champlain from the Atlantic refugium, as suggested by genetic evidence from lake cisco *Coregonus artedi* (Turgeon & Bernatchez 2001). Our yellow perch mtDNA control region haplotype 1 probably already was widespread preglacially and then represented in the Mississippian and Atlantic refugia populations but was more common in the west. Today, haplotype 1 remains more abundant in the west.

The Atlantic coastal refugium formed a warm enclave of diverse habitats in coastal plains and estuaries east of the Appalachian Mountains (Schmidt 1986; Bernatchez 1997), which colonized contemporary northeastern and northcentral populations (Russell *et al.* 2009). This region supports high species richness and endemism today (Griffiths 2010), as discerned for yellow perch. The northeastern migrating populations split to found those we sampled in Maine and those along the eastern seaboard route to the Hudson River; both are very divergent today. The St. Johns River population is less diverse and presumably experienced a founder event and/or genetic bottleneck. Its pattern appears to fit the leading-edge dispersal hypothesis (Hewitt 1996, 1999).

Southern isolated and relict populations

Both southerly unglaciated regions sampled for yellow perch—the South Atlantic and Gulf coastal regions—are believed to be historically older populations (*c.* 2.78–

1.81 Ma), which probably accumulated distinct haplotypes and alleles over time. Homing behaviour to natal sites may be more pronounced in these oldest populations, which could be tested using relative straying percentages.

Yellow perch from the South Atlantic coast—including the Chesapeake Bay and Albemarle Sound populations—are unusual in inhabiting brackish estuarine waters during most of their lives, with travel up connected tributaries in spring spawning run aggregations to lay their eggs in freshwater (Muncy 1962). They are believed to spend their entire lives within their natal system and thus appear uniquely adapted to a mesohaline lifestyle. Dispersal through these estuarine habitats may be facilitated by freshwater discharge from their upper portions (Gibson & Najjar 2000). To the best of our knowledge, few other percids have appreciable saline tolerances, excepting *Sander marinus* from the Caspian Sea (Craig 2000) and *S. lucioperca* in Caspian and Baltic Sea estuaries (HELCOM 2006).

Our results indicate that the South Atlantic coastal region houses a unique variety of yellow perch mtDNA haplotypes and μsat alleles. There is no evidence of present genetic connectivity between the Chesapeake Bay and Albemarle Sound populations, despite their common evolutionary history, as suggested by our mtDNA haplotype data. Their respective upper freshwater reaches facilitate some limited gene flow confined within each system (Grzybowski *et al.* 2010). During global climate warming, the unique genetic diversity of these euryhaline populations might provide an important genetic reservoir for yellow perch in the event that some inland waters become more saline.

The present study also analysed rare and isolated relict native populations at the southern border of the yellow perch's native distribution, from the Chattahoochee and Apalachicola rivers in the Gulf coastal region (Lee *et al.* 1980). These areas house unique mtDNA haplotypes and μsat alleles that are highly differentiated from those in the South Atlantic coastal region, reflecting long-term isolation. Gulf and South Atlantic coastal population groups probably were isolated by drainage patterns around Georgia's Altamaha River, which separates tributaries to the southwest, forming a barrier together with the southern edge of the Appalachian Mountains (Church *et al.* 2003). Similar divergences distinguish Gulf coastal populations of the hermit crab *Pagurus longicarpus* (Young *et al.* 2002), tiger salamander *Ambystoma tigrinum* (Church *et al.* 2003) and millipedes of the genus *Narceus* (Walker *et al.* 2009).

The Chattahoochee and Apalachicola rivers are located in the same watershed, yet their yellow perch populations are distinguished by high θ_{ST} divergences despite apparent opportunity for gene flow. They each have small population sizes, underwent bottlenecks, and their spawning groups do not appear to mix. Likewise, walleye spawning in the Gulf coastal relict region of the North/Tombigbee rivers system comprise a rare relict population with low genetic diversity, unique genotypes and high divergence from other areas (Stepien *et al.* 2009).

Genetic patterns in the face of rapid climate change

Evaluating diversity and divergence patterns resulting from postglacial dispersal and adaptation in new environments, and the genetic reservoirs comprising isolated relict groups, may help us to predict the challenges faced by taxa during this era of rapid climate and habitat alterations. Populations along the lower latitudinal fringes of a species' native range probably house valuable genetic adaptations to warmer climates (Hampe & Petit 2005). In effect, global warming patterns rapidly are extending the northward postglacial expansion trajectory of many taxa; meanwhile, their southerly rear-edge groups may experience greater isolation, habitat reduction and bottlenecks. However, these southern genotypes may move northward, given connection opportunity. The diverse South Atlantic coastal yellow perch populations may prove especially well-adapted to tolerating salinity fluctuations and increasing water temperatures, facilitating their northward coastal migration, if sea levels rise to eventually connect low-lying estuaries, which are currently isolated by barrier island and sandbar systems.

The growing realm of molecular genomics will increasingly resolve the adaptations that underlie patterns of genetic diversity and diversity discerned here (see Allendorf *et al.* 2010; Avise 2010; Ouborg *et al.* 2010). Elucidating such adaptive genetic variation will help us to predict the response of specific populations to changing environments, new habitat regimes and exploitation pressure. Our waterscape genetic approach provides a bridge for understanding habitat connectivity and genetic distribution patterns, applied to the unique challenges faced by aquatic taxa due to constrained dispersal and gene flow via connected waterways. This investigation shows that the genetic structure of today's yellow perch populations reflects interplay among climatic events, ephemeral waterway connections, population sizes and probably spawning group philopatry. Interpreting the historical and present-day factors that shape population structure may aid conservation of genetic diversity despite ongoing anthropogenic changes.

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C.A.S.'s Great Lakes Genetics Laboratory (GLGL) at the Lake Erie Centre of the University of Toledo focuses on conservation genetics and genomics of native fishes and on invasion genetics of nonindigenous species. This study is part of a series on percid genetic patterns, dating to publications since 1995. This manuscript is part of O.J.S.-V.'s PhD dissertation study in the GLGL. O.J.S.-V. now is working on yellow perch aquaculture, nutrition, and genetics as a postdoctoral fellow at the USDA Agricultural Research Service in Milwaukee, Wisconsin. The GLGL also is investigating the evolutionary genetics and genomics of walleye *Sander vitreus* (see our 2009 Molecular Ecology paper), smallmouth bass *Micropterus dolomie*u (2007 Molecular Ecology paper), round goby *Neogobius melanostomus* (2009 and 2010 Molecular Ecology papers), tubenose goby *Proterorhinus semilunaris* and the dreissenid mussels *Dreissena polymorpha* and *D. bugensis*. Additional information and updates are available at http://www.utoledo.edu/nsm/lec/research/glgl/index.html.

Data accessibility

DNA sequences: GenBank Accessions: 1 = FJ155931, 2 = FJ155932, 3 = FJ155933, 4 = FJ155934, 5 = FJ155935, 6 = FJ155936, 7 = FJ155937, 8 = FJ155938, 9 = FJ155939, 10 = FJ155940, 11 = FJ155941, 12 = FJ155942, 13 = FJ155943, 14 = FJ155944, 15 = FJ155945, 16 = FJ155946, 17 = FJ155947, 18 = FJ155948, 19 = FJ155949, 20 = FJ155950, 21 = FJ155951, 22 = JX454954, 23 = JX454955, 24 = X454956, 25 = JX454957, and 26 = JX454958.

Arlequin-formatted nuclear microsatellite and mitochondrial haplotype input files, as well as Nexus-formatted mitochondrial haplotype alignments files, are available at http://www.datadryad.org. doi: 10.5061/dryad.91rg5.

Appendix I

Summary statistics for 15 μsat loci across the 24 spawning groups of yellow perch

Locus	N_A	Size range (bp)	F_{IS}	F_{IT}	F_{ST}
*Svi*2	18	184–218	0.149	0.455	0.360
*Svi*3	14	112–156	0.161	0.401	0.287
*Svi*4	42	108–198	0.101	0.235	0.149
*Svi*7	14	162–212	0.328	0.516	0.280
*Svi*17	30	96–190	0.170	0.280	0.133
*Svi*33	51	76–178	0.246	0.311	0.087
*YP*13	23	214–280	0.289	0.536	0.348
*YP*17	16	191–241	0.133	0.344	0.243
*Mpf*1	53	171–347	0.143	0.184	0.048
*Mpf*2	51	203–311	0.131	0.162	0.036
*Mpf*3	27	103–179	0.048	0.198	0.158
*Mpf*4	35	171–247	0.172	0.254	0.100
*Mpf*5	24	127–171	0.086	0.317	0.253
*Mpf*6	21	100–164	0.182	0.396	0.261
*Mpf*7	29	128–200	0.050	0.184	0.141
Total	448	—	0.150	0.299	0.175

N_A, number of alleles; bp, base pairs; F_{IS}, average differentiation within a spawning group; F_{IT}, deviation in the total sample; F_{ST}, mean genetic divergence between pairs of spawning groups.

Appendix II
Number and relative frequency (in parentheses) of yellow perch mtDNA control region haplotypes (1–26) per sampling site (A–X)

Locality	*N*	1	2	3	4	5	6	7	8	9	10	11	12	13
A. Upper Mississippi R. sites	18	9 (0.50)	9 (0.50)	—	—	—	—	—	—	—	—	—	—	—
B. L. Winnipeg, MB	12	12 (1.00)	—	—	—	—	—	—	—	—	—	—	—	—
C. St. Louis Bay, MN, L. Superior	25	25 (1.00)	—	—	—	—	—	—	—	—	—	—	—	—
D. Muskegon L., MI, L. Michigan	30	24 (0.80)	4 (0.13)	—	—	2 (0.07)	—	—	—	—	—	—	—	—
E. Grand Haven, MI, L. Michigan	15	10 (0.67)	3 (0.20)	—	—	2 (0.13)	—	—	—	—	—	—	—	—
F. Thunder Bay, MI, L. Huron	15	8 (0.56)	—	—	—	—	—	—	—	—	—	—	—	—
G. Saginaw Bay, MI, L. Huron	30	26 (0.87)	3 (0.10)	—	—	1 (0.03)	—	—	—	—	—	—	—	—
H. Anchor Bay, MI, L. St. Clair	10	10 (1.00)	—	—	—	—	—	—	—	—	—	—	—	—
I. Monroe, MI, L. Erie	40	38 (0.95)	1 (0.03)	—	1 (0.03)	—	—	—	—	—	—	—	—	—
J. South Bass Isl., OH, L. Erie	29	28 (0.93)	—	—	—	—	—	—	—	—	—	—	—	—
K. Fairport, OH, L. Erie	10	7 (0.70)	2 (0.20)	—	—	1 (0.10)	—	—	—	—	—	—	—	—
L. Perry, OH, L. Erie	40	33 (0.83)	4 (0.10)	—	1 (0.03)	—	—	—	1 (0.03)	—	1 (0.03)	—	—	—
M. Pt. Colborne /Pt. Albino, ON, L. Erie	30	30 (1.00)	—	—	—	—	—	—	—	—	—	—	—	—
N. Dunkirk, NY, L. Erie	39	36 (0.93)	1 (0.03)	1 (0.03)	—	—	—	—	—	1 (0.03)	—	—	—	—
O. Rochester, NY, L. Ontario	14	13 (0.93)	—	—	—	—	—	—	—	—	—	—	1 (0.07)	—
P. Burlington, VT, L. Champlain	30	15 (0.50)	—	—	—	—	—	—	—	—	—	—	—	—
Q. Sebasticook R., ME	21	4 (0.19)	—	—	—	—	—	—	—	—	—	—	—	5 (0.24)
R. St. Johns R., ME	14	—	—	—	—	—	—	—	—	—	—	—	—	3 0.30)
S. Hudson R., NY	16	4 (0.29)	—	—	—	—	—	—	—	—	—	—	—	—
T. Bush R., Chesapeake Bay, MD	23	—	—	—	—	—	—	—	—	—	—	—	—	—
U. Scuppernong R., Albemarle S., NC	28	—	—	—	—	—	—	—	—	—	—	—	—	—
V. Morgan Ck., Cape Fear, NC	4	—	—	—	—	—	—	—	—	—	—	—	—	1 (0.25)

Continued

Locality	*N*	1	2	3	4	5	6	7	8	9	10	11	12	13
W. Chattahoochee R., Gulf Coast, GA	12	—	—	—	—	—	—	—	—	—	—	—	—	—
X. Apalachicola R., Gulf Coast, FL	3	—	—	—	—	—	—	—	—	—	—	—	—	—
Total	508	335 (0.67)	27 (0.05)	1 (0.00)	2 (0.00)	6 (0.01)	—	—	1 (0.00)	1 (0.00)	1 (0.00)	—	1 (0.00)	9 (0.02)

Locality	14	15	16	17	18	19	20	21	22	23	24	25	26
A. Upper Mississippi R. sites	—	—	—	—	—	—	—	—	—	—	—	—	—
B. L. Winnipeg, MB	—	—	—	—	—	—	—	—	—	—	—	—	—
C. St. Louis Bay, MN, L. Superior	—	—	—	—	—	—	—	—	—	—	—	—	—
D. Muskegon L., MI, L. Michigan	—	—	—	—	—	—	—	—	—	—	—	—	—
E. Grand Haven, MI, L. Michigan	—	—	—	—	—	—	—	—	—	—	—	—	—
F. Thunder Bay, MI, L. Huron	—	—	—	—	—	—	—	—	7 (0.44)	—	—	—	—
G. Saginaw Bay, MI, L. Huron	—	—	—	—	—	—	—	—	—	—	—	—	—
H. Anchor Bay, MI, L. St. Clair	—	—	—	—	—	—	—	—	—	—	—	—	—
I. Monroe, MI, L. Erie	—	—	—	—	—	—	—	—	—	—	—	—	—
J. South Bass Isl., OH, L. Erie	—	—	—	—	—	—	—	1 (0.07)	—	—	—	—	—
K. Fairport, OH, L. Erie	—	—	—	—	—	—	—	—	—	—	—	—	—
L. Perry, OH, L. Erie	—	—	—	—	—	—	—	—	—	—	—	—	—
M. Pt. Colborne/ Pt. Albino, ON, L. Erie	—	—	—	—	—	—	—	—	—	—	—	—	—
N. Dunkirk, NY, L. Erie	—	—	—	—	—	—	—	—	—	—	—	—	—
O. Rochester, NY, L. Ontario	—	—	—	—	—	—	—	—	—	—	—	—	—
P. Burlington, VT, L. Champlain	—	—	—	—	—	—	15 (0.50)	—	—	—	—	—	—
Q. Sebasticook R., ME	2 (0.10)	1 (0.05)	—	9 (0.43)	—	—	—	—	—	—	—	—	—
R. St. Johns R., ME	—	—	—	7 (0.70)	—	—	—	—	—	—	—	—	—

Continued

Locality	14	15	16	17	18	19	20	21	22	23	24	25	26
S. Hudson R., NY	—	—	—	—	—	—	—	—	—	10 (0.71)	—	—	—
T. Bush R., Chesapeake Bay, MD	—	—	—	—	—	—	—	—	—	—	17 (0.74)	6 (0.26)	—
U. Scuppernong R., Albemarle S., NC	—	—	—	18 (0.64)	—	—	—	—	—	—	—	—	10 (0.36)
V. Morgan Ck., Cape Fear, NC	—	—	1 (0.25)	1 (0.25)	—	1 (0.25)	—	—	—	—	—	—	—
W. Chattahoochee R., Gulf Coast, GA	—	—	—	—	2 (0.17)	10 (0.83)	—	—	—	—	—	—	—
X. Apalachicola R., Gulf Coast, FL	—	—	—	—	—	3 (1.00)	—	—	—	—	—	—	—
Total	2 (0.00)	1 (0.00)	1 (0.00)	35 (0.07)	2 (0.00)	14 (0.03)	15 (0.03)	2 (0.00)	7 (0.01)	10 (0.02)	17 (0.03)	6 (0.01)	10 (0.02)

Appendix III

Pairwise tests of yellow perch population sample heterogeneity using the F_{ST} analogue θ_{ST} (Weir & Cockerham 1984) for 15 µsat loci (below diagonal) and mtDNA control region sequences (above diagonal)

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X
A. Upper Mississippi R. sites	—	*0.552*	*0.522*	0.219	0.117	0.397	*0.290*	0.392	*0.422*	*0.430*	0.230	0.097	*0.449*	*0.552*	*0.399*	*0.359*	*0.558*	*0.798*	*0.714*	*0.972*	*0.393*	*0.806*	*0.888*	0.929
B. L. Winnipeg, MB	*0.202*	—	0.000	0.080	*0.200*	*0.505*	0.052	0.000	0.008	0.034	0.050	0.239	0.000	0.000	0.050	*0.483*	*0.633*	*0.875*	*0.787*	*0.984*	*0.454*	*0.904*	*0.948*	*1.000*
C. St. Louis Bay, MN, L. Superior	*0.116*	*0.202*	—	0.069	0.175	*0.473*	0.042	0.000	0.002	0.026	0.041	0.206	0.000	0.000	0.036	*0.458*	*0.606*	*0.858*	*0.765*	*0.982*	*0.429*	*0.888*	*0.941*	*1.000*
D. Muskegon L., MI, L. Michigan	*0.125*	*0.232*	*0.134*	—	0.000	*0.487*	0.000	0.012	0.020	0.037	0.000	0.000	0.041	0.080	0.040	*0.441*	*0.615*	*0.845*	*0.774*	*0.978*	*0.448*	*0.860*	*0.910*	*0.945*
E. Grand Haven, MI, L. Michigan	*0.193*	*0.271*	*0.183*	*0.055*	—	0.374	0.005	0.072	0.098	0.111	0.013	0.000	0.123	0.200	0.095	0.359	*0.525*	*0.775*	*0.688*	*0.971*	*0.366*	*0.777*	*0.876*	*0.920*
F. Thunder Bay, MI, L. Huron	*0.137*	*0.194*	*0.137*	*0.046*	*0.054*	—	*0.492*	0.334	*0.550*	*0.499*	*0.537*	0.322	*0.551*	*0.505*	0.388	*0.458*	*0.488*	*0.525*	0.113	*0.719*	0.190	0.420	*0.555*	0.416
G. Saginaw Bay, MI, L. Huron	*0.144*	*0.190*	*0.127*	*0.037*	*0.055*	*0.018*	—	0.000	0.000	0.013	0.000	0.000	0.012	0.052	0.022	*0.452*	*0.620*	*0.854*	*0.778*	*0.980*	*0.450*	*0.873*	*0.922*	*0.962*
H. Anchor Bay, MI, l. St. Clair	*0.217*	*0.320*	*0.226*	*0.130*	*0.148*	*0.124*	*0.127*	—	0.000	0.000	0.000	0.074	0.000	0.000	0.000	0.362	*0.492*	*0.764*	*0.653*	*0.974*	0.329	*0.774*	*0.901*	1.000
I. Monroe, MI, L. Erie	*0.196*	*0.251*	*0.181*	*0.070*	*0.069*	*0.026*	*0.050*	*0.133*	—	0.001	0.001	0.079	0.000	0.008	0.007	*0.504*	*0.666*	*0.885*	*0.815*	*0.984*	*0.494*	*0.906*	*0.941*	*0.977*
J. South Bass Isl., OH, L. Erie	*0.311*	*0.369*	*0.267*	*0.183*	*0.244*	*0.166*	*0.187*	*0.279*	*0.167*	—	0.021	0.101	0.004	0.034	0.018	*0.469*	*0.626*	*0.864*	*0.782*	*0.982*	*0.452*	*0.888*	*0.935*	*0.980*

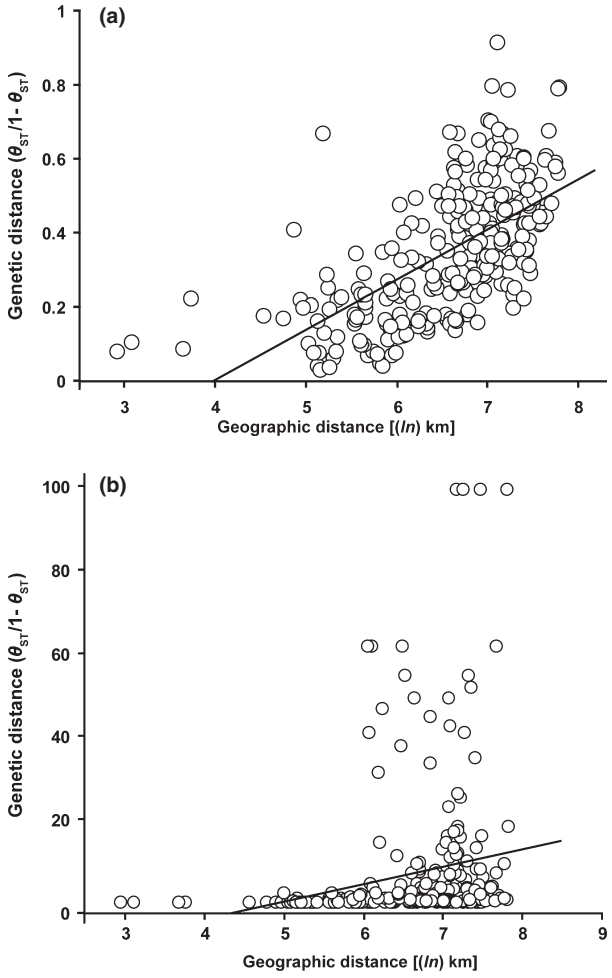
Continued

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X
K. Fairport, OH, L. Erie	*0.282*	*0.368*	*0.257*	*0.135*	*0.172*	*0.105*	*0.135*	*0.164*	*0.074*	*0.210*	—	0.000	0.024	0.050	0.024	*0.475*	0.651	*0.864*	*0.805*	*0.979*	*0.489*	*0.877*	*0.916*	*0.944*
L. Perry, OH, L. Erie	*0.226*	*0.285*	*0.209*	*0.090*	*0.108*	*0.045*	*0.078*	*0.153*	0.008	*0.163*	*0.076*	—	0.109	0.239	0.090	0.327	*0.485*	*0.742*	*0.645*	*0.969*	0.327	*0.732*	*0.869*	0.929
M. Pt. Colborne /Pt. Albino, ON, L. Erie	*0.236*	*0.287*	*0.206*	*0.101*	*0.109*	*0.050*	*0.083*	*0.158*	*0.016*	*0.177*	*0.089*	*0.014*	—	0.000	0.000	*0.504*	*0.665*	*0.884*	*0.815*	*0.984*	*0.494*	*0.905*	*0.940*	*0.976*
N. Dunkirk, NY, L. Erie	*0.255*	*0.337*	*0.245*	*0.118*	*0.138*	*0.089*	*0.116*	*0.174*	*0.049*	*0.198*	*0.098*	*0.052*	*0.060*	—	0.050	*0.483*	*0.633*	*0.875*	*0.787*	*0.984*	*0.454*	*0.904*	*0.948*	*1.000*
O. Rochester, NY, L. Ontario	*0.244*	*0.353*	*0.213*	*0.116*	*0.177*	*0.110*	*0.128*	*0.093*	*0.122*	*0.227*	*0.184*	*0.125*	*0.121*	*0.147*	—	0.396	*0.535*	*0.799*	*0.698*	*0.976*	*0.367*	*0.819*	*0.909*	0.981
P. Burlington, VT, L. Champlain	*0.247*	*0.285*	*0.175*	*0.208*	*0.237*	*0.193*	*0.196*	*0.278*	*0.227*	*0.239*	*0.297*	*0.248*	*0.230*	*0.284*	*0.246*	—	*0.362*	*0.513*	*0.701*	*0.917*	*0.332*	*0.373*	*0.363*	0.250
Q. Sebasticook R., ME	*0.337*	*0.395*	*0.263*	*0.298*	*0.326*	*0.277*	*0.288*	*0.356*	*0.318*	*0.362*	*0.386*	*0.343*	*0.330*	*0.362*	*0.328*	*0.211*	—	0.002	*0.669*	*0.881*	*0.238*	0.000	*0.374*	0.305
R. St. Johns R., ME	*0.301*	*0.369*	*0.212*	*0.240*	*0.310*	*0.228*	*0.235*	*0.315*	*0.265*	*0.307*	*0.341*	*0.281*	*0.279*	*0.320*	*0.268*	*0.237*	*0.173*	—	*0.702*	*0.928*	0.214	0.000	*0.526*	0.479
S. Hudson R., NY	*0.228*	*0.288*	*0.150*	*0.120*	*0.171*	*0.102*	*0.121*	*0.209*	*0.124*	*0.197*	*0.187*	*0.134*	*0.120*	*0.177*	*0.130*	*0.148*	*0.251*	*0.193*	—	*0.705*	0.294	*0.631*	*0.742*	0.646
T. Bush R., Chesapeake Bay, MD	*0.268*	*0.296*	*0.186*	*0.221*	*0.259*	*0.213*	*0.211*	*0.268*	*0.260*	*0.310*	*0.320*	*0.287*	*0.275*	*0.312*	*0.232*	*0.207*	*0.195*	*0.181*	*0.190*	—	*0.600*	*0.935*	*0.958*	*0.963*
U. Scuppernong R., Albemarle S., NC	*0.312*	*0.350*	*0.225*	*0.274*	*0.312*	*0.260*	*0.261*	*0.326*	*0.305*	*0.359*	*0.374*	*0.336*	*0.322*	*0.356*	*0.304*	*0.253*	*0.233*	*0.228*	*0.234*	*0.112*	—	0.137	*0.298*	0.190
V. Morgan Ck., Cape Fear, NC	*0.249*	0.362	*0.166*	*0.224*	*0.295*	*0.220*	*0.208*	*0.308*	*0.283*	*0.393*	*0.394*	*0.325*	*0.310*	*0.352*	*0.290*	*0.240*	*0.260*	*0.250*	*0.205*	*0.159*	*0.168*	—	0.345	0.213
W. Chattahoochee R., Gulf Coast, GA	*0.348*	*0.436*	*0.288*	*0.312*	*0.367*	*0.301*	*0.308*	*0.373*	*0.353*	*0.405*	*0.437*	*0.380*	*0.376*	*0.392*	*0.360*	*0.310*	*0.297*	*0.314*	*0.316*	*0.239*	*0.295*	*0.311*	—	0.000
X. Apalachicola R., Gulf Coast, FL	*0.367*	0.434	*0.313*	*0.324*	*0.389*	*0.309*	*0.305*	*0.377*	*0.367*	*0.404*	0.472	*0.397*	*0.390*	*0.433*	0.348	*0.321*	*0.365*	*0.358*	*0.330*	*0.265*	*0.342*	0.367	0.393	—

Regular text = not significant, underlined = significant at 0.05 level, underlined italics = remained significant following sequential Bonferroni correction (Rice 1989). All comparison results were congruent with exact tests of differentiation (Goudet *et al.* 1996).

Appendix IV

Mantel (1967) pairwise test for relationship between genetic distance ($\theta_{ST}/1 - \theta_{ST}$) and natural logarithm of geographical distance (km) among yellow perch population samples using (a) 15 μsat loci ($P < 0.001$, $R^2 = 0.39$, $y = 0.14x - 0.57$), and (b) mtDNA control region sequences ($P < 0.001$, $R^2 = 0.041$, $y = 4.13x - 20.31$).



Appendix V

Per cent assignment of yellow perch individuals (in rows) to (a) spawning samples (in columns), (b) major geographic regions and (c) putative glacial refugia.

(a)

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V
A. Upper Mississippi R. sites	**50**	—	6	11	—	11	6	—	6	—	—	—	—	—	—	—	—	—	—	—	—	—
B. L. Winnipeg, MB	—	**75**	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C. St. Louis Bay, MN, L. Superior	—	—	**88**	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
D. Muskegon L., MI, L. Michigan	—	—	—	**63**	—	8	15	—	5	—	3	—	—	—	—	—	—	—	—	—	—	—
E. Grand Haven, MI, L. Michigan	—	—	—	12	**36**	24	8	—	12	—	—	—	4	—	—	—	—	—	—	—	—	—
F. Thunder Bay, MI, L. Huron	—	—	—	—	—	**58**	10	—	21	—	2	—	2	—	—	—	—	—	—	—	—	—
G. Saginaw Bay, MI, L. Huron	—	—	—	—	—	44	**44**	—	3	—	3	—	—	—	—	—	—	—	—	—	—	—
H. Anchor Bay, MI, l. St. Clair	—	—	—	—	—	—	3	**85**	3	—	—	—	—	—	—	—	—	—	—	—	—	—
I. Monroe, MI, L. Erie	—	—	—	—	—	8	4	—	**58**	—	10	—	15	—	—	—	—	—	—	—	—	—
J. South Bass Isl., OH, L. Erie	—	—	—	—	—	—	—	—	—	**97**	3	—	—	—	—	—	—	—	—	—	—	—
K. Fairport, OH, L. Erie	—	—	—	—	—	—	—	—	5	—	**95**	—	—	—	—	—	—	—	—	—	—	—
L. Perry, OH, L. Erie	—	—	—	—	—	8	—	—	58	—	—	**19**	15	—	—	—	—	—	—	—	—	—
M. Pt. Colborne/Pt. Albino, ON, L. Erie	—	—	—	—	—	10	—	—	30	—	8	—	**55**	—	—	—	—	—	—	—	—	—
N. Dunkirk, NY, L. Erie	—	—	—	—	—	6	—	—	19	—	4	—	—	**71**	—	—	—	—	—	—	—	—
O. Rochester, NY, L. Ontario	—	—	—	—	—	—	—	—	27	—	—	—	—	—	**53**	—	—	—	—	—	—	—
P. Burlington, VT, L. Champlain	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	**100**	—	—	—	—	—	—
Q. Sebasticook R., ME	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	**81**	—	—	—	—	—
R. St. Johns R., ME	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	**60**	—	—	—	—
S. Hudson R., NY	—	—	—	—	—	—	—	—	6	—	—	—	—	—	—	—	—	—	**56**	—	—	—
T. Bush R., Chesapeake Bay, MD	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	**84**	—	—
U. Scuppernong R., Albemarle S., NC	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	**88**	—
V. Morgan Ck., Cape Fear, NC	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	**92**

(b)

	Northwest Lake Plains	Great Lakes region	Lake Champlain	North US Atlantic coastal	South US Atlantic coastal	US Gulf coastal
A. Upper Mississippi R. sites	**17**	78	—	—	—	—
B. L. Winnipeg, MB	**92**	8	—	—	—	—
C. St. Louis Bay, MN, L. Superior	—	**52**	—	—	—	—
D. Muskegon L., MI, L. Michigan	—	**100**	—	—	—	—
E. Grand Haven, MI, L. Michigan	—	**100**	—	—	—	—
F. Thunder Bay, MI, L. Huron	—	**100**	—	—	—	—
G. Saginaw Bay, MI, L. Huron	—	**94**	—	—	—	—

Continued

(b)

	Northwest Lake Plains	Great Lakes region	Lake Champlain	North US Atlantic coastal	South US Atlantic coastal	US Gulf coastal
H. Anchor Bay, MI, L. St. Clair	—	**97**	—	—	—	—
I. Monroe, MI, L. Erie	—	**100**	—	—	—	—
J. South Bass Isl., OH, L. Erie	—	**100**	—	—	—	—
K. Fairport, OH, L. Erie	—	**100**	—	—	—	—
L. Perry, OH, L. Erie	—	**100**	—	—	—	—
M. Pt. Colborne/Pt. Albino, ON, L. Erie	—	**100**	—	—	—	—
N. Dunkirk, NY, L. Erie	—	**100**	—	—	—	—
O. Rochester, NY, L. Ontario	—	**100**	—	—	—	—
P. Burlington, VT, L. Champlain	—	—	**93**	3	—	—
Q. Sebasticook R., ME	—	—	—	**84**	—	—
R. St. Johns R., ME	—	—	—	**93**	—	—
S. Hudson R., NY	—	44	—	**44**	—	—
T. Bush R., Chesapeake Bay, MD	—	—	—	—	**91**	—
U. Scuppernong R., Albemarle S., NC	—	—	—	—	**100**	—
V. Morgan Ck., Cape Fear, NC	—	—	—	—	**50**	—
W. Chattahoochee R., Gulf coast, GA	—	—	—	—	—	**83**

(c)

	Missourian refugium	Mississippian refugium	Atlantic coastal refugium and relicts	Gulf coastal relicts
A. Upper Mississippi R. sites	**6**	94	—	—
B. L. Winnipeg, MB	**37**	—	3	—
C. St. Louis Bay, MN, L. Superior	**96**	4	—	—
D. Muskegon L., MI, L. Michigan	—	**95**	—	—
E. Grand Haven, MI, L. Michigan	—	**83**	—	—
F. Thunder Bay, MI, L. Huron	—	**100**	—	—
G. Saginaw Bay, MI, L. Huron	—	**103**	—	—
H. Anchor Bay, MI, L. St. Clair	—	**97**	—	—
I. Monroe, MI, L. Erie	—	**100**	—	—
J. South Bass Isl., OH, L. Erie	—	**100**	—	—
K. Fairport, OH, L. Erie	—	**100**	—	—
L. Perry, OH, L. Erie	—	**100**	—	—
M. Pt. Colborne/Pt. Albino, ON, L. Erie	—	**100**	—	—
N. Dunkirk, NY, L. Erie	—	**100**	—	—
O. Rochester, NY, L. Ontario	—	**93**	—	—
P. Burlington, VT, L. Champlain	—	—	**100**	—
Q. Sebasticook R., ME	—	—	**88**	—
R. St. Johns R., ME	—	—	**82**	—
S. Hudson R., NY	—	6	**94**	—
T. Bush R., Chesapeake Bay, MD	—	—	**94**	—
U. Scuppernong R., Albemarle S., NC	—	—	**100**	—

Continued

(c)	Missourian refugium	Mississippian refugium	Atlantic coastal refugium and relicts	Gulf coastal relicts
V. Morgan Ck., Cape Fear, NC	—	—	**100**	—
W. Chattahoochee R., Gulf coast, GA	—	—	—	**100**

Assignment tests used a simulated population size of 10 000 individuals per site, with a rejection level of 0.01 (Cornuet *et al.* 1999) in GENECLASS2 (Piry *et al.* 2004). Bold values on diagonal denote self-assignment. Underlined = Highest percentage assignment.

Appendix VI
Summary statistics of Bayesian population assignment as implemented in Structure (Pritchard *et al.* 2000; Pritchard & Wen 2004) for *K* = 17 groups using 15 μsat loci

	Inferred population clusters																
Locality	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
A. Upper Mississippi R. sites	0.013	0.009	0.003	0.003	0.010	0.049	0.082	0.018	0.012	0.054	0.008	0.002	0.696	0.021	0.005	0.011	0.003
B. L. Winnipeg, MB	0.006	0.002	0.002	0.006	0.004	0.005	0.008	0.004	0.005	0.004	0.003	0.003	0.927	0.005	0.004	0.011	0.002
C. St. Louis Bay, MN, L. Superior	0.006	0.006	0.004	0.005	0.009	0.015	0.862	0.007	0.008	0.014	0.006	0.009	0.009	0.007	0.018	0.009	0.006
D. Muskegon L., MI, L. Michigan	0.019	0.013	0.006	0.004	0.012	0.109	0.007	0.012	0.017	0.660	0.009	0.006	0.056	0.018	0.011	0.037	0.004
E. Grand Haven, MI, L. Michigan	0.045	0.004	0.006	0.003	0.038	0.121	0.006	0.017	0.029	0.644	0.006	0.003	0.039	0.012	0.007	0.018	0.003
F. Thunder Bay, MI, L. Huron	0.043	0.010	0.005	0.005	0.027	0.531	0.017	0.017	0.039	0.037	0.017	0.004	0.028	0.093	0.016	0.108	0.003
G. Saginaw Bay, MI, L. Huron	0.023	0.010	0.004	0.007	0.017	0.642	0.014	0.014	0.017	0.088	0.009	0.009	0.011	0.021	0.036	0.074	0.004
H. Anchor Bay, MI, l. St. Clair	0.012	0.010	0.003	0.004	0.008	0.018	0.006	0.852	0.011	0.019	0.005	0.006	0.012	0.010	0.007	0.013	0.003
I. Monroe, MI, L. Erie	0.195	0.007	0.004	0.005	0.063	0.123	0.015	0.018	0.081	0.038	0.019	0.005	0.014	0.153	0.012	0.243	0.004
J. South Bass Isl., OH, L. Erie	0.015	0.006	0.002	0.003	0.011	0.015	0.008	0.007	0.015	0.011	0.850	0.002	0.006	0.021	0.004	0.021	0.003
K. Fairport, OH, L. Erie	0.048	0.003	0.002	0.003	0.019	0.011	0.004	0.021	0.808	0.012	0.024	0.002	0.008	0.011	0.006	0.018	0.002
L. Perry, OH, L. Erie	0.288	0.007	0.004	0.004	0.055	0.043	0.007	0.010	0.074	0.018	0.022	0.002	0.009	0.196	0.011	0.248	0.003
M. Pt. Colborne/Pt. Albino, ON, L. Erie	0.281	0.011	0.009	0.008	0.065	0.033	0.007	0.008	0.043	0.012	0.020	0.008	0.009	0.370	0.010	0.101	0.005
N. Dunkirk, NY, L. Erie	0.064	0.012	0.003	0.004	0.705	0.015	0.005	0.013	0.060	0.012	0.015	0.004	0.008	0.023	0.009	0.046	0.004
O. Rochester, NY, L. Ontario	0.029	0.588	0.015	0.010	0.018	0.010	0.009	0.144	0.022	0.012	0.013	0.003	0.005	0.066	0.014	0.038	0.004
P. Burlington, VT, L. Champlain	0.013	0.005	0.015	0.871	0.006	0.004	0.018	0.005	0.007	0.005	0.006	0.006	0.008	0.010	0.009	0.007	0.004
Q. Sebasticook R., ME	0.007	0.042	0.793	0.017	0.012	0.007	0.005	0.006	0.009	0.007	0.006	0.031	0.007	0.011	0.007	0.008	0.024
R. St. Johns R., ME	0.011	0.011	0.642	0.006	0.014	0.010	0.060	0.006	0.016	0.004	0.034	0.041	0.010	0.012	0.088	0.016	0.018
S. Hudson R., NY	0.011	0.021	0.013	0.088	0.009	0.014	0.009	0.007	0.015	0.019	0.008	0.009	0.007	0.009	0.743	0.013	0.005
T. Bush R., Chesapeake Bay, MD	0.003	0.007	0.022	0.009	0.005	0.004	0.003	0.004	0.003	0.004	0.003	0.902	0.004	0.004	0.010	0.003	0.008
U. Scuppernong R., Albemarle S., NC	0.003	0.004	0.015	0.003	0.003	0.003	0.005	0.002	0.003	0.003	0.003	0.934	0.004	0.003	0.006	0.003	0.003
V. Morgan Ck., Cape Fear, NC	0.007	0.004	0.031	0.006	0.004	0.007	0.285	0.007	0.004	0.007	0.002	0.573	0.014	0.004	0.018	0.005	0.022
W. Chattahoochee R., Gulf Coast, GA	0.002	0.003	0.008	0.006	0.002	0.002	0.004	0.003	0.002	0.003	0.002	0.030	0.014	0.002	0.003	0.002	0.912
X. Apalachicola R., Gulf Coast, FL	0.002	0.817	0.002	0.009	0.002	0.002	0.008	0.002	0.002	0.002	0.005	0.002	0.004	0.004	0.003	0.002	0.133

Optimal *K* = 17 (pp = 0.999) was determined from Δ*K* likelihood evaluations (Evanno *et al.* 2005).

Appendix VII

Relationships among yellow perch mtDNA control region haplotypes evaluated using Maximum Likelihood (ML) in PHYML 3.0 (Guindon *et al.* 2010). Members of the family Percidae were used to better define relationships: *Gymnocephalus cernua* (GenBank #AF025355.1; Stepien *et al.* 1998; Stepien *et al.* 2005, *G. baloni* (AF025360.1), *G. schraetser* (AF025361.1), *Perca fluviatilis* (Y14724), *Sander vitreus* (AF162272), *S. canadensis* (U90618.1) and *Percina maculata* (PMU90623).