Evolutionary Relationships, Population Genetics, and Ecological and Genomic Adaptations of Perch (Perca)

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Evolutionary Relationships, Population Genetics, and Ecological and Genomic Adaptations of Perch (*Perca*)

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ABSTRACT

The latest results about the evolutionary, biogeographic, and population genetic relationships of the three species comprising the percid fish genus *Perca* are presented, explained, and discussed. New analyses from new data dated the origin of the genus to an estimated 19.8 million years ago (mya) during the early Miocene Epoch, and the distribution of ancestral *Perca* likely extended across the North Atlantic Land Bridge until the mid-Miocene. The earliest evolutionary bifurcation led to the diversification of the European perch *P. fluviatilis* from the lineage shared by the common ancestor of the North American yellow perch

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P. flavescens and the Eurasian Balkash perch *P. schrenkii.* The latter two species diverged during the later Miocene, after the Land Bridge was closed. The European and yellow perches are both widely distributed across their respective continents, with biogeographic areas housing high genetic distinctiveness. Population genetic structure in their northern regions were shaped by post-glacial colonization patterns from multiple refugia, whose admixture increased diversity. Today's spawning groups are modest in genetic diversity yet very divergent from one another, which may reflect an apparent tendency of perch to live with relatives throughout their lives. There is a disconnect between the genetic divisions among populations and the delineation of fishery management units in the yellow perch, which is of concern. Employing a combined fisheries management and genetics/genomic approach will provide further understanding to help maintain the genetic diversity and unique adaptations of perch populations in the face of increasing anthropogenic influences, including climate change.

Keywords: Balkhash perch, biogeography, conservation genetics, evolutionary patterns, European perch, fisheries management, genomics, *Perca flavescens*, *Perca fluviatilis*, *Perca schrenkii*, phylogenetics, phylogeography, population genetics, yellow perch

2.1 Evolutionary and Biogeographic History of *Perca*

The percid genus *Perca* contains three economically and ecologically important species, which are top piscivores in North America and Eurasia. The yellow perch *P. flavescens* Mitchill, 1814 is endemic to North America, whereas two *Perca* species are native to Eurasia—the European perch *P. fluviatilis* Linnaeus, 1758 and the Balkhash perch *P. schrenkii* Kessler, 1874. Both the yellow perch and the European perch are widespread across much of their respective continents (Figs. 1 and 2), where they support popular recreational and commercial fisheries. They each have been widely introduced for angling outside their native ranges. Perch also serve as an important model species in ecotoxicology studies (e.g., Chapter 10, this volume). The goals of this chapter are to summarize the current knowledge and recent study results about their evolutionary and population genetic diversification, with implications and suggestions for further research.

The Balkhash perch is native to Lakes Balkhash and Alakolin Kazakhstan, where it supported abundant fisheries during the 1930s and 1940s (Sokolovsky et al. 2000). The Lake Balkhash fishery collapsed, however, contemporary harvests remain in the Lake Alakol region (Sokolovsky et al. 2000); the species also occurs in associated catchments extending into China (Berg 1965). During the 1960s and 1970s, the Balkhash perch was introduced to various water bodies in Uzbekistan, Kazakhstan, and Middle Asia (Kamilov 1966; Nuriyev 1967; Pivnev 1985). The Balkhash perch is classified in "The IUCN of Threatened Species" (v2013.2) as "data deficient" (http://www.iucnredlist.org/). Chapter 3 (this volume) is dedicated to this rare species.

As the phylogenetic relationships of the Balkhash perch to the other two *Perca* species was unresolved, we harvested sequence data from NIH GenBank, obtained new samples to sequence (by the Stepien laboratory), analyzed two mitochondrial genes
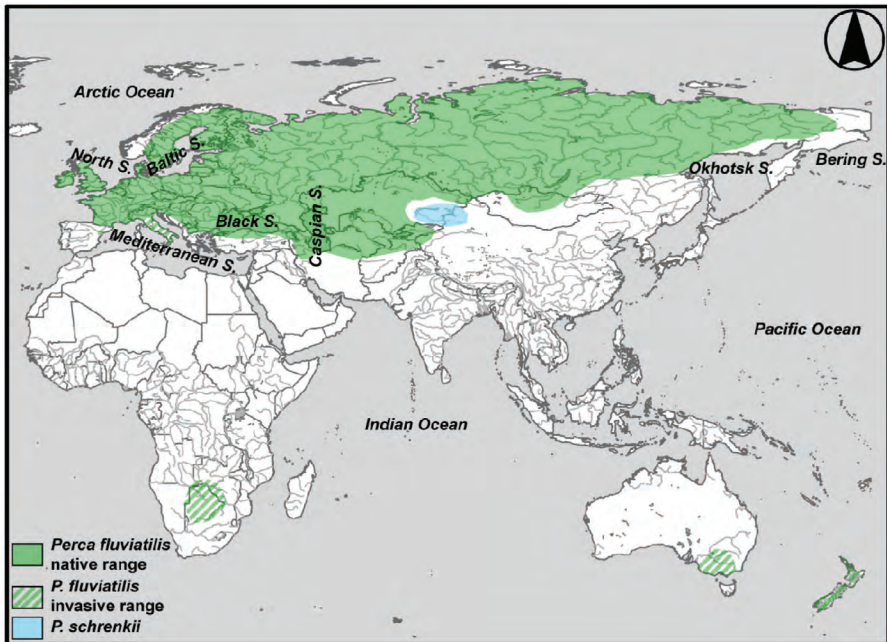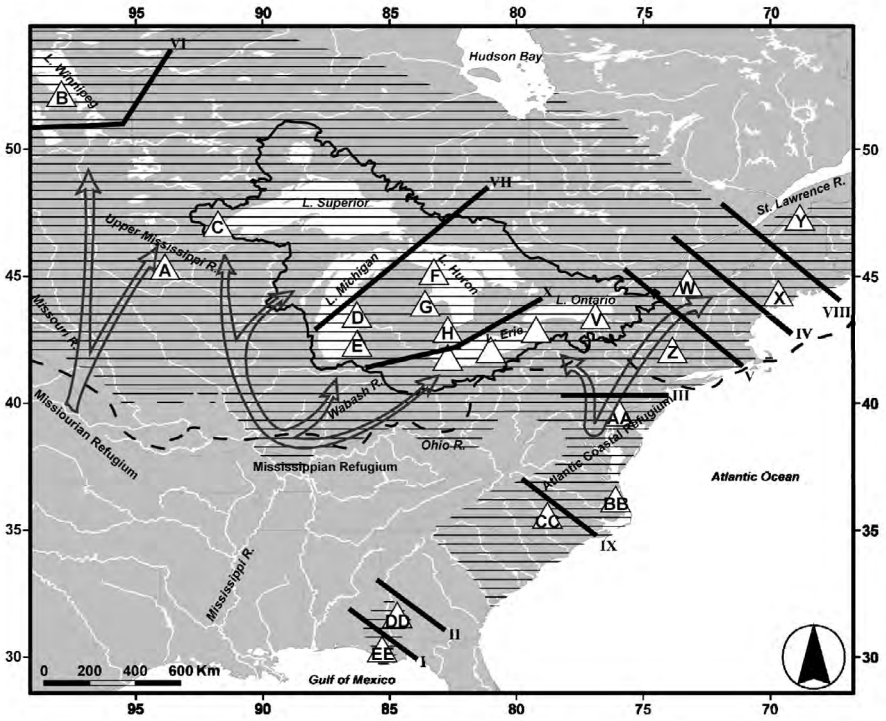
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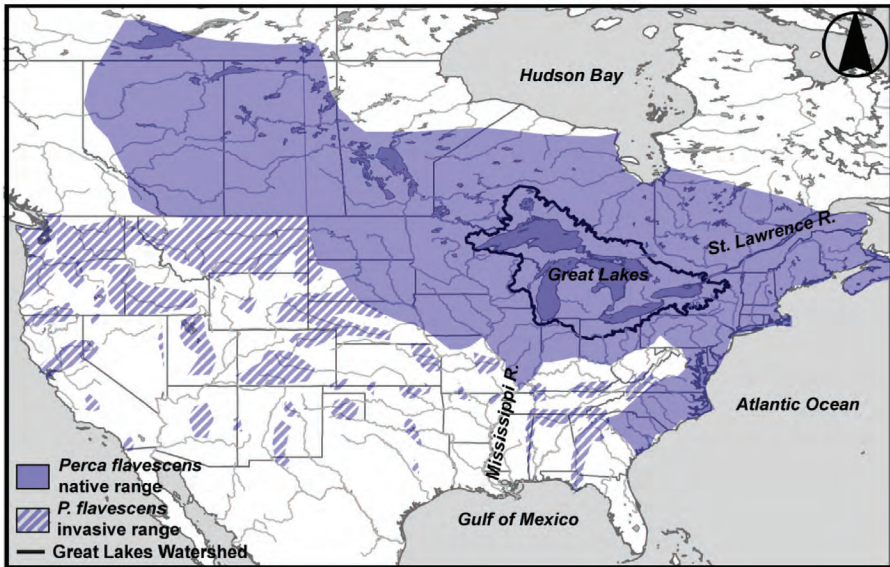
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Fig. 1. Maps showing the native and invasive ranges of *Perca* spp. in (A) North America and (B) Eurasia, using information adapted from Collette and Bănărescu (1977), Craig (2000), Page and Burr (2011), and Fuller and Neilson (2012).
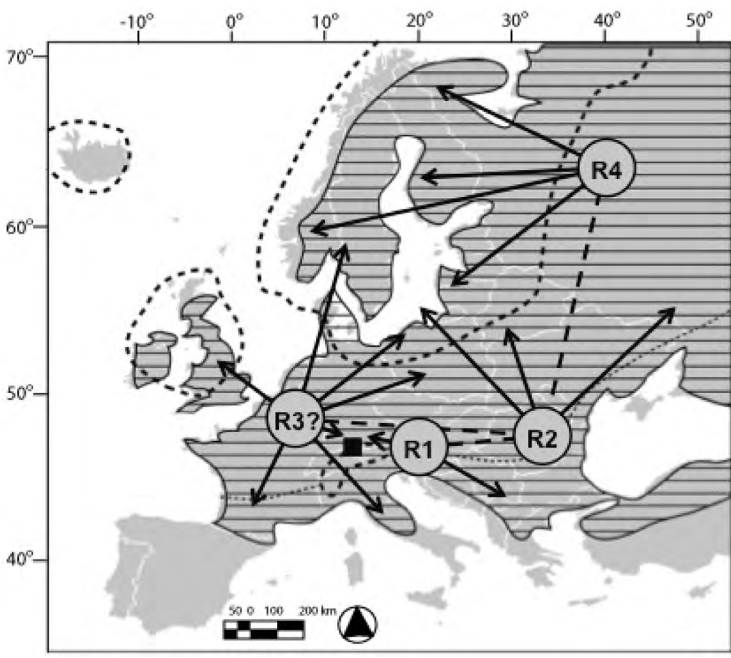
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Fig. 2. contd....

and a nuclear DNA gene region, and conducted new phylogenetic analyses. A new phylogeny (Fig. 3), based on concatenated DNA sequence data from the mitochondrial (mt) cytochrome *b* (cyt*b*) and cytochrome *c* oxidase I (COI) genes, and the nuclear recombination-activating gene intron 1 (RAG1), was determined for the present study by the Stepien laboratory using Bayesian analysis in MrBAYES v3.2.1 (Ronquist and Huelsenbeck 2003). We also conducted separate analyses on each gene, whose results were congruent to those obtained from the concatenated gene tree (Fig. 3). Results demonstrate that the genus *Perca* is monophyletic and well-supported (with 1.0 Bayesian posterior probability and 100% maximum likelihood bootstrap support).

Fossil record calibration data indicate that the genus *Perca* originated by an estimated 19.8 million years ago (mya) during the early Miocene Epoch (Fig. 3). It thus shares a similar biogeographic origin and pattern with the percid genus *Sander* (see recent phylogeny by Haponski and Stepien 2013). DNA sequence data indicated that the genus *Perca* is monophyletic and comprises three well-defined species (Fig. 3), which likewise is supported by morphological characters (see Craig et al. 2000). As indicated by the DNA data (Fig. 3), the primary division in the genus separates out the European perch (*P. fluviatilis*) from the Balkhash and yellow perch; the latter shared a more recent common ancestry. The Balkhash and yellow perch are sister species (nearest relatives), but are each highly distinct, having diverged an estimated 13.4 mya during the mid-Miocene Epoch. The common distribution of the ancestral *Perca* might have extended bi-continentally across either the North Atlantic Land Bridge and/or the Beringia Land Bridge, which once linked the continents across the Atlantic and the Pacific oceans, respectively (see Fig. 2). However, given that the native distribution of *P. flavescens* is exclusively east of the Rocky Mountains in North America and extends to the Atlantic Coast (Fig. 1A) and the distribution of *P. fluviatilis* extends northwest to the Atlantic Coast in Eurasia and is absent from far southeastern Asia (Fig. 1B), the distribution of their once-common ancestor most likely extended across the North Atlantic Land Bridge. This is concordant with findings by Wiley (1992)

Fig. 2. Maps showing the distributions of the North American yellow perch *Perca flavescens* (A) and the European perch *P. fluviatilis* (B), with their former areas of glacial refugia noted. A. Sampling locations for yellow perch (triangles) referred to in this study. Thick dashed line indicates the maximum extent of the Wisconsinan glaciations, arrows denote likely routes of post-glacial population colonizations (adapted from Mandrak and Crossman 1992; Stepien et al. 2012; Sepulveda-Villet and Stepien 2012). Grey lines (solid = microsatellite data, dashed = mtDNA control region sequences) denote major barriers to gene flow calculated based on the relationship between geographic coordinates (latitude and longitude) and genetic divergence (F_{ST}) using BARRIER v2.2 analysis (Manni et al. 2004, http://www.mnhn.fr/mnhn/ecoanthropologie/software/ barrier.html). Results are modified from Sepulveda-Villet and Stepien 2012, with genetic barriers ranked I–V for the microsatellite and 1–5 for the mtDNA control region data sets, in order of their decreasing magnitude. B. Map showing the distribution (hatched area) and postulated areas of former glacial refugia (R1–R4) for *P. fluviatilis* in Europe. Hatched lines indicate phylogenetic relationships between mtDNA haplotypes that originated in the refugia, arrows indicate postglacial dispersal pathways. The position of refugium R3 is somewhat unclear, as indicated by a question mark. The area surrounded by a heavy hatched line indicates the extent of the ice during the last glaciation (the Weichselian glaciation) and the glacier covering the Alps. The light hatched line indicates the southern border of the permafrost during the same time. The square indicates the position of the Lake Constance area. This figure was modified from Fig. 6 of Nesbø et al. (1999) and Fig. 1 of Hewitt (1999).
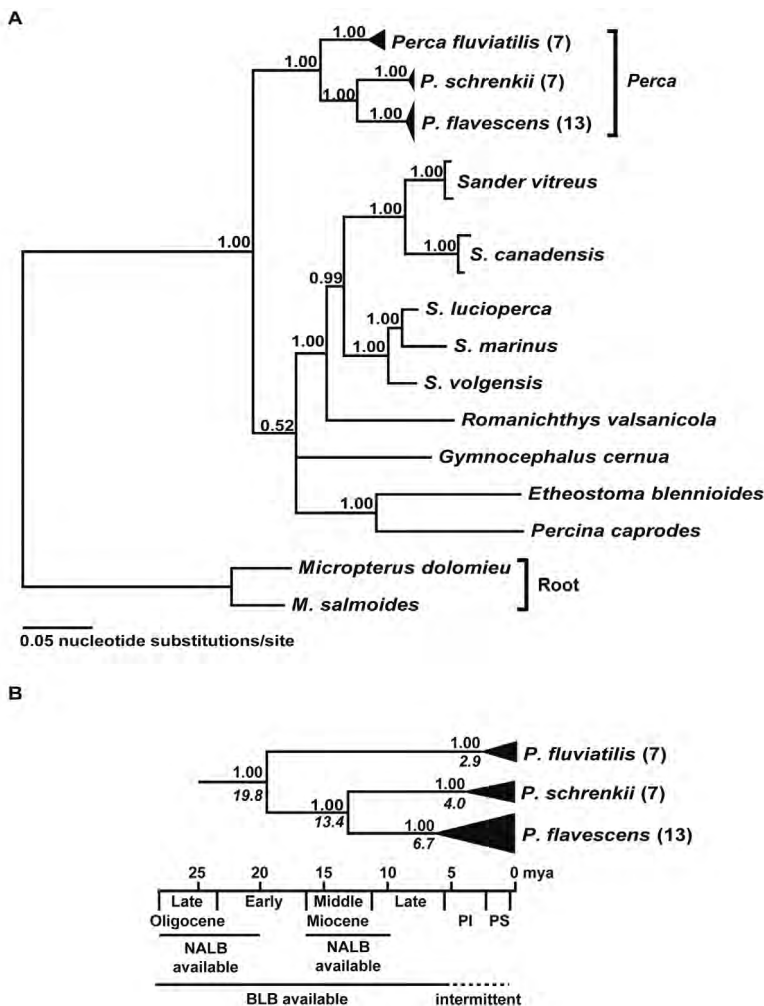
Fig. 3. Phylogeny of *Perca*. (A) Bayesian phylogenetic tree of mtDNA cytochrome *b* sequence haplotypes for the genus *Perca* and members of the family Percidae, determined for this study using concatenated sequence data set from three genes: mitochondrial cytochrome *b* (cyt*b*) and cytochrome *c* oxidase I (COI), and the nuclear recombination-activating gene intron 1 (RAG1), calculated using MrBAYES v3.2.1 (Ronquist and Huelsenbeck 2003, http://mrbayes.sourceforge.net). The program jMODELTEST v2 (Darriba et al. 2012, https://code.google.com/p/jmodeltest2/) was employed to select the best substitution model. The relationships among the *Perca* from the combined concatenated gene data were identical to this from separate analyses of all three genes. Tree is rooted to *Micropterus* based on its hypothesized close relationship to the Percidae, according to Song et al. (1998) and Sloss et al. (2004).

(B) Time-calibrated phylogeny for *Perca* derived using BEAST. Dates for the availability of the North Atlantic Land Bridge (NALB) were determined from Tiffney (1985) and Denk et al. (2011), and for the Bering Land Bridge (BLB) from Gladenkov et al. (2002). PI = Pliocene, PS = Pleistocene.

Above nodes = Bayesian posterior probability (pp) support. Below nodes in italics = estimated divergence times (millions of years) from BEASTv1.71 (Drummond et al. 2012, http://beast.bio.ed.ac.uk/), using the fossil calibration point of 12.0 mya for the genus Micropterus, and three molecular calibration points: 15.4 mya for the origin of the North American Sander, 13.8 mya for the Eurasian Sander, and 9.1 mya for the divergence between S. lucioperca and S. marinus, adapted from Haponski and Stepien (2013).

and Carney and Dick (2000). Moreover, a recent paper for the similarly distributed pikeperch genus *Sander,* likewise pointed to historic connection over the North Atlantic Land Bridge (Haponski and Stepien 2013). The North Atlantic Land Bridge appears to have been disrupted during the estimated interval of 17–20 mya, which matches this estimated time period for *Perca* taxon divergence, determined using BEAST 1.7 analyses (Drummond et al. 2012) and fossil date calibrations shown in Fig. 3. It may be that, given the phylogeny and these dates, this differentiation between *P. fluviatilis* and the *P. flavescens*/*schrenkii* linage began during this disruption in the North Atlantic Land Bridge. The lineages leading to the *P. schrenkii* and *P. flavescens* species later differentiated over the 4.4–6.7 to 13.4 mya time range, as indicated on Fig. 3.

2.2 Broadscale Biogeographic Patterns

2.2.1 Population Relationships Shaped by Glaciations and Colonizations

The yellow perch has a wide native geographic distribution that extends across much of the northeast and northcentral regions of North America, with a few isolated relict populations in the southeast (Figs. 1A and 2A). It inhabits a diversity of lacustrine and fluvial habitats, ranging from large to small in geographic areas, with its most extensive habitats and greatest abundances occurring in the Laurentian Great Lakes—especially in Lake Erie (Scott and Crossman 1973; Hubbs and Lagler 2004) and the St. Lawrence River system (Bernatchez and Giroux 2012).

   In the northern regions of the yellow perch's range, the habitats and basins of the Great Lakes region were formed and reshaped by the Laurentian Ice Age glaciations, leading to their present configuration about 4,000–12,000 years ago (ya). Similarly in Europe, the most recent Pleistocene cold stages, especially the Weichselian glaciation 13,000–25,000 ya, shaped the habitats of many freshwater fish species—including the European perch (Nesbø et al. 1999). During the glaciations, perches and other aquatic species migrated to waters south of the ice sheets, where their populations were concentrated in restricted areas, known as glacial refugia (Hocutt and Wiley 1986).

   Three primary North American glacial refugia are recognized (marked on Fig. 2A), which are: the Mississippian refugium in the central U.S., the Missourian refugium to the west, and the Atlantic refugium to the east (Bailey and Smith 1981; Crossman and McAllister 1986; Mandrak and Crossman 1992). Following the glacial meltwaters, yellow perch and other aquatic taxa migrated along tributary pathways leading from the refugia into the reformed water bodies of the Great Lakes and other northerly habitats (see Fig. 2A). Today's northern populations of yellow perch and other fishes appear to retain the signatures of their genetic origins from the respective glacial refugia (summarized by Sepulveda-Villet and Stepien 2012 for yellow perch). The yellow perch, although now adapted to the large inland "seas" that comprise the Great Lakes, had its ecological and evolutionary origins in fluvial systems rather than large, lacustrine basins.

   A very similar picture occurred in Europe (Fig. 2B). Many European freshwater fish species were driven from their original ranges and their distribution restricted to refugia situated in the three Mediterranean peninsulas: the Iberian (Atlantic-Mediterranean refugium), Italian (Adriatic-Mediterranean refugium), and Balkan

peninsulas (Pontic-Mediterranean refugium) (Hewitt 1999; Schmitt 2007), or in eastern continental regions into Asia or in northerly refugia bordering the ice shields (Stewart and Lister 2001). Later, with the glacial retreats, populations dispersed from their respective refugia and re-expanded their ranges. For European perch, a phylogeographic study by Nesbø et al. (1999) indicated the existence of four different refugia (labelled R1–R4 on Fig. 2B), from where European perch commenced their most recent colonisation patterns. The Danubian refugium (R1) presumably served as a founder population that led to few of the present European perch lineages (Nesbø et al. 1999; Behrmann-Godel et al. 2004). Most contemporary European perch populations trace their origins to the other three refugia (R2–R4) (Nesbø et al. 1999).

2.2.2 Phylogeographic Patterns of the European Perch

The European perch possesses a complex evolutionary history that has been delineated through phylogeographic studies. During the last Ice age in Central Europe, a wide plain of permafrost and cold steppe stretched between the northern main ice sheet and the southern mountain ranges—including the Alps—forming a very cold and dry environment (Fig. 2B) (Hewitt 1999). During this time, many freshwater fish species were driven from their original ranges, with their distributions restricted to refugia situated southward and/or eastward of the ice shield (Taberlet et al. 1998; Stewart and Lister 2001; Schmitt 2007).

When the ice later retreated, the populations dispersed again from their respective European refugia and re-expanded their ranges. As supported for other freshwater fish species in Europe, including chub *Leuciscus cephalus* (Durand et al. 1999) and burbot *Lota lota* (Barluenga et al. 2006), the European perch followed a hypothesized two-step expansion model. In the first step, descendants of an eastern lineage (refuge R2 on Fig. 2B), extensively colonized Central Eastern and western Europe likely during the Riss-Würm interglacial (between 115,000–126,000 ya). These survived the next glacial period in various refugia that were located either in Western European rivers, such as Rhine and Rhone (refuge R3 on Fig. 2B), in eastern drainages that enter the Black Sea (refuge R2), and/or in northeastern rivers (refuge R4). During the second step, at the end of the Würm period (~10,000 ya), range expansions took place from the Western stocks into all Atlantic drainages, and from the eastern and northeastern stocks into the rest of Europe. Through these pathways, the lineages reached and met together in the Baltic Sea region, resulting in a high level of heterogeneity (Nesbø et al. 1999).

During this recolonization process in Central Europe, several lineages that diverged in refugial allopatry came into secondary contact (Taberlet et al. 1998; Hewitt 2004a). For European perch, contact between refugial lineages has been indicated in drainages that either enter or postglacially entered the Baltic Sea, the Danube River, and the Lake Constance area (Nesbø et al. 1999; Behrmann et al. 2004). Several studies have identified a contact zone for Atlantic and Danubian fish lineages along the French-German border and in the western Alps, which corresponds to the closest area between the Rhine and Danube rivers (Taberlet et al. 1998; Hewitt 2004b). Lineages in that area possess genetic signatures from both the eastern Danubian and

the western cryptic Alpine or Atlantic refugia (see, e.g., Durand et al. 1999; Nesbø et al. 1999; Bernatchez 2001; Volckaert et al. 2002).

Lake Constance is a large pre-alpine lake located in the center of the contact zone between the Rhine and the Danube river systems (Figs. 2B and 4). It was formed after the last glacial period (Würm) with the retreat of the Alpine Rhine glacier, 10,000–15,000 ya (Fig. 4; Keller and Krayss 2000; Behrmann-Godel et al. 2004). It appears that the two neighboring systems in the Rhine and Danube rivers were connected only briefly at the end of the last recessional stage of the glacier (Wagner 1960; Keller and Krayss 2000). With the glacial retreat, melt water streams and proglacial lakes were formed (Fig. 4A–C; Wagner 1960; Keller and Krayss 2000), which provided a potential temporary colonization that could have been used by Danubian fish lineages
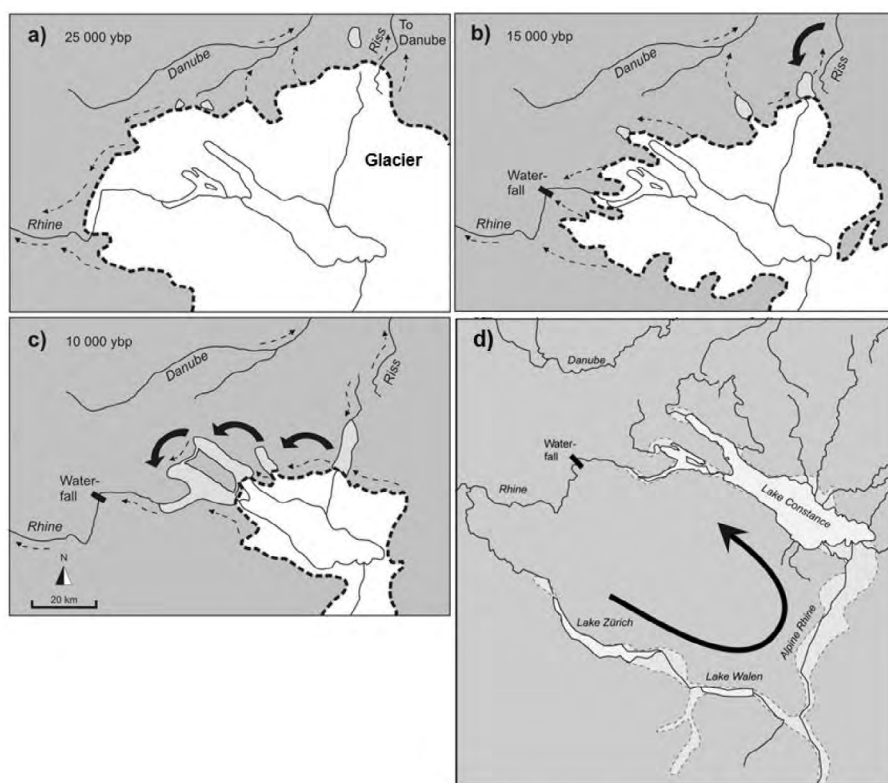

Fig. 4. Colonization route of Danubian (a–c) and Atlantic (d) haplotypes of *P. fluviatilis* into Lake Constance. a) During the last glacial maximum the Alpine glacier extended almost to the Danube system and melt water (hatched arrows) was running into the Danube. b) With the retreating glacier, huge proglacial lakes formed where perch from the Danube system could potentially have entered (black arrow) using the melt water streams as "colonization bridges", whereas colonization directly from the Rhine upstream was prevented by the Rhine waterfall. d) Postglacial connection of the Rhine and the Lake Constance region via Lakes Zürich and Walen after the last glacial period (redrawn after Wagner 1960). The arrow indicates the potential colonization route for Atlantic fish lineages via the connected lake system (area within dashed lines). Figure modified from Behrmann-Godel et al. 2004 and J. Behrmann-Godel, M. Barluenga, A. Meyer, and W. Salzburger, unpublished.

to colonize the lake; this has been shown for European perch, and burbot (Behrmann-Godel et al. 2004; Barluenga et al. 2006). At the end of the glacial period, the Lake Constance region became isolated westward from the upper Rhine River by a 23 meter high Rhine waterfall (Fig. 4c), which cutoff the upstream migration of Atlantic fish lineages (Behrmann-Godel et al. 2004). Directly after the retreat of the Alpine Rhine glacier, the water level of Lake Constance was 410 meters above sea level (15 meters higher than today). Lake Constance then was part of a huge postglacial lake system, which extended along the valley of the Alpine Rhine and connected them via the Linth River and through lakes Walen and Zürich (Fig. 4d). This connection existed until the outflowing Rhine River had excavated its channel, lowering Lake Constance to its present level of 395 meters above sea level. This connection putatively was used by Atlantic lineages of European perch, burbot, bullhead, and the vairone *Telestes muticellus* to colonize the region, which then came into secondary contact with the Danubian lineages within the Lake Constance area (Behrmann-Godel et al. 2004; Barluenga et al. 2006; Behrmann-Godel et al., unpublished).

2.2.3 Contemporary Broadscale Population Relationships of Yellow Perch

Contemporary haplotypes of the yellow perch in North America appear to trace to ~6.0 million years ago (mya; Sepulveda-Villet and Stepien 2012, Fig. 5). Regional distinctiveness of yellow perch metapopulations is very apparent, with those from the south and north, and east versus west, being highly differentiated (Table 2, Figs. 2A, 4–6, also see Stepien et al. 2009; Sepulveda-Villet and Stepien 2012). Divergences of the southern yellow perch haplotypes appear to date to ~2.5–3.6 mya, whereas the northern haplotypes share a common ancestry estimated ~0.6–4.2 mya among them (Fig. 5; Sepulveda-Villet and Stepien 2012).

Pronounced genetic demarcations delineate that the most unique yellow perch populations are located in six major geographic regions: Northwest Lake Plains, Great Lakes watershed, Lake Champlain, North Atlantic coastal, South Atlantic coastal, and Gulf coastal (Figs. 2A and 4–6; Sepulveda-Villet and Stepien 2012). The Atlantic coastal yellow perch populations possess high endemism today (Griffiths 2010), as evidenced by their genetic diversity and unique alleles (Table 1; Sepulveda-Villet and Stepien 2012). Substantial genetic diversity in the southerly, unglaciated populations may be due to their long undisturbed history for evolution and local adaptation (April et al. 2013). The South Atlantic coastal yellow perch populations are adapted to mesohaline conditions, and likely readily migrate from fresh to brackish waters (Grzybowski et al. 2010). The South Atlantic and Gulf coastal haplotypes are more closely related to each other than to those from the North Atlantic region (Sepulveda-Villet and Stepien 2012).

In comparison, the southern Gulf relict population of yellow perch sampled has relatively lower heterozygosity (Table 1), which is characteristic of its small population size, bottlenecks, and genetic drift. Yet, it also possesses a high number and proportion of private alleles, indicative of long-term isolation and distinctiveness (Table 1; Figs. 2A, 4–6). The relict Gulf coastal population appears related to, yet distinct from, populations of the southeast Atlantic seaboard (Sepulveda-Villet et al. 2009; Sepulveda-Villet and Stepien 2012).
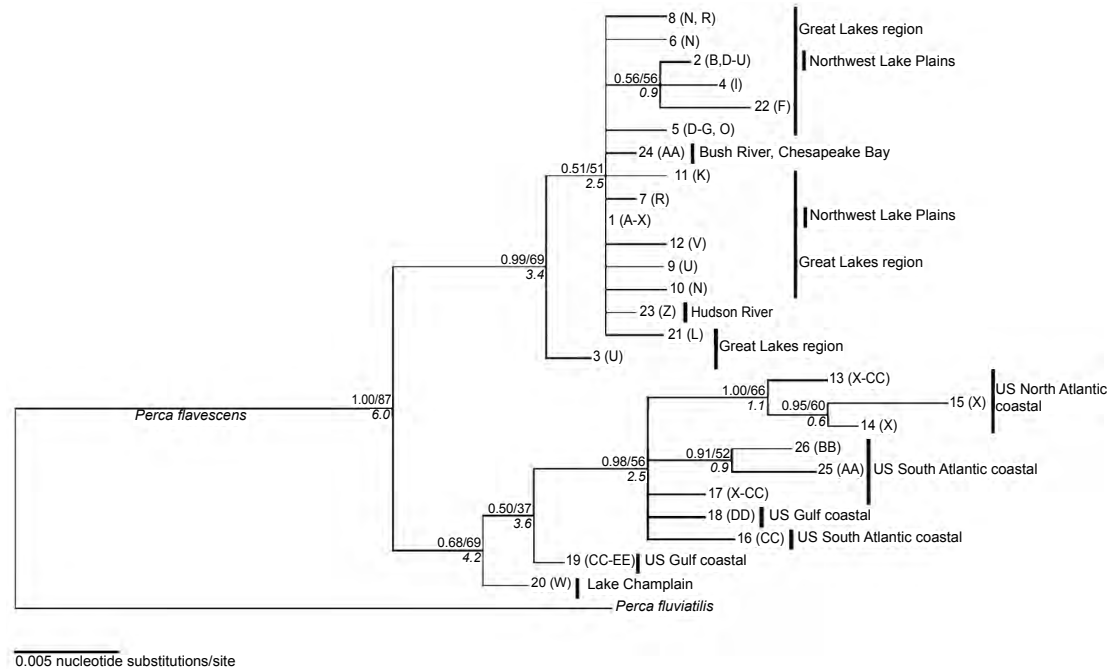
Fig. 5. Bayesian phylogenetic tree of mtDNA control region sequence haplotypes for yellow perch, calculated using MrBAYES v3.2.1 (Ronquist and Huelsenbeck 2003, http://mrbayes.csit.fsu.edu/). Values above nodes = Bayesian posterior probability/percentage support from 2,000 bootstrap pseudo-replications in ML with PHYML v3.0 (Guindon et al. 2010, http://www.atgc-montpellier.fr/ phyml/); those with ≥0.50 pp and ≥50% bootstrap support are reported. jMODELTEST v2 (Darriba et al. 2012, https://code.google.com/p/jmodeltest2/) selected the most likely model of nucleotide substitution for construction of the phylogenetic trees and divergence time estimates. Values below nodes in italics = estimated divergence times (given as millions of years) as determined in r8s v1.71 (Sanderson 2003, http://loco.biosci.arizona.edu/r8s/) and BEAST v1.71 (Drummond et al. 2012, http://beast.bio.ed.ac.uk/Main_Page#Citing_BEAST). Divergence times were calibrated using three fossil and four molecular calibration points following Haponski and Stepien (2013b, 2014). Letters in parentheses denote sampling sites in which haplotypes were recovered (see Fig. 2 map). Vertical bars denote general geographical regions.
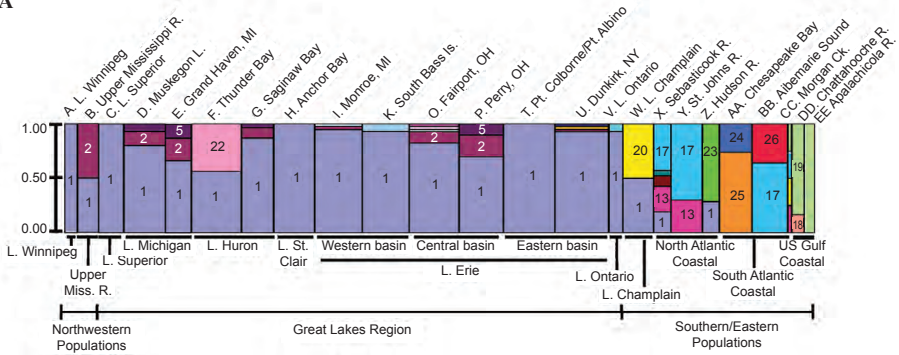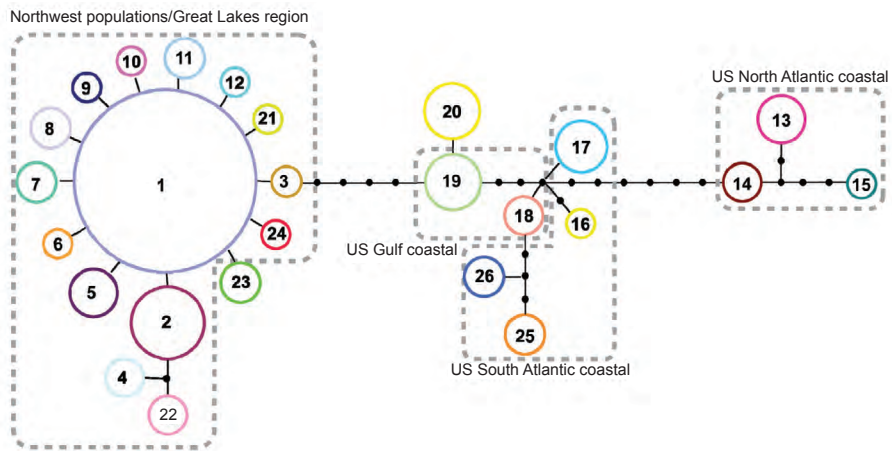
Fig. 6. MtDNA haplotypes of yellow perch across North America (modified from Sepulveda-Villet et al. 2009; Sepulveda-Villet and Stepien 2012). (A) MtDNA control region haplotype frequencies calculated using GENEPOP v4.0 (Rousset 2008, http://kimura.univ-montp2. fr/~rousset/Genepop.htm), and Microsoft Excel 2008 (Redmond, VA). Vertical black lines separate different spawning groups (lettered). Major geographic regions are indicated in the bottom rule. (B) Parsimony network of relationships among yellow perch mtDNA control region haplotypes constructed using TCS v1.21 (Clement et al. 2000, http://darwin. uvigo.es/software/ tcs.html). Circles are sized according to total observed frequency of the haplotype. 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. Circle colors reflect haplotype identities as portrayed in Fig. 6A.

Yellow perch in the Northwest Lake Plains region of North America (Fig. 2A: Lake Winnipeg and the upper Mississippi River) trace their descent to Missourian refugium colonists (Sepulveda-Villet et al. 2009; Sepulveda-Villet and Stepien 2012). Today, the overall differences in these populations from other regions is apparent in Figs. 2A and 6, with the latter depicting a Bayesian STRUCTURE analysis of populations, based on nuclear DNA microsatellite loci (Table 1) which shows that

Table 1. Yellow perch metapopulation regions tested, sample size (N), and mean genetic variability values from (A) 15 microsatellite loci and (B) mtDNA control region sequences. Microsatellite data include: observed (H_O) heterozygosity, inbreeding coefficient (F_{IS}), number of μsat alleles across all loci (N_A), allelic richness (A_R), proportion of private alleles (P_{PA}), and proportion of full siblings (Sib). Values for mtDNA include number of haplotypes (N_H), haplotypic diversity (H_D), and proportion of private haplotypes (P_{PH}). Values were calculated using the programs GENEPOP v4.0 (Rousset 2008, http://kimura.univ-montp2.fr/~rousset/Genepop.htm), FSTAT v2.9.3.2 (Goudet 1995, 2002, http://www2.unil.ch/popgen/softwares/fstat.htm), ARLEQUIN v3.1.5.3 (Excoffier and Lischer 2010, http://cmpg.unibe.ch/software/arlequin35/), and CONVERT v1.31 (Glaubitz 2004, http://www.agriculture.purdue.edu/fnr/html/faculty/rhodes/students%20and%20staff/glaubitz/software.htm). Data are summarized and adapted from Sepulveda-Villet and Stepien (2012).

Locality	A. Nuclear Microsatellite DNA Loci						B. mtDNA Control Region Haplotypes			
	N	H_O	F_{IS}	N_A	A_R	P_{PA}	N	H_D	N_H	P_{PH}
Total (or Mean)	892	0.53	0.145	442	8.39	(0.04)	664	0.73	0.029	111
1. Lake Winnipeg	12	0.49	−0.010	68	4.53	0.02	12	0.00	1	0.00
2. Upper Mississippi R. watershed	18	0.52	0.165	112	7.47	0.04	18	0.53	2	0.00
Great Lakes region (3–9):	459	0.55	0.206	363	9.97	0.14	459	0.22	14	0.07
3. Lake Superior	25	0.64	0.080	119	7.93	0.01	25	0.00	1	0.00
4. Lake Michigan	65	0.54	0.174	298	9.93	0.05	65	0.34	3	0.00
5. Lake Huron	80	0.61	0.135	355	11.83	0.02	80	0.40	4	0.15
6. Lake St. Clair	86	0.59	0.098	225	13.22	0.03	39	0.00	1	0.00
Lake Erie:	401	0.55	0.116	313	13.26	0.09	235	0.21	12	0.03
7. Western Basin, L. Erie	189	0.55	0.100	259	12.87	0.05	77	0.27	4	0.03
8. Eastern Basin, L. Erie	212	0.54	0.122	270	13.00	0.06	88	0.07	4	0.03
9. Lake Ontario	62	0.55	0.122	213	13.79	0.04	15	0.13	2	0.07
10. Northeastern populations	60	0.50	0.236	347	7.71	0.05	60	0.48	3	0.29
11. Southeastern populations	68	0.60	0.132	349	7.78	0.06	68	0.63	7	0.62
12. US Gulf coastal region	15	0.39	0.346	108	3.60	0.07	15	0.15	2	0.13

the Lake Winnipeg and Upper Mississippi River populations are different from those in most of the Great Lakes. Yellow perch from western Lake Superior also are very distinctive based on microsatellite DNA data (Fig. 7, Sepulveda-Villet and Stepien 2012). Glacial Lake Agassiz initially occupied much of the Hudson Bay watershed (including Lake Winnipeg), which probably had some southern drainage to Lake Superior (Mandrak and Crossman 1992; Rempel and Smith 1998), facilitating fish movements 8,500–13,000 ya. Ice later blocked this passage (Saarnisto 1974; Teller and Mahnic 1988), isolating the yellow perch populations in our Northwest Lake Plains sites, as is shown by their high divergences from other areas (denoted by distinct colors on Fig. 7, Sepulveda-Villet and Stepien 2012). The Lake Superior region was long covered in ice, except for glacial Lake Duluth in the west until ~8,500–9,000 ya, thus isolating its yellow perch gene pools. Most of the Great Lakes fauna—especially in Lakes Huron, Michigan, St. Clair, and western Lake Erie (Underhill 1986; Mandrak

Table 2. Genetic divergence F_{ST} (Weir and Cockerham 1984) pairwise comparisons among yellow perch regional metapopulations, based on: A. nuclear DNA microsatellite loci (below diagonal) and B. mtDNA control region sequence data (above diagonal), using FSTAT v2.9.3.2 (Goudet 1995, 2002, http://www2.unil.ch/popgen/softwares/fstat.htm) and ARLEQUIN v3.1.5.3 (Excoffier and Lischer 2010, http://cmpg.unibe.ch/software/arlequin35/), with significance tested through 100,000 replicates. Results are congruent to those from exact tests of differentiation comparisons. Note that spawning populations are grouped together in metapopulation regions for purpose of comparison, thus please consult the original papers to examine fine-scale patterns. *= significant with sequential Bonferroni correction (Rice 1989), *italics* = significant at 0.05 prior to Bonferroni correction. Not bold, not * = not significant. Results are modified from Sepulveda-Villet and Stepien (2011, 2012).

| Population Region	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
1. Lake Winnipeg	–	0.552*	0.522*	0.191*	0.081*	0.392*	0.395*	0.490*	0.399*	0.249*	0.501*	0.895*
2. Upper Mississippi R.	0.202*	–	0.000	0.087*	0.107*	0.000	0.012	0.006	0.050	0.282*	0.548*	0.949*
3. Lake Superior	0.116*	0.202*	–	0.077*	0.096	0.000	0.008	0.010	0.036	0.266*	0.531*	0.943*
4. Lake Michigan	0.137*	0.228*	0.142*	–	0.119*	0.027	0.037*	0.059*	0.054	0.322*	0.584*	0.914*
5. Lake Huron	0.133*	0.183*	0.128*	0.030	–	0.045	0.205*	0.177*	0.069	0.189*	0.433*	0.537*
6. Lake St. Clair	0.217*	0.320*	0.226*	0.122*	0.117*	–	0.026	0.044	0.029	0.197*	0.468*	0.909*
7. Lake Erie, Western Basin	0.217*	0.271*	0.198*	0.074*	0.055	0.147*	–	0.002	0.023*	0.455*	0.701*	0.951*
8. Lake Erie, Eastern Basin	0.218*	0.274*	0.202*	0.079*	0.053	0.145*	0.014*	–	0.004	0.404*	0.659*	0.956*
9. Lake Ontario	0.244*	0.353*	0.213*	0.125*	0.111*	0.093*	0.118*	0.111*	–	0.225*	0.492*	0.915*
10. Northeastern populations	0.204*	0.246*	0.133*	0.166*	0.148*	0.222*	0.185*	0.188*	0.179*	–	0.215*	0.240*
11. Southeastern populations	0.250*	0.279*	0.169*	0.222*	0.203*	0.259*	0.273*	0.274*	0.231*	0.117*	–	0.436*
12. Gulf coastal region	0.290*	0.361*	0.237*	0.273*	0.251*	0.320*	0.317*	0.320*	0.294*	0.180*	0.186*	–
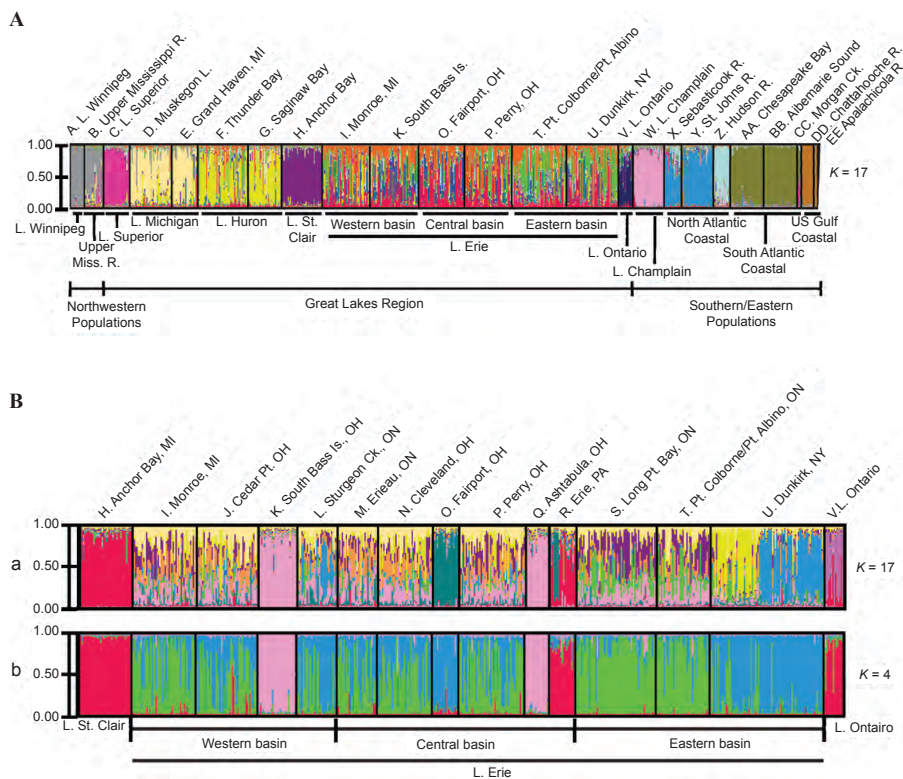
Fig. 7. Estimated comparative population structure for yellow perch from Bayesian STRUCTURE v2.3.3 analyses (Pritchard et al. 2000; Pritchard and Wen 2004, http://pritchardlab.stanford.edu/structure.html) for (A) 24 spawning groups using 15 nuclear DNA microsatellite loci (modified from Sepulveda-Villet and Stepien 2012), for which optimal K = 17; and (B) 15 Lake Erie spawning groups at optimal (a) K = 10 and (b) K = 4 four (adapted from Sepulveda-Villet and Stepien 2011); in reference to outlying groups from Lake St. Clair and L. Ontario. Analyses were run with 100,000 burn-in and 500,000 replicates. Optimal K values were determined by posterior probabilities (Pritchard et al. 2000) and the ΔK method of Evanno et al. (2005). Thin vertical lines represent individuals and thicker bars separate spawning groups at given locations; these are partitioned into K colored segments that represent estimated population group membership. Note that there is no correspondence between the colors of A and B.

and Crossman 1992; Todd and Hatcher 1993; Stepien et al. 2009, 2010)—trace their origins to the Mississippian refugium. In particular, Lake Erie's formation dates to glacial Lake Maumee (~14,000 ya), which then drained west via the Ohio River to the Mississippi, then switched outlets during several lake stages, with its current outlet draining east into Lake Ontario (~10,000 ya) (Underhill 1986; Larson and Schaetzl 2001; Strange and Stepien 2007). As a consequence, Lake Erie yellow perch today are geographically isolated and genetically differentiated from most other Great Lakes populations. Notably, Lake Erie physically is separated from Lake Ontario by Niagara Falls and from the upper Great Lakes by the narrow and short Detroit River, which drains Lake St. Clair. Yellow perch from Lake St. Clair clearly are separated

from those spawning in Lake Erie (note the color difference between the red-colored population from Lake St. Clair versus the mixed colors in Lake Erie in Fig. 7B); these appear on opposite sides of a genetic barrier (X), determined from BARRIER v2.2 analysis (Manni et al. 2004), shown in Fig. 2A.

More information about the evolutionary origin of yellow perch stems from mtDNA studies. Thus, yellow perch mtDNA control region haplotype 1 (Figs. 6A and B) likely was widespread pre-glacially and was represented in both the Mississippian and Atlantic refugia populations, but was more common in the west. Today, yellow perch haplotype 1 remains more abundant in the west (see Fig. 6A), apparently reflecting retention of its original predominant proportions in populations colonized from the Mississippian refugium and is only slightly represented in those descendants from the Atlantic refugium to the present day.

The Atlantic coastal refugium (Fig. 2A) formed a warm enclave of diverse habitats in coastal plains and estuaries east of the Appalachian Mountains (Schmidt 1986; Bernatchez 1997); yellow perch from that refugium migrated north to colonize the northeastern and north central regions after the glaciations (Russell et al. 2009; Sepulveda-Villet and Stepien 2012). The northeastern migrating populations split to found the yellow perch populations in Maine (colored blue, sites X and Y, on Fig. 7A) and the Hudson River (colored light blue, site Z); both are very divergent today (also see mtDNA haplotypes on Fig. 6A).

Lake Champlain (site W) drains into the St. Lawrence River and its yellow perch appear to trace to joint origins from the Atlantic and Mississippian refugia, but today has a very divergent genetic composition from other locations (see unique haplotype 20 on Figs. 5 and distinct colors for Lake Champlain yellow perch on Figs. 5A and 6A, denoting different genetic composition). Lake Champlain received meltwaters from glacial Lake St. Lawrence (~11,600 ya), and then Lake Agassiz (~8,000–10,900 ya) and glacial Lake Barlow-Ojibway (~8,000–9,500 ya). This convergence of meltwaters 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 and Vilks 1994; Sepulveda-Villet and Stepien 2012). Regional flooding presumably led to colonization of Lake Champlain by aquatic taxa from the Atlantic refugium, as suggested by genetic evidence from lake cisco *Coregonus artedi* (Turgeon and Bernatchez 2001) and lake whitefish *C. clupeaformis* (Bernatchez and Dodson 1991); the Lake Champlain yellow perch population appears to reflect joint contributions from the Atlantic and Mississippian refugia (see Fig. 6; Sepulveda-Villet and Stepien 2012).

Variable evolutionary, demographic, and colonization history of the species also impacts the extent of population divergence observed throughout its range of distribution. The greatest inter-population divergences are observed in the upper Mississippi River and the Gulf Coast, reaching a genetic divergence Fixation Index (F_{ST}) value = 0.361, based on microsatellite data (Table 2; Sepulveda-Villet and Stepien 2012). The greatest difference for the mitochondrial DNA data likewise occurs between the same population pair (F_{ST} = 0.949, Table 2). Pronounced divergence also was observed among geographically isolated small populations from northwestern Québec and northeastern Ontario (average F_{ST} = 0.378) (Bourret et al. 2008). Some of the most divergent yellow perch population groups also distinguished the Gulf

Coast (mean F_{ST} = 0.275 among 11 pairwise comparisons), the upper Mississippi River (0.257), the southeast Atlantic Coast (0.224), and then Lake Winnipeg (0.203). Likewise, these population groups appeared highly differentiated according to their mtDNA, in relative order of: the Gulf Coast (mean F_{ST} = 0.786), the southeast Atlantic Coast (0.506), Lake Winnipeg (0.424), and then Lake Erie (0.255).

The relationship between genetic and geographic distances (measured by nearest waterway) is illustrated on Fig. 8A, which indicates broadscale correspondence across
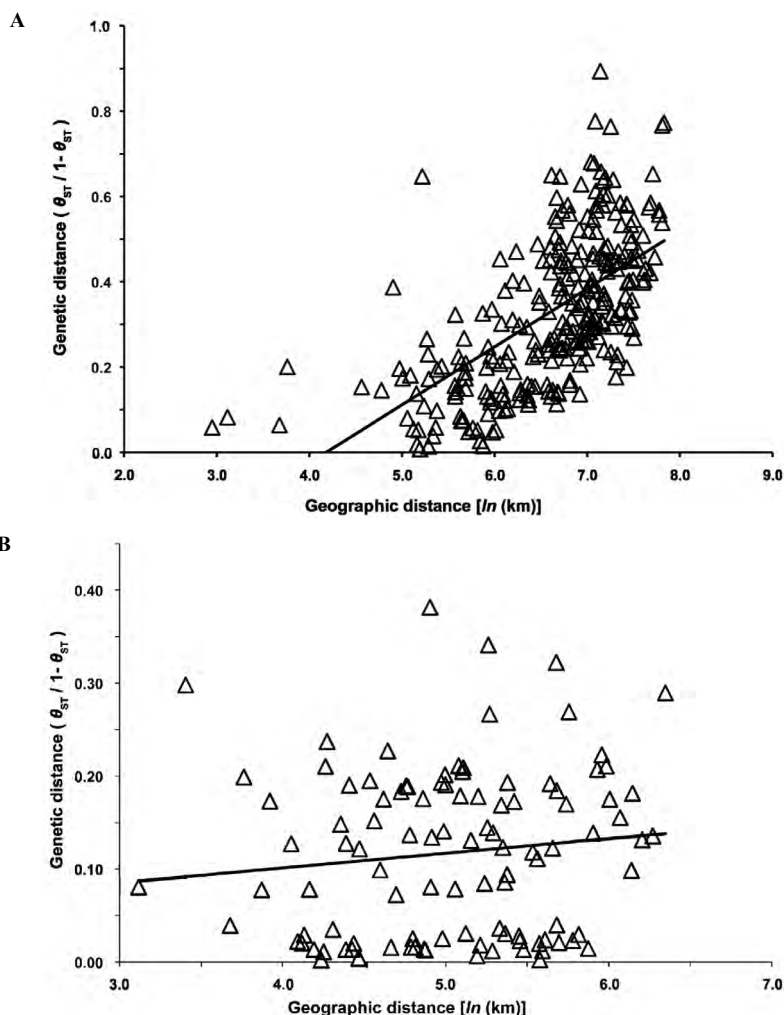

Fig. 8. Mantel (1967) pairwise tests using GENEPOP v4.0 (Rousset 2008, http://kimura.univ-montp2.fr/~rousset/Genepop.htm), with 10,000 permutations, for the relationship between genetic distance (θ_{ST}/1-θ_{ST}) and natural logarithm of geographic distance (kilometers) (A) across the native North American range of yellow perch populations from North America ($p < 0.001$, R^2 = 0.39, $y = 0.14x–0.57$; modified from Sepulveda-Villet et al. 2012), and (B) among Lake Erie spawning groups ($p = 0.212$, $R^2 = 0.024$, $y = 0.016x–0.038$; modified from Sepulveda-Villet and Stepien 2011). Note there is no significant relationship in the fine-scale analysis (B).

the range. Thus, there is an overall isolation by genetic distance pattern. However, some populations in relatively close proximity are distinguished by much greater than expected genetic distances, as indicated by the results of the BARRIER analysis (Manni et al. 2004), shown in Fig. 2. The Bayesian STRUCTURE analyses also denote a substantial number of distinctive population groups of yellow perch (K = 17, Fig. 7A). Overall, these results illustrate that pronounced population genetic differentiation in perch may stem from a variety of sources, including: long-term geographic separation, geographic distance separating populations, barriers to dispersal, and genetic drift.

In summary, earlier biogeographic investigations based on fish distribution and knowledge of geological and glacial history led to diverse hypotheses regarding the evolutionary history of the yellow and European perches. Present-day detailed knowledge of the evolutionary history of both species summarized in this chapter stems from recent large-scale phylogeographic and population genetic analyses using mitochondrial DNA and nuclear DNA microsatellite markers, which has led to new insights and consensus. Altogether, these studies have revealed a predominant role of historical to modern biogeography for interpreting contemporary patterns of genetic diversity in both species. In particular, regions that have remained the most stable in time (e.g., were less affected by glaciations) are generally characterized by more pronounced genetic diversity, both at the intra- and inter-specific levels. Higher genetic diversity is also observed in zones of secondary contacts between evolutionary lineages that previously evolved in geographic isolation. Thus, history has played an important role in determining the genetic diversity and its differentiation in perch species across both continents.

2.3 Perch Life Histories and Population Genetic Implications

While historical contingency has deeply influenced broad scale patterns of genetic diversity in perches, it is also clear that the species, and their biological and ecological characteristics also play an important role. In particular, a remarkable similarity in major life history characteristics (Craig 2000) and population genetic implications are shared by both the yellow perch and the European perch across both continents, which invokes their common evolutionary history. Here we introduce some major life history characteristics and population genetic implications for both species and highlight similarities and differences.

2.3.1 Population Genetic Structuring of Reproductive Groups

Cued by gradual changes in water temperature and photoperiod, *Perca* species aggregate to spawn in late spring to early summer on shallow reef complexes in lacustrine systems or slow-moving tributaries (Scott and Crossman 1973; Coles 1981; Wang and Eckmann 1994; Carlander 1997; Jansen et al. 2009; Chapter 3, Chapter 7). Spawning is related to spring water temperatures and starts at >10ºC. Because it is mainly dictated by temperature, spawning occurs much earlier in the southern reaches of their ranges, and much later in the extreme north (Thorpe 1977; Carlander 1997; Craig 2000). Spring spawning migrations of yellow perch and European perch

are relatively short and it is believed that they return to specific natal sites in shallow waters (Aalto and Newsome 1990; Carlander 1997; Craig 2000; Sepulveda-Villet and Stepien 2012).

Yellow perch captured and tagged during spawning season and released many kilometers distant in the Eastern Basin of Lake Erie were found to return to their tagging locations (MacGregor and Witzel 1987), implicating homing. Separate studies by Clady (1977), Rawson (1980), and Ontario Ministry of Natural Resources (2011) likewise found that most yellow perch tagged during spawning were recovered at or very close to their initial spawning locations in subsequent years. Yellow perch spawning groups located just a few kilometers apart (17 kilometers) in central Lake Erie diverged from one another in genetic and morphological composition (Kocovsky et al. 2013). This genetic divergence suggests that Lake Erie yellow perch populations are highly structured and likely congregate in natal groups at specific spawning locations (Sepulveda-Villet and Stepien 2012; Sullivan and Stepien 2014, 2015). Aalto and Newsome (1990) removed yellow perch egg masses from given spawning sites, which led to fewer fish returning to that location in subsequent years than in control sites, suggesting that they returned to the same spawning areas year after year. It is hypothesized that imprinting occurs during the early life history of yellow perch and European perch, with their highly developed olfactory systems used to detect natal spawning sites and/or the pheromones of neighbors and relatives (see Horal 1981; Gerlach et al. 2001). As observed in Lake Erie, most recaptures of thousands of tagged yellow perch from Lake Saint-Louis in the St. Lawrence River, Québec, were made within 10 kilometers from tagging sites (Leclerc et al. 2008). Moreover, movements between the two areas were limited, with only 4% of recaptured yellow perch found in alternate locations over a 3-year period (Dumont 1996). As a consequence, significant genetic differences were observed between yellow perch sampled on the north vs. south shores of the lake (Leclerc et al. 2008).

Genetic composition of yellow perch spawning groups differs significantly from location to location across broad and fine geographic scales (Sepulveda-Villet and Stepien 2011, 2012; Sullivan and Stepien 2014). However, some significant differences have been found at some of the same locations from year to year (Sullivan and Stepien 2015). This local genetic variability suggests that although yellow perch may spawn together with a specific group (believed to be their natal group), specific spawning locations may vary from year to year. A similar pattern was found for European perch in Lake Erken, Sweden by Bergek and Olsson (2009). When comparing perch aggregations caught at four different locations in the lake, consistent genetic differentiation was found among these locations over time. However, local European perch groups were genetically differentiated when comparing perch from the same location from different years (Bergek and Olsson 2009).

The spawning process is similar in both species. During the spawning season, males move into the spawning areas first, arriving before females by a few weeks and lingering longer at the sites (Scott and Crossman 1973; Craig 2000; Simon and Wallus 2006). The female perch lays a long gelatinous egg strand (up to 2.1 meters long), which contains 10,000 to 40,000 eggs, over submerged vegetation or other structures at night or in early morning. As the egg mass is released by the female, it

is externally fertilized by a cluster of 2–25 males, who closely follow the female and often are in close proximity to other spawning clusters (Scott and Crossman 1973; Mangan 2004; Simon and Wallus 2006).

2.3.2 Early Life History and Population Patterns

Soon after hatching in littoral areas, the young-of-the-year move into deeper water as juveniles in late spring, where they occupy a wide variety of habitats (Craig 2000). As a consequence, Parker et al. (2009) found that age one juvenile yellow perch differed in morphology and genetically at 12 nuclear DNA microsatellite loci between populations in Lake Huron and Lake Michigan, with those from Lake Huron having deeper, longer bodies and larger dorsal fins. The researchers also discerned morphological and genetic differences between juveniles living in nearshore versus wetland habitats in Lake Michigan. Juveniles inhabiting nearshore areas from both lakes had deeper, longer bodies and larger dorsal fins than did those occupying wetlands, which might reflect an adaptive response to predators and open-water cruise swimming. Although phenotypic differences between habitats across the lakes were hypothesized to reflect plasticity between phenotypic and genetic divergence (Parker et al. 2009), a genetic basis for such variation cannot be ruled out, given the evidence for some reproductive isolation based on genetic data. Bergek and Björklund (2009) discerned a very similar genetic and morphological divergence pattern for European perch from the east coast of Sweden in the Baltic Sea between local populations sampled at two different spatial scales, a near scale (300 m–2 kilometers) and a far scale (2–13 kilometers). The morphological differences between them were hypothesized to reflect phenotypic plasticity, but again, a genetic basis could not be ruled out.

2.3.3 Adult Perch Movements and Migrations: Implications for Genetics

After the spawning season, adult perch movements largely are determined by habitat complexity, food availability, and foraging capacity (Radabaugh et al. 2010). Likewise, juvenile and adult yellow perch and European perch typically occur in shoals, which may facilitate foraging and predator avoidance (Helfman 1984; Craig 2000). Interestingly, shoals of European perch have been shown to contain large numbers of related individuals; they are believed to recognize each other from chemical and physical cues (Gerlach et al. 2001; Behrmann-Godel et al. 2006). However, whether the shoals of yellow perch likewise are structured based on kinship has not yet been evaluated (see Sullivan and Stepien 2015).

A study of yellow perch tag returns by Haas et al. (1985) determined that post-spawning movements are moderate; individuals tagged at Lake Erie spawning sites did not move upstream through the corridor connecting Lake Huron to Lake Erie, which is termed the Huron-Erie Corridor (HEC), connecting the two Lakes via the St. Clair River, Lake St. Clair, and the Detroit River. Some yellow perch that were tagged in Lake St. Clair migrated to nearby tributaries (Haas et al. 1985). Note that although individuals may move among water bodies to feed, their reproductive groups determine their overall population genetic structures.

A tagging study of European perch in prealpine Lake Constance, Germany discerned moderate movements of adults beyond the spawning season (Godel 1999). Tagged perch occupied home ranges of approximately 500 meters, located along distinct depth contours (ca. 10 meter water depth in summer, Fig. 9), within which they spent several days to weeks. Typically, their home ranges were located near structures that resembled fish nurseries (submerged wooden structures built by fishers in Lake Constance) or near harbors. During this stationary time in the home range, their typical behavioral patterns revealed highest activity levels during or close to dusk and dawn, low activity during the day, and no activity at night (Fig. 10). After a period ranging from two days to three weeks, most perch individuals became migratory and began to move straightforward along the shoreline between 1 and 20 kilometers longitudinally for a few hours to a few days before they again settled to occupy a new home range (Fig. 9). Congruent with movement patterns depicted in previous studies, evidence for yellow perch metapopulations in Lake Ontario embayments were discerned by otolith microchemistry (Murphy et al. 2012), indicating discrete assemblages in connected bays and impoundments, as were found among spawning groups along Lake Erie coastal sites (Fig. 7B, Fig. 11; Sepulveda-Villet and Stepien 2011; Sullivan and Stepien 2015). These populations likely display seasonal mixing, as described by Parker et al. (2009).
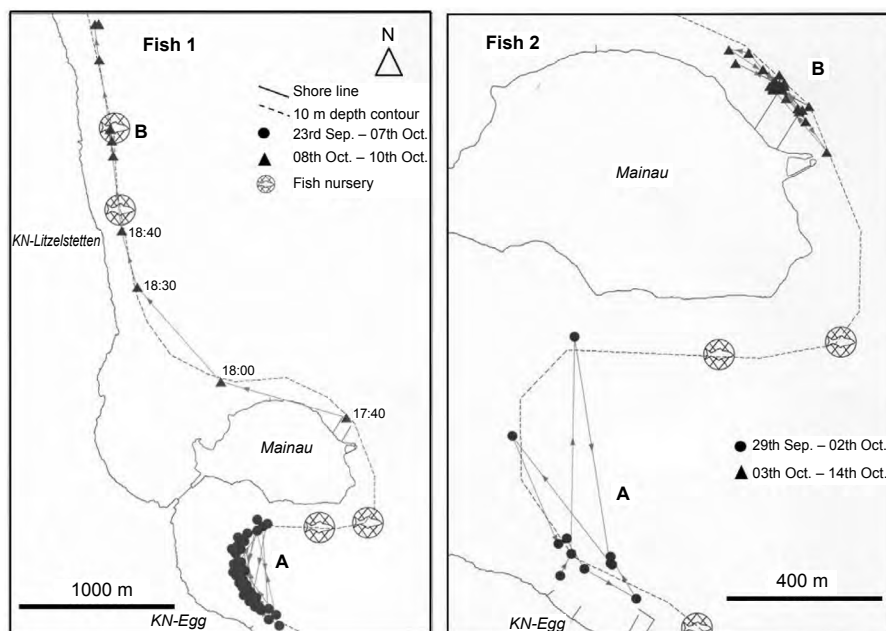

Fig. 9. Swimming paths of two individual European perch during a tagging study using ultrasonic transmitters in Lake Constance near the isle of Mainau. Dots and triangles are fish positionings, arrows indicate swimming direction. For Fish 1, time (CET) of positionings is given for a migratory movement in the evening of the 08th October, where the fish moved from home range A to home range B.
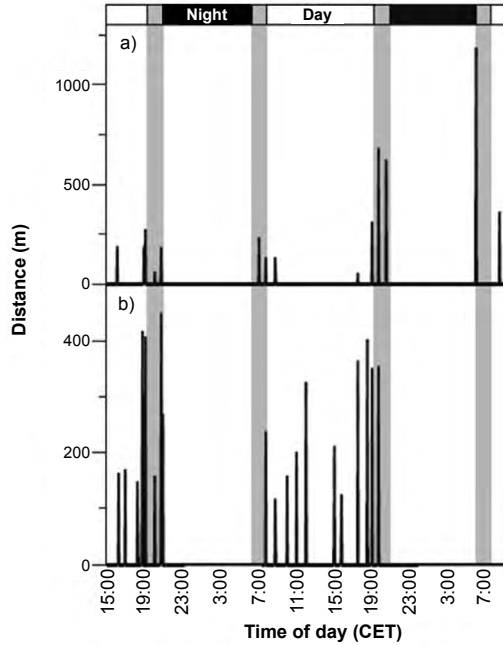
Fig. 10. Swimming activity for two European perch (a, b) during 48 h observation periods in Lake Constance. Fish were tagged with ultrasonic transmitters. Activity is given as swimming distance between two positionings. Perch typically showed highest activity during or close to twilight or during the day and no activity at night.
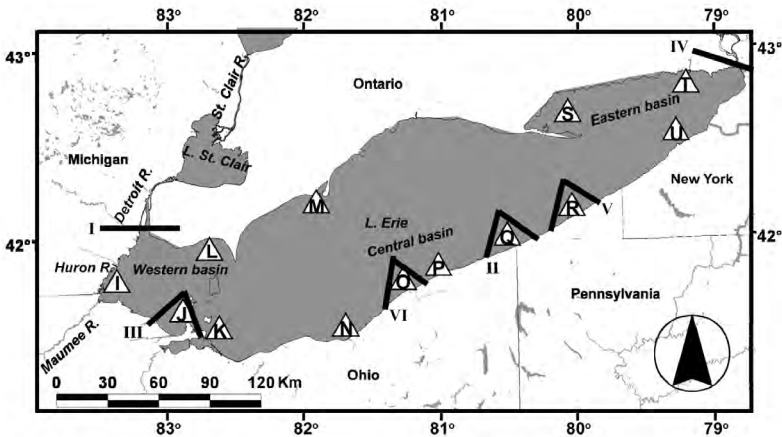

Fig. 11. Fine-scale map of Lake Erie in the North American Laurentian Great Lakes showing locations of yellow perch spawning groups (triangles) tested and genetic barriers delineating specific groups from 15 nuclear microsatellite loci and BARRIER v2.2 analysis (Manni et al. 2004, http://www.mnhn.fr/mnhn/ecoanthropologie/software/ barrier.html), which are ranked I–VI, in order of their decreasing magnitude. Sites of spawning groups are lettered, as follows: I. Monroe, MI; J. Cedar Pt., OH; K. S. Bass Isl., OH; L. Sturgeon Ck., ON; M. Erieau, ON; N. Cleveland, OH; O. Fairport, OH; P. Perry, OH; Q. Ashtabula, OH; R. Erie, PA; S. Long Pt. Bay, ON; T. Pt. Colborne, ON; U. Dunkirk, NY. Figure was modified from results of Sepulveda-Villet and Stepien (2011, 2012).

2.4 Influence of Habitat Connectivity, Isolation, and Dispersal on Population Genetic Patterns

In addition to the role of intrinsic species characteristics described above, patterns of population structure in both yellow and European perch are influenced by habitat characteristics and landscape, which directly impact their dispersal capability and connectivity. Large connected spans of suitable habitats, as found in the Great Lakes basins and tributaries for yellow perch, offer a variety of environmental resources for robust and diverse populations, reflecting the interplay between migration opportunity and localized adaptation (see Lindsay et al. 2008; Vandewoestijne et al. 2008; Kunin et al. 2009).

Aquatic habitats frequently are connected by narrow and relatively ephemeral connections that link populations during migration and dispersal, but whose habitats may pose distinct biological challenges. For example, small connecting channels may offer limited food and shelter, and extensively differ in size and habitat complexity, which then influence the distribution of population genetic variability. In other areas, such as in the St. Lawrence River, patches of suitable habitat for reproduction and nursing for yellow perch may be separated by extensive stretches of unsuitable habitats, which also may result in meta-population dynamics (e.g., Mingelbier et al. 2008) that will influence the distribution of genetic diversity. In contrast, isolated relict populations having little connectivity may possess lower overall genetic diversity due to the influences of genetic drift, bottlenecks, and selection (Moran and Hopper 1983; Petit et al. 2003; Coulon et al. 2012; Sepulveda-Villet and Stepien 2012).

2.4.1 Population Genetic Diversity Comparisons

The overall genetic diversity of yellow perch is relatively low compared to freshwater fishes in general (DeWoody and Avise 2000). For instance, it is much lower than in walleye for both nuclear DNA (mean heterozygosity is 0.53 for yellow perch versus 0.73 for walleye) and mtDNA sequence variability (mean haplotypic diversity is 0.31 for yellow perch versus 0.77 for walleye) (Stepien et al. 2012; Sepulveda-Villet and Stepien 2012; Haponski and Stepien 2014). The relatively low diversity for yellow perch likewise was revealed by other genetic data sets, including allozymes (Leary and Booke 1982; Todd and Hatcher 1993; Moyer and Billington 2004), mtDNA restriction fragment length polymorphisms (RFLPs) (Billington 1993; Moyer and Billington 2004), mtDNA sequences (Sepulveda-Villet et al. 2009; Sepulveda-Villet and Stepien 2012), as well as nuclear microsatellites (Miller 2003; Bourret et al. 2008; Leclerc et al. 2008; Sepulveda-Villet and Stepien 2011, 2012; Sullivan and Stepien 2014, 2015), and single nucleotide polymorphisms (SNPs; Bélanger-Deschênes et al. 2013).

Overall mtDNA genetic diversity of yellow perch roughly matches that of the European perch (Refseth et al. 1998; Nesbø et al. 1998, 1999), which also has relatively low allozymic genetic diversity (Gyllensten et al. 1985; Bodaly et al. 1989). In fact, relatively low genetic diversity in both mtDNA and nuclear DNA appears characteristic of the genus *Perca*. Some individual yellow perch spawning groups possess a relatively high degree of kin relationship (see Table 1), which may result in lower variability within samples (Sullivan and Stepien 2015). Genetically similar

individuals of European perch have been found to aggregate with one another (Gerlach et al. 2001), recognizing their relatives via olfactory cues at the fry life stage and beyond (Behrmann-Godel et al. 2006). Kin recognition by olfactory cues has not yet been studied in yellow perch, but might yield important insights on their fine-scale population structure and the distribution of their respective diversities.

Across most of their North American ranges, yellow perch populations exhibit relatively consistent levels of genetic variability for the nuclear microsatellite data (Table 1; Sepulveda-Villet and Stepien 2012). Less genetic diversity is found in some of the northwest populations and the Gulf coastal region; both areas house small, isolated populations that likely experienced bottlenecks. In contrast, population genetic diversities are relatively high across the Great Lakes and in the southeastern populations (Sepulveda-Villet and Stepien 2012). The southeastern populations were never glaciated, and thus maintained relatively stable population sizes. In contrast, the Great Lakes populations were founded from variable combinations of the Missourian, Mississippian, and Atlantic glacial refugia (Stepien et al. 2009; Sepulveda-Villet and Stepien 2012). The Great Lakes populations today exhibit relatively high genetic diversities as a result of this admixture of founding from multiple refugia, in combination with their large population sizes and abundant habitat expanses. These factors appear to have superseded any effects of bottlenecks stemming from their former restriction to glacial refugia during the Pleistocene and any founder effects during the subsequent post-glacial resurgence to new habitats opened in the modern-day Great Lakes.

Levels of mitochondrial DNA diversity, measured as haplotypic diversity (Table 1), are comparatively quite low for yellow perch. MtDNA diversity in populations is much more influenced by bottlenecks as its theoretical effective population size is just ¼ that of nuclear DNA (see Avise 2004). As a consequence, values of haplotypic diversity of yellow perch are much lower than their nuclear diversity levels. This may reflect a history of bottlenecks for yellow perch, with most of the Great Lakes and the northwestern populations dominated by a single yellow perch haplotype (haplotype 1 of Fig. 6). Nuclear DNA diversity levels for yellow perch populations overall also are relatively modest (Sepulveda-Villet and Stepien 2011) in comparison to walleye from the same regions (Stepien et al. 2009, 2012; Haponski and Stepien 2014).

Private alleles are those that are found only in a specific population or set of populations. In the Great Lakes overall, 14% of nuclear microsatellite alleles and 7% of the mitochondrial haplotypes were private in yellow perch (Table 1). In Lake Erie, 9% of the microsatellite alleles and 3% of the mitochondrial haplotypes were private. In the Gulf Coastal population, 7% of yellow perch microsatellite alleles and 13% of the mitochondrial haplotypes were private (Table 1, Fig. 6). Thus, these distributions reflect appreciable differentiation among metapopulations.

2.4.2 Fine-scale Population Genetic Structure in Yellow Perch and European Perch

Although relationships among yellow perch populations typically follow a broad-scale pattern of genetic isolation by geographic distance (Fig. 8A), relationships among

spawning groups within individual lakes do not reflect geographic distance (Figs. 4 and 8B). Some closely situated spawning groups are markedly different, whereas others are more closely related. Fine-scale relationships among yellow perch spawning groups appear to be driven by spawning aggregations, natal homing behavior, and localized adaptations, rather than due to simple geographic connectivity (see Sepulveda-Villet and Stepien 2011, 2012; Kocovsky et al. 2013; Sullivan and Stepien 2014, 2015).

Sepulveda-Villet and Stepien (2011) found significant differences at 15 microsatellite loci among Lake Erie yellow perch at spawning sites (shown in Fig. 7B), discerning no relationship between genetic distance and geographic distance between sampling locations. Kocovsky and Knight (2012) reported similar trends using morphometric data from yellow perch sampled from many of the same spawning locations used by Sepulveda-Villet and Stepien (2011). Yellow perch spawning groups in the Central Basin of Lake Erie that are separated by 17–94 kilometers were distinguished by significant genetic divergences of $F_{ST} = 0.016–0.056$ using the same 15 loci, and also displayed significant morphological differences (Kocovsky et al. 2013). Grzybowski et al. (2010) described fine-scale genetic structure between yellow perch spawning in Lake Michigan open water versus those in Green Bay, also from microsatellite data ($F_{ST} = 0.126$).

Such differentiation among spawning groups within a system appears to result from spawning site philopatry to specific natal locations, maintained from generation to generation. European perch form long-term population groups of related individuals, according to microsatellite data (Behrmann-Godel et al. 2006; Bergek and Björklund 2007, 2009). Reproductive success was significantly lower in breeding experiments when two subpopulations were hybridized, with reduced pre-zygotic and post-zygotic fitness manifested by lower fertilization rates and less hatching success (Behrmann-Godel and Gerlach 2008). One of the likely barriers to gene flow for European perch thus is reproductive isolation, either via kin recognition using olfactory cues (Gerlach et al. 2001; Behrmann et al. 2006) or due to reduced hybrid fitness between sympatric but divergent cohorts (Behrmann-Godel and Gerlach 2008). Likewise, it is possible that yellow perch returning to natal locations are guided by olfactory information imprinted during early stages of their life history. If so, it may be the primary mechanism for maintaining divergence among spawning aggregations, but this hypothesis remains to be tested.

There apparently is no effect of gender in the establishment of these fine-scale genetic structure trends, as both male and female yellow perch have analogous genetic patterns, and thus appear to have similar site fidelity (Sepulveda-Villet and Stepien 2011, 2012; Sullivan and Stepien 2015). Eight spawning groups from Lake Erie locations (sites on Fig. 11) were all genetically distinguishable from one other (mean $F_{ST} = 0.068 \pm 0.008$, range = 0.002–0.168), but some also differed in allelic composition between two sampling time periods (2001–2004 versus 2009), at ~1/4 the magnitude of the difference among locations. Sullivan and Stepien (2015) found significant differences among yellow perch spawning groups and between different sampling years at some of these sites. An example of annual variation within the yellow perch spawning group sampled at Van Buren Bay in eastern Lake Erie is given in Table 3. A study by Demandt (2010) likewise found significant variations in microsatellite allelic

Table 3. Fine-scale pairwise genetic divergences for yellow perch spawning at Dunkirk NY in eastern Lake Erie sampled in six different collection years: 1985, 2001, 2004, 2008, 2009, and 2010, based on 15 nuclear DNA microsatellite loci (modified from Sullivan and Stepien 2015). Sample sizes are in parentheses. Calculations used *F*STAT v2.9.3.2 (Goudet 1995, 2002, http://www2.unil.ch/popgen/softwares/fstat.htm) and ARLEQUIN v3.1.5.3 (Excoffier and Lischer 2010, http://cmpg.unibe.ch/software/arlequin35/), with 100,000 replicates to test for significance. * = All were significantly different following sequential Bonferroni correction (Rice 1989).

Year (N)	1985 (34)	2001 (37)	2004 (48)	2008 (30)	2009 (30)
2001 (37)	0.037*	–			
2004 (48)	0.056*	0.055*	–		
2008 (30)	0.125*	0.138*	0.141*	–	
2009 (30)	0.041*	0.072*	0.088*	0.105*	–
2010 (36)	0.011*	0.041*	0.057*	0.113*	0.014*

frequencies of European perch among sampling years for a population in Sweden. This observation suggests a similar trend for annual variability at spawning sites for both yellow and European perch.

Yellow perch spawning groups varied among individual sampling years and age cohorts, with the 2003 cohort being the most distinctive of those sampled (Sepulveda-Villet and Stepien 2011, 2012; Sullivan and Stepien 2014, 2015). This 2003 cohort was an especially large and successful group for yellow perch recruitment in Lake Erie (YPTG 2013). Spawning groups of yellow perch contained high numbers of full siblings (mean = 18.5%, ranging to 75% for the 2001 age cohort spawning at Van Buren Bay in eastern Lake Erie; Sullivan and Stepien 2015). Temporal genetic divergence at spawning locations was not explained by genetic isolation over time, but appeared to be due to yellow perch spawning in kin-related groups, which varied slightly from year to year. Spatial patterns were attributed to limited migration and natal homing, whereas temporal patterns may reflect kin group structuring and differential reproductive success (Sullivan and Stepien 2015).

Although there is ample evidence for fine scale population structuring in both yellow and European perch, there may be some exceptions to this, as exemplified by the population structure revealed in a landscape genetics study of yellow perch from the St. Lawrence River. Leclerc et al. (2008) employed a landscape genetics approach to document the population genetic structure of yellow perch using microsatellite markers, assess to what extent the structure was explained by landscape heterogeneity, and interpret the relevance of interactions between genetics and landscape for management and conservation. Genetic analysis of 1715 individuals from 16 localities, distributed across 310 kilometers in the freshwater section of the Saint Lawrence River, revealed a modest level of genetic structuring (F_{ST} = 0.039). BARRIER analysis (Manni et al. 2004), which combined geographical and genetic information, identified three zones of restricted gene flow. These delineated just four distinct populations over a large geographic distance (Fig. 12). Results showed that physical barriers (e.g., occurrence of dams) played a more important role on gene flow and genetic structure than waterway geographical distance. The authors also found correlations between genetic differentiation and the presence of distinct water masses, and with fragmentation of
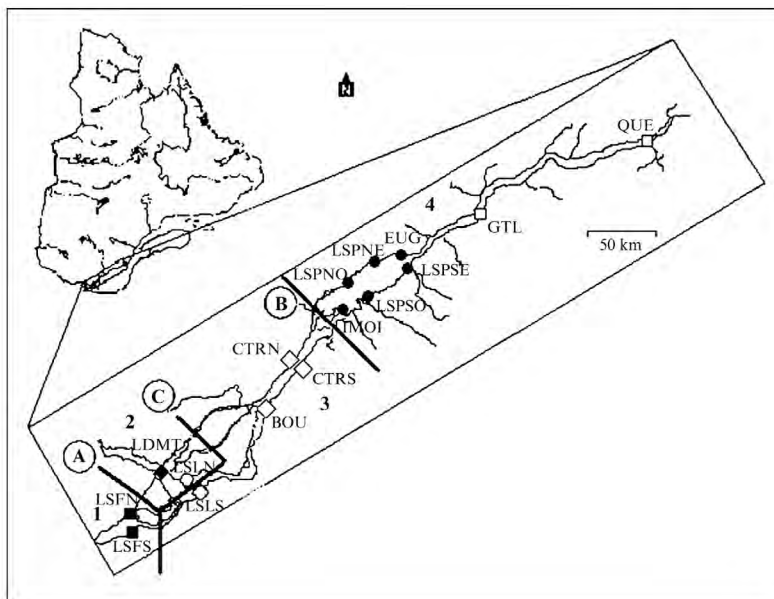
Fig. 12. Areas of population genetic breaks among yellow perch along the St. Lawrence River system identified by BARRIER 2.2 analysis (Manni et al. 2004) using Monmonier's algorithm in the study by Leclerc et al. (2008). Genetic barriers that were retained under the majority-rule criterion are identified by order of importance (A, B, and C). These barriers separated the system into four genetically distinct populations: (1) Lake Saint-François; (2) North of Lake Saint-Louis and Lake des Deux-Montagnes; (3) South of Lake Saint-Louis downstream to Contrecoeur; (4) and Lake Saint-Pierre downstream to Quebec City. Symbols denote sampling locations, from west to east, dark squares, Lake Saint-François; black diamonds, Lake des Deux-Montagnes; white circles, Lake Saint-Louis; white diamonds, fluvial section from Boucherville to Contrecoeur; black circles, Lake Saint-Pierre; white squares, fluvial section from Gentilly to Quebec City.

spawning habitats. The study also showed that landscape genetics is a powerful means to identify environmental barriers to gene flow, which create genetic discontinuities in apparently highly connected aquatic landscapes.

2.5 Applications to Perch Population Maintenance and Restoration

As molecular-based population dynamics and structure analyses increasingly provide ways to better assess past and present levels of diversity in fish populations, a need for greater use of these techniques has been proposed in concert with traditional management approaches. For instance, dating to the mid-1800s, yellow perch was stocked (artificially introduced to new areas) to many areas of North America to support recreational fishery and to provide fishing opportunity (USFWS/GLFC 2010). These introductions sometimes mixed nonindigenous hatchery broodstock with local genotypes. Molecular analyses may help to discern whether stocking may have partly blurred the evolutionary history of the species and may have impacted the genetic integrity of some indigenous populations. Today's fishery managers increasingly

recognize the importance of preserving local population variability, and it is advisable to perform any supplementation solely with native genotypes specific to that particular locale. The most prudent action still remains to protect the habitats of locally adapted populations and avoid negative effects of overexploitation, thereby circumventing any "need" to stock.

Understanding and maintaining yellow perch population structure are critically important fisheries-management goals designated by the Great Lakes Fishery Commission (Ryan et al. 2003; GLFC 2011). For example, the findings of just four biological units in the study by Leclerc et al. (2008), were in contrast with the current basis for yellow perch management and thus called for a re-evaluation of management strategy of the species in this system. This also has been true for Lake Erie yellow perch, for which genetic data reveal many more population subunits than the number that are managed for (Fig. 7B, 11; Sepulveda-Villet and Stepien 2011; Kocovsky et al. 2013; Sullivan and Stepien 2014, 2015). When demographic data on exploited fisheries are collected on a larger scale than population subunits, valuable data may be lacking for management decisions to conserve local genetic and morphological diversity and adaptedness.

Fish habitats in the Great Lakes, including the St. Lawrence River, Lake Erie, Lake St. Clair, and connecting tributaries were subject to extensive and deleterious changes in the 20th and 21st centuries, marked by loss of wetlands, channelization of major streams, construction of dams, oxygen depletion, shoreline modification, siltation of spawning areas, nutrient enrichment, water-quality deterioration, sand and gravel extraction, and invasive species introductions (Trautman 1981; Bolsenga and Herdendorf 1993; Fielder 2002; Hoff 2002; Ryan et al. 2003; Mailhot et al., Chapter 5 of this volume). Discerning whether and how perch adapted and coped with such pronounced environmental disturbance is crucial, and may provide significant insights into how populations will respond in the future.

Molecular tools that inform about adaptive differences between populations as well as population response to environmental stressors are readily available, yet these have been largely untapped in perch studies. As one example of informative applications of recent genomic tools, Bélanger-Deschênes et al. (2013) documented functional polymorphisms of chronically metal-contaminated wild yellow perch. Based on a *de novo* transcriptome scan; they first contrasted subsets of individuals from clean and contaminated lakes to identify 87 candidate annotated coding SNPs. Candidate genotypes and liver metal concentration were obtained in 10 populations (N = 1,052) and a genome scan distinguished outliers between polluted and unpolluted sites: one nuclear (cyclin G1 gene) and two mitochondrial (cytochrome *b* and NADH dehydrogenase subunit 2) genes also displayed allelic correlation to mean liver cadmium concentration. Based on associated functions and inter-population differentiation, the authors proposed that contaminated perch may have been selected for fast life cycle completion involving the p53 pathway and memorization impairment mitigation through this long-term potentiation pathway. In accordance with predicted evolutionary trajectory for stressed and energy deprived organisms, adapted perch would not compensate for repair mechanism inhibition, instead reallocating energy towards growth and favoring inexpensive impairment mitigation adaptations over costly detoxification. Overall, this study showed that a few dozen generations of

selection apparently drove rapid, potentially adaptive evolution by selecting for alleles that increased perch fitness in polluted environments. This result is in line with the growing evidence that human-driven environmental change may cause rapid evolutionary change that must be taken into consideration for sound management and conservation strategies (Smith and Bernatchez 2008).

More recently, somatic and genetic markers were employed to evaluate the reproductive health of yellow perch populations for which fisheries monitoring revealed reduced recruitment, in urbanized and developed streams of the Chesapeake Bay watershed (Blazer et al. 2013). Results showed gonadal anomalies and changes in DNA integrity in those yellow perch population samples. These findings suggest that pollution can significantly impact reproduction and recruitment, the effects of which can be detected with molecular markers.

Genetic findings to date, as illustrated in this chapter, reveal that most perch populations have appreciable genetic diversity and significantly differ from other populations, both nearby and distant, despite and sometimes because of anthropogenic influences. These diversity and divergence patterns may translate to localized adaptations, which merit preservation. Accordingly, we recommend conserving their genetic composition and differentiation patterns by maintaining and restoring spawning habitats, and continued careful management of fisheries.

2.6 Conclusions and Perspectives for Future Research

Temperatures are predicted to increase over the next 50 years, with those in the North American Great Lakes region predicted to increase by 5–5.5ºC to become more like today's Gulf of Mexico Coast (Hayhoe et al. 2010). 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 and Jump 2011), as occurred during Pleistocene glaciations (Oberdorff et al. 1997; Davis and Shaw 2001; Soltis et al. 2006) and is ongoing today (Araújo and Rahbek 2006; Harris and Taylor 2010).

Bergek et al. (2010) suggested that environmental factors other than geographic distance distinguished European perch spawning groups, implicating water temperature differences among groups spawning in various habitats during the spring. The onset of perch spawning is highly controlled by spring season water temperature, in combination with day length (see Chapter 7 for an extensive review on the topic). Water temperatures need to be below 10°C during the winter to ensure gonad maturation and reproductive success (Hokanson 1977; Dabrowski et al. 1996). Spring spawning of perches is initiated by a rise in water temperature above 10ºC along with increasing day length; spawning occurs over a very short period of time (approximately 14 days). By manipulating water temperature and day length, Dabrowski et al. (1996) delayed yellow perch spawning for several months. Bergek et al. (2010) tested different environmental parameters including: salinity, turbidity, surface temperature in August, mean temperature in April (the spawning time of European perch at the location analyzed), and mean water depth for their correlation with genetic differentiation of spawning groups analyzed from spawning places along an environmental gradient.

Of all parameters tested, only mean temperature in April correlated significantly with genetic isolation of various spawning groups. Similarly, yellow perch populations were significantly affected by water level fluctuations of glacial lakes in North Dakota, with their greatest recorded abundances and body weights occurring during high water periods (Dembkowski et al. 2013), underscoring potential deleterious effects of increased evaporation and water losses linked to climate change.

These findings highlight the importance of spawning sites and localized variations governing relationships among the associated reproductive groups for yellow perch and European perch. It appears likely that genetic structure among spawning localities will continue to reflect a product of the interplay between ancestral lineages and environmental variation among spawning areas, rather than simple isolation by distance. If this concept holds true, then we should expect effects on genetic diversity and composition from the increasing pace of climate change and higher surface water temperatures with shifting population distributions.

In addition, there might be a number of indirect effects affecting the genetic structure of perch populations, such as an alteration of the exposure to parasites and pathogens (Poulin 2006; Chapter 8 in this volume). It is well known that the interaction between hosts and parasites is controlled by the environment (Wolinska and King 2009). For example, the period of parasite transmission can be prolonged, and the abundance and virulence of distinct pathogens and parasites may be increased by rising temperatures (e.g., Poulin 2006). Alien parasites and diseases may be favored and cause epizootic outbreaks in naïve host populations that either lack the genetic adaptations to reduce pathogenicity or to defend the invaders (Marcogliese 2001; Britton et al. 2011; Behrmann-Godel et al. 2013). For example, the recent outbreaks and deleterious fish die-offs of the viral hemorrhagic septicemia virus (VHS) in the Great Lakes, which first appeared ~2005, may be related to climate change (see Pierce and Stepien 2012). Additionally the cumulative effects that multiple stressors exert on native species, including anthropogenic pollutants in combination with parasites or pathogens currently are raising a major concern (see section 10.3 in Chapter 10 for further discussion on this topic). For example, Vidal-Martínez et al. (2010) and Marcogliese and Pietrock (2011) discussed their negative effects on immune function and animal health. The exact details of the effect of a changing environment on host-parasite interactions are hard to predict due to reciprocal evolutionary effects among multiple factors. This coevolution first will affect the genes that play major roles in infection and susceptibility of parasites and hosts, respectively (Woolhouse et al. 2002; Stepien et al. 2015). However they may cause local coadaptation, which is a prerequisite for further population sub structuring. The antagonistic co-evolution is believed to be the major driver of the extraordinarily high polymorphism usually found for infection and resistance alleles in parasites and their hosts, as evidenced by the major histocompatibility complex (MHC) genes in vertebrate hosts. It has already been shown that MHC classII receptor genes in European perch are highly variable (Michel et al. 2009; Oppelt et al. 2012) and it was recently found that a long-term rise in temperature (over 35 years) strongly affected those genes resulting in a massive change in MHC variability and an alteration of the cycling pattern of several MHC alleles in a European perch population enclosed in an artificially heated Swedish lake (Björklund et al. 2015). This observation indicated strong selection on the MHC

classII receptor genes of perch via an alteration of their parasitic community. Future studies will reveal whether such long-term changes in temperature will indeed result in stable changes of the genetic composition of perch populations.

Evaluating diversity and divergence patterns resulting from post-glacial 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. In effect, climate change patterns rapidly are extending the northward post-glacial expansion trajectory of many taxa in north temperate regions; meanwhile their southerly rear-edge groups may experience greater isolation, habitat reduction, and bottlenecks. The southern genotypes may move northward, given connection or transport opportunity, and likely house valuable genetic adaptations to warmer climates (Hampe and Petit 2005). For example, the diverse Atlantic coastal yellow perch populations in the southeastern U.S. 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. Distributional changes in populations are significant in the context that they may interbreed with long-term native populations in the north. It is possible that the adaptive potential of native populations may be either positively or negatively influenced by these changes.

Due to the uncertain nature and amplitude of climate change it is difficult to predict how genetic diversity would be expected to respond to climate change or how one would use such information to interpret climate shifts. Nevertheless, it may prove useful to employ functional genomics (e.g., genome-wide genotyping at coding gene regions) monitoring in other to temporally track what biological functions are most associated (and therefore most affected) by climate change.

Warming temperatures and increases in storm events may influence fish population structure and overall productivity via biological and climate-related effects as outlined by Newbry and Ashworth (2004). For example, Hill and Magnuson (1990) suggested that changes in bioenergetics accompanying climate change might modify growth and prey consumption, thereby affecting food-web dynamics. Shuter and Post (1990) suggested that an increase of 4°C may move the distributional limit of yellow perch northward and, depending on lake morphometry and productivity, might also greatly affect survival, relative year-class strength, and ecosystem carrying capacity. Moreover, climate change may affect various regions of the distribution range of perches and other taxa in unpredictable ways, resulting in habitat fragmentation and leading to genetic diversification. To date, yellow and European perch populations possess relatively consistent levels of genetic diversity and high local distinctiveness. These appear to have been maintained despite anthropogenic habitat loss, degradation, fragmentation, and exploitation, likely offset by their large population sizes and the relative abundance of habitats.

Genetic structure of today's perch populations reflects interplay among climatic events, ephemeral waterway connections, population sizes, and likely spawning group philopatry. Delineation of the genomic adaptations that underlie the patterns of genetic diversity and diversity described here will aid predictions of likely response to changing environments, new habitat areas, and exploitation pressures (see Allendorf et al. 2010; Avise 2010). The study of Bélanger-Deschênes (2013) described above, as well as the

use of transcriptomics to investigate population response to pollutants (Pierron et al. 2011; Bougas et al. 2013; Couture et al. Chapter 10 this volume), clearly illustrate the benefits of taking advantage of the modern genomics toolbox for perch management and conservation. A combined fisheries management and genetics/genomic approach will provide a bridge for understanding the unique challenges faced by aquatic taxa due to their constrained dispersal and gene flow via habitat connectivity. Understanding the historical and present day factors that shaped today's populations may aid their continued conservation in the face of future challenges.

2.7 Acknowlegements

2.8 References

Aalto, S.K. and G.E. Newsome. 1990. Additional evidence supporting demic behavior of a yellow perch (*Perca flavescens*) population. Can. J. Fish. Aquat. Sci. 47: 1959–1962.

Aldenhoven, J.T., M.A. Miller, P.S. Corneli and M.D. Shapiro. 2010. Phylogeography of nine spine sticklebacks (*Pungitius pungitius*) in North America: glacial refugia and the origins of adaptive traits. Mol. Ecol. 19: 4061–4076.

Allendorf, F.W., P.A. Hohenlohe and G. Luikart. 2010. Genomics and the future of conservation genetics. Nature Rev. Genet. 11: 697–710.

April, J., R. Hanner, R. Mayden and L. Bernatchez. 2013. Metabolic rate and climatic fluctuations shape continental wide pattern of genetic divergence and biodiversity in fishes. Plos One 8: e70296.

Araújo, M.B. and C. Rahbek. 2006. How does climate change affect biodiversity? Science 313: 1396–1397.

Avise, J.C. 2004. Molecular Markers, Natural History, and Evolution, 2nd edn. Sinauer Associates, Sunderland, Massachusetts.

Avise, J. 2010. Conservation genetics enters the genomics era. Conserv. Genet. 11: 665–669.

Azizishirazi, A., W.A. Dew, H.L. Forsyth and G.G. Pyle. 2013. Olfactory recovery of wild yellow perch from metal contaminated lakes. Ecotoxicol. Environ. Safety 88: 42–47.

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

Barluenga, M., M. Sanetra and A. Meyer. 2006. Genetic admixture of burbot (Teleostei: *Lota lota*) in Lake Constance from two European glacial refugia. Mol. Ecol. 15: 3583–600.

Barton, B.A. and T.P. Barry. 2011. Reproduction and environmental biology. pp. 199–231. *In*: B.A. Barton (ed.). Biology, Management, and Culture of Walleye and Sauger. American Fisheries Society, Bethesda, Maryland.

Behrmann-Godel, J., G. Gerlach and R. Eckmann. 2004. Postglacial colonization shows evidence for sympatric population splitting of European perch (*Perca fluviatilis* L.) in Lake Constance. Mol. Ecol. 13: 491–497.

Behrmann-Godel, J., G. Gerlach and R. Eckmann. 2006. Kin and population recognition in sympatric Lake Constance perch (*Perca fluviatilis* L.): Can assortative shoaling drive population divergence? Behav. Ecol. Sociobiol. 59: 461–468.

Behrmann-Godel, J. and G. Gerlach. 2008. First evidence for postzygotic reproductive isolation between two populations of European perch (*Perca fluviatilis* L.) within Lake Constance. Front. Zool. 5: 1–7.

Behrmann-Godel, J., S. Roch and A. Brinker. 2014. Gill worm *Ancyrocephalus percae* (Ergens 1966) outbreak negatively impacts the Eurasian perch *Perca fluviatilis* L. stock of Lake Constance, Germany. J. Fish Dis. 37: 925–930.

Bélanger-Deschênes, S., P. Couture, P.G. Campbell and L. Bernatchez. 2013. Evolutionary change driven by metal exposure as revealed by coding SNP genome scan in wild yellow perch (*Perca flavescens*). Ecotoxicology 22: 938–957.

Beletsky, D., D.M. Mason, D.J. Schwab, E.S. Rutherford, J. Janssen, D.F. Clapp and J.M. Dettmers. 2007. Biophysical model of larval yellow perch advection and settlement in Lake Michigan. J. Great Lakes Res. 33: 842–866.

Bergek, S. and M. Björklund. 2007. Cryptic barriers to dispersal within a lake allow genetic differentiation of European perch. Evolution. 61: 2035–2041.

Bergek, S. and M. Björklund. 2009. Genetic and morphological divergence reveals local subdivision of perch (*Perca fluviatilis* L.). Biol. J. Linn. Soc. 96: 746–758.

Bergek, S. and J. Olsson. 2009. Spatiotemporal analysis shows stable genetic differentiation and barriers to dispersal in the European perch (*Perca fluviatilis* L.) Evol. Ecol. Res. 11: 827–840.

Bergek, S., G. Sundblad and M. Björklund. 2010. Population differentiation in perch *Perca fluviatilis*: environmental effects on gene flow? J. Fish. Biol. 76: 1159–1172.

Bernatchez, L. and J.J. Dodson. 1991. Phylogeographic structure in mitochondrial DNA of the Lake Whitefish (*Coregonusclupeaformis*) in North America and its relationships to Pleistocene glaciations. Evolution 45: 1016–1035.

Bernatchez, L. 1997. Mitochondrial DNA analysis confirms the existence of two glacial races of rainbow smelt *Osmerusmordax* and their reproductive isolation in the St. Lawrence River estuary (Quebec, Canada). Mol. Ecol. 6: 73–83.

Bernatchez, L. 2001. The evolutionary history of brown trout (*Salmo trutta* L.) inferred from phylogeographic, nested clade, and mismatch analyses of mitochondrial DNA variation. Evolution 55: 351–379.

Bernatchez, L. and M. Giroux. 2012. Les Poissons d'eau douce du Québec et leur répartition dans l'est du Canada. Editions Broquet 348 p.

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

Björklund, M., T. Aho and J. Behrmann-Godel. 2015. Isolation over 35 years in a heated biotest basin causes selection on MHC class IIß genes in the European perch (*Perca fluviatilis* L.) Ecol. Evol. 5(7): 1440–1455. 5: DOI: 10.1002/ece3.1426.

Blazer, V.S., A.E. Pinkney, J.A. Jenkins, L.R. Iwanowicz, S. Minkkinen, R.O. Draugelis-Dale and J.H. Uphoff . 2013. Reproductive health of yellow perch *Perca flavescens* in selected tributaries of the Chesapeake Bay. Sci. Total Environ. 447: 198–209.

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

Bolsenga, S.J. and C.E. Herdendorf. 1993. Lake Erie and Lake St. Clair Handbook. Wayne State University Press, Detroit, Michigan.

Bougas, B., E. Normandeau, F. Pierron, P.G.C. Campbell, L. Bernatchez and P. Couture. 2013. How does exposure to nickel and cadmium affect the transcriptome of yellow perch (*Perca flavescens*)— Results from a 1000 candidate-gene microarray. Aquat. Toxic. 142-143C: 355–364.

Bourret, V., P.P. Couture, P.C.G. Campbell and L. Bernatchez. 2008. Evolutionary toxicology of wild yellow perch (*Perca flavescens*) populations chronically exposed to a polymetallic gradient. Aquatic Toxicology 86: 76–90.

Bozek, M.A., D.A. Baccante and N.P. Lester. 2011. Walleye and sauger life history. pp. 233–301. *In*: B.A. Barton (ed.). Biology, Management, and Culture of Walleye and Sauger. American Fisheries Society. Bethesda, Maryland.

Britton, J.R., J. Pegg and C.F. Williams. 2011. Pathological and ecological host consequences of infection by an introduced fish parasite. PLoS ONE 6 (10): e26365.

Carlander, K.D. 1997. Handbook of Freshwater Fishery Biology, Vol. 3: Life History Data on Ichthyopercid and Percid Fishes of the United States and Canada. Iowa State University Press. Ames, Iowa.

Carney, J.P. and T.A. Dick. 2000. The historical ecology of yellow perch (*Perca flavescens* [Mitchill]) and their parasites. Journal of Biogeography 27: 1337–1347.

Clady, M.D. 1977. Distribution and relative exploitation of yellow perch tagged on spawning grounds in Oneida Lake. NY Fish. Game J. 24: 46–52.

Clement, M., D. Posada and K.A. Crandall. 2000. TCS: A computer program to estimate gene genealogies. Mol. Ecol. 9: 1657–1660. Available at http://darwin.uvigo.es/software/tcs.html

Coles, T. 1981. The distribution of perch, *Perca fluviatilis* L. throughout their first year of life in LlynTegid, North Wales. Arch. Fisch. 15: 193–204.

Collette, B.B., M.A. Ali, K.E.F. Hokanson, M. Nagiec, S.A. Smirnov, J.E. Thorpe, A.H. Weatherly and J. Willemsen. 1977. Biology of the percids. J. Fish. Res. Board Can. 34: 1891–1899.

Coulon, A., J.W. Fitzpatrick, R. Bowman and I.J. Lovette. 2012. Mind the gap: Genetic distance increases with habitat gap size in Florida scrub jays. Biol. Letters 8: 582–585.

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

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

Dabrowski, K., R.E. Ciereszko, A. Ciereszko, G.P. Toth, S.A. Christ, D. El-Saidy and J.S. Ottobre. 1996. Reproductive physiology of yellow perch (*Perca flavescens*): environmental and endocrinological cues. J. Appl. Ichthyol. 12: 139–148.

Darriba, D., G.L. Taboada, R. Doallom and D. Posada. 2012. jModelTest 2: More models, new heuristics and parallel computing. Nat. Methods 9: 772. Available at http://code.google.com/p/jmodeltest2/.

Davis, M.B. and R.G. Shaw. 2001. Range shifts and adaptive responses to quaternary climate change. Science 292: 673–679.

Demamdt, M.H. 2010. Temporal changes in genetic diversity of isolated populations of perch and roach. Conserv. Genet. 11: 249–255.

Dembkowski, D.J., S.R. Chipps and B.G. Blackwell. 2013. Response of walleye and yellow perch to water-level fluctuations in glacial lakes. Fish. Man. and Ecol. 21: 89–95.DOI: 10.1111/fme.12047.

DeWoody, J.A. and J.C. Avise. 2000. Microsatellite variation in marine, freshwater and anadromous fishes compared with other animals. J. Fish. Biol. 56: 461–473.

Diekmann, O.E. and E.A. Serrão. 2012. Range-edge genetic diversity: locally poor extant southern patches maintain a regionally diverse hotspot in the seagrass *Zostera marina*. Mol. Ecol. 7: 1647–1657.

Drummond, A.J., M.A. Suchard, D. Xie and A. Rambaut. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. Mol. Biol. Evol. 29: 1969–1973. Available at http://beast.bio.ed.ac.uk/Main_Page#Citing_BEAST.

Dumont, P. 1996. Comparaison de la dynamique des populations de perchaudes (*Perca flavescens*) soumises a des niveaux differents de stress anthropique. Ministere de l'Environnement et de la Faune, Service de l'amenagemetn et de l'exploitation de la faune. Repport technique 06–46. Montreal, Canada.

Durand, J.D., H. Persat and Y. Bouvet. 1999. Phylogeography and postglacial dispersion of the chub (*Leuciscus cephalus*) in Europe. Mol. Ecol. 8: 989–97.

Evanno, G., S. Regnaut and J. Goudet. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Mol. Ecol. 14: 2611–2620.

Excoffier, L. and H.E. Lischer. 2010. ARLEQUIN suite ver. 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. Mol. Ecol. Resour. 10: 564–567. Available at http://cmpg.unibe.ch/software/arlequin35/.

Faber, J.E. and C.A. Stepien. 1997. The utility of mitochondrial DNA control region sequences for analyzing phylogenetic relationships among populations, species, and genera of the Percidae. pp. 129–144. *In*:

T.D. Kocher and C.A. Stepien (eds.). Molecular Systematics of Fishes. Academic Press, London, England.

Ferguson, M.M. and G.A. Duckworth. 1997. The status and distribution of lake sturgeon, *Ascipenser fulvescens*, in the Canadian provinces of Manitoba, Ontario and Quebec: A genetic perspective. Environ. Biol. Fishes. 48: 299–309.

Fielder, D.G. 2002. Sources of walleye recruitment in Saginaw Bay, Lake Huron. N. Am. J. Fish. Manage. 22: 1032–1040.

Fulford, R.S., J.A. Rice, T.J. Miller, F.P. Binkowski, J.M. Dettmers and B. Belonger. 2006. Foraging selectivity by larval yellow perch (*Perca flavescens*): implications for understanding recruitment in small and large lakes. Can. J. Fish. Aquat. Sci. 63: 28–42.

Gerlach, G., U. Schardt, R. Eckmann and A. Meyer. 2001. Kin–structured subpopulations in European perch (*Perca fluviatilis* L.). Heredity 86: 213–221.

Glaubitz, J.C. 2004. CONVERT: A user–friendly program to reformat diploid genotypic data for commonly used population genetic software packages. Mol. Ecol. Notes 4: 309–310. http://www.agriculture.purdue.edu/fnr/html/faculty/rhodes/students%20and%20staff/glaubitz/software.htm.

GLFC (Great Lakes Fishery Commission). 2011. Strategic vision of the Great Lakes Fishery Commission 2011–2020. Great Lake Fish. Comm. Spec. Pub. Ann Arbor, Michigan. Available at http://www.glfc.org/pubs/SpecialPubs/StrategicVision2012.pdf.

Godel. 1999. Seasonal migrations of perch *Perca fluviatilis* L. in Lake Constance (in German) Master thesis, University of Konstanz.

Goudet, J. 1995. Fstat version 1.2: a computer program to calculate *F* statistics. J. Hered. 86: 485–486.

Goudet, J. 2002. Fstat version 2.9.3.2. Available at http://www2.unil.ch/popgen/softwares/fstat.htm.

Griffiths, D. 2010. Pattern and process in the distribution of North American freshwater fish. Biol. J. Linn. Soc. 100: 46–61.

Grzybowski, M., O.J. Sepulveda-Villet, C.A. Stepien, D. Rosauer, F. Binkowski, R. Klaper, B.S. Shepherd and F. Goetz. 2010. Genetic variation of 17 wild yellow perch populations from the Midwest and east coast analyzed via microsatellites. Trans. Am. Fish. Soc. 139: 270–287.

Guindon, S., J.F. Dufayard, V. Lefort, M. Anisimova, W. Hordijk and O. Gascuel. 2010. New Algorithms and methods to estimate maximum–likelihood phylogenies: assessing the performance of PhyML 3.0. Systematic Biol. 59: 307–321. Available at http://www.atgc–montpellier.fr/phyml/.

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

Haas, R.C., W.C. Bryant, K.D. Smith and A.J. Nuhfer. 1985. Movement and harvest of fish in Lake St. Clair, St. Clair River, and Detroit River. Final Report Winter Navigation Study U.S. Army Corps of Engineers.

Hampe, A. and A.S. Jump. 2011. Climate relicts: Past, present, future. Ann. Rev. Ecol. Evol. Syst. 42: 313–333.

Hampe, A. and R. Petit. 2005. Conserving biodiversity under climate change: The rear edge matters. Ecol. Lett. 8: 461–467.

Haponski, A.E. and C.A. Stepien. 2013a. Genetic connectivity and diversity of walleye (*Sander vitreus*) spawning groups in the Huron-Erie Corridor. J. Great Lakes Res. 49: 89–100.

Haponski, A.E. and C.A. Stepien. 2013b. Phylogenetic and biogeographic relationships of the *Sander* pikeperches (Perciformes: Percidae): Patterns across North America and Eurasia. Biol. J. Linn. Soc. 110: 156–179.

Haponski, A.E. and C.A. Stepien. 2014. A population genetic window into the past and future of the walleye *Sander vitreus*: Relation to historic walleye and the extinct blue pike variant. BMC Evol. Biol. 14: 133.

Harris, L.N. and E.B. Taylor. 2010. Pleistocene glaciations and contemporary genetic diversity in a Beringian fish, the broad whitefish, *Coregonusnasus* (Pallas): Inferences from microsatellite DNA variation. J. Evol. Biol. 23: 72–86.

Hayhoe, K., J. VanDorn, T. Croley, N. Schlegal and D. Wuebbles. 2010. Regional climate change projections for Chicago and the US Great Lakes. J. Great Lakes Res. 36: 7–21.

Helfman, G. 1984. School fidelity in fishes: the yellow perch pattern. Anim. Behav. 32: 663–672.

Hewitt, G.M. 1999. Post–glacial re-colonization of European biota. Biol. J. Linn. Soc. 68: 87–112.

Hewitt, G.M. 2004a. The structure of biodiversity—insights from molecular phylogeography. Front. Zool. 1: 4.

Hewitt, G.M. 2004b. Genetic consequences of climatic oscillations in the Quaternary. Philos. T. R. Soc. B. 359: 183–195.

Hill, D.K. and J.J. Magnuson. 1990. Potential effects of global climate warming on the growth and prey consumption of Great Lakes fish. Trans. Am. Fish. Soc. 119: 265–275.

Hoagstrom, C.W. and C.R. Berry. 2010. The native range of walleyes in the Missouri River drainage. N. Am. J. Fish. Manage. 30: 642–654.

Hocutt, C.H. and E.O. Wiley. 1986. The Zoogeography of the North American Freshwater Fishes. Wiley, New York 880 pp.

Hoff, M.H. 2002. A rehabilitation plan for walleye populations and habitats in Lake Superior. Great Lakes Fish. Comm. Misc. Pub. 2003-01. Ann. Arbor, Michigan.

Hokanson, K.E.F. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. J. Fish. Res. Brd. Can. 34: 1524–1550.

Horrall, R.M. 1981. Behavioral stock-isolating mechanisms in Great Lakes fishes with special reference to homing and site imprinting. Can. J. Fish. Aquat. Sci. 38: 1481–1496.

Hubbs, C.L. and K.F. Lagler. 2004. Fishes of the Great Lakes Region (G.R. Smith, revised). University of Michigan. Ann. Arbor, Michigan.

Jansen, A.C., B.D.S. Graeb and D.W. Willis. 2009. Effect of a simulated cold-front on hatching success of yellow perch eggs. J. Freshwater Ecol. 24: 651–655.

Jones, M.L., J.K. Netto, J.D. Stockwell and J.B. Mion. 2003. Does the value of newly accessible spawning habitat for walleye (*Stizostedionvitreum*) depend on its location relative to nursery habitats? Can. J. Fish. Aquat. Sci. 60: 1527–1538.

Kamilov, G. 1966. New data on the composition of ichthyofauna of reservoirs in Uzbekistan. pp. 110–111 (in Russian). *In*: Biological Background of Commercial Fishery in Reservoirs of Middle Asia and Kazakhstan. Alma-Ata, Kainar.

Keller, O. and E. Krayss. 2000. Die Hydrographie des Bodenseeraums in Vergangenheit und Gegenwart. Ber. St. Gall. Naturw. Ges. 89: 39–56.

Kerr, S.J., B.W. Corbett, N.J. Hutchinson, D. Kinsman, J.H. Leach, D. Puddister, L. Stanfield and N. Ward. 1997. Walleye habitat: A synthesis of current knowledge with guidelines for conservation. Percid Community Synthesis, Walleye Habitat Working Group, Ontario Ministry of Natural Resources, Peterborough.

Kocovsky, P.M. and C.T. Knight. 2012. Morphological evidence for discrete stocks of yellow perch in Lake Erie. J. Great Lakes Res. 38: 534–539.

Kocovsky, P.M., T.J. Sullivan, C.T. Knight and C.A. Stepien. 2013. Genetic and morphometric differences demonstrate fine–scale population substructure of the yellow perch *Perca flavescens*: Need for redefined management units. J. Fish. Biol. 82: 2015–2030.

Kornis, M.S., N. Mercado-Silva and M.J. Vander Zanden. 2012. Twenty years of invasion: a review of *Neogobiusmelanostomus* biology, spread, and ecological implications. J. Fish. Biol. 80: 235–285.

Kunin, W.E., P. Vergeer, T. Kenta, M.P. Davey, T. Burke, F.I. Woodward, P. Quick, M-E. Mannarelli, N.S. Watson-Haigh and R. Butlin. 2009. Variation at range margins across multiple spatialscales: Environmental temperature, population genetics and metabolomic phenotype. P. R. Soc. B. 276: 1495–1506.

Larson, G. and R. Schaetzl. 2001. Origin and evolution of the Great Lakes. J. Great Lakes Res. 27: 518–546.

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

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

Li, S. and J.A. Mathias. 1982. Causes of high mortality among cultured larval walleyes. Trans. Am. Fish. Soc. 111: 710–721.

Lindsay, D.L., K.R. Barr, R.F. Lance, S.A. Tweddale, T.J Hayden and P.L. Leberg. 2008. Habitat fragmentation and genetic diversity of an endangered, migratory songbird, the golden-cheeked warbler (*Dendroicachrysoparia*). Mol. Ecol. 17: 2122–2133.

MacGregor, R.B. and L.D. Witzel. 1987. A twelve year study of the fish community in the Nanticoke Region of Long Point Bay, Lake Erie. Lake Erie Fisheries Assessment Unit Report 1987–3. Ontario Ministry of Natural Resources, Port Dover.

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

Mangan, M.T. 2004. Yellow perch production and harvest strategies for semi-permanent wetlands in Eastern South Dakota. M.S. Thesis, Wildlife and Fisheries Sciences, South Dakota State University, South Dakota.

Manni, F., E. Guérard and E. Heyer. 2004. Geographic patterns of (genetic, morphologic, linguistic) variation: How barriers can be detected by using Monmonier's algorithm. Hum. Biol. 76: 173–190. Available at http://www.mnhn.fr/mnhn/ecoanthropologie/software/barrier.html.

Manning, N.F., C.M. Mayer, J.M. Bossenbroek and J.T. Tyson. 2013. Effects of water clarity on the length and abundance of age-0 yellow perch in the Western Basin of Lake Erie. J. Great Lakes Res. 39: 295–302.

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

Marcogliese, D.J. 2001. Implications of climate change for parasitism of animals in the aquatic environment. Can. J. Zool. 79: 1331–1351.

Marcogliese, D.J. and M. Pietrock. 2011. Combined effects of parasites and contaminants on animal health: parasites do matter. Trends Parasitol. 27: 123–130.

Michel, C., L. Bernatchez and J. Behrmann-Godel. 2009. Diversity and evolution of MHII beta genes in a non-model percid species—the Eurasian perch (*Perca fluviatilis* L.). Mol. Immunol. 46: 3399–3410.

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

Mingelbier, M., P. Brodeur and J. Morin. 2008. Spatially explicit model predicting the spawning 578 habitat and early stage mortality of Northern pike (*Esoxlucius*) in a large system: the 579 St. Lawrence River between 1960 and 2000. Hydrobiologia 601: 55–69.

Moran, G.F. and S.D. Hopper. 1983. Genetic diversity and the insular population structure of the rare granite rock species, *Eucalyptus caesia* Benth. Aust. J. Bot. 31: 161–172.

Moyer, G.R. and N. Billington. 2004. Stock structure among yellow perch populations throughout North America determined from allozyme and mitochondrial DNA analysis. pp. 96–97. *In*: T.P. Barry and J.A. Malison (eds.). Proceedings of Percis III: The Third International Percid Fish Symposium. University of Wisconsin Sea Grant Institute, Madison, Wisconsin.

Murdoch, M.H. and P.D. Hebert. 1997. Mitochondrial DNA evidence of distinct glacial refugia brown bullhead (*Ameiurusnebulosus*). Can. J. Fish. Aquat. Sci. 54: 1450–1460.

Murphy, S., N. Collins, S. Doka and B. Fryer. 2012. Evidence of yellow perch, largemouth bass and pumpkinseed metapopulations in coastal embayments of Lake Ontario. Environ. Biol. Fish. 95: 213–226

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

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

Newbrey, M.G. and A.C. Ashworth. 2004. A fossil record of colonization and response of lacustrine fish populations to climate change. Can. J. Fish. Aquat. Sci. 61: 1807–1816.

Nuriyev, H. 1967. Occurrence of Balkhash perch in Kattakurgan reservoir (pool of Zeravshan River). pp. 208–209 (in Russian). *In*: Biological background of commercial fishery in reservoirs of Middle Asia and Kazakhstan (summeries of reports). Balkhash, Kazakhstan.

Oberdorff, T., B. Hugueny and J.-F. Guégan. 1997. Is there an influence of historical events on contemporary fish species richness in rivers? Comparisons between western Europe and North America. J. Biogeogr. 24: 461–467.

OMNR (Ontario Ministry of Natural Resources). 2011. 2006–2009 Annual Report. Lake Erie MU.

Oppelt, C. and J. Behrmann-Godel. 2012. Genotyping MHC classIIB in non-model species by reference strand-mediated conformational analysis (RSCA). Con. Gen. Res. 4: 841–844.

Parker, A.D., C.A. Stepien, O.J. Sepulveda-Villet, C.B. Ruehl and D.G. Uzarski. 2009. The interplay of morphology, habitat, resource use, and genetic relationships in young yellow perch. Trans. Am. Fish Soc. 138: 899–914.

Petit, R.J., I. Aguinaglade, J.-L. de Beaulieu, C. Bittkau, S. Brewer, R. Cheddadi, R. Ennos, S. Fineschi, D. Grivet, M. Lascoux, A. Mohanty, G. Müller-Starck, B. Demesure-Musch, A. Palmé, J.P. Martín, S. Rendell and G.G. Vendramin. 2003. Glacial refugia: Hotspots but not melting pots of genetic diversity. Science 300: 1563–1565.

Pierce, L.R. and C.A. Stepien. 2014. Evolution and biogeography of an emerging quasi species: Diversity patterns of the fish viral hemorrhagic septicemia virus (VHSv). Mol. Phyl. Evol. 63: 327–341.

Pierron, F., E. Normandeau, M.A. Defo, P.G.C. Campbell, L. Bernatchez and P. Couture. 2011. Effects of chronic metal exposure on wild fish populations revealed by high-throughput cDNA sequencing. Ecotoxicology 6: 1388–1399.

Pivnev, I. 1985. Fish species in pool of Chu and Talas rivers. pp. 189 (in Russian). Frunze: Ilim.

Poulin, R. 2006. Global warming and temperature-mediated increases in cercarial emergence in trematode parasites. Parasitology 132: 143–151.

Pritchard, J.K. and W. Wen. 2004. Documentation for STRUCTURE software: Ver. 2.3.3. Stanford University. Available at http://pritchardlab.stanford.edu/software.html.

Pritchard, J.K., M. Stephens and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. Genetics 155: 945–959.

Provan, J. and K.D. Bennett. 2008. Phylogeographic insights into cryptic glacial refugia. Trends Ecol. Evol. 23: 564–571.

Radabaugh, N.B., W.F. Bauer and M.L. Brown. 2010. A comparison of seasonal movement patterns of yellow perch in simple and complex lake basins. N. Am. J. Fish. Manage. 30: 179–190.

Rawson, M.R. 1980. Yellow perch movements. Ohio Department of Natural Resources Job Program Report, Dingell–Johnson Project Number F–35–R–18, Study Number. 4, November 1 1979–June 30, 1980.

Redman, R.A., S.J. Czesny and J.M. Dettmers. 2013. Yellow Perch Population Assessment in Southwestern Lake Michigan. INHS Technical Report 2013 (25., Division of Fisheries, Illinois Department of Natural Resources, Champaign, IL.

Refseth, U.H., C.L. Nesbø, J.E. Stacy, L.A. Vøllestad, E. Fjeld and K.S. Jakobsen. 1998. Genetic evidence for different migration routes of freshwater fish into Norway revealed by analysis of current perch (*Perca fluviatilis*) populations in Scandinavia. Mol. Ecol. 7: 1015–1027.

Rempel, L.L. and D.G. Smith. 1998. Postglacial fish dispersal from the Mississippi refuge to the Mackenzie River basin. Can. J. Fish. Aquat. Sci. 55: 893–899.

Rice, R.M. 1989. Analyzing tables of statistical tests. Evolution. 43: 223–225.

Rodrigues, C.G. and G. Vilks. 1994. The impact of glacial lake runoff on the Goldthwait and Champlain Seas: The relationship between glacial Lake Agassiz runoff and the younger dryas. Quat. Sci. Rev. 13: 923–944.

Ronquist, F. and J.P. Huelsenbeck. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics. 19: 1572–1574. http://mrbayes.csit.fsu.edu/. (v3.1.2 2005).

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

Rousset, F. 2008. Genepop'008: A complete re–implementation of the Genepop software for Windows and Linux. Mol. Ecol. Resour. 8: 103–106. Available at http://kimura.univmontp2.fr/ ~rousset/ Genepop.htm.

Russell, D.A., F.J. Rich, V. Schneider and J. Lynch-Stieglitz. 2009. A warm thermal enclave in the Late Pleistocene of the south-eastern United States. Biol. Rev. 84: 173–202.

Ryan, P.A., R. Knight, R. MacGregor, G. Towns, R. Hoopes and W. Culligan. 2003. Fish-community goals and objectives for Lake Erie. Great Lakes Fishery Commission Special Publication 03–02.

Saarnisto, M. 1974. The deglaciation history of the Lake Superior region and its climatic implications. Quatern. Res. 4: 316–339.

Sanderson, M.J. 2003. r8s: inferring absolute rates of molecular evolution and divergence times in the absence of a molecular clock. Bioinformatics 19: 301–302. Available at http://loco.biosci.arizona.edu/r8s/.

Schmidt, R.E. 1986. Zoogeography of the northern Appalachians. pp. 137–159. *In*: C.H. Hocutt and E.O. Wiley (eds.). The Zoogeography of North American Freshwater Fishes. John Wiley and Sons, New York.

Schmitt, T. 2007. Molecular biogeography of Europe: Pleistocene cycles and postglacial trends. Front. Zool. 4: 11.

Scott, W.B. and E.J. Crossman. 1973. Freshwater fishes of Canada. J. Fish. Res. Board Can. 184: 1–196.

Sepulveda-Villet, O.J., A.M. Ford, J.D. Williams and C.A. Stepien. 2009. Population genetic diversity and phylogeographic divergence patterns of the yellow perch (*Perca flavescens*). J. Great Lakes Res. 35: 107–119.

Sepulveda-Villet, O.J. and C.A. Stepien. 2011. Fine-scale population genetic structure of the yellow perch *Perca flavescens* in Lake Erie. Can. J. Fish. Aquat. Sci. 68: 1435–1453.

Sepulveda–Villet, O.J. and C.A. Stepien. 2012. Waterscape genetics of the yellow perch (*Perca flavescens*): Patterns across large connected ecosystems and isolated relict populations. Mol. Ecol. 21: 5795–5826.

Shuter, B.J. and J.R. Post. 1990. Climate, population viability, and the zoogeography of temperate fishes. Trans. Am. Fish Soc. 119: 314–336.

Simon, T.P. and R. Wallus. 2006. Reproductive Biology and Early Life History of Fishes in the Ohio River Drainage, Vol. 4: Percidae–Perch, Pikeperch, and Darters. CRC Taylor and Francis, Boca Raton, Florida.

Sloss, B.L., N. Billington and B.M. Burr. 2004. A molecular phylogeny of the Percidae (Teleostei, Perciformes) based on mitochondrial DNA sequence. Mol. Phylogenet. Evol. 32: 545–562.

Smith, T.B. and L. Bernatchez (eds.). 2008. Evolutionary change in human-altered environments. Mol. Ecol. 17: 1–8.

Sokolovsky, V., S. Galouschak and V. Skakun. 2000. Current condition of Balkhash perch *Perca schrenki* (Percidae) in lakes of Alakol system. Problems of Ichthyology 40(2): 228–234.

Soltis, D.E., A.B. Morris, J.S. McLachlan, P.S. Manos and P.S. Soltis. 2006. Comparative phylogeography of unglaciated eastern North America. Mol. Ecol. 15: 4261–4293.

Song, C.B., T.J. Near and L.M. Page. 1998. Phylogenetic relations among percid fishes as inferred from mitochondrial cytochrome *b* DNA sequence data. Mol. Phylogenet. Evol. 10: 343–353.

Stepien, C.A. and J.E. Faber. 1998. Population genetic structure, phylogeography, and spawning philopatry in walleye (*Stizostedionvitreum*) from mtDNA control region sequences. Mol. Ecol. 7: 1757–1769.

Stepien, C.A., A.K. Dillon and M.D. Chandler. 1998. Genetic identity, phylogeography, and systematics of ruffe *Gymnocephalus* in the North American Great Lakes and Eurasia. J. Great Lakes Res. 24: 361–378.

Stepien, C.A., J.E. Brown, M.E. Neilson and M.A. Tumeo. 2005. Genetic diversity of invasive species in the Great Lakes versus their European source populations: Insights for risk analysis. Risk Anal. 25: 1043–1060.

Stepien, C.A., D.J. Murphy and R.M. Strange. 2007. Broad- to fine-scale population genetic patterning in the smallmouth bass *Micropterus dolomieu* across the Laurentian Great Lakes and beyond: An interplay of behaviour and geography. Mol. Ecol. 16: 1605–1624.

Stepien, C.A., D.J. Murphy, R.N. Lohner, O.J. Sepulveda–Villet and A.E. Haponski. 2009. Signatures of vicariance, postglacial dispersal, and spawning philopatry: Population genetics and biogeography of the walleye *Sander vitreus*. Mol. Ecol. 18: 3411–3428.

Stepien, C.A., D.J. Murphy, R.N. Lohner, A.E. Haponski and O.J. Sepulveda–Villet. 2010. Status and delineation of walleye (*Sander vitreus*) genetic stock structure across the Great Lakes. pp. 189–223. *In*: E. Roseman, P. Kocovsky and C. Vandergoot (eds.). Status of Walleye in the Great Lakes: Proceedings of the 2006 Symposium. Great Lakes Fishery Commission Technical Report 69, Ann. Arbor.

Stepien, C.A., J.A. Banda, D.J. Murphy and A.E. Haponski. 2012. Temporal and spatial genetic consistency of walleye (*Sander vitreus*) spawning groups. Trans. Am. Fish Soc. 141: 660–672.

Stepien, C.A., L.R. Pierce and D. Leaman, M. Niner and B. Shepherd. 2015. Genetic diversification of an emerging pathogen: A decade of mutation by the fish Viral Hemorrhagic Septicemia (VHS) virus in the Laurentian Great Lakes. In review.

Stewart, J.R. and A.M. Lister. 2001. Cryptic northern refugia and the origins of the modern biota. Trends. Ecol. Evol. 16: 608–613.

Strange, R.M. and C.A. Stepien. 2007. Genetic divergence and connectivity among river and reef spawning groups of walleye (*Sander vitreus*) in Lake Erie. Can. J. Fish. Aquat. Sci. 64: 437–448.

Sullivan, T.J. and C.A. Stepien. 2014. Genetic diversity and divergence of yellow perch spawning populations across the Huron–Erie Corridor, from Lake Huron through western Lake Erie. J. Great Lakes Res. 40: 101–109.

Sullivan, T.J. and C.A. Stepien. 2015. Temporal population genetic structure of yellow perch (*Perca flavescens*) spawning groups in the lower Great Lakes. Trans. Am. Fish Soc. 144: 211–226. DOI: 10.1080/00028487.2014.982260.

Taberlet, P., L. Fumagalli, A.-G. Wust-Saucy and J.F. Cosson. 1998. Comparative phylogeography and postglacial colonization routes in Europe. Mol. Ecol. 7: 453–464.

Teller, J.T. and P. Mahnic. 1988. History of sedimentation in the northwestern Lake Superior basin and its relation to Lake Agassiz overflow. Can. J. Earth Sci. 25: 1660–1673.

Thorpe, J.E. 1977. Morphology, physiology, behaviour and ecology of *Perca fluviatilis* L. and *Perca flavescens* Mitchill J. Fish. Res. Board Can. 34: 1504–1514.

Timmerman, A.J. 1995. Walleye assessment and enhancement projects in the middle Grand River watershed 1987–1995. Ontario Ministry of Natural Resources, Cambridge District, Guelph.

Todd, T.N. and C.O. Hatcher. 1993. Genetic variability and glacial origins of yellow perch (*Perca flavescens*) in North America. Can. J. Fish. Aquat. Sci. 50: 1828–1834.

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

Truemper, H.A. and T.E. Lauer. 2005. Gape limitation and piscine prey size-selection by yellow perch in the extreme southern area of Lake Michigan, with emphasis on two exotic prey items. J. Fish. Biol. 66: 135–149.

Turgeon, J. and L. Bernatchez. 2001. Mitochondrial DNA phylogeography of lake cisco (*Coregonusartedi*): evidence supporting extensive secondary contacts between two glacial races. Mol. Ecol. 10: 987–1001.

Underhill, J.C. 1986. The fish fauna of the Laurentian Great Lakes, the St. Lawrence lowlands, Newfoundland, and Labrador. pp. 105–136. *In*: C.H. Hocutt and E.O. Wiley (eds.). The Zoogeography of North American Freshwater Fishes. John Wiley and Sons, New York.

USFWS/GLFC (United States Fish and Wildlife Service/Great Lakes Fishery Commission). 2010. Great Lakes Fish Stocking database. U.S. Fish and Wildlife Service, Region 3 Fisheries Program, and Great Lakes Fishery Commission. Available at ttp://www.glfc.org/fishstocking/.

Vandewoestijne, S., N. Schtickzelle and M. Baguette. 2008. Positive correlation between genetic diversity and fitness in a large, well-connected metapopulation. BMC Biol. 6: 46.

Vidal-Martínez, V.M., D. Pech, B. Sures, S.T. Purucker and R. Poulin. 2010. Can parasites really reveal environmental impact? Trends Parasitol. 26: 44.

Volckaert, F.A.M., B.H. Hänfling, B. Hellmans and G.R. Carvalho. 2002. Timing of the population dynamics of bullhead *Cottusgobio* (Teleostei: Cottidae) during the Pleistocene. J. Evol. Ecol. 15: 930–944.

Wagner, G. 1960. Einführung in die Erd- und Landschaftsgeschichte mit besonderer Berücksichtigung Süddeutschlands, Verlag der Hohenlohe´schen Buchhandlung F. Rau, Öhringen.

Wang, N. and R. Eckmann. 1994. Distribution of perch (*Perca fluviatilis* L.) during their first year of life in Lake Constance. Hydrobiologia 277: 135–143.

Weir, B.S. and C.C. Cockerham. 1984. Estimating *F*–statistics for the analysis of population structure. Evolution 38: 1358–1370.

Wiley, E.O. 1992. Phylogenetic relationships of the Percidae (Teleostei: Perciformes): A preliminary hypothesis. pp. 247–267. *In*: R.L. Mayden (ed.). Systematics, Historical Ecology, and North American Freshwater Fishes. Stanford University Press, Stanford (CA).

Wilson, C.C. and P.D. Hebert. 1996. Phylogeographic origins of lake trout (*Salvelinus namaycush*) in eastern North America. Can. J. Fish. Aquat. Sci. 53: 2764–2775.

Wolinska, J. and K.C. King. 2009. Environment can alter selection in host–parasite interactions. Trends Parasitol. 25: 236–244.

Woolhouse, M.E.J., J.P. Webster, E. Domingo, B. Charlesworth and B.R. Levin. 2002. Biological and biomedical implications of the co-evolution of pathogens and their hosts. Nature Genetics 32: 569.

YPTG (Yellow Perch Task Group of the Lake Erie Committee, Great Lakes Fishery Commission). 2013. Report of the Lake Erie yellow perch task group. Great Lakes Fishery Commission Ann Arbor. Available at http://www.glfc.org/lakecom/lec/YPTG_docs/annual_reports/YPTG_report_2013.pdf.

Zhao, Y., M.L. Jones, B.J. Shuter and E.F. Roseman. 2009. A biophysical model of Lake Erie walleye (*Sander vitreus*) explains interannual variations in recruitment. Can. J. Fish. Aquat. Sci. 66: 114–125.