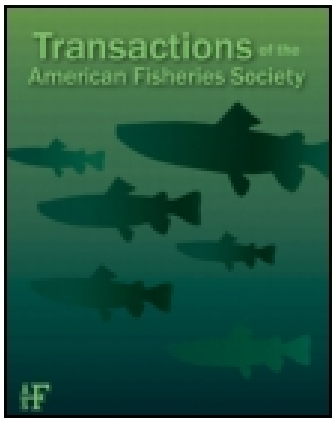

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ARTICLE

Temporal Population Genetic Structure of Yellow Perch Spawning Groups in the Lower Great Lakes

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Abstract

This study tested the hypothesis that the genetic composition of Yellow Perch *Perca flavescens* spawning groups at specific sites remained consistent among years or age-cohorts; this likely would influence spatial population structure and be important for delineating management units. Previous studies identified that spawning groups genetically differed among locations across fine geographic scales, but it was unknown whether these patterns persisted from year to year. We analyzed 15 nuclear DNA microsatellite loci from Yellow Perch spawning at six Lake Erie locations in 2009 in reference to two out-groups spawning in Lakes St. Clair and Ontario. Results were compared with a prior study of samples from the same locations that had been collected in various years, ranging from 2001 to 2005. We evaluated consistency for two of the spawning groups across multiple birth-year-cohorts. Results indicated that the levels of genetic diversity were similar across all spawning groups and years. All eight spawning groups genetically differed from one other, with their allelic compositions varying between the two sampling periods. Some variation occurred among individual sampling years and birth-cohorts, with the 2003 cohort being the most distinctive. Sampling groups contained relatively high proportions of full siblings (mean = 18.5%, ranging to 75% for the 2001 birth-cohort spawning at the eastern Lake Erie site), yet inbreeding appeared relatively low. Differences at sampling sites over time did not appear to reflect genetic drift but may instead suggest that spawning groups reproduce in slightly different locations from year to year or perhaps within a given season; this merits examination. Spatial and temporal patterns may reflect kin-group structuring and differential reproductive success, in which strong year-classes dominate spawning groups and impact genetic structure.

The designation and application of management units (MUs) is a widely used approach to monitor and manage sustainable harvesting of populations in given areas (Begg et al. 1999; Schwartz et al. 2007), which may need to be adjusted via adaptive management for future conditions (Kocovsky et al. 2013; Shelton 2014). However, MUs that are based primarily on geography often are not biologically relevant (Waples and Gaggiotti 2006; Palsboll et al. 2007), and their mismatch can lead to reduced genetic diversity, productivity, and population size (Reiss et al. 2009). Genetic data provide a powerful tool to delineate stock structure, identify unique genetic variation and potential local adaptations, and may be used to help focus action at a biologically relevant scale (Pracheil et al. 2012; Rice et al. 2012; Allendorf et al. 2013).

The Yellow Perch *Perca flavescens* (family Percidae) is a popular sport and commercial fishery species, whose geographic distribution extends across much of the northeast and central regions of North America (summarized by Sepulveda-Villet and Stepien 2012; Stepien et al., in press). Its greatest abundances, most extensive habitats, and largest fisheries co-occur in the lower Laurentian Great Lakes, especially in Lake Erie, whose population levels have undergone frequent and poorly understood fluctuations (Scott and Crossman 1973; Hubbs and Lagler 2004; Kocovsky et al. 2013). Notably,

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Yellow Perch population sizes declined in the lower Great Lakes over the 1960s through 1985, which is attributed to a combination of exploitation, poor water quality, and changes in prey species (Henderson and Nepszy 1989; Tyson and Knight 2001). In response to improved management and habitat conditions, the Yellow Perch has undergone a shallow recovery in Lake Erie from 1985 to the present, averaging ~180 million individuals and ranging from 43 million to 501 million per year since 1990 (Munawar et al. 2005; YPTG 2014). Lake Erie Yellow Perch are managed under the jurisdiction of the Great Lake Fishery Commission's Lake Erie Committee, with recommendations from the Yellow Perch Task Group, which employs an MU framework to set annual quotas. In recent years, the fishery has been dominated by a few large year-classes (particularly 2003 and 2007), followed by poorer recruitment in subsequent cohorts (YPTG 2014). Understanding the temporal and spatial genetic stock structure (Ryan et al. 2003) that underlies these population fluctuations may provide important information for maintaining the fishery.

Studies of spawning behavior coupled to genetic data comprise a powerful approach to identify reproductive groups and discern population structure. Yellow Perch undergo short migrations in late spring to early summer, aggregating to spawn on shallow reef complexes in lacustrine systems or slow-moving tributaries, where females drape egg masses that are fertilized by two to five males (Scott and Crossman 1973; Carlander 1997; Jansen et al. 2009). It is believed that Yellow Perch return to specific reproductive sites (Aalto and Newsome 1990; Carlander 1997; Craig 2000), which is supported by genetic data (Sepulveda-Villet and Stepien 2011, 2012; Stepien et al., in press) and tagging data (Clady 1977; Rawson 1980; MacGregor and Witzel 1987; Ontario Ministry of Natural Resources 2011). Aalto and Newsome (1990) removed Yellow Perch egg masses from given spawning sites, which led to fewer fish returning to those locations than to control sites in subsequent years, suggesting that they returned to the same spawning areas year after year (potentially their natal location). Yellow Perch spawning groups located just a few kilometers apart (17 km) in central Lake Erie were found to diverge from one another in genetic and morphological compositions (Kocovsky et al. 2013). Reproductive groups of Yellow Perch have been shown to be genetically differentiated, suggesting that they likely congregate in natal groups at specific spawning locations (Sepulveda-Villet and Stepien 2012; Sullivan and Stepien 2014). It is hypothesized that imprinting occurs during the early life history of Yellow Perch and of the related European Perch *Perca fluviatilis*, with their highly developed olfactory systems used to detect natal spawning sites and/or the pheromones of neighbors and relatives (Horrall 1981; Gerlach et al. 2001; Stepien et al., in press).

Although Yellow Perch may spawn together with a specific group (believed to be their natal group), their exact spawning locations may vary somewhat from year to year. Notably, Bergek and Olsson (2009) compared spawning aggregations of European Perch caught at four different locations in Lake Erken in Sweden, consistently finding significant genetic differentiation among the samples. However, the local spawning groups also genetically differed from year to year when sampled at the same locations (Bergek and Olsson 2009).

Sepulveda-Villet and Stepien (2011) analyzed Yellow Perch spawning groups in Lake Erie using 15 nuclear microsatellite loci, finding consistent levels of genetic diversity among spawning groups and that nearly all groups were distinguishable by allelic composition and frequencies. However, the sampling design was limited since each spawning group was sampled just once and different collection years were used. That experimental design may have confounded the interpretation of spatial versus temporal patterns.

The present study thus investigates whether Yellow Perch genetic composition remains consistent among collection years and age-cohorts at specific spawning sites, which may influence spatial population structure and be important for defining MUs.

METHODS

Sample collection, DNA extraction, and PCR amplification.—Reproductive-condition adult Yellow Perch were sampled by state and federal agency biologists from eight spawning sites, which are labeled A–H on Figure 1. Six of them were located in Lake Erie (B–G), and two out-groups were from spawning locations in Lakes St. Clair (A) and Ontario (H). Lake Erie is connected to Lake St. Clair by the Detroit River to the west and to Lake Ontario via the Niagara River to the east (Figure 1). Samples were collected in single collecting events, made at the same time or in consecutive days at the same location, either using single 10–20-min bottom trawls at ~5.6 km/h or using overnight gill nets. The numbers of male and female fish were determined in some cases, but this information was not always available (Supplementary Table S.1. in the online version of this article). Fin clips were preserved in 95% ethanol in the field. We compared results from 2009 (this study) to those from single collections of spawning Yellow Perch made during 2001–2005 at the same locations (reported by Sepulveda-Villet and Stepien 2011). At one eastern Lake Erie location (site G; Dunkirk, New York), we intensively analyzed year-to-year temporal variability, comparing individuals spawning there in 1985, 2001, 2004, 2008, 2009, and 2010. The DNA from the Dunkirk 1985 sample was obtained from extractions of uncleaned dried fish scales. Spawning adults from Dunkirk collected in all years except 2009 and from site B (Monroe, Michigan) in western Lake Erie were aged using scale annuli by the agencies who collected the samples, allowing comparisons to be made among age-cohorts (Tables S.2, S.3) that contained more than five individuals.

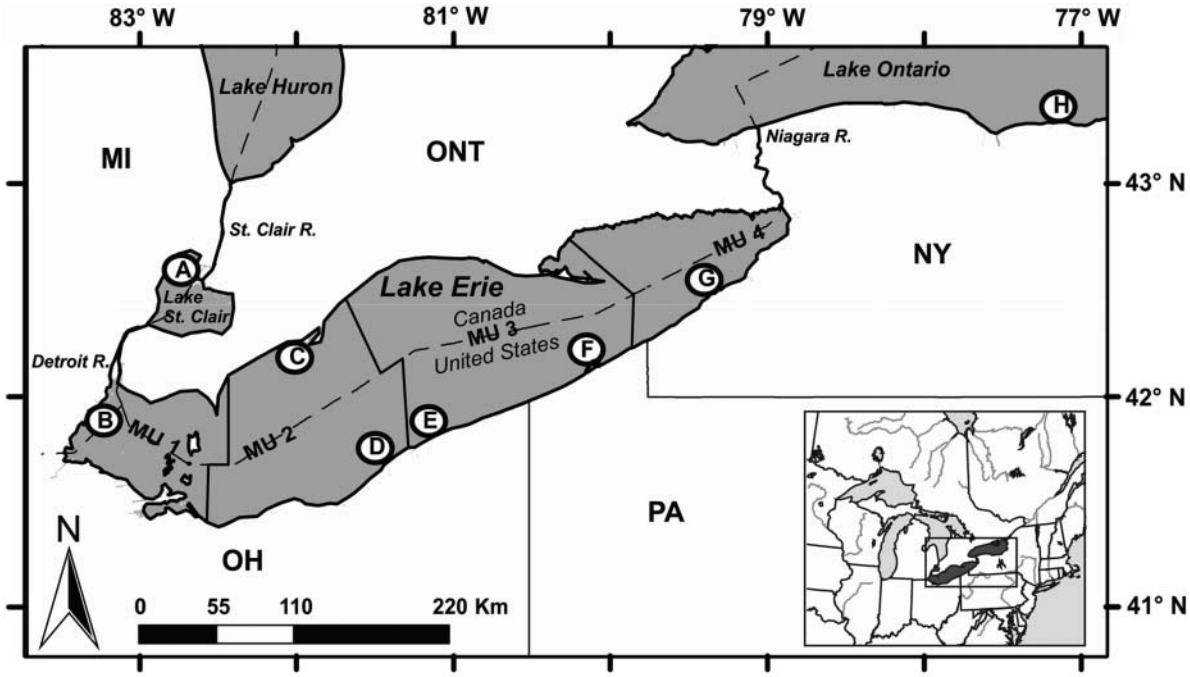

FIGURE 1. Map showing sampling sites (A–H) of spawning Yellow Perch. The thin solid lines separate Lake Erie into management units (MU1–MU4; www.glfc.com), and the thin dashed line shows the international boundary between United States and Canadian waters. Abbreviations are as follows: MI = Michigan, OH = Ohio, PA = Pennsylvania, NY = New York, and ONT = Ontario.

The methods and conditions for data collection and analysis of 15 nuclear DNA microsatellite loci (Table 1) matched those used in our laboratory for the 2001–2005 samples. Genomic DNA from the ethanol-preserved fin clips was extracted and purified using DNeasy Qiagen kits (QIAGEN, Valencia, California), and dried scale samples were extracted according to Hutchinson et al. (1999); all aliquots were frozen, labeled, and archived. With the scale samples, loci *Svi7*, *Svi17*, and *Mpf1* failed to amplify, attributed to lower template quality. Therefore, analyses for the 1985 samples were based on the other 12 loci.

TABLE 1. Summary PCR parameters and genetic variation statistics for 15 nuclear DNA microsatellite loci across Yellow Perch spawning populations. Abbreviations are as follows: T_A = PCR annealing temperature, N_A = number of alleles per locus, F_{IS} = mean deviation from Hardy–Weinberg equilibrium within subpopulations, F_{ST} = mean deviation among subpopulations, and F_{IT} = the total deviation.

Locus and total	Reference	T_A (°C)	N_A	Size range (bp)	F_{IS}	F_{ST}	F_{IT}
Svi2	Eldridge et al. (2002)	54	6	202–216	0.042	0.017	0.072
Svi3	Eldridge et al. (2002)	54	15	130–160	0.061	0.050	0.108
Svi4	Borer et al. (1999)	62	33	108–190	−0.005	0.041	0.030
Svi7	Eldridge et al. (2002)	53	13	158–194	−0.041	0.015	−0.022
Svi17	Borer et al. (1999)	60	24	142–190	0.071	0.033	0.102
Svi33	Borer et al. (1999)	60	41	100–178	0.093	0.194	0.256
YP13	Li et al. (2007)	54	18	223–268	0.099	0.171	0.375
YP17	Li et al. (2007)	56	11	205–292	0.011	0.031	0.046
Mpf1	Grzybowski et al. (2010)	56	49	231–341	0.053	0.009	0.059
Mpf2	Grzybowski et al. (2010)	56	49	213–333	0.025	0.011	0.034
Mpf3	Grzybowski et al. (2010)	54	21	107–149	−0.100	0.036	−0.062
Mpf4	Grzybowski et al. (2010)	58	36	173–243	0.086	0.044	0.126
Mpf5	Grzybowski et al. (2010)	54	16	127–169	0.117	0.202	0.310
Mpf6	Grzybowski et al. (2010)	54	13	124–162	−0.068	0.022	−0.047
Mpf7	Grzybowski et al. (2010)	53	23	142–192	−0.025	0.033	0.008
Total			368		0.028	0.061	0.099

The protocol for polymerase chain reactions (PCRs) followed that of Sepulveda-Villet and Stepien (2011, 2012), using the same positive and negative controls; these provided an important measure of consistency between the two sampling periods. Amplification products were analyzed on our ABI 3130XL Genetic Analyzer with GENEMAPPER 3.7 software (Applied Biosystems, Foster City, California). Output profiles were reviewed manually together by Sepulveda-Villet and T. J. Sullivan to confirm the correct identification of allelic size variants.

Evaluation of microsatellite loci.—Population samples were tested for conformance to Hardy–Weinberg Equilibrium (HWE) expectations at each locus, with significance evaluated using the Markov Chain Monte Carlo method using 1,000 randomization procedures (Guo and Thompson 1992) in GENEPOP 4.0 (Rousset 2008). Any deviations were analyzed for excess or deficiency of homozygotes. Loci were tested for linkage disequilibrium; levels of significance for both tests were adjusted using sequential Bonferroni corrections (Rice 1989) to reduce type I error. The possible presence of nonamplified (null) alleles was tested with MICRO-CHECKER 2.3.3 (van Oosterhout et al. 2004, 2006). Lastly, each locus was evaluated for neutrality or possible selection using the program BayeScan2.1, whose results were unaffected by geographic structuring (Foll and Gaggiotti 2008). Loci that were identified as possibly subject to selection were evaluated further by comparing observed diversity and divergence estimates with and without those loci (Tables S.4–S.13).

Estimating genetic diversity.—To test whether genetic diversity or levels of inbreeding varied among sampling groups or age-cohorts, we compared (1) the expected and observed heterozygosity values (H_E and H_O), (2) the inbreeding statistic (F_{IS}) in GENEPOP, (3) the number of alleles (N_A), (4) the allelic richness (A_R; number of alleles per locus independent of sample size [Mousadik and Petit 1996]) with *F*STAT 2.9.3.2 (Goudet 2002), and (5) the numbers (N_{PA}) and proportions (P_{PA}) of private alleles using CONVERT 1.31 (Glaubitz 2004). We evaluated whether observed heterozygosity or allelic richness values differed among samples using Friedman's rank-sum tests in the R statistical software suite 2.15.2 (R Development Core Team 2012), with loci treated as blocks per spawning population.

Influence of potential outliers and related individuals.—Population genetic metrics and analyses (i.e., F_{ST} and sibship estimates) assume neutral polymorphic loci, whose variation reflects population demographics, size, and structure (see Vitalis et al. 2001; Allendorf et al. 2013). Outlier loci may be under selection, leading to bias in measuring these parameters for populations. Similarly, kin structure within population samples also may bias interpretations of population patterns (Allendorf and Phelps 1981; Vera et al. 2010). Both of these biases may impact divergence and diversity estimates since they can skew allele frequencies. To avoid possible biases within our dataset, we computed diversity and divergence metrics without potential outlier loci and after the removal of family groups. Results showed that their removals had no significant effects; thus, we retained the loci and individuals in favor of increased power and sample size (Tables S.4–S.13).

Spatial and temporal population genetic structure.—To investigate whether genetic composition varied significantly among spawning populations (for each sampling period), sampling years, collection years (at Dunkirk, New York), and age-cohorts (at Monroe, Michigan, and Dunkirk), unbiased θ estimates of *F*-statistics (Weir and Cockerham 1984) and their levels of significance were calculated in *F*STAT. Since models using θ_{ST} (the F_{ST} metric of Weir and Cockerham 1984) have been shown to have greater resolution among recently diverged populations (Balloux and Lugon-Moulin 2002), they were employed here. Pairwise comparisons additionally were conducted using a nonparametric (exact *G*) procedure (Raymond and Rousset 2005), whose probability was estimated using the Markov Chain Monte Carlo method in GENEPOP. That approach does not assume a normal distribution and is not influenced by sample size, but may have less statistical power (Goudet et al. 1996). Sequential Bonferroni corrections (Rice 1989) were used to reduce the potential for type I error in all pairwise comparisons.

Analysis of molecular variance (AMOVA; Excoffier et al. 1992) in ARLEQUIN 3.5.12 (Excoffier and Lischer 2010) was performed across all loci and locus by locus to evaluate whether genetic composition varied significantly temporally and spatially. We conducted two AMOVA tests, which partitioned genetic variation (1) first among the eight spawning groups and then between the two sampling periods (2001–2005 and 2009), emphasizing spatial variation, and (2) first between the two sampling periods and then among the eight spawning groups, emphasizing temporal variation. These tests used the dataset for the eight spawning groups and the two sampling periods (2001–2005 and 2009). The AMOVA additionally examined whether genetic variation was differentially partitioned among age-cohorts (born in 1998, 1999, 2001, 2002, and 2003) for the Monroe (site B) and Dunkirk (site G) sites. Those age-cohort years were used since they were well represented at both spawning locations, facilitating comparisons.

The presence of full siblings in spawning samples (95% probability) was evaluated using COLONY (Jones and Wang 2010), which analyzes allele frequencies with maximum likelihood. Lakewide spawning samples first were analyzed without a subsetting (Table 2). Yellow Perch spawning at the Monroe and Dunkirk sites were then analyzed separately for each collection year and then separately by birth-year-cohort (Tables 3, 4). The COLONY runs were made using the following conditions: diploidy, polygamy, no prior for sibship size or complexity, unknown population allele frequency, and medium run with high precision.

TABLE 2. Sample data and genetic parameters for Yellow Perch spawning populations based on variation at 15 nuclear microsatellite loci. Included are the collection date, sample size (N), observed (H_O) and expected (H_E) heterozygosity, deviation from Hardy–Weinberg equilibrium within subpopulations (F_{IS}), number of alleles across all loci (N_A), allelic richness (A_R), number of private alleles (N_{PA}), proportion of private alleles (P_{PA}), and number and percentage of individuals identified as full siblings (Sibs) from COLONY analyses (Jones and Wang 2010). Lake Erie management unit designations are indicated as MU1–MU4 (YPTG 2014).

Locality, total, and mean	Date	N	$H_O \pm$ SE	$H_E \pm$ SE	$F_{IS} \pm$ SE	N_A	$A_R \pm$ SE	N_{PA}	P_{PA}	Sibs
				2001–2005						
A) Lake St. Clair	May 26, 2005	39	0.53 ± 0.08	0.60 ± 0.08	0.10 ± 0.07	152	6.8 ± 1.2	5	0.03	8 (21%)
Lake Erie (B–G)	2001–2004	203	0.54 ± 0.06	0.61 ± 0.07	0.11 ± 0.03	254	16.9 ± 2.7	94	0.37	42 (21%)
B) Monroe, Michigan (MU1)	April 13, 2004	48	0.56 ± 0.07	0.63 ± 0.07	0.10 ± 0.03	184	7.8 ± 1.3	4	0.02	6 (13%)
C) Erieau, Ontario (MU2)	April 15, 2003	30	0.55 ± 0.08	0.54 ± 0.08	−0.02 ± 0.02	146	7.2 ± 1.3	2	0.01	4 (13%)
D) Fairport, Ohio (MU2)	April 19, 2003	20	0.51 ± 0.08	0.50 ± 0.08	−0.03 ± 0.03	94	5.5 ± 0.9	5	0.05	4 (20%)
E) Perry, Ohio (MU3)	April 28, 2003	48	0.52 ± 0.07	0.59 ± 0.08	0.08 ± 0.03	111	7.4 ± 1.3	6	0.05	10 (21%)
F) Erie, Pennsylvania (MU3)	May 5, 2001	20	0.51 ± 0.08	0.55 ± 0.07	0.08 ± 0.07	109	6.3 ± 1.2	0	0.00	4 (20%)
G) Dunkirk, New York (MU4)	May 5, 2001	37	0.54 ± 0.06	0.60 ± 0.06	0.09 ± 0.05	143	6.6 ± 1.0	4	0.03	14 (38%)
H) Lake Ontario	July 16, 2002	14	0.52 ± 0.07	0.62 ± 0.06	0.16 ± 0.06	100	6.9 ± 1.1	1	0.01	0 (0%)
Total (2001–2005)		256	0.54 ± 0.06	0.63 ± 0.07	0.14 ± 0.04	279	18.6 ± 2.8			50 (20%)
Mean (2001–2005)		32	0.54 ± 0.07	0.58 ± 0.07	0.08 ± 0.05	130	6.8 ± 1.2	4	0.03	4.5 (20%)
				2009						
A) Lake St. Clair	June 3, 2009	47	0.62 ± 0.07	0.64 ± 0.07	−0.05 ± 0.02	176	7.5 ± 1.3	9	0.05	14 (30%)
Lake Erie (B–G)	April 21–May 5, 2009	226	0.58 ± 0.08	0.58 ± 0.08	0.02 ± 0.02	293	19.5 ± 3.2	89	0.30	39 (17%)
B) Monroe, Michigan (MU1)	April 21, 2009	30	0.57 ± 0.07	0.66 ± 0.09	−0.12 ± 0.04	127	6.2 ± 0.9	1	0.01	3 (10%)
C) Erieau, Ontario (MU2)	May 5, 2009	36	0.54 ± 0.09	0.52 ± 0.07	0.02 ± 0.06	145	6.3 ± 1.0	4	0.03	4 (11%)
D) Fairport, Ohio (MU2)	April 30, 2009	48	0.57 ± 0.08	0.56 ± 0.08	−0.02 ± 0.03	173	7.1 ± 1.2	7	0.04	8 (17%)
E) Perry, Ohio (MU3)	April 30, 2009	48	0.56 ± 0.08	0.56 ± 0.08	−0.01 ± 0.03	171	7.0 ± 1.2	10	0.06	14 (29%)
F) Erie, Pennsylvania (MU3)	May 12, 2009	34	0.57 ± 0.07	0.61 ± 0.08	0.08 ± 0.02	180	8.1 ± 1.4	13	0.07	2 (6%)
G) Dunkirk, New York (MU4)	May 13, 2009	30	0.57 ± 0.09	0.54 ± 0.08	−0.06 ± 0.04	133	6.6 ± 1.2	5	0.04	8 (27%)
H) Lake Ontario	April 24, 2009	48	0.55 ± 0.08	0.59 ± 0.07	0.09 ± 0.06	190	7.8 ± 1.5	15	0.08	2 (4%)
Total (2009)		321	0.58 ± 0.08	0.60 ± 0.07	0.02 ± 0.02	340	22.6 ± 3.6			55 (17%)
Mean (2009)		40	0.57 ± 0.08	0.59 ± 0.08	−0.02 ± 0.04	162	7.1 ± 1.2	8	0.05	6.9 (17%)

Population structure was assessed through the Bayesian-based program STRUCTURE 2.3.4 (Pritchard et al. 2000; Pritchard and Wen 2004). Results were compared from 10 independent runs at $K = 1$ (a single spawning group) to $K = 24$ (1.5 times the number of sampling sites), with burn-ins of 100,000 and 500,000 replicates. We evaluated the consistency among runs, the probabilities of individual assignments to groups, and the log-likelihood values. Optimal K scenarios were determined via the posterior probability procedure of Pritchard et al. (2000) and ΔK likelihood from Evanno et al. (2005) using STRUCTURE HARVESTER (Earl and von Holdt 2012). A neighbor-joining tree of Yellow Perch population samples based on Nei's (1972) genetic distances for 15 microsatellite loci was conducted using POPULATIONS 1.2.32 (Langella 2002) with 1,000 bootstrap replicates.

Correspondence between genetic distances ($\theta_{ST}/1-\theta_{ST}$) and geographic distances (shortest waterway distances) was tested using ISOLDE in GENEPOP (Rousset 1997). The regression line fit and significance were calculated using the procedure in Mantel (1967) with 1,000 permutations. We similarly examined possible relationships between the genetic distances and time (years) separating the Dunkirk age-cohorts.

RESULTS

Genetic Diversity

All loci were unlinked and conformed to expectations of HWE after sequential Bonferroni correction. Tests indicated no evidence of null alleles, large allele dropouts, or stuttering. A total of 368 alleles were recovered for the 15 loci, averaging 24.5 alleles/locus and ranging from 6 at *Svi2* to 49 at *Mpf1* and *Mpf2* (Table 1). Based on F_{ST} values, *Mpf5*, *YP13*, and *Svi33* showed the greatest divergence among spawning sites. These loci were not under the influence of natural selection, according to BayeScan2.1, and were retained in our analyses since they were in HWE and dropping them did not affect the relative genetic diversity or divergence estimates nor the significance of tests (Tables S.4–S.13). For the 1985 scale samples from Dunkirk alone, just a single locus (*Mpf6*) showed some potential null alleles but was in HWE, and no other samples had that issue. This may have been due to template quality. Since the other loci for that sample were scored reliably, all loci were used for our analyses.

All spawning groups possessed similar levels of genetic diversity, which also was consistent between the two sampling periods (2001–2005 and 2009; Table 2). Notably, observed heterozygosity values were consistent across the spatial distribution of all spawning groups in both 2001–2005 and 2009 (2001–2005: $\chi^2 = 2.9$, df = 7, $P = 0.89$; 2009: $\chi^2 = 7.2$, df = 7, $P = 0.41$). Allelic richness values fluctuated more (2001–2005: $\chi^2 = 14.5$, df = 7, $P = 0.04$; 2009: $\chi^2 = 16.6$, df = 7, $P = 0.02$; Table 2). For the 2001–2005 samples, allelic richness appeared highest at Monroe (site B) and lowest at Fairport, Ohio (site D); in 2009, they were highest at Erie, Pennsylvania (site F), and lowest at Monroe (B). At the Erie (site F) and Lake Ontario (site H) sites, more private alleles were recovered in 2009.

Levels of genetic diversity (H_O) for Yellow Perch spawning at Dunkirk (site G) in eastern Lake Erie were consistent across the six collection years ($\chi^2 = 13.9$, df = 5, $P = 0.92$; Table 3). Allelic richness varied ($\chi^2 = 21.8$, df = 5, $P = 0.001$; Table 3), being greatest in 1985 and lowest in 2004. Birth-year-cohorts from Dunkirk and Monroe (site B) displayed different patterns. Heterozygosity of the Dunkirk cohorts remained similar from 1980 to 2008 ($\chi^2 = 7.5$, df = 14, $P = 0.92$; Table 4), but Monroe in western Lake Erie showed variation (1997–2004: $\chi^2 = 20.1$, df = 6, $P = 0.003$), being higher in the 2001 and 2002 cohorts (Table 4). Allelic richness differed among the Dunkirk age-cohorts ($\chi^2 = 32.3$, df = 14, $P = 0.004$; Table 4), being greatest in 1980, 1981, and 1982. In contrast, allelic richness remained similar for all cohorts from Monroe ($\chi^2 = 9.3$, df = 6, $P = 0.16$; Table 4). Private alleles were recovered in all collection years (Table 3) and in nearly all Dunkirk cohorts (Table 4), reaching a high of 0.10 in 1980. Private alleles comprised greater proportions in the earlier cohorts (1980–1982). At Monroe, all cohorts contained private alleles, whose proportions ranged from 0.05 (1999) to 0.16 (1998) (Table 4). Private alleles appeared to decline in the later samples from Dunkirk and Monroe.

Spatial and Temporal Population Genetic Structure

The genetic compositions of Yellow Perch spawning groups were significantly distinct from all other spawning groups (Table 5). They did not follow a pattern of genetic isolation by geographic distance (2001–2005: $y = 0.00007x + 0.09$, $R^2 = 0.036$, $P = 0.22$; Figure 2A; 2009: $y = 0.00003x + 0.04$, $R^2 = 0.078$, $P = 0.054$; Figure 2B). In 2009, spawning

TABLE 3. Sample data and genetic parameters for Yellow Perch spawning at Dunkirk, New York, in western Lake Erie for six collection years (1985–2010; 12 loci). Data include the collection date, sample size (N), observed (H_O) and expected (H_E) heterozygosity, deviation from Hardy–Weinberg equilibrium within subpopulations (F_{IS}), number of alleles across all loci (N_A), allelic richness (A_R), number of private alleles (N_{PA}), proportion of private alleles (P_{PA}), and number and percentage of individuals identified as full siblings (Sibs) by COLONY (Jones and Wang 2010). Allelic richness values were based on 30 individuals.

Date, total, and mean	N	$H_O \pm$ SE	$H_E \pm$ SE	$F_{IS} \pm$ SE	N_A	$A_R \pm$ SE	N_{PA}	P_{PA}	Sibs
May 16, 1985	34	0.54 ± 0.09	0.64 ± 0.07	0.20 ± 0.07	144	11.1 ± 2.1	23	0.16	10 (29%)
May 15, 2001	37	0.57 ± 0.06	0.61 ± 0.06	0.08 ± 0.06	116	8.7 ± 1.5	14	0.12	14 (38%)
May 13, 2004	48	0.59 ± 0.08	0.55 ± 0.06	−0.09 ± 0.07	110	7.4 ± 1.3	10	0.09	26 (54%)
May 13, 2008	30	0.55 ± 0.08	0.56 ± 0.09	−0.01 ± 0.02	121	9.7 ± 2.1	11	0.09	4 (13%)
May 13, 2009	30	0.57 ± 0.09	0.53 ± 0.08	−0.06 ± 0.05	111	8.9 ± 1.9	11	0.10	13 (43%)
May 13, 2010	36	0.58 ± 0.09	0.59 ± 0.09	0.01 ± 0.03	141	10.6 ± 2.0	9	0.06	10 (28%)
Total	215	0.57 ± 0.08	0.62 ± 0.07	0.09 ± 0.05	237	19.7 ± 3.3			77 (36%)
Mean	35.8	0.57 ± 0.08	0.58 ± 0.08	0.02 ± 0.05	124	9.4 ± 1.8	12	0.10	13 (36%)

TABLE 4. Sample data and genetic parameters for birth-year-cohorts from two Lake Erie locations, Dunkirk, New York (born in 1980–2008; 12 loci), and Monroe, Michigan (born in 1997–2004; 15 loci). Allelic richness values were based on six individuals for Dunkirk and five individuals for Monroe, in order to standardize comparisons. See Table 3 for column heading definitions.

Birth-cohort, total, and mean	N	$H_O \pm$ SE	$H_E \pm$ SE	$F_{IS} \pm$ SE	N_A	$A_R \pm$ SE	N_{PA}	P_{PA}	Sibs
Dunkirk, New York									
1980	9	0.53 ± 0.10	0.63 ± 0.08	0.23 ± 0.09	79	5.3 ± 0.9	8	0.10	0 (0%)
1981	13	0.58 ± 0.07	0.66 ± 0.07	0.12 ± 0.06	90	5.1 ± 0.7	6	0.07	0 (0%)
1982	12	0.51 ± 0.11	0.65 ± 0.07	0.27 ± 0.10	91	5.2 ± 0.8	7	0.08	0 (0%)
1995	9	0.56 ± 0.07	0.60 ± 0.05	0.07 ± 0.08	55	3.9 ± 0.4	1	0.02	0 (0%)
1996	6	0.51 ± 0.08	0.65 ± 0.07	0.21 ± 0.11	49	4.1 ± 0.5	2	0.04	2 (33%)
1998	14	0.60 ± 0.09	0.56 ± 0.07	−0.06 ± 0.07	75	4.1 ± 0.6	6	0.08	6 (43%)
1999	7	0.57 ± 0.07	0.63 ± 0.05	0.12 ± 0.11	53	4.2 ± 0.5	1	0.02	0 (0%)
2000	10	0.58 ± 0.10	0.55 ± 0.08	−0.05 ± 0.08	65	4.2 ± 0.6	2	0.03	0 (0%)
2001	16	0.61 ± 0.07	0.58 ± 0.06	−0.07 ± 0.07	98	4.2 ± 0.5	5	0.05	12 (75%)
2002	17	0.57 ± 0.08	0.54 ± 0.07	−0.05 ± 0.07	73	3.9 ± 0.6	4	0.05	4 (24%)
2003	10	0.58 ± 0.11	0.55 ± 0.09	0.01 ± 0.08	68	4.4 ± 0.8	1	0.01	0 (0%)
2005	17	0.55 ± 0.07	0.60 ± 0.08	0.07 ± 0.05	99	4.8 ± 0.7	6	0.06	2 (12%)
2006	6	0.57 ± 0.11	0.61 ± 0.10	0.08 ± 0.07	60	5.0 ± 0.9	2	0.03	0 (0%)
2007	14	0.59 ± 0.09	0.61 ± 0.09	0.01 ± 0.04	91	5.0 ± 0.8	3	0.03	2 (14%)
2008	13	0.57 ± 0.10	0.55 ± 0.09	−0.03 ± 0.02	84	4.6 ± 0.8	0	0.00	0 (0%)
Total	173	0.57 ± 0.07	0.63 ± 0.07	0.10 ± 0.05	226	18.8 ± 3.3			28 (15%)
Mean	12	0.57 ± 0.09	0.60 ± 0.10	0.06 ± 0.07	75	4.5 ± 0.7	4	0.05	1.9 (16%)
Monroe, Michigan									
1997	8	0.57 ± 0.07	0.63 ± 0.08	0.08 ± 0.04	84	4.3 ± 0.67	7	0.08	0 (0%)
1998	18	0.52 ± 0.08	0.61 ± 0.08	0.15 ± 0.06	130	4.5 ± 0.62	21	0.16	2 (11%)
1999	5	0.52 ± 0.09	0.55 ± 0.09	0.02 ± 0.06	60	4.0 ± 0.62	3	0.05	0 (0%)
2001	11	0.70 ± 0.09	0.59 ± 0.07	−0.17 ± 0.05	100	4.3 ± 0.53	12	0.12	0 (0%)
2002	7	0.67 ± 0.09	0.56 ± 0.07	−0.16 ± 0.05	67	3.8 ± 0.44	5	0.07	0 (0%)
2003	12	0.61 ± 0.09	0.56 ± 0.08	−0.07 ± 0.05	88	3.9 ± 0.51	8	0.09	0 (0%)
2004	7	0.61 ± 0.07	0.61 ± 0.07	0.00 ± 0.03	68	3.8 ± 0.51	4	0.06	0 (0%)
Total	68	0.60 ± 0.08	0.60 ± 0.07	0.02 ± 0.02	194	12.9 ± 2.20			2 (3%)
Mean	9.7	0.60 ± 0.08	0.59 ± 0.05	−0.01 ± 0.02	85	4.1 ± 0.56	8.6	0.09	0.3 (3%)

samples from the nearby locations of Fairport, Ohio (site D), and Perry, Ohio (site E), which were separated by just 23 km, did not significantly differ in genetic composition. However, they differed using the nonparametric exact G-test, which is less sensitive to low sample size (reviewed by Allendorf et al. 2013). The magnitude of the overall divergence among spawning groups was lower in 2009 than for the 2001–2005 samples.

The STRUCTURE results with delta K indicated highest support for $K = 3$, 6, and 8 population groups (Figure 3b, c). Some cross assignment between the two sampling periods occurred at the $K = 3$ level but very little at the $K = 6$ and 8 levels, except for the Lake Ontario (site H) out-group samples (Figure 3a). High self-assignments characterized samples from Lake St. Clair (site A), Fairport (site D), Erie (site F), and Dunkirk (site G) for the 2001–2005 sampling period but were less pronounced in 2009. Several spawning groups displayed a mixed assignment signature in 2009 at $K = 3$, 6, and 9, with proximate locations at Fairport and Perry appearing very similar. This mirrored the trend of lower pairwise divergence values among sampling locations in 2009 (Table 5). The neighbor-joining tree showed some clustering by year-group; however, no relationships among spawning groups were supported by bootstrap values > 0.50 (Supplementary Figure S.1); this may reflect a high degree of within-sample variation.

The first AMOVA scenario (comparing the eight spawning groups and then the two sampling periods within each spawning group) revealed significant partitioning of genetic variation between the two sampling periods (Table 6), similar to their significant pairwise divergence values (Table 5). Annual variation (1985–2010) likewise was shown in the pairwise comparisons at Dunkirk (Table 7). The second AMOVA scenario revealed significant variation among both year-groups and the spawning groups within each year-group (Table 6).

TABLE 5. Pairwise genetic divergences of spawning Yellow Perch between year-groups at a given site (2001–2005 versus 2009 in bold italics, along diagonal) and between sampling locations (2001–2005 below diagonal; 2009 above diagonal) given as θ_{ST}/ (exact *G*). An asterisk indicates significance following sequential Bonferroni correction (Rice 1989); all samples significantly differed with the exact *G*-tests. An infinite value given by the exact *G*-test is indicated by "Inf." The mean divergence among the spawning sites in the 2001–2005 samples was 0.094 ± 0.016 and was 0.042 ± 0.004 among the sites in 2009. The mean divergence between the two sampling time periods was 0.076 ± 0.0080. Locations B–G are in Lake Erie.

Location and mean	A	B	C	D	E	F	G	H	Mean (2009)
A) Lake St. Clair	***0.138*/(Inf.)***	0.030*/(Inf.)	0.044*/(Inf.)	0.065*/(Inf.)	0.052*/(Inf.)	0.044*/(Inf.)	0.040*/(Inf.)	0.033*/(Inf.)	0.044 ± 0.005
B) Monroe, Michigan	0.133*/(Inf.)	***0.026*/(Inf.)***	0.042*/(Inf.)	0.069*/(Inf.)	0.048*/(Inf.)	0.055*/(Inf.)	0.061*/(Inf.)	0.051*/(Inf.)	0.051 ± 0.005
C) Erieau, Ontario	0.159*/(Inf.)	0.015*/(73.9)	***0.037*/(Inf.)***	0.056*/(Inf.)	0.047*/(Inf.)	0.037*/(Inf.)	0.033*/(94.3)	0.045*/(Inf.)	0.043 ± 0.003
D) Fairport, Ohio	0.156*/(Inf.)	0.072*/(Inf.)	0.072*/(Inf.)	***0.114*/(Inf.)***	0.002/(50.8)	0.030*/(Inf.)	0.038*/(Inf.)	0.056*/(Inf.)	0.045 ± 0.009
E) Perry, Ohio	0.151*/(Inf.)	0.007*/(71.4)	0.012*/(54.5)	0.073*/(Inf.)	***0.041*/(Inf.)***	0.028*/(Inf.)	0.037*/(Inf.)	0.049*/(Inf.)	0.038 ± 0.007
F) Erie, Pennsylvania	0.083*/(Inf.)	0.110*/(Inf.)	0.121*/(Inf.)	0.145*/(Inf.)	0.114*/(Inf.)	***0.135*/(Inf.)***	0.014*/(97.1)	0.034*/(Inf.)	0.034 ± 0.005
G) Dunkirk, New York	0.168*/(Inf.)	0.029*/(Inf.)	0.036*/(Inf.)	0.085*/(Inf.)	0.028*/(Inf.)	0.124*/(Inf.)	***0.064*/(Inf.)***	0.034*/(Inf.)	0.037 ± 0.005
H) Lake Ontario	0.122*/(Inf.)	0.074*/(Inf.)	0.101*/(Inf.)	0.139*/(Inf.)	0.071*/(Inf.)	0.149*/(Inf.)	0.075*/(Inf.)	***0.055*/(Inf.)***	0.043 ± 0.004
Mean (2001– 2005)	0.139 ± 0.011	0.063 ± 0.018	0.074 ± 0.021	0.106 ± 0.015	0.065 ± 0.020	0.121 ± 0.008	0.078 ± 0.020	0.104 ± 0.012	***0.076 ± 0.008***

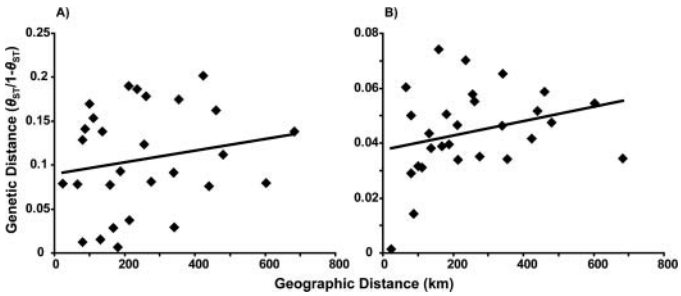

FIGURE 2. Mantel (1967) regression analyses of the pairwise relationships between genetic distance ($\theta_{ST}/1 - \theta_{ST}$) and geographic distance (km) for Yellow Perch spawning samples in **(A)** 2001–2005 ($y = 0.00007x + 0.09$, $R^2 = 0.036$, $P = 0.218$) and **(B)** 2009 ($y = 0.00003x + 0.04$, $R^2 = 0.078$, $P = 0.054$).

The AMOVA results indicated significant variation among age-cohorts at specific spawning sites (Table 6). Pairwise comparisons at Dunkirk (Table 8) and Monroe (Table 9) revealed significant genetic divergence among many of their age-cohorts. At both sites, the 2003 cohort markedly differed from the others (Tables 8, 9). The isolation-by-time test showed that genetic distance among the age-cohorts at Dunkirk was not explained by their separation times ($y = 0.0009x + 0.078$, $R^2 = 0.026$, $P = 0.67$).

Results from COLONY analyses (Jones and Wang 2010) indicated that spawning group samples averaged 20% full siblings in 2001–2005 and 17% in 2009 (Table 2). However, each family contained just a few individuals (2–3 individuals); there were multiple families present in each sample.

Yellow Perch spawning at Dunkirk averaged 36% full siblings overall, ranging from 13% in 2008 to 54% in 2004 (Table 4), and the numbers of siblings significantly varied among sampling years ($\chi^2 = 16.1$, df = 4, $P = 0.007$). Age-cohorts spawning at Dunkirk averaged 16% full siblings, ranging from 0% to 75%. Since our sample sizes were relatively low, this may reflect stochasticity. The values for Yellow Perch spawning at Monroe averaged just 3% full siblings among all age-cohorts, ranging from 0% to 11% for individual cohorts (Table 4).

DISCUSSION

This study identified consistent levels of heterozygosity and slight variations in allelic richness for spawning groups and

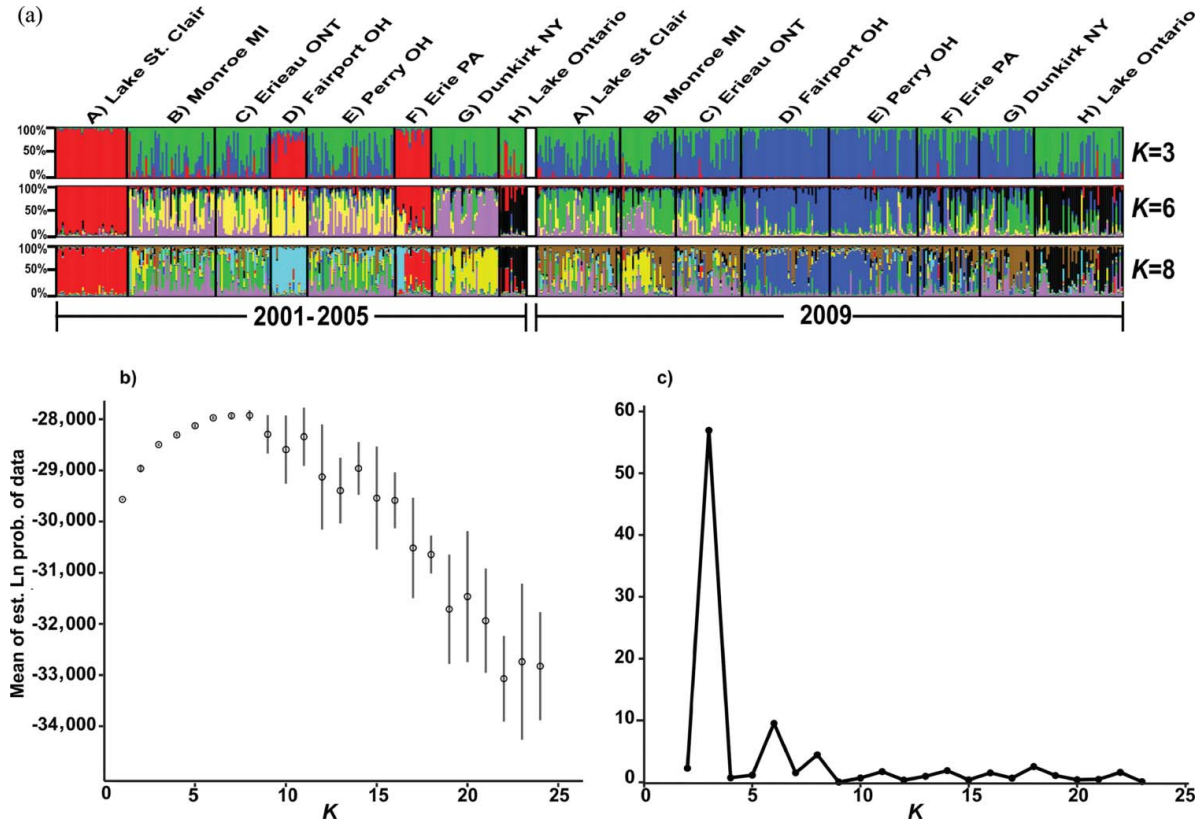

FIGURE 3. Population relationships from Bayesian STRUCTURE analysis (Pritchard et al. 2000; Pritchard and Wen 2004) and **(a)** a diagram showing $K = 3$, 6, and 8 population groups. The black lines separate spawning samples, and individuals are represented by thin vertical lines; colors show the estimated membership to a population group. The results for each possible K based on STRUCTURE HARVESTER (Earl and von Holdt 2012) are shown for **(b)** Ln(Pd); Pd = probability of data and **(c)** ΔK.

TABLE 6. Hierarchical analysis of molecular variance (AMOVA; Excoffier et al. 1992), showing the distribution of genetic variation among the spawning groups and between the two sampling periods (2001–2005 versus 2009), between the two sampling periods and among their eight spawning groups, and between the groups spawning at Monroe, Michigan, and Dunkirk, New York, and among their birth-year-cohorts. The loci that significantly supported each partition based on locus-by-locus AMOVA tests also are provided. An asterisk indicates a significant difference.

Source of variation	% Variation	df	Fixation index	*P*-value	Number of supporting loci
Among the eight spawning groups	< 0.01	7	< 0.001	0.598	5: *Svi2*, *Svi7*, *Svi17*, *YP17*, *Mpf3*
Between the two sampling periods (2001–2005 and 2009)	7.76	8	0.077	< 0.001*	All 15
Between the two sampling periods (2001–2005 and 2009)	1.71	1	0.017	< 0.001*	2: *Svi33*, *Mpf5*
Among the eight spawning groups	6.23	14	0.063	< 0.001*	All 15
Between spawning groups (Monroe and Dunkirk)	1.78	1	0.018	0.001*	4: *Svi3*, *Svi4*, *Mpf3*, *Mpf7*
Among birth-year-cohorts (born in 1998, 1999, 2001, 2002, 2003)	4.56	8	0.046	< 0.001*	14: *Svi3*, *Svi4*, *Svi7*, *Svi17*, *Svi33*, *YP13*, *YP17*, *Mpf1*, *Mpf2*, *Mpf3*, *Mpf4*, *Mpf5*, *Mpf6*, *Mpf7*

age-cohorts of Yellow Perch. The genetic composition of spawning groups diverged at geographic scales finer than known previously. Spawning groups and age-cohorts were characterized by temporal variation in genetic composition and somewhat inconsistent genetic structuring. This result indicates that individuals may not spawn in the same areas from year to year or may change locations within a spawning season. Yellow Perch spawning groups may experience conditions of differential reproductive success, whereby strong year-classes dominate the system and impact population structure. The population influence of strong year-classes renders the geographic delineation of MUs more difficult yet is important for understanding the harvest of Lake Erie Yellow Perch spawning groups.

Spatial and Temporal Genetic Diversity Patterns

The levels of genetic diversity recovered in the present study ($H_O = 0.56 \pm 0.08$) matched those determined for Yellow Perch spawning groups using the same 15 microsatellite loci across Lake Erie ($H_O = 0.56 \pm 0.08$; Sepulveda-Villet and Stepien 2011), the Great Lakes (0.55 ± 0.02; Sepulveda-Villet and Stepien 2012), and over the North American range (0.53 ± 0.02; Sepulveda-Villet and Stepien 2012). Diversity values for Yellow Perch appeared lower than those estimated for the related European Perch (based on just five microsatellite loci, $H_O = 0.79$, Demandt 2010; and for six loci, $H_O = 0.73$, Bergek and Olsson 2009; none of which were the loci used here). This difference between the two species may reflect bias from the limited number of loci selected for those

TABLE 7. Pairwise genetic divergences (θ_{ST} below the diagonal and exact *G* above the diagonal) of spawning Yellow Perch from Dunkirk, New York, on eastern Lake Erie sampled in six different collection years (1985, 2001, 2004, 2008, 2009, and 2010). An asterisk indicates a significant difference following sequential Bonferroni correction (Rice 1989) and Inf. = infinite.

Year (*N*) and mean	1985	2001	2004	2008	2009	2010
1985 (34)		Inf*	Inf.*	Inf.*	Inf.*	Inf.*
2001 (37)	0.037*		Inf.*	Inf.*	Inf.*	Inf.*
2004 (48)	0.056*	0.055*		Inf.*	Inf.*	Inf.*
2008 (30)	0.125*	0.138*	0.141*		Inf.*	Inf.*
2009 (30)	0.041*	0.072*	0.088*	0.105*		52.4*
2010 (36)	0.011*	0.041*	0.057*	0.113*	0.014*	
Mean ± SE	0.054 ± 0.019	0.069 ± 0.018	0.079 ± 0.017	0.124 ± 0.007	0.064 ± 0.016	0.047 ± 0.018

TABLE 8. Pairwise genetic divergences (θ_{ST} below the diagonal and exact G above the diagonal) of birth-cohorts at Dunkirk, New York (born in 1980–2008). An asterisk indicates a significant difference following sequential Bonferroni correction (Rice 1989) and Inf. = infinite.

Birth-cohort (N) and mean	1980	1981		1995	1996	1998	1999	2000	2001	2002	2003	2005	2006	2007	2008
1980 (9)		33.4	35.2	69.4*	55.4*	66.1*	48.3	60.8*	60.9*	74.3	Inf.*	Inf.*	24.0	35.7	29.3
1981 (13)	0.002		73.1*		67.6*	89.8*	53.4*	69.7*	96.4*	105.2	Inf.*	Inf.*	46.2	49.1*	46.4
1982 (12)	0.003	0.000	64.9*		71.5*	95.2*	50.1*	64.2*	99.8*	Inf.	Inf.*	Inf.*	29.7	45.9	45.3
1995 (9)	0.052	0.048	0.059		68.0*	41.9	37.3	78.7*	77.0*	77.0	Inf.*	Inf.*	69.2*	65.5*	61.1*
1996 (6)	0.070	0.068*	0.073	0.077		65.1*	34.0	104.9*	111.9*	Inf.	102.0*	120.7*	65.2*	83.3*	89.1*
1998 (14)	0.041	0.042*	0.062*	0.030	0.066		37.1	Inf.*	Inf.*	Inf.	Inf.*	Inf.*	74.5*	69.4*	78.4*
1999 (7)	0.031	0.024	0.036	0.009	0.034	0.011		73.4*	59.9*	67.3	70.0	70.2	39.0	50.8*	42.9
2000 (10)	0.057*	0.057*	0.062*	0.077*	0.142*	0.088*	0.067*		34.6	49.9	Inf.*	Inf.*	55.4*	Inf.*	59.4*
2001 (16)	0.044*	0.056*	0.065*	0.047*	0.117*	0.074*	0.042	0.006		30.1	Inf.*	Inf.*	63.0*	96.4*	78.4*
2002 (17)	0.040*	0.052*	0.048*	0.053*	0.093*	0.064*	0.046	0.033	0.014		Inf.*	Inf.*	69.9*	81.1*	79.0*
2003 (10)	0.117*	0.102*	0.120*	0.135*	0.172*	0.149*	0.079	0.115*	0.104*	0.125*		31.6	41.9	Inf.*	Inf.*
2005 (17)	0.092*	0.071*	0.101*	0.105*	0.150*	0.114*	0.062	0.082*	0.086*	0.106*	0.009		48.0	Inf.*	Inf.*
2006 (6)	0.000	0.018	0.008	0.071	0.098	0.071*	0.031	0.061	0.054*	0.054	0.070	0.058		41.0	34.1
2007 (14)	0.000	0.009	0.014	0.045*	0.094*	0.039*	0.031	0.057*	0.055*	0.043*	0.100*	0.071*	0.009		17.6
2008 (13)	0.011	0.016	0.027	0.063*	0.117*	0.054*	0.037	0.060*	0.067*	0.055*	0.111*	0.073*	0.025	0.000	
Mean ± SE	0.040 ± 0.010	0.040 ± 0.008	0.048 ± 0.010	0.062 ± 0.008	0.098 ± 0.010	0.065 ± 0.009	0.039 ± 0.005	0.069 ± 0.009	0.059 ± 0.008	0.059 ± 0.008	0.108 ± 0.010	0.084 ± 0.009	0.045 ± 0.008	0.041 ± 0.009	0.051 ± 0.009

TABLE 9. Pairwise genetic divergences (θ_{ST} below the diagonal and exact *G* above the diagonal) of birth-cohorts at Monroe, Michigan (born in 1997–2004). An asterisk indicates a significant difference following sequential Bonferroni correction (Rice 1989).

Birth-cohort (*N*) and mean	1997	1998	1999	2001	2002	2003	2004
1997 (8)		19.6	20.0	22.7	30.5	50.8*	30.3
1998 (18)	0.000		31.3	42.6	36.5	79.4*	53.4*
1999 (5)	0.000	0.019		22.4	30.5	40.2	35.5
2001 (11)	0.000	0.021*	0.006		29.1	52.0*	37.9
2002 (7)	0.001	0.014	0.004	0.010		28.4	20.5
2003 (12)	0.010	0.030*	0.015	0.024*	0.000		26.7
2004 (7)	0.000	0.022*	0.018	0.019*	0.000	0.000	
Mean ± SE	0.002 ± 0.002	0.018 ± 0.004	0.010 ± 0.003	0.013 ± 0.004	0.004 ± 0.002	0.013 ± 0.005	0.010 ± 0.004

studies. Genetic diversity of the Yellow Perch also was much lower than that of Walleye *Sander vitreus,* including spawning groups across Lake Erie (nine microsatellite loci; 0.70 ± 0.01; Strange and Stepien 2007), the Great Lakes (0.71 ± 0.011, Stepien et al. 2009), and the overall North American range (Stepien et al. 2009, 2010; Haponski and Stepien 2014), despite sharing about the same geographic range and belonging to the same family (Percidae).

The present study identified consistent levels of heterozygosity and slight variations in allelic richness between Yellow Perch spawning groups sampled across Lake Erie and between the two time periods (2001–2005 versus 2009). In contrast, allelic richness values were similar among spawning groups of Walleye across Lake Erie but differed in heterozygosity levels, being appreciably higher in the eastern basin than in the western basin (Strange and Stepien 2007; Stepien et al. 2012). Differences in the distribution of genetic diversity between the two percid species may be related to refugia and colonization histories, contemporary demographic differences, species-specific behavior during spawning, or a combination of these factors (Stepien et al. 2009, in press; Sepulveda-Villet and Stepien 2011, 2012).

In our study, allelic richness values fluctuated among the six sampling years and 15 birth-year-cohorts for the Dunkirk spawning group but did not follow an apparent pattern. In contrast, Yellow Perch spawning at Monroe displayed increased heterozygosity in recent birth-cohorts. Populations of other fishes exhibited temporal genetic stability in the number of alleles and heterozygosity values over generations, including Atlantic Salmon *Salmo salar* (Tessier and Bernatchez 2002; Lage and Kornfield 2006), Rainbow Trout *Oncorhynchus mykiss* (Heath et al. 2002), and Walleye (Stepien et al. 2012). However, populations of the Atlantic Cod *Gadus morhua* (Hutchinson et al. 2003) and the New Zealand Snapper *Pagrus auratus* (Hauser et al. 2002) underwent temporal changes, marked by declines in heterozygosity and the numbers of alleles. Those reductions were linked to high levels of exploitation from commercial and recreational fishing. The variations we observed among birth-cohorts likely reflected sampling stochasticity due to our small sample sizes, meriting caution in interpretation. Future research that examines genetic diversity and composition among birth-cohorts, along with their demographic characters, should employ larger numbers of samples. Such results would provide important information about the contribution of individual birth-cohorts to lakewide population genetic structure, diversity, and demography.

Genetic Divergence Patterns across Spatial and Temporal Scales

The present results show that the genetic compositions of Yellow Perch spawning groups differed across Lake Erie, to a greater degree and at a much smaller geographic scale than was known previously (also see Sepulveda-Villet and Stepien 2011, 2012). These fine-scale genetic demarcations also were recovered when morphological variation was analyzed among closely situated Yellow Perch spawning groups in Lake Erie (Kocovsky and Knight 2012; Kocovsky et al. 2013).

Kin recognition has been suggested as a behavioral factor that structures the spawning groups of the European Perch (Gerlach et al. 2001; Behrmann-Godel et al. 2006). European Perch in Lake Constance were found to aggregate with genetically related individuals, which grouped near other schools sharing genetic similarity (Gerlach et al. 2001). Olfactory recognition of related individuals played an important role governing schooling behavior (Behrmann-Godel et al. 2006). Whether kin recognition also structures the spawning groups of Yellow Perch may be important to know for understanding population structure in relation to MUs. Closely related individuals may avoid inbreeding by recognizing their kin and avoiding them at the time of fertilization, an idea that remains to be tested (see Stepien et al., in press).

Although the genetic composition of Yellow Perch spawning groups diverged among locations, this magnitude of difference was less in 2009 than in 2001–2005. The genetic divisions that distinguished the gene pools of the spawning groups varied between the two sampling time periods. In a similar pattern, European Perch differed in genetic composition among locations in Lake Erken, Sweden, showing significant fluctuations from year to year (Bergek and Olsson 2009). In comparison, Walleye spawning groups in Lake Erie exhibited both spatial and temporal consistency of genetic composition (Stepien et al. 2012).

It is likely that the population genetic patterns recovered for Yellow Perch are influenced by a combination of factors. First, the Yellow Perch from the second sampling period (2009) were collected at spawning time all in the same year, resulting in much less sampling variability than for the previous collection (that spanned 2001–2005; see Sepulveda-Villet and Stepien 2011). Second, the 2009 samples contained a preponderance of the prolific 2003 year-class (YPTG 2014). Research by Strange and Stepien (2007) and Stepien et al. (2012) hypothesized an increase in genetic connectivity of Walleye spawning groups along Lake Erie's southern shore during reproduction that year. The 2003 Yellow Perch year-class also may have been the product of greater genetic mixing among spawning groups (see Sepulveda-Villet and Stepien 2011; Kocovsky and Knight 2012; Kocovsky et al. 2013), resulting in the differences we observed.

Yellow Perch that were collected in different years at given spawning sites varied in genetic composition, yet overall diversity within spawning sites was relatively consistent. Similarly, Rainbow Trout exhibited temporal genetic fluctuations, with numbers of alleles and heterozygosity remaining relatively similar (Heath et al. 2002). Spawning groups of European Perch were significantly differentiated among years at four locations, with all sites remaining different (Bergek and Osslon 2009). Age-cohorts (sampled from 1988 to 1996) of the European White Seabream *Diplodus sargus* varied in heterozygosity and were highly divergent (Lefant and Planes 2002; Planes and Lefant 2002). Similar patterns were identified in populations of Kelp Bass *Paralabrax clathratus*, with adult and larval gene pools varying across a season of larval settlement (Selkoe et al. 2006). Significant temporal divergence was discerned across five collection years for a European Perch spawning group in Sweden from 1977 to 2000 (Demandt 2010). That study also discerned a significant relationship between genetic divergence and time (Demandt 2010), in contrast to our Mantel test results here for Yellow Perch. Both Kelp Bass and European Perch aggregate in kin-groups (Gerlach et al. 2001; Selkoe et al. 2006) and experience high fecundity and high mortality at early life history stages (type III survivorship). Those life history characters may lead to differential reproductive output for some adults, whereby a few individuals produce most of the surviving progeny (Hedgecock 1994), a situation that results in strong temporal genetic variability of populations due to some individuals passing on a greater number of genes to the next cohort. This scenario may also lead to a strong year-class effect, whereby certain cohorts dominate the spawning groups and impact the spatial and temporal structure of populations. Differential reproductive outputs and selection likewise may shape temporal genetic patterns of these Yellow Perch age-cohorts, collection years, and spawning groups. Further genetic investigations are needed to elucidate the mechanisms behind these patterns and to understand their impacts on stock structure.

CONCLUSIONS

An understanding of the genetic composition, diversity, and spatial stock structure is essential for effective management of Yellow Perch, given its economic, social, and ecological value in the Great Lakes ecosystem. Our genetic analyses identified insights into the dynamic nature of the spatial and temporal patterns underlying genetic population structure. Significant genetic differences support the hypothesis of populations structured at a scale finer than the current MUs for Lake Erie (Sepulveda-Villet and Stepien 2011, 2012; Kocovsky and Knight 2012; Kocovsky et al. 2013; YPTG 2014). Since multiple distinct genetic stocks are grouped together within a single MU, overexploitation of subgroups might occur. Our study identifies temporal fluctuations in the genetic compositions of spawning groups and age-cohorts that may make genetic-based MUs difficult to delineate and that requires further investigation. Further research to determine the extent and effects of annual variability on population structure, and to identify the influence of differential reproductive and recruitment success, is necessary for focusing management practices at a relevant biological scale. The present study illustrates the importance of continued genetic monitoring as a management tool and the importance of coupling this information with long-term demographic data (age structure, population size, movements, etc.) at finer scales than that of the current MUs. Continued sampling of fish populations, accompanied by analysis of their genetic data and genomic adaptations, will allow for further investigation into the extent and impacts of annual variation and differential reproduction success, which may facilitate conservation of genetic diversity.

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