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Microsatellite DNA Loci Reveal Genetic Structure of Yellow Perch in Lake Michigan

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Abstract.—The genetic population structure of yellow perch *Perca flavescens* was assessed, with a focus on spawning groups within Lake Michigan. Six microsatellite DNA loci were evaluated, which had heterozygosities ranging from 0.21 to 0.86 in samples from seven Lake Michigan locations and six others in the north-central United States. Genetic variation within samples was somewhat higher in Lake Michigan than in surrounding inland lakes. Genetic variation was also higher in the north-central United States than in a sample from the eastern United States. Exact tests for population differentiation and the fixation index R_{ST} indicated little differentiation among spawning groups within southern Lake Michigan or Green Bay (pairwise R_{ST} values, −0.005 to +0.014; $P > 0.05$ after sequential Bonferroni correction for multiple tests). However, spawning groups in Green Bay were distinct from those in Lake Michigan, and all inland locations were distinct from one another as well as from those in Lake Michigan ($P < 0.01$). All north-central U.S. samples were considerably different from the eastern U.S. sample (pairwise R_{ST} values 0.67–0.72). Although the sample sizes for northern Lake Michigan were limited, these fish grouped more closely with those from southern Lake Michigan than with those from Green Bay. There thus is evidence for the proposition that the yellow perch in Lake Michigan proper should be managed separately from those in Green Bay.

Yellow perch *Perca flavescens* is the only native Great Lakes fish that has sustained substantial uninterrupted commercial and sport harvests over the past century. The number of Lake Michigan yellow perch caught by anglers far exceeds that of other Great Lakes fish. Until recently, yellow perch composed approximately 85% of the lakewide sport fisheries catch (Great Lakes Fishery Commission 1995). Populations have fluctuated during the past several decades, with large declines in the 1960s followed by rebounds at most locations in the early 1980s (Francis et al. 1996). During the late 1980s and early 1990s, yellow perch recruitment declined at several Great Lakes locations, particularly southern Lake Michigan, prompting concern over the ability of the fishery to recover (Francis et al. 1996). Commercial fishing has been closed in the waters of southern Lake Michigan, quotas have been reduced in Green Bay, and sport harvests have been severely curtailed. The causes for the decline of yellow perch are under investigation, with a strong focus on factors related to the predemersal survival of young fish, including changes in predator and prey communities (Makauskas and Clapp 2001). The recent decline in yellow perch has prompted renewed interest in the potential genetic structuring of these populations within Lake Michigan (Clapp and Dettmers 2002).

Little is known about the population structure of yellow perch. The existence of independent breeding groups in individual lakes has been proposed on the basis of age structure comparisons, patterns of egg mass deposition, and experimental manipulations of egg masses (Aalto and Newsome 1989, 1990). In contrast, low variation within and among populations has limited the use of genetic markers for discriminating populations of yellow perch in the central United States (Leary and Booke 1982; Todd and Hatcher 1993; Billington 1996; Robillard et al. 1996; Fields et al. 1997). Leary and Booke (1982) found 19 allozyme loci to be effectively monomorphic (common allele frequency > 0.99) in samples from 13 sites in Green Bay and Lake Michigan. Robillard et al. (1996) found few polymorphisms in samples from four Lake Michigan sites in analyses of allozymes, mitochondrial DNA, and randomly amplified polymorphic DNA (RAPD). More variable genetic markers are needed to assess the potential genetic population structure among yellow perch in this geographical area.

The objective of the present study was to describe the genetic variation within and among yel-

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low perch populations from Lake Michigan and the surrounding region using microsatellite DNA markers. Microsatellite loci developed for another percid, walleye *Stizostedion vitreum*, were evaluated for their ability to detect genetic variation in yellow perch. Six loci were used to test the null hypothesis that there is genetic homogeneity (i.e., no genetic structure) among yellow perch spawning groups in Lake Michigan and Green Bay. The genetic patterns within the lake were contrasted with those found among several inland populations from the region. The presence of a genetic structure among the populations in Lake Michigan would be consistent with reproductive isolation caused by limited movement by individuals or fidelity to natal sites (i.e., returning to the place of birth to spawn) on the part of yellow perch, as has been shown for walleyes in the Great Lakes (Stepien and Faber 1998; McParland et al. 1999). Where reproductively isolated populations occur, they should be managed as separate stocks.

Methods

Sample collections.—Collections were obtained from 14 sampling locations, 7 from various spawning sites in Lake Michigan, 6 from inland lakes in the north-central United States, and one from Vermont in the eastern United States (Figure 1). In the spring of 2000, state natural resource agency personnel collected adult yellow perch in the spawning stage at two Green Bay and three southern Lake Michigan sites. Green Bay is the largest bay of Lake Michigan and is separated from the main body of the lake by an approximately 45-km opening with numerous islands. Fin clips stored in 95% ethanol or air-dried scales were obtained for genetic analyses. Additional samples were obtained from archived scale collections of adult perch from inland lakes. To assess the temporal stability of the data, replicate samples were taken from archived scale and spine collections from one southern Lake Michigan location (Milwaukee) sampled in 1998 and from Green Bay in 1997. Sample sizes ranged from 45 to 82. Extracted DNA from a previous genetics study was obtained for smaller collections from two northern Lake Michigan locations, Bailey's Harbor ($n = 15$) and Grand Traverse Bay ($n = 30$). These two samples were only included in certain analyses, as described below.

Genetic analysis.—DNA was extracted from tissue samples using 200 μL of a 5%-Chelex (Sigma Chemical Co., St. Louis, Missouri) solution following the protocol of Miller and Kapuscinski (1996). A single scale or a 2-mm^2 piece of spine or fin tissue was used for each preparation.

Thirteen microsatellite loci developed for walleyes were evaluated for cross-species utility in yellow perch: *Svi4, Svi6, Svi17, Svi18, Svi26,* and *Svi33* from Borer et al. (1999) and *Svi2, Svi3, Svi5, Svi7, Svi14, Svi16,* and *Svi20* from Eldridge et al. (2002). Microsatellite amplification via the polymerase chain reaction (PCR) was performed in a 96-well plate. Each 15-μL PCR reaction contained 6 μL of Chelex extraction as the DNA template, 0.4 μM each of the forward and reverse primers for one locus, 0.25 mM of each deoxynucleotide triphosphate, 2.0 mM $MgCl_2$, and 0.5 units *Taq* polymerase and 1× manufacturer's reaction buffer (Promega, Madison, Wisconsin). One primer of each pair was labeled with a fluorescent dye (Fam, Hex, or Tet). Amplification was carried out in a Hybaid Omn-E thermocycler (ThermoHybaid, Franklin, Massachusetts) using the following protocol: 5 min initial denaturation at 95°C; 10 cycles of 30 s denaturation at 94°C, 45 s annealing at 48°C, and 45 s elongation at 72°C; 25 cycles with the same conditions except for a reduction of the annealing temperature to 89°C; and a final elongation of 10 min at 72°C.

PCR products were visualized in two ways. To confirm the amplification of products and obtain rough estimates of product size, the products were visualized on a 14-cm × 16-cm nondenaturing 8%-acrylamide gel stained with ethidium bromide. To score alleles, the products of individual PCR reactions were pooled and electrophoresed on an ABI Prism 377 DNA sequencer (Perkin-Elmer Applied Biosystems) at the Advanced Genetic Analysis Center, University of Minnesota, St. Paul. Each lane contained an internal size standard for allele sizing. Genotypes were determined using Genescan and Genotyper software (PE Applied Biosystems 1996a, 1996b). Each plate contained a negative control without DNA to detect potential PCR contamination, and each gel contained a positive control using a sample that had previously been genotyped to standardize allele scoring among gels.

Data analysis.—Using six polymorphic loci identified in the initial screening, we quantified the within-population genetic variation as the number of alleles per locus in each sample and the observed and expected heterozygosities. Conformity with Hardy–Weinberg expectations was tested using exact tests (Guo and Thompson 1992). To assess among-population genetic variation, exact tests were performed for population differentiation (Ray-

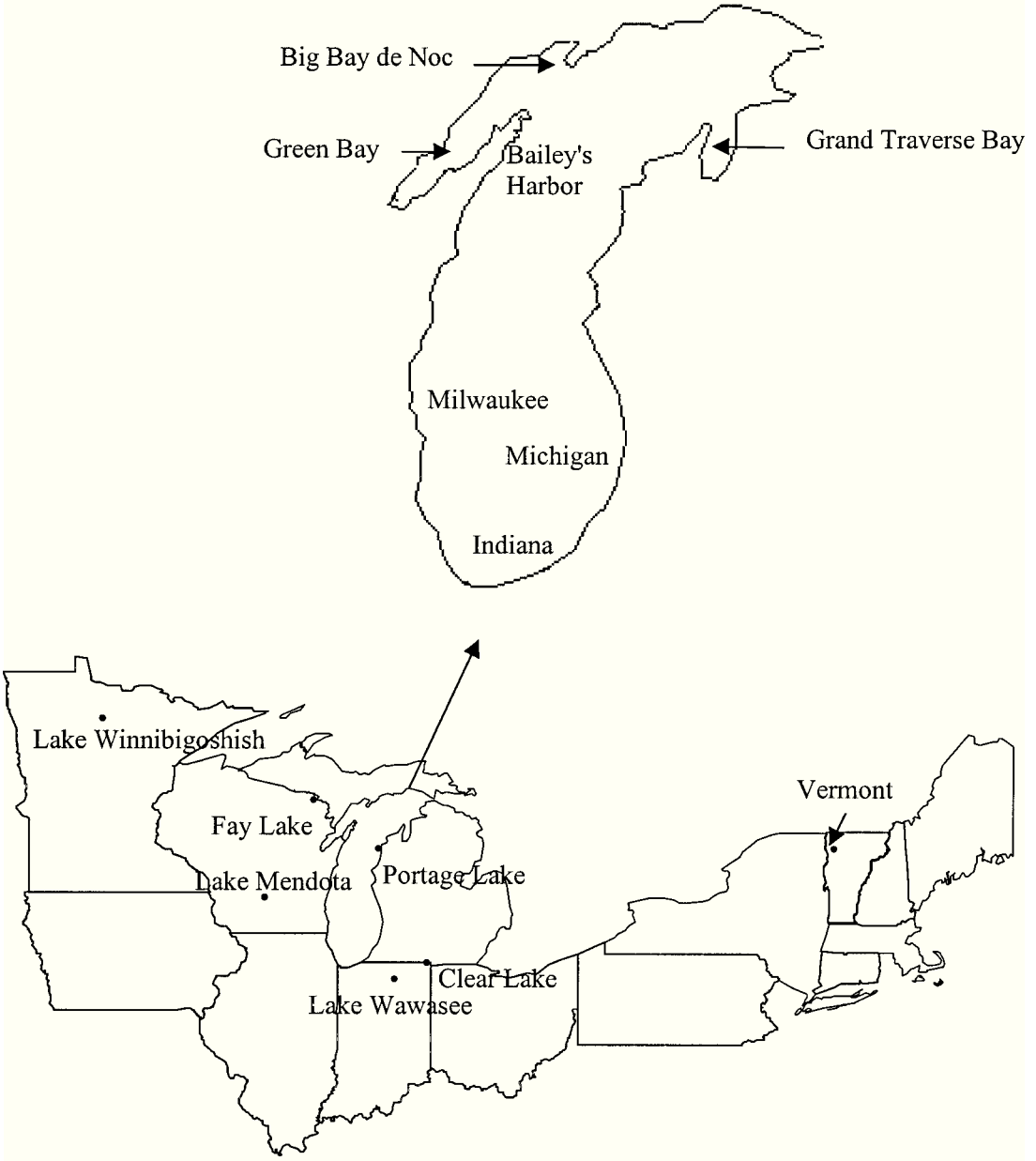

FIGURE 1.—Yellow perch sampling locations in Lake Michigan and Green Bay (upper map) and elsewhere in the north-central and eastern United States (lower map), with sample size and year of collection in parentheses: southern Green Bay (60, 1997; and 52, 2000); Big Bay de Noc (51, 2000); Milwaukee (59, 1998; and 76, 2000); Indiana (82, 2000); Michigan (58, 2000); Grand Traverse Bay (30, 1995); Bailey's Harbor (15, 1995); Lake Winnibigoshish (59, 1996) and Lake Mendota (70, 1993) in the Mississippi River drainage; Fay Lake (45, 1998), Portage Lake (61, 1999), and Lake Wawasee (74, 1997) in the Lake Michigan basin; Clear Lake (60, 1992) in the Lake Erie basin; and Lake Champlain, Vermont (45, 1998) in the St. Lawrence River drainage.

mond and Rousset 1995) between each pair of locations under the null hypothesis of identical allelic distribution between samples. These analyses were conducted using the software program Tools for Population Genetic Analysis (available from Mark Miller, Utah State University, http://bioweb.usu.edu/mpmbio/index.htm). Population structure was assessed by estimating values of R_{ST}, an analog of

TABLE 1.—Genetic variation at six microsatellite loci among yellow perch from 14 sampling locations. For each location, values are given for sample size (n), number of alleles (A), frequency of the most common allele (f; size in base pairs indicated in parentheses), and observed (H_o) and expected heterozygosity (H_e). The means in the next-to-last column are for all locations except Vermont. See Figure 1 for information on sampling locations.

	Lake Michigan							Other north-central U.S. lakes							
	Green Bay			Southern main lake											
Locus	Green Bay (1997)	Green Bay (2000)	Big Bay de Noc	Milwaukee (1998)	Milwaukee (2000)	Indiana	Michigan	Lake Mendota	Fay Lake	Portage Lake	Lake Wawasee	Clear Lake	Lake Winnibigoshish	Mean	Vermont
Svi2															
n	44	51	50	57	74	82	58	67	45	51	74	59	54		42
A	3	3	3	4	3	4	4	2	2	5	2	4	2	3.2	6
f (214)	0.37	0.40	0.46	0.69	0.67	0.75	0.66	0.25	0.70	0.49	0.36	0.28	0.03		0.14
H_o	0.57	0.37	0.47	0.47	0.44	0.54	0.51	0.10	0.04	0.58	0.03	0.14	0.04	0.33	0.62
H_e	0.57	0.42	0.50	0.55	0.48	0.48	0.45	0.10	0.04	0.61	0.03	0.14	0.04	0.34	0.64
Svi3															
n	43	20	31	50	42	73	58	64	45	55	68	33	39		35
A	5	5	5	6	3	5	5	4	3	6	5	2	6	4.6	4
f (141)	0.93	0.88	0.89	0.90	0.94	0.91	0.89	0.85	0.97	0.79	0.64	0.99	0.90		0.77
H_o	0.14	0.25	0.16	0.20	0.12	0.15	0.20	0.26	0.09	0.38	0.54	0.03	0.15	0.21	0.37
H_e	0.13	0.24	0.21	0.19	0.11	0.16	0.21	0.27	0.08	0.37	0.55	0.03	0.19	0.21	0.20
Svi4															
n	41	51	50	29	73	66	55	67	44	56	68	40	57		41
A	20	17	15	11	17	21	15	12	11	17	15	10	12	14.8	5
f (160)	0.15	0.16	0.14	0.28	0.31	0.21	0.28	0.26	0.06	0.21	0.23	0.20	0.06		0.01
H_o	0.90	0.90	0.88	0.93	0.88	0.82	0.93	1.00	0.89	0.84	0.90	0.71	0.88	0.88	0.10
H_e	0.90	0.88	0.89	0.86	0.85	0.89	0.87	0.85	0.83	0.90	0.84	0.83	0.79	0.86	0.10
Svi6															
n	54	44	41	36	59	70	54	59	39	51	74	45	42		45
A	22	19	21	18	23	26	21	14	10	30	19	12	13	19.1	8
f (178)	0.08	0.02	0.07	0.44	0.53	0.36	0.44	0.01	0.00	0.12	0.10	0.44	0.00		0.00
H_o	0.96	0.98	0.90	0.83	0.78	0.82	0.76	0.90	0.90	0.98	0.92	0.83	1.00	0.89	0.59
H_e	0.86	0.87	0.88	0.77	0.72	0.83	0.79	0.84	0.76	0.95	0.90	0.74	0.85	0.83	0.56
Svi7															
n	58	44	39	45	64	64	58	61	37	42	66	53	56		38
A	5	6	5	4	4	5	4	3	2	4	3	2	4	3.9	3
f (186)	0.62	0.61	0.69	0.89	0.85	0.88	0.92	0.89	0.27	0.75	0.91	0.98	0.50		0.15
H_o	0.57	0.45	0.43	0.22	0.25	0.25	0.15	0.23	0.38	0.47	0.15	0.04	0.45	0.31	0.27
H_e	0.50	0.51	0.47	0.20	0.28	0.23	0.15	0.21	0.40	0.40	0.17	0.04	0.52	0.31	0.21
Svi17															
n	55	41	41	47	64	62	58	57	35	35	57	51	51		43
A	8	6	10	7	8	7	9	7	5	6	7	5	5	6.9	3
f (156)	0.37	0.40	0.46	0.69	0.67	0.75	0.66	0.25	0.70	0.49	0.36	0.28	0.03		0.14
H_o	0.75	0.59	0.68	0.46	0.42	0.38	0.44	0.49	0.51	0.47	0.82	0.63	0.35	0.54	0.62
H_e	0.72	0.60	0.69	0.50	0.52	0.43	0.54	0.54	0.47	0.68	0.77	0.67	0.38	0.58	0.63
Mean, all loci															
A	10.5	9.3	9.8	8.3	9.7	11.3	9.7	7.0	5.5	11.3	8.5	5.8	7.0	8.7	4.6
H_e	0.61	0.59	0.61	0.51	0.49	0.50	0.50	0.47	0.43	0.65	0.54	0.41	0.46	0.52	0.39

the fixation index F_{ST} that accounts for the proposed mode of microsatellite mutation, using RSTCALC (Goodman 1997). A sequential Bonferroni correction for multiple comparisons was made for the exact tests and R_{ST} (Rice 1989; $\alpha = 0.05$, $k = 91$ [i.e., 91 pairwise comparisons among 14 samples]). Because of small sample sizes, the two samples from northern Lake Michigan were not used in these analyses.

Population relationships were examined further with the chord distance of Cavalli-Sforza and Edwards (1967) using the Gendist component of the PHYLIP software package (Felsenstein 2002). A neighbor-joining tree was constructed for the 14

larger samples from 1,000 bootstrap resamplings over loci using the software components Seqboot, Neighbor, and Consense to visualize the genetic structure among populations.

For Lake Michigan locations, the power of the loci was tested for correct assignment of fish to their source population using the jackknife procedure of the software WHICHRUN (Banks and Eichert 2000). For this purpose, the samples from the four locations in southern Lake Michigan were combined to form a single source population for that region, and the samples from Grand Traverse Bay and Bailey's Harbor were combined to form a single source population from northern Lake Michigan; the three samples from Green Bay formed a third hypothesized source. Assignments were made by determining which source population had the highest likelihood of producing the genotype of an individual fish, given the allele frequencies in each source and assuming Hardy–Weinberg equilibrium within each source population. Only five loci were used for this analysis because data for *Svi3* were lacking for Grand Traverse Bay and Bailey's Harbor.

Results

Microsatellite Variation

In preliminary studies, 12 of 13 *Svi* microsatellites amplified yellow perch DNA. Of the 12, 4 loci were monomorphic or had very low variation (*Svi14, Svi16, Svi18,* and *Svi20*), and 2 loci were variable but amplified inconsistently (*Svi5* and *Svi33*). The remaining 6 loci (*Svi2, Svi3, Svi4, Svi6, Svi7,* and *Svi17*) were used to assess genetic variation in the samples.

All six loci were polymorphic in all sample collections (Table 1). The mean number of alleles per locus in samples from north-central U.S. locations was 8.7 (range, 3.2–19.1). Mean expected heterozygosity per locus was 0.52 (0.21–0.86). These values were considerably lower in Vermont (4.6 and 0.39, respectively), the one location in the eastern United States. Higher numbers of alleles per locus and higher expected heterozygosity were generally observed in Lake Michigan samples than in those from inland lakes in the north-central United States (Table 1). One exception was Portage Lake, but this lake is connected to eastern Lake Michigan by a channel. Green Bay samples had similar numbers of alleles as but consistently higher heterozygosity than those in southern Lake Michigan. The higher heterozygosity in Green Bay was consistent across all six loci (Table 1).

TABLE 2.—Common alleles in Lake Champlain, Vermont, yellow perch that were rare or absent in the north-central United States. Shown are the highest frequencies of the given allele(s) for any one sampling location within the group (seven locations within Lake Michigan and Green Bay and six locations from other north-central U.S. lakes).

Locus	Allele size(s) (base pairs)	Allele frequency: Vermont	Allele frequency: Lake Michigan and Green Bay	Allele frequency: Other north-central U.S. lakes
Svi2	188, 190, 210	0.60	0.00	0.00
Svi4	114	0.95	0.06	0.00
Svi6	146, 148, 150, 152, 154	0.88	0.00	0.00
Svi7	190	0.84	0.04	0.01[a]
Svi17	180	0.59	0.01	0.00

[a] Allele found in Portage Lake and Lake Winnibigoshish.

Among north-central U.S. samples, there were only 20 alleles unique to a single location. The highest frequency of a unique allele was 0.15 for *Svi4* in the sample from Lake Wawasee. The sample from Portage Lake had the highest number of unique alleles (6), with frequencies of 0.01–0.11. In contrast, the sample from Vermont had many unique or high-frequency alleles that were rare in the north-central United States (Table 2). For all loci except *Svi3* (the locus with the lowest variation), Vermont had alleles at frequencies of 0.59–0.95 that were entirely absent from or occurring at frequencies of no more than 0.06 in any of the north-central U.S. samples. At least one of these high-frequency Vermont alleles was found in each Lake Michigan sample. The only other samples with these alleles were those from Portage Lake and Lake Winnibigoshish.

All loci in all samples conformed to Hardy–Weinberg expectations after sequential Bonferroni correction for multiple tests ($\alpha = 0.05$, $k = 84$ [6 loci $\times$ 14 samples]). Single-test *P*-values less than 0.05 were only observed in more than one sample for loci *Svi4* (three samples) and *Svi6* (two samples). Single-test *P*-values less than 0.05 were only observed for more than one locus in Lake Mendota and Clear Lake (two loci each). The widespread distribution of low *P*-values among samples and loci suggests that there is no general deviation from Hardy–Weinberg equilibrium at any sampling location or locus.

Genetic Population Structure

The various methods of assessing population differentiation all suggested similar relationships

among the sampling locations. Exact tests indicated no significant differences ($P > 0.05$ after sequential Bonferroni correction) in allelic distributions among samples from southern Lake Michigan (Milwaukee, Indiana, and Michigan), including the two samples taken from Milwaukee in separate years (1998 and 2000). Exact tests also indicated no difference between the samples from southern Green Bay in 1997 and Big Bay de Noc (in northern Green Bay). Here too, the two temporal samples from Green Bay showed no difference, demonstrating the stability of the data for Green Bay and Lake Michigan locations. However, the comparison between Green Bay in 2000 and Big Bay de Noc did show a significant difference ($P < 0.05$). Comparisons between pairs of locations from southern Lake Michigan and Green Bay showed significant divergence, as did all pairwise comparisons involving lakes outside of Lake Michigan (i.e., those between Lake Michigan and the inland locations and those between all inland locations; $P < 0.01$).

The R_{ST} index also provided no evidence for population structure within southern Lake Michigan or Green Bay (Table 3). Within these areas, comparisons between sample pairs were not significant, including Green Bay in 2000 and Big Bay de Noc. Like the exact tests, the values of R_{ST} indicated significant differences between pairs from southern Lake Michigan and Green Bay and between all pairs of inland lakes ($R_{ST} > 0$, $P < 0.05$ after sequential Bonferroni correction). However, R_{ST} was not significantly greater than zero for three comparisons between Lake Michigan and inland lake samples, namely, Green Bay in 1997 and Fay Lake, Green Bay in 1997 and Lake Winnibigoshish, and Indiana and Lake Wawasee (Table 3). By contrast, the fixation index F_{ST} was significant for all of these comparisons (data not shown). Fay Lake drains into Green Bay and Lake Wawasee drains into southern Lake Michigan; Lake Winnibigoshish, however, is in the upper Mississippi River watershed.

Genetic distances and the resulting tree construction illustrate the genetic similarity of two groups of samples (Table 3 and Figure 2). Very small genetic distances were found among southern Lake Michigan locations (0.007–0.010) and among Green Bay locations (0.011–0.015) (Table 3). Locations within each of these groups were adjacent on the tree diagram (Figure 2). The Green Bay samples, however, were quite distinct from those of southern Lake Michigan. The genetic distances between Green Bay and the inland locations

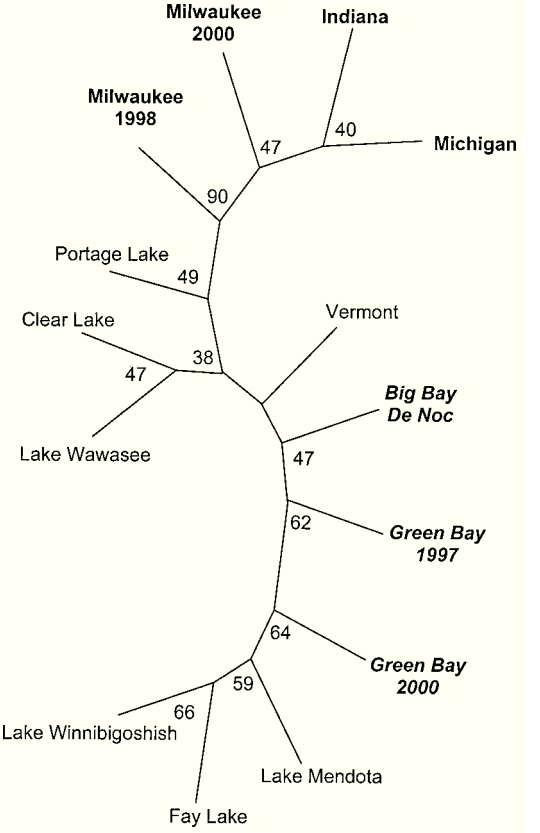

FIGURE 2.—Tree diagram constructed from the genetic distance matrix using the chord distance of Cavalli-Sforza and Edwards (1967) for samples of yellow perch from 14 locations. Locations in southern Lake Michigan are in bold type and those in Green Bay in bold italics (see Figure 1 for further information on sampling locations). The numbers at the forks are the percentages of 1,000 bootstrap resamplings that produced trees with the same grouping of sampling locations. Branch lengths are not proportional to genetic distances (see Table 3 for distance values).

from various drainages (0.019–0.048, excluding Vermont) were similar to those between pairs from Green Bay and southern Lake Michigan (0.024–0.037) (Table 3). On the tree diagram, the Green Bay sampling locations clustered on a separate branch from that containing the southern Lake Michigan locations (Figure 2).

Three major groupings were formed from all samples both within and outside of Lake Michigan (Figure 2). One branch contained the Green Bay locations along with Fay Lake, which is in the Green Bay watershed, and the two Mississippi drainage locations, Lakes Mendota and Winnibigoshish. A second branch contained the southern

Lake Michigan locations and the three lakes in the Lake Michigan (Portage Lake and Lake Wawasee) and Lake Erie (Clear Lake) watersheds. Finally, all of the north-central U.S. locations clustered together and were distant from the easternmost location in Vermont (genetic distances, 0.109–0.141).

Population Assignment

Individual fish from Green Bay and Lake Michigan were accurately assigned to their source populations when the latter were combined (Table 4). Eighty-five percent of Green Bay individuals were correctly assigned to Green Bay and 91–93% of Lake Michigan individuals to either southern or northern Lake Michigan. Within Lake Michigan, assignment accuracy was poor. Only 54% and 53% of the southern and northern fish, respectively, were assigned to their correct source, with most of the incorrect fish assigned to the other Lake Michigan source population.

Discussion

This study is the first extensive examination of genetic variation within and among populations of yellow perch in Lake Michigan and the surrounding region using microsatellite DNA markers. Although previous studies from this region using allozymes or mitochondrial DNA restriction fragment length polymorphisms (Leary and Booke 1982; Todd and Hatcher 1993; Robillard et al. 1996; Billington 1996; Fields et al. 1997) had not revealed much genetic variation, we found appreciable polymorphism at nuclear DNA microsatellite loci. Up to 36 alleles per locus were detected, and single-locus heterozygosity values ranged from 0.21 to 0.86. This level of genetic variation allowed evaluation of population structure within Lake Michigan and a comparison of the level of differentiation within the lake with that among the lake and regional inland populations. The spawning groups in southern Lake Michigan comprised a single, genetically homogeneous population, and those within Green Bay also appeared to be homogeneous. In contrast, the spawning populations in Green Bay were as divergent from those in southern Lake Michigan as those in noncontiguous inland lakes and should continue to be managed separately.

The lack of genetic divergence among spawning groups within southern Lake Michigan and Green Bay may be explained in part by the movements of adult yellow perch. The Indiana and Michigan samples were taken approximately 50 km apart. Although tagging studies in Lake Michigan have found that over one-third of recaptures occurred at distances greater than 40 km, even up to 3 years after tagging no more than 7% of recaptures occurred at distances greater than 100 km (S. Robillard, Illinois Natural History Survey, personal communication). Further, J. E. Marsden (University of Vermont, personal communication) showed that most yellow perch stayed within about 170 km of their tagging site and that 41% were captured within 1.6 km of their original site. The straight-line distances between Milwaukee and the other southern Lake Michigan sites and those between Green Bay sites are about 150 km, which would imply that there are limited movements among these areas. Adult movements, therefore, may not adequately explain the lack of population structure.

The movements of larval yellow perch may further enhance population mixing among the sample locations in southern Lake Michigan and Green Bay. Larval perch are pelagic and may move with currents, effectively mixing many of the offspring produced at various spawning sites. Netting studies have demonstrated significant offshore movements of larval yellow perch in southern Lake Michigan (Makauskas and Clapp 2001). Currents in Lake Michigan tend to flow southward along the western shore and northward along the eastern shore. In addition, distinct circular patterns are formed in the northern and southern sections of the lake (Beletsky et al. 1999). These currents may provide enough movement of larval perch to genetically homogenize the yellow perch population over broad regions of the lake, at least over generations.

The lack of genetic structure over broad areas within southern Lake Michigan and Green Bay contrasts with findings for some smaller lakes. Previous nongenetic studies have suggested that reproductively isolated stocks of yellow perch occur within Lochaber Lake, Nova Scotia (Aalto and Newsome 1989, 1990). In addition, tagging and genetic studies of the closely related Eurasian perch *Perca fluviatilis* have shown stock structure within Lake Windermere, United Kingdom (Kipling and Le Cren 1984; Bodaly et al. 1989). These studies suggest that in some systems perch either exhibit limited movements or return to their natal sites, leading to distinct populations. Lake Windermere is long and narrow, with distinct northern and southern basins. In contrast, Lake Michigan is wide and open, allowing for the development of mixing currents as described earlier. Green Bay is

TABLE 3.—Matrix of chord genetic distances (above diagonal; Cavalli-Sforza and Edwards 1967) and R_{ST} fixation indices (below diagonal; standard errors in parentheses) for all pairwise comparisons between samples of yellow perch from 14 locations. Measures were derived from data for six microsatellite loci. Values of R_{ST} in bold italic were not significantly greater than zero ($P > 0.05$ after sequential Bonferroni correction).

Location (year)	Green Bay (1997)	Green Bay (2000)	Big Bay de Noc	Milwaukee (1998)	Milwaukee (2000)	Indiana	Michigan
Green Bay (1997)		0.011	0.012	0.028	0.026	0.024	0.029
Green Bay (2000)	***0.012***		0.015	0.035	0.037	0.032	0.037
	(0.002)						
Big Bay de Noc	***−0.005***	***0.007***		0.027	0.027	0.023	0.030
	(0.001)	***(0.002)***					
Milwaukee (1998)	0.076	0.087	0.085		0.009	0.009	0.010
	(0.002)	(0.003)	(0.002)				
Milwaukee (2000)	0.087	0.117	0.092	***0.006***		0.009	0.008
	(0.002)	(0.003)	(0.002)	***(0.001)***			
Indiana	0.043	0.059	0.041	***0.012***	***0.014***		0.007
	(0.001)	(0.002)	(0.001)	***(0.001)***	***(0.001)***		
Michigan	0.075	0.089	0.079	***0.000***	***0.014***	***0.002***	
	(0.002)	(0.002)	(0.002)	***(0.001)***	***(0.001)***	***(0.000)***	
Lake Mendota	0.047	0.034	0.035	0.152	0.160	0.096	0.140
	(0.002)	(0.002)	(0.002)	(0.003)	(0.003)	(0.002)	(0.003)
Fay Lake	***0.023***	0.067	0.055	0.172	0.198	0.140	0.176
	(0.002)	(0.003)	(0.003)	(0.005)	(0.004)	(0.003)	(0.004)
Portage Lake	0.072	0.068	0.051	0.155	0.165	0.101	0.132
	(0.002)	(0.002)	(0.002)	(0.003)	(0.002)	(0.002)	(0.002)
Lake Wawasee	0.068	0.066	0.045	0.059	0.051	***0.028***	0.045
	(0.002)	(0.002)	(0.002)	(0.002)	(0.001)	***(0.001)***	(0.001)
Clear Lake	0.060	0.078	0.055	0.103	0.086	0.075	0.118
	(0.002)	(0.003)	(0.003)	(0.002)	(0.003)	(0.002)	(0.003)
Lake Winnibigoshish	***0.025***	0.068	0.052	0.167	0.177	0.137	0.173
	(0.002)	(0.003)	(0.002)	(0.004)	(0.004)	(0.002)	(0.004)
Vermont	0.677	0.708	0.685	0.717	0.701	0.700	0.716
	(0.003)	(0.002)	(0.002)	(0.002)	(0.002)	(0.002)	(0.002)

isolated from the main body of Lake Michigan, and its yellow perch are divergent from those in the lake. Within Green Bay, there is some indication of differentiation between the northern and southern bay, as indicated by a significant exact test between Big Bay de Noc and Green Bay in 2000. Differentiation within Green Bay may be consistent with the reduced likelihood of larval perch mixing by currents in this smaller body of water. However, no differentiation was found in the exact-test comparison with Green Bay in 1997 or in R_{ST} comparisons among Green Bay locations.

The large genetic differences between the eastern U.S. population and all north-central populations are consistent with the results of allozyme studies and presumably derive from the existence of separate glacial refugia for the populations from the two regions (Todd and Hatcher 1993). Todd and Hatcher (1993) found a clear distinction, including a fixed allelic difference, among populations east and west of (approximately) Lake Erie and suggested that there has been little postglacial dispersal across this boundary. The present results generally concur; however, there were no fixed differences. The presence of common ''eastern alleles'' almost exclusively in the Lake Michigan and Green Bay samples (Table 2; Portage Lake connects with Lake Michigan) suggests that the Great Lakes may be providing a conduit for some movement across this boundary.

The patterns of genetic variation among spawning groups found by this study suggest that the yellow perch in Lake Michigan should be managed under the assumption that there are at least two distinct stocks, a Green Bay stock and a southern Lake Michigan stock. In contrast, there is no genetic evidence for the presence of multiple stocks within these two regions. Lack of population differentiation may indicate substantial interbreeding among groups of fish (although the lack of detectable genetic structure does not preclude biologically meaningful stock structure; see Waples 1998). Therefore, within southern Lake Michigan, and likely within Green Bay, what may be single reproductive stocks are affected by management actions. The stock in southern Lake Michigan is under the jurisdiction of management agencies from four different states. These agencies should

TABLE 3.—Extended.

Location (year)	Lake Mendota	Fay Lake	Portage Lake	Lake Wawasee	Clear Lake	Lake Winnibigoshish	Vermont
Green Bay (1997)	0.027	0.034	0.027	0.035	0.037	0.029	0.120
Green Bay (2000)	0.019	0.030	0.034	0.033	0.048	0.026	0.125
Big Bay de Noc	0.030	0.042	0.023	0.034	0.039	0.041	0.109
Milwaukee (1998)	0.051	0.060	0.024	0.039	0.035	0.071	0.118
Milwaukee (2000)	0.055	0.061	0.026	0.040	0.035	0.068	0.120
Indiana	0.051	0.058	0.025	0.040	0.037	0.067	0.115
Michigan	0.057	0.068	0.025	0.039	0.036	0.075	0.121
Lake Mendota		0.039	0.050	0.034	0.048	0.025	0.135
Fay Lake	0.186 (0.005)		0.059	0.058	0.069	0.032	0.138
Portage lake	0.097 (0.002)	0.125 (0.002)		0.040	0.044	0.064	0.124
Lake Wawasee	0.064 (0.001)	0.173 (0.003)	0.064 (0.002)		0.034	0.052	0.136
Clear Lake	0.065 (0.003)	0.214 (0.007)	0.155 (0.002)	0.063 (0.001)		0.062	0.129
Lake Winnibigoshish	0.089 (0.002)	0.049 (0.003)	0.144 (0.002)	0.154 (0.002)	0.109 (0.003)		0.141
Vermont	0.722 (0.002)	0.703 (0.002)	0.668 (0.002)	0.690 (0.002)	0.709 (0.002)	0.678 (0.003)	

coordinate their regulations and management decisions because impacts on the waters of one state will affect the common perch population (Francis et al. 1996). The Yellow Perch Task Group formed by the Lake Michigan Committee of the Great Lakes Fishery Commission provides an appropriate venue for information sharing and coordinated management of this shared resource (Makauskas and Clapp 2001).

TABLE 4.—Likelihood-based population assignments for yellow perch from Lake Michigan based on five microsatellite loci (i.e., with *Svi3* removed; see Methods). Green Bay samples consist of samples from Green Bay in 1997 and 2000 and Big Bay de Noc; southern Lake Michigan samples consist of samples from Milwaukee in 1998 and 2000, Indiana and Michigan; northern Lake Michigan samples consist of samples from Bailey's Harbor and Grand Traverse Bay.

	Assigned source population		
Known sample	Green Bay	Southern Lake Michigan	Northern Lake Michigan
Green Bay	0.85	0.06	0.09
Southern Lake Michigan	0.07	0.54	0.39
Northern Lake Michigan	0.09	0.38	0.53

The Green Bay spawning groups are distinct from those in Lake Michigan, which supports their management as separate stocks. It has long been noted that the characteristics of the yellow perch populations in Green Bay and Lake Michigan differ (e.g., Wells 1977). Wisconsin currently regulates its sport and commercial fisheries differently in Green Bay and Lake Michigan waters, although Michigan does not (Makauskas and Clapp 2001). The reproductive isolation of the Green Bay and Lake Michigan stocks may have allowed these stocks to develop biological differences (e.g., fecundity and growth rates) that affect their response to exploitation. Population modeling and harvest management should continue separately for these two stocks (Wisconsin Department of Natural Resources 1995). The strong differentiation between the Green Bay and Lake Michigan populations provided reasonably accurate determination of source populations, with 85–93% correct assignment when northern and southern Lake Michigan were combined (Table 4). This ability may be use-

ful for enforcement of harvest regulations specific to the two areas.

Insufficient samples were available to make conclusive recommendations concerning the entire extent of Lake Michigan. When the two northern Lake Michigan samples were included in a tree diagram, they clustered with southern Lake Michigan rather than Green Bay locations (data not shown) despite the geographic closeness of the northern locations to Green Bay (Figure 1). Within Lake Michigan, the southern and northern individuals were correctly assigned to their source population at rates of only 54% and 53%, respectively (Table 4), which is indicative of the genetic similarity between the northern and southern samples. However, in a preliminary study using more loci but fewer samples, exact tests indicated differentiation between Grand Traverse Bay and Milwaukee in 1998 ($P < 0.05$ after sequential Bonferroni correction). Major currents would tend to support partial isolation of the northern and southern portions of the lake. Grand Traverse Bay in particular provides for potential isolation of yellow perch from the currents of the open area of the lake. Additional samples with increased numbers of individuals should be examined to make further recommendations concerning Lake Michigan.

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