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[Article]

Genetic Assessment of Lake Sturgeon Population Structure in the Laurentian Great Lakes

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Abstract.—Many populations of lake sturgeon *Acipenser fulvescens* have decreased in size throughout the Great Lakes basin. To implement management strategies such as stocking, it is important to understand the genetic structure of lake sturgeon spawning populations. Lake sturgeon from 27 spawning locations (25 from the Great Lakes basin and 2 from the Hudson Bay drainage) were analyzed using 12 microsatellite loci. Population structure was detected at different spatial scales. At the largest scale, consistent genetic breaks were observed among three clusters of spawning populations: (1) Hudson Bay–northern Lake Superior, (2) southern Lake Superior, and (3) the rest of the Great Lakes. These clusters were identified using a Bayesian approach that does not define the populations a priori. Within each of the three clusters, sublevels of genetic structure were detected. These sublevel clusters accounted for 8.82% of the genetic variation ($P < 0.000$), while differences among populations within the clusters accounted for 3.72% of the genetic variation ($P < 0.000$). At the smallest scale, significant genetic differentiation was detected between most sampled locations through pairwise genetic differentiation index (F_{ST}) tests and pairwise contingency tests. Lake sturgeon showed greater genetic differentiation in Lake Superior than elsewhere, which could be due to the lake's bathymetry. The lower genetic resolution observed elsewhere in the Great Lakes could be due to more recent colonization events. The results can be used to delineate management units and to select appropriate donor populations for supplementation or reintroductions.

Lake sturgeon *Acipenser fulvescens* inhabit the Great Lakes basin, Hudson Bay drainage, and the Mississippi River system, and the Great Lakes represent approximately 25% of the species' range (Harkness and Dymond 1961). Lake sturgeon population abundances in each of the three major drainages are much reduced from historic levels (Hay-Chmielewski and Whelan 1997; Auer 1999a; Stewart and Watkinson 2004). Populations at many locations within the Great Lakes basin are estimated to be 1% of their historic sizes (Hay-Chmielewski and Whelan 1997). Declines have been attributed to overfishing, habitat loss, and the hydrological changes and migration impediments caused by dams (Auer 1999a). Although some of these problems have been solved, many lake sturgeon populations have not experienced a substantial increase in size, resulting in concern for the long-term viability of this species in the basin. Lake sturgeon are listed as either endangered or threatened in 19 of the 20 states within the species' historic range in the United States (Auer 1999a; Aadland et al. 2005). Lack of population recovery at some locations may be due to lake sturgeon life history characteristics, such as late age of sexual maturity (14–20 years for females: Harkness and Dymond 1961), intermittent spawning (females spawn approximately every 6 years: Harkness and Dymond 1961), and limited recruitment resulting from low numbers of spawning fish (as seen in white sturgeon *A. transmontanus*: Anders et al. 2002).

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Fishery management agencies in the basin are attempting to facilitate the recovery of lake sturgeon populations through regulations and habitat restoration measures (Welsh 2004), such as modification of flow regimes at hydropower facilities. Several agencies are interested in taking more active management approaches (e.g., stocking, fish transfers) for which genetic analyses are critical in guiding decisions. Populations across the entire Great Lakes system can be delineated using neutral microsatellite DNA markers to detect levels of genetic exchange between spawning locations. Identification of populations and subsequent grouping of genetically similar populations can be used to delineate management units and to help choose donor populations for stocking that will preserve existing genetic structure.

The objective of this study was to determine the genetic relationships of lake sturgeon at spawning locations throughout the Great Lakes basin in order to further our understanding about the number and distribution of genetic management units, which would facilitate the selection of donor populations used in stocking. The tested null hypothesis was that lake sturgeon represent a single panmictic population throughout the Great Lakes basin. Successful recaptures of marked lake sturgeon have shown that they are capable of long-distance movements; lake sturgeon captured in one of the five Great Lakes have subsequently been captured in a different lake within the system (Gunderman et al. 2004), making this hypothesis plausible. An alternative hypothesis is that lake sturgeon return with high fidelity to their natal rivers to reproduce. A few lake sturgeon have been captured, marked, and later recaptured at the same spawning location, which supports the possibility of spawning site fidelity (Lyons and Kempinger 1992; Auer 1999b). This hypothesis has also been supported by genetic data in lake sturgeon (McQuown et al. 2003; DeHaan et al. 2006) and other sturgeon species (e.g., Waldman et al. 2002; Wirgin et al. 2005). The research presented in this paper expands on existing lake sturgeon genetic studies to assess patterns of genetic differentiation on a large geographic scale using additional microsatellite loci. By examining genetic structure on a geographic scale that encompasses the majority of lake sturgeon spawning populations remaining in the Great Lakes basin, we will gain a better understanding about the delineation of genetic management units throughout the Great Lakes.

Methods

Sample collection.—Thirty-five spawning locations throughout the Great Lakes basin and the Hudson Bay drainage were sampled, and successful sampling occurred at 27 locations (Table 1; Figure 1). Pectoral or dorsal fin clips or sections of the pectoral fin ray from adult lake sturgeon were collected for genetic analysis. Samples from Lake Champlain represent two spawning sites (Lamoille and Winooski rivers). These samples were pooled to obtain an adequate sample size for Lake Champlain. Samples from four of the Great Lakes spawning locations (Menominee, Wolf, St. Lawrence, and Des Prairies rivers) were originally analyzed by McQuown et al. (2003) and were included in the data analysis. The two locations within the Hudson Bay drainage, the Mattagami River (originally analyzed by McQuown et al. 2003) and Rainy River–Lake of the Woods system (samples described in Rusak and Mosindy 1997), were also included in the study.

Sampling techniques consisted of bottom-set gill nets fished perpendicular to the current and baited setlines fished consistent with techniques described by Thomas and Haas (1999). Capture start and end date varied from year to year. Sampling was initiated at the beginning of the spawning run when water temperature reached 10°C or upon learning of the presence of adult lake sturgeon at the spawning grounds. Duration of capture effort in a particular river varied depending upon availability of resources but generally lasted from 1 to 2 weeks. All sampling was conducted during the spawning period. However, due to difficulty in accessing spawning adults at a few sites (Mattagami, Kaminstiquia, and Detroit rivers and Lake Champlain), samples from adults of unverified spawning condition were used from these locations. Set lines were baited with cut ciscoes *Coregonus artedi*, whole round goby *Neogobius melanostomus*, salmon roe, or squid. Gill nets and set lines were set during morning hours and lifted the next morning (i.e., a 1-night set). Gill-net sets were fished in the same general locations during all years; however, specific locations were not consistent due to changes in water velocity, water depth, stream morphology, and instream debris.

Laboratory techniques.—All populations were analyzed for variation at 13 microsatellite loci. Microsatellite data were available for 4 of the 13 loci in the four populations studied by McQuown et al. (2003). These samples were reanalyzed for variation at the remaining nine microsatellite loci.

For fish collected from locations not previously analyzed, genomic DNA was extracted from approximately 25 mg of each fin clip or fin ray by use of the Wizard SV 96 Genomic DNA Purification System (Promega), the DNeasy Tissue Kit (Qiagen), or the GenElute Mammalian Genomic DNA Miniprep Kit (Sigma). Thirteen disomic microsatellite loci with tetranucleotide repeat motifs (*AfuG9*, *AfuG56*, *AfuG63*,

TABLE 1.—Sampled locations, number of samples collected and analyzed, and sampling years in a study of lake sturgeon genetic structure in the Great Lakes and associated drainages. In the spawning column, Y indicates that samples were collected from spawning adults, and N indicates samples that were collected from adults for which spawning condition could not be confirmed.

Location	Collected samples	Analyzed samples	Sampling years	Spawning
Hudson Bay				
Mattagami River (Ontario [ON])	40	40	1997	N
Rainy River–Lake of the Woods (Minnesota [MN]–ON)	27	27	1988–1989	Y
Lake Superior				
Bad River (Wisconsin [WI])	148	136	2001–2003	Y
White River (WI)	45	43	2001–2003	Y
Pigeon River (MN–ON)	2	0	2003	N
Kaministiquia River (ON)	87	85	2001	N
Black Sturgeon River (ON)	58	57	2003	Y
Pic River (ON)	33	33	2002–2003	Y
Black River (ON)	1	0	2002	Y
Little Black River (ON)	0		2002	
White River (ON)	0		2003	
Michipicoten River (ON)	1	1	2003	Y
Batchawana River (ON)	7	6	2003	Y
Chippewa River (ON)	1	1	2003	Y
Goulais River (ON)	44	43	2000–2004 (excl. 2002)	Y
Lake Michigan				
Menominee River (Michigan [MI]–WI)	21	21	1995	Y
Wolf River (WI)	30	30	1995	Y
Lake Huron				
Mississaugi River (ON)	96	52	2001, 2003	Y
Nottawasaga River (ON)	8	8	2002–2003	Y
Spanish River (ON)	51	47	2003, 2005	Y
Thessalon River (ON)	3	3	2003	Y
Magnetawan River (ON)	0		2003	
Serpent River (ON)	0		2003	
Rifle River (MI)	0		2003	
Eastern Lake Nipissing (South River, ON)	36	35	2003	Y
Western Lake Nipissing (Sturgeon River, ON)	41	40	2001, 2003	Y
Lake Erie				
St. Clair River (MI–ON)	56	50	2002–2003	Y
Detroit River (MI–ON)	36	33	2000–2002	N
Lake Ontario–St. Lawrence River				
Lower Niagara River (New York [NY]–ON)	21	20	1999–2002	Y
Black River (NY)	11	11	2005	Y
Trent River (NY)	0			
Grasse River (NY)	38	28	2006	Y
St. Lawrence River (NY–Quebec [QC])	54	54	1995	Y
Des Prairies River (QC)	15	14	1994–1995	Y
Lake Champlain	37	25	1998–2001	N

AfuG74, *AfuG112*, *AfuG122*, *AfuG160*, *AfuG195*, *AfuG204* [Welsh et al. 2003]; *Afu68* [May et al. 1997]; *Afu68b* [McQuown et al. 2002]; *Aox27* [King et al. 2001]; *Spl120* [McQuown et al. 2000]) were amplified using the polymerase chain reaction (PCR). Ten nanograms of extracted DNA were amplified at 12 of the microsatellite loci (*AfuG9* excluded) in 10-μL reactions consisting of 20-mM tris-HCl (pH 8.4), 50-mM KCl, 0.8-mM deoxynucleotide triphosphates (dNTPs), 1.0–1.75-mM $MgCl_2$, 0.2-μM forward primer (labeled with 6-carboxyfluorescein [FAM], tetrachloro-6-carboxyfluorescein [TET], or hexachloro-6-carboxyfluorescein [HEX]), 0.2-μM unlabeled reverse primer, and 0.4 units of *Taq* DNA polymerase (enzyme number 2.7.7.7; IUBMB 1992). For locus *AfuG9*, 10-μL PCR reactions consisted of 50-mM tris-HCl (pH 8.3), 10-mM KCl, 5-mM $(NH_4)_2SO_4$, 0.2-mM dNTPs, 2-mM $MgCl_2$, 0.2-μM FAM-labeled forward primer, 0.2-μM unlabeled reverse primer, and 2 units of FastStart *Taq* DNA polymerase. BioRad PTC100 thermocyclers were used, and amplification parameters (excluding *AfuG9*, *AfuG56*, and *Spl120*) were as follows: 95°C for 1.5 min; 30 cycles of 95°C for 1.0 min, 52°C or 55°C for 45 s, and 72°C for 2.0 min; a plus-A extension of 60°C for 45 min; and a 4°C hold. Further optimization of *AfuG9* due to inconsistent amplification resulted in the following amplification parameters for this locus: 95°C for 4 min; 40 cycles of 95°C for 30 s, 52°C for 30 s, and 72°C for 45 s; 72°C for 7 min; and a 4°C hold. The following protocol was used for the amplification of *AfuG56* and

FIGURE 1.—Locations of spawning sites in the Great Lakes and associated drainages, where lake sturgeon were sampled for a study of population genetic structure.

Spl120 to eliminate the amplification of a secondary locus: 94°C for 1 min; 20 cycles of 92°C for 30 s and 70°C for 40 s (using a 0.5°C decrease in the second step for each cycle); 20 cycles of 92°C for 30 s and 60°C for 40 s (using a 1-s increase in the second step for each cycle); and a 4°C hold. Amplified samples were then diluted at ratios from 1:2 to 1:20 (depending on the locus), and 1 μL of diluted product was added to 4 μL of loading buffer (36% formamide, 12% loading dye, 1.4% 6-carboxy-x-rhodamine [ROX]-labeled 400HD ladder); at this point, loci were pooled into four groups. The amplified product was separated on a 5.5% acrylamide gel running at 2,600 V for 6,000 scans on a BioRad BaseStation. Gels were analyzed using the accompanying Cartographer software.

Statistical analyses.—Populations with fewer than 10 samples (Batchawana, Michipicoten, Chippewa, Thessalon, and Nottawasaga rivers) were excluded from the majority of analyses because accurate allele frequency estimates could not be obtained. These samples were, however, included in the STRUCTURE analysis (detailed later) because it is conducted on the individual level and can ignore population information.

Allelic frequencies were calculated and the occurrence of private alleles (i.e., alleles found in only one of the sampled populations) was detected. Genetic diversity within each population was measured as allelic richness (number of alleles corrected for differences in sample size; El Mousadik and Petit 1996) and heterozygosity. Allelic richness was calculated using the software FSTAT (Goudet 2001). The program Genetic Data Analysis (GDA; Lewis and Zaykin 2001) was used to test for differences between observed and expected heterozygosity values (Hardy–Weinberg equilibrium [HWE]) for each locus within each sampling location. Using the GDA software, all possible pairs of loci were tested for the nonrandom association of alleles (linkage disequilibrium [LD]) after eliminating confounding effects from loci that deviated from HWE. Significance of tests was assessed after a sequential Bonferroni correction for multiple comparisons (Rice 1989). Loci that consistently deviated from HWE in the majority of sampled populations were eliminated from subsequent analyses.

Genetic differentiation between each pair of spawning populations was measured using the Weir and Cockerham (1984) estimator of the genetic differentiation index F_{ST} (estimated in Arlequin software [Schneider et al. 2000]) and pairwise contingency tests of allele frequency heterogeneity (Raymond and

Rousset 1995) estimated in Tools for Population Genetic Analyses software (Miller 1997). Both measures are useful in testing the null hypothesis of panmixia, and the results of the pairwise contingency tests are useful in estimating the number of populations (Waples and Gaggiotti 2006). Values of F_{ST} can range from 0 to 1 (0 = no genetic differentiation; 1 = complete differentiation at all loci). The significance of pairwise F_{ST} comparisons was based on 1,023 permutations. For the pairwise contingency tests, 10 batches of 2,000 permutations each were run and 1,000 dememorization steps were used. Significance of both the pairwise F_{ST} and contingency tests was assessed after a sequential Bonferroni correction (Rice 1989). The F_{ST} values and their significance were also calculated for locations with multiple sampling years to test for temporal stability.

Visual analyses of the genetic relationships among spawning populations were conducted through the construction of a neighbor-joining tree based on the Cavalli-Sforza and Edwards (1967) chord distance in PHYLIP software (Felsenstein 2004). This distance measure was selected because simulation studies have shown that it is one of the most accurate genetic distance measures for microsatellite analyses (Takezaki and Nei 1996). Bootstrap values demonstrating statistical support for groupings in the tree were calculated based on 10,000 replicates.

A factorial correspondence analysis (FCA), which explains a maximal amount of genetic variation using a minimal number of factors, also provided a means for visualizing genetic relationships among spawning populations. The program GENETIX was used for the FCA analysis (Belkhir et al. 2002). Alleles were coded according to the method described by She et al. (1987). For each allele, an individual was coded as 0 (allele absent), 1 (heterozygous), or 2 (homozygous). Therefore, each allele is an independent variable, as opposed to other multivariate analyses that use a combined parameter (Roques et al. 2001). Individuals are then projected into a multidimensional space defined by the factors. Because of the large number of individuals analyzed, the centers of gravity for each population were instead projected.

A Bayesian approach for identifying population clusters was implemented using STRUCTURE software (Pritchard et al. 2000). Without using previous information about sampling location, STRUCTURE tests the likelihood of various numbers of population clusters (K), given the genetic data and based on HWE and LD. Values of K ranging from 1 to 23 were tested using five replicates for each value of K, a burn-in period of 10,000 iterations, and 50,000 Markov-chain Monte Carlo iterations after the burn-in period. An admixture model (describing the possibility of mixed ancestry in individuals) was assumed based on the level of admixture inferred from the data. It was also assumed that allele frequencies were correlated among populations. These assumptions were recommended by Falush et al. (2003) for the detection of subtle population structure. The $\log_e$(likelihood) values were plotted, and consistent genetic discontinuities were identified among the most likely values of K. Due to the large number of sampled spawning locations and STRUCTURE's reputed difficulty in detecting more than 10 populations (Pearse and Crandall 2004), the first run of STRUCTURE was conducted using all 27 spawning locations to detect the clusters at the largest spatial scale. Clusters were determined by identifying those populations that consistently grouped apart for several likely values of K. For each cluster detected in the first run, possible values of K (ranging from 1 to [the number of sampling locations within the cluster + 3]) were tested under the same assumptions as the initial analysis to allow detection of sublevel population structure (Evanno et al. 2005). Subclusters were also identified by observing consistent genetic discontinuities for several likely K values. Values of K exceeding the number of sampled locations were tested to allow for the possibility of multiple populations existing at a single location.

An analysis of molecular variance (AMOVA; Excoffier et al. 1992) was conducted for the clusters identified based on pairwise F_{ST} values, contingency tests, the neighbor-joining tree, the FCA, and the STRUCTURE analysis. The approach is similar to a standard analysis of variance but takes into account the number of mutational differences between genotypes. Through AMOVA, the amount of covariance due to differences between individuals within a population, differences between populations within a cluster, and differences between clusters can be assessed. Significance of the tests was based on 1,000 permutations.

Results

Within-Population Genetic Diversity

The total number of alleles observed at each locus ranged from 2 to 12 (Table A.1). Potential private alleles were observed in Lake Champlain, eastern Lake Nipissing, western Lake Nipissing, and the Rainy, Bad, White, Menominee, Wolf, and St. Lawrence rivers. All private alleles were observed at a low frequency (0.01–0.06). Average allelic richness of each population ranged from 2.76 (Grasse River) to 4.07 (St. Lawrence River). Average expected heterozygosity of each population ranged from 0.46 (Grasse River) to 0.63 (lower Niagara River), and the overall average was 0.56.

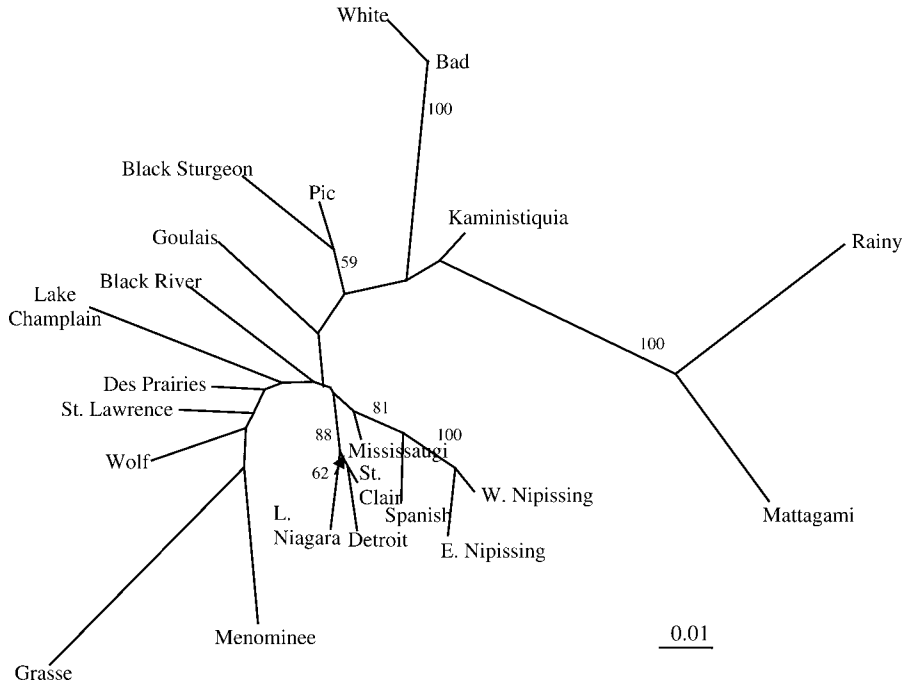

FIGURE 2.—Neighbor-joining tree based on Cavalli-Sforza and Edwards' (1967) chord distances determined from analysis of 12 microsatellite loci in 22 spawning populations of lake sturgeon from the Great Lakes basin (see Figure 1 for locations). Bootstrap values (percentage of replicates supporting the group) exceeding 50% are displayed.

Hardy–Weinberg Equilibrium and Linkage Disequilibrium

A significant heterozygote deficiency was observed in 15 of the 22 spawning populations at locus *AfuG122* ($P < 0.0003$) and in 4 populations (Mattagami, Bad, White, and Detroit rivers) at locus *Afu68* ($P < 0.0003$). These deficits are probably due to the presence of a null allele (Pyatskowit et al. 2001; Welsh and May 2006). Because a large number of populations deviated from HWE at *AfuG122*, this locus was dropped from all subsequent analyses. The St. Lawrence River population deviated from HWE at *AfuG122* and at two additional loci (*AfuG160* and *AfuG204*). Five spawning populations (Bad, Kaministiquia, Black Sturgeon, and Spanish rivers and Lake Champlain) had one to three locus pairs that exhibited LD ($P < 0.0003$), and such locus pairs were not consistent between populations.

Population Differentiation

Pairwise F_{ST} values ranged from 0.00 to 0.22 and demonstrated that most spawning populations were genetically distinct from each other (Table 2). The Black and Des Prairies rivers had the smallest sample sizes and probably lacked sufficient power to detect a significant difference. Goudet et al. (1996) demonstrated that pairwise F_{ST} tests have reduced power when unbalanced sampling schemes are used. Excluding these two populations, population comparisons with nonsignificant F_{ST} values included (1) Bad River versus White River; (2) western Lake Nipissing versus eastern Lake Nipissing; and (3) Detroit, St. Clair, and lower Niagara rivers. Mean F_{ST} for all 20 Great Lakes populations was 0.09. Populations from the Hudson Bay drainage were highly distinct from Great Lakes basin populations (Table 2). All F_{ST} values between temporal samples within the same sampling location were 0.01 or lower except in the Detroit River ($F_{ST} = 0.03$). No F_{ST} values between temporal samples were significant.

Pairwise contingency tests had a greater number of significant results than did F_{ST} analyses. This is probably due to the increased power of contingency tests with unbalanced sampling. The only nonsignificant pairwise contingency tests were those conducted for the Detroit and St. Clair rivers, the St. Clair and lower Niagara rivers, and the Des Prairies and St. Lawrence rivers (Table 2).

Identification of Population Clusters

Among the Great Lakes, Lake Superior had the greatest number of distinct population clusters. The

TABLE 2.—Chi-square values from pairwise contingency tests (above diagonal) and pairwise genetic differentiation index (F_{ST}) values (below diagonal) for 22 spawning populations of lake sturgeon in the Great Lakes basin. Comparisons in bold italic type were nonsignificant after sequential Bonferroni correction ($P > 0.02$ for contingency tests; df = 24; $P > 0.002$ for F_{ST} comparisons).

Population	Mattagami River	Rainy River	Bad River	White River	Kaministiquia River	Goulais River	Black Sturgeon River	Pic River	Menominee River	Wolf River	Mississaugi River
Mattagami River		121	199	200	190	207	206	213	220	217	221
Rainy River	0.10		187	187	182	220	174	173	203	195	196
Bad River	0.17	0.19		43	203	190	170	176	188	218	210
White River	0.19	0.22	***0.00***		188	175	164	164	174	196	220
Kaministiquia River	0.16	0.18	0.11	0.14		168	197	142	177	165	164
Goulais River	0.16	0.19	0.08	0.10	0.07		178	124	126	118	109
Black Sturgeon River	0.15	0.12	0.12	0.14	0.10	0.06		110	149	176	187
Pic River	0.16	0.14	0.11	0.13	0.06	0.05	0.03		116	137	108
Menominee River	0.21	0.21	0.13	0.17	0.11	0.07	0.08	0.06		70	93
Wolf River	0.20	0.22	0.14	0.16	0.13	0.05	0.08	0.07	0.04		79
Mississaugi River	0.17	0.20	0.13	0.15	0.11	0.03	0.07	0.06	0.05	0.02	
Eastern Lake Nipissing	0.18	0.20	0.13	0.14	0.10	0.04	0.08	0.06	0.09	0.06	0.03
Western Lake Nipissing	0.18	0.22	0.13	0.13	0.09	0.03	0.10	0.08	0.08	0.06	0.02
Spanish River	0.19	0.25	0.15	0.16	0.11	0.04	0.13	0.11	0.12	0.08	0.03
Detroit River	0.17	0.19	0.12	0.14	0.08	0.03	0.10	0.06	0.06	0.05	0.02
St. Clair River	0.17	0.17	0.10	0.12	0.08	0.03	0.07	0.04	0.04	0.04	0.02
Lower Niagara River	0.18	0.18	0.10	0.12	0.09	0.03	0.08	0.07	0.06	0.05	0.03
Black River	0.10	0.15	0.08	0.10	0.07	***0.02***	0.05	0.04	0.10	***0.05***	***0.03***
Grasse River	0.26	0.26	0.18	0.20	0.20	0.12	0.13	0.12	0.09	0.08	0.07
Des Prairies River	0.14	0.16	0.09	0.11	0.11	***0.03***	0.08	0.05	***0.04***	***0.03***	***0.02***
St. Lawrence River	0.19	0.19	0.15	0.17	0.13	0.05	0.09	0.07	0.04	0.03	0.04
Lake Champlain	0.15	0.16	0.14	0.16	0.14	0.08	0.10	0.08	0.12	0.09	0.07

neighbor-joining tree showed that the Bad and White rivers (south shore of Lake Superior) consistently grouped together (Figure 2) and the Pic and Black Sturgeon rivers (north shore) grouped together, albeit with less support. In general, longer branch lengths (indicating greater genetic distance) separated the spawning populations of Lake Superior from those of the other Great Lakes, and most spawning populations in Lake Superior did not group together, indicating substantial population genetic structure in this lake. The genetic distinctiveness observed in Lake Superior was diminished at the Goulais River, a spawning location that was more geographically proximate to the rest of the Great Lakes. In the remaining Great Lakes, lake sturgeon appeared to be more genetically similar; more populations grouped together in the neighbor-joining tree, and branch lengths were shorter (Figure 2). The tree also corroborated nonsignificant pairwise F_{ST} values by grouping spawning lake sturgeon from the Detroit, St. Clair, and lower Niagara rivers with high bootstrap support.

The FCA highlighted the differences within Lake Superior. The south shore contained spawning populations that were highly differentiated from all other Great Lakes populations, including others within Lake Superior (Figure 3). According to the FCA, spawning individuals in the Bad and White rivers had approximately the same level of genetic differentiation from other Great Lakes spawning populations as did spawning fish in the Hudson Bay drainage. Two less-distinct clusters were also observed within the remainder of the Great Lakes populations.

The STRUCTURE analysis revealed three upper-level clusters, which were further divided into sublevel clusters. Certain populations consistently grouped in different clusters for several of the most likely values of K (i.e., between 3 and 8; Figure 4A), allowing for the identification of three clusters. The three upper-level clusters were (1) Hudson Bay–northern Lake Superior (Mattagami, Rainy, Kaministiquia, Black Sturgeon, and Pic rivers); (2) southern Lake Superior (Bad and White rivers); and (3) remaining Great Lakes locations. Populations represented by only a single individual (Michipicoten and Chippewa rivers) did not group strongly with any given population and were instead split between two clusters. For the Michipicoten River individual, the highest membership coefficient was that for cluster 1 (0.55), followed by cluster 3 (0.38). For the Chippewa River individual, the highest membership coefficient was for cluster 3 (0.59), followed by cluster 1 (0.36). A similar pattern was also observed at other Lake Superior locations in the same geographic vicinity. The Goulais and Pic rivers had relatively low membership coefficients for the identified clusters: 0.65 for Goulais River fish in association with cluster 3 and 0.58 for Pic River fish in association with cluster 1.

Possible values of K were tested to identify sublevels of population structure within each of the three upper-

TABLE 2.—Extended.

Population	E. Lake Nipissing	W. Lake Nipissing	Spanish River	Detroit River	St. Clair River	Lower Niagara River	Black River	Grasse River	Des Prairies River	St. Lawrence River	Lake Champlain
Mattagami River	232	232	207	230	238	205	157	217	209	238	214
Rainy River	214	218	211	213	223	198	156	188	209	217	202
Bad River	209	206	220	209	212	191	156	225	163	201	187
White River	207	186	207	188	195	166	150	226	131	204	188
Kaministiquia River	187	173	187	199	201	161	122	196	133	201	189
Goulais River	141	117	130	116	125	94	77	204	81	176	129
Black Sturgeon River	193	210	226	179	184	168	114	199	155	212	179
Pic River	142	158	183	123	130	139	82	185	86	159	150
Menominee River	149	156	166	127	130	118	122	153	61	84	135
Wolf River	134	147	158	111	118	94	74	150	55	88	141
Mississaugi River	121	111	132	86	96	78	71	157	60	123	131
Eastern Lake Nipissing		48	138	102	103	107	110	178	102	150	137
Western Lake Nipissing	***0.01***		109	93	110	119	83	192	97	153	143
Spanish River	0.04	0.02		141	167	126	85	169	103	168	133
Detroit River	0.02	0.03	0.05		***22***	51	92	170	82	128	121
St. Clair River	0.02	0.03	0.06	***0.00***		***40***	85	170	77	150	142
Lower Niagara River	0.04	0.03	0.05	***0.02***	***0.01***		75	175	56	115	140
Black River	***0.03***	***0.03***	***0.03***	***0.03***	***0.03***	***0.03***		167	50	91	93
Grasse River	0.10	0.11	0.14	0.10	0.07	0.08	0.14		152	158	162
Des Prairies River	0.06	0.04	0.06	***0.04***	0.03	***0.02***	***0.01***	0.09		***32***	84
St. Lawrence River	0.06	0.05	0.07	0.04	0.03	0.02	0.05	0.06	***0.01***		143
Lake Champlain	0.07	0.08	0.10	0.07	0.05	0.07	***0.04***	0.11	***0.05***	0.06	

level clusters. Three sublevel clusters were identified within upper-level cluster 1 (Figure 5A): one sublevel cluster represented Hudson Bay, and two sublevel clusters represented northern Lake Superior. The Michipicoten River individual grouped with the Black Sturgeon and Pic rivers (membership coefficient = 0.75). A single sublevel cluster was identified in upper-level cluster 2, indicating that lake sturgeon of the Bad and White rivers in Lake Superior were not genetically distinct.

Two sublevel clusters were observed in the remainder of the Great Lakes (upper-level cluster 3; Figure 5B). However, the sublevel clusters were less discrete than those of Lake Superior, as indicated by the lower membership coefficients and the number of populations containing individuals with different memberships. This is probably due to STRUCTURE's lack of resolving power when genetic differentiation is low or moderate (Waples and Gaggiotti 2006), as was observed in these regions of the Great Lakes. The first sublevel cluster consisted primarily of individuals from the Goulais, Batchawana, Spanish, and Thessalon rivers and Lake Nipissing. The second sublevel cluster consisted of individuals from the Chippewa (membership coefficient = 0.82), Menominee, Wolf, Black, Grasse, St. Lawrence, and Des Prairies rivers and Lake Champlain. The Mississaugi, Nottawasaga, Detroit, St. Clair, and lower Niagara rivers contained an approximate equal mixture of individuals from the two clusters.

The results of the AMOVA showed that the subclusters identified by the STRUCTURE analysis maximized the percentage of variation between clusters and minimized the percentage of variation between populations within a cluster. Variation among clusters accounted for 8.82% of the total variation ($P < 0.000$), and variation among populations within clusters accounted for 3.72% of the total ($P < 0.000$). The remainder of the variation was due to differences among individuals within populations.

Discussion

Within-Population Genetic Diversity

Genetic diversity, as measured by allelic richness and heterozygosity, was relatively consistent among the different populations, despite substantial differences between populations in population size and status. The average expected heterozygosity across all populations was 0.56, which is consistent with the heterozygosity observed for most freshwater fishes (DeWoody and Avise 2000). This retention of genetic diversity may be due to the life history of the lake sturgeon. As observed in another long-lived species, the copper redhorse *Moxostoma hubbsi*, a long generation time may protect a species from a rapid loss of genetic diversity despite decreased population size (Lippé et al. 2006).

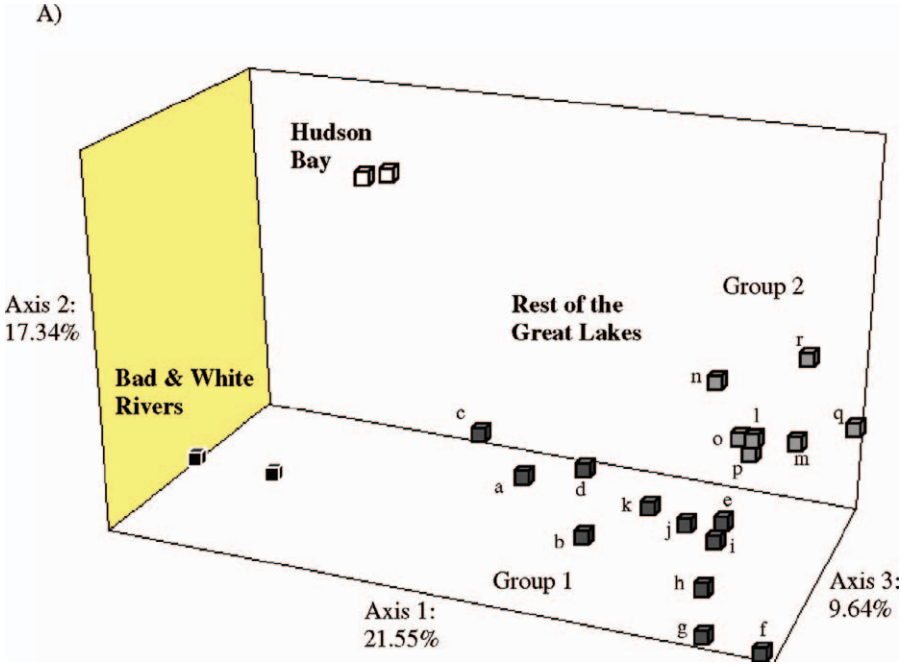

FIGURE 3.—Factorial correspondence analysis (FCA) based on 12 microsatellite loci in 22 spawning populations of lake sturgeon from the Great Lakes basin (see Figure 1 for locations); 49.16% of the total genetic variation is shown. Collections from the Bad and White rivers in the Lake Superior drainage (black cubes) are as different from the rest of the Great Lakes populations (dark and light gray cubes) as are the two Hudson Bay collections (white cubes). Axis 3 separates the other Great Lakes populations into two groups. Group 1 (dark gray cubes) includes (a) Kaministiquia River, (b) Goulais River, (c) Black Sturgeon River, (d) Pic River, (e) Mississaugi River, (f) eastern Lake Nipissing, (g) western Lake Nipissing, (h) Spanish River, (i) Detroit River, (j) St. Clair River, and (k) lower Niagara River. Group 2 (light gray cubes) includes (l) Menominee River, (m) Wolf River, (n) Black River, (o) Grasse River, (p) Des Prairies River, (q) St. Lawrence River, and (r) Lake Champlain.

Lake sturgeon from the Grasse River in Lake Ontario had the lowest genetic diversity, possibly due to a population bottleneck. This population includes both resident and migratory stocks because of a barrier located 12 river kilometers upstream (Carlson 1995), and the resident stock may have declined due to a decrease in accessibility of the St. Lawrence River.

The highest genetic diversity was observed at the St. Lawrence and lower Niagara River locations, despite the relatively small size of their respective spawning runs. Lake sturgeon sampled at the St. Lawrence River also had an excess of homozygotes at *AfuG160*, which could be due to inadvertent sampling of multiple populations, resulting in an apparent heterozygote deficit (i.e., Wahlund effect: Wahlund 1928). The St. Lawrence River population was sampled below the Moses–Saunders Dam, which impedes upstream migration and could result in congregation of multiple spawning populations. The representation of these multiple populations may also lead to the higher allelic richness observed at this location. The high heterozygosity observed in lake sturgeon from the lower Niagara River could be attributable to a recent recolonization event and the subsequent breeding with the remnant population (discussed in the next section).

Population Differentiation and Clustering

The majority of spawning populations within the Great Lakes basin were genetically distinct from each other, supporting the findings of McQuown et al. (2003) and DeHaan et al. (2006). Based on standard interpretations of F_{ST} (Wright 1978), the spawning locations in the Hudson Bay drainage and the Bad and White rivers in Lake Superior generally were highly differentiated (F_{ST} = 0.15–0.25) from others in the Great Lakes basin. The Kaministiquia River was moderately differentiated (F_{ST} = 0.05–0.15) from the rest of the Great Lakes spawning populations. Outside of Lake Superior, low to moderate levels of genetic differentiation were detected. Based on pairwise F_{ST}, lake sturgeon at most spawning locations can be considered different populations. Because of small sample sizes, however, pairwise F_{ST} comparisons

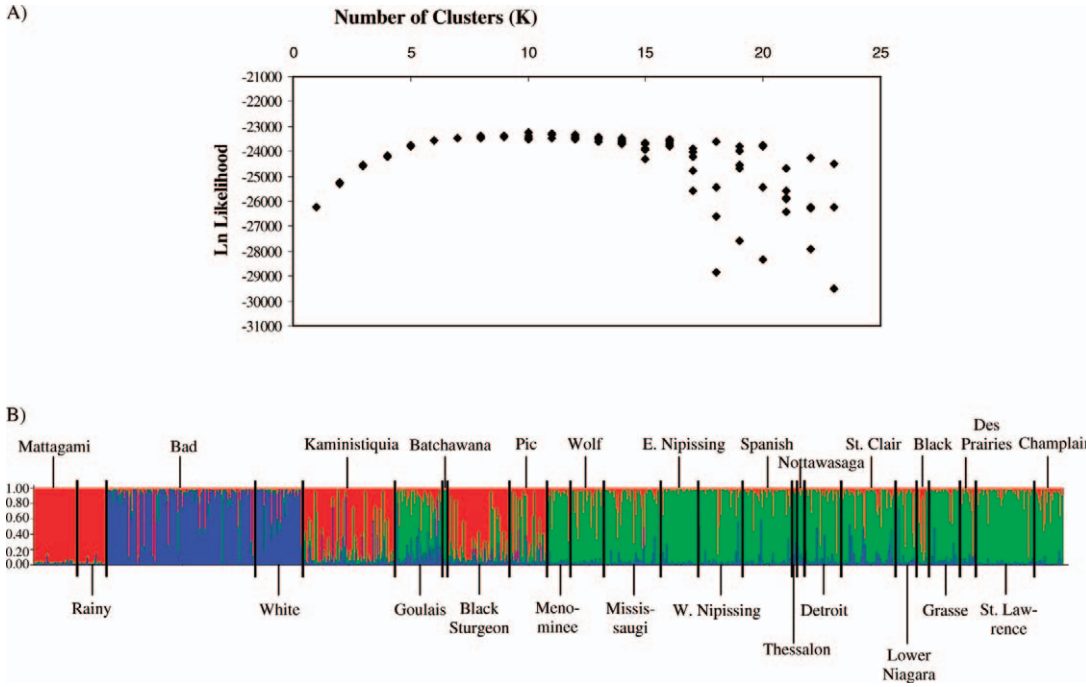

FIGURE 4.—Results from STRUCTURE analysis used to detect upper-level clustering based on 12 microsatellite loci in 27 spawning populations of lake sturgeon from the Great Lakes basin (see Figure 1 for locations): **(A)** $\log_e$(likelihood) values for cluster numbers (K) from 1 to 23 (5 replicates/cluster value) and **(B)** membership coefficients (y-axis) for each individual (represented by thin vertical lines) in relation to the three different upper-level clusters (represented as green, red, and blue). Dark black lines separate the sampling locations. Populations from which only one individual was sampled (Michipicoten and Chippewa rivers) are not visible on the plot but are described in the text.

lacked sufficient statistical power to detect significant differences between certain populations.

The pairwise contingency tests resulted in a greater number of significant comparisons. These tests confirmed that most lake sturgeon populations are genetically distinct, with a few exceptions. The lack of genetic differentiation between populations in the Detroit and St. Clair rivers may indicate that the Detroit River fish belonged to the St. Clair River spawning population. The samples obtained from the Detroit River were not from actively spawning individuals. Although spawning sites have been documented in the Detroit River, the sampled fish may have returned to the St. Clair River to spawn. Radiotelemetry of lake sturgeon indicated that fish migrated between the Detroit River and Lake St. Clair (Caswell et al. 2004). Alternatively, the fish collected in the Detroit River may have been St. Clair River individuals that now use the Detroit River for spawning.

Despite the large geographic distance between the Detroit River–St. Clair River system and the lower Niagara River, low levels of genetic differentiation were observed between these populations. The lower Niagara River population supported both commercial and recreational fisheries until the 1940s, when the population drastically declined and fisheries collapsed (Aug 1992). Between 1980 and 1994, only two documented lake sturgeon captures occurred in the lower Niagara River (Carlson 1995). Catch per unit effort in a recent assessment of the population indicated low lake sturgeon abundance in the river (Hughes et al. 2005). Juvenile age-classes dominated the population; ages ranged from 1 to 23 years, and the majority of fish were younger than age 10 (Hughes et al. 2005). These age data provide evidence for a new or recovering population. Recolonization of the lower Niagara River by individuals from Lake Huron or Lake Erie moving downstream or through the Welland Canal (although little evidence exists that the canal is a movement corridor [Daniels 2001]), could explain the lack of genetic differentiation observed between populations of the Detroit River–St. Clair River system and the lower Niagara River.

Although most lake sturgeon populations are

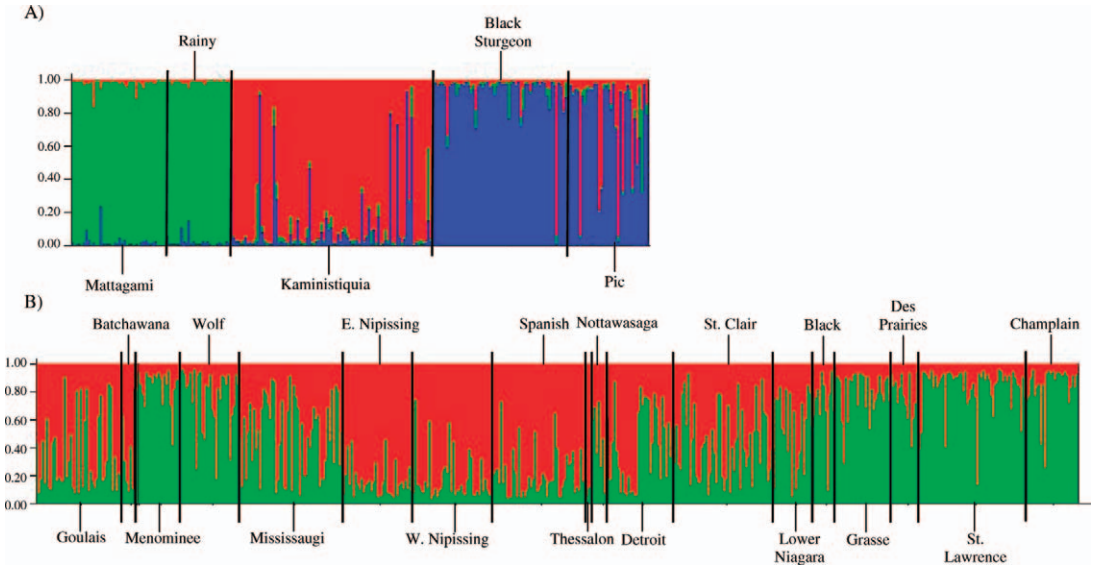

FIGURE 5.—Membership coefficients from STRUCTURE analyses to detect sublevel structuring within three upper-level clusters based on 12 microsatellite loci in 27 spawning populations of lake sturgeon from the Great Lakes basin (see Figure 1 for locations): **(A)** upper-level cluster 1, which describes Hudson Bay–northern Lake Superior, and **(B)** upper-level cluster 3, which describes the remaining Great Lakes. Maximum value of clusters (K) tested was the number of sampling locations + 3; within a panel, each sublevel cluster is represented by a different color. Upper-level cluster 2 (southern Lake Superior) is not displayed because the most likely K-value was 1.

genetically distinct from each other, populations can be grouped together according to genetic similarity. The Mattagami and Rainy River populations (Hudson Bay drainage) consistently grouped together in all clustering analyses, as did the Bad and White River populations (Lake Superior). The STRUCTURE analysis was able to detect clusters within Lake Superior; however, the software did not perform as well for other Great Lakes populations, which appeared to experience moderate to high levels of gene flow. In general, the genetic data indicated five groups of populations within the Great Lakes: (1) Bad and White rivers; (2) Kaministiquia River; (3) Black Sturgeon and Pic rivers; (4) Goulais, Batchawana, Spanish, and Thessalon rivers and Lake Nipissing; and (5) Menominee, Wolf, Black, Grasse, and St. Lawrence rivers and Lake Champlain. Remaining populations could not be reliably assigned to a single cluster.

Great Lakes lake sturgeon can move freely between lakes. Lake Ontario, once isolated by Niagara Falls, is now connected to the other Great Lakes through locks in the Welland Canal. However, movement of lake sturgeon through the canal has not been documented. Despite the potential for interlake movement, lake sturgeon appear to exhibit fidelity to spawning and foraging grounds. Isolation of populations in the Great Lakes may primarily be a result of the life history characteristic of homing to natal tributaries. Tagging studies have shown that lake sturgeon home to the same tributary, spawning grounds, and foraging grounds (Auer 1999a; Hochleithner and Gessner 1999; Stewart and Watkinson 2004). Despite the fact that several thousand lake sturgeon have been tagged and released back into Lake Superior, none have been recaptured outside of the basin, and there is no evidence of fish spawning in more than one river. In contrast, lake sturgeon in Lakes Michigan, Huron, Erie, and St. Clair have moved between multiple lakes. One individual tagged in the Wolf River (a tributary to Green Bay, Wisconsin) moved as far as Lake Erie, and a fish from Lake Huron was subsequently captured in Lake Michigan (R. Bruch, Wisconsin Department of Natural Resources [WDNR], Green Bay, personal communication). However, the majority of lake sturgeon tagged in Green Bay remain within that basin (Gunderman et al. 2004). In Lake Huron, lake sturgeon in Georgian Bay are infrequently captured outside of the bay and fish from southern Lake Huron are associated with the St. Clair River and Lake St. Clair (Thomas and Haas 1999).

Potential explanations for the differences in genetic structure in Lake Superior and the remaining Great Lakes include habitat characteristics. Among the Great Lakes, Lake Superior has the greatest surface area and

depth (average depth = 147 m; Fuller and Shear 1995). Lake sturgeon prefer depths less than 10 m, where abundant food is available (Becker 1983). Steep shoreline areas and cold water in Lake Superior may limit movement along the shoreline, as has been observed in the other Great Lakes. This is particularly the case along Minnesota's north shore and the northeast shoreline in Ontario, where depths exceeding 60 m are found very close to shore. Many lake sturgeon stocked in the St. Louis River have moved into Lake Superior; however, few have been captured east of Bark Point, where areas near the shoreline are deep (S. Schram, WDNR, Bayfield, personal communication). Therefore, the limited amount of shallow habitat available in Lake Superior may present a dispersal barrier for lake sturgeon within the lake.

Historically, the outlet to Lake Superior was a relatively narrow expanse of shallow rapids at Sault Ste. Marie, Ontario. The locks, dams, bypass channels, and shallow rapids that currently exist at the outlet probably continue to preclude interlake fish movement. The other Great Lakes experience high water flow between the basins and wide connecting waters that may facilitate dispersal. Between Lakes Michigan and Huron, the Straits of Mackinac are 5 km wide and 40 m deep, and water flows sometimes reverse from eastward to westward. These strong hydrologic connections between the lower lakes may explain the populations' reduced genetic differentiation relative to Lake Superior and the high membership coefficients for some individuals in association with clusters outside of their sampled location. Additionally, the low membership coefficients observed for Lake Superior populations close to Lake Huron allow for the possibility of gene flow between the eastern portion of Lake Superior and the other Great Lakes.

The observed genetic structure may also be an artifact of recent historical influences. The Great Lakes basin was covered with ice until approximately 15,000 years ago (Underhill 1986). Mandrak and Crossman (1992) hypothesized that during glaciation, lake sturgeon relocated to the Mississippian refugium and recolonized the Great Lakes by three dispersal routes. The genetic structure in Lake Superior could be due to the use of multiple dispersal routes into the lake, while the lack of resolution in the other Great Lakes may indicate the use of a single dispersal route.

The genetic diversity observed here for lake sturgeon is similar to that seen in other acipenserids. Atlantic sturgeon *A. oxyrinchus*, found along the Atlantic coast and the Gulf of Mexico, were found to exhibit high levels of genetic differentiation between rivers used for spawning (Stabile et al. 1996; Wirgin et al. 2002; Dugo et al. 2004). Grunwald et al. (2002) used mitochondrial DNA control region sequence data to study genetic structuring in shortnose sturgeon *A. brevirostrum*. Significant differences in haplotype frequencies were observed at the level of individual rivers between known spawning populations. Wirgin et al. (2005) also detected significant differences between the nearest neighbors of several river locations. Similar patterns were also observed in anadromous sturgeon species along the Pacific coast of North America. Population structure was detected in white sturgeon within a single river, reflecting postglacial dispersal patterns (Smith et al. 2002). The use of microsatellites detected genetic structuring of green sturgeon *A. medirostris* along the Pacific coast, resulting in the identification of two management units (Israel et al. 2004). As with lake sturgeon, these genetic studies support the likelihood of natal homing in North American sturgeon species.

Management Implications

Several Great Lakes management agencies are interested in expanding stocking efforts to actively restore lake sturgeon populations; however, outbreeding depression can be a risk with such programs. Results from genetic analyses indicate that most lake sturgeon populations are genetically distinct. Stocking practices should preserve the existing genetic structure in order to maintain population identity, preserve native genetic lineages, and ensure the representation of maximum adaptive potential throughout the species' range (Miller and Kapuscinski 2003). Interbreeding of genetically divergent stocks may result in outbreeding depression or reduced fitness in the F_1 or F_2 generation due to loss of local adaptations or disruption of co-adapted gene complexes (Lynch 1991). Alternatively, outbreeding can result in hybrid vigor (increased fitness in hybrids) due to the masking of deleterious alleles (Remington and O'Malley 2000). In populations that are highly inbred and experiencing detrimental fitness consequences, very low levels of immigration can improve the fitness of the population (Tallmon et al. 2004). Straying of large numbers of stocked individuals could exceed the low levels of immigration required to improve fitness without diluting locally adaptive alleles. Lake sturgeon populations show no evidence of inbreeding depression, and no correlation between genetic diversity and population size has been observed (DeHaan et al. 2006); therefore, supplementation with individuals from genetically divergent populations is not a recommended management strategy.

Outbreeding depression could result from stocking individuals in areas where a native population still exists or from straying of stocked individuals that subsequently breed with remnant spawning popula-

tions. Outbreeding depression has been well documented in salmonids after the mating of individuals from genetically distinct populations (e.g., Gilk et al. 2004; Granath et al. 2004). Outbreeding between populations of largemouth bass *Micropterus salmoides* with F_{ST} values of 0.05 (comparable to those observed in this study) resulted in increased infectious disease susceptibility (Goldberg et al. 2005). Consequently, to avoid the potential for outbreeding depression, caution should be exercised when making stocking decisions. Additionally, some spawning populations have not yet been sampled and these remnant populations may retain high levels of genetic distinctiveness.

The methods used here to detect population structure can also be used to delineate management units with utility for stocking. Using the traditional genetic definition of a management unit, populations that have significant allele frequency differences at nuclear loci would constitute separate management units (Moritz 1994). With this definition, most of the populations in this study would be considered separate management units. Although this fine-scale delineation may be appropriate for some management goals, flexibility in management unit definition needs to be incorporated to accommodate different management objectives. Alternative delineations of management units take into account relevant demographic and ecological parameters (Crandall et al. 2000; Palsbøll et al. 2006).

Demographic and ecological characteristics are fairly consistent among Great Lakes lake sturgeon populations. Growth rates and age–length curves reported from throughout the lake sturgeon range suggest similarities among collections from particular latitudes regardless of the major drainage basin (Harkness and Dymond 1961; Scott and Crossman 1973; Becker 1983; Peterson et al. 2002; Stewart and Watkinson 2004). Growth rates decrease with lower mean annual air temperature and increasing latitude (Hochleithner and Gessner 1999). Age at maturity varies slightly among males and females but is consistent throughout the range of lake sturgeon. Morphological characteristics have been suggested as a means to differentiate lake sturgeon stocks (Harkness and Dymond 1961). However, early work by Harkness and Dymond (1961) was concerned with species identification, while more recent work has concluded that the 41 morphological characteristics analyzed did not allow stock separation in the St. Lawrence River (Guenette et al. 1992). Throughout their range, lake sturgeon reportedly spawn in rapids or fast-flowing water during April through June and spawning is initiated at water temperatures of 11–12°C (Harkness and Dymond 1961; Scott and Crossman 1973; Becker 1983; Auer 1999a; Stewart and Watkinson 2004). Lake sturgeon spawning on wave-swept shorelines and along islands has been reported for inland lakes (Harkness and Dymond 1961; Becker 1983) and may be a characteristic used to delineate management units. Although reported by Scott and Crossman (1973) for Lakes Erie and Ontario, spawning on offshore reefs or along rocky shorelines of the Great Lakes has not been confirmed (Auer 1999a). Because of the similarities in life history among lake sturgeon populations, genetic studies provide useful information for delineating management units.

In the case of lake sturgeon management, most stocking occurs at locations where populations have been extirpated. Therefore, the genetic risk of outbreeding depression results from the straying of stocked individuals into remnant spawning populations. To delineate a relevant management unit, managers could estimate the rate of straying of stocked sturgeon to different locations throughout the Great Lakes. Factors to consider when determining the likelihood of straying include distance between sites, intervening habitat, and stocking methods that improve imprinting. The F_{ST} value corresponding to that level of migration could be calculated (assuming a Wright–Fisher island population model). A suitable donor population with the desired F_{ST} value could then be selected to maintain current levels of genetic differentiation. Sampling of additional spawning locations in both the USA and Canada (particularly in Lakes Huron, Erie, and Ontario) and genetic data compilation with other laboratories will further elucidate genetic relationships that are useful for identifying units for management and conservation.

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Appendix follows

Appendix: Allelic Frequencies for Great Lakes Lake Sturgeon Populations

TABLE A.1.—Allele sizes (base pairs [bp]) and frequencies at 13 microsatellite loci in lake sturgeon collected from 22 spawning locations in the Great Lakes basin. Allele frequencies in bold italic font indicate potential private alleles.

Locus	Allele size (bp)	Matta-gami R.	Rainy R.	Bad R.	White R.	Kaminis-tiquia R.	Goulais R.	Black Sturgeon R.	Pic R.	Menomi-nee R.	Wolf R	Missis-saugi R.
AfuG9	120	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	124	0.06	0.08	0.27	0.33	0.06	0.11	0.04	0.05	0.05	0.07	0.09
	128	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.02
	132	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.03	0.09	0.00
	136	0.00	0.00	0.00	0.00	0.04	0.09	0.00	0.02	0.00	0.03	0.00
	140	0.14	0.00	0.50	0.54	0.25	0.51	0.40	0.33	0.43	0.52	0.48
	144	0.60	0.21	0.10	0.07	0.36	0.17	0.13	0.21	0.38	0.09	0.24
	148	0.03	0.00	0.00	0.00	0.04	0.00	0.00	0.05	0.13	0.10	0.02
	152	0.18	0.37	0.13	0.06	0.26	0.06	0.41	0.35	0.00	0.05	0.15
	156	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.02	0.00
	160	0.00	0.27	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00
	168	0.00	***0.02***	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
AfuG56	258	0.00	***0.02***	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	262	0.09	0.06	0.11	0.09	0.37	0.18	0.25	0.27	0.09	0.07	0.09
	266	0.61	0.50	0.64	0.71	0.35	0.71	0.52	0.68	0.91	0.90	0.89
	274	0.30	0.43	0.26	0.20	0.28	0.11	0.24	0.05	0.00	0.03	0.02
AfuG63	127	0.00	0.00	0.23	0.13	0.66	0.49	0.20	0.35	0.21	0.27	0.38
	135	0.31	0.19	0.00	0.00	0.00	0.02	0.12	0.03	0.08	0.05	0.05
	139	0.35	0.65	0.30	0.38	0.22	0.39	0.55	0.48	0.39	0.53	0.45
	143	0.34	0.17	0.47	0.47	0.11	0.10	0.12	0.11	0.32	0.15	0.13
	147	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.03	0.00	0.00	0.00
AfuG74	218	0.11	0.07	0.60	0.63	0.62	0.64	0.55	0.70	0.83	0.78	0.57
	222	0.30	0.46	0.31	0.26	0.16	0.21	0.34	0.09	0.11	0.03	0.09
	226	0.59	0.46	0.09	0.12	0.22	0.15	0.11	0.21	0.06	0.18	0.34
	230	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
AfuG112	240	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	***0.02***	0.00
	244	0.05	0.04	0.27	0.29	0.22	0.17	0.32	0.39	0.34	0.23	0.33
	248	0.17	0.15	0.01	0.00	0.02	0.00	0.00	0.00	0.06	0.00	0.00
	252	0.00	0.02	0.08	0.07	0.01	0.24	0.13	0.17	0.19	0.20	0.12
	256	0.57	0.59	0.21	0.26	0.57	0.41	0.13	0.18	0.22	0.27	0.32
	260	0.21	0.20	0.41	0.35	0.14	0.17	0.38	0.24	0.06	0.14	0.04
	264	0.00	0.00	0.02	0.03	0.00	0.01	0.04	0.02	0.13	0.14	0.18
	268	0.00	0.00	0.00	0.00	0.03	0.00	0.01	0.00	0.00	0.00	0.00
AfuG122	147	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	151	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	155	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00
	159	0.04	0.19	0.31	0.40	0.14	0.04	0.01	0.06	0.00	0.10	0.19
	163	0.01	0.04	0.03	0.00	0.11	0.00	0.02	0.16	0.00	0.03	0.02
	167	0.43	0.33	0.50	0.36	0.45	0.32	0.11	0.13	0.21	0.53	0.19
	171	0.43	0.15	0.09	0.08	0.09	0.45	0.57	0.41	0.57	0.22	0.34
	175	0.08	0.30	0.02	0.05	0.19	0.16	0.29	0.25	0.17	0.02	0.26
	179	0.00	0.00	0.06	0.11	0.01	0.03	0.00	0.00	0.02	0.10	0.00
	183	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	187	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	***0.02***	0.00	0.00
AfuG160	127	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00
	131	0.00	0.00	0.00	0.00	0.06	0.05	0.08	0.03	0.14	0.08	0.05
	135	0.49	0.67	0.19	0.12	0.58	0.62	0.61	0.76	0.76	0.67	0.75
	139	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
	143	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.02	0.00
	147	0.44	0.17	0.65	0.74	0.34	0.34	0.13	0.14	0.02	0.23	0.17
	151	0.08	0.17	0.15	0.14	0.02	0.00	0.18	0.08	0.00	0.00	0.02
AfuG195	161	0.33	0.61	0.61	0.64	0.58	0.45	0.71	0.67	0.80	0.60	0.57
	165	0.68	0.39	0.38	0.36	0.42	0.55	0.29	0.33	0.20	0.40	0.43
	169	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	173	0.00	0.00	***0.01***	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
AfuG204	141	1.00	1.00	0.99	1.00	0.98	0.70	0.78	0.95	0.63	0.58	0.61
	145	0.00	0.00	0.01	0.00	0.02	0.30	0.22	0.05	0.38	0.42	0.39
Afu68	108	0.28	0.00	0.07	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	112	0.47	0.91	0.53	0.50	0.44	0.31	0.42	0.47	0.62	0.40	0.24
	116	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.02	0.02	0.03
	120	0.00	0.00	0.01	0.04	0.01	0.07	0.28	0.22	0.05	0.12	0.20
	124	0.00	0.00	0.07	0.11	0.15	0.21	0.08	0.11	0.00	0.13	0.28
	128	0.08	0.02	0.03	0.01	0.35	0.00	0.06	0.02	0.31	0.32	0.24

TABLE A.1.—Extended.

Locus	Eastern Lake Nipissing	Western Lake Nipissing	Spanish R.	Detroit R.	St. Clair R.	Lower Niagara R.	Black R.	Grasse R.	Des Prairies R.	St. Lawrence R.	Lake Champlain
AfuG9	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	***0.06***
	0.06	0.08	0.09	0.14	0.20	0.13	0.09	0.30	0.08	0.19	0.35
	0.19	0.05	0.09	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
	0.01	0.00	0.02	0.00	0.01	0.00	0.05	0.34	0.04	0.11	0.04
	0.00	0.00	0.01	0.03	0.05	0.03	0.14	0.00	0.08	0.08	0.06
	0.40	0.44	0.35	0.39	0.33	0.38	0.23	0.18	0.27	0.06	0.10
	0.24	0.40	0.30	0.38	0.27	0.15	0.09	0.11	0.19	0.26	0.10
	0.01	0.00	0.01	0.05	0.05	0.03	0.14	0.00	0.12	0.09	0.27
	0.07	0.04	0.06	0.02	0.08	0.30	0.14	0.04	0.15	0.17	0.04
	0.01	0.00	0.00	0.00	0.00	0.00	0.14	0.04	0.08	0.03	0.00
	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
AfuG56	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.29	0.18	0.14	0.15	0.21	0.15	0.06	0.00	0.04	0.04	0.16
	0.70	0.80	0.83	0.79	0.73	0.78	0.94	0.98	0.96	0.95	0.84
	0.01	0.03	0.03	0.06	0.07	0.08	0.00	0.02	0.00	0.01	0.00
AfuG63	0.41	0.55	0.70	0.42	0.34	0.38	0.36	0.00	0.25	0.33	0.15
	0.00	0.00	0.04	0.03	0.07	0.03	0.18	0.00	0.00	0.08	0.37
	0.44	0.36	0.14	0.35	0.39	0.30	0.27	0.68	0.36	0.39	0.31
	0.13	0.09	0.12	0.17	0.18	0.25	0.18	0.32	0.36	0.15	0.17
	0.01	0.00	0.00	0.03	0.02	0.05	0.00	0.00	0.04	0.06	0.00
AfuG74	0.47	0.48	0.50	0.53	0.58	0.48	0.41	0.68	0.67	0.65	0.48
	0.07	0.15	0.10	0.06	0.10	0.20	0.27	0.00	0.04	0.07	0.02
	0.46	0.38	0.40	0.41	0.32	0.33	0.32	0.32	0.25	0.25	0.50
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.04	0.00
AfuG112	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.47	0.41	0.36	0.33	0.35	0.18	0.05	0.16	0.30	0.44	0.30
	0.00	0.00	0.00	0.02	0.00	0.00	0.45	0.00	0.00	0.06	0.02
	0.02	0.00	0.01	0.15	0.12	0.18	0.05	0.00	0.05	0.08	0.14
	0.20	0.28	0.53	0.25	0.23	0.32	0.00	0.75	0.35	0.28	0.52
	0.14	0.14	0.02	0.10	0.08	0.08	0.05	0.09	0.10	0.08	0.02
	0.18	0.18	0.05	0.12	0.23	0.24	0.10	0.00	0.10	0.03	0.00
	0.00	0.00	0.02	0.03	0.00	0.00	0.30	0.00	0.10	0.04	0.00
AfuG122	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.01	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	***0.02***	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.09	0.09	0.01	0.15	0.00	0.16	0.12	0.06	0.17
	0.14	0.02	0.18	0.03	0.01	0.00	0.14	0.00	0.00	0.05	0.08
	0.56	0.29	0.04	0.31	0.22	0.35	0.14	0.14	0.35	0.29	0.25
	0.08	0.29	0.43	0.40	0.56	0.38	0.64	0.00	0.38	0.30	0.42
	0.00	0.02	0.23	0.16	0.18	0.13	0.09	0.57	0.12	0.13	0.08
	0.22	0.38	0.04	0.02	0.02	0.00	0.00	0.13	0.00	0.10	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	***0.04***	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
AfuG160	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
	0.09	0.10	0.00	0.00	0.03	0.00	0.00	0.00	0.18	0.16	0.00
	0.66	0.59	0.56	0.79	0.77	0.68	0.60	0.90	0.57	0.68	0.73
	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.05	0.00
	0.26	0.31	0.37	0.21	0.20	0.33	0.40	0.10	0.21	0.11	0.23
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
AfuG195	0.69	0.61	0.49	0.67	0.74	0.65	0.50	0.85	0.46	0.63	0.56
	0.31	0.38	0.51	0.33	0.26	0.35	0.50	0.15	0.54	0.37	0.44
	0.00	***0.01***	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
AfuG204	0.73	0.61	0.53	0.77	0.70	0.55	0.86	0.54	0.64	0.51	0.77
	0.27	0.39	0.47	0.23	0.30	0.45	0.14	0.46	0.36	0.49	0.23
Afu68	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.14	0.15	0.12	0.39	0.42	0.43	0.30	0.25	0.54	0.55	0.40
	0.24	0.20	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00
	0.30	0.23	0.26	0.06	0.13	0.10	0.25	0.27	0.18	0.14	0.54
	0.27	0.25	0.40	0.39	0.29	0.15	0.35	0.00	0.11	0.07	0.02
	0.03	0.14	0.13	0.15	0.08	0.23	0.10	0.30	0.11	0.14	0.04

TABLE A.1.—Continued.

Locus	Allele size (bp)	Matta-gami R.	Rainy R.	Bad R.	White R.	Kaminis-tiquia R.	Goulais R.	Black Sturgeon R.	Pic R.	Menomi-nee R.	Wolf R.	Missis-saugi R.
	132	0.17	0.07	0.04	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	136	0.00	0.00	0.19	0.11	0.01	0.08	0.00	0.00	0.00	0.00	0.00
	140	0.00	0.00	0.05	0.11	0.04	0.20	0.15	0.19	0.00	0.00	0.00
	144	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.02	0.00
	152	0.00	0.00	0.00	***0.01***	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Afu68b	153	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00
	157	0.01	0.00	0.08	0.04	0.01	0.09	0.19	0.05	0.05	0.00	0.10
	161	0.00	0.00	0.01	0.00	0.00	0.02	0.00	0.03	0.20	0.00	0.02
	165	0.06	0.30	0.00	0.00	0.01	0.06	0.00	0.03	0.03	0.08	0.11
	169	0.00	0.04	0.03	0.05	0.03	0.06	0.04	0.05	0.05	0.00	0.07
	173	0.06	0.02	0.22	0.26	0.45	0.26	0.10	0.28	0.28	0.13	0.14
	177	0.06	0.00	0.10	0.02	0.05	0.19	0.20	0.11	0.13	0.42	0.25
	181	0.48	0.39	0.02	0.06	0.22	0.12	0.37	0.33	0.10	0.08	0.09
	185	0.00	0.02	0.36	0.28	0.01	0.09	0.00	0.03	0.08	0.00	0.16
	189	0.33	0.20	0.00	0.00	0.04	0.01	0.01	0.05	0.03	0.22	0.00
	193	0.00	0.04	0.17	0.29	0.18	0.10	0.02	0.05	0.08	0.05	0.06
	197	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.02	0.00
Aox27	130	1.00	1.00	0.75	0.62	0.92	0.80	0.99	0.88	0.98	0.95	0.90
	134	0.00	0.00	0.16	0.21	0.04	0.05	0.01	0.11	0.02	0.00	0.05
	138	0.00	0.00	0.09	0.17	0.04	0.15	0.00	0.02	0.00	0.05	0.05
Spl120	254	0.21	0.28	0.31	0.40	0.55	0.46	0.38	0.58	0.47	0.52	0.59
	256	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	258	0.01	0.04	0.29	0.37	0.08	0.31	0.26	0.11	0.14	0.05	0.08
	262	0.13	0.07	0.18	0.07	0.15	0.16	0.23	0.16	0.28	0.12	0.14
	266	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.03	0.00	0.00	0.00
	274	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.15	0.01
	278	0.23	0.04	0.04	0.01	0.04	0.03	0.00	0.02	0.03	0.07	0.08
	282	0.39	0.09	0.18	0.14	0.15	0.00	0.09	0.00	0.03	0.10	0.02
	286	0.01	0.46	0.01	0.00	0.03	0.03	0.04	0.10	0.00	0.00	0.07
	290	0.00	***0.02***	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	294	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

TABLE A.1.—Extended. Continued.

Locus	Eastern Lake Nipissing	Western Lake Nipissing	Spanish R.	Detroit R.	St. Clair R.	Lower Niagara R.	Black R.	Grasse R.	Des Prairies R.	St. Lawrence R.	Lake Champlain
	0.00	0.00	0.00	0.00	0.02	0.10	0.00	0.00	0.04	0.04	0.00
	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00
	0.01	0.04	0.00	0.00	0.04	0.00	0.00	0.18	0.04	0.00	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Afu68b	0.00	0.00	0.00	0.00	0.03	0.03	0.00	0.00	0.00	0.00	0.03
	0.00	0.00	0.02	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.03
	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.04	0.04	0.05
	0.00	0.00	0.07	0.03	0.00	0.03	0.05	0.00	0.23	0.09	0.39
	0.10	0.08	0.00	0.22	0.17	0.15	0.05	0.00	0.00	0.06	0.00
	0.20	0.14	0.27	0.28	0.28	0.40	0.14	0.43	0.19	0.20	0.16
	0.39	0.24	0.18	0.33	0.30	0.28	0.27	0.22	0.12	0.40	0.18
	0.00	0.13	0.08	0.00	0.01	0.03	0.32	0.06	0.23	0.06	0.03
	0.07	0.10	0.12	0.13	0.14	0.08	0.00	0.30	0.12	0.07	0.00
	0.03	0.00	0.00	0.02	0.03	0.00	0.00	0.00	0.00	0.04	0.13
	0.20	0.29	0.26	0.00	0.01	0.03	0.18	0.00	0.08	0.01	0.00
	0.01	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00
Aox27	0.77	0.65	0.88	0.71	0.71	0.65	0.86	0.96	0.75	0.76	0.75
	0.06	0.17	0.01	0.05	0.11	0.03	0.05	0.00	0.11	0.12	0.15
	0.17	0.18	0.11	0.24	0.18	0.33	0.09	0.04	0.14	0.13	0.10
Spl120	0.24	0.49	0.54	0.55	0.56	0.37	0.69	0.04	0.50	0.43	0.35
	0.10	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.38	0.21	0.32	0.18	0.21	0.18	0.00	0.40	0.14	0.07	0.28
	0.07	0.09	0.07	0.02	0.01	0.03	0.13	0.24	0.18	0.15	0.35
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.22	0.00
	0.18	0.08	0.02	0.14	0.04	0.18	0.00	0.28	0.11	0.10	0.00
	0.00	0.00	0.02	0.00	0.03	0.11	0.13	0.04	0.04	0.03	0.03
	0.01	0.03	0.02	0.11	0.15	0.13	0.06	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00