Genetically Derived Estimates of Contemporary Natural Straying Rates and Historical Gene Flow among Lake Michigan Lake Sturgeon Populations

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Abstract

Natural rates of straying are difficult to quantify over large spatial scales using direct observations, particularly for long-lived fish species characterized by delayed sexual maturity and long interspawning intervals. Using multilocus microsatellite genotypes and likelihood-based statistical methods, we quantified rates of immigration and emigration for six genetically differentiated (mean $F_{ST} = 0.041$) lake sturgeon *Acipenser fulvescens* populations in Lake Michigan based on adults ($n = 437$) captured in tributaries during the spawning season. Estimated rates of straying were high (mean = 0.105), asymmetrical, and highly variable across populations. We found no significant association between the total length (a surrogate measure of age) of individuals that strayed and those that did not. Linear distance between streams was more predictive of straying rates and F_{ST} than least-cost distances estimated based on lakescape features (bathymetry and lake current patterns). Historical rates of gene flow estimated using coalescent analysis indicated a fully parameterized model with variable evolutionarily effective population sizes (θ; range, **0.684–0.989**),

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and variable and nonsymmetrical migration rates best explained the genetic data. Comparatively high estimates of relative historical gene flow from several numerically depressed populations suggest that these populations were once larger contributors to basinwide gene flow than indicated by estimates of contemporary straying rates. High rates of interpopulation straying contrast with high F_{ST}, suggesting that straying rates are poor indicators of successful reproduction following dispersal.

The propensity for individuals to return to spawn in their natal streams is of ecological and managerial importance. For example, in Pacific salmon *Oncorhynchus* spp. the tendency to stray (i.e., disperse to a stream other than an individual's stream of origin to spawn) is important for the colonization of new or previously extirpated streams (Milner 1987; Milner et al. 2000; Anderson et al. 2008). Straying does not necessarily result in gene flow to the destination population because immigrants may not successfully breed or may be selected against based on prezygotic (e.g., population differences in mate preference) or postzygotic (e.g., reduced offspring fitness via outbreeding depression; Lynch 1991) factors. Source–sink dynamics whereby population numbers are sustained by immigration of individuals from other populations can result in stable populations over generations (Ayllon et al. 2006). Resource managers' concerns about straying are exemplified by conservation hatchery programs (Mobrand et al. 2005), which often adopt strict rearing and release policies to facilitate imprinting to natal waters in order to minimize straying (Scholz et al. 1978; Candy and Beacham 2000). Additionally, in locations where limited harvest of numerically depressed species is permissible, regulations often are established based on assessments of the risk associated with the potential harvest of individuals from numerically less abundant, nontarget populations that may have strayed into the population subject to legal harvest (Policansky and Magnuson 1998; Bott et al. 2009).

Many variables can affect the likelihood of individuals straying. Natal philopatry is observed in many fish species and is believed to result from responses to site-specific olfactory signals detected during migration to spawning areas (Leggett 1977; Quinn 1993). Demographic parameters such as gender, age, and population size also may influence probabilities of straying (Hard and Heard 1999). Individuals originating from populations that are reproductively isolated temporally and spatially have lower expectations of straying than geographically proximal populations that spawn at similar times (Tallman and Healey 1994). Habitat quality also has the potential to affect the tendency of individuals to stray from a particular stream, whether the differences in quality are of anthropogenic (Quinn and Fresh 1984) or natural origin (Leider 1989). Fish produced in hatcheries have been shown to stray more than their wild counterparts (Quinn 1993; Mortensen et al. 2002); however, juveniles that are properly imprinted to target streams are generally more likely to home (Pascual et al. 1995; Dittman and Quinn 1996).

The methods used to quantify straying rates and movement patterns have traditionally included telemetry (Auer 1999) and capture–mark–recapture (Quinn 1993; Mortensen et al. 2002). Tag loss detracts from the usefulness of direct tagging methods when estimating population size and straying rates (Miranda 2002; Smith et al. 2002). Additionally, certain species have life history characteristics that make the implementation of direct straying estimators difficult. For instance, species with long generation times require long-term studies that extend until first reproduction occurs (Wirgin et al. 1997). Extended interspawning intervals and long-distance migrations between reproductive episodes also present challenges for collecting adequate numbers of recaptures from physical tags for accurate assessments of movements.

Molecular techniques can be used to study straying when opportunities to employ direct tagging are limited or impractical (Hansen et al. 2001). Examples of indirect genetic methods being implemented successfully to quantify rates of straying are found in Miller et al. (2001), D'Amelio et al. (2008), and Homola et al. (2010). Moreover, if there is sufficient genetic variation between populations, samples obtained from a single capture can be used to determine an individual's population of origin based on individual assignment testing (Cornuet et al. 1999).

Applications of genetic techniques for species such as lake sturgeon *Acipenser fulvescens* are especially important to elucidate information on straying due to aspects of the species' ecology. Lake sturgeon are a long-lived potamodromous fish species that reach reproductive maturity in 15–25 years, depending on sex (Harkness and Dymond 1961; Houston 1987). Through time, natal philopatry has resulted in genetically distinct lake sturgeon populations throughout the Great Lakes (DeHaan et al. 2006; Welsh et al. 2008) and has facilitated the use of genetic markers as a means of detecting individuals occupying nonnatal habitats (Bott et al. 2009; Homola et al. 2010).

The primary objective of this study was to quantify basinwide straying rates of Lake Michigan lake sturgeon to examine alternative hypotheses about the factors that may contribute to straying rates and directionality, including population demography, lakescape features, and stream environmental features. Given the levels of spatial genetic structure previously documented among Great Lakes lake sturgeon populations (DeHaan et al. 2006; Welsh et al. 2008), we hypothesized that straying among populations would be limited. Furthermore, we expected

that straying would be associated with the age of the straying in-
dividuals (i.e., younger fish would stray more frequently) and the
geographic proximity of natal and destination streams (closer
streams would have a higher likelihood of receiving strays). We
also hypothesized that contemporary straying rates would reflect
a lower preference for streams with a high degree of anthro-
pogenic disturbance (e.g., dam construction), reflecting recent
declines in the amount and quality of spawning habitat available
relative to historical levels. To test these hypotheses, the specific
objectives of this study were to (1) quantify the direction and
rates of straying among lake sturgeon populations ($n = 7$; sample
size $= 437$) that spawn in tributaries to Lake Michigan, (2) eval-
uate the influence of demographic and environmental variables
on straying rates, (3) quantify the relationships among straying
rates, genetic variation, and interstream geographic distance,
and (4) estimate historic rates of gene flow to facilitate compar-
isons with the rates of straying in contemporary populations.

METHODS

Sample collection.—Adult lake sturgeon were sampled from
Wisconsin tributaries to Lake Michigan, including the lower Fox
River during 2000 ($n = 28$), 2001 ($n = 17$), and 2004 ($n = 25$);
the Menominee River during 2002 ($n = 23$) and 2005 ($n = 41$);
the Oconto River during 2002 ($n = 9$), 2003 ($n = 10$), 2004 ($n
= 6$), and 2007 ($n = 2$); and the Peshtigo River during 2001 ($n
= 23$), 2002 ($n = 22$), 2004 ($n = 14$), 2007 ($n = 1$), and 2009 ($n
= 35$) (Figure 1). Adult lake sturgeon also were sampled from
the following Michigan tributaries: the Kalamazoo River during
2004 ($n = 4$), 2005 ($n = 4$), and 2009 ($n = 9$); the Manistee
River during 2000 ($n = 30$), 2001 ($n = 17$), 2002 ($n = 36$),
2003 ($n = 16$), and 2004 ($n = 7$); and the Muskegon River
during 2002 ($n = 7$), 2003 ($n = 10$), 2004 ($n = 7$), 2005 ($n =
12$), 2008 ($n = 8$), and 2009 ($n = 14$) (Figure 1). Individuals
were selected for analysis based on their physical presence at
or near spawning areas in each stream during the spawning
season (April 15 through June 15). Lake sturgeon were captured
using long-handed dip nets, gill nets, seines, or electrofishing.
Upon capture, a 1-cm^2 portion of the dorsal or caudal fin was
collected from each individual for genetic analysis and stored in
a uniquely marked scale envelope. Sex and maturity status were
not apparent for all fish at the time of sampling. Consequently,
only individuals of at least the minimum expected size at sexual
maturity for either sex (>110 cm) were included in analyses.

Laboratory analysis.—DNA was extracted from fin tissue
using QIAGEN DNeasy kits (Qiagen, Inc., Valencia, California)
according to manufacturer's specifications. DNA was quantified
using a NanoDrop spectrophotometer (NanoDrop Technolo-
gies, Thermo Scientific, Wilmington, Delaware) and diluted to
a concentration of 20 ng/μL. All individuals were genotyped
at twelve microsatellite loci: *AfuG68* (May et al. 1997), *Afu68b*
(McQuown et al. 2002), *Spl120* (McQuown et al. 2000),
Aox27 (King et al. 2001), *AfuG9*, *AfuG160*, *AfuG63*, *AfuG74*,
AfuG204, *AfuG195*, *AfuG56*, and *AfuG112* (Welsh et al. 2003).
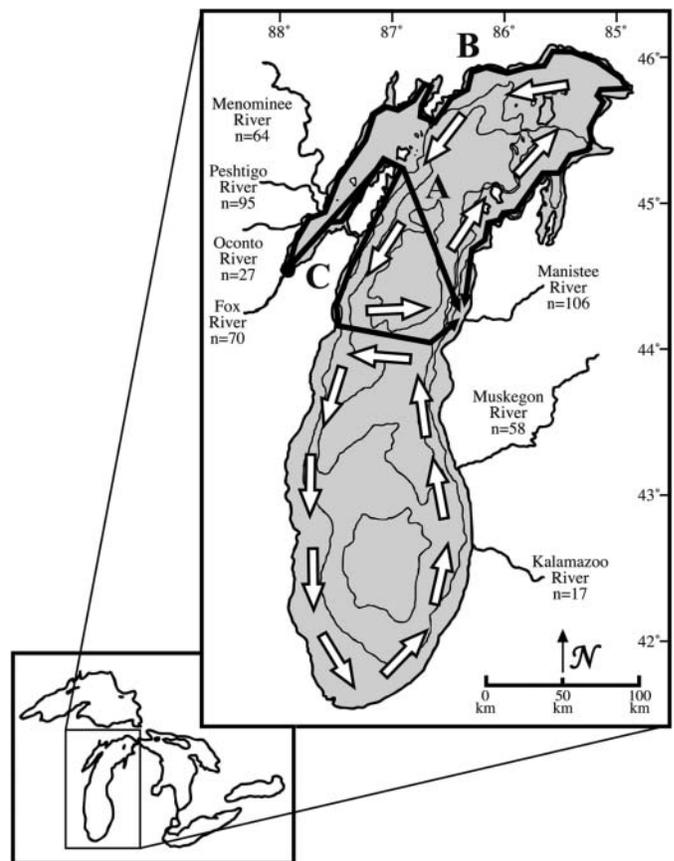Polymerase chain reactions (PCR) were conducted in 25-μL

FIGURE 1.   Visual representation of the three alternative connectivity scenar-
ios evaluated using genetic data for lake sturgeon from seven remnant spawning
populations in the Lake Michigan basin with generalized surface water cur-
rents indicated by white arrows. Distance measurements were quantified based
on direct open water distance (A), shoreline distance (B), and surface current
distance (C).

volumes containing 100 ng of template DNA, 2.5 μL of 10 ×
PCR buffer (1 M tris-HCl, 1.5 M MgCl$_2$, 1 M KCl, 10% gelatin,
10% NP-40, and 10% triton X), and 0.8 mM deoxynucleotide
triphosphates, 10 pm fluorescently labeled forward and unla-
beled reverse primers, sterile water, and 0.5 U *Taq* polymerase.
Polymerase chain reactions were performed using Robocycler
96 thermocyclers (Stratagene, Inc., La Jolla, California) under
the conditions detailed in Homola et al. (2010). Amplified PCR
products were visualized on 6% denatured polyacrylamide gels
using an FMBIO II scanner (Hitachi Software Engineering
Co., Ltd., Yokohama, Japan). Allele size was determined by
comparison with lake sturgeon samples of known genotype and
based on molecular size standards. Genotype scores were con-
firmed by independent scoring by two experienced laboratory
personnel.

Statistical analysis.—Measures of genetic diversity were es-
timated for each population to quantify the degree of differ-
entiation among the lake sturgeon populations. Estimates of
allele frequency, exact tests for Hardy–Weinberg equilibrium,
and measures of genetic diversity, including allelic richness

(A), observed (H_o) and expected (H_e) heterozygosity, were estimated using the computer program GENEPOP (version 4; Raymond and Rousset 1995). GENEPOP also was used to evaluate significant differences among the genotypic frequencies of each population using a Fisher's exact test. Fixation indexes, including measures of the interpopulation variance in allele frequency (F_{ST}) and the variation among individuals within populations (F_{IS}), were estimated as described by Weir and Cockerham (1984) using the program FSTAT (version 2.9.3.1; Goudet 2001). A Bonferroni correction was used to adjust significance to account for multiple tests. Similarities in allelic frequency prompted the grouping of individuals from the Peshtigo and Oconto rivers for all analyses ($F_{ST} = 0.0006$; DeHaan et al. 2006; Bott et al. 2009). Gametic disequilibrium was assessed to provide estimates of locus independence from other loci in each population using GENEPOP, and a Bonferroni correction was used to adjust alpha levels.

Multilocus microsatellite data were analyzed in program STRUCTURE 2.2 (Pritchard et al. 2000; Falush et al. 2003) to detect the occurrence of population structure without a priori knowledge of putative populations. Data were analyzed using an admixture model assuming correlated frequencies to probabilistically assign individuals to putative genetic clusters using a 100,000 burn-in period, 200,000 Markov chain–Monte Carlo iterations, and a number of possible populations (K) ranging from 1 to 8; this analysis was repeated 10 times to ensure consistency across runs. An upper limit of $K = 8$ was chosen to allow for individuals not originating from one of the seven sampling locations to be placed in a separate group. The Web-based program STRUCTURE HARVESTER (Earl and vonHoldt 2012) was used to summarize estimates of the likelihood of K given the data for each K and replicate to estimate the number of clusters that best fit the data based on the mean likelihood $L(K)$ and its variance and estimates of ΔK (Evanno et al. 2005).

Identification of presumed first-generation migrants (i.e., individuals that strayed from a presumed natal stream to a different stream at the time of spawning) for each population was determined using the program GENECLASS (version 2.0.h; Cornuet et al. 1999). Estimates of emigration and immigration based on individual assignments of first-generation migrants will hereafter be referred to as representing measures of "contemporary rates of straying." Assignment criteria followed the recommendations in Paetkau et al. (2004) and are detailed in Homola et al. (2010). Mean contemporary rates of straying across all populations were calculated by dividing the total number of individuals that were genetically determined to have strayed by the sum of all individuals sampled from their population of origin. Immigration rates were estimated for each population by dividing the number of strays found in each stream by the total number of individuals sampled in that stream. Emigration rates for each population were estimated by dividing the total number of strays found in each population by the total number of individuals sampled originating from that population regardless of capture location. Disparities between the number of immi-

grating and emigrating individuals for a stream were evaluated using a Fisher's exact test.

Statistical tests to assess potential nonrandomness in the contemporary migration pattern were conducted as follows. Let N_j denote the number of fish in sample j (i.e., the sample from population j), and let N_{ij} denote the number of these fish that originated in population i. Since all sampled fish originated in one of the six populations, $N_j = \Sigma_i N_{ij}$ for every j. The inferred number of sampled fish N_i' that were in each population i before migrating is given by $N_i' = \Sigma_j N_{ij}$. To test the null hypothesis that migration was random, we viewed premigration values N_i' as fixed and postmigration values N_{ij} as the result of random sampling from the premigration values. We conducted two such tests, differing in the extent of assumed randomness in migration.

The first test assumes completely random migration. We assumed that all N_i' premigration fish from population i left their natal population and randomly chose one of the six populations to join, with the probability of joining any particular population being 1/6. The expected number $E(N_{ij})$ of postmigration fish in sample j that originated in population i is given by $E(N_{ij}) = N_i'/6$ for all combinations of i and j. We quantified the overall discrepancy between the observed and expected numbers of fish in cells of sample matrix $\mathbf{N} = [N_{ij}]$ using test statistic $X^2 = \Sigma_{i,j} [N_{ij} - E(N_{ij})]^2/E(N_{ij})$. For our data, the values of $E(N_{ij})$ in all cells of the expected sample matrix are greater than 1, so X^2 will have an approximately chi-squared (χ^2) distribution with 30 degrees of freedom. We therefore tested the null hypothesis of completely random migration by determining whether the probability that $\chi^2(30) > X^2_{obs}$ is less than 0.05, where X^2_{obs} is the observed value of X^2.

The second test permits partially nonrandom migration. Here we assumed that only a fraction m of the premigration fish from each population randomly chose one of the six populations to join, while the remaining fraction $1 - m$ intentionally returned to their natal population. The expected number of postmigration fish in sample j that originated in population i is given by $E(N_{ij}) = mN_i'/6$ for $i \neq j$ and by $E(N_{ii}) = (1 - m)N_i' + mN_i'/6 = (1 - 5m/6)N_i'$ for $i = j$. The value of parameter m is unknown but can be estimated from the data using the estimator $m = (6/5)[1 - \Sigma_i N_{ii}/\Sigma_i N_i']$, which for our data yields $m = 0.124$. As in the previous test, we quantified the overall discrepancy between the observed and expected numbers of fish in the cells of the sample matrix using test statistic X^2. Here, however, the values of $E(N_{ij})$ in several cells of the expected sample matrix are well below 1, so it is not safe to assume that X^2 has an approximately chi-squared distribution. We therefore constructed the complementary cumulative distribution function of X^2 by Monte Carlo simulation and used it to test the null hypothesis of partially nonrandom migration by determining whether the probability that $X^2 > X^2_{obs}$ is less than 0.05.

The relationships between demographic characteristics, the proximity of natal streams relative to other populations, and stream habitat availability and the straying rates of individuals

from each population were quantified. A two-sample *t*-test assuming unequal variances was used to test the null hypothesis that there was no difference in the total body lengths of individuals that strayed and that of those that returned to their stream of origin to spawn. Length was assumed to be a surrogate measure of age (Bruch et al. 2009). Fisher's exact test was employed to evaluate the null hypothesis that there was an equal likelihood to stray for a lake sturgeon native to a Green Bay (Wisconsin) western basin tributary as there was for an individual native to an eastern basin (Michigan) stream. Additionally, Fisher's exact test was used to examine the null hypothesis that a straying individual was equally likely to stray to a stream on the same side of the basin as their natal stream as they were to migrate to a stream on the opposite side of the basin. The effects of the amount of spawning habitat available before the first migration barrier on straying rates were examined using Spearman's rank correlation coefficient. Measures of spawning habitat availability from previous published studies were used (O'Neal 1997; Tonello 2004; Wesley 2005; Daugherty et al. 2009) with the availability for the Oconto and Peshtigo rivers being the mean amount of accessible habitat for each of the two streams.

Linear regression analysis was used to characterize the relationships between degree of interpopulation variance in allele frequency ($F_{ST}/[1 - F_{ST}]$), interpopulation straying rate, and geographic distance between populations. The interpopulation straying rate was calculated as the total number of first-generation migrants between two stream populations divided by the total number of individuals analyzed for both populations. Interstream distances were estimated based on the direct open-water distances between river mouths and using least-cost paths (Spear et al. 2010) based on two river connectivity criteria: (1) shoreline distance based on lake sturgeon depth limitations and (2) distances estimated based on prevailing surface current patterns (Figure 1). Direct open-water distance was estimated as the shortest straight-line distance across water between two steams (Figure 1, segment A). Shoreline distance was the shortest distance between two river mouths following shoreline bathometric contours (Figure 1, segment B). The depth limitations used to estimate shoreline distances were based on descriptions of the species' depth limitations (approximately 18.2 m; Harkness and Dymond 1961). Water depths were determined using Lake Michigan bathymetric data (U.S. National Oceanic and Atmospheric Administration). A third measure of connectivity was based on water current patterns. Shoreline distance was estimated following two counterclockwise patterns consistent with the prevailing water currents in the northern and southern portions of Lake Michigan (Figure 1, segment C; Beletsky and Schwab 2001). All distances were measured between river mouths using Google Earth (version 5.2.1.1588; earth.google.com).

The relative rates of historical gene flow and evolutionary effective population sizes for the Lake Michigan lake sturgeon populations were based on coalescence analyses from multilocus microsatellite genotypes estimated using the program MIGRATE, version 3.1.6 (Beerli 2002). Historical rates are referred to as "relative" because they can only be compared with similarly derived rates (i.e., these rates are not directly comparable with contemporary straying rates). The evolutionary effective population size ($\theta = 4N_e\mu$) for nuclear loci was estimated, where N_e is the evolutionary effective total population size and μ is the rate of mutation to new alleles. The number of migrants per generation (N_em) among lake sturgeon populations was calculated based on the model with the best fit among the six evaluated models. Model 1 is an *N*-island model that assumes equal values of θ and equal interpopulation rates of gene flow. Model 2 allows for a variable θ and assumes constant and symmetrical pairwise rates of gene flow among populations. Model 3 assumes equal values of θ and variable and asymmetrical rates of gene flow among populations. Model 4 was designed to evaluate the hypothesis of predominately east–west migration and assumes equal values of θ and variable rates of gene flow among populations on the same or different sides of Lake Michigan. Model 5 also segregates the lake basin into eastern and western sides, assuming that θ is equal and that gene flow rates are equal and symmetrical between populations that spawn on the same side of the basin but possibly different between populations on different sides of the basin. Model 6 is a fully parameterized model, estimating θ for each population and allowing for different and asymmetrical pairwise gene flow rates. A maximum likelihood search of the parameter space included ten short chains (1,000 genealogies per chain), four long chains (10,000 genealogies per chain), and four adaptively heated chains (start temperatures = 1, 1.5, 3, and 10,000; swapping interval = 1). Three independent runs were conducted to evaluate evidence of convergence of all estimated parameters. Empirical estimates of F_{ST} were used for the first run, and output estimates were used during subsequent runs. Each model was evaluated for goodness of fit using a log-likelihood ratio test, and the model best supported by the data was determined based on Akaike's information criterion (Burnham and Anderson 2002). Log-likelihood ratio test statistics are equivalent to a chi-square distribution with degrees of freedom equal to the difference in the number of parameters estimated in the models (Beerli and Felsenstein 2001).

Potential asymmetry in historical gene flow between populations of different effective sizes N_e was assessed as follows: Let m_{ij} ($i \neq j$) denote the relative migration rate from population i to j. Model 6 above allows estimates of m_{ij} and m_{ji} to differ and also allows effective population sizes to differ. For each pair of populations, we calculated the net relative migration rate $m_{ij} - m_{ji}$, where i is the population with the larger effective population size (based on θ, assuming equal mutation rates μ across all populations). This yielded 15 net migration rates. Under the null hypothesis that the direction of net migration is random, there is an equal chance that the sign of $m_{ij} - m_{ji}$ will be positive or negative. A sign test was used to test this hypothesis against the one-sided alternative that positive signs occur more frequently than negative signs, indicating that net migration

TABLE 1. Measures of genetic diversity for seven Lake Michigan breeding populations of lake sturgeon. Abbreviations are as follows: n = sample size, k = mean number of alleles, A = allelic richness, H_o = observed gene diversity within individuals, H_e = expected gene diversity among individuals, and F_{IS} = Wright's inbreeding coefficient (all estimates not significantly different from zero).

Population	n	Diversity measure				
		k	A	H_o	H_e	F_{IS}
Fox River	70	4.83	3.78	0.520	0.517	−0.003
Menominee River	64	4.33	3.66	0.472	0.482	0.021
Oconto–Peshtigo rivers	122	4.83	3.67	0.539	0.534	−0.009
Kalamazoo River	17	3.58	3.41	0.508	0.499	−0.010
Manistee River	106	4.58	3.70	0.509	0.532	0.043
Muskegon River	58	4.42	3.74	0.569	0.549	−0.039
Mean values	72.83	4.43	3.66	0.519	0.519	0.000

tended to be directed from larger to smaller effective population sizes.

Potential dependence of the total migration rate between pairs of populations (sum of migration rates m_{ij} and m_{ji}) on the corresponding interpopulation geographic distance was assessed by linear regression. The 15 estimates of $m_{ij} + m_{ji}$ were regressed against the corresponding interpopulation distances D_{ij} and the null hypothesis that the slope equals zero was tested.

Comparison of measures of interpopulation straying and coalescent-based estimates of historical rates of interpopulation gene flow was conducted using a Mantel test implemented in program PASSAGE, version 2.0 (Rosenberg and Anderson 2011). Significant association between the elements of both matrices was evaluated using a permutation randomization test (Legendre 2000) and reported as a *t*-test.

RESULTS

Measures of Genetic Diversity within and among Populations

The levels of genetic diversity based on allelic richness (range, 3.41–3.78) and the observed (range, 0.472–0.569) and expected (range, 0.482–0.549) heterozygosity were similar across populations (Table 1). Following Bonferroni corrections, all populations conformed to Hardy–Weinberg expectations at all loci except for one locus for the Fox River (*AfuG56*), one for the Manistee River (*AfuG160*), and one for the Menominee River (*AfuG56*). The F_{IS} values were not statistically different from zero (range, −0.039 to +0.043; $P > 0.05$). Gametic disequilibrium was found in 3 out of a possible 396 locus combinations (0.76%). Nonindependence was found in the Manistee River population (between *Afu68* and *Afu68b*) and the Oconto–Peshtigo population (between *Afu68b* and *AfuG56* and between *Afu68b* and *Spl120*).

All populations were significantly differentiated genetically based on the estimated interpopulation variance in allele frequency ($F_{ST} = 0.041 \pm 0.006$; Table 2) and pairwise Fisher's exact tests ($P < 0.001$ for all pairings). The F_{ST}-related alpha values were adjusted to 0.003 (0.05/15) following sequential Bonferroni correction (Rice 1989). The greatest level of genetic similarity was found between the Oconto–Peshtigo rivers and the Fox River ($F_{ST} = 0.018$; $P < 0.003$ after sequential Bonferroni correction), which likely is a result of their close geographic proximity (approximate shoreline distance of 60 km). The largest level of interpopulation variance was estimated between the Menominee River and the Kalamazoo River ($F_{ST} = 0.08$; $P < 0.003$), which are located on opposite sides of the basin. It must be noted that lake sturgeon from the lower Fox River were not genetically differentiated from the large Wolf River spawning population that resides upstream in Lake

TABLE 2. Pairwise interpopulation estimates of F_{ST} based on 12 microsatellite loci for six lake sturgeon populations in Lake Michigan, 2000–2009 ($P < 0.003$ for all comparisons). The populations from the Peshtigo and Oconto rivers were combined for analysis because of a lack of significant differences in allele frequency.

River	Fox	Menominee	Oconto–Peshtigo	Kalamazoo	Manistee	Muskegon
Fox		0.044	0.018	0.063	0.044	0.027
Menominee			0.034	0.080	0.060	0.053
Oconto–Peshtigo				0.060	0.044	0.038
Kalamazoo					0.052	0.048
Manistee						0.026
Muskegon						

Winnebago (DeHaan et al. 2006). A portion of the Wolf River–Lake Winnebago population out-migrates into Lake Michigan and returns to spawn in the lower Fox River below the first dam (Elliott and Gunderman 2008). Therefore, fish characterized as being from the lower Fox River also could have originated from the Wolf River spawning population.

Based on the estimated $L(K)$ (mean $\pm$ SD log probability of the data given K over 10 replicates; ΔK method), the best estimate was five genetic clusters. The average estimated posterior probability of individual assignment to each of the five clusters was 0.532. The average membership coefficient for individuals that strayed was 0.104. Based on posterior probabilities of individual assignment, each Wisconsin tributary represented a genetic cluster. On the eastern side of the basin, individuals from the Muskegon River were members of a cluster and individuals from the Manistee and Kalamazoo rivers were members of a cluster. Individuals identified by GENECLASS as strays all had higher posterior probabilities associated with their population of assignment than with the population of capture. Based on ΔK, the estimated number of genetic clusters was two, corresponding to the eastern (Michigan) and western (Wisconsin) basin tributaries, and the relative degree of genetic differentiation among populations from the same side of the basin (mean $F_{ST} = 0.029$; $P < 0.003$) was less than between populations from different sides of the basin (mean $F_{ST} = 0.052$; $P < 0.003$; Table 2). Higher average posterior probabilities of assignment (mean $=$ 0.762) appear to result from higher interpopulation variance in allele frequency among tributaries on different sides of the basin (Table 2). Individuals identified as strays from a different region in the basin (Michigan versus Wisconsin) had a higher posterior probability of cluster assignment to their population by GENECLASS than to the population of capture.

Estimates of Contemporary and Historical Interpopulation Exchange

The contemporary straying rate across all populations was estimated to be 0.105, and asymmetrical patterns of emigration and immigration were estimated for all streams; however, statistical significance was only found for the Oconto–Peshtigo rivers (Table 3). For example, the Manistee River population had an immigration rate (0.085) that exceeded the rate of emigration (0.067), although the rates were statistically indistinguishable ($P = 0.8$). In contrast, the Oconto–Peshtigo rivers were more than three times as likely to receive immigrants from other populations as they were to export individuals (immigration $= 0.139$, emigration $= 0.045$; $P = 0.046$; Table 3).

The pattern of contemporary migration was nonrandom. The null hypothesis of random migration was rejected, regardless of whether it was assumed that all fish migrated randomly ($X^2_{obs} =$ 1,688.53, Prob[$\chi^2(30) > X^2_{obs}$] $\ll 0.001$) or that only a fraction of each population migrated randomly ($X^2_{obs} = 62.86$, Prob[$X^2 > X^2_{obs}$] $\ll 0.001$). Straying individuals that originated from streams on the eastern side of the basin were equally likely to move into streams on the opposite side of the basin (0.055) as

they were to stray to other eastern basin streams (0.033; $P = 0.44$). Similarly, Green Bay origin lake sturgeon were equally likely to stray to other Green Bay tributaries (0.074) as they were to traverse the basin (0.043; $P = 0.187$). The number of individuals straying from eastern to western tributaries also did not differ significantly from the number of individuals straying from western to eastern tributaries ($P = 0.651$).

Relative rates of historical gene flow based on coalescence analysis indicated that model 6 (the full model with variable θ and different, nonsymmetrical migration) was the model that best fit our genetic data (Table 4). Estimates of evolutionary effective population size (θ) varied from 0.684 in the Kalamazoo River to 0.989 in the Oconto–Peshtigo rivers, although estimates for five of six populations were fairly concordant (0.905–0.989; Table 5). Estimates of relative gene flow from coalescence analysis ranged from 0 (Kalamazoo River to Menominee River) to 22 (Oconto–Peshtigo rivers to Fox River; Table 5). Parameter estimates suggested that historical gene flow between populations was asymmetrical, even among geographically proximal streams. For example, the estimated relative straying rate from the Manistee River to the Muskegon River was 14.77, a value greater than that from the Muskegon River into the Manistee River (5.23; Table 5). The greatest magnitude of asymmetric migration was estimated between the Kalamazoo and Oconto–Peshtigo rivers, with a 19.93 times greater rate of gene flow from the Oconto–Peshtigo rivers into the Kalamazoo River (11.282) than from the Kalamazoo into the Oconto–Peshtigo rivers (0.566). Mantel analyses revealed no evidence for significant association between rates of historical gene flow and contemporary rates of straying ($r = 0.339$, $t = 1.39$, $P = 0.145$).

Impacts of Demographic and Environmental Variables

Analyses indicated no significant relationships between demographic and environmental variables and contemporary rates of straying. On average, the body size of resident individuals exceeded that of strays (straying individuals: 140.9 ± 3.16 cm; resident individuals: 146.6 ± 1.33 cm). However, lake sturgeon body size was not predictive of an individual's likelihood to stray ($t = 1.68$; $P = 0.099$). The proximity (km) of a migration barrier (dam) to the mouth of a tributary, a measure of the amount of spawning habitat available, was not significantly correlated with net rates of straying ($\rho = 0.486$; $P = 0.324$).

Linear regressions to quantify the relationships between the estimated contemporary rates of straying and lakescape features (which were hypothesized to affect the occupancy of open-water lake habitats and the direction of straying) indicated that the direct open-water distance between streams (mean $= 235$ km, SD $= 144$ km, range $= 27$–457 km) was a better predictor of straying rates ($r^2 = 0.316$, $P = 0.029$; Figure 2a) than least-cost distance estimates derived from either of two distance models: shoreline distance (mean $= 411$ km, SD $= 282.5$ km, range $= 30$–740 km; $r^2 = 0.101$, $P = 0.075$) and distance based on surface current patterns (mean $= 502$ km, SD $= 342.7$ km, range $= 49$–1,160 km; $r^2 = 0.061$, $P > 0.190$).

TABLE 3. Results from individual assignment tests estimating the number ($P < 0.05$) of first-generation migrant (straying) lake sturgeon captured during the breeding season within a stream, estimations of immigration and emigration rates for each population, and Fisher's exact test results for immigration versus emigration comparisons.

Presumed population of origin	Total number of individuals across Lake Michigan basin assigned to stream[a]	Individuals strayed into						Emigration rate	Emigration versus immigration P-value
		Green Bay			Eastern basin				
		Fox River	Menominee River[b]	Oconto–Peshtigo rivers	Kalamazoo River	Manistee River	Muskegon River		
Fox River	75 ($n = 70$)		2 (0.029)	5 (0.071)	0 (0.000)	5 (0.071)	0 (0.000)	0.160	0.465
Menominee River	72 ($n = 64$)	1 (0.016)		7 (0.109)	1 (0.016)	0 (0.000)	3 (0.047)	0.167	0.115
Oconto–Peshtigo rivers	110 ($n = 122$)	2 (0.016)	1 (0.008)		0 (0.000)	1 (0.008)	1 (0.047)	0.045	0.046
Kalamazoo River	16 ($n = 17$)	0 (0.000)	0 (0.000)	1 (0.059)		1 (0.059)	0 (0.008)	0.125	1.000
Manistee River	104 ($n = 106$)	2 (0.019)	1 (0.009)	2 (0.019)	1 (0.009)		1 (0.000)	0.067	0.800
Muskegon River	60 ($n = 58$)	2 (0.035)	0 (0.000)	2 (0.035)	1 (0.017)	2 (0.035)	1 (0.009)	0.117	0.765
Immigration rate		0.100	0.063	0.139	0.176	0.085	0.086		

[a] The values in parentheses are the numbers of individuals captured in each river.
[b] The values in parentheses are the proportions of fish from each river listed across the top that strayed into the river in the left column (e.g., for the Menominee River, the proportion is 2/70 = 0.029).

TABLE 4. Summary and quantitative comparison of different coalescence models of interpopulation gene flow (m_{ij}) and evolutionary effective population size (θ) for six Lake Michigan lake sturgeon populations based on 12 microsatellite loci.

Model	Hypothesis	AIC	ΔAIC	Number of parameters
6	Full model, variable θ and m_{ij}	3,753.2	0	36
5	Constant θ, within east–west basin symmetrical m_{ij}	6,292.7	2,539.5	27
4	Constant θ, crossbasin symmetrical m_{ij}	6,477.0	2,723.8	25
3	Constant θ, variable m_{ij}	3,798.5	45.3	32
2	Variable θ, symmetrical m_{ij}	8,789.4	5,036.2	24
1	N-Island model	9,631.0	5,877.8	2

Contemporary interpopulation rates of straying were significantly related to the direct open-water distance between streams ($r^2 = 0.316$, $P = 0.029$), with increased rates of straying estimated for interpopulation pairs in close geographic proximity (Figure 2a). Standardized measures of interpopulation variance in allele frequency ($F_{ST}/[1 - F_{ST}]$) were not significantly related ($r^2 = 0.236$, $P = 0.066$) to stream proximity. However, the positive relationship is likely to be ecologically meaningful (Figure 2b) given the relatively small number of populations in the basin. The standardized variance in allele frequency ($F_{ST}/[1 - F_{ST}]$) was significantly related to interpopulation rates of straying ($r^2 = 0.461$, $P = 0.012$; Figure 2c).

Relative rates of historical gene flow were biased in the direction from larger to smaller effective population size (sign test; $P = 0.018$). Additionally, the total historical rate of gene flow between pairs of populations (i.e., the sum of rates in both directions) showed a statistically significant linear decline with increasing interpopulation distance (slope $= -0.026$; adjusted $R^2 = 0.260$, $P = 0.030$). Thus, historical gene flow tended to be directed from larger to smaller populations and to decline with increasing distance between populations.

DISCUSSION

We combined coalescence analyses estimating historical interpopulation gene flow with assignment tests identifying first-generation migrants to estimate contemporary straying rates in order to characterize rates of lake sturgeon interpopulation exchange. Comparisons of contemporary straying rates and directionality with historical gene flow and directionality provided a means of evaluating the possible effects of population size, age structure, and stream spawning habitat availability that have varied over many decades.

Temporal Variation in Movement of Straying Individuals

Movement patterns among the lake sturgeon populations spawning in Lake Michigan tributaries appear to have varied over time. While attaching specific time frames to coalescence analyses is highly speculative, our estimates provide a cumulative history of gene flow since modern population genetic structuring began to form following the most recent glacial retreat (Bernatchez and Wilson 1998). The relatively high historical

rates of gene flow for lake sturgeon originating in the Oconto–Peshtigo and Manistee rivers suggest that historically the populations that spawn in those tributaries were major contributors to basinwide gene flow (Table 5). However, contemporary estimates of emigration rates for individuals originating in the Oconto and Peshtigo rivers (0.045; Table 3) and Manistee River (0.067; Table 3) are among the lowest for any tributary of Lake Michigan. While the relative rates of emigration appear to be lower than those for other populations (Table 3), the relative rates of immigration to those streams seem to be greater than long-term trends inferred from coalescence analysis (Table 5). Despite the evident temporal stochasticity in specific interstream exchanges, both historic gene flow and contemporary straying rates showed nonrandom movement patterns ($P < 0.05$). This suggests a consistent trend of source–sink dynamics throughout the basin and that populations which were once major sources of straying individuals (net exporters) later became recipients (net importers). Mantel analyses failed to document significant associations between contemporary rates of straying estimates and historical gene flow.

The differences in the relative rates of immigration and emigration are suggestive of changes in numerical abundance or habitat quality and access to spawning sites. For example, the historical estimates of gene flow associated with the Oconto–Peshtigo rivers revealed higher rates of gene flow away from than into the system (Table 5). Based on our contemporary straying estimates, a reversed trend is suggested, with more fish immigrating (0.139) than emigrating (0.045; $P = 0.046$; Table 3). One potential explanation of this difference is that current immigration into the Peshtigo, Oconto, and other rivers from the lower Fox River has increased due to the disruption of upstream movements into the upper Fox River by dams located only 7 km upstream from Lake Michigan (Daugherty et al. 2009); by contrast, in the historical period the upper Fox and Wolf rivers were connected to Lake Michigan. Moreover, because of the close geographic proximity of the Wolf River spawning grounds to the headwaters of the Oconto and Peshtigo rivers, olfactory cues influencing Wolf–Fox River fish that had migrated into Green Bay might attract fish to the Oconto or Peshtigo River. Another potential explanation of the differences between historic gene flow and contemporary straying is alteration of the olfactory cues used for homing by the vast changes in watershed land

TABLE 5. Parameter estimates for migration rates (m_{ij} or m_{ij}/μ) and θ ($4N_e\mu$) with 95% confidence intervals in parentheses for six Lake Michigan lake sturgeon populations for the model of best fit (model 6; see Table 4).

| Source population	θ	Migration to					
		Fox River	Menominee River	Oconto–Peshtigo rivers	Kalamazoo River	Manistee River	Muskegon River
Fox River	0.940 (0.894–0.989)		5.578 (4.939–6.271)	4.350 (4.025–4.692)	4.786 (3.768–5.970)	2.147 (1.868–2.452)	2.847 (2.406–3.338)
Menominee River	0.905 (0.860–0.953)	7.283 (6.533–8.089)		3.115 (2.841–3.406)	0.650 (0.325–1.146)	1.815 (1.559–2.098)	2.296 (1.899–2.746)
Oconto–Peshtigo rivers	0.989 (0.963–1.016)	22.000 (20.659–23.399)	13.109 (12.111–14.159)		11.282 (9.660–13.077)	15.539 (14.765–16.339)	14.285 (13.269–15.351)
Kalamazoo River	0.684 (0.605–0.781)	0.549 (0.363–0.791)	0.000 (0.000–0.039)	0.566 (0.454–0.695)		0.875 (0.700–1.077)	1.653 (1.327–2.029)
Manistee River	0.921 (0.892–0.953)	11.275 (10.317–12.283)	10.117 (9.247–11.040)	4.873 (4.525–5.242)	15.796 (13.884–17.876)		14.767 (13.738–15.848)
Muskegon River	0.942 (0.893–0.995)	3.499 (2.984–4.069)	4.224 (3.671–4.829)	2.412 (2.172–2.670)	6.533 (5.322–7.916)	5.234 (4.782–5.702)	
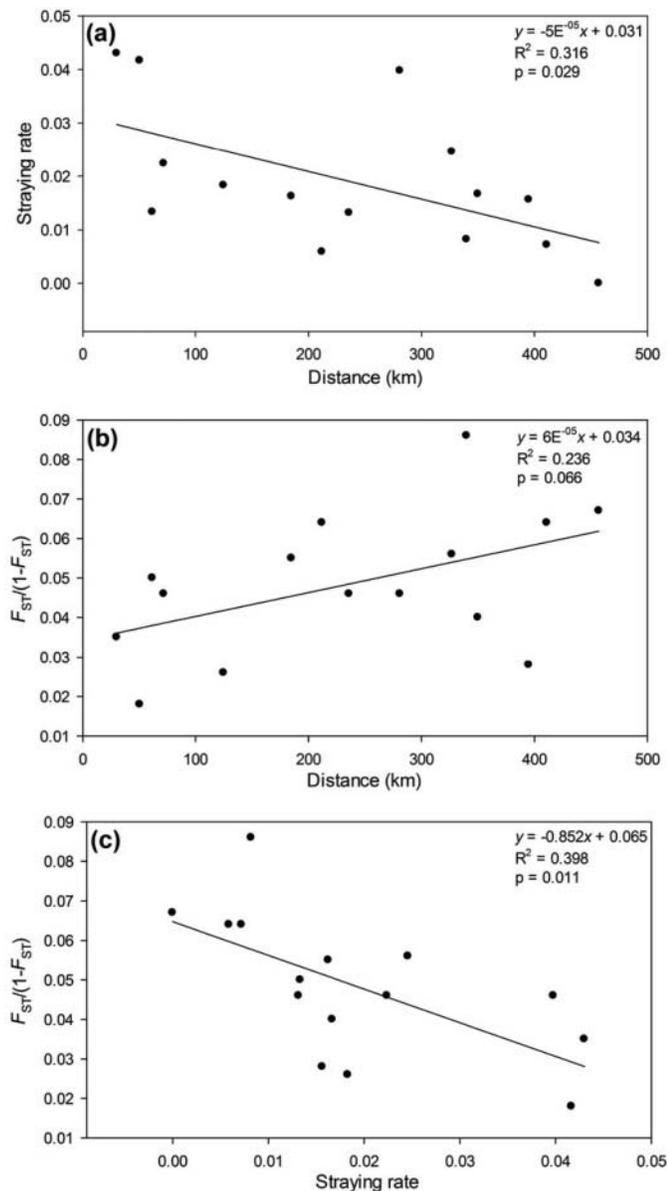
FIGURE 2. Linear regression analyses describing the relationships between measures of interpopulation genetic structure and predictor variables: **(a)** interpopulation straying rate and Euclidean open-water distance, **(b)** interpopulation genetic differentiation ($F_{ST}/[1 - F_{ST}]$) and distance, and **(c)** $F_{ST}/(1 - F_{ST})$ and interpopulation straying rate.

use (currently industrial and agricultural as opposed to historically forest dominated; Cole et al. 1998). Higher contributions by strays originating in the Muskegon and Manistee rivers to the Fox, Oconto, Peshtigo, and Menominee rivers than by those originating in other rivers reinforce the historical importance of Michigan populations to basinwide gene flow (Table 5).

Emigration rate estimates are typically calculated per capita and therefore are difficult to ascertain without accurate population abundance estimates. Considering lake sturgeon biology (i.e., long interspawning intervals and delayed reproductive maturity), the available abundance estimates for the analyzed populations have prohibitively high levels of uncertainty to be useful in estimating demographic parameters. The method that we used to estimate emigration rates relies on the assumption that sampling effort was equal among streams, which is difficult to achieve when sampling occurs across broad geographic and temporal scales. Ongoing research throughout the Great Lakes is working to improve the accuracy and precision of abundance estimates that then could be used for the estimation of demographic parameters such as immigration, emigration, recruitment, and death rates. Additionally, reliable abundance estimates would benefit our data by adding context to the contemporary straying rates that we estimated. For instance, a population with a relatively low emigration rate might contribute a larger absolute number of strays to the basinwide population than a population with a high emigration rate but low abundance.

Given the evidence of significant interpopulation genetic differentiation across the Great Lakes basin previously reported (DeHaan et al. 2006; Welsh et al. 2008), we anticipated low levels of straying in the populations investigated. However, we documented a relatively high contemporary straying rate (10.45%). This estimate of straying likely underestimates the actual value due to our criterion ($P < 0.05$) for population assignment decisions. For instance, if we were to relax the assignment criterion to $P < 0.10$, the number of strays would increase from 45 ($P < 0.05$) to 87 ($P < 0.10$). The estimated 10.45% straying rate conflicts with the relatively high F_{ST} and nonsignificant F_{IS} values we estimated, suggesting either that the individuals that stray are reproductively unsuccessful (Hendry 2004) or that contemporary straying rates are not reflective of historical rates of gene flow. The natural straying rates that we documented are higher than those in the literature. Notably, a 3.5% straying rate has been documented among two Lake Superior populations of naturally produced lake sturgeon (Homola et al. 2010). Additionally, the straying rates of naturally produced Atlantic salmon *Salmo salar* in the River Imsa, Norway, were estimated to be 6% with no correlation between straying rates and age; however, an increased straying tendency was documented, with longer elapsed time before entering a stream to spawn (Jonsson et al. 2003).

Demographic and Environmental Effects on Straying

Body length was used as a surrogate measure of age to evaluate whether age was a factor contributing to the likelihood of straying since the species' extended time to sexual maturity could result in high straying rates relative to other species. Age and the differences in age structure characterizing different populations likely are not the predominant factors associated with the documented contemporary straying rates. However, the changing size and age structure of each population must be considered, since most Great Lakes lake sturgeon populations are dominated by younger individuals as a result of recent increasing recruitment due to the cessation of harvests and increasing water quality.

Examination of the amount of stream habitat available for spawning revealed little difference between streams that differ in contemporary straying rates. Hay-Chmielewski and Whelan (1997) assessed the suitability of several Michigan tributaries for lake sturgeon spawning using the criteria of population status, discharge, gradient, barriers, spawning habitat, and river temperature. The Kalamazoo, Manistee, Menominee, and Muskegon rivers all were characterized as highly suitable for lake sturgeon reproduction. Additionally, Daugherty et al. (2009) detailed habitat suitability for sturgeon in all of the Green Bay tributaries, allowing comparison of reproductive potential between rivers, and Benson (2006) and Elliott and Gunderman (2008) documented successful reproduction in the Peshtigo, Oconto, and lower Fox rivers. Our analyses detected no significant association between the length of river accessible for spawning and straying rates. In Lake Michigan tributaries, the length of accessible potential spawning habitat has been greatly reduced from historical levels and may contribute to the relatively high levels of straying.

The positive correlation between the length (km) of riverine habitat available for spawning before the first dam and contemporary straying rates, while not statistically significant, is suggestive of an ecologically important correlation. Anthropogenically driven change to spawning areas caused by dam construction may have contributed to incongruities between historic gene flow and contemporary straying rates. Even if a dam is situated upstream of historic spawning grounds, it likely reduces recruitment when downstream habitats are altered by elevated water temperature and changes in flow regimes and substrate composition (Williams and Wolman 1984). Even if rates of gene flow have remained constant over time, low recruitment and numerically depressed population numbers (Hay-Chmielewski and Whelan 1997) likely greatly reduced effective population size, thereby magnifying the effects of genetic drift.

An alternative explanation for the temporal heterogeneity in relative rates of straying versus interpopulation measures of straying is that historical saturation of spawning habitat created density-dependent straying (e.g., Ware and Schweigert 2001). This notion is supported by the general directionality of historical gene flow from populations with higher effective population sizes to ones with lower effective population sizes. Significant reductions in lake sturgeon abundance over the past century may have altered straying propensities across the basin. Once highly abundant throughout the Great Lakes, lake sturgeon are currently far below 1% of their historic levels as a result of habitat degradation, water pollution, and overexploitation (Hay-Chmielewski and Whelan 1997; Elliott 2008).

Linear regression analyses were suggestive of relationships between alternative measures of stream proximity (direct open-water, shoreline, and surface water current straying patterns) and contemporary straying rates. The extended spawning intervals of lake sturgeon (Forsythe et al. 2012) were expected to increase the likelihood of individuals straying along the relatively shallow-water depth contours that conform to the species' maximum depth threshold (18.2 m; Harkness and Dymond 1961) despite their having to travel a longer distance to remain in shallower waters. However, the relative lack of support for least-cost paths that consider the species' maximum depth threshold (shoreline distance) and surface water current patterns suggests that lake sturgeon traverse deeper waters than previously believed.

The populations analyzed showed a significant relationship between F_{ST} and rates of straying (Figure 2c). Whitlock and McCauley (1999) suggested that equating F_{ST} to the number of individuals in a population (N) multiplied by the rate of straying (m) is unrealistic given that migration rarely occurs as assumed by Sewall Wright's island model. Wright (1943) hypothesized that the variance in gene frequencies among different populations would be related to the number of individuals migrating to or from each population. Model comparisons (Table 4) revealed that the island model, which assumes equal population size and equal and reciprocal migration, was the least supported model evaluated. The significant negative relationship documented between straying rate and F_{ST} provides evidence supporting Wright's isolation-by-distance model (Figure 2c; Wright 1943). Similarly, analyses indicate a negative relationship between straying rate and distance (Figure 2a) and a positive relationship between F_{ST} and distance (Figure 2b), as predicted in Slatkin (1993). This scenario also was documented in chum salmon *Oncorhynchus keta*, which showed a higher degree of genetic dissimilarity than predicted by the relatively high estimated straying rate (Tallman and Healey 1994).

Aspects of sample collection may have influenced study results. However, due to the inherent interannual variability in fish spawning events, we do not believe that these factors reduce the applicability of our findings. There is considerable variation among the years of our sample collection due to the constraints involved in the simultaneous sampling of seven different streams across a large geographic area and several management boundaries. Since sampling occurred over multiple years, the individuals included in our study represent a composite from multiple spawning periods for each population, thereby reducing the bias that would occur if samples were only collected during a single season. Moreover, considering the lake sturgeon's long interspawning interval (average 2–3 years for males, 3–7 years for females; Forsythe et al. 2012), using samples obtained over multiple years would be preferable to obtain a representative sample from each population. In addition, efforts were made to ensure that all of the individuals included in our baseline populations were present in each stream for spawning purposes by only analyzing individuals captured in streams during dates of known spawning activity (April 15–June 15). The individuals included in our analyses were >110 cm in length to ensure that they were at least the minimum expected size at sexual maturity; however, since male lake sturgeon spawn at a younger age than females, some individuals included in the analyses might have been immature females.

Management Implications

Relative rates of historical gene flow estimated by means of coalescence analysis and contemporary rates of straying estimated by assignments of first-generation migrants during the spawning season are not necessarily representative of the degree of demographic independence. The degree to which population growth is affected by straying (demographic connectivity) often is independent of gene flow (Lowe and Allendorf 2010). Long-term tracking using genetic or direct tagging recaptures would be necessary to determine the extent of lake sturgeon straying over longer time periods (i.e., whether individuals return for one or more breeding seasons) to evaluate the importance of demographic connectivity to population stability. Considering the numerically depressed state of all Great Lakes lake sturgeon populations and the asymmetric dispersal of straying individuals from all of the populations we analyzed, changes in the demographic connectivity within the basin could shift source populations to an overall negative growth rate (Lowe and Allendorf 2010). Moreover, low recruitment for Great Lakes lake sturgeon as a result of spawning habitat degradation (Hay-Chmielewski and Whelan 1997) may have increased the dependence of population stability on immigration from other populations (Waples and Gaggiotti 2006).

Improved understanding of lake sturgeon straying will supply the information necessary to enhance the effectiveness of conservation and management efforts. Knowledge of population composition, individual movement tendencies, and historical population characteristics are critical for informing the best possible management practices (Hay-Chmielewski and Whelan 1997; Holey et al. 2000). Determining the contemporary straying rates of Lake Michigan lake sturgeon and comparing them with historic gene flow levels provide the quantitative information necessary for setting long-term management goals aimed at lake sturgeon restoration. Additionally, understanding the straying patterns of lake sturgeon is particularly important considering their reduced population sizes (Hay-Chmielewski and Whelan 1997; Elliott 2008), which may make the species more susceptible to nontarget harvest (Bott et al. 2009) or site-specific pollution events. The correlations analyzed between straying rates, stream geographic proximity, and F_{ST} provide insight into a stage of lake sturgeon life history that is difficult to gain through conventional direct-observation methods.

Population supplementation through the release of hatchery-reared individuals is a common management strategy to augment numerically depressed populations in many fishes (Quinn 1993; Mortensen et al. 2002; Smith et al. 2002), including lake sturgeon (Hay-Chmielewski and Whelan 1997; Schram et al. 1999). Stocking of lake sturgeon could result in elevated levels of straying, as seen in other species (Quinn 1993; Mortensen et al. 2002), including other sturgeon species (Smith et al. 2002). A variation of stocking known as streamside rearing is currently being undertaken across the Lake Michigan basin in hopes of reducing the likelihood of straying for stocked fish (Elliott 2008).

The data presented here represent a valuable baseline for future comparisons when hatchery-reared fish mature.

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