Journal of Great Lakes Research xxx (2010) xxx–xxx

Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

Genetic assessment of straying rates of wild and hatchery reared lake sturgeon (*Acipenser fulvescens*) in Lake Superior tributaries

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ARTICLE INFO

Article history:
Received 29 March 2010
Accepted 16 July 2010
Available online xxxx

Communicated by Carol Stepien

Index words:
Lake sturgeon
Straying
mtDNA
Lake Superior

ABSTRACT

Natal philopatry in lake sturgeon (*Acipenser fulvescens*) has been hypothesized to be an important factor that has lead to genetically distinct Great Lakes populations. Due to declining abundance, population extirpation, and restricted distribution, hatchery supplementation is being used to augment natural recruitment and to reestablish populations. If hatchery-reared lake sturgeon is more likely to stray than naturally produced individuals, as documented in other well-studied species, outbreeding could potentially jeopardize beneficial site-specific phenotypic and genotypic adaptations. From 1983 to 1994, lake sturgeon propagated using eggs taken from Lake Winnebago adults (Lake Michigan basin) were released in the St. Louis River estuary in western Lake Superior. Our objective was to determine whether these introduced individuals have strayed into annual spawning runs in the Sturgeon River, Michigan. Additionally, we estimated a natural migration rate between the Sturgeon River and Bad River, Wisconsin populations. Presumed primiparous lake sturgeon sampled during Sturgeon River spawning runs from 2003 to 2008 were genotyped at 12 microsatellite loci. Genotypic baselines established for the Sturgeon River ($n=101$), Bad River ($n=40$), and Lake Winnebago river system ($n=73$) revealed a relatively high level of genetic divergence among populations (mean $F_{ST}=0.103$; mean $R_{ST}=0.124$). Likelihood-based assignment tests indicated no straying of stocked Lake Winnebago strain lake sturgeon from the St. Louis River into the Sturgeon River spawning population. One presumed primiparous Sturgeon River individual likely originated from the Bad River population. Four first-generation migrants were detected in the Sturgeon River baseline, indicating an estimated 3.5% natural migration rate for the system.

Introduction

The predisposition of individuals to return to natal waters for reproduction has been widely described in many fishes and has important consequences at the individual and population levels (Leggett, 1977; Miller et al., 2001; Palmer et al., 2005). The ability of individuals to migrate to a distinct spawning area or to reside in a particular region often will result in reproductive isolation among populations (Leggett, 1977). Consequently, homing to natal sites can facilitate the evolution of beneficial site-specific genotypic and phenotypic adaptation over time. In sturgeon species, existing data suggest some degree of homing associated with natal philopatry (Auer, 1996; Stabile et al., 1996; Tranah et al., 2001), resulting in genetically distinct populations (DeHaan et al., 2006; Welsh et al., 2008).

Site-specific adaptations can be jeopardized by interpopulation breeding when a particular strain of a species is stocked into an environment that differs from its origin. Outbreeding often reduces the fitness-related benefits gained through site-specific genotypic and phenotypic adaptation throughout subsequent generations (Lynch, 1991). This effect can be extended throughout an ecosystem by straying, resulting in reduced fitness for multiple populations (Edmands, 2007). Conversely, limited interbreeding between populations can enhance gene diversity and reduce the risks posed by inbreeding in numerically depressed populations due to the presence of disadvantageous alleles, thereby improving fitness of offspring (Remington and O'Malley, 2000). Excessive straying of stocked individuals could quickly exceed the low number required for interbreeding to be beneficial.

From 1983 to 1994, the Minnesota and Wisconsin Departments of Natural Resources stocked 864,500 lake sturgeon into the St. Louis

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0380-1330/$ – see front matter © 2010 Published by Elsevier B.V. on behalf of International Association for Great Lakes Research.
doi:10.1016/j.jglr.2010.08.011

River estuary in western Lake Superior. These releases included 736,000 fry, 128,000 fingerlings, and 500 yearlings (Schram et al., 1999). Eggs used for propagation originated from the Lake Winnebago strain (Lake Michigan watershed) (Schram et al., 1999). Maturation of this hatchery-reared lake sturgeon in recent years has led to suspicions of straying and possible attempted reproduction in the annual spawning runs of other Lake Superior populations. Schram (2007) documented capture of these individuals up to 300 km from their original tagging location. Movements of this magnitude are not unusual for native Lake Superior populations of lake sturgeon, which have been documented dispersing up to 280 km between spawning events (Auer, 1999).

Migration of hatchery-reared lake sturgeon into a native population has not been previously studied. The most significant obstacle to observation is the species' delayed maturation of 14–33 years in females and 12–22 years in males (Hay-Chmielewski and Whelan, 1997). Straying has been documented in stocked shortnose sturgeon (*Acipenser brevirostrum*), an amphidromous species that reaches sexual maturity much earlier than lake sturgeon. In this case, researchers found stocked shortnose sturgeon had strayed up to 278 km in a time span of only 5.2 years (Smith et al., 2002). It is also important to note that physical tagging techniques were utilized by Smith et al. (2002) to monitor movement, with tag loss being a considerable problem (72.2% loss). Our genetic-based approach to detecting migration eliminates this problem. The development of highly variable genetic markers, such as microsatellite DNA, has allowed for discrimination among different lake sturgeon populations (DeHaan et al., 2006; Welsh et al., 2008), thereby facilitating assignment of population of origin on an individual basis. Numerous studies on sturgeon species have successfully utilized multi-locus microsatellite genotyping techniques for a variety of purposes (Stabile et al., 1996; Tranah et al., 2001; Israel et al., 2004; Bott et al., 2009). When sufficient genetic variability exists between neighboring populations, it is then possible to identify first generation migrants (immigrants from populations other than the location of capture), as well as determine their population of origin (Cornuet et al., 1999). This technique has been used successfully by researchers when determining populations of origin in lake sturgeon (DeHaan et al., 2006), as well as other species (Narum et al., 2008; Sloss et al., 2008).

The objective of this study was to determine whether Lake Winnebago strain lake sturgeon stocked into the St. Louis River were straying into the spawning runs in the Sturgeon River. Detection of straying then was compared to estimates of a natural straying rate between the Sturgeon River and the nearest population, in the Bad River, Wisconsin. These three populations represent three of the five lake sturgeon populations in U.S. waters of Lake Superior (Auer, 2003). Since 1998, additional stocking of Sturgeon River strain individuals has occurred in the Ontonagon River, a Lake Superior tributary located between the Bad and Sturgeon River, although these individuals would not have reached a size consistent with those we sampled and have no bearing on our study.

Materials and methods

Study area and sample collection

Baseline samples were collected by sampling lake sturgeon spawning in the Sturgeon River, Michigan from 2001 to 2008 ($n = 525$), the Bad River, Wisconsin ($n = 40$, Fig. 1) and the Fox River of the Lake Winnebago system, Wisconsin ($n = 73$) from 1999 to 2003. DeHaan et al. (2006) showed that the lake sturgeon throughout the Lake Winnebago system is genetically indistinguishable. Individuals included in baselines were selected by size in order to reflect the demographic distribution of the samples taken from each stream when possible (size range = 114–178 cm). Adult lake sturgeon were sampled from 2003 to 2008 during spring spawning runs in the Sturgeon River ($n = 161$; size range = 98–181 cm). Fin clips were taken from the dorsal fin of the captured fish and subsequently dried and stored in individually marked envelopes. A subsample was then taken for analysis based on the body size of a likely primiparous fish (males ≤ 120 cm total length, females ≤ 135 cm total length, $n = 39$), which is consistent with ages of the lake sturgeon that were stocked in the St. Louis River.

Laboratory analysis

DNA was extracted from the dried fin clips using QIAGEN DNeasy kits (Qiagen, Inc.) using manufacturer's specifications. Stock DNA was quantified on a NanoDrop spectrophotometer 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*, *AfuG63*, *AfuG74*, *AfuG204*, *AfuG195*, *AfuG56* and *AfuG112* (Welsh et al., 2003). Microsatellite polymerase chain reactions (PCR) were conducted in 25 μL volumes containing 100 ng of template DNA, 2.5 μL of 10X 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 deoxy-nucleotide-triphosphates (dNTPs), 10 pm fluorescently labeled forward and unlabeled

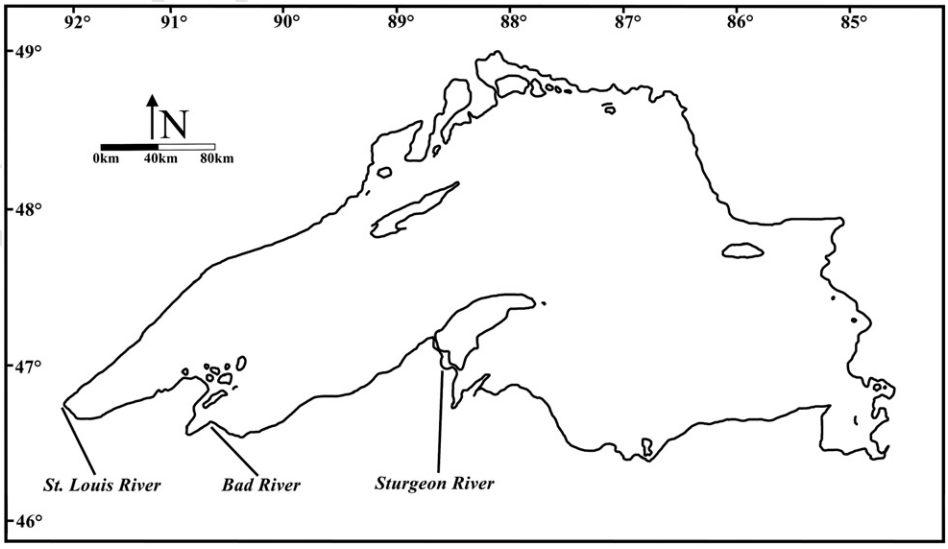

Fig. 1. Location of two rivers sampled for lake sturgeon (1999–2008) in Lake Superior and location of Lake Winnebago sturgeon stocking near Duluth, MN (1983–1994).

reverse primers, sterile water, and 0.5 U Taq polymerase. Reactions were performed using Robocycler 96 thermocyclers (Stratagene, Inc., La Jolla, California). PCR amplification was performed under the following process: 94 °C for 2 min for 1 cycle, followed by 94° for 1 min, locus-specific annealing temperature for 1 min, and 72 °C for 1 min for a locus-specific number of cycles (as described in DeHaan et al., 2006; Welsh et al., 2008), then 72 °C for 2.5 min for 1 cycle. Microsatellite PCR amplification products were visualized on 6% denatured polyacrylamide gels using the Hitachi (Tokyo, Japan) FMBIO II scanner. Resulting allele sizes were determined by comparison to lake sturgeon samples of known genotype. All genotypes were scored independently by two laboratory personnel.

Statistical analysis

Estimates of allele frequencies and Hardy–Weinberg equilibrium tests were conducted using the computer program GENEPOP (version 4, Raymond and Roussett, 1995) and further quantified using estimates of F_{IS} established using methods consistent with Weir and Cockerham (1984). Measures of genetic diversity were examined within individuals (H_o) and among individuals (H_e) within samples, per locus, and averaged over loci using the program GENEPOP. Genetic variation was measured using the pair-wise genetic differential index (F_{ST}, Cornuet et al., 1999). Due to the rate at which microsatellite alleles mutate, additional measures of inter-population differentiation that use the frequency and evolutionary relationships (i.e., differences in allele size or number (n) of tandem repeats of the core motif (e.g., $[CA]_n$)) may provide additional inferences about historical genetic relationships among populations (Slatkim, 1995; Roussett, 1996). Accordingly, we estimated R_{ST} (Roussett, 1996; Goodman, 1997) using program FSTAT version 2.9.3.1 (Goudet, 2001). Previous studies have shown considerable genetic variation among our tested populations (DeHaan et al., 2006; Welsh et al., 2008). Gametic disequilibrium was examined to provide estimates of locus independence from other loci in each population. Estimates of gametic disequilibrium and allelic richness were examined using FSTAT. A Bonferroni correction was used to adjust significance to account for multiple tests.

Assignment of unknown individuals' population of origin was performed using the frequency-based method described in Paetkau et al. (1995) using the program GENECLASS (version 2.0.h, Cornuet et al., 1999). We also used the program GENECLASS to detect first-generation migrants (immigrants from another population). Following recommendations outlined in Paetkau et al. (2004), we used the frequency-based approach described by Paetkau et al. (1995) and Monte Carlo resampling protocols using the ratio of likelihoods (L = L_home/L_max likelihood, Paetkau et al., 2004), where L_home and L_max are the likelihoods of an individual's multi-locus genotype to have arisen in the population genotyped or the population of most likely origin, respectively. We simulated 10,000 individuals and a 0.05 type I error rate to establish statistical support for individuals straying from populations other than the stream in which the individual was sampled (L_home). Based upon previous research indicating sources of possible migration (DeHaan et al., 2006; Welsh et al., 2008), our established baseline populations represent the three possible sources of immigrants into these three systems, which is a requisite for the chosen assignment method (Paetkau et al., 2004).

Results

Measures of genetic diversity

Measures of genetic diversity indicated the lowest diversity in the Fox River (Lake Winnebago system), and highest diversity in the Bad River (Table 1). Allelic richness was lowest in the Bad River population (3.97), and highest in Fox River population (4.38, Table 1). Although allelic richness was similar between the Sturgeon and Fox Rivers, expected heterozygosity (H_e) values of 0.540 and 0.519 (Table 1), respectively, offer evidence of appreciable genetic diversity in those populations. Gametic disequilibrium was found in three of 198 possibilities (1.51%), all in the Sturgeon River population (attributed to chance), where non-independence was found between *AfuG68B* and *AfuG9*, *AfuG68B* and *AfuG112*, and *AfuG63* and *AfuG56*. Mean estimates of inter-population variance in allele frequency (F_{ST}) was estimated to be 0.103. We estimated R_{ST} to be slightly higher (0.124 over all loci) due to differences in the frequency of alleles and differences in allele size (see Table A in DeHaan et al., 2006 for description of allele sizes and frequencies for lake sturgeon populations across the upper Great Lakes including the three populations described herein).

Table 1
Measures of genetic diversity for two Lake Superior (Sturgeon River and Bad River, 1999–2008) and one Lake Winnebago, Wisconsin region (Fox River, 1999–2003) breeding populations of lake sturgeon.

		Diversity measures				
Population	n	k	A	H_o	H_e	F_{IS}
Sturgeon R.	101	4.75	4.35	0.53	0.540	0.03
Bad R.	40	4	3.97	0.58	0.560	−0.04
Fox R.	73	4.83	4.38	0.520	0.52	0

n, sample size; k, number of alleles; A, allelic richness; H_o, observed gene diversity within individuals; H_e, expected gene diversity among individuals; F_{IS}, Wright's inbreeding coefficient.

Detection of St. Louis River and natural straying

We found no evidence of Lake Winnebago strain lake sturgeon in the Sturgeon River spawning population. There was one occurrence of a presumed primiparous individual from the Bad River population present during Sturgeon River spawning activity ($p = 0.016$). Four individuals originating in the Bad River were apparent in the Sturgeon River population (p-values ranged from 0.0031 to 0.0264). There was no evidence of first-generation migrants in the Bad River. A 3.5% natural straying rate was estimated from the presence of the five individuals which strayed into the spawning runs of the Sturgeon River.

Discussion

Our results support previous research findings detailing levels of population genetic structure of lake sturgeon in the Laurentian Great Lakes and their tributaries. Detection of high levels of genetic divergence (mean $F_{ST} = 0.103$; mean $R_{ST} = 0.124$) among the sampled streams corresponds with estimates of inter-population variance in allele frequency described previously, including the populations characterized in the present study. Welsh et al. (2008) described inter-population F_{ST} among 20 Great Lakes populations (ranging from 0.00 to 0.22; mean = 0.09). Examination of 11 Great Lakes populations by DeHaan et al. (2006), yielded a range of F_{ST} of 0.000 to 0.147 (mean = 0.055). Additionally, our estimation of natural migration rate is concordant with that of DeHaan et al. (2006), who used a coalescent-based analysis (Beerli, 2002) to estimate higher historical levels of migration from the Bad River to the Sturgeon River than from the Sturgeon River to the Bad River. Bott (2006) found a similar asymmetrical migration pattern in Lake Michigan where data showed individuals migrating exclusively from the eastern side of the basin to the west. Studies of lake sturgeon straying among breeding populations during the reproductive season using direct measures such as telemetry and tag returns are lacking. However, we believe the indirect estimates of west to east dispersal documented in our genetic analysis and described previously (DeHaan et al., 2006) could be an

Please cite this article as: Homola, J.J., et al., Genetic assessment of straying rates of wild and hatchery reared lake sturgeon (*Acipenser fulvescens*) in Lake Superior tributaries, J Great Lakes Res (2010), doi:10.1016/j.jglr.2010.08.011

indicator of future movements of stocked Lake Winnebago strain lake sturgeon from the St. Louis River when they reach reproductive maturity and may stray to neighboring near-shore habitats and streams.

The degree of straying inferred between the Lake Superior populations of lake sturgeon that we investigated was expected. Although little research has quantified straying rates in sturgeon species, we can make inferences based on previous lake sturgeon research and the straying rates of other species that exhibit natal philopatry. Research focused on estimating lake sturgeon gene flow in the Great Lakes suggests that some degree of straying does occur (DeHaan et al., 2006; Welsh et al., 2008), although it is impossible to make a direct comparison between straying rates and gene flow without further investigation. Limited straying is common in other species that demonstrate natal fidelity. For example, pink salmon (*Oncorhynchus gorbuscha*), has exhibited straying rates ranging from 4.4 to 6.9% (Mortenson et al., 2002). Hatchery-reared American shad (*Alosa sapidissima*), another species with strong natal fidelity, has been documented to have a 0.2% straying rate (Hendricks et al., 2002).

Future monitoring of straying of lake sturgeon stocked in the St. Louis River is recommended. Despite our lack of evidence suggesting a presence of Lake Winnebago strain individuals in the Sturgeon River population, future investigation is warranted to quantify migration. The effects of outbreeding on the remnant population of lake sturgeon in the Sturgeon River by Lake Winnebago strain individuals could be important due to the drastically contrasting habitats within which each have evolved. Lake Winnebago is a comparatively small (557 km^2) lake system containing two tributaries used by spawning lake sturgeon, the Wolf and Upper Fox Rivers, with the Lower Fox River draining Lake Winnebago to Lake Michigan. Lake Winnebago is a shallow (mean depth 4.7 m, max. 6.4 m) eutrophic lake that is isolated from Lake Michigan by a series of dams and locks downstream from the lake (Choudhury et al., 1996). In contrast, Lake Superior is a large (82,100 km^2) oligotrophic lake with a mean depth of 148 m, with approximately 71% of its depth greater than 100 m (Assel et al., 2003).

Individuals genotyped for this study were sampled from 2003 through 2008 and represented a possible age distribution of the hatchery-reared Lake Winnebago strain of 9–25 years. Although the timing of sampling that occurred for our study allowed sufficient maturation time for most of the individuals in question, the likelihood of St. Louis River migrants appearing in the spawning runs of nearby streams may increase over the next 10–15 years as remaining individuals reach maturity.

Since the stocking of Lake Winnebago strain lake sturgeon into the St. Louis River was discontinued in 1994 (Schram et al., 1999), there has been an increasing emphasis on the use of population genetic theory and empirical genetic data to guide supplementation prescriptions (Welsh et al., 2010). A renewed stocking effort in the St. Louis River from 1998 to 2000 using a Lake Superior source population (Sturgeon River, Michigan) (Schram, 2007) reflected growing consensus of the importance of embracing genetic concepts. Use of a strain of similar genetic structure to the native population is currently accepted as an important factor to increase the long range viability of reintroduced lake sturgeon (Welsh et al., 2010).

Effective management necessitates a fundamental understanding of rates of straying that occur in natural populations. No barriers exist in the Great Lakes to prevent lake sturgeon from migrating long distances, even between lake basins. The lake sturgeon's life history characteristics likely also play an important role in influencing contemporary levels of spatial population structure (Waldman et al., 2002) and propensity for straying could vary among different regions in the Great Lakes. Life history characteristics including delayed sexual maturity (approximately 15–20 years), long intervals between spawning (up to 7 years), and extensive migrations between spawning periods (Houston, 1987; Auer 1999) suggest that natural rates of straying may be high. These characteristics also make the collection of tag return data difficult for this species.

The results from this study provide evidence within a portion of one Great Lake basin for heterogeneity in dispersal direction of lake sturgeon relative to population of origin, adding important information to a poorly understood area of sturgeon biology. Although other studies (e.g., Rusak and Mosindy, 1997; Auer 1999; Knights et al., 2002; Haxon, 2003) have examined patterns of lake sturgeon movement, the methods used in this study allowed analysis of sample sizes far greater than those that are possible via direct methods, with samples taken over a span of time that would have been difficult with direct methods. Other Great Lake basins are characterized by different physical and biotic conditions that may differentially affect the rate and direction of dispersal among breeding populations. Comparisons of straying among different regions of the Great Lakes that are characterized by different environmental conditions would serve to generalize findings reported in this study, and will help inform more effective conservation and management actions for lake sturgeon.

Acknowledgments

This study was funded by the College of Agriculture and Natural Resources undergraduate research program at Michigan State University and the Michigan Department of Natural Resources and Environment.

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Please cite this article as: Homola, J.J., et al., Genetic assessment of straying rates of wild and hatchery reared lake sturgeon (*Acipenser fulvescens*) in Lake Superior tributaries, J Great Lakes Res (2010), doi:10.1016/j.jglr.2010.08.011

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Please cite this article as: Homola, J.J., et al., Genetic assessment of straying rates of wild and hatchery reared lake sturgeon (*Acipenser fulvescens*) in Lake Superior tributaries, J Great Lakes Res (2010), doi:10.1016/j.jglr.2010.08.011