

Genetic Evidence for Hybridization of Pallid and Shovelnose Sturgeon

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Abstract

To determine the genetic origin of individual sturgeon that are morphologically intermediate to pallid (*Scaphirhynchus albus*) and shovelnose (*Scaphirhynchus platorhynchus*) sturgeon, we combined previously published mitochondrial DNA (mtDNA) and microsatellite data with additional microsatellite data. Two sympatric populations of pallid and shovelnose sturgeon from the upper Missouri River and a sympatric population containing pallid, shovelnose, and putative pallid-shovelnose hybrids from the Atchafalaya River were analyzed using an index of hybridization and a principle components analysis of individual relatedness scores. The addition of new microsatellite data improved our ability to genetically differentiate individual pallid and shovelnose sturgeon collected in both areas. Our methods distinguished morphologically intermediate Atchafalaya River sturgeon, which appear to be genetically intermediate between pallid and shovelnose sturgeon. The results support a hybrid origin for morphologically intermediate individuals, although it is unclear whether they are all first-generation hybrids or if some are the result of subsequent backcrossing with the more common shovelnose sturgeon.

The pallid sturgeon (*Scaphirhynchus albus*) was first described by Forbes and Richardson (1905) as a morphological variant of the shovelnose sturgeon (*Scaphirhynchus platorhynchus*), based on morphometric and meristic differentiation and on respective maximum size of 1500 mm and 900 mm standard length as adults (Bailey and Cross 1954; Carlson et al. 1985; Keenlyne et al. 1994b). The two species also have differing geographic distributions and spawning habitat preferences (Kallemeyn 1989). The shovelnose sturgeon is relatively common and widely distributed throughout the Mississippi, Missouri, Ohio, and Tennessee Rivers, including many major tributaries (Carlson et al. 1985). The pallid sturgeon is less abundant and limited to the main channels of the Missouri, Yellowstone, and lower Mississippi Rivers, where they occur sympatrically with shovelnose sturgeon (Carlson et al. 1985; Mayden and Kuhuda 1997). Pallid sturgeon prefer larger river channels with swift, turbid flows and rocky or sandy substrate, whereas shovelnose sturgeon prefer slower flows and shallow pools associated with sandbars and channel edges (Carlson et al. 1985; Dwyer and Sandoval 1993; Forbes and Richardson 1905; Kallemeyn 1989).

Morphologically intermediate forms identified as hybrids are found in more than half of the pallid sturgeon's range (Keenlyne et al. 1994a). Hybrid identification is based on morphologic intermediacy or the inconsistency of some characters (e.g., barbel size and position, scute patterns, and

coloration) (Carlson et al. 1985). Morphologic hybrids are mostly restricted to the lower end of the pallid sturgeon's distribution, including the Mississippi and Atchafalaya Rivers in Louisiana. Damming and channelization have degraded or potentially removed the pallid sturgeon's preferred spawning habitat (Kallemeyn 1989). These alterations have been implicated in the species' decline and eventual listing as endangered in 1990 under the Endangered Species Act (U.S. Department of the Interior, U.S. Fish and Wildlife Service 1990). Interspecific hybridization is frequently documented in habitat that has been modified naturally or by human-induced forces (Arnold 1997; Avise 1994; Campton 1987; Dowling and Secor 1997). Fishes are especially susceptible to interspecific hybridization due to external fertilization (in most species) and generally weak ethological barriers (Campton 1987). A high alleged incidence of hybridization in the lower Mississippi and Atchafalaya Rivers (Keenlyne et al. 1994a) has caused concern regarding the potential negative effects of hybridization on the rare pallid sturgeon (Carlson et al. 1985).

Morphologic intermediacy can be misleading when determining if hybridization has occurred between two morphotypes. First-generation hybrids are not always morphologically intermediate to the parental types (Neff and Smith 1979), while morphologic intermediacy does not always indicate that hybridization has taken place (Wayne

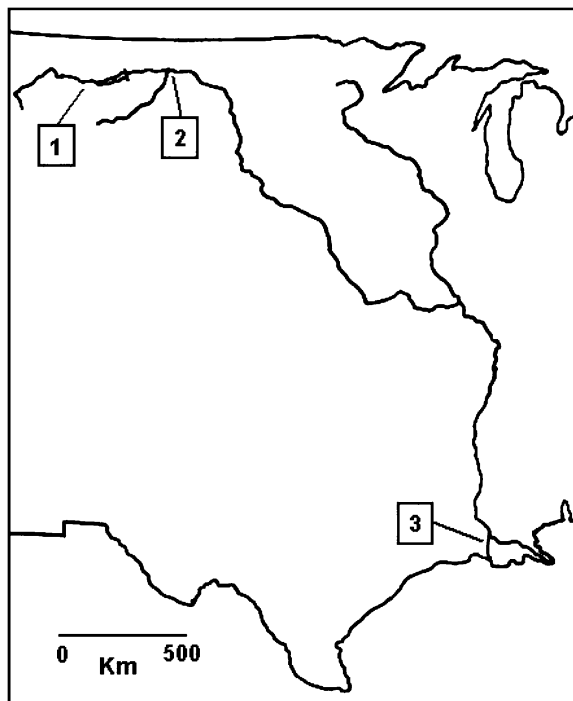


Figure 1. Geographic localities in the central United States from which pallid, shovelnose, and putative pallid-shovelnose hybrid sturgeon were collected (sample sizes and standard lengths in parentheses): (1) Upper Missouri River above Fort Peck Lake: pallid ($n = 8$, mean SL = 1298 mm, range = 1207–1387 mm) and shovelnose ($n = 10$, mean SL = 754 mm, range = 588–897 mm) sturgeon; (2) Upper Missouri River below Fort Peck Dam, including confluence of the lower Yellowstone River: pallid ($n = 11$, mean SL = 1456 mm, range = 1016–1540 mm) and shovelnose ($n = 10$, mean SL = 525 mm, range = 326–600 mm) sturgeon; (3) Atchafalaya River: pallid ($n = 10$, mean SL = 747 mm, range = 567–840 mm) and shovelnose ($n = 17$, mean SL = 549 mm, range = 429–654 mm) sturgeon, and putative pallid-shovelnose hybrids ($n = 9$, mean SL = 673 mm, range = 551–722 mm). Adapted from Campton et al. 2000.

and Jenks 1991). A detailed genetic investigation focusing on morphologically intermediate pallid and shovelnose sturgeon would provide more information about the origin of this group.

Early genetic investigations did not demonstrate genetic differentiation between pallid and shovelnose sturgeon. In the first genetic study concerning these species, 3 of 37 allozyme loci examined were polymorphic in both species with similar allele frequencies (Phelps and Allendorf 1983). A subsequent study using restriction enzyme analysis of five protein-coding loci also failed to distinguish the two species (Morizot 1994). Pallid and shovelnose sturgeon also showed little mitochondrial DNA (mtDNA) sequence divergence in the control region (Campton et al. 2000) and the cytochrome *b* gene (Simons et al. 2001). However, Campton et al. (2000)

found significant haplotype frequency differences between pallid and shovelnose sturgeon from the Missouri and Atchafalaya Rivers. Tranah et al. (2001) examined variation at microsatellite loci using the same samples from Campton et al. (2000) and found that allele frequencies differed significantly between pallid and shovelnose sturgeon from the Missouri and Atchafalaya Rivers. In addition, allele frequencies for morphologic hybrids from the Atchafalaya River differed significantly from those of pallid sturgeon and were statistically indistinguishable from shovelnose sturgeon (Tranah et al. 2001).

This study extends the studies of Campton et al. (2000) and Tranah et al. (2001) to determine if morphologically intermediate individuals found in the lower Mississippi River basin are of hybrid origin. By combining data from both studies with additional microsatellite data and using individual-based analyses, we seek to determine if patterns of morphological differentiation are consistent with genetic data.

Materials and Methods

Sampling Sites and Specimen Collection

Pallid and shovelnose sturgeon were examined from two Missouri River (MR), Montana sites and one Atchafalaya River (AR), Louisiana site (Figure 1). Blood and fin samples were collected by personnel from state and federal agencies in 1992 and archived. Each specimen was measured (mm SL) and classified as a pallid sturgeon, shovelnose sturgeon, or morphologic hybrid sturgeon based on the criteria of Keenlyne et al. (1994a,b). In the upper MR, pallid ($n = 19$) and shovelnose ($n = 19$) sturgeon were sampled 400 km upstream of Fort Peck Lake and downstream of Fort Peck Dam at the confluence of the Yellowstone and Missouri Rivers. Pallid ($n = 10$), shovelnose ($n = 18$), and morphologic hybrid sturgeon ($n = 10$) were also obtained from the AR site in the lower Mississippi River basin.

Microsatellites

Archived genomic DNA stored in TE buffer (Sambrook et al. 1989) was obtained for individuals classified morphologically as pallid, shovelnose, and hybrids from the three localities. All samples were analyzed with four microsatellite loci (*Spl 101*, *Spl 105*, *Spl 106*, and *Spl 173*) developed from a shovelnose sturgeon genomic library (McQuown et al. 2000). Genomic DNA was amplified in 15 μ l reactions containing 20 mM Tris-HCl, pH 8.4, 50 mM KCl, 1.5 mM MgCl₂, 0.5 mM dNTPs, 0.5 μ M primers, and 0.5 units *Taq* DNA polymerase (GIBCO). Reaction mixtures were amplified using the following procedure: 94°C for 2 min, 30 cycles at 94°C for 30 s, 52°C for 30 s, 72°C for 1 min, and a final step at 72°C for 5 min. Amplification products were mixed 1:1 with 98% formamide loading dye, denatured for 3 min at 95°C and cooled on ice before running on 5% denaturing acrylamide gels at 60W for 30 min. Products were fluorescently visualized using the agarose and Vistra Green

Table 1. Percent assignment and misassignment using the “critical population method” of WHICHLOCI 1.0 (Banks et al. 2003)

	n	5 Loci ^a		9 Loci ^b		10 Loci ^c	
		assigned	mis-assigned	assigned	mis-assigned	assigned	mis-assigned
P-MR	19	82.8	4.9	95.6	4.8	96.6	4.4
S-MR	19	52.2	8.4	82.4	2.6	89.2	1.7
P-AR	10	86.6	7.4	95.8	4.6	98.8	4.4
S-AR	18	66.4	8.9	75.6	1.4	73.2	0.6
H-AR	10	63.2	7.7	87.2	4.8	92.4	3.4
Average		70.2	7.5	87.3	3.6	90.0	2.9

The following locus combinations were used: (a) five microsatellite loci from Tranah et al. (2001); (b) five microsatellite loci from Tranah et al. (2001) with four new microsatellite loci; (c) five microsatellite loci from Tranah et al. (2001) with four new microsatellite loci and mtDNA control region data from Campton et al. (2000). Sample sites for pallid sturgeon (P), shovelnose sturgeon (S), and morphologic hybrid (H) sturgeon are the Missouri River (MR) and Atchafalaya River (AR). Assignments were based on minimum 95% assignment and maximum 5% misassignment thresholds with no threshold log-likelihood ratio implemented.

overlay procedure of Rodzen et al. (1998) and scanned with a Molecular Dynamics 595 fluorimager. Alleles were sized using FragneNT analysis (Molecular Dynamics, Sunnyvale, CA).

We assembled a dataset that combined codominant genotypes classified from four new microsatellite loci (*Spl 101*, *Spl 105*, *Spl 106*, and *Spl 173*; primers from McQuown et al. 2000) and five microsatellite loci from Tranah et al. (2001) (*Afu 19*, *Afu 34*, *Afu 68*, and *Afu 57*; primers from May et al. 1997; and *Aox 27*; primer from King et al. 2001) with mtDNA control region data from Campton et al. (2000).

Analyses

To determine if the addition of four microsatellite loci increased resolving power we assessed the percent assignment and misassignment for the following locus combinations: (1) five microsatellite loci from Tranah et al. (2001); (2) five microsatellite loci from Tranah et al. (2001) with four new microsatellite loci; and (3) five microsatellite loci from Tranah et al. (2001) with four new microsatellite loci and mtDNA control region data from Campton et al. (2000). Using the “critical population method” of WHICHLOCI 1.0 (Banks et al. 2003), an individual-based assignment method, we tested the accuracy of assignment for individual pallid, shovelnose, and morphologic hybrid sturgeon to each population. Assignment accuracy was based on a minimum assignment threshold of 95% and a maximum misassignment threshold of 5%, with no threshold log-likelihood ratio implemented. Running trial assignments with individual and combined datasets allows us to rank their effectiveness for correct population assignment and tendency for false assignments.

Observed heterozygosity (H_o), expected heterozygosity (H_e), inbreeding coefficient (F_{IS}) (Weir and Cockerham 1984), and deviations from Hardy-Weinberg expectations were calculated with GENEPOP 3.0 (Raymond and Rousset 1995). An index of relatedness (R_{XY}) was calculated for all individuals ($n = 76$) using Relatedness 4.2 (Queller and Goodnight 1989). Principal components analysis (PCA) and clustering were performed for relatedness values with

Statistica for Windows version 5.1 (Statsoft Inc.). The hybrid index (I_H) of Campton and Utter (1985) was used to quantitatively analyze the likelihood of hybrid origin for the putative hybrid individuals. This index measures the relative probability that a composite genotype arose by random mating within each of the two source species; in this case, pallid and shovelnose sturgeon. The index ranges from 0.0 to 1.0 and will be close to one of these values when an individual genotype has a high probability of belonging to either species, respectively. The expectation is that genotypically intermediate individuals (hybrids) would have an index value that is intermediate to that of pallid and shovelnose sturgeon. We first validated the performances of R_{XY} and I_H on reproductively isolated sturgeon from the Missouri River before examining the morphologically intermediate individuals from the Atchafalaya River.

Results

The addition of four microsatellite loci to the combined Tranah et al. (2001) and Campton et al. (2000) datasets improved individual assignment accuracy to 90.0% and decreased the rate of misassignment to 2.9% (Table 1). A range of 2 to 11 alleles was observed per microsatellite locus (all of which displayed patterns consistent with disomic inheritance) and randomized tests showed greater than 95% genotypic distributions to conform to Hardy-Weinberg expectations (Table 2). No linkage disequilibrium was detected. For details about the mtDNA control region haplotypes see Campton et al. (2000).

The first two R_{XY} PCA factors cluster individual MR pallid and shovelnose sturgeon into two groups with no interspecific overlap and account for 52% of the variance among samples (Figure 2a). The R_{XY} PCA analysis of AR pallid, shovelnose, and putative hybrid sturgeon accounts for 35% of the variance among samples (Figure 2b). Pallid and shovelnose sturgeon formed distinct groups (with the exception of a single pallid sturgeon sample), while morphologic hybrids formed a loosely clustered group largely intermediate to pallid and shovelnose sturgeon.

Table 2. Allele frequencies, observed heterozygosity (H_O), expected heterozygosity (H_E), inbreeding coefficient (F_{IS}), sample sizes (N), for all sturgeon populations based on nine microsatellite loci. Sample sites for pallid sturgeon, shovelnose sturgeon, and morphologic hybrid sturgeon are the Missouri River (MR) and the Atchafalaya River (AR). Asterisks denote deviations from Hardy-Weinberg expectations for which significant ($\alpha = 0.05$) F_{IS} values were obtained

Locus	Allele	Population					
		P – MR	S – MR	P – AR	S – AR	H – AR	
Afu 19	(N)	19	18	10	18	10	
	122	0.66	0.64	1.00	0.89	0.45	
	125	0.34	0.36	0.00	0.11	0.55	
	H_O	0.26	0.50	0.00	0.22	0.50	
	H_E	0.46	0.47	0.00	0.20	0.52	
	F_{IS}	0.44	-0.06	1.00	-0.10	0.04	
Afu 34	(N)	19	19	10	18	10	
	139	0.18	0.13	0.00	0.03	0.15	
	143	0.03	0.00	0.00	0.00	0.00	
	147	0.45	0.76	0.80	0.81	0.80	
	151	0.00	0.03	0.05	0.00	0.00	
	155	0.03	0.00	0.00	0.00	0.00	
	159	0.29	0.05	0.15	0.17	0.00	
	163	0.03	0.00	0.00	0.00	0.00	
	167	0.00	0.00	0.00	0.00	0.05	
	171	0.00	0.03	0.00	0.00	0.00	
	H_O	0.58	0.37	0.30	0.28	0.40	
	H_E	0.70	0.41	0.35	0.33	0.35	
	F_{IS}	0.18	0.10	0.16	0.17	-0.14	
	Afu 68	(N)	19	19	10	18	10
113		0.00	0.00	0.00	0.03	0.00	
117		0.00	0.13	0.10	0.03	0.15	
121		0.00	0.05	0.20	0.22	0.15	
125		0.16	0.53	0.15	0.36	0.20	
129		0.16	0.05	0.20	0.11	0.05	
133		0.00	0.00	0.05	0.00	0.00	
137		0.61	0.08	0.15	0.06	0.25	
141		0.08	0.13	0.15	0.17	0.20	
145		0.00	0.03	0.00	0.03	0.00	
H_O		0.47	0.74	0.90	0.83	1.00	
H_E		0.59	0.69	0.88	0.80	0.85	
F_{IS}		0.21	-0.06	-0.02	-0.05	-0.18	
Afu 57		(N)	17	19	10	17	9
	144	0.06	0.55	0.10	0.53	0.39	
	147	0.94	0.45	0.90	0.47	0.61	
	H_O	0.12	0.16	0.00	0.59	0.78	
	H_E	0.11	0.51	0.19	0.51	0.50	
	F_{IS}	-0.03	0.70*	1.00*	-0.15	-0.60	
Aox 27	(N)	16	19	10	18	10	
	121	0.31	0.29	0.50	0.28	0.40	
	125	0.66	0.50	0.10	0.58	0.30	
	129	0.03	0.21	0.40	0.14	0.30	
	H_O	0.69	0.68	0.60	0.44	0.90	
	H_E	0.49	0.64	0.61	0.58	0.69	
	F_{IS}	-0.44	-0.07	0.02	0.24	-0.32	
	Spl 101	(N)	17	18	10	18	10
		286	0.50	0.08	0.45	0.36	0.30
		290	0.21	0.06	0.10	0.14	0.25
294		0.18	0.53	0.25	0.28	0.20	
298		0.00	0.22	0.20	0.00	0.05	
302		0.00	0.03	0.00	0.03	0.05	
306		0.00	0.06	0.00	0.03	0.10	
310		0.12	0.03	0.00	0.11	0.05	
314		0.00	0.00	0.00	0.03	0.00	
318		0.00	0.00	0.00	0.03	0.00	
H_O		0.76	0.78	0.70	0.94	0.90	
H_E		0.68	0.68	0.72	0.78	0.83	
F_{IS}		-0.12	-0.16	0.03	-0.22	-0.09	
Spl 105		(N)	18	19	10	18	10
	120	0.00	0.03	0.00	0.00	0.00	
	124	0.00	0.00	0.00	0.06	0.00	
	128	0.33	0.45	0.45	0.28	0.45	

Table 2. Continued

Locus	Allele	Population					
		P – MR	S – MR	P – AR	S – AR	H – AR	
	132	0.61	0.53	0.35	0.36	0.35	
	136	0.00	0.00	0.05	0.08	0.05	
	140	0.00	0.00	0.10	0.06	0.05	
	144	0.06	0.00	0.05	0.14	0.10	
	152	0.00	0.00	0.00	0.03	0.00	
	H_O	0.56	0.47	0.50	0.89	0.60	
	H_E	0.53	0.54	0.69	0.78	0.69	
	F_{IS}	-0.06	0.12	0.29	-0.14	0.14	
	Spl 106	(N)	18	16	10	18	10
		218	0.03	0.00	0.05	0.03	0.05
222		0.00	0.03	0.00	0.03	0.00	
226		0.00	0.00	0.00	0.06	0.10	
230		0.00	0.09	0.00	0.06	0.10	
234		0.00	0.22	0.10	0.14	0.00	
238		0.61	0.19	0.40	0.19	0.30	
242		0.00	0.09	0.10	0.06	0.10	
246		0.31	0.28	0.35	0.28	0.25	
250		0.03	0.03	0.00	0.03	0.00	
254		0.03	0.06	0.00	0.11	0.10	
258		0.00	0.00	0.00	0.03	0.00	
H_O		0.44	0.94	0.90	0.78	0.70	
H_E		0.55	0.84	0.73	0.87	0.85	
F_{IS}	0.19	-0.12	-0.25	0.10	0.18		
Spl 173	(N)	18	19	8	18	9	
	180	0.00	0.29	0.06	0.28	0.00	
	184	0.22	0.03	0.19	0.19	0.00	
	188	0.39	0.42	0.31	0.14	0.72	
	192	0.03	0.13	0.38	0.08	0.06	
	196	0.17	0.08	0.06	0.14	0.06	
	200	0.17	0.05	0.00	0.08	0.17	
	204	0.03	0.00	0.00	0.08	0.00	
	H_O	0.44	0.68	0.50	0.78	0.56	
	H_E	0.76	0.73	0.77	0.85	0.47	
F_{IS}	0.43*	0.07	0.36*	0.09	-0.19		

I_H scores grouped individual MR pallid and shovelnose sturgeon at opposite ends of the histogram with no overlap at intermediate values (Figure 3a). Atchafalaya River pallid and shovelnose sturgeon also had distinctly different distributions of I_H scores (Figure 3b). Morphologic hybrids formed a genotypically intermediate group whose I_H scores overlapped with those of shovelnose sturgeon (Figure 3b).

Discussion

In assessing the microsatellite (Tranah et al. 2001) and mtDNA data (Campton et al. 2000), Allendorf et al. (2001) suggest that pallid and shovelnose sturgeon from the lower Mississippi River never evolved complete reproductive isolation or are undergoing substantial hybridization. The mtDNA control region divergence (2.06%) observed by Campton et al. (2000) and the mean F_{ST} values (0.16) reported by Tranah et al. (2001) for pallid and shovelnose sturgeon from the Atchafalaya River are less than what is typically observed between species, suggesting that these populations may not represent distinct evolutionary lineages (Allendorf et al. 2001). Allendorf et al. (2001) argue that these populations may not have been distinct lineages long enough to accumulate sufficient sequence divergence to warrant species status. Alternatively, there may be no pure pallid sturgeon remaining in what is essentially a hybrid group in the lower Mississippi River (Allendorf et al. 2001).

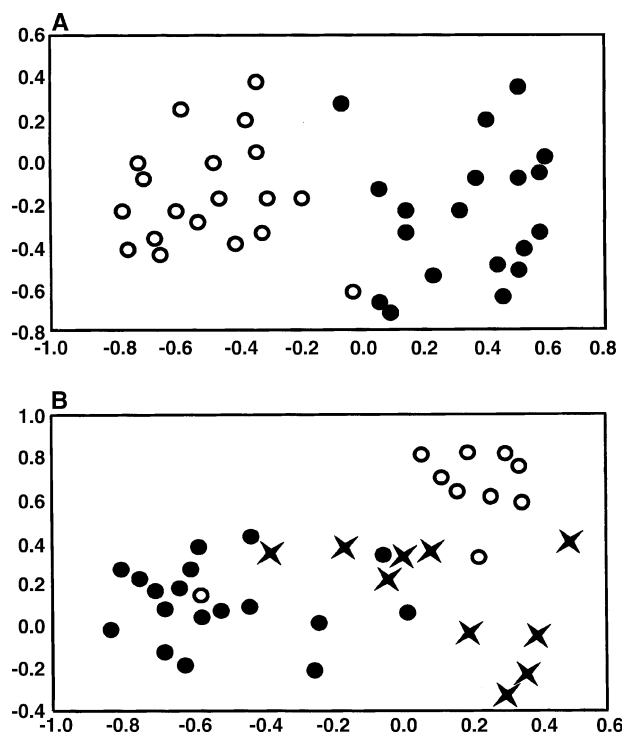


Figure 2. Factor map of two main principle components axes based on R_{XY} for MR pallid (open), shovelnose (solid), and morphologic hybrid sturgeon (X). (A) Missouri River pallid and shovelnose sturgeon: the first two axes extracted by a maximum-likelihood method explained 52% of the total variance; (B) Atchafalaya River pallid, shovelnose, and putative pallid-shovelnose hybrids: the first two axes extracted by a maximum-likelihood method explained 35% of the total variance.

When considering the morphologic hybrids, the microsatellite data suggest that they are more similar to shovelnose sturgeon (Tranah et al. 2001), while the mtDNA data (Campton et al. 2000) suggest that the putative hybrids are more similar to pallid sturgeon, perhaps due to sex-specific or nonreciprocal crossing. These early results suggest that pallid sturgeon females may be contributing to the first-generation hybrid population and that some hybrids may be the result of backcrossing with the more abundant shovelnose sturgeon.

By combining the new microsatellite loci with the Campton et al. (2000) and Tranah et al. (2001) datasets, we have increased the power to distinguish individual pallid sturgeon from shovelnose sturgeon in regions of natural sympatry. The I_H scores and R_{XY} multivariate plots indicate that morphologic hybrids contain a mixture of parental composite genotypes. As demonstrated in both upper Missouri River populations and with the Atchafalaya River population, each analysis clearly separates pallid and shovelnose sturgeon. If the putative hybrids had simply represented misidentified pallid or shovelnose sturgeon, those individuals would have grouped with either species in the analysis of AR sturgeon. In both tests, the putative hybrid

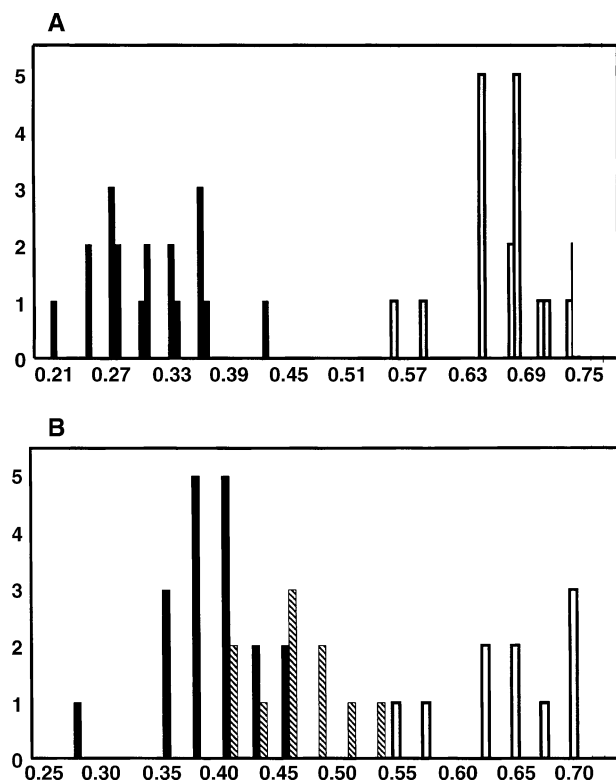


Figure 3. Hybrid index scores for pallid (open), shovelnose (solid), and putative pallid-shovelnose hybrid sturgeon (striped): (A) Missouri River and (B) Atchafalaya River. Index scores are on the x-axis and number of samples on the y-axis.

individuals are intermediate to AR pallid and shovelnose sturgeon, as would be expected with a population composed of mixed genetic origin. In addition, the putative hybrid individuals overlapped with shovelnose sturgeon at the higher range of their I_H scores and in the multivariate plot of R_{XY} . This overlap of the hybrid individuals with shovelnose sturgeon may be explained by hybrid individuals backcrossing with shovelnose sturgeon, which are more abundant in the Atchafalaya River. Campton and Utter (1985) used I_H to demonstrate natural hybridization between steelhead and coastal cutthroat trout in regions of sympatry. The occurrence of two genotypic classes, representing rainbow and coastal cutthroat trout, was evident for index values that were close to 1.0 and 0.0. Intermediate I_H scores supported the presence of a third group from a different location, which Campton and Utter (1985) interpreted as evidence of natural hybridization.

Although there are many factors that can induce interspecific hybridization, it is often a biological response to the alteration of spawning habitat wherein conditions become favorable for two species to overlap (Arnold 1997; Avise 1994; Campton 1987; Dowling and Secor 1997). Hybridization between pallid and shovelnose sturgeon is mostly documented from the lower Mississippi and Atchafalaya Rivers (Carlson et al. 1985; Keenlyne et al. 1994a). Hydroelectric, flood control, and navigation projects

in the Mississippi River basin began in the 1930s and river engineering continues today. Damming and dredging have decreased water velocity and transformed large, wide channels into relatively clear and cold pools, altering preferred spawning substrate (Dryer and Sandoval 1993; Kallemeyn 1989). Water impoundment hinders migration to spawning areas and prevents the deposition of sediments and organic material. Such alterations have likely “hybridized the habitat” (Schmulbach 1974) and changed the ecological relationship between species. Ecologically hybrids were more closely associated with shovelnose rather than pallid sturgeon (Carlson et al. 1985). Hybrid and shovelnose sturgeon occurred in similar habitats and were sampled together more frequently than hybrids and pallid sturgeon. However, hybrid and pallid sturgeon were both found to be piscivorous, unlike shovelnose sturgeon, which feed on benthic macro-invertebrates.

Introgression can lead to the loss of locally adapted populations and eradicate the genetic diversity necessary for future evolutionary potential. Of particular concern is the homogenization of two or more taxa into a single, indistinguishable unit, as is occurring with native cutthroat and introduced rainbow trout in western North America (Allendorf and Leary 1998). Introgression with a more abundant species can also cause the genetic assimilation of a rare species (Arnold 1997; Campton 1987). These are major concerns when the hybrid forms are viable and more abundant than the progenitors in their original habitat, because they compete for food and spawning resources (Arnold 1997). Hybridization may not be as much of a concern if the hybrids are less fit genetically or ecologically, although this could result in wasted reproductive output of a rare species. From an evolutionary standpoint, hybridization may salvage maximum genetic diversity and lead to novel adaptations, allowing a higher fitness in a rapidly changing environment (Arnold 1997). O'Brien et al. (1990) also argued that introgression could infuse genetic diversity into a rare or endangered species or subspecies, and potentially increase the fitness of that taxon (e.g., Florida panther).

The combined data and analysis presented herein strongly suggests that pallid and shovelnose sturgeon from the lower Mississippi River are reproductively distinct groups undergoing hybridization. It is unclear whether the pallid-shovelnose hybrids are the product of first-generation hybridization between pallid and shovelnose sturgeon, or if they are the result of subsequent backcrossing with the more abundant shovelnose sturgeon (as demonstrated by the Atchafalaya River I_H scores). More ecological information is needed to determine if the hybrids are an independent group that is becoming adapted to altered habitat, if they are directly competing with pallid sturgeon for food resources and spawning opportunities, or if they are even reproductively viable. It is possible that the presence of hybrid pallid and shovelnose sturgeon indicates a response to human-induced alteration to the lower Mississippi and Atchafalaya Rivers (Allendorf et al. 2001). If hybridization between pallid and shovelnose sturgeon in the lower Mississippi River is a natural

biological response to changing environmental pressures it will likely continue as long as the aquatic habitat is altered by human activity.

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