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ARTICLE

Patterns of Population Structure Vary Across the Range of the White Sturgeon

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Abstract

Critical unknowns surrounding the basic biology of White Sturgeon *Acipenser transmontanus* have hindered management and conservation efforts. Population genetic data may be used to address some of these uncertainties, but previous examinations of population structure in White Sturgeon have been limited by the highly duplicated nature of the species' genome. We report results from an analysis of White Sturgeon population structure within and among drainages using 13 polysomic microsatellite loci. Genetic diversity levels varied widely among regions, and the lowest levels were observed in the endangered Kootenai River Distinct Population Segment and the highest levels were detected in regions with access to estuarine and marine habitat. Patterns of within-drainage population structure varied, and no structure was detected in the Sacramento–San Joaquin drainage and a complex pattern of isolation by distance was revealed in the Columbia–Snake River drainage. These results contrast a previously published evaluation of a White Sturgeon population structure in the Fraser River, which revealed several genetically distinct populations within a single drainage. Examination of population structure among drainages, including from samples collected across the species range, revealed six populations. Populations in the Sacramento–San Joaquin, Kootenai, lower Fraser, and upper Fraser River drainages were distinct. The complex isolation-by-distance pattern discovered in the within-drainage analysis of the Columbia–Snake River drainage was supported by the among-drainage population structure analysis. Our results provide little support for the practice of managing each impounded reach of the Columbia–Snake River system as a genetically distinct population as adjacent reaches show little to no genetic divergence in these analyses. Variation in patterns of population structure across the species range indicates that the scale of spawning site fidelity for White Sturgeon varies regionally, which has implications for recruitment failure mitigation.

The White Sturgeon *Acipenser transmontanus* is the largest fish inhabiting the freshwaters of the West Coast of North America and ranges from Ensenada, Mexico, to the Gulf of Alaska (Moyle 2002). Spawning populations occur in the Sacramento–San Joaquin, Columbia–Snake, and Fraser rivers (Figure 1). White Sturgeon are long-lived, late-maturing fish that may attain 80 + years of age, and the age of sexual maturity in females increases with increasing latitude (12–34 years: Scott and Crossman 1973; Moyle 2002). Like most North American sturgeons, White Sturgeon experienced severe harvest pressure at the turn of the 20th century due to high demand for caviar and flesh. The near collapse of White Sturgeon populations led to fishery restrictions and closures across the species' range (Craig and Hacker 1940; Rieman and Beamesderfer 1990; Moyle 2002).

The current status of White Sturgeon varies widely across the species range. They are highly abundant in the lower Columbia River where a small commercial and a large recreational fishery exists (McCabe and Tracy 1994). Recreational fisheries for White Sturgeon are found in the other regions of the Columbia River, as well as the Sacramento–San Joaquin, Snake, and Fraser rivers. However, several impounded reaches in the main-stem Columbia and Snake rivers contain collections of White Sturgeon unable to sustain harvest due to low abundance. Additionally, White Sturgeon are listed under the Species at Risk Act

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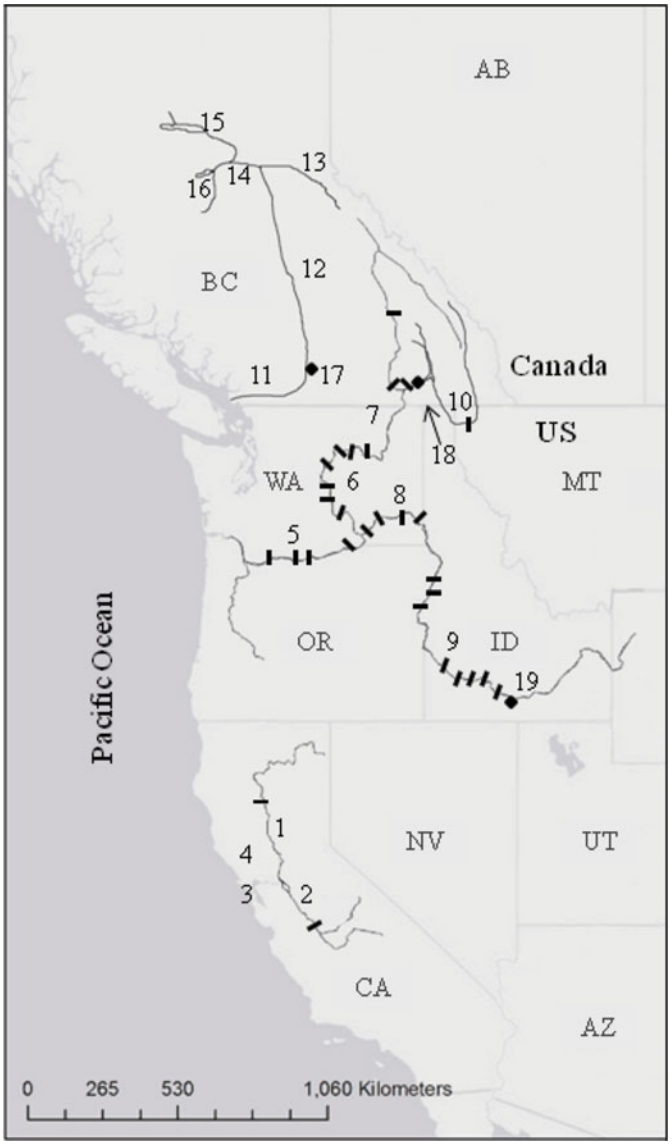

FIGURE 1. Distribution map for White Sturgeon. Triangles indicate natural dispersal barriers while dashes indicate approximate locations of major impoundments. 1, Sacramento River; 2, San Joaquin River; 3, San Pablo–Suisun Bays; 4, Napa River; 5, lower Columbia River; 6, middle Columbia River; 7, Transboundary Reach; 8, lower Snake River; 9, middle Snake River; 10, Kootenai River; 11, lower Fraser River; 12, middle Fraser River; 13, upper Fraser River; 14, Nechako River; 15, Stuart Lake; 16, Fraser Lake; 17, Hells Gate; 18, Bonnington Falls; 19, Shoshone Falls.

in Canada and the Kootenai River Distinct Population Segment (DPS) is listed under the Endangered Species Act in the United States (USFWS 1994; COSEWIC 2003; DFO 2007). Factors currently limiting White Sturgeon populations include habitat degradation, habitat fragmentation, modification of seasonal flow regimes by impoundment, pollution, nonnative species, and overharvest. In some areas (upper Columbia, Kootenai, and Nechako rivers), partial to complete recruitment failure lasting for decades or more have shifted the age structure of White Sturgeon populations and continue to threaten their persistence (Hildebrand et al. 1999; Anders et al. 2002; McAdam et al. 2005). Conservation aquaculture programs currently sustain White Sturgeon reproduction in the upper Columbia and Kootenai rivers (Ireland et al. 2002; Drauch Schreier and May 2011; Drauch Schreier et al. 2012b).

Management and conservation efforts for White Sturgeon may be improved by resolving several critical unknowns surrounding the basic biology of the species. First, it is unknown how many White Sturgeon populations exist. Different impounded reaches of the Columbia and Snake rivers have been managed as separate populations (Parsley et al. 2007), but there is no genetic evidence to support these designations. Additionally, biologists have assumed high spawning site fidelity in White Sturgeon due to their migratory reproductive behavior, but some tagging data has suggested that spawning site fidelity may occur on a broader scale in sturgeon than in anadromous species such as salmonids (Lyons and Kempinger 1992; Rusack and Mosindy 1997). Knowledge of spawning site fidelity may help managers address environmental variables that may be contributing to White Sturgeon recruitment failure. Population genetic data may be used to delineate White Sturgeon populations, and the scale of population structure within and among drainages would shed light on the scale of White Sturgeon spawning site fidelity.

The extent of previous population genetic analyses of White Sturgeon was once limited by the highly duplicated nature of the species' genome. White Sturgeon are ancient octoploids, possessing ~240 chromosomes (Birstein and Vasil'ev 1987), and nuclear loci, such as microsatellites, may be found in four or eight copies (Rodzen and May 2002; Drauch Schreier et al. 2011). Initial examinations of population structure used allozymes or mitochondrial DNA (Bartley et al. 1985; Brown et al. 1992a, 1992b; Setter and Brannon 1992). Although these studies provided preliminary evidence of genetic structure on a coarse scale, the markers used did not provide enough resolution to examine fine-scale patterns of population structure within drainages. More recent examinations of population structure using microsatellites have provided finer resolution. Smith et al. (2002) used four microsatellites in conjunction with mitochondrial control region sequence data to identify four populations in the Fraser River drainage. Using eight polysomic microsatellites, Rodzen et al. (2004) reported a significant global F_{ST} of 0.11 in an examination of population structure that included samples from several regions in the Columbia, Fraser, and Sacramento rivers. However, no study to date has provided a detailed examination of genetic structure with exhaustive sample coverage including all regions of the species' range.

We used 13 polysomic microsatellite loci to examine White Sturgeon population structure across the species' range. Geographic sample coverage was increased in this study compared with previous studies. We analyzed samples from nearly all reaches of each of the three drainages containing spawning populations of White Sturgeon. Study goals were to (1) characterize

genetic diversity within and among regions inhabited by White Sturgeon and (2) examine patterns of population structure both within and among drainages to provide data that could be used in management and conservation practices for White Sturgeon.

METHODS

Sample collection and DNA extraction.—Tissue samples were collected throughout the three major drainages containing spawning populations of White Sturgeon: the Sacramento–San Joaquin, Columbia–Snake, and Fraser River drainages (Figure 1; Table 1). Within heavily impounded rivers such as the Columbia and Snake rivers, care was taken to obtain samples from nearly all impounded reaches. The majority of samples were collected from subadult and adult fish during routine population monitoring by state, federal, and tribal management agencies or public utility companies.

The Qiagen PureGene DNA extraction kit was used to extract DNA from tissue and the Qiagen DNeasy blood and tissue kit was used to extract DNA from blood samples. The DNA was quantified on a Fujifilm FLA 5100 fluorimager and diluted to 20 ng. Polymerase chain reactions (PCRs) were performed in Life Technologies (LT) GeneAmp 9700 thermal cyclers using fluorescently labeled primers for 13 microsatellite loci as described in Drauch Schreier et al. (2012b). A total of 1.0 μL of diluted PCR product was added to 8.85 μL of highly deionized formamide (The Gel Company) and 0.15 μL of Rox 400 HD size standard (LT). Genotyping was conducted on either an LT ABI 3130xl or 3730 genetic analyzer using GeneMapper version 4.0 software. Positive controls were genotyped on each platform to ensure conformity of allele binning between instruments. Due to the highly duplicated nature of the White Sturgeon genome, it was impossible to determine how many copies of each allele were present in an individual and microsatellites could not be genotyped as codominant loci.

TABLE 1. Samples used for examination of rangewide population structure in White Sturgeon. Impounded reaches in each regional designation on the Columbia–Snake River system are listed in order from downstream to upstream.

Drainage or region	River reach or estuary	*N*	Tissue type
Sacramento–San Joaquin River (S–SJ)	San Pablo Bay	135	Fin clip
	Suisun Bay	480	Fin clip
	Sacramento River	42	Fin clip
	Napa River	3	Fin clip
Lower Columbia River	Columbia River estuary[a] (CRE)	97	Pectoral fin ray
	The Dalles Pool (DD)	59	Fin clip
	John Day Pool (JD)	59	Fin clip
Middle Columbia River	McNary Pool (MCN)	28	Fin clip
	Priest Rapids Pool (PR)	4	Fin clip
	Wanapum Pool (WN)	30	Fin clip
	Rock Island Pool (RI)	4	Fin clip
	Rocky Reach Pool (RR)	9	Fin clip
	Wells Pool (WP)	11	Fin clip
	Chief Joseph Pool (CJ)	5	Fin clip
Upper Columbia River	Transboundary Reach (TR)	330	Fin clip
	Kootenai (KT)	98	Fin clip
Lower Snake River	Lower Monumental Pool (LM)	48	Fin clip
	Little Goose Pool (LG)	49	Fin clip
	Lower Granite to Hells Canyon (HC)	97	Fin clip
Middle Snake River	Brownlee to Swan Falls (BR)	28	Blood
	Swan Falls to CJ Strike (SF)	47	Fin clip
	CJ Strike to Bliss (CJS)	41	Fin clip
	Lower Salmon to Upper Salmon Falls (LSF)	19	Fin clip
	Upper Salmon Falls to Shoshone (USF)	50	Fin clip
Lower Fraser River, below Hells Gate	SG-1	38	Fin clip
	SG-2	38	Fin clip
Upper Fraser River, above Hells Gate	Middle Fraser River (SG-3)	40	Fin clip
	Nechako River/Stuart Lake/Fraser Lake (NK/SL/FL)	86	Fin clip
	Upper Fraser (UF)	47	Fin clip

[a]From the mouth of the Columbia River estuary to Bonneville Dam.

Instead, each microsatellite allele was treated as a present–absent dominant locus, producing a binary allelic phenotype represented by numerals 1 and 0 for each individual (Rodzen and May 2002; Israel et al. 2009; Pfeiffer et al. 2011). Although these dominant loci could not be tested for deviation from Hardy–Weinberg equilibrium or linkage equilibrium, we followed the inheritance of these markers in known families of White Sturgeon to confirm that all loci were transmitted from parent to offspring in patterns conforming to Mendelian laws of inheritance (Rodzen and May 2002; Drauch Schreier et al. 2011).

Analysis of duplicates.—The program GenoType (Meirmans and Tienderen 2004) was used to identify duplicate samples in the White Sturgeon data set. We determined the rate of allelic dropout across 13 loci to be 1.2%; therefore, we allowed up to two mismatches in identifying duplicate samples. One individual from each pair of duplicate samples was removed from the data set before further analyses were conducted.

Genetic diversity.—The number of shared and private alleles was calculated in GenAlEx version 6.3 (Peakall and Smouse 2006) to characterize levels of genetic diversity in each region sampled. The range in sample sizes made direct comparison of genetic diversity levels among regions untenable (Table 1). Therefore, we used a random number generator in Microsoft Excel 2007 to create a subsample of each region equal to the smallest sample size in the data set ($N = 60$; lower Fraser) and recalculated numbers of alleles and private alleles to make comparisons.

An analysis of molecular variation (AMOVA) was conducted in GenAlEx version 6.3 (Peakall and Smouse 2006) to examine the proportion of genetic diversity partitioned within and among regions. We conducted 9,999 random permutations to assess the significance of Phi-PT (Peakall et al. 1995), an F_{ST} analog most appropriate for dominant data that provides a measure of pairwise genetic divergence. We used a sequential Bonferroni correction (Rice 1989) to account for multiple pairwise comparisons using $\alpha = 0.05$.

Within-drainage population structure.—We first explored population structure within river drainages. Within-drainage population structure analysis of the Fraser River system has been published elsewhere (Drauch Schreier et al. 2012a), and we will consider only within-drainage population structure of the Sacramento–San Joaquin and Columbia–Snake River drainages here. The program Structure version 2.3.3 (Pritchard et al. 2000) was used to explore the number of possible populations (K) existing within the Sacramento–San Joaquin and Columbia–Snake River drainages. Binary allelic phenotypes were treated as dominant genetic data in Structure with the "absent" state considered the recessive allele (Falush et al. 2007). This approach has been used successfully to examine population structure in other polyploid species (Andreakis et al. 2009; Israel et al. 2009). Exploratory analyses were first performed using a relatively short burn-in (50,000) and small number of iterations (100,000) to test the likelihood of $K = 1$ to $K = 20$ for each river system and ascertain the general shape of the likelihood curve. Longer analyses (burn-in 500,000; 1,000,000 iterations) were conducted only for the most likely range of K values found in the exploratory analyses (Pritchard et al. 2010; Table 2). Each Structure analysis used the admixture model and assumed correlated allele frequencies among populations. We conducted six replicates for each K. The LOCPRIOR model (Hubisz et al. 2009), which incorporates sampling location information as a prior when found to be informative by Structure, was used to increase the program's ability to identify the true K in the presence of weak differentiation among populations. Structure results were interpreted in several ways. First, the mean likelihood value, ln Pr($X|K$), for each possible number of populations was examined in the program Structure Harvester (Earl and von Holdt 2012). The K with the highest likelihood value was interpreted as the best estimate of the number of populations in each river system. However, this method has a tendency to overestimate K, particularly when analyzing dominant data (Pritchard et al. 2010). Therefore, we also used the ΔK metric of Evanno et al. (2005) to interpret Structure results for each system. When multiple K values seemed equally likely via examination of the likelihood function and ΔK, individual Q values were examined to select the most likely K. In this analysis, a Q value represents an individual's proportional membership in each population identified by Structure. We used the program CLUMPP (Jakobsson and Rosenberg 2007) to compile individual assignments across all replicates for the most likely K, and individual Q values were plotted in the program Distruct 1.1 (Rosenberg 2003) for visual examination.

TABLE 2. Structure analyses conducted for White Sturgeon population delineation. Exploratory analyses consisted of a burn-in of 50,000 with 100,000 iterations. Full analyses used a 500,000 burn-in and 1,000,000 iterations.

River system	Exploratory analysis	Full analysis
Sacramento–San Joaquin	$K = 1$ to $K = 20$	$K = 1$ to $K = 6$
Columbia–Snake	$K = 1$ to $K = 20$	$K = 1$ to $K = 10$
Rangewide	$K = 1$ to $K = 20$	$K = 1$ to $K = 10$

Range-wide population structure.—Structure 2.3.3 was then used to examine White Sturgeon population structure among drainages across the species' range (Sacramento–San Joaquin, Columbia–Snake, Fraser rivers). The computational time of analyzing all 2,056 samples in Structure was prohibitive. Therefore, all populations delineated by the within-drainage analysis with more than 100 samples were randomly subsampled in Excel 2007 so no more than 100 individuals from each population were included in the range-wide analysis. This reduced the total number of samples in the range-wide analysis to 855. Exploratory analyses (burn-in 50,000 with 100,000 iterations) examined the likelihood of $K = 1$ to $K = 20$, while full analyses (burn-in 500,000 with 1,000,000 iterations) explored $K = 1$ to $K = 10$ (Table 2). The admixture model was used and correlated allele frequencies among populations assumed. Six replicates were conducted for each K. As for the within-drainage analyses, the

LOCPRIOR model was implemented when sampling location was informative and Structure results were interpreted by examining the ln Pr($X|K$) function, the ΔK metric, and individual Q values. The program CLUMPP compiled individual assignments across replicates for the most likely K, and individual Q values were plotted in Distruct 1.1 for visual examination.

We used the re-allocation procedure in the program AFLPOP (Duchesne and Bernatchez 2002) to independently corroborate the genetic distinctiveness of White Sturgeon populations identified by Structure across the species range. The re-allocation procedure randomly sampled individuals from predefined source populations and used dominant allele frequencies to determine the likelihood that the individual belonged in that population. A population with many correct re-allocations and few misallocations or nonallocations would represent a genetically distinct population. The assignment of a sample to its population of origin was a correct re-allocation, while the assignment of a sample to a different population was a misallocation. If a population had few correct re-allocations and many misallocations or nonallocations, its status as a genetically distinct population may be questioned. The program AFLPOP uses a threshold minimum log difference (MLD) value to re-allocate individuals to a population. We first used the "Simulation: many iterations" procedure to select the appropriate MLD value to maximize the number of correct re-allocations while minimizing the rate of nonallocations. Ten simulations were conducted and 1,000 genotypes were randomly generated for each population. The MLD value that maximized the number of correct re-allocations and minimized the number of nonallocations in the simulated populations was MLD = 0.8. We used a zero-frequency replacement value of $1/(N + 1)$. Only samples without missing data could be included in this analysis. We distinguished between the Columbia River estuary and the remaining Columbia–Snake River system as two separate populations for the purpose of this analysis based on results of the within-drainage Structure analyses (see Results).

We conducted a second AMOVA in GenAlEx version 6.3 to examine how genetic diversity was partitioned among populations identified by Structure across the species range. Random permutations were conducted (9,999) to assess the significance of Phi-PT, and a Bonferroni correction was conducted to account for multiple pairwise comparisons. The corrected P-value denoting significance at $\alpha = 0.05$ was 0.002. Principal coordinates analysis (PCA) was conducted with Phi-PT data in GenAlEx version 6.3 to visualize genetic relationships among populations. A PCA uses a distance matrix to illustrate similarities between cases, which in this instance are populations identified by Structure.

RESULTS

Analysis of Duplicate Samples

A total of 19 sample pairs were classified as duplicates in the White Sturgeon genotype database, two pairs from the Sacramento–San Joaquin River and 17 pairs from the Columbia–Snake River. Nine of these duplicate pairs originated from the Transboundary Reach of the Columbia River. Samples from this region were originally collected for a site fidelity study, and several individuals were recaptured in different locations and tissue was collected multiple times. Remaining duplicate pairs originated from the Columbia River estuary (including the Columbia River below Bonneville Dam), the Kootenai River, and the Lower Granite to Hells Canyon reach of the Snake River. No duplicates were detected in the Fraser River (Drauch Schreier et al. 2012a). Duplicate pairs exhibited zero ($N = 8$) or one ($N = 9$) mismatch while two pairs possessed two mismatches.

Genetic Diversity

From 13 microsatellite loci, a total of 275 alleles were detected. The number of alleles per microsatellite locus ranged from 7 (*AciG2*) to 31 (*Atr109*, *Atr117*; see Table A.1). The total number of alleles found within regions ranged from 97 (Kootenai River) to 236 (Sacramento–San Joaquin River; Table 3). No private alleles were detected in the Kootenai or middle Snake rivers, while the Sacramento–San Joaquin River had the highest number of private alleles (18; Table 3). When the total number of alleles and private alleles were recalculated for the subsampled regions ($N = 60$), the highest level of genetic diversity was detected in the lower Fraser River, from which 198 alleles and 13 private alleles were detected (Table 4). Similarly high levels of genetic diversity were detected in the other two regions that had access to marine habitat, the Sacramento–San Joaquin and lower Columbia rivers (Table 4).

A Phi-PT value of 0.09 ($P = 0.0001$) revealed significant levels of genetic differentiation among regions; 9% of genetic diversity was partitioned among regions while 91% of the variation was found within regions. An examination of pairwise Phi-PT values showed significant levels of genetic differentiation among nearly all comparisons and the highest levels were between the Kootenai River and all other regions (Table 5). The

TABLE 3. Total number of alleles and private alleles detected in White Sturgeon within regions. N refers to the sample size while A_T is the total number of alleles and A_P the total number of private alleles detected across 13 microsatellite loci.

Region	N	A_T	A_P
Sacramento–San Joaquin	660	236	18
Lower Columbia	214	217	3
Middle Columbia	91	178	1
Transboundary Reach	328	187	1
Kootenai	376[a]	97	0
Lower Snake	194	192	4
Middle Snake	184	123	0
Lower Fraser	60	198	10
Upper Fraser	112	133	1

[a]This value calculated from genetic monitoring data set for the Kootenai River population (Drauch Schreier et al. 2012b).

TABLE 4. Genetic diversity measures in White Sturgeon corrected for unequal samples sizes among regions. Total number of alleles and private alleles detected within regions after subsampling to smallest population sample size ($N = 60$). N refers to the sample size while A_T is the total number of alleles and A_P the total number of private alleles detected across 13 microsatellite loci.

Region	N	A_T	A_P
Sacramento–San Joaquin	60	196	8
Lower Columbia	60	189	2
Middle Columbia	60	172	3
Transboundary Reach	60	160	2
Kootenai	60	77	0
Lower Snake	60	164	2
Middle Snake	60	107	1
Lower Fraser	60	198	13
Upper Fraser	60	124	1

middle Columbia population was not significantly differentiated from the lower Columbia or lower Snake populations. The lowest levels of genetic differentiation were found in populations from the lower Columbia, middle Columbia, Transboundary Reach, and lower Snake River regions. Similarly low levels of divergence were found for one out-of-drainage comparison, between the lower Columbia and lower Fraser rivers (Table 5). The middle Snake population showed low differentiation from that in the lower Snake River but showed higher levels of divergence from those in the Columbia River regions. Interestingly, the lower Fraser population showed higher levels of genetic divergence from that of the upper Fraser River than it did from the Sacramento–San Joaquin and lower Columbia populations (Table 5).

Within-Drainage Population Structure

Sacramento–San Joaquin River system.—Exploratory analyses with Structure suggested that the most likely number of populations (K) in the Sacramento–San Joaquin River sample was between one and six, so more extensive exploration of the data were conducted for those values of K. Examination of likelihood values, ln Pr($X|K$), from the full analysis indicated that the Sacramento–San Joaquin River system was most likely a single population (Figure 2A). The Evanno method suggested that $K = 4$ was the most likely number of populations in the Sacramento–San Joaquin River system. However, when Structure assumed four populations, each individual was assigned evenly to each population (mean Q values = 0.23, 0.25, 0.24, and 0.26), suggesting this was an overestimate of the true population number. It is important to note that ΔK cannot evaluate the likelihood of $K = 1$, so a comparison between the likelihood of $K = 1$ and $K = 4$ by this method was not possible.

Columbia–Snake River.—In the Columbia–Snake River drainage, sampling location labels were found to be informative by Structure (mean $r = 0.15$) and the LOCPRIOR model was employed. Examination of ln Pr($X|K$) and ΔK both indicated the most likely number of populations was three (Figure 2B). In the main-stem Columbia River, from the lower Columbia River reach to the Transboundary Reach and including the lower Snake River (Lower Monumental Pool to Hells Canyon), individuals assigned to two populations, and membership to the second population increased on an upstream cline (Figure 3). Individuals in the middle Snake River (Brownlee Pool to Upper Salmon Falls Pool) assigned strongly to the second population with high Q values (mean $Q = 0.99$). The Kootenai River was identified as a distinct population, and all individuals from the Kootenai River assigned to a single genetic cluster with high Q values (mean $Q = 0.99$). In subsampling for the range-wide population structure analysis, we distinguished between the Columbia River estuary (downstream population), the Columbia–lower Snake rivers (The Dalles Pool to Transboundary Reach on the Columbia River, Lower Monumental Pool to Hells Canyon on the Snake River), and middle Snake River (Brownlee to Upper Salmon Falls; upstream population).

Range-wide Population Structure

Sampling information was found to be informative in the rangewide Structure analysis (mean $r = 0.05$) and the

TABLE 5. Pairwise genetic divergence among regions inhabited by White Sturgeon. Phi-PT values are below the diagonal and P-values are above the diagonal. S–SJ = Sacramento–San Joaquin, LC = lower Columbia, MC = middle Columbia, TR = Transboundary Reach, KT = Kootenai, LS = lower Snake, MS = middle Snake, LF = lower Fraser, and UF = upper Fraser. Bonferroni corrected significant values ($P \leq 0.0001$) are indicated with the letter z.

Region	S–SJ	LC	MC	TR	KT	LS	MS	LF	UF
S–SJ		0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
LC	0.043 z		0.0005	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
MC	0.084 z	0.023		0.0001	0.0001	0.0050	0.0001	0.0001	0.0001
TR	0.093 z	0.029 z	0.026 z		0.0001	0.0004	0.0001	0.0001	0.0001
KT	0.222 z	0.171 z	0.169 z	0.156 z		0.0001	0.0001	0.0001	0.0001
LS	0.094 z	0.025z	0.016	0.010	0.186 z		0.0001	0.0001	0.0001
MS	0.171 z	0.083 z	0.050 z	0.050 z	0.240 z	0.022 z		0.0001	0.0001
LF	0.040 z	0.022 z	0.055 z	0.057 z	0.193 z	0.056 z	0.118 z		0.0001
UF	0.122 z	0.065 z	0.082 z	0.079 z	0.209 z	0.075 z	0.136 z	0.082 z	

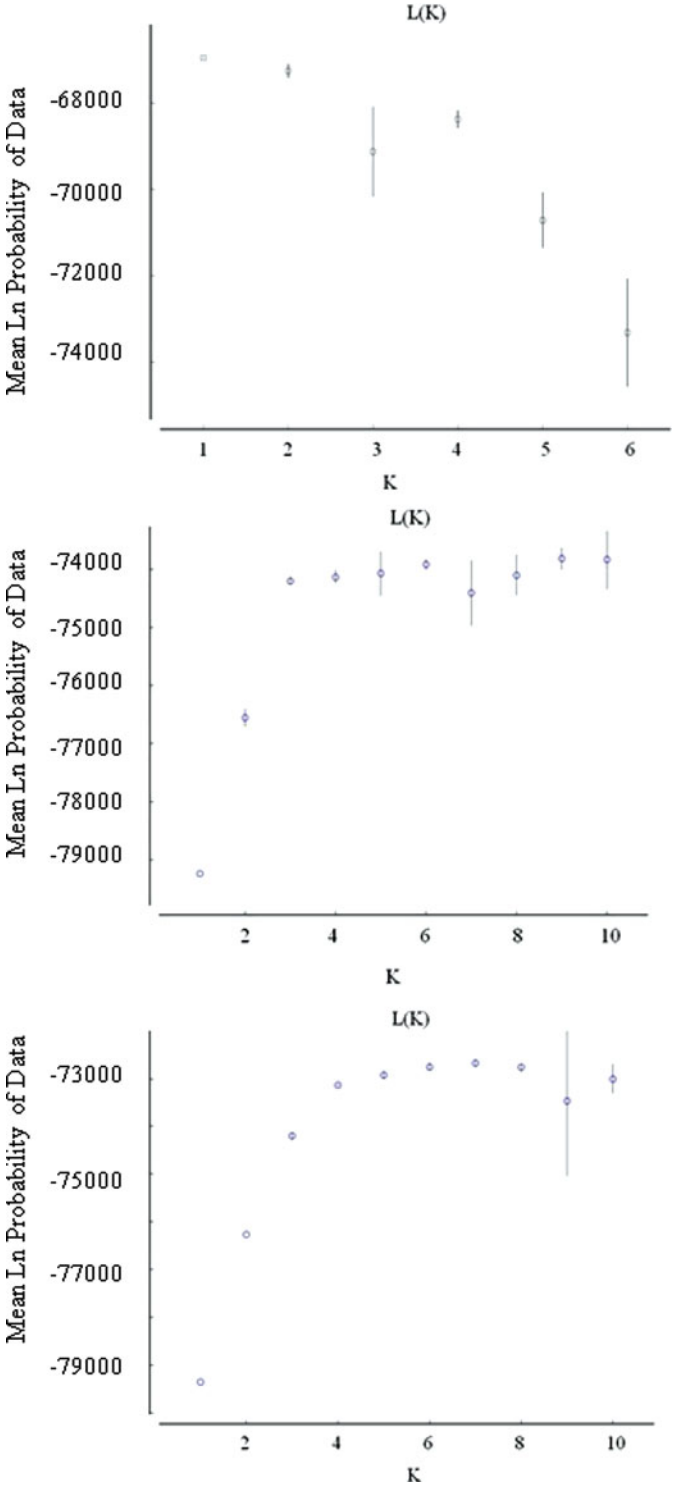

FIGURE 2. Mean ln Pr($X|K$) values for Structure examination of population structure (**A**) within the Sacramento–San Joaquin River system, (**B**) within the Columbia–Snake River drainage, and (**C**) among drainages across the species' range. Vertical lines denote SD.

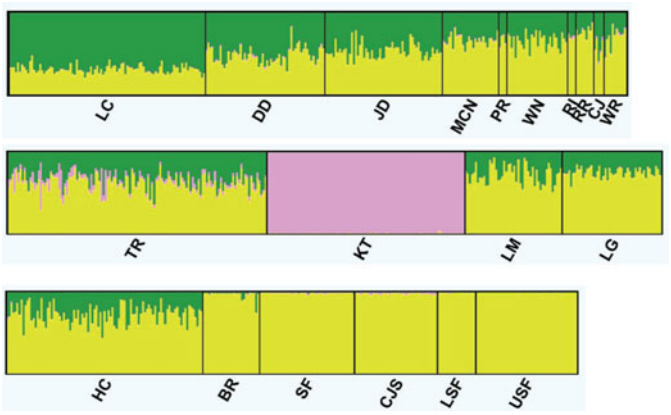

FIGURE 3. Bar histogram output from Structure depicting individual assignments in the Columbia–Snake River drainage. Each bar represents one individual genome, each color represents a genetic cluster identified by Structure, and the proportion of each color in each bar represents the proportional assignment of each individual to each cluster. See Table 1 for population abbreviations. [Figure available online in color.]

LOCPRIOR model was implemented by Structure. The ln Pr($X|K$) plot suggested that the most likely number of populations was between four and seven (Figure 2C), while ΔK suggested two was the true number of populations. The slope of the curve between $K = 1$ and $K = 2$ indeed exhibited the greatest rate of change, but the likelihood plot clearly indicated that $K = 2$ was not the most likely number of populations. We used our knowledge of the species' life history and the results of the within-drainage Structure analyses and regional Phi-PT analyses to conclude that $K = 6$ was the most likely number of populations in the data set.

When $K = 6$ was assumed, the Sacramento–San Joaquin (mean $Q = 0.97$), middle Snake (mean $Q = 0.94$), Kootenai (mean $Q = 0.99$), lower Fraser (mean $Q = 0.77$), and upper Fraser cluster (mean $Q = 0.96$) were five distinct populations (Figure 4). Individuals sampled downstream of McNary Dam on the Columbia River tended to assign to a "lower Columbia" cluster (mean $Q = 0.51$) or were split evenly between the "lower Columbia" and "middle Snake" clusters. Individuals sampled from the McNary Reservoir to the Transboundary Reach tended to assign to the "middle Snake" cluster (mean $Q = 0.60$), although an isolation-by-distance pattern was still evident at this level (Figure 4). Individuals from the lower Snake River tended to assign to the "middle Snake" cluster (mean $Q = 0.68$).

The AFLPOP re-allocation analysis was able to correctly re-allocate most individuals to the population from which they were sampled (Figure 5). The populations from the Sacramento–San Joaquin, Kootenai, and upper Fraser rivers were the most distinct, with a high rate of correct re-allocations and few non-allocations. Few individuals from the lower Fraser population were misallocated but the nonallocation rate was higher than that of the upper Fraser population. The highest rates of misallocation or nonallocation were found for the Columbia River estuary and Columbia–Snake River populations (Figure 5).

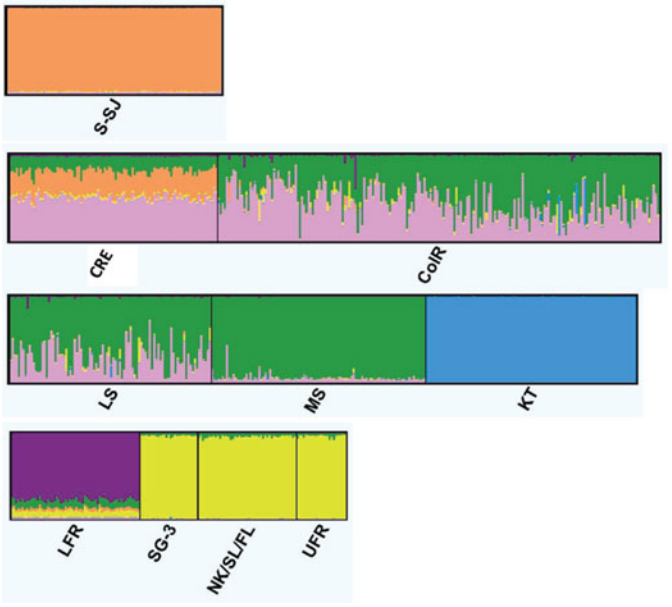

FIGURE 4. Bar histogram outputs from Structure depicting individual assignments in the rangewide data set. Each bar represents one individual genome, each color represents a genetic cluster identified by Structure, and the proportion of each color in each bar represents the proportional assignment of each individual to each cluster. S–SJ = Sacramento–San Joaquin River, CRE = Columbia River estuary, ColR = Columbia River (DD to TR), LS = lower Snake River, MS = middle Snake River, KT = Kootenai River, LFR = lower Fraser River, SG-3 = middle Fraser River, NK/SL/FL = Nechako River/Stuart Lake/Fraser Lake, UFR = upper Fraser River. See Table 1 for more information regarding population abbreviations.

When individuals were parsed into the six populations identified by Structure, the Phi-PT value increased to 0.10 (P = 0.0001), meaning the proportion of genetic diversity partitioned among populations was 10%. Further partitioning the Fraser River above Hells Gate into two populations to account for cryptic substructure (Drauch Schreier et al. 2012a) did not change the proportion of genetic diversity detected within populations. An examination of pairwise Phi-PT values for populations identified by Structure revealed similar patterns as the Phi-PT analysis based on sampling regions, and the highest levels of divergence occurred between the Kootenai River and all other populations (Table 6). All pairwise comparisons were significant. The lowest levels of genetic differentiation were found between the Columbia River estuary and the lower Fraser River. Relatively low levels of genetic differentiation were detected between the Columbia River estuary and the remaining Columbia–Snake River system (Table 6). As found in the regional analysis, the lower Fraser population showed higher levels of genetic divergence from the Fraser River above Hells Gate than it did from the Sacramento–San Joaquin, Columbia River estuary, and Columbia–Snake populations (Table 6). The PCA separated the Kootenai River population from all others along axis 1, while other populations were primarily distinguished along axis 2 (Figure 6A). All populations with access to marine habitat were found in the lower left quadrant of Figure 6A. A second PCA was conducted without the Kootenai River outlier. In the PCA without the Kootenai River population, less similarity was evident between the Columbia–Snake River population and upper Fraser River population (Figure 6B). A close genetic relationship between the Columbia River estuary and lower Fraser populations was shown although the similarity was less pronounced when the Kootenai population was removed (Figure 6B).

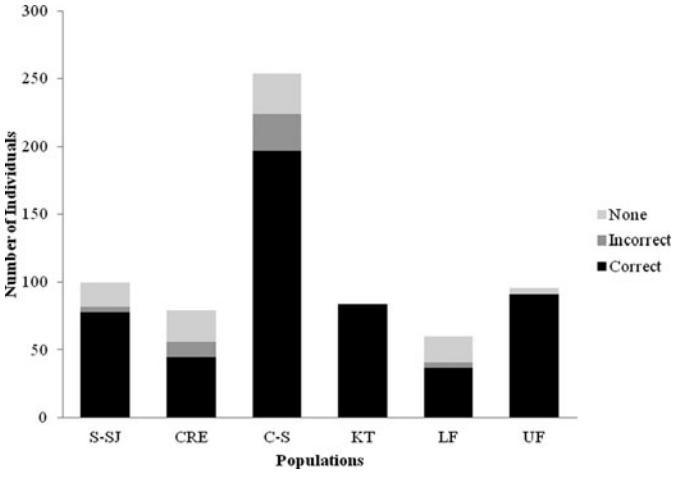

FIGURE 5. Re-allocation of White Sturgeon to populations identified by Structure in the program AFLPOP, MLD = 0.8. See Figure 4 for definition of abbreviations.

TABLE 6. Pairwise Phi-PT values for the six populations of White Sturgeon identified by rangewide Structure analysis. S–SJ = Sacramento–San Joaquin, CRE = Columbia River estuary, C–S (The Dalles Dam to Transboundary Reach, lower Snake, middle Snake), KT = Kootenai, LF = lower Fraser, and UF = upper Fraser. All values were significant ($P < 0.0001$).

Population	S–SJ	CRE	C–S	KT	LF	UF
S–SJ						
CRE	0.030					
C–S	0.100	0.045				
KT	0.225	0.181	0.167			
LF	0.041	0.020	0.053	0.209		
UF	0.128	0.078	0.067	0.215	0.083	

DISCUSSION

We have reported a range of genetic diversity levels and revealed differing patterns of population structure among White Sturgeon collections within and among drainages across the species' range. Populations suggested by Structure generally corresponded to regional designations (Table 1), with the exception of the Columbia–Snake River drainage. Both within-drainage and range-wide population structure analyses in this study and in Drauch Schreier et al. (2012a) recognized distinct populations inhabiting the Sacramento–San Joaquin, Kootenai, lower Fraser, and upper Fraser rivers, and substructure was

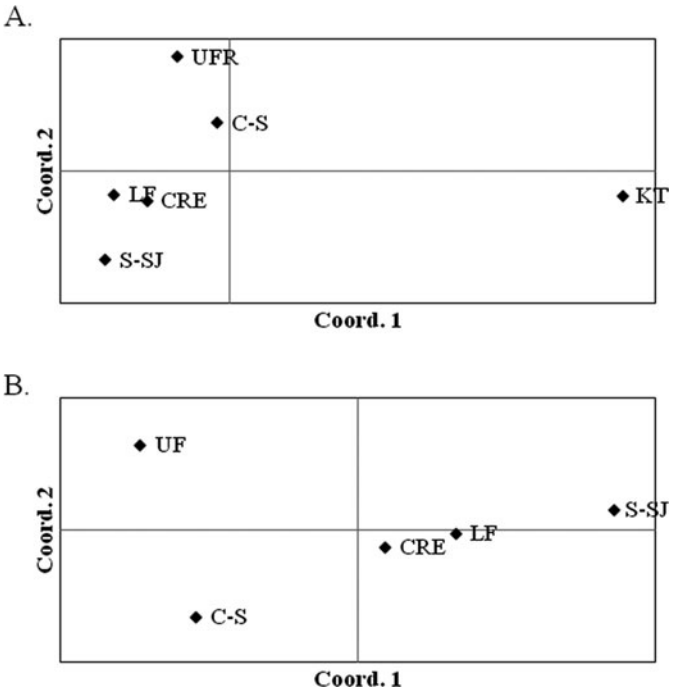

FIGURE 6. Principle coordinates analysis of White Sturgeon populations identified by Structure in range-wide analysis. S–SJ = Sacramento–San Joaquin River, CRE = Columbia River estuary, C–S = The Dalles to Transboundary Reach of Columbia River, lower Snake River, and middle Snake River, KT = Kootenai River, LF = lower Fraser River, and UF = upper Fraser River. (**A**) PCA conducted with the Kootenai River population. (**B**) PCA excluding the Kootenai River population.

identified in the upper Fraser River. Within-drainage and range-wide analyses for the Columbia–Snake River system indicated that these fish from this drainage are distinct, but the pattern of population structure within the Columbia–Snake system is complex. There appear to be two populations, one each associated with the downstream and upstream extents of the system, and individuals sampled between the Columbia River estuary and middle Snake River exhibited varying degrees of admixture between these two populations. This pattern is consistent with isolation by distance and net downstream gene flow.

Genetic Diversity

The Atlantic Sturgeon *A. oxyrinchus oxyrinchus*, distributed along the East Coast of North America, exhibits high levels of microsatellite genetic diversity in the middle of its range, while populations in regions at the northern and southern extremes of its range possess less genetic diversity (King et al. 2001). This pattern is not replicated in White Sturgeon. Genetic diversity levels in White Sturgeon were highest in regions with access to ocean habitat (Sacramento–San Joaquin River, Columbia River estuary, lower Fraser River) and lowest in upriver regions (middle Snake River, upper Fraser River above Hells Gate, Kootenai River). Very low levels of genetic diversity in White Sturgeon in the Kootenai River were expected based on findings of other studies (Rodzen et al. 2004; Drauch Schreier et al. 2012b). White Sturgeon inhabiting the Kootenai River were isolated from the rest of the Columbia River by Bonnington Falls 10,000–12,000 years ago (Northcote 1973), and very low levels of genetic diversity suggest that the Kootenai population was founded by few individuals. Genetic diversity loss in the Kootenai River may have been exacerbated by decades-long recruitment failure in this population (Ireland et al. 2002).

Within-Drainage Population Structure

Sacramento–San Joaquin River system—The Sacramento–San Joaquin River system contains a single population even though, historically, this system contained two rivers with available spawning habitat. This pattern has been observed for Atlantic Sturgeon in the Edisto and Combahee rivers on the East Coast, where no population structure is detected among the two rivers, both of which empty into St. Helena's Sound, South Carolina (Waldman et al. 2002; Grunwald et al. 2008). Although flows on the San Joaquin River have been significantly reduced by agricultural diversion of water for ~60 years (Pelley 2009), capture of adult White Sturgeon and their larvae in the San Joaquin River (Kohlhorst 1976; Dubois et al. 2009, 2010), and on the San Joaquin side of the delta (Stevens and Miller 1970), suggests that spawning has occurred in the San Joaquin historically. Additionally, White Sturgeon eggs were sampled in the San Joaquin River in the springs of 2011 ($N = 23$) and 2012 ($N > 60$) across multiple sites (Z. Jackson, U.S. Fish and Wildlife Service, personal communication). The lack of population structure in the Sacramento–San Joaquin system despite likely historical and possibly contemporary spawning in both rivers suggests that (1) there is a high rate of gene flow between them, enough to prevent the accumulation of significant genetic differences, or (2) a genetically distinct San Joaquin population existed but is now functionally extinct due to low survival in the river. Examination of tissue samples collected from adults in the Sacramento–San Joaquin system before modification of the San Joaquin River would allow us to distinguish between these two scenarios.

Columbia–Snake River system.—The pattern of population structure within the Columbia–Snake River system is more complex than that in the Sacramento–San Joaquin River. The within-drainage analysis of population structure suggests that three populations exist in the Columbia River drainage. One is the Kootenai River population, which is highly divergent from all other White Sturgeon populations. The distinctiveness of the Kootenai River population is probably due to its history of isolation and subsequent genetic drift. Structure analyses identified two other clusters in the Columbia–Snake River system, one associated with lower Columbia River and another associated with the middle Snake cluster at the upstream extent of the Snake River, and individuals in the middle Columbia River, Transboundary Reach and lower Snake River exhibited signs of admixture between the two clusters. It is likely that this pattern is due to isolation by distance along the length of the Columbia–Snake River system and possibly net downstream gene flow.

Before the Columbia and Snake rivers were impounded, White Sturgeon had the ability to migrate unimpeded from the Columbia River estuary upstream to Columbia Lake on the Columbia River and Shoshone Falls on the Snake River. However, the patterns of population structure revealed here suggest that historically there has been some degree of spawning site fidelity in Columbia–Snake White Sturgeon, and one population has spawned in areas farther upstream in the middle Snake River and another population has spawned lower in the Columbia River system. As contemporary spawning sites are known to be distributed throughout the Columbia River even in the presence of impoundments (Parsley and Kappenman 2000), it is likely that multiple spawning sites were located throughout the system historically.

The genetic signature of the upstream population found in individuals sampled in the lower reaches of the Columbia River also may be explained by the net downstream export of genes via downstream dispersal of individuals through one or more impoundments on the Columbia River. Net downstream gene flow over natural barriers in the Columbia River may occur as well. Several individuals in the Transboundary Reach, directly downstream of Bonnington Falls, showed some ancestry in the Kootenai River population, but no individuals in the Kootenai River showed ancestry in the Columbia–Snake River (Figure 3). While downstream entrainment of White Sturgeon through certain dams on the Columbia–Snake River system and natural barriers may occur, upstream movement remains relatively rare (Parsley et al. 2007) and is impossible at Bonnington Falls. Therefore, genes from the upstream reaches are exported to downstream reaches, but reciprocal gene flow is often not possible.

Range-wide Population Structure

A hierarchical approach to examining population structure both on a within-drainage and range-wide scale with Structure allowed us to detect fine-scale population structure within rivers, as well as evaluate genetic relationships among White Sturgeon populations inhabiting different drainages. When we examined White Sturgeon across the species range in Structure, $K = 4$ through $K = 7$ had similar likelihoods and variances. In this scenario, selecting the lowest value for K that is biologically reasonable is recommended (Pritchard et al. 2010). However, when $K = 4$ was assumed (data not shown), individuals from the Sacramento–San Joaquin River, Columbia River estuary, and lower Fraser River essentially assigned to a single cluster. When $K = 5$ is assumed (data not shown), the Sacramento–San Joaquin population was found to be distinct, but the Columbia River estuary and lower Fraser River collections were nearly identical, showing membership to a Sacramento–San Joaquin group and a Columbia River group. These two outcomes are contrary to our understanding of sturgeon species biology, as most sturgeon species exhibit some degree of natal philopatry, often on the scale of drainages (King et al. 2001; Israel et al. 2004; Welsh et al. 2008; but see Smith et al. 2002), and other studies have shown the genetic distinctiveness of the Sacramento–San Joaquin population (Bartley et al. 1985). Although recaptures of tagged individuals suggest that White Sturgeon do migrate to nonnatal estuaries (Chadwick 1955; Galbreath 1985; Brennan and Cailliet 1991; DeVore et al. 1999; Welch et al. 2006), we have no evidence to indicate that these migrations are for spawning. When $K = 7$ (data not shown), no individuals assigned to the seventh cluster, suggesting this was an overestimate of the number of populations in the data set. We used our knowledge of the species' life history and the results of the within-drainage Structure analysis to conclude that $K = 6$ was the most likely number of populations in the range-wide data set. This is supported by the authors of Structure, who suggest that program users strongly consider the biological feasibility of their results when determining the number of populations in their data set (Pritchard et al. 2010).

On the range-wide scale, Structure and AFLPOP analyses revealed that White Sturgeon from each of the Sacramento–San Joaquin, middle Snake, Kootenai, lower Fraser, and upper Fraser (above Hells Gate) rivers are genetically distinct populations. The genetic signature of the Sacramento–San Joaquin population is evident in the Columbia River estuary collection suggesting that some low level of gene flow occurs between the two systems. The PCA using populations defined by Structure also corroborates the hypothesis that some gene flow (historical or contemporary) occurs between all three populations that have access to marine habitat (Sacramento–San Joaquin River, Columbia River estuary, lower Fraser River), as all three populations cluster in the same quadrant of the PCA plot that includes the Kootenai River (Figure 6A). When the Kootenai population is removed as an outlier, the populations with ocean access still appear more closely related to each other than to the Columbia–Snake or upper Fraser populations (Figure 6B). It is uncertain whether the very close relationship identified between the Columbia River estuary and lower Fraser River is due to contemporary gene flow or recent coalescence because the lower Columbia River is thought to be one source for postglacial recolonization of the lower Fraser River (McPhail and Lindsay 1986; Brown et al. 1992b).

Population Structure in other Acipenserids

Studies applying nuclear markers to examine range-wide population structure have been conducted in several acipenserid species, including Atlantic Sturgeon, Green Sturgeon *A. medirostris*, and Lake Sturgeon *A. fulvescens*. All studies reveal significant population structure although it is found at various hierarchical levels depending on species. In Atlantic Sturgeon, populations are structured at the drainage level, with distinct populations in most rivers that contain a spawning population (King et al. 2001). Hierarchical patterns of population structure were revealed in Lake Sturgeon in the Great Lakes basin by Welsh et al. (2008) using disomic microsatellite data. At the highest level of population structure, individuals spawning in rivers in the (1) Hudson Bay–northern Lake Superior, (2) southern Lake Superior, and (3) the remaining Great Lakes clustered

together, although substructure was detected among some rivers in these larger geographic groups.

Few other studies have studies have examined sturgeon population structure within river drainages. Dugo et al. (2004) observed significant population structure in Gulf Sturgeon *A. oxyrinchus desotoi* among drainages and also within the Pascagoula River, revealing evidence for a second, previously unknown spawning population within the Pascagoula River. The finest scale examination of population structure in sturgeon is that of Welsh and McLeod (2010), which showed that no population structure existed among five Lake Sturgeon spawning sites located within 30.5 km on the Namakan River, Ontario (Welsh and McLeod 2010).

Only two genetically divergent populations have been identified in the Green Sturgeon, which is sympatric with White Sturgeon across its range on the West Coast. The Northern Distinct Population Segment (NDPS) of Green Sturgeon spawns in the Klamath and Rogue rivers while the threatened Southern Distinct Population Segment (SDPS) spawns in the Sacramento River (NMFS 2003). In contrast to the patterns we see in White Sturgeon in the Columbia–Snake River system and Fraser River, no within-drainage structure has been detected with disomic and tetrasomic microsatellite markers in the Green Sturgeon SDPS or NDPS (Drauch Schreier et al. 2012a; Israel et al. 2009).

Differences in patterns of population structure between White Sturgeon and the Atlantic Sturgeon, Gulf Sturgeon, Green Sturgeon, and Lake Sturgeon may to due to differences in life history strategies between the species. Atlantic Sturgeon, Gulf Sturgeon, Green Sturgeon, and Lake sturgeon all leave their natal drainage as subadults and range widely in marine or lentic habitat during nonreproductive times. Atlantic Sturgeon, Gulf Sturgeon, and Green sturgeon commonly migrate to nonnatal estuaries, although these movements are probably for feeding and not reproduction (King et al. 2001; Dugo et al. 2004; Grunwald et al. 2008; Israel et al. 2009). In contrast, White Sturgeon generally remain in freshwater or estuarine habitat associated with their natal drainage, and although marine movements of individuals have been documented (Chadwick 1955; Galbreath 1985; Brennan and Cailliet 1991; DeVore et al. 1999; Welch et al. 2006), these movements do not appear to be a significant component of their life history strategy. The species of North American sturgeon that has a life history most similar to White Sturgeon is the Shortnose Sturgeon *A. brevirostrum* of the East Coast. The Shortnose Sturgeon spends the majority of its life in its freshwater or estuary habitat of its natal drainage, although marine migrations among estuaries have been documented (Grunwald et al. 2002). Studies using mitochondrial DNA markers have detected significant levels of population structure in Shortnose Sturgeon among drainages and it is thought that population structure patterns in Shortnose Sturgeon have largely been shaped by phylogeographic forces (Grunwald et al. 2002). However, the Shortnose Sturgeon exhibits a higher ploidy level than White Sturgeon (Blacklidge and Bidwell 1993; Kim et al. 2005) and no studies using nuclear markers to examine population structure have been published.

Management Implications

Management and conservation of White Sturgeon can be enhanced by an improved understanding of genetic relationships among White Sturgeon populations across the species' range. In the Columbia–Snake River system, collections of individuals trapped between impoundments are often treated as "populations" for the purpose of management and conservation (Parsley et al. 2007). Our genetic analysis with microsatellite markers does not provide support for the management of impounded reaches as distinct populations. Evidence of gene flow between geographically proximate regions, either due to historical movement between regions that are now impounded or due to unidirectional downstream movement over dams, suggests that the genetic units be defined on a larger scale. It would be difficult to divide the Columbia River system into distinct genetic units for management as strong genetic differentiation only exists between White Sturgeon inhabiting the system's extremes (Columbia River estuary and middle Snake River) and little genetic divergence is observed among White Sturgeon collections throughout most of the system. It would be useful to reevaluate population structure in the Columbia–Snake River when codominant single nucleotide polymorphism markers become available for White Sturgeon to determine whether more fine-scale patterns of population structure could be revealed.

It is important to note that impoundment is a relatively recent disturbance when considering the long generation time of sturgeons. Only ~3–4 White Sturgeon generations have passed since the first impoundment was constructed on the Columbia River. It is likely that not enough time has passed since the beginning of habitat fragmentation for it to have significantly altered patterns of population structure. For example, the first dam constructed on the Columbia River, Rock Island Dam, isolates the upper four reservoirs of the middle Columbia River and the Transboundary Reach from the rest of the river. However, the within-drainage Structure analysis reveals very little difference in proportional population membership among collections ranging from the McNary Dam reservoir (several impoundments downstream) to the Transboundary Reach. Over time, however, genetic divergence among White Sturgeon collections isolated in impounded regions is expected to increase, depending on the rate of downstream migration, which probably varies by impoundment. Uppermost regions of the Columbia–Snake River system are expected to differentiate more quickly due to isolation.

Hatchery supplementation is being considered for various impounded reaches of the Columbia River to mitigate for hydroelectric projects and to improve White Sturgeon fisheries. We recommend selecting broodstock from the reach where stocking is to occur or from geographically proximate impounded reaches. We advise against selecting broodstock from the lower Columbia River for stocking into the Transboundary Reach or middle Snake River, and vice versa, to preserve any

unique genetic differences that may exist at the upstream and downstream extremes of the species range. Any supplemental stocking program for White Sturgeon should select a source population (or populations) containing many sexually mature adults that may be used as broodstock to allow for a multiyear stocking program. As many wild adults as possible should be spawned annually to preserve high levels of wild genetic diversity (e.g., Kootenai River conservation aquaculture program: Ireland et al. 2002; Drauch Schreier et al. 2012b).

Management of chronic recruitment failure in White Sturgeon may be improved by a greater understanding of different aspects of spawning behavior, including spawning site fidelity. The range-wide population structure analysis supports the notion that sturgeon exhibit natal fidelity at the drainage scale, although, we found that White Sturgeon spawning behavior within drainages varies. The Sacramento–San Joaquin and Fraser River systems represent two extremes. No population structure was detected in the former while evidence of reach-specific spawning site fidelity was found in the latter. Although no barriers separate the middle Fraser River from the Nechako River, each contains a distinct spawning population (Smith et al. 2002; Drauch Schreier et al. 2012a). The Columbia–Snake River system, on the other hand, exhibits intermediate levels of population structuring, and evidence of gene flow exists between geographically proximate reaches, but isolation by distance exists at extreme ends of the drainage. Few studies have examined spawning site fidelity of other sturgeon species within drainages. Several studies using site tagging or genetic data to examine Lake Sturgeon spawning behavior report the use of multiple spawning sites in a river within and among years by some individuals (Lyons and Kempinger 1992; Rusack and Mosindy 1997; Welsh and McLeod 2010). Applying the theory of Wright (1931), the use of multiple spawning sites by a few individuals would be enough to reduce genetic differentiation among different spawning populations.

As factors responsible for recruitment failure probably vary between locations, knowledge of how White Sturgeon select available spawning habitat (spatially and temporally) will improve managers' abilities to pinpoint the causes of recruitment failure and provide mitigation. Our results suggest that the scale of spawning site fidelity in sturgeon is broader than the salmonid model, and gene flow between geographically proximate spawning sites occurs in the Columbia–Snake River system and possibly the Sacramento–San Joaquin River system. This suggests that for some populations, recruitment failure is best managed on a larger scale than a "per spawning site" basis, at least in regions where fish use multiple spawning sites.

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APPENDIX: DETAILED RESULTS

Table A1. Numbers of alleles, allelic size ranges, and copy numbers of White Sturgeon microsatellites observed in genotypes from samples collected across the species' range. The allelic size ranges were determined using primers published in Rodzen and May (2002) and Börk et al. (2008). The copy number is to the number of locus copies detected by these primers in the polyploid White Sturgeon genome, as inferred from inheritance data (Drauch Schreier et al. 2011).

Locus	Number of alleles	Allelic size range (bp)	Copy number
AciG 2	7	261–299	4
AciG 35	21	238–306	12?
AciG 52	25	170–242	8
AciG 53	9	210–258	4
AciG 110	24	260–351	8
AciG 140	10	154–184	4
As015	20	177–237	8
Atr 105	10	125–161	4
Atr 107	30	178–268	8
Atr 109	31	212–304	8
Atr 117	31	193–281	8
Atr 1101	9	128–160	4
Atr 1173	24	237–322	8

APPENDIX REFERENCES

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