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ARTICLE

Influences of Hatchery Supplementation, Spawner Distribution, and Habitat on Genetic Structure of Chinook Salmon in the South Fork Salmon River, Idaho

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Abstract

We evaluated the genetic influence of hatchery supplementation on distinct naturally spawning populations of Chinook salmon *Oncorhynchus tshawytscha* in the South Fork Salmon River (SFSR), Idaho. Genetic tissue samples were collected from unmarked natural-origin and McCall Fish Hatchery (MFH)-reared Chinook salmon carcasses, and fish were identified by an adipose fin clip at five main-stem sites located both upstream and downstream of a seasonal exclusionary weir in the upper SFSR. We evaluated allele frequency data across 95 single-nucleotide polymorphism loci to determine the extent of genetic differentiation among collections. Genetic distance analyses and homogeneity tests indicated little subpopulation distinction in the upper SFSR. The weak overall genetic structure (global $F_{ST} = 0.010$) is likely reflective of a population diversity similar to the historical structure with introgression by MFH stock in the naturally spawning population of the upper SFSR. Further analyses were conducted to evaluate the genetic structure among the upper SFSR and spawning aggregates in two adjacent SFSR tributaries: the Secesh River, which is devoid of any hatchery stocking, and Johnson Creek, where a discrete supplementation program has been implemented using only Johnson Creek fish. Our results indicated variable abundances of SFSR hatchery spawners distributed spatially among the three main watersheds. Gene flow appears to be restricted and genetic differentiation to be relatively large despite substantial hatchery releases in the upper SFSR. Three historical aggregates of Chinook salmon appear to persist in the SFSR metapopulation, where variable hatchery influences are coincident with the distribution of suitable spawning habitat and watershed-specific management objectives.

The South Fork Salmon River (SFSR) is a major spawning tributary for a single run of spring/summer Chinook salmon *Oncorhynchus tshawytscha* in the Snake River basin of Idaho. In terms of historical salmon abundances and exploitation, it was considered to be one of the most important subbasins in the entire Columbia River basin (IDFG 1985). Currently, Snake River fall-run and spring/summer-run Chinook salmon are both listed as threatened under the Endangered Species Act (ESA).

In the SFSR and throughout the Pacific Northwest, hatchery propagation of salmon has become a fundamental component of population management. Hatchery supplementation can be beneficial for boosting spawner abundance in populations that have experienced a decline in natural production. Hatcheries are also instrumental in aiding reintroduction where populations have been extirpated (Narum et al. 2007b; Backman et al. 2009). However, hatchery fish have been known to represent a potential

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conservation risk for natural spawning wild populations when the two forms co-occur (Theriault et al. 2011). Supplementation stocks introduce a potentially disruptive aspect to natural mosaics of population structure through the erosion of adaptive gene complexes and functional population homogenization. Such modified selection regimes may result in decreased survival in the natural environment (Berejikian and Ford 2004; Kostow et al. 2003). Among Chinook salmon and other *Oncorhynchus* spp., hatchery-origin fish may be less fit, exhibit lower genetic diversity, and experience decreased survival (Hindar et al. 1991; Ryman et al. 1994; Waples 1994; McLean et al. 2005; Ford et al. 2006). Moreover, the propensity for straying among hatchery-origin Chinook salmon is significantly higher than is observed for natural-origin fish (Hard and Heard 1999; Candy and Beacham 2000), further confounding the genetic relationship among putative wild populations (Waples 1991).

Mounting concerns regarding hatchery influences have prompted fisheries managers to more cautiously evaluate supplementation protocols and the scope of their implementation. Restricting reproductive interaction or genetic introgression between nonendemic hatchery-origin salmon and putative wild populations may be facilitated by operation of exclusionary weirs used to limit stream access, fin marking to physically distinguish fish, subsequent hatchery-targeted selective harvests, and interception and removal of hatchery-origin adults. Monitoring and evaluation of supplementation and conservation hatchery programs is recognized as a necessary component for measuring their success (HSRG 2009). As a result, hatchery operation has seen major reform in recent years. Many supplementation programs have moved away from rearing segregated and often exogenous stocks, substituting fully integrated broodstocks derived exclusively from natural spawning local sources (Miller and Kapuscinski 2003; Mobrand et al. 2005). Such programs are intended to provide a demographic boost in natural production among populations in decline (Hedrick et al. 2000; Berejikian et al. 2008) while minimizing genetic differences and maintaining similar levels of variability among hatchery and natural population components (Mobrand et al. 2005; Heggenes et al. 2006; Eldridge and Killebrew 2008; Small et al. 2009).

In order to properly gauge the magnitude of genetic distinction among natural-spawning populations, it is important to implement genetic monitoring that represents or accounts for both natural- and hatchery-origin population components that likely have influence. In addition, such distinctions may also be shaped by behavior in conjunction with landscape, where spawner spatial distribution is also likely to affect genetic relationships (Williamson et al. 2010). Favorable spawning habitat is present in the upper reaches of the three adjacent and converging watersheds in the SFSR (Figure 1; Young and Blenden 2011). Areas utilized for spawning are spatially separated by areas of unsuitable spawning habitat marked by high gradient and large rock or boulder substrate. Previous studies utilizing allozymes (Waples et al. 1993) and microsatellite markers (Narum et al. 2007b) have noted a relatively high degree of genetic structure within the SFSR compared with many Snake River drainages, but specific ecological or demographic influences for delineating the genetic structure require further exploration. Three putative historical and distinct aggregate populations of spring/summer Chinook salmon populations occur among three primary watersheds of the SFSR subbasin (ICTRT 2003). Local supplementation programs are currently in operation to address conservation concerns and to augment sport and tribal harvest of Chinook salmon in the area (Young and Blenden 2011). Between the adjacent watersheds, the contribution of hatchery-origin individuals to total production in natural-spawning populations may be variable across stream sections, including those upstream of weirs.

In this study, we used allele frequency data compiled across a suite of single nucleotide polymorphism (SNP) loci to examine the existing level of population diversity in the SFSR subbasin. One of our primary objectives was to investigate the degree to which intense hatchery supplementation for harvest augmentation has influenced the genetic structure of the Chinook salmon population in the upper SFSR, an area where returning hatchery fish are proportionally present in large numbers. Our analyses were designed to specifically test whether or not the natural-spawning and hatchery supplementation components of the upper SFSR population appear genetically similar. Our efforts further focused on testing for genetic differentiation among spatially segregated spawning aggregates of Chinook salmon in three adjacent watersheds of the SFSR, including the upper SFSR. We investigated potential adverse effects of the upper SFSR supplementation program on apparent population aggregate distinctions among watersheds, expecting that the persistence of putative historical populations is facilitated by a patchy distribution of habitat and philopatric behavior of the species. Differences are further likely to be spatially coincident with the pursuit of specific low-impact or conservation hatchery management agendas in the basin. However, it is likely that the spawning aggregate in the upper SFSR, where hatchery fish have been present and numerous, may appear wholly integrated with supplementation stock. We suggest that the results of our evaluation will be generally valuable to managers weighing alternative plans for population rehabilitation and harvest opportunities. The information may be particularly applicable in other complex systems with multiple management objectives, where jeopardy (genetic or otherwise) to wild salmon populations remains an overarching concern.

STUDY AREA

The SFSR is a tributary of the Salmon River, and its confluence is located at approximately river kilometer (rkm) 212 of the Salmon River in the Snake River basin of Idaho. The SFSR drains three primary watersheds each known to support a spawning population of spring/summer Chinook salmon: (1) the upper main-stem SFSR upstream of the confluence with the East Fork SFSR (EFSFSR), (2) the EFSFSR draining from the

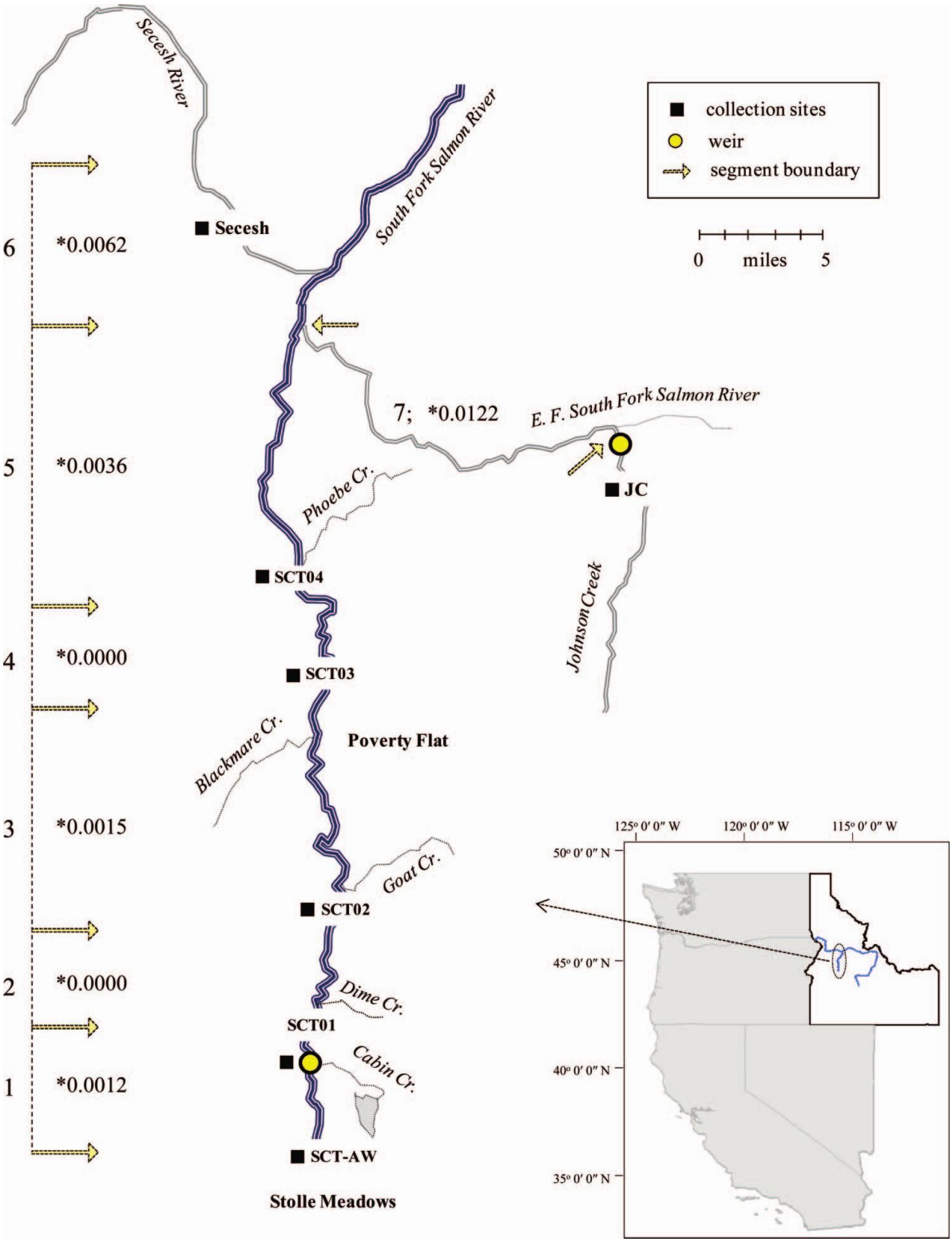

FIGURE 1. Map of the study area in the SFSR subbasin. Sampling locations inclued two adjacent watersheds: Johnson Creek (JC) and Secesh River. Five upper SFSR collection sites include fish interrogated at the upper SFSR adult weir and one site near Stolle Meadow (SCT-AW) upstream of the weir, two sites in the upper SFSR main stem downstream of the weir (SCT01 and SCT02), and two sites downstream of Poverty Flat (SCT03 and SCT04) in a lower section of the upper SFSR main stem. Collection locations are associated with stream segments for analysis using StreamTree (Kalinowski et al. 2008). Stream segments are numbered on the left margin (and center for number 7). Fitted or "mapped" genetic distances are also shown at left (asterisks). Correlation of the pairwise F_{ST} between collections and the fitted distances of stream sections bounding those collections was significant ($r^2 = 0.93$, $P < 0.001$). [Figure available in color online.]

east into the SFSR at rkm 60, and (3) Secesh River draining from the west into the SFSR at rkm 58 (Figure 1).

Spawning activity is limited in much of the lower section of the upper SFSR (Figure 1), and the distribution of suitable spawning habitat upstream of the EFSFSR confluence is patchy, areas of good-to-excellent habitat being separated by areas of unsuitable or unfavorable spawning habitat. Within the upper SFSR, extensive though patchy areas of moderate-to-excellent spawning habitat is present from Phoebe Creek to a region upstream of the upper SFSR weir. For example, the Stolle Meadows area is characterized by nearly continuous excellent spawning habitat. Both Johnson Creek (a tributary of the EFSFSR) and the Secesh River contain localized areas of excellent Chinook salmon spawning habitat. However, like the upper SFSR, the lower sections of both Secesh River and the EFSFSR downstream of Johnson Creek (approximately 30 km of river) support limited spawning and are characterized by steep gradient, relatively high velocity flows, and large rocky substrate.

Interpreting the impacts of supplementation throughout the SFSR first requires a thorough understanding of recent hatchery sources and implementation history. Each of the three watersheds in the study area is managed differently with specific management strategies. The upper SFSR remains the most complex, balancing conservation and supplementation with harvest. An upper SFSR hatchery stock (HAT) was established for mitigated harvest augmentation through the Lower Snake River Compensation Program (LSRCP). These fish are reared at the Idaho Department of Fish and Game McCall Fish Hatchery (MFH). Substantial hatchery-selective sport harvest and a nonselective tribal harvest have been ongoing. Broodstock for the program was initially collected (from 1978 to 1980) at Little Goose and Lower Granite dams in the lower Snake River, and at an upper SFSR weir (Figure 1; Hutchinson 1982). Although the timing of those broodstock collections coincided with normal return times for SFSR spring/summer-run Chinook salmon, they likely comprised spring/summer-run fish from throughout the Snake River region (i.e., unknown origins). After 1980, all broodstock collections have occurred entirely at the SFSR weir.

Through brood year (BY) 1989, approximately one-third of hatchery-released fish were marked with an adipose fin clip and coded wire tag (CWT); the remainder had no distinguishing marks or tags. Thus, both the hatchery broodstock and naturally spawning fish were presumably an admixture of marked and unmarked hatchery- and natural-origin fish (Frew 1986; Cochnauer and Elam 1990). Beginning in BY1990, all hatchery-origin juveniles were marked with an adipose fin clip, and in 1996 the hatchery program became completely segregated by initiating the exclusive use of adipose-clipped broodstock (Howell et al. 1985). No segregated hatchery-origin fish were intentionally released upstream of the weir in the upper SFSR, but weir operation from 1980 to 2007 routinely saw highly variable weir efficiencies, prompting construction of a more-robust weir in 2007. Prior to 2007, a significant number of segregated hatchery-origin fish were able to escape upstream undetected.

The other two major spawning population aggregates in the subbasin, Johnson Creek and Secesh River, have distinct management objectives. In Johnson Creek, an adult exclusionary weir has been in operation since 1998 for broodstock collection and directed fish passage in a watershed-specific conservation hatchery program. Hatchery spawned fish are locally derived and intended to boost local natural spawner abundance (Rabe et al. 2006). Only returning natural-origin fish are utilized for broodstock, and a majority of natural-origin fish and all hatchery-origin fish are passed upstream of the weir. Hatchery-origin fish are marked with a CWT and a visible implanted elastomer tag but are not adipose fin clipped. Since 2001, all stray hatchery fish (identified by absence of the adipose fin) encountered at the weir have been removed from Johnson Creek. Although targeted nontribal harvest is not permitted, tribal harvest is allowed. In contrast to Johnson Creek, the Secesh River is a low-impact stream, minimally managed in support of natural spawning. In the Secesh River, there is no use of exclusionary weirs and no directed hatchery supplementation, sport harvest is prohibited, and tribal harvest is limited.

METHODS

Sample collection.—Tissue samples for genetic analysis were extracted from opercle or caudal fin tissue of live adult fish captured at a weir located in Johnson Creek and from juveniles sampled during operation of a rotary screw trap in Secesh River. In the upper SFSR, samples were obtained from carcasses encountered during spawning ground surveys at five locations in the upper SFSR from 2000 to 2002. Some carcasses at the site upstream of the SFSR adult weir were sampled from 2005 to 2007 (Figure 1). Sample sizes (n) across collections ranged from 35 to 115 (Table 1). Tissue samples were immediately stored in individually labeled vials containing either a 95% solution of nondenatured ethanol or a lysis buffer (0.5 M EDTA, pH 8.0; 2 M tris, pH 7.5; 5 M NaCl, 20% sodium dodecyl sulfate).

Throughout this evaluation, "natural-origin" is used to refer to all progeny of naturally spawning Chinook salmon that were reared in the natural environment as indicated by the absence of tags or fin marks (parental origin may be either wild- or hatchery-origin). The segregated MFH stock released in the upper SFSR is identified as "HAT." Five upper main-stem SFSR collection sites, identified by SCT, are (1) Stolle Meadows, located upstream of the weir (including natural-origin fish sampled at the weir during upstream migration; SCT-AW); (2) a stream section from the weir downstream to Dime Creek (SCT-01); (3) from Dime Creek downstream to an unnamed tributary approximately 2 km upstream of Goat Creek (SCT-02); (4) a section extending 1.1 km downstream from Blackmare Creek in the Poverty Flat area (SCT-03); and (5) from Lodgepole Campground to immediately downstream of Phoebe Creek (SCT-04; Figure 1; Table 1). For analyses,we evaluated 11 groups (POPs) partitioned from among the five upper SFSR carcass collection sites and adjacent watersheds. Due to small annual sample

TABLE 1. Numbers of fish (*n*) collected. Samples span five sampling sites in the upper South Fork Salmon River (SFSR) and three sites in adjacent tributaries. Samples were partitioned into 11 analysis populations (POPs): four natural-origin (NOR) groups identified by stream sections (SCTs) downstream of the upper SFSR weir, NOR groups sampled at or upstream of the upper SFSR weir (SCT-AW), adipose-marked McCall Fish Hatchery stock grouped into three return-year collections (HAT), and three populations from adjacent SFSR watersheds. The Johnson Creek (JC) sample includes fish identified by coded wire tag detection to differentiate Johnson Creek supplementation fish (JCsupp) from a natural population component (JC). Collection years are identified in parentheses. All upper SFSR natural-origin analysis populations were pooled by location across sample years.

	SFSR collection site(s)						Adjacent SFSR watersheds		
POP	SCT01	SCT02	SCT03	SCT04	Weir	Above weir	JC weir	Secesh	Total (*n*)
(1) HAT (2000)	16	28	0	0					44
(2) HAT (2001)	12	16	9	10					47
(3) HAT (2002)	0	0	0	0	31	16[a]			47
(4) SCT01 (2000–2002)	40								40
(5) SCT02 (2000–2002)		49							49
(6) SCT03 (2000–2002)			35						35
(7) SCT04 (2000–2002)				60					60
(8) SCT-AW (2005–2007)					26[b]	89			115
(9) JC (2002)							90		92
(10) JCsupp (2002)							88		88
(11) Secesh (2001)								81	81

[a] Although directed passage upstream of the weir excluded HAT stock, some HAT carcasses were encountered in surveys of this area.
[b] Weir samples were collected from 2000 to 2002.

sizes, temporal collections of natural-origin fish were pooled for analysis by stream sections corresponding to the five sites (Table 1). The HAT fish, identified by an adipose fin clip, were pooled across all five upper SFSR collection sites but partitioned temporally by three return years (2000, 2001, and 2002). This included HAT fish sampled during weir captures. An additional three POPs for comparison among watersheds included Secesh River and two population components from Johnson Creek: the integrated supplementation component (JCsupp) and natural-origin fish (JC).

Laboratory protocols.—Genomic DNA was extracted from digested tissue samples using a standard Qiagen DNeasy protocol and a Qiagen 3000 robotic pipetting system. Prior to amplification of SNP loci using Taqman assays (Applied Biosystems), an initial polymerase chain reaction (PCR) "preamp" step was implemented using whole genomic DNA and unlabeled primers to jumpstart SNP amplification via increased copy number of target DNA regions. The cycling regime and PCR conditions for the preamp step were as follows: one initial cycle of 95°C for 15 min, 14 cycles of 95°C for 15 s, 60°C for 4 min, and a final dissociation step. Samples were genotyped for 95 SNP markers (see Table A.1 in the appendix in the online version of this article) with TaqMan chemistry (Campbell and Narum 2008) and Fluidigm 96.96 dynamic array chips to generate high-throughput genotyping. (For additional details on locus or primer specifications, locus optimizations, and characterization of Chinook salmon populations using this panel of SNP markers, see Hess et al. 2011a, 2011b; Matala et al. 2011.) Chips contained one genotype indicator sample and one no-template control sample as a quality control measure. Sample cocktails included 2.5 μL TaqMan 2 × master mix (Applied Biosystems), 0.05 μL Gold *Taq* polymerase, 0.25 μL GT load buffer, 0.2 μL H_2O, and 2.0 μL preamp DNA template. Single SNP assays were prepared in a 5.3-μL reaction mix (per sample) containing the following reagents: 2.5 μL DA load buffer, 0.25 μL Rox dye, 1 μL H_2O, and 1.25 μL primer–probe. Fluidigm 96.96 dynamic array chips were loaded with assay cocktail dispensed at 4.5 μL per well and sample cocktail dispensed at 5.0 μL per well. Chip loading and amplification was completed following standard manufacturers protocol on a Fluidigm IFC controller, and chips were imaged and scored on a Fluidigm EP1 imager using Fluidigm SNP Genotyping Analysis Software version 2.1.1. Carcass samples often provide poor quality or quantity (or both) of viable DNA relative to fresh tissue, and our final sample sizes were pared based on individual genotyping success. Successful genotyping for a given sample was defined proportionally as less than 10% missing data (i.e., missing data at no more than nine SNP loci).

Statistical analysis.—Descriptive statistics (including number of samples analyzed per population per locus, the unbiased heterozygosity (H_E; Nei 1978), and observed heterozygosity [H_O]) were generated using the analysis program GenAlEx version 6.2 (Peakall and Smouse 2006). The Markov Chain Monte Carlo approximation of Fisher's exact test implemented in GENEPOP version 3.3 (1,000 batches with 1,000 iterations; Raymond and Rousset 1995) was used to test for deviations from HWE expectations, evaluated across SNP loci and populations; we used this test to evaluate potential nonrandom mating within populations or possible marker amplification problems (e.g., null alleles). Index of inbreeding (F_{IS}) identifies the direction of deviations (e.g., heterozygote deficit) and was also evaluated

using GENEPOP. Linkage disequilibrium was tested for all pairs of loci across populations using a simulated exact test in GENEPOP. For all pairs of loci with significant nonrandom association or "linkage," we reconstructed the (unknown) gametic phase of multilocus genotypes, thereby creating a phased constituent genotype for each locus pair using the ELB algorithm implemented in ARLEQUIN version 3.5 (Excoffier et al. 2005). The significance level ($\alpha = 0.05$) was corrected for multiple tests across 95 loci using a modified version of the BY–false discovery rate (FDR) method (Benjamini and Yekutieli 2001) as presented in Narum (2006) in order to reduce false positives for both HWE and linkage tests; this resulted in a critical threshold for significance of 0.0060 and 0.0057, respectively.

The program LOSITAN (Antao et al. 2008) was used to evaluate the relationship between F_{ST} and H_e (expected heterozygosity) for all loci in an island model, to identify outlier loci having excessively high or low F_{ST} compared with neutral expectations; such loci would be candidates for selection. Eliminating nonneutral "outlier" loci is necessary before computing many population genetic parameters (e.g., F_{ST}, Nm, Ne), as the assumption of neutrality can be biased by outliers (Luikart et al. 2003). We used data simulations based on 50,000 replicates for all SNP loci under an infinite alleles model, a simulation mean F_{ST} of 0.008, and a 0.99 confidence interval (CI). Outlier loci lying above or below these quantiles may be under directional or balancing selection, respectively, in some populations.

GENEPOP (Raymond and Rousset 1995) was used to calculate locus-specific and global F_{ST} (θ of Weir and Cockerham 1984), which indicates the proportion of total variation attributed to differences among collections; a 95% CI around F_{ST} was generated in FSTAT version 2.9.3.2 (Goudet 2001). A matrix of pairwise F_{ST} among pairs of collections was generated in GENEPOP. Pairwise F_{ST} significance was tested using ARLEQUIN version 3.1, and critical values were adjusted for multiple tests using the modified BY-FDR method (Narum 2006). Analysis of molecular variance was conducted on a locus-specific basis and overall across watersheds using ARLEQUIN version 3.5 (Excoffier et al. 2005). The AMOVA was first performed on the Johnson Creek and Secesh River analysis populations to determine the appropriateness of grouping those collections. The temporal HAT and upper SFSR analysis populations were similarly evaluated to determine if HAT should be evaluated as a separate group in overall AMOVA.

The program StreamTree (Kalinowski et al. 2008) was used to map genetic differentiation between collection sites (analysis populations) to the intermediate stream segments between them. The method employs a modified least-squares approach commonly used to construct phylogenetic trees, where the stream network is analogous to the topology or branching pattern of the tree. The method is used to infer or explore factors within the physical environment that may influence genetic variation in the absence of isolation by distance, such as barriers, habitat corridors, or headwater connections. When the sum of fitted (or "mapped") genetic distances approaches the observed genetic distance (F_{ST}) between collections, genetic variation among putative populations may be inferred geographically, in association with landscape features, even if geographic distance is not directly correlated. The HAT collections, which were collected from throughout the upper SFSR, cannot be associated directly with specific stream segment and were not included in the StreamTree.

A pairwise matrix of Nei's standard genetic distance (Nei 1972) and an unrooted neighbor-joining (NJ) tree were generated using PHYLIP version 3.68 (Felsenstein 2008). The NJ tree displays the relationship among all populations as their respective proximities in the tree topology, where the sum of branch lengths represents the genetic distance between any two populations. The SEQBOOT option was implemented to generate 1,000 simulated data sets, and a consensus topology with bootstrap support was generated using the CONSENSE option in PHYLIP. In addition, a microsatellite data set was constructed with contributed data previously described in Narum et al. (2007b) for the Snake River basin, including Johnson Creek and Secesh River. We incorporated existing microsatellite genotypic data collected in our laboratory that included the previously described temporal HAT collections and natural-origin samples from the upper SFSR. We reconfigured the reported NJ tree topology of Narum et al. (2007b) using all available data in order to draw regional comparisons and evaluate similarity among SFSR samples represented in a larger Snake River basin context.

The analysis program GenAlEx version 6.2 (Peakall and Smouse 2006) was used to conduct multivariate principal coordinate analysis (PCA) to graphically display patterns or clusters of genetic similarity among 11 analysis populations. The method reduces redundant variables into a smaller subset of the most informative, where each successive PCA axis explains proportionately less of the total variation. Generally, the first two to three axes will reveal most of the separation among distinct groups. We used both the option to convert the distance matrix (the pairwise F_{ST} matrix generated in GENEPOP) to a covariance matrix and the standardization option which divides the covariance input by $\sqrt{n-1}$.

RESULTS

Descriptive Statistics

The mean expected heterozygosity per locus ranged from 0.000 to 0.495 across collections (Table A.1). We observed fixed-allele frequencies for a single allele at each of nine loci (Table A.1). A private allele was observed in group SCT03 at SNP locus *Ots_ASPAT-196*, and in group HAT2000 at *Ots_LWSop-638*. Since minor allele frequency was very low for both private alleles, each single observation may be the result of laboratory error, but genotypes were confirmed by replication of results in a quality-control run and all populations were otherwise fixed for the alternate allele at both loci. Among 1,045 total HWE tests, we observed 20 departures from

TABLE 2. Analysis of molecular variance results. The populations defined in Table 1 were partitioned into pairs of groups for testing: JC versus Secesh River, POPs 9–10 versus POP 11, HAT versus upper SFSR NOR, POPs 1–3 versus POPs 4–8, upper SFSR versus adjacent tributaries, and POPs 1–8 versus POPs 9–11. The sources and percentages of variation are defined as follows: Va = among group, Vb = among populations within groups, and Vc = within populations. Values in bold italics are statistically significant at $\alpha < 0.05$. Tests were conducted with 10,000 permutations.

Source of variation	df	Sum of squares	Variance components	Percent variation	*P*-value
		JC versus Secesh River			
Va	1	46.647	0.116	1.220	0.328
Vb	1	21.610	0.068	0.720	***<0.000***
Vc	519	4,832.787	9.312	98.060	***<0.000***
Total/F_{ST}	521	4,901.044	9.496	(0.019)	
		HAT versus upper SFSR NOR			
Va	1	15.860	0.010	0.110	0.051
Vb	6	71.429	0.023	0.250	***<0.000***
Vc	866	8,182.047	9.448	99.650	***<0.000***
Total/F_{ST}	873	8,269.336	9.482	(0.003)	
		Upper SFSR versus adjacent tributaries			
Va	1	59.417	0.061	0.640	***0.018***
Vb	9	155.546	0.065	0.680	***<0.000***
Vc	1,385	13,014.834	9.397	98.680	***<0.000***
Total/F_{ST}	1,395	13,229.797	9.523	(0.013)	

expected genotypic proportions across groups. Four departures occurred at mitochondrial locus *Ots_C3N3* (all other collections were fixed at this locus); this deviation was expected due to lack of heterozygous genotypes owing to exclusive maternal inheritance of the marker. The remaining 16 deviations spanned 10 to 11 analysis groups and 14 different loci; there was no indication of collection- or locus-specific deviations. A plot of expected heterozygosity and genetic distance (F_{ST}) generated in LOSITAN indicated that no loci were outliers or candidates for either balancing or directional selection. Tests for linkage disequilibrium across 11 total analysis groups revealed two pairs of loci that remained significantly out of equilibrium after a BY-FDR adjustment ($P < 0.0057$). Apparent linked locus pairs were *Ots_FGF6A* and *Ots_FGF6B_1* (11 analysis pops), and *Ots_hsc71–3′-488* and *Ots_hsc71–5′-453* (in 4 of 11 pops); data for all four loci were retained by generating composite phased genotypes per pair. The resulting data set available for all subsequent population analyses included 84 of the original 95 loci (reduced by nine fixed SNPs and two phased locus pairs).

Population Genetic Structure Analysis

For the 11 groups of Chinook salmon evaluated in the upper SFSR and two adjacent tributaries, the AMOVA by polymorphic loci revealed among-group variation (Va) ranging from Va less than 0 to Va equal to 4.65 (Table A.1). The mean (weighted average) among-group variation from AMOVA per locus was 1.04%. There was no significant difference in among-group variation for the Secesh River versus Johnson Creek analysis populations, nor for the temporal HAT versus upper SFSR collections (Table 2). Subsequently, an overall AMOVA across watersheds, testing all upper SFSR analysis populations combined versus Secesh River–Johnson Creek, did reveal significant among-group variation (Table 2). Across the entire data set (84 loci and 11 analysis populations), we observed locus-specific, among-group variation that ranged from F_{ST} less than 0.00 to $+0.046$. The overall or global estimate of 0.010 was significantly greater than 0 (95% CI = 0.008–0.013). Patterns of population pairwise variation (F_{ST}) differed among the 11 analysis populations in comparisons across the three watersheds (Table 3). Significant differentiation was observed between the Johnson Creek and Secesh River collections, and both were significantly different from all upper SFSR groups, including HAT collections. Among natural-origin collections from the upper SFSR, SCT04 showed the greatest overall distinction from HAT, and the only significant difference among upper SFSR groups was observed between SCT02 and SCT04. Temporal variation among hatchery groups was evident, where HAT2000 was significantly different from HAT2001; moreover, the greatest variation occurred between HAT2000 and upper SFSR natural-origin groups in comparisons with the other temporal hatchery collections (Table 2). The least amount of among-group variation was observed in comparisons involving SCT01 and SCT03 (neither of which exhibit differentiation from any other collection in the upper SFSR). The SCT-AW population (Stolle Meadow upstream of the weir) was only significantly different from the HAT2000 group in the upper SFSR. The comparison of the Johnson Creek collection and SCT02 collection in the upper SFSR had the largest observed pairwise F_{ST} detected in this study (0.0219).

We demonstrated genetic similarity or distinction among the 11 analysis groups through phylogenetic relationships in the topology of an unrooted NJ phylogram (Figure 2). The confidence or concordance (>50%) of the topology is indicated with

TABLE 3. Pairwise comparisons of among-group variation (F_{ST}). Results are based on 84 single-nucleotide polymorphism multilocus genotypes. The lower left half-matrix displays pairwise F_{ST} values for each pairwise comparison, while the upper right half-matrix provides the corresponding statistical significance (P-value). Asterisks following values in bold italics indicate a significant result after adjustment for multiple tests ($P < 0.0108$; Narum 2006). Mean pairwise values were calculated across all pairwise comparisons on a per-group basis.

Analysis group	HAT2000	HAT2001	HAT2002	SCT01	SCT02	SCT03	SCT04	SCT-AW	JC	JCsupp	Secesh
HAT2000		0.0010	0.3496	0.1133	0.0000	0.0137	0.0000	0.0010	0.0000	0.0000	0.0000
HAT2001	***0.0072****		0.0381	0.0664	0.0928	0.2334	0.0029	0.0703	0.0000	0.0000	0.0000
HAT2002	0.0005	0.0035		0.4658	0.0586	0.1084	0.0147	0.0527	0.0000	0.0000	0.0000
SCT01	0.0025	0.0030	–0.0001		0.5566	0.2852	0.6260	0.1914	0.0000	0.0000	0.0000
SCT02	***0.0084****	0.0028	0.0035	–0.0005		0.1543	0.0098	0.0772	0.0000	0.0000	0.0000
SCT03	0.0063	0.0014	0.0032	0.0015	0.0027		0.1455	0.0039	0.0000	0.0000	0.0000
SCT04	***0.0118****	***0.0059****	0.0040	–0.0010	***0.0046****	0.0023		0.1104	0.0000	0.0000	0.0000
SCT-AW	***0.0070****	0.0020	0.0025	0.0011	0.0021	0.0060	0.0015		0.0000	0.0000	0.0000
JC	***0.0135****	***0.0135****	***0.0140****	***0.0117****	***0.0181****	***0.0118****	***0.0152****	***0.0130****		0.0000	0.0000
JCsupp	***0.0182****	***0.0202****	***0.0179****	***0.0210****	***0.0219****	***0.0167****	***0.0204****	***0.0191****	***0.0075****		0.0000
Secesh	***0.0143****	***0.0086****	***0.0117****	***0.0096****	***0.0102****	***0.0111****	***0.0118****	***0.0121****	***0.0172****	***0.0196****	
Mean pairwise	0.0090	0.0068	0.0061	0.0049	0.0074	0.0063	0.0076	0.0066	0.0135	0.0183	0.0126

bootstrap values at the nodes in a consensus tree. Results revealed a relatively large distance at an internal node, separating a subcluster containing all upper SFSR groups from collections in two adjacent tributaries. Johnson Creek and Secesh River branch lengths were also characterized by relatively large distances from the same internal node. In the upper SFSR many of the natural-origin groups cluster in relatively close proximity (SCT01, SCT02, SCT04, and SCT-AW), but confidence in this subcluster relationship is not substantiated with adequate bootstrap support. The largest concordant branch length, indicating greatest genetic distance among the 11 groups, was observed for the two Johnson creek collections. The only other significant consensus node occurred at the branch separating the HAT2000 and HAT2002 samples from remaining populations. This indicates relatively large temporal variation within the hatchery program. The inset topology (Figure 2), representing the SFSR groups in a Snake River basinwide view, displays relatively short intermediate genetic distances between all SFSR groups that also cluster in close association as an overall distinct group, indicating local similarity compared with other major subbasins in the Snake River basin region.

Spatial PCA analysis of the 11 analysis populations resulted in a primary axis, accounting for 45.1% of the total variation, that appeared to separate groups accurately into adjacent stream regions or watersheds (Figure 3). Overall, the first three axes explained greater than 78% of the total variation. Further, the plot corroborates the degree of relative similarity between the three temporal HAT sample groups and their proximity to upper SFSR groups observed in the phylogeographic analysis.

Results of the StreamTree analysis indicate significant correlation ($r^2 = 0.93$, $P < 0.0001$) between observed F_{ST} genetic distance and summed fitted distances between all pairs of analysis populations (Figure 1). Testing for no difference between fitted distance and observed genetic distance across stream segments, we determined that landscape is significantly associated with the distribution of genetic differentiation. The greatest proportion of the total fitted distance occurred in the stream segments that culminate at the confluence of the EFSFSR and the SFSR, bounded by collections in SCT04 (near Phoebe Creek), and the JC and SECESH collection sites (Figure 1). These sites (and intermediate stream segments 5–7) are spatially discrete, separated by nonspawning habitat and extreme hydrologic conditions. They account for nearly all of the total variation, calculated as the summed genetic distances across all stream segments (Figure 1).

DISCUSSION

Our genetic evaluation of Chinook salmon in the SFSR provides information about the population structure within the upper SFSR and between populations in adjacent watersheds that represent putative historical spawning aggregates. Results from the NJ tree complement those from a previous study (Narum et al. 2007b) that described local similarity among the Johnson Creek and Secesh River populations when those populations were viewed in broader context throughout the Snake River basin (Figure 2, inset). Our findings elaborate on Narum et al. (2007b) by further indicating that this local similarity extends to the upper SFSR and the hatchery supplementation stock. Although divergent, the genetic distances between upper SFSR, JC, and Secesh collections in phylogenetic analyses were complementary in scale to regional similarities identified by Narum et al. (2007b). The upper SFSR population appears to be highly introgressed with HAT, yet exogenous early broodstock sources from the lower Snake River do not appear to have had a lasting genetic influence within the observed SFSR population

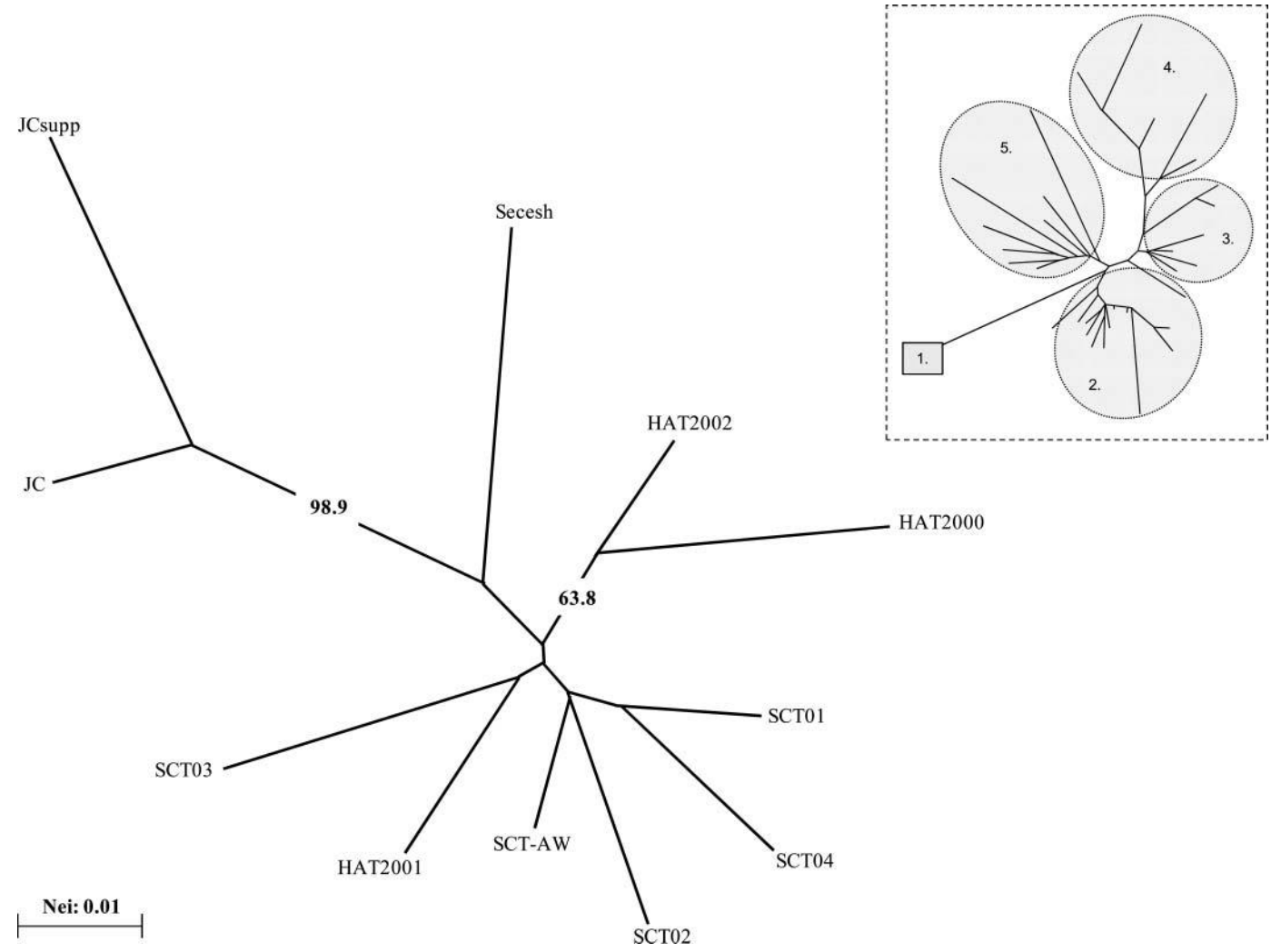

FIGURE 2. A neighbor-joining (NJ) radial tree based on Nei's unbiased distances. Bootstrap support for the topology (>50%) is shown at nodes. Natural-origin and supplementation stock from Johnson Creek are shown separately; HAT is partitioned by temporal collections from 2000 to 2002. The inset topology (NJ tree and Nei's distance) represents SFSR collections in broader context and is reconfigured from Narum et al. (2007b) using microsatellite data. Clusters in the inset tree are (1) Imnaha River; (2) Grand Ronde River and Clearwater River; (3) SFSR, including three upper SFSR groups, two Johnson Creek groups, and Secesh River; (4) Middle Fork Salmon River; and (5) Upper Salmon River.

structure. In other words, a regional distinction persists despite potential nonlocal effects of broodstocks that originated as mixed-stock collections (Keifer et al. 1992; Myers et al. 1998).

From overall diversity analyses, it appears that introgression of HAT fish is prevalent throughout the upper SFSR (the greatest influence being in SCT01 and SCT02). It has been common for hatchery-origin fish to spawn in suitable habitat regions just downstream of the weir. In fact, carcass and spawning surveys have shown that ad-clipped hatchery fish comprise a predominate proportion (approximately 80%) of all fish on the spawning grounds (Young and Blenden 2011). From 1996 through 2008, the proportion of HAT carcasses recovered from stream sections was relatively stable (SCT01 = 70.6% [SE = 3.8], SCT02 = 73.1% [SE = 3.6], SCT03 = 23.5 [4.14], and SCT04 = 14.37 [SE = 3.68]; Young and Blenden 2011). Population SCT04 is the furthest downstream group in our analyses and was also the most differentiated from HAT in F_{ST} diversity.

We have identified a common and substantial homogenizing effect by stocked hatchery-origin fish throughout the sampled area in the upper SFSR. Therefore, in addition to introgression mediated in the hatchery, it is likely that putative natural-origin fish in these collections may be the progeny of naturally spawning HAT fish. Although the SFSR weir was constructed to exclude passage of HAT and to protect the upstream natural-origin population from introgression, high water usually delayed its installation. This allowed a significant portion of returning HAT fish to escape upstream of the trap, with consequently ample opportunity for HAT introgression into the natural-origin population in the Stolle Meadows area. Given this outcome, we would expect that areas upstream of the weir would be characterized

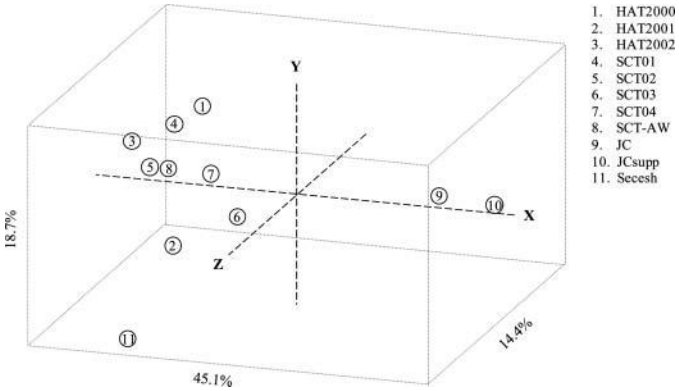

FIGURE 3. A three-dimensional (3-D) PCA plot showing the ordinal association of 11 analysis groups in the SFSR. Proportion of total variation explained by each of the first three PCA axes is shown. A Microsoft Excel macro for conversion of data to a 3-D scatter plot graphic is available as freeware (http://faculty.fuqua.duke.edu/∼kamakura/bio/WagnerKamakuraDownloads.htm).

by a hatchery influence of similar magnitude to those sections just downstream of the weir. In fact, our findings point to an in-basin hatchery influence occurring irrespective of upstream or downstream proximity to the weir.

A new weir was constructed in 2007 to better manage upstream passage. Because continued weir operation has limited or excluded passage of marked fish with far greater efficiency since 2007, it is unclear whether or not genetic introgression of natural-origin Chinook salmon would occur disproportionately upstream versus downstream of the upper SFSR weir in the long term. Regardless, starting in 2010 an integrated broodstock program was initiated for the upper SFSR, the intent being to minimize future risks to the NOR population. This new program utilizes a local integrated broodstock comprising both population components, and the management of natural- and hatchery-origin composition passed upstream of the weir is based on proportions dictated by the run size of natural-origin fish. With these management changes, we would predict that integration will buffer against potential demographic differentiation in the upper SFSR that might otherwise occur upstream of the weir. It should be noted that a similar, experimental integrated supplementation program began in the early 1990s to investigate natural productivity of hatchery by natural-origin crosses (Bowles and Leitzinger 1991); that effort was halted in 2002.

We detected significant differentiation between Johnson Creek, Secesh River, and all remaining groups in the upper SFSR (Figures 2, 3). Landscape genetic methods were used to identify how genetic diversity or variation is distributed throughout the stream corridors within our study and revealed significant correlation of fitted genetic distance with pairwise F_{ST} results. Specifically, locations of geographic features and available habitat appear to be a major influence in the distribution of genetic variation (Figure 1). From this analysis, genetic variation between groups is not well supported by either the fitted or mapped genetic differences associated with the collection sites in the upper SFSR corridor (downstream of the weir), marked by nearly continuous moderate-to-excellent spawning habitat. In contrast, the mapped genetic difference in the unsampled region between the three watersheds, defined by stream segments 5–7 and characterized by unsuitable spawning habitat, explain nearly all of the genetic variation in this analysis; the effect is presumably similar to isolation by distance, though not necessarily correlated with distance.

Our interpretation of the genetic structure results leads us to the reasonable conclusion that the distribution of genetic variation we observed can be attributed to habitat discontinuity and the landscape (see Keefer et al. 2004; Olsen et al. 2010). The lower sections of the three major watersheds are characterized by extreme in-stream conditions related to gradient and flow rate, and unsuitable spawning substrate. Collections bounded by stream segment 7 (Figure 1) are fish that experience restricted upstream travel via a weir in Johnson Creek, which is located downstream of nearly all suitable spawning habitat. However, it is not likely that directed passage or exclusion has facilitated the observed differentiation since in 2002 the Johnson Creek weir had been operational for less than one Chinook salmon generation. Our collections would have been the progeny of adult fish that returned prior to weir operation, including any stray HAT and natural- origin fish from the upper SFSR. Nevertheless, the proportion of stray hatchery fish documented in Johnson Creek from 1998 to 2009 has averaged only 3.44% (0.55–7.46%; Rabe et al. 2006; Rabe and Nelson 2007, 2008, 2009, 2010) and represents a minimal genetic influence in that stream. Therefore, stream segment 7 (Figure 1) is largely represented by the geography and hydrology downstream of the Johnson Creek weir, an area believed to support a paucity of redds compared with numbers observed in upstream reaches. We speculate that the Secesh River is also relatively well differentiated from all upper SFSR analysis populations and Johnson Creek by similar mechanisms and the same reasoning. Recall that in Secesh River, exclusion of HAT or other migrants from outside the watershed is not facilitated by weir operations. Rates of stray hatchery fish documented in Secesh River from 1996 to 2010 have averaged only 3.8% (0.50–16.00%; R. Kinzer, Nez Perce Tribe Department of Fisheries, personal communication).

The degree of genetic differentiation observed through genetic distance analyses among Secesh River, Johnson Creek, and upper SFSR is consistent with philopatric divergence among geographically proximate groups (McIsaac and Quinn 1988; Candy and Beacham 2000; Beacham et al. 2003; Hendry et al. 2003; Waples et al. 2004). Results of a comparable magnitude and significance have been shown among natural-origin populations in an adjacent upstream subbasin within the Salmon River system (Middle Fork Salmon River; Neville et al. 2007) and previously in the SFSR subbasin (Narum et al. 2007b). The putative wild Chinook salmon population aggregations in these three areas remain largely intact despite substantial releases of MFH stock (HAT) for supplementation and harvest augmentation in the upper SFSR.

It should be noted that assignment tests and Bayesian analyses (STRUCTURE) were conducted but not reported. Those tests failed to provide any meaningful results. The lack of information stemmed from low (albeit significant) pairwise F_{ST} diversity among watersheds. Such tests conducted on an individual-by-individual basis are highly sensitive to the magnitude of F_{ST}. Small sample sizes in some collections and the biallelic (low polymorphic) nature of the marker type also likely contributed to the limited population membership fidelity we observed in those analyses (Kalinowski 2004; Morin et al. 2009; Hess et al. 2011b; but see Smith et al. 2008). This outcome can be particularly common when attempting to identify dissimilarity among populations characterized by subtle differences on a fine geographic scale, as is the case with Chinook salmon in the SFSR. Yet even with the expectation that some straying between the three regions in this study may be a regular occurrence, we observed varying degrees of group distinction (gene flow is not absent, but it is restricted).

Philopatry among Chinook salmon is well documented (Hasler and Scholz 1983; McIsaac and Quinn 1988; Quinn et al. 1991) and may be a significant force shaping populations and defining units of productivity. It is often more straightforward to resolve population distinctions on a large geographic scale where gene flow and isolation by distance are more readily detectable. However, the distribution of suitable spawning habitat and the homing behavior of locally adapted population segments may produce fine-scale genetic structure between adjacent stream sections or watersheds (Beacham et al. 2006). Studies have identified correlations between hydrology or geography (or both) and differences in migratory behavior and genetic structure (Keefer et al. 2004; Olsen et al. 2010). Genetic structure between populations may persist despite gene flow (Neville et al. 2007), and while straying is thought to be necessary to buffer loss of genetic diversity in salmon (Milner and Bailey 1989), the rate of straying among wild fish compared with hatchery-origin fish has been shown to be relative low (Quinn 1993; Heard et al. 1995). Proportions of observed stray HAT fish and levels of population genetic differentiation from this study suggest low levels of hatchery straying across a relatively small spatial scale in the SFSR basin.

Concern over ESA-listed stocks of Chinook salmon in the Snake River basin (both fall-run and spring/summer-run) has led to increased monitoring efforts and development of management strategies that are primarily intended to increase the viability and abundance of depleted natural populations in many systems (Mobrand et al. 2005; HSRG 2009). Mitigating for resource losses may include implementing the use of nonlocal hatchery stocks for reintroduction, harvest augmentation, or both (Venditti et al. 2006; Bradley et al. 2009), or development of supplementation programs to manage and conserve extant populations and fisheries. However, these efforts need to be carefully evaluated over time to assess the extent of introgression, relative risks of hybridization (Narum et al. 2007a; Kinziger et al. 2008), and demographic and genetic influences on the natural populations. Intended supplementation benefits typically hinge on strategies and hatchery programs that are watershed specific. In reality, such programs are often contentious (see Gross 1988 versus Waples 1994), much of the controversy being centered on the genetic risks associated with supplementation (Hindar et al. 1991; Ryman and Laikre 1991; Waples 1994). However, hatchery supplementation is capable of helping combat the risk of extinction in natural populations (Hedrick et al. 1994; Cummings et al. 1997; Hedrick et al. 2000; Olsen et al. 2000; Matala et al. 2009) or providing short-term demographic boosts (Araki et al. 2007a; Berejikian et al. 2008) that may benefit fisheries with low impact on existing populations (Heggenes et al. 2006; Eldridge and Killebrew 2008; Matala et al. 2008; Small et al. 2009).

Overall, management actions in the upper SFSR appear to have fulfilled the harvest mitigation responsibility of the MFH (USACE 1975) with minimal adverse effects on adjacent spawning aggregates in the primary production regions encompassed by our study. Our analyses suggest that there has been no discernable long-lasting influence to the contemporary genetic diversity in the upper SFSR or the SFSR basin resulting from exogenous stocks. In the context of hatchery influence, we made the assumption that no influence equates to population structure that would have been present "presupplementation," but in the upper SFSR we cannot distinguish between a lack of historic structure and complete homogenization by the MFH stock. Distribution of habitat in a central corridor and philopatry appear to be enough to maintain genetic differentiation between a population aggregate directly supplemented with upper SFSR stock and those that are alternatively managed among the SFSR metapopulation.

For fisheries professionals weighing supplementation as a harvest or recovery strategy, the implications of our study results are cautionary but optimistic, particularly in the range of anadromous Pacific salmonids. Throughout this region, the "hatchery" debate might be the most polarizing of contemporary management issues and studies describing hatchery–natural interactions are accumulating (Heggenes et al. 2011; Theriault et al. 2011), yet no single conclusion can be used to generally represent the outcome of supplementation. Whether or not hatchery supplementation can offer an intended benefit that significantly balances or outweighs the risks and costs will arguably require managers to evaluate the unique attributes of each system individually. Many factors, both environmental and genetic, may affect the success of supplementation programs, from choice of release or acclimation sites (Williamson et al. 2010) to mate choice and breeding designs (DuPont-Nivet et al. 2006). The scope of fitness consequences in one stream (e.g., see Araki et al. 2007a, 2007b, 2007c) probably does not equate to the same outcome everywhere else or necessarily represent the risks across species. Ours is one case (but see also Heggenes et al. 2011) that suggests it is perhaps feasible to implement a large-scale supplementation program, with significant harvest benefit, while not measurably affecting adjacent populations.

Nonetheless, in all cases involving supplementation, preventing the loss of genetic identity, variability, and other consequences of introgression should be the primary focus of thorough and often long-term monitoring and evaluation efforts.

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