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GENETIC PARENTAGE ANALYSIS OF SPRING CHINOOK SALMON ON THE SOUTH SANTIAM RIVER: INSIGHTS INTO POPULATION PRODUCTIVITY AND REINTRODUCTION STRATEGIES

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SUMMARY

Upper Willamette River spring Chinook salmon (*Oncorhynchus tshawytscha*) are listed as threatened under the U.S. Endangered Species Act. On the South Santiam River, a tributary of the Willamette River, recovery of spring Chinook salmon is limited by the effects of Foster Dam, which, along with Green Peter Dam, inundates and blocks access to ~ 85% of the population's historical spawning habitat. In 1996, the Oregon Department of Fish and Wildlife initiated reintroductions of spring Chinook salmon above Foster Dam in order to re-establish natural production on historical spawning and rearing grounds. Here we use genetic parentage analysis to evaluate the contribution of salmon reintroductions to subsequent adult recruitment to the South Santiam River at Foster Dam. The parentage of salmon sampled as carcasses below Foster Dam was also examined to estimate reintroduction program contributions to below-dam recruitment. We used the parentage assignments to estimate the fitness of Chinook salmon released above Foster Dam. We also examined the influence of reintroduced salmon origin (hatchery or wild), release date, and release location on fitness.

Most salmon released above Foster Dam in 2012 (74%) and 2013 (66%), the years for which we had near complete genetic sampling of potential parents, were progeny of reintroduced salmon. Reintroduced salmon also produced up to 15% of salmon recruits to the South Santiam River below the dam, as estimated from 2013 returns. Overall, adult offspring recruitment to the South Santiam River appears to be meeting or even marginally exceeding replacement of reintroduced parents, with cohort replacement rates (CRR) for the 2007 and 2008 populations estimated at 0.96 and 1.16, respectively. However, the effective population size (N_e) of the reintroduced population was estimated at 100 individuals (95% C.I. = 93.9 – 107.0) in 2007 and 138 individuals (95% C.I. = 131.4 – 144.5) in 2008, substantially lower than the census population size (2007: N = 403; 2008: N = 700).

The total lifetime fitness among reintroduced salmon was highly variable, with individual salmon producing between 0-38 adult progeny. In all of the release years but 2007, females achieved higher fitness compared to males. Later release dates during the spawning migration were also associated with higher fitness. However, this effect may reflect higher rates of prespawn mortality occurring above Foster Dam in earlier compared to later release groups and was exclusive to release years comprised of primarily HOR salmon (i.e. 2007 and 2008).

Moreover, in 2008, the only year comprising a mixed origin population (i.e. HOR and NOR), parental pairs involving an HOR individual achieved significantly lower mean fitness (2.4±2.5 offspring) compared to pairs comprised of an NOR male and female (6.4±5.1 offspring). As the reintroduction program has moved in recent years towards releasing salmon that are solely of natural origin, we predict that population productivity derived from the program will continue to increase.

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INTRODUCTION

Upper Willamette River spring Chinook salmon (*Oncorhynchus tshawytscha*) are listed as threatened under the U.S. Endangered Species Act. On the South Santiam River, a tributary of the Willamette River, recovery of spring Chinook salmon is limited by the effects of Foster Dam, which, along with Green Peter Dam, inundates and blocks access to ~ 85% of the population's historical spawning habitat (ODFW and NMFS, 2011; Figure 1). Efforts to re-establish a natural spawning population of spring Chinook salmon above Foster Dam began in 1996, when the Oregon Department of Fish and Wildlife (ODFW) initiated releases of hatchery origin (HOR) fish above the dam (NMFS 2008). In response to the recommendations of the Willamette Biological Opinion (NMFS 2008), unmarked (i.e. not adipose fin-clipped), presumed natural origin (NOR) salmon have been integrated into the reintroduction program since 2008. Since 2009, all releases above Foster Dam have been unmarked salmon (Table 1). Unmarked salmon are assumed to be NOR, however, this group may include up to 30% HOR fish, as estimated from otolith-tagging studies (C. Sharpe, ODFW, personal communication; also see methods).

Tissue samples for genetic analysis have been collected from reintroduced spring Chinook salmon since 2007. Here we use genetic parentage analysis to evaluate the contribution of salmon reintroductions to subsequent adult recruitment to the South Santiam River at Foster Dam. The parentage of salmon sampled as carcasses below Foster Dam was also examined to estimate reintroduction program contributions to below-dam recruitment. From our parentage assignments, we also examined individual-based estimates of fitness of reintroduced salmon and investigated how different management strategies, such as releasing salmon above the dam at different times and locations, and of different origins (HOR vs. NOR), may influence fitness. We define *fitness* as the number of adults recruiting to the South Santiam River during 2010-2013 that assigned as progeny of an individual reintroduced above the dam in a previous year (i.e. 2007 and onwards). Salmon recruiting to the South Santiam River during 2010-2012 and 2011-2013 will include all major adult age classes (i.e. 3, 4, and 5 year olds; Figure 2) of progeny for the 2007 and 2008 reintroduced populations, respectively. Therefore, for salmon reintroduced above Foster Dam in 2007 and 2008, we estimated *total lifetime fitness* (TLF).

Our study carries out the following objectives:

1. Using genetic parentage assignments, estimate the number of adult Chinook salmon released above Foster Dam during 2010-2013 that were progeny of reintroduced salmon (see Figure 2).

2. Estimate the extent to which reintroduced salmon contribute to adult recruitment to the South Santiam River below Foster Dam.

3. Estimate *cohort replacement rate* (CRR), or "the number of future spawners produced by a spawner" (Botsford and Brittnacher 1998) for the 2007 and 2008 reintroduced populations as an indicator of population productivity.

4. Using patterns of multilocus microsatellite linkage disequilibrium found among progeny, estimate effective population size (N_e) of the reintroduced populations in 2007 and 2008.

5. Estimate *total lifetime fitness* (TLF) of spring Chinook salmon reintroduced above the dam in 2007 and 2008, and *fitness*, based on 3 and 4 year old offspring returns, of salmon reintroduced above the dam in 2009.

6. Examine the influence of origin (HOR vs. NOR), release date, and release location on the fitness of spring Chinook salmon reintroduced above Foster Dam.

Split-basin management has been identified as a goal of the recovery plan for UWR spring Chinook salmon (ODFW and NMFS 2011), that is, supporting the recovery of natural salmon production in upper basins (i.e. above dams) while maintaining hatchery mitigation activities below dams. This study is examining the extent to which reintroduction activities are supporting wild spring Chinook salmon production above Foster Dam and subsequent wild adult recruitment to the upper basin of the South Santiam River.

Our research also addresses the information needs of Reasonable and Prudent Alternative (RPA) 9.5.1(4) of the Willamette Project Biological Opinion (NMFS 2008) in determining the fitness of hatchery fish in the wild, RPA 4.1 (restoration of productivity by outplanting Chinook salmon above dams), RPA 4.7 (increase the percent of outplanted adults that successfully spawn through development of new release locations), RPA 6.2.3 (continue adult Chinook salmon outplanting, Willamette basin-wide), and RPA 9.3 (monitoring the effectiveness of fish passage facilities and strategies at Project dams).

Methods

Study area

Foster Dam is located on the South Santiam River, Oregon, at 44° 24′ 59.45″ N, 122° 40′ 9.31″ W (Figure 1). The dam stands 38m high and impounds approximately 0.035 km^3 of water in Foster Lake, the reservoir contained above the dam. Dam operations began in 1968, and at the same time, a salmon hatchery was built on the main stem of the South Santiam River.

Spring Chinook salmon reintroduction program

Attempts to re-establish a natural spawning population of spring Chinook salmon above Foster Dam began in 1996. Above-dam releases of externally marked hatchery fish (i.e. adipose fin-clipped individuals) were terminated in 2009 (Table 1). Also, since 2009, three release locations, Calkins Park, Gordon Road, and Riverbend have been in use; prior to this, all fish were released at Gordon Road (Figure 1). Reintroduction operations typically begin in early May or June and run to the end of September or early October in each year. Appendix 1 provides a summary of the number of fish released by date in each year.

The Oregon Department of Fish and Wildlife (ODFW) began collecting tissue samples from individuals released above Foster Dam in 2007. In this first year, 64% of released fish were tissue-sampled, whereas in later years (2008 and onwards), 100% of released fish were sampled (Table 1). All tissue samples were stored in 95% ethanol. In addition, since 2011, all released salmon have been floy-tagged to facilitate individual identification in the field.

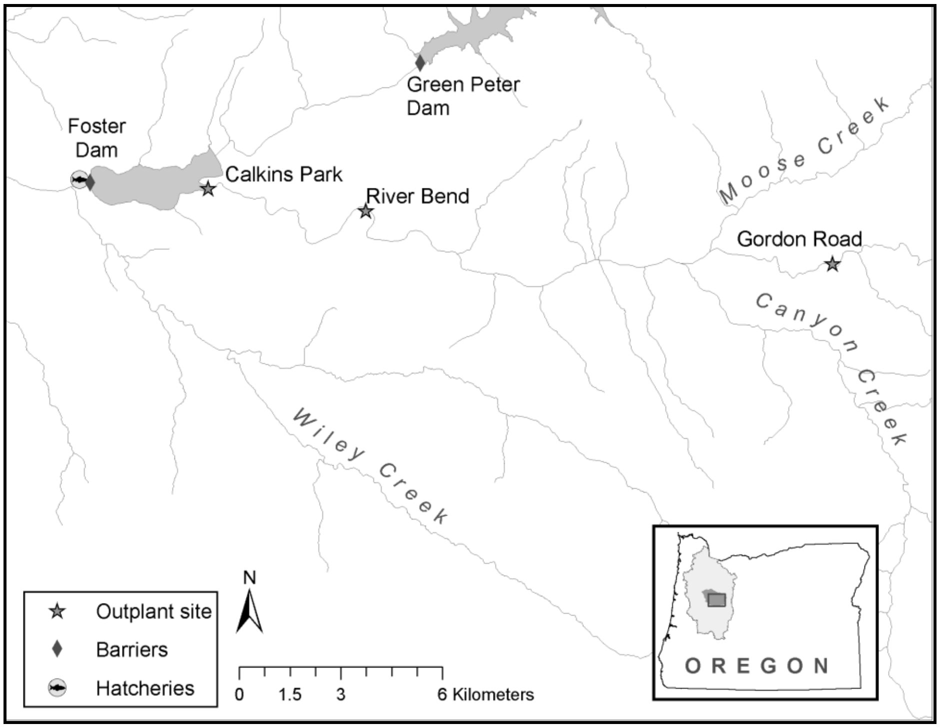

Figure 1. Location of Foster Dam on the South Santiam River, Oregon. Also indicated are the three locations used for spring Chinook salmon reintroductions on the South Santiam River; Calkins Park, River Bend, and Gordon Road.

Spring Chinook salmon below Foster Dam

Tissue samples were also collected in the fall of 2011 (N = 148), 2012 (N = 67), and 2013 (N = 164) from NOR Chinook salmon carcasses recovered during spawning surveys on stretches of the South Santiam River below Foster Dam. While samples collected from carcasses represent only a fraction of salmon returning to the South Santiam River, we included these samples in our parentage analysis to 1) evaluate the relative contribution of the reintroduction program to the productivity of the below dam population, 2) provide more accurate estimates of fitness for reintroduced salmon, and 3) explore the extent to which gene flow is being maintained between the above and below dam populations.

Carcass surveys above Foster Dam

Surveys for redds and salmon carcasses are also used to provide quantitative estimates of spawning activity above Foster Dam by ODFW. Otoliths are collected from the carcasses during the surveys and later examined in the laboratory for thermal marks - temperature induced changes in otolith growth rate which lead to a distinct banding pattern - a method used by hatcheries to identify HOR salmon (Volk et al. 1999). Otolith data were available for salmon carcasses above Foster Dam during 2011 (N = 277), 2012 (N = 240), and 2013 (N = 202), which allowed us to estimate the proportion of unmarked HOR salmon found in the release population in each year. Of these, 53 (19%), 78 (32%), and 20 (10%) individuals in 2011, 2012, and 2013, respectively, were identified as HOR from otolith marks (C. Sharpe, ODFW, personal communication). Twenty-seven, 18, and 14 of these otolith-marked (but not adipose fin-clipped) individuals could be identified from floy tags retained on carcasses in 2011, 2012, and 2013, respectively. These individuals were excluded from the parentage analysis since they were identified as progeny of hatchery origin salmon (Table 1).

Table 1. Summary of spring Chinook salmon reintroductions above Foster Dam during 2007-2013 on the South Santiam River. Indicated are the number of salmon of natural (NOR) or hatchery (HOR) origin, as determined from adipose fin clips, and of each sex that were released above the dam.

Year	Releases[a]	NOR/HOR	Number genotyped	Number individuals (duplicate genotypes)[b]	Females[c]	Males[c]	Unmarked HOR[d]	HOR identified[e]
2007	403	18/385	252	252 (0)	125	127	-	-
2008	700	163/527	690	659 (31)	218	441	-	-
2009	434	434/0	425	412 (13)	158	254	-	-
2010	705	705/0	702	700 (2)	233	467	-	-
2011	1210	1210/0	1205	1203 (2)	526	677	53/277	27
2012	1046	1046/0	1021	1010 (11)	423	587	78/240	18
2013	940	940/0	932	931 (1)	403	528	20/202	14

[a] Based on ODFW field records.
[b] Total number of individuals released above Foster Dam that were successfully genotyped. In brackets are the number of individuals determined to have been sampled repeatedly, via comparisons of multilocus microsatellite genotypes (see methods), either due to field sampling error or fallbacks of released salmon over the dam. Duplicate samples were removed from the parentage analysis.
[c] Number of male and female Chinook salmon released above Foster Dam who were genotyped and included in parentage analysis. Sex was determined genetically using the sex-linked marker, *Oty*3 (see methods).
[d] Unmarked HOR individuals released above Foster Dam as determined from the analysis of thermal marks on otoliths/total number of unmarked salmon examined for thermal marks on otoliths.
[e] Number of unmarked HOR fish that we were able to identify using floy tags retained on the carcass; these individuals were removed from the parentage analysis.

Genetic parentage analysis

Chinook salmon released above Foster Dam and those sampled as carcasses below the dam were genotyped at a suite of 11 microsatellite loci: *Ots201*, *Ots208b*, *Ots209*, *Ots211*, *Ots212, Ots215, Ots249*, *Ots253*, *Ots311*, *Ots409*, and *Ots515* (Banks et al. 1999; Naish and Park 2002; Greig et al. 2003). We also used the sex-linked marker, *Oty3*, to determine sex (Brunelli et al. 2008).

Using the protocol of Ivanova et al. (2006), we isolated whole genomic DNA from tissue samples. Polymerase chain reaction (PCR) was then used to amplify each of the 12 markers. PCR products and a DNA size standard were visualized on an ABI 3730xl DNA analyzer and allele size were scored in GeneMapper software (Applied Biosystems, Inc., Foster City, CA). DNA degrades rapidly post-mortem in salmon (Copeland et al. 2009), but we were able to genotype a total of 66/148 (45%), 47/67 (70%), and 80/164 (49%) individuals sampled in 2011, 2012, and 2013, respectively, as carcasses below Foster Dam. In contrast, we isolated DNA and successfully genotyped 98-99% of samples collected from live salmon reintroduced above the dam (Table 1, Appendix 1). All molecular work was performed at the Marine Fisheries Genetics Laboratory at Hatfield Marine Sciences Center, Newport, Oregon.

The 11 microsatellite loci were highly polymorphic, exhibiting between 18 and 61 alleles. For the three release years in which we are examining fitness (2007-2009), the loci provided an average non-exclusion probability for a candidate parental pair of 4.6×10-17, as estimated by CERVUS v. 3.0 (Kalinowski et al. 2007). Analyses in Genepop v. 4.2 (Raymond & Rousset 1995) indicated that allele frequencies at most loci conformed to Hardy-Weinberg expectations, albeit there was a consistent trend towards a heterozygote deficit at *Ots209* and *Ots208b* across all years (Table 2), suggesting that these loci exhibit null alleles (non-amplifying alleles; Dharmarajan et al. 2013). To avoid bias in parent-offspring assignments arising from null alleles, we used a maximum-likelihood approach to identify male and female parents (Harrison et al. 2013).

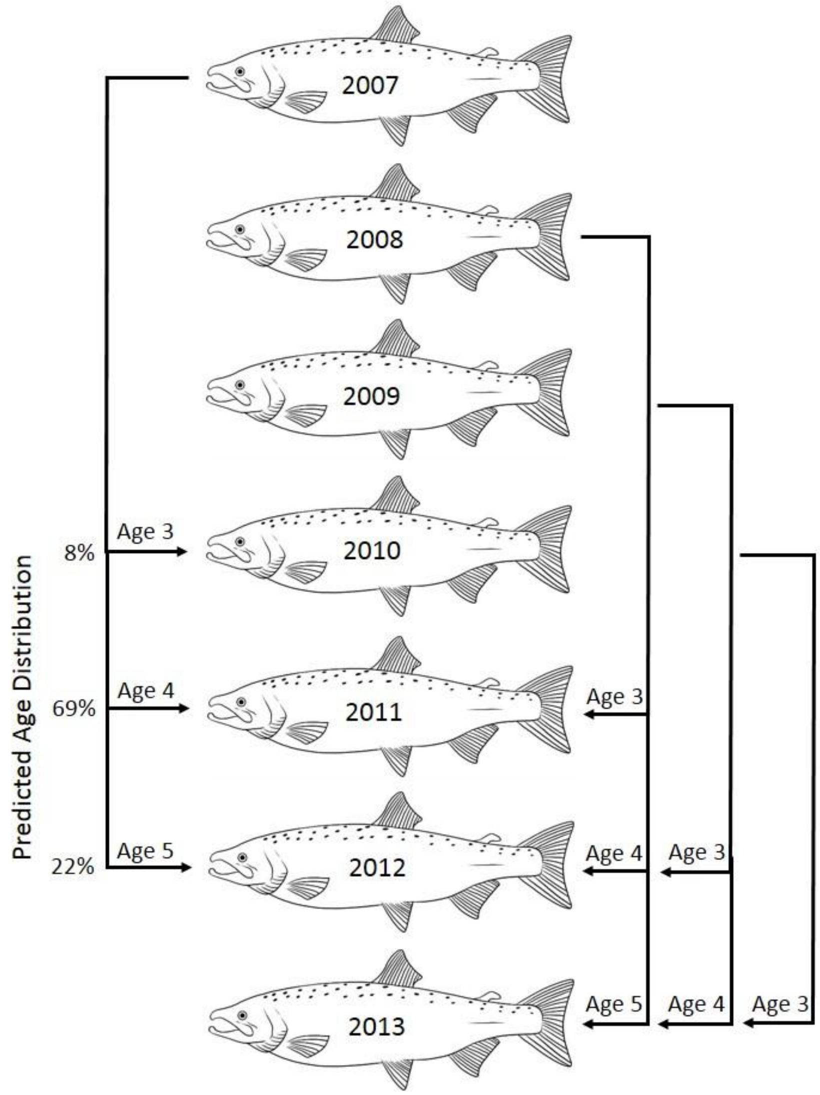

Figure 2. Parentage assignments for spring Chinook salmon in the South Santiam River, Oregon. The majority of Chinook salmon in the South Santiam River (~99%) return to spawn as three, four, or five year olds. Therefore, salmon that returned to the South Santiam River during 2010-2013 are possible progeny of salmon reintroduced above Foster Dam since 2007. The age distribution of adult salmon in the South Santiam River is based on unpublished data provided by C. Sharpe (ODFW).

To estimate the number of salmon returning to the South Santiam River during 2010-2013 that were progeny of salmon from the reintroduction program, we compared the multilocus microsatellite genotypes of putative progeny (i.e. above and below Foster Dam), to the genotypes of adults reintroduced above the dam during 2007-2010 (putative parents), as indicated in Figure 2. These comparisons were conducted in the maximum-likelihood parentage assignment program CERVUS. Parentage assignments were made using a strict (95% confidence) assignment criterion. In addition, we used the PLS-FL likelihood algorithm implemented in COLONY v. 2.0 (Jones and Wang 2010) to construct kinship groups based on putative offspring and parental genotypes and to confirm the parentage assignments from CERVUS. We conducted this second analysis as CERVUS's likelihood-based parentage assignment method requires an accurate estimate of the number of parents contributing to a cohort (Harrison et al. 2013); unknown parental contributions to the 2010-2013 releases, i.e. from below dam spawners, unsampled hatchery broodstock, or strays from other systems, could therefore impact assignment accuracy using this program. Moreover, simulation studies have suggested that COLONY's assignment protocol is the most accurate of current pedigree construction methods (Harrison et al. 2013). In COLONY, pedigrees for the 2010-2013 cohorts were constructed using a long run length and the polygamous male and female setting. Allele dropout and general error rates were set to 1% each per locus. The genotyping error rate was estimated empirically in the Marine Fisheries Genetics Laboratory by re-genotyping a randomly selected individual from each 96-well DNA plate (N = 57).

Table 2. Summary of genetic variation observed in spring Chinook salmon released above Foster Dam on the South Santiam River, Oregon, 2007-2013. The total number of alleles observed at each locus is shown across all years (K). The observed heterozygosity (H_O), expected heterozygosity (H_E), and the significance of a test for heterozygote deficit (P), a potential indicator of null alleles (Dharmarajan et al. 2013), is indicated for each of the 11 microsatellite loci used for the parentage assignments. P-values for microsatellite loci showing evidence of heterozygote deficit (P < 0.05) are indicated in boldface.

		2007			2008			2009			2010			2011			2012			2013		
Locus	K	H_O	H_E	P	H_O	H_E	P	H_O	H_E	P	H_O	H_E	P	H_O	H_E	P	H_O	H_E	P	H_O	H_E	P
Ots201b	27	0.89	0.90	0.270	0.91	0.90	0.628	0.88	0.90	0.125	0.87	0.91	**0.001**	0.90	0.91	0.056	0.91	0.90	0.142	0.91	0.90	0.784
Ots209	58	0.88	0.94	<**0.001**	0.90	0.95	<**0.001**	0.94	0.95	0.084	0.91	0.95	<**0.001**	0.91	0.95	<**0.001**	0.92	0.94	<**0.001**	0.94	0.94	0.233
Ots249	34	0.96	0.94	0.944	0.95	0.94	0.864	0.92	0.93	**0.022**	0.95	0.94	0.737	0.94	0.94	0.720	0.94	0.94	0.943	0.93	0.94	0.132
Ots253b	27	0.88	0.92	**0.034**	0.90	0.92	0.115	0.92	0.92	0.725	0.90	0.92	**0.028**	0.89	0.92	**0.015**	0.89	0.91	0.063	0.89	0.92	**0.001**
Ots215	36	0.97	0.95	0.838	0.94	0.95	**0.015**	0.94	0.95	0.134	0.97	0.95	0.596	0.95	0.95	0.224	0.95	0.95	0.225	0.95	0.95	0.746
OtsG311	53	0.97	0.95	0.964	0.96	0.95	0.919	0.97	0.96	0.798	0.95	0.96	0.436	0.95	0.96	0.090	0.96	0.95	0.867	0.96	0.96	0.484
OtsG409	61	0.97	0.96	0.973	0.95	0.95	0.083	0.94	0.95	0.128	0.95	0.95	0.071	0.96	0.95	0.167	0.95	0.95	0.469	0.95	0.94	1.000
Ots211	26	0.87	0.91	0.215	0.94	0.92	1.000	0.90	0.92	0.191	0.91	0.92	0.305	0.92	0.91	0.936	0.91	0.91	0.565	0.91	0.92	0.585
Ots208b	38	0.89	0.93	<**0.001**	0.94	0.94	0.064	0.92	0.94	**0.038**	0.92	0.94	0.121	0.91	0.94	**0.003**	0.91	0.94	**0.011**	0.93	0.94	<**0.001**
Ots212	25	0.90	0.90	0.520	0.91	0.90	0.996	0.89	0.89	0.152	0.88	0.90	0.053	0.90	0.90	0.439	0.90	0.90	0.477	0.91	0.90	1.000
Ots515	18	0.88	0.87	0.455	0.88	0.88	0.157	0.88	0.86	0.841	0.85	0.87	0.113	0.86	0.87	0.059	0.88	0.88	0.542	0.87	0.87	0.866

Duplicate genotypes

We compared genotypes among individuals within each release year using GenAlEx (Peakall and Smouse 2012) to identify potential "fallbacks" over Foster Dam. "Fallbacks" refer to adults that fall or spill over the dam following reintroduction above the dam. These individuals may be re-trapped and re-released above the dam, and therefore re-sampled, at a later date. Duplicate genotypes could also reflect sampling errors in the field. Regardless of the process, repeated sampling of individuals will contribute to ambiguous assignments between parents and offspring and possibly inflate estimates of fitness for parents. Thus, genotypes that were identical at all loci were assumed to represent a single individual and the redundant genotypes were removed from the dataset. Genotypes that matched at all but one locus were also removed, as the probability of observing a near-identical multilocus genotype at 10 of the microsatellite loci used in this study was extremely low ($< 1\times10^{-20}$) in each year.

Parentage assignment rates and release date

A recent study of spring Chinook salmon from the South Fork McKenzie River indicated that later returning salmon (post Sept. 1) assigned at a lower rate as progeny of salmon reintroduced above Cougar Dam compared to earlier returns (Banks et al. 2013). This result may be suggestive of increased movement of salmon from other populations (i.e. from below the dam or other rivers, or unmarked HOR fish) towards the dam later in the spawning migration. We investigated whether parentage assignment rate varied with date of release above Foster Dam in each of 2010, 2011, 2012 and 2013 using generalized linear models (GLM) that incorporated a binomial distribution for the dependent "assignment success" variable and a logit link function. The models were run in JMP v. 10, using a critical value $\alpha = 0.05$.

Cohort replacement rate (CRR)

We estimated cohort replacement rate (CRR), or "the number of future spawners produced by a spawner" (Botsford and Brittnacher 1998), for salmon reintroduced above Foster Dam as an indicator of population productivity. In most years of our study, the sex ratio of salmon released above Foster Dam was male-biased (Table 1), and therefore, population productivity is likely to be constrained by the number of females in the population. Thus, we estimated CRR from the number of three, four, and five year old female progeny produced by females reintroduced above Foster Dam in 2007 and 2008. That is, CRR was calculated as:

$$CRR = \frac{Nf_3 + Nf_4 + Nf_5}{Nf_P}$$

where Nf_3, Nf_4, and Nf_5, represent the number of three, four, and five year old female progeny that assigned to a female parent (Nf_P) from a given year.

Effective population size

We estimated the effective population size (N_e) of the reintroduced populations in 2007 and 2008 using the linkage disequilibrium (LD) method of Waples and Do (2008), as implemented in the program NeEstimator v.2 (Do et al. 2014). N_e was estimated for each reintroduction year from patterns of linkage disequilibrium in the multilocus microsatellite genotypes of adult progeny. N_e was calculated using a minimum allele frequency of 0.02. We report our estimate of N_e for each release year (2007 and 2008) ± 95% confidence intervals. The confidence intervals around N_e were determined using a jackknife re-sampling method which estimates variance in LD through the sequential elimination of pairs of loci from the calculation (Waples and Do 2008).

Fitness of reintroduced salmon

We estimated *total lifetime fitness* (TLF) for salmon reintroduced above Foster Dam during 2007 based on the number of progeny identified in the reintroduced populations in 2010-2012 and from carcass samples collected below the dam during 2011-2012. TLF of salmon released above the dam in 2008 was estimated from the number of progeny that returned to the South Santiam River, both to Foster Dam and below the dam, during 2011-2013. We estimated *fitness* for the 2009 cohort from the number of adult progeny that recruited to Foster Dam and below the dam in 2012 and 2013 (i.e. as three and four year old progeny; Figure 2). A preliminary estimate of *fitness* for salmon released above Foster Dam during 2010 was calculated based on the number of three year old progeny identified in 2013.

Predictors of fitness

We used a GLM that incorporated a Poisson distribution and log link function to examine the influence of sex, release date, and the interaction between release date and sex on the TLF of spring Chinook salmon released above Foster Dam during 2007. It should be noted that in 2007, only three release dates, all in September (Appendix 1), were used for reintroductions. Therefore, in 2007, compared to later years, we had limited insight into the potential influence of release date on TLF.

We used a similar approach to examine factors influencing the TLF of salmon reintroduced above Foster Dam during 2008. However, in addition to variation in release date, salmon reintroduced above Foster Dam in 2008 were of mixed origin, i.e. HOR and NOR. Therefore, we examined the influence of release date, sex, origin, and the interaction between sex and origin, and sex and release date on TLF in our initial model. In our final model, we excluded the interaction terms as they were not significant predictors of variation in TLF.

Several studies have suggested that interactions between parental genomes (i.e. non-additive genetic effects) can affect the fitness of salmonids (Pitcher and Neff 2006; Araki et al. 2007; Evans et al. 2010; Whitcomb et al. 2014). Thus, we were also interested in the potential influence of parental pair type, with respect to male and female origin, on the TLF of salmon released above Foster Dam in 2008. Parental pairs in this year could comprise a HOR male and female, a NOR male and female, or a mix of HOR and NOR males and females. We examined differences in TLF among the four parental pair types using a generalized linear mixed model (GLMM), which incorporated male ID and female ID as random effects in the model. The random ID effects were included in the model to account for multiple mating by males and females which resulted in repeated measures of TLF for some individuals. As we were interested in differences in TLF among pairs that were known to have successfully mated (i.e. independent of the influence of sexual selection processes and pre-spawn mortality effects on fitness), we only examined differences in TLF of parental pairs with at least one adult offspring that returned to the South Santiam River during 2011-2013.

In 2007 and 2008, Chinook salmon were reintroduced above Foster Dam at only one location, Gordon Road (Figure 1). However, three reintroduction locations were used in 2009: Gordon Road, Calkins, and Riverbend (Figure 2). Therefore, in our initial model, the effect of date, location, and sex, and the interaction between sex and release date on fitness was investigated using a GLM that incorporated a Poisson distribution and a log link function. The interaction term was not a significant predictor of variation in fitness and was excluded from the final model. Given the preliminary nature of the fitness estimates for salmon released above the dam in 2010, we did not statistically examine any factors contributing to variation in fitness.

All Poisson GLMs included a correction for overdispersion in the fitness estimates. Models were run in JMP v. 10, using a critical value $\alpha = 0.05$. Means are reported ± 1SD unless otherwise indicated.

RESULTS

Duplicate genotypes and fallbacks at Foster Dam

In six of the seven years included in our study (2008-2013), we identified multiple samples with identical genotypes (Table 1). The majority of the duplicates (46/60) were derived from samples collected on the same day, suggesting that they resulted from field sampling error. However, in 2009, 2012, and 2013, respectively, nine, four, and one of these duplicates appear to be Chinook salmon fallbacks, as the time between sample collections was 56 ± 16 days.

Parentage assignments and inferred age at return

A total of 48 (7%) salmon released above Foster Dam during 2010 assigned as progeny of salmon released above the dam during 2007 (Table 3). The 7% assignment rate is close to the expected proportion of three year old adult returns typically observed in the South Santiam River (Figure 2). For the 2011 releases above Foster Dam, 34% (404/1176) of individuals were identified as progeny of parents released above the dam during 2007 or 2008. The majority of progeny returned to the South Santiam River as four year olds (i.e. assigned to 2007 parents; 329/404 or 82%) and to a lesser extent as three year olds (i.e. assigned to 2008 parents; 74/404 or 18%).

Seventy-four percent (731/992) of salmon released above the dam during 2012 were identified as progeny of salmon reintroduced above the dam during 2007-2009 (Table 3). The majority of assigned progeny were four year olds, i.e. assigned to parents released above Foster Dam in 2008 (532/731 or 73%). Twenty-one percent (150/731) and 7% (52/731) of assigned progeny were identified as five and three year olds, respectively, i.e. progeny of parents reintroduced above Foster Dam during 2007 and 2009, respectively (Table 3). The apparent age structure of assigned progeny is likely to be partially influenced by incomplete sampling of potential parents in 2007.

A smaller proportion of salmon released above Foster Dam during 2013 assigned as the progeny of reintroduced salmon (66% or 601/917) compared to in 2012. Seventy-eight percent (468/601) returned as four year olds and 18% returned as five year olds (107/601). Only 4% (26/601) of salmon returned as three year olds in 2013 (Table 3); these individuals were progeny of salmon released above Foster Dam in 2010. An extreme flooding event occurred in the fall of 2010, which may have destroyed many of the spring Chinook salmon redds within the upper basin of the South Santiam River, and may be driving the relatively low proportion of three year old offspring observed in 2013 compared to in 2010-2012.

We genotyped a total of 193 tissue samples collected from carcasses below Foster Dam during 2011-2013 (Table 3), and across years, an average of 12% (23/193) were identified as progeny of Chinook salmon released above Foster Dam in previous years (Table 3).

Reintroduction date and parentage assignment rates

We found a near-significant positive relationship between release date and parentage assignment rates for spring Chinook salmon reintroduced above Foster Dam in 2010 ($\chi^2_1 = 2.94$, $P = 0.086$, Figure 3). However, as we were only able to discern parentage of a small proportion of salmon reintroduced above the dam in 2010, this relationship may not provide an accurate representation of the influence of spawning migration timing on assignment rates. Indeed, for salmon released above Foster Dam in 2012 and 2013, the years for which we genetically sampled the majority of putative parents from the reintroduction program (i.e. in 2007-2009 and 2008-2010, respectively), we detected a significant negative influence of release date on assignment rate (2012: $\chi^2_1 = 21.09$, $P < 0.001$; 2013: $\chi^2_1 = 32.22$, $P < 0.001$; Figure 3). For the 2011 releases, we did not detect a relationship between release date and parentage assignment success ($\chi^2_1 = 0.01$, $P = 0.918$). However, our ability to assign progeny in this year was limited to salmon sampled and reintroduced above Foster Dam during 2007-2008.

Table 3. Summary of progeny assigned to spring Chinook salmon reintroduced above Foster Dam on the South Santiam River, Oregon, using genetic parentage analysis. The parentage assignment approach is depicted in Figure 2. Indicated are the number of progeny assigned to a parental pair, or to a male or female parent only, in each year.

		2007			2008			2009			2010			Total assigned
Progeny	N*	Pair	Female	Male	Pair	Female	Male	Pair	Female	Male	Pair	Female	Male	
2010 releases	700	9	18	21	-	-	-	-	-	-	-	-	-	48 (7%)
2011 releases	1176	131	18	169	44	12	18	-	-	-	-	-	-	404 (34%)
2011 carcass	66	0	2	4	0	0	0	-	-	-	-	-	-	6 (9%)
2012 releases	992	50	30	70	386	68	78	27	6	16	-	-	-	731 (74%)
2012 carcass	47	1	0	1	1	1	1	0	0	0	-	-	-	5 (11%)
2013 releases	917	-	-	-	75	11	21	391	29	48	10	10	6	601 (66%)
2013 carcass	80	-	-	-	1	1	1	5	1	2	0	0	1	12 (15%)

*Total number of individuals genotyped after accounting for duplicate sampling and unmarked HOR fish identified from thermal marks on otoliths.

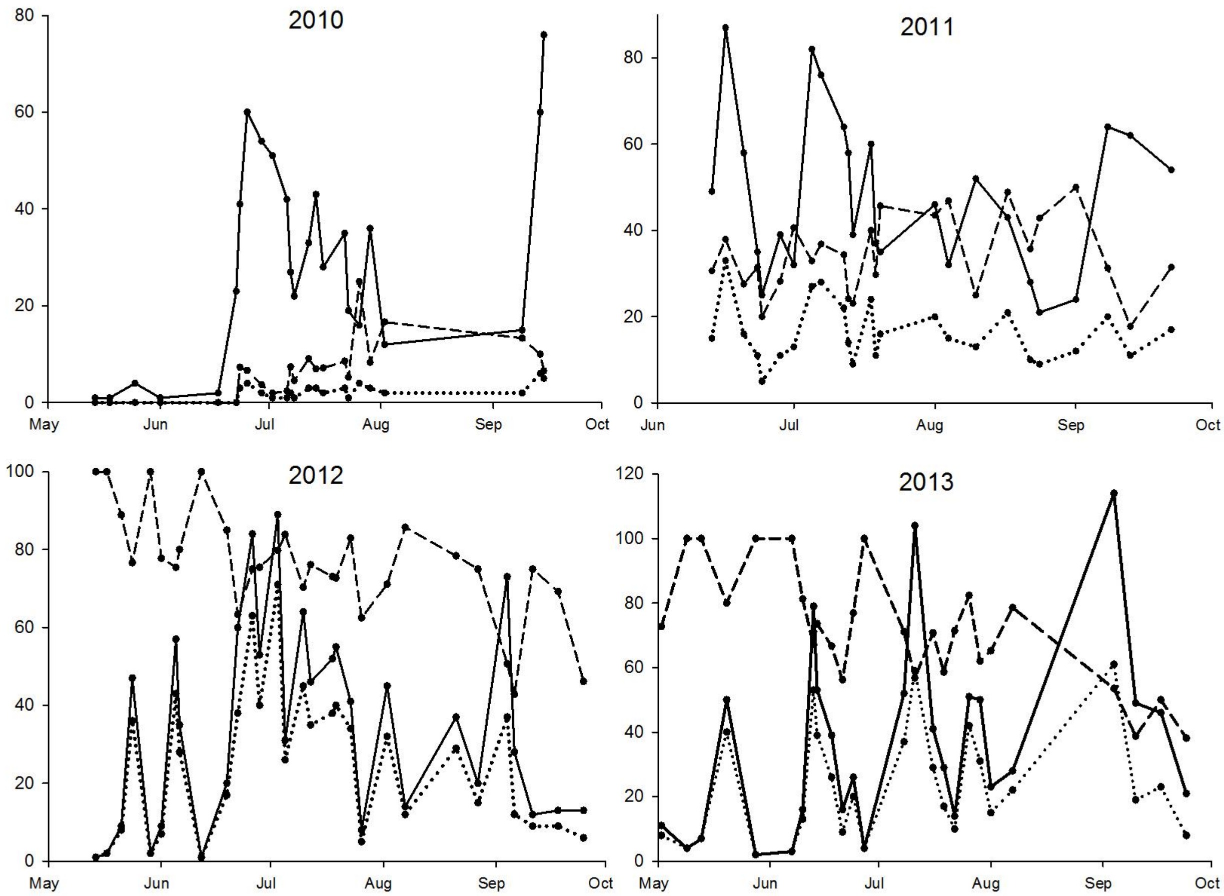

Figure 3. The influence of release date on parentage assignment rates for spring Chinook salmon reintroduced above Foster Dam on the South Santiam River, Oregon, in 2010, 2011, 2012, and 2013. In each year, the total number of salmon released above Foster Dam (solid black line) is plotted by release date. Also plotted by release date are the number (dotted line) and percent (dashed line) of salmon identified as progeny of salmon previously reintroduced above Foster Dam. Spring Chinook salmon are released above Foster Dam beginning in May/June of each year, with operations ceasing in September/October, depending on the timing of the spawning migration.

Cohort replacement rate

In total, 120 females that returned to the South Santiam River (119 released above the dam, 1 sampled as a carcass below the dam) during 2010-2012 assigned as progeny of the 125 females released above the dam in 2007, which resulted in a CRR of 0.96. A total of 253 (252 released above the dam, 1 sampled as a carcass below the dam) females that returned to the South Santiam River during 2011-2013 assigned as progeny of the 219 females released above Foster Dam during 2008, resulting in a CRR of 1.16. When examined separately for HOR and NOR females released above the dam during 2008, the CRR was similar (NOR: 1.10; HOR: 1.13). Note that the independent estimates of CRR for HOR and NOR females are lower than the overall CRR in 2008 because the origin of some females was unknown. These females were therefore excluded from the origin-specific calculations.

Effective population size

N_e of the reintroduced population in 2007 was estimated at 100 individuals (95% C.I. = 93.9 – 107.0). For the reintroduced population in 2008, N_e was estimated at 138 individuals (95% C.I. = 131.4 – 144.5). In contrast, the census population size in 2007 was 400 and in 2008 was 700.

Fitness of reintroduced spring Chinook salmon

We observed pronounced variation in fitness among spring Chinook salmon reintroduced above Foster Dam (Figure 4). As estimated from three, four, and five year old adult offspring returns to the South Santiam River, male and female TLF for the 2007 release year ranged from 0-38 and 0-19, respectively (Table 4). Overall, ~61% (154/252) of salmon sampled and released above the dam in 2007 produced at least one adult offspring returning to the South Santiam River (Figure 4). There was a trend towards males achieving higher TLF compared to females in 2007, though sex, on its own, was not a significant predictor of TLF (Tables 4-5). Instead, release date and the interaction between release date and sex were significantly associated with TLF. Specifically, males who were released above the dam on the last release day, September 21, exhibited higher TLF than females (Table 5).

In contrast to 2007, only 38% (249/660) of salmon released above the dam in 2008 produced at least one adult offspring (Figure 4). TLF ranged from 0-24 in males and from 0-26 in females. TLF varied significantly between males and females and with release date of the parent. Specifically, females exhibited higher TLF compared to males (Table 4-5) and TLF was positively associated with release date above Foster Dam (Table 5).

We found no evidence of a difference in individual-based estimates of TLF between HOR and NOR salmon released above Foster Dam during 2008 (Tables 4-5). However, given that the majority of salmon released above the dam were HOR, we were also interested in the potential influence of parental pair type (origin) on TLF. Sample sizes of observed matings between NOR males and NOR females were limited (N = 5). Nevertheless, NOR×NOR pairs exhibited significantly higher TLF compared to the other parental pair types (Table 6, Figure 5). NOR females mated to HOR males exhibited TLF values intermediate to that of HOR×HOR pairs and NOR×NOR pairs, whereas pairs comprised of HOR females and NOR males showed similar TLF to HOR×HOR pairs (Table 6, Figure 5).

Neither release date nor location was associated with the fitness of salmon released above Foster Dam in 2009, at least as currently estimated from 2012 (three year old) and 2013 (four year old) adult offspring returns (Table 3). Similar to what was observed in 2008, females exhibited higher fitness than males (Tables 3-4) and overall, 46% (190/412) of reintroduced salmon produced at least one 3 or 4 year old adult offspring. Interestingly, the mean and range of fitness values observed in 2009 is already comparable to, or marginally exceeding, TLF estimates for salmon reintroduced above Foster Dam in 2007 and 2008 (Figure 4). This suggests that the productivity of the 2009 reintroduced population will be higher than that observed in previous years.

We assigned few progeny to salmon reintroduced above Foster Dam in 2010

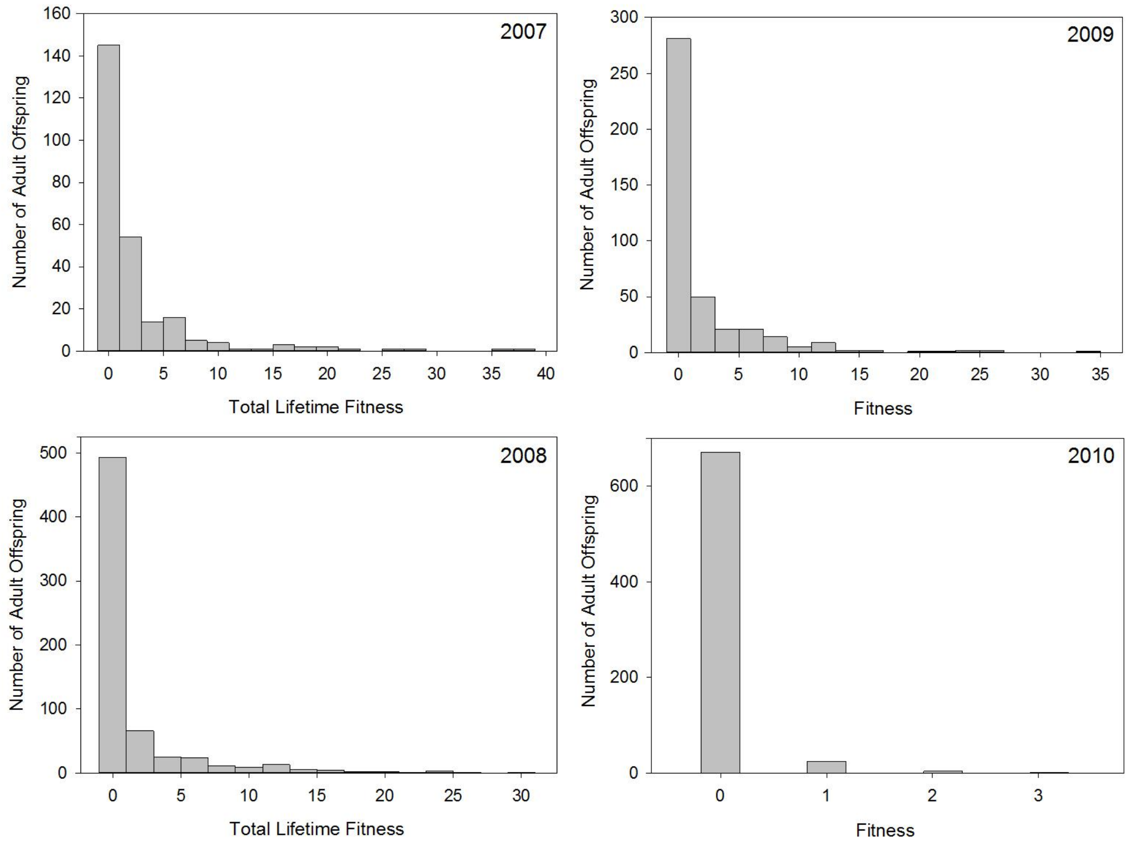

Figure 4. Fitness of spring Chinook salmon released above Foster Dam on the South Santiam River, Oregon, 2007-2010. Fitness was estimated from the number of adult progeny returning to the river in subsequent years. *Total lifetime fitness* is shown, as estimated from the number of three, four, and five year old progeny returning to the South Santiam River, for salmon reintroduced above Foster Dam during 2007 and 2008. *Fitness* of salmon reintroduced above Foster Dan during 2009 and 2010 is currently estimated from the number of adult progeny returning to the South Santiam River during 2012 and 2013, and 2013, respectively.

Table 4. Summary of fitness estimates for male and female spring Chinook salmon reintroduced above Foster Dam on the South Santiam River, Oregon, between 2007-2010. The *total lifetime fitness* (TLF) of salmon released above Foster Dam during 2007 and 2008 was estimated from the number of adult offspring returning to the South Santiam River during 2010-2012 and 2011-2013, respectively. Estimates of *fitness* for salmon reintroduced above Foster Dam during 2009 are based on 3 and 4 year old adult offspring returns during 2012-2013. For 2010, *fitness* is preliminarily estimated from 3 year old adult offspring returns during 2013.

		Adult offspring				
		Mean	Median	SD	Minimum	Maximum
2007 TLF – HOR salmon	male	3.57	1	6.92	0	38
	female	2.15	1	3.22	0	19
2008 TLF – HOR salmon	male	1.50	0	3.32	0	24
	female	2.65	0	4.94	0	26
2008 TLF – NOR salmon	male	1.13	0	3.69	0	25
	female	2.94	0	5.63	0	30
2009 Fitness – NOR salmon	male	1.89	0	4.33	0	35
	female	2.89	1	4.63	0	24
2010 Fitness – NOR salmon	male	0.04	0	0.22	0	2
	female	0.07	0	0.32	0	3

Table 5. Results of generalized linear models examining the influence of sex, release date, release location (variable in 2009), and origin (i.e. HOR or NOR, variable in 2008) on the fitness of spring Chinook salmon reintroduced above Foster Dam during 2007-2009. *Total lifetime fitness* (TLF) for the 2007 and 2008 releases was estimated from the number of adult progeny returning to the South Santiam River during 2010-2012 and 2011-2013, respectively. *Fitness* of the 2009 releases was estimated from the number of 3 and 4 year old progeny that returned to the South Santiam during 2012-2013. The hypothesis that each factor's effect on fitness is zero was tested with the chi-square (χ^2) statistic. P-values falling below the critical α (0.05) are in boldface. Estimates (β) of parameter effects on fitness are indicated when significant.

	2007 TLF				2008 TLF				2009 Fitness		
	χ^2 (df)	β	P		χ^2 (df)	β	P		χ^2 (df)	β	P
Model	61.65 (3)		<**0.001**	Model	50.37 (3)		<**0.001**	Model	12.86 (4)		**0.012**
Sex [F]	3.16 (1)	-	0.075	Sex [F]	13.24 (1)	0.29	<**0.001**	Sex	6.19 (1)	0.25	**0.013**
Date	31.99 (1)	1.04×10^{-6}	<**0.001**	Date	32.70 (1)	2.48×10^{-7}	<**0.001**	Date	1.39 (1)	-	0.238
Date × Sex [F]	6.65 (1)	-4.43×10^{-7}	**0.010**	Origin [NOR]	0.16 (1)	-	0.687	Location	0.53 (2)	-	0.767

n.b. For each discrete factor (e.g. sex, origin), the reference parameter is indicated in parentheses.

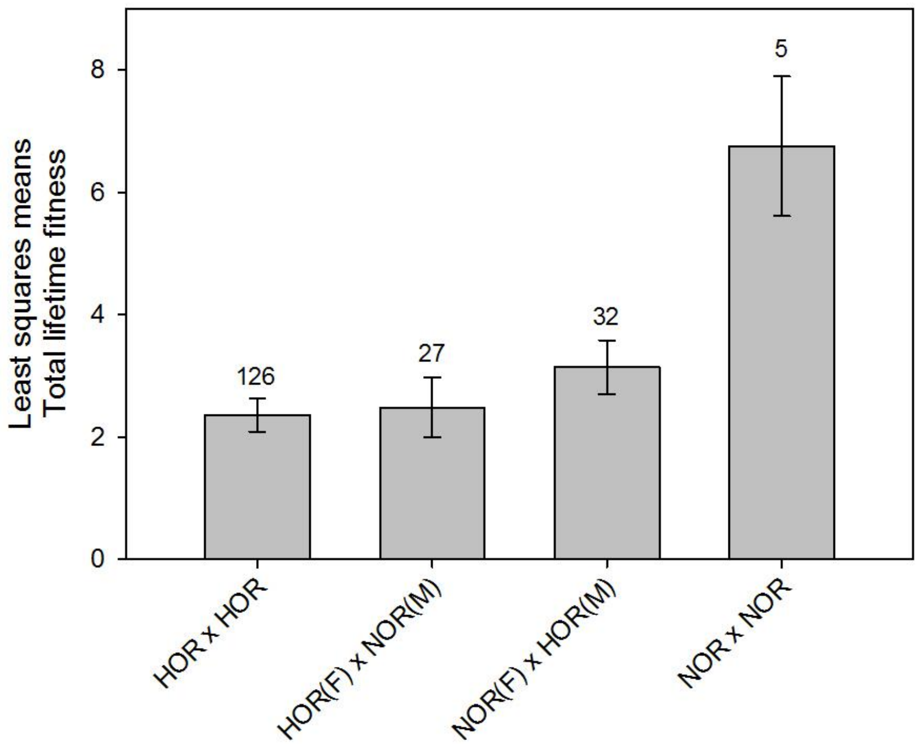

Figure 5. The influence of parental pair type (origin) on the *total lifetime fitness* (TLF) of salmon released above Foster Dam during 2008. Parental pairs comprised: hatchery origin (HOR) male and female pairs (HOR × HOR), HOR females mated to natural origin (NOR) males (HOR[F] × NOR[M]), NOR females mated to HOR males (NOR[F] × HOR[M]), and NOR male and female pairs (NOR × NOR). The statistical analysis associated with this figure is reported in Table 6. Here the least squares means of TLF ± 1SE, which corrects for multiple mating (repeated observations of individuals), are shown. Sample sizes of each parental pair type observed in this year are indicated above the error bars.

Table 6. Results of a generalized linear mixed model examining the influence of parental pair origin on the *total lifetime fitness* (TLF) of spring Chinook salmon released above Foster Dam during 2008. Parental pairs comprised: hatchery origin (HOR) male and female pairs (HOR × HOR), HOR females that mated with natural origin (NOR) males (HOR[F] × NOR[M]), NOR females that mated with HOR males (NOR[F] × HOR[M]), and NOR male and female pairs (NOR × NOR). The model fit is reported as an adjusted R^2 and the effect of parental pair type on TLF was tested using the F-statistic. Numerator (num) and denominator (denom) degrees of freedom (DF) are reported for the model. The model included male and female ID as random effects in order to account for multiple mating (repeated observations) of males and females. Estimates (β) of parameter effects on fitness are indicated when significant. P-values falling below the critical α (0.05) are in boldface.

	R^2	F	DF (num,denom)	P
Model (parental pair)	-0.28	5.16	3,75.6	**0.003**
Parameter estimates (TLF relative to HOR × HOR)			β	P
		NOR × NOR	3.07	**0.038**
		HOR[F] × NOR[M]	-1.21	**0.015**
		NOR[F] × HOR[M]		0.234

DISCUSSION

Spring Chinook salmon reintroductions have been implemented on the South Santiam River to support natural salmon production above Foster Dam. We used genetic parentage analysis methods to examine the contribution of the reintroduction program to subsequent wild (NOR) adult salmon recruitment above the dam. We also used parentage analysis to estimate reintroduction program contributions to below-dam salmon recruitment. From the parentage assignments, we estimated the fitness of reintroduced salmon and examined the influence of various reintroduction strategies on fitness, including the effects of releasing salmon of hatchery versus natural origin, and at different times and locations, above Foster Dam.

Our major findings indicated that:

1. Most salmon reintroduced above Foster Dam in 2012 (74%) and 2013 (66%) were progeny of salmon reintroduced above the dam in a previous year. For the 2010 and 2011 releases, 7% and 34%, respectively, were progeny of reintroduced salmon. The lower parentage assignment rates in 2010-2011 compared to in 2012-2013 are due to incomplete sampling of parents; i.e. no tissue samples were collected pre-2007 and only 64% of reintroduced salmon were sampled in 2007.

2. The reintroduction program is contributing to spring Chinook salmon recruitment below Foster Dam. Parentage analysis of salmon sampled as carcasses below Foster Dam in 2011, 2012, and 2013 indicated that 9%, 11%, and 15%, respectively, were progeny of reintroduced salmon. The higher parentage assignment rate in later years is most likely related to near-complete sampling and genotyping of the reintroduced population since 2008.

3. The cohort replacement rate, our index of population productivity, for the reintroduced population in 2007 was 0.96 and in 2008 was 1.16.

4. The effective population size (N_e) of the reintroduced population in 2007 was 100 individuals (95% C.I. = 93.9 – 107.0), and in 2008, 138 individuals (95% C.I. = 131.4 – 144.5).

5. We detected a significant negative relationship between reintroduction date and parentage assignment rate in 2012 and 2013, the years for which we had near-complete sampling of putative parents from the reintroduction program.

6. Most salmon (61%) released above Foster Dam during 2007 produced adult progeny that returned to and were subsequently released above the dam during 2010-2012. However, in 2008, only 38% of released salmon produced progeny that were released above Foster Dam during 2011-2013. Estimates of fitness for the 2009 releases are preliminary (based on 3 and 4 year old progeny), but indicate that at least 46% of salmon reintroduced above Foster Dam during 2009 produced adult progeny that were released above the dam during 2012-2013.

7. Total lifetime fitness (TLF) was highly variable among individuals, ranging from zero to 38 progeny. On average, the TLF of salmon released above Foster Dam in 2008 was lower than in 2007. In 2008, but not 2007, females exhibited higher TLF than males. In both years, release date was positively associated with TLF.

8. Releases above Foster Dam in 2008 comprised a mix of hatchery and natural origin salmon. Individual-based estimates of fitness for the hatchery and natural origin salmon were not significantly different. However, parental pairs involving a hatchery origin individual achieved significantly lower fitness (2.4±2.5 offspring) compared to pairs comprised of a natural origin male and female (6.4±5.1 offspring).

Productivity of reintroduced population

For salmon released above Foster Dam in 2012 and 2013, parentage analyses indicated that most (74% in 2012; 66% in 2013) were progeny of salmon reintroduced above the dam in previous years (2007-2010). Moreover, the reintroduction program produced up to 15% of adults recruiting to the South Santiam River basin below Foster Dam, as estimated from 2013 returns. A small proportion of salmon reintroduced above the dam subsequently fall over the dam and survive to be re-released at a later date. The fallback frequencies detected in this study are likely minimum estimates of this phenomenon given that individuals falling over the dam would need to survive, be re-trapped, and re-released above the dam. Fallbacks could also remain and subsequently spawn below the dam. Additional studies are needed to fully evaluate the extent to which fallbacks and/or the progeny of reintroduced salmon are contributing to below dam spawning activity.

The number of female progeny produced by reintroduced females (i.e. the Cohort Replacement Rate) was close to one in both 2007 and 2008, suggesting that offspring recruitment to the South Santiam River met or marginally exceeded population replacement. However, the effective population size (N_e) of the reintroduced population in 2007 and 2008, estimated at 100 and 138, respectively, was only a fraction of the census size. It is recommended that managers maintain a minimum N_e of ~ 50-100 to avoid inbreeding depression and ~ 500-1000 to retain the long term evolutionary potential of a population (Jamieson and Allendorf 2012; Frankham et al. 2014). Thus, the long-term adaptive potential of the reintroduced population may be of concern given current relatively low estimates of effective population size. However, the reintroduced population is not entirely isolated - our parentage analysis suggests that gene flow is being maintained between the above and below dam populations, which will mitigate for the low effective population size of the reintroduced population in a given year. Overall, our findings suggest that the reintroduction program is a promising method of increasing natural spring Chinook salmon production within the upper basin of the South Santiam River.

Unassigned salmon reintroduced above Foster Dam

In each of the release years examined in this study, there were reintroduced salmon for which only a male or female parent was identified or no parents were identified. Several possibilities could explain the occurrence of salmon with missing parents in our parentage analysis. First, despite thorough sampling of putative parents from the reintroduction program since 2008, in each year there remained a few salmon that were not sampled and/or successfully genotyped (see Appendix 1). Second, it is possible that resident individuals present above Foster Dam are contributing to reproduction in the system. Male Chinook salmon can mature at 1-2 years of age, remain resident, and spawn precocially in freshwater (Taylor 1989; Quinn and Myers 2005). While a resident freshwater life history does not typically occur in female Chinook salmon, populations that face high mortality during migration and/or from passage through dams may be more likely to express or evolve resident behaviors (Taylor 1989; Waples et al. 2007). Recent evidence has shown that resident female Chinook salmon occur in some reservoirs above UWR dams (Romer and Monzyk in press).

It is also possible that unmarked HOR fish, NOR salmon originating from the South Santiam River below Foster Dam, and/or strays from other populations were reintroduced above the dam. Data provided by ODFW indicates that in some years up to 32% of salmon released above Foster Dam are unmarked HOR fish. Moreover, although salmonids are largely philopatric, some individuals stray from their natal stream environments to locate suitable spawning habitat (Dittman et al. 2010; Westley et al. 2013). Notably, our parentage assignment rate declined with reintroduction date in 2012 and 2013, similar to the pattern observed in the genetic parentage study of spring Chinook salmon reintroduced above Cougar Dam on the South Fork McKenzie River (Banks et al. 2013). This pattern is suggestive of increased immigration by salmon from other "populations" towards Foster and Cougar dams late in the spawning migration.

Tissue samples have been collected from below-dam carcasses since 2011, so it will be possible, beginning in 2014, to quantify below-dam spawner contributions to the reintroduction program. It would also be informative to collect tissue samples from South Santiam hatchery broodstock and incorporate these individuals into the parentage analysis of reintroduced salmon. This would facilitate (1) the identification of any unmarked HOR individuals reintroduced above Foster Dam, (2) fitness estimates for HOR salmon following reintroduction, (3) estimates of introgression with wild salmon above Foster Dam, and (4) eventual fitness estimates for the wild-born progeny of hatchery origin fish.

Factors affecting spring Chinook salmon fitness

As the reintroduction program continues to evolve and adopt best practices, it will be important for managers to limit anthropogenic factors that may adversely affect the fitness of salmon released above Foster Dam. For salmon reintroduced above Foster Dam in 2007 and 2008, it appears that later release dates were associated with higher total lifetime fitness. A previous study of spring Chinook salmon in the Willamette River basin showed that salmon released above dams at later dates were more likely to experience lower rates of pre-spawn mortality (PSM) following release, compared to salmon released earlier in the spawning migration (Keefer et al. 2010). Rates of PSM experienced by later-migrating spring Chinook salmon throughout the spawning migration are not currently available. Therefore we cannot rule out the possibility that earlier and later migrants experience similar rates of PSM but in different geographical locations (i.e. above vs. below dams, respectively). Moreover, in contrast to the patterns observed for the 2007 and 2008 releases, the fitness of salmon released above the dam in 2009 was not associated with release date, suggesting that it does not generally affect the fitness of reintroduced salmon (also see Keefer *et al.* 2010). It is possible that the environmental conditions experienced above the dam in 2009 may have been more favorable for salmon reproduction and/or survival than in previous years. However, 2009 was also the first year in which only natural origin salmon were released above the dam, a factor that may drive interannual differences in the performance of reintroduced salmon (Araki et al. 2007; Anderson et al. 2013). Indeed, the fitness of the 2009 releases, as currently estimated from 3 and 4 year old offspring returns to the South Santiam River, already meet or exceed mean total lifetime fitness estimates of salmon released above the dam in 2007 and 2008. Overall, it appears that later-arriving migrants, on average, achieve higher fitness than earlier arriving salmon, a result that is likely to be at least partly driven by differential PSM experienced following release above Foster Dam. Moreover, the effect of release timing on fitness was not generally observed across years, suggesting that interannual environmental differences experienced by the reintroduced populations or differences in the composition of the fish released above the dam are also critical to fitness.

Previous studies have suggested that hatchery origin salmon experience lower fitness when breeding in the wild compared to wild salmon (Araki et al. 2007; Anderson et al. 2013). While we did not detect a difference in individual-based estimates of fitness for hatchery and natural origin salmon, the fitness of natural origin parental pairs was more than twice that of parental pairs involving a hatchery origin mate. In steelhead (*O. mykiss*), Araki et al. (2007) similarly demonstrated that the reproductive success of wild × hatchery and hatchery × hatchery parental pairs is lower than parental pairs of wild origin. Overall, our results suggest that the fitness of natural origin males and females, as estimated on an individual level, is likely constrained by mating with a hatchery origin individual. The move towards exclusively reintroducing salmon of natural origin above Foster Dam therefore appears to be a prudent measure to boost the intrinsic productivity of this population.

Conclusions

Overall, our results suggest that the reintroduction program for spring Chinook salmon on the South Santiam River is demographically viable, with the number of progeny recruiting to the river meeting or exceeding replacement of the reintroduced parent population. As the program continues to evolve, there are a number of management actions that may help to ensure the continued recovery of the population. First, our results point to better fitness outcomes for parental pairs of spring Chinook salmon comprised of natural origin individuals, suggesting that reintroductions of only natural origin salmon should remain a priority for the program. Second, despite the apparent success of the program in terms of achieving population replacement, the effective number of breeders (N_e) in the population is substantially lower than that recommended for the maintenance of adaptability over evolutionary timescales (Jamieson & Allendorf 2012). Importantly, the effective population size of the spring Chinook salmon UWR ESU is substantially greater than in the South Santiam alone, which may facilitate longer-term adaptation across the contributing populations. This finding also suggests that some caution is warranted when utilizing census population size, which greatly exceeds our estimates of N_e, to evaluate the viability of the reintroduced population (Shrimpton and Heath 2003). High rates of PSM are likely driving much of the observed discrepancy between effective and census population sizes. Investigations of productivity and effective population size of reintroduced populations comprised of entirely natural origin salmon are now needed to evaluate the long-term potential of the reintroduction program.

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Appendix 1

Releases of spring Chinook salmon above Foster Dam on the South Santiam River, Oregon, summarized by release date, 2007-2013. Numbers of released salmon are summarized by release date, sex, and origin i.e. hatchery origin (HOR) or natural origin fish (NOR). Origin was assessed in the field via the absence (HOR) or presence (NOR), respectively, of an adipose fin. In brackets following release numbers are the number of fish successfully genotyped.

Year	Date	HOR		NOR		Origin unknown*		Total released	Not genotyped
		Males	Females	Males	Females	Males	Females		
2007	Sept. 7	100 (98)	75 (72)	0	0	0	0	175	5
	Sept. 11	8	24	0	0	0	0	32	0
	Sept. 21	21	31 (29)	0	0	0	0	52	2
	Total	129	130	0	0	0	0	259[a]	7
2008	Aug. 6	61	27 (26)	22	3	1	0	114	1
	Aug. 16	49	35 (34)	45	1	0	0	130	1
	Sept. 25	33	15	15	0	0	0	63	0
	Oct. 1	88 (87)	35	12	19	0	0	154	1
	Oct. 2	107 (106)	50 (46)	11 (9)	30	0	10	280	7
	Total	338	162	105	53	1	10	669	10
2009	Jun. 24	0	0	8	3	0	0	11	0
	Jul. 2	0	0	21	23 (22)	0	0	44	1
	Jul. 6	0	0	30 (26)	21 (20)	0	0	51	5
	Jul. 9	0	0	4	8	0	0	12	0
	Jul. 14	0	0	17	12	0	0	29	0
	Jul. 15	0	0	5	3	0	0	8	0
	Jul. 30	0	0	11	5	0	0	16	0
	Aug. 10	0	0	19	18	0	0	37	0
	Aug. 12	0	0	31 (30)	26	0	0	57	1
	Aug. 19	0	0	11	2	0	0	13	0
	Aug. 26	0	0	4	2	0	0	6	0
	Sept. 2	0	0	34	4	0	0	38	0
	Sept. 8	0	0	25 (23)	5	0	0	30	2
	Sept. 15	0	0	24	17	0	0	41	0
	Sept. 22	0	0	15	10	0	0	25	0
	Sept. 29	0	0	2	1	0	0	3	0
	Total	0	0	261	160	0	0	421	9
2010	May 14	0	0	0	1	0	0	1	0
	May 18	0	0	1	0	0	0	1	0
	May 25	0	0	2	2	0	0	4	0
	Jun. 1	0	0	0	1	0	0	1	0
	Jun. 17	0	0	1	1	0	0	2	0
	Jun. 22	0	0	12	11	0	0	23	0
	Jun. 23	0	0	18	23	0	0	41	0
	Jun. 25	0	0	39	21	0	0	60	0

	Jun. 29	0	0	34	20	0	0	54	0
	Jul. 2	0	0	35	17 (16)	0	0	52	1
	Jul. 6	0	0	19	22	0	0	41	0
	Jul. 7	0	0	19	8	0	0	27	0
	Jul. 8	0	0	20	2	0	0	22	0
	Jul. 12	0	0	22	11	0	0	33	0
	Jul. 14	0	0	29	15 (14)	0	0	44	1
	Jul. 16	0	0	16	12	0	0	28	0
	Jul. 22	0	0	25	9	0	0	34	0
	Jul. 23	0	0	10	9	0	0	19	0
	Jul. 26	0	0	10	6	0	0	16	0
	Jul. 29	0	0	24	12	0	0	36	0
	Aug. 2	0	0	9	3	0	0	12	0
	Sept. 9	0	0	14	1	0	0	15	0
	Sept. 14	0	0	32	29 (28)	0	0	61	1
	Sept. 15	0	0	76	0	0	0	76	0
	Total	0	0	467	236	0	0	703	3
2011	Jun. 13	0	0	24	25	0	0	49	0
	Jun. 16	0	0	37	51 (50)	0	0	88	1
	Jun. 20	0	0	29	29	0	0	58	0
	Jun. 23	0	0	19	16	0	0	35	0
	Jun. 24	0	0	14	11	0	0	25	0
	Jun. 28	0	0	25	14	0	0	39	0
	Jul. 1	0	0	17	15	0	0	32	0
	Jul. 5	0	0	46 (45)	37	0	0	83	1
	Jul. 7	0	0	40	36	0	0	76	0
	Jul. 12	0	0	34	31 (30)	0	0	65	1
	Jul. 13	0	0	33	25	0	0	58	0
	Jul. 14	0	0	20	19	0	0	39	0
	Jul. 18	0	0	34	26	0	0	60	0
	Jul. 19	0	0	20	17	0	0	37	0
	Jul. 20	0	0	20	15	0	0	35	0
	Aug. 1	0	0	21	25	0	0	46	0
	Aug. 4	0	0	17	15	0	0	32	0
	Aug. 10	0	0	23	29	0	0	52	0
	Aug. 17	0	0	28	15	0	0	43	0
	Aug. 22	0	0	18	11	0	0	29	0
	Aug. 24	0	0	15	6	0	0	21	0
	Sept. 1	0	0	17	7	0	0	24	0
	Sept. 8	0	0	49	15	0	0	64	0
	Sept. 13	0	0	41	21	0	0	62	0
	Sept. 22	0	0	37	17	0	0	54	0
	Sept. 28	0	0	2 (0)	0	0	0	2	2
	Total	0	0	680	528	0	0	1208	5
2012	May 10	0	0	1 (0)	0	0	0	1	1
	May 14	0	0	0	1	0	0	1	0
	May 17	0	0	0	2	0	0	2	0
	May 21	0	0	7	2	0	0	9	0
	May 24	0	0	23	24	0	0	47	0
	May 29	0	0	1	1	0	0	2	0
	Jun. 1	0	0	3	6	0	0	9	0

	Jun. 5	0	0	29 (28)	28	0	0	57	1
	Jun. 6	0	0	20	15	0	0	35	0
	Jun. 12	0	0	0	1	0	0	1	0
	Jun. 19	0	0	11	9	0	0	20	0
	Jun. 22	0	0	26	34	0	0	60	0
	Jun. 26	0	0	42	42	0	0	84	0
	Jun. 28	0	0	29	24	0	0	53	0
	Jul. 3	0	0	47	42	0	0	89	0
	Jul. 5	0	0	19	13	0	0	32	0
	Jul. 10	0	0	38	26	0	0	64	0
	Jul. 12	0	0	20	25	0	0	45	0
	Jul. 18	0	0	35 (33)	18	0	0	53	2
	Jul. 19	0	0	34	21	0	0	55	0
	Jul. 23	0	0	26 (21)	23 (19)	0	0	49	9
	Jul. 26	0	0	10 (0)	8	0	0	18	10
	Aug. 2	0	0	27	18	0	0	45	0
	Aug. 7	0	0	7	7 (6)	0	0	14	1
	Aug. 21	0	0	26	11	0	0	37	0
	Aug. 27	0	0	14	7 (6)	0	0	21	1
	Sept. 4	0	0	56	11	0	0	67	0
	Sept. 6	0	0	22	5	0	0	27	0
	Sept. 11	0	0	10	2	0	0	12	0
	Sept. 18	0	0	11	2	0	0	13	0
	Sept. 25	0	0	12	1	0	0	13	0
	Total	0	0	606	429	0	0	1035	25
2013	May 2	0	0	8	3	0	0	11	0
	May 9	0	0	2	2	0	0	4	0
	May 13	0	0	5	2	0	0	7	0
	May 20	0	0	26 (24)	26	0	0	52	2
	May 28	0	0	1	1	0	0	2	0
	Jun. 7	0	0	1	2	0	0	3	0
	Jun. 10	0	0	14 (13)	3	0	0	17	1
	Jun. 13	0	0	46	33	0	0	79	0
	Jun. 14	0	0	24	29	0	0	53	0
	Jun. 18	0	0	18	21	0	0	39	0
	Jun. 21	0	0	7	9	0	0	16	0
	Jun. 24	0	0	13	13	0	0	26	0
	Jun. 27	0	0	1	3	0	0	4	0
	Jul. 8	0	0	28	24	0	0	52	0
	Jul. 11	0	0	53	51	0	0	104	0
	Jul. 16	0	0	23	18	0	0	41	0
	Jul. 19	0	0	9	20	0	0	29	0
	Jul. 22	0	0	12	2	0	0	14	0
	Jul. 26	0	0	26	25	0	0	51	0
	Jul. 29	0	0	23	27	0	0	50	0
	Aug. 1	0	0	11	12	0	0	23	0
	Aug. 7	0	0	14	14	0	0	28	0
	Sept. 4	0	0	85	29	0	0	114	0
	Sept. 10	0	0	31 (30)	19	0	0	50	1
	Sept. 17	0	0	35	11 (10)	0	0	46	1
	Sept. 24	0	0	18 (16)	6 (5)	0	0	24	3
	Total	0	0	534	405	0	0	939	8

[*]Data on origin missing from field records
[a]Total number of fish released above the dam in 2007 was 403, according to ODFW field records; tissue samples were collected from a subsample of released spring Chinook salmon in this year.
[b] In addition to three females and five males, one individual of unknown sex was released above Foster and not tissue-sampled on this day.