AN EVALUATION OF SPRING CHINOOK SALMON REINTRODUCTIONS ABOVE DETROIT DAM, NORTH SANTIAM RIVER, USING GENETIC PEDIGREE ANALYSIS

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SUMMARY

For approximately two decades, hatchery-origin (HOR) spring Chinook salmon have been released ("outplanted") above Detroit Dam on the North Santiam River. Here we used genetic parentage analysis to evaluate the contribution of salmon outplants to subsequent natural-origin (NOR) salmon recruitment to the river.

Despite sampling limitations encountered during several years of the study, we were able to determine that most NOR salmon sampled in 2013 (59%) and 2014 (66%) were progeny of outplanted salmon. We were also able to estimate fitness, a cohort replacement rate (CRR), and the effective number of breeders (N_b) for salmon outplanted above Detroit Dam in 2009. On average, female fitness was ~5× (2.72:0.52 progeny) that of males and fitness was highly variable among individuals (range: 0-20 progeny). It is likely that the highly skewed male:female sex ratio (~6:1) among outplanted salmon limited reproductive opportunities for males in 2009. The CRR was 1.07, as estimated from female replacement. However, when considering all outplanted salmon CRR was 0.54, suggesting that sex ratio skew influenced overall population productivity. The N_b of the 2009 outplant cohort was 130.7 (95% C.I. = 123.4-138.6), leading to an N_b/N_c (effective number of breeders / reintroduced cohort census size) ratio of 0.17.

Taken together, this study provides a baseline for future investigations of the viability of salmon reintroductions above the Detroit-Big Cliff dam complex on the North Santiam River. With additional sampling in 2015, estimates of cohort replacement, total lifetime fitness, and N_b will be possible for the 2010 outplant cohort, which comprised the largest release of HOR fish above Detroit Dam since tissue sampling of outplanted salmon began. Moreover, fitness estimates for salmon outplanted in 2010 will provide some insight into reproductive success and population productivity under a relatively even male:female sex ratio, albeit at a much higher breeding density than in 2009.

INTRODUCTION

Adult spring Chinook salmon (*Oncorhynchus tshawytscha*) are released above USACE dams throughout the Upper Willamette River (UWR) basin to facilitate dispersal to historical habitats and increase the abundance of naturally produced fish. The North Santiam River is a major tributary of the UWR and supports both hatchery (HOR) and natural-origin (NOR) spring Chinook salmon. For approximately two decades, spring Chinook salmon have been released ("outplanted") above Detroit Dam, yet the contribution of this program to adult salmon recruitment to the North Santiam River remains unknown.

Our research is aimed at addressing this uncertainty by estimating the fitness (the number of adult salmon produced by a given spawner) of adult Chinook salmon released above Detroit Dam and evaluating the influence of reintroduction strategies (e.g. date and location of release) on reproductive performance. This work will meet the specific information needs of Reasonable and Prudent Alternative (RPA) 9.5.1(4) of the Willamette Project Biological Opinion (NMFS 2008) in determining the reproductive success of hatchery fish in the wild. Results of the research will also address RPA 4.1 (restoration of productivity by outplanting Chinook 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 outplanting, Willamette basin-wide), and RPA 9.3 (monitoring the effectiveness of fish passage facilities and strategies at Willamette Project dams).

Outplanting programs on other rivers within the UWR basin currently release marked, HOR fish, unmarked, presumed NOR fish, or some combination of unmarked (NOR) and marked (HOR) spring Chinook salmon. Except for a subset of fish in 2010, only HOR spring Chinook salmon have been released above Detroit Dam on the North Santiam River. Our study evaluates the productivity of salmon released above Detroit Dam, within the context of current passage conditions, to inform management decisions regarding the future use of NOR spring Chinook salmon in outplanting operations.

Objectives

1. Determine the number and proportion of unmarked adult Chinook salmon, sampled at various locations on the North Santiam River (i.e. Minto fish collection facility, spawning grounds, Bennett Dam) in 2010-2014, that were progeny of spring Chinook salmon outplanted above Detroit Dam (2007-2011), and from these assignments, examine the age structure of adult progeny. Salmon outplants during 2010 included 50 NOR salmon; these fish were considered as both possible progeny (i.e. of salmon outplanted in 2007) and possible parents of NOR salmon recruits during 2013-2014.

2. Estimate the fitness of spring Chinook salmon outplanted above Detroit Dam in 2007-2010. This estimate will be based on parentage analysis of unmarked adult Chinook salmon sampled at Bennett Dam (2011), Minto fish collection facility (2013 and 2014), as well as unmarked salmon encountered on the spawning grounds below Big Cliff Dam (2011-2014).

3. Estimate the effects of release date and location on the fitness of spring Chinook salmon outplanted above Detroit Dam in 2007-2010.

4. Estimate Cohort Replacement Rate (CRR), or "the number of future spawners produced by a spawner" for spring Chinook salmon released above Detroit Dam in 2009.

5. Estimate the effective number of breeders among salmon outplanted in 2009.

METHODS

Spring Chinook salmon migration on the North Santiam River is impeded by two large dams, Big Cliff and Detroit, which are located at 44° 45′ 3.6″ N, 122° 16′ 59.16″ W and 44° 43′ 15.44″ N, 122° 14′ 59.27″ W, respectively (Figure 1). Dam operations began in the early 1950s as did operation of the original Minto fish collection facility which was used to collect broodstock for Marion Forks Fish Hatchery, located upstream of the dams. A new fish collection facility was built at Minto in 2011-2012, and became operational in 2013. The new facility is used to collect hatchery broodstock and to assist with salmon passage around the dams.

HOR salmon outplanting above Detroit Dam was initiated in the 1990s. Multiple release locations have been used during outplanting, including Cooper Ridge, Cleater Bend and Road 096 on the Breitenbush River, and direct released into Detroit Reservoir (Figure 1).

Since 2007, tissue samples have been collected from outplanted fish, though in some years, only a subset of individuals were sampled. Specifically, in 2008, 205 salmon were outplanted and 129 tissue-sampled. In 2009, hatchery records indicated that over 1000 salmon were released above Detroit Dam, but only 806 tissue samples were received by our lab. Moreover, records provided by ODFW indicated that 269 of the 806 salmon released above the dam were NOR. Hatchery outplant records contradict this, indicating that all releases were HOR salmon, consistent with the current outplant policy on the North Santiam River. Thus, in our analyses we have assumed that all salmon released above Detroit Dam in 2009 were HOR and that salmon origin (HOR/NOR) was incorrectly recorded for some fish in that year.

ODFW records also indicated that 34 HOR salmon males were released at Shelburn Road in 2009, below the dams and Minto, which contradicts hatchery outplant records. Supporting the hatchery records, our pedigree results indicated that several of the “Shelburn” males mated with outplanted females, suggesting that they were actually released above the dam. Thus, we have included these males in our analysis of salmon outplanted in 2009.

In 2010, 2735 salmon were released above Detroit and 2198 were tissue-sampled. Among the outplanted salmon, 50 NOR salmon were released as part of a radiotelemetry study; these fish represent possible three year old progeny of salmon outplanted in 2007 as well as parents of the 2013 and 2014 adult progeny.

It is important to note that incomplete sampling of outplanted salmon (i.e. putative parents) will affect our ability to assign NOR progeny that recruit back to the system in subsequent years; we note throughout the report where estimates of outplant program contributions to NOR recruitment are likely to be downwardly biased as a result of incomplete sampling.

NOR recruitment and carcass surveys for adult offspring

Beginning in 2011, tissue samples were collected from NOR carcasses during spawning ground surveys. We used these samples to examine the contribution of salmon outplanting operations to recruitment below Big Cliff and Detroit dams. In addition, a small number of tissue samples, collected in 2011 from unmarked adult salmon used in a disease challenge experiment conducted by ODFW and Oregon State University, were examined as possible progeny of outplanted salmon (Table 1).

Tissue-sampling at Minto ceased in 2011-2012 during the new facility's construction. However, since 2013, NOR salmon recruits to the new Minto fish collection facility have been tissue-sampled and subsequently released to the river above Minto Dam, but below Big Cliff Dam (Table 1). These NOR recruits represent possible progeny of outplanted HOR salmon (2008-2011; Figure 2). All tissue samples collected from Chinook salmon were stored in 95% ethanol for future genetic analysis.

As carcass samples represent only a fraction of salmon returning to the river, offspring assignments to the 2007 and 2008 outplant cohorts will be minimum estimates of fitness and should be interpreted with caution.

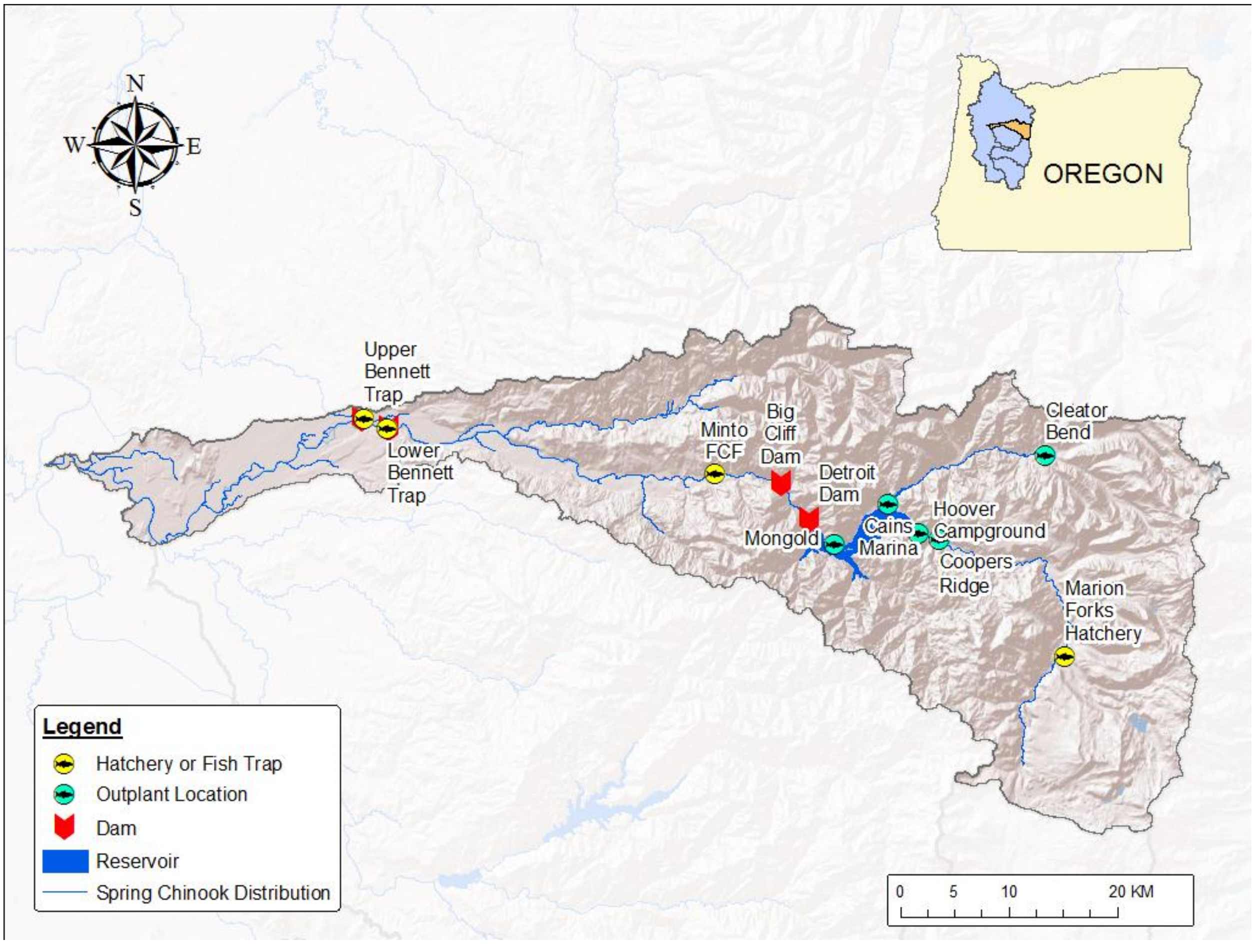


Figure 1. Location of the North Santiam River in Oregon. Shown are the locations of Big Cliff and Detroit dams, Minto fish collection facility (FCF) and the locations used in spring Chinook salmon outplanting operations.

Genetic parentage analysis

Using the protocol of Ivanova et al. (2006), whole genomic DNA was isolated from tissue samples. Each sample was then genotyped at 12 microsatellite loci: *Ots201*, *Ots211*, *Ots212*, *Ots215*, *OtsG249*, *OtsG311*, *OtsG409*, *OtsG474*, *Ots515*, *Ssa408*, *Ogo4*, and *Ogo2* (Olsen et al. 1998, Cairney et al. 2000, Williamson et al. 2002, Naish and Park 2002, Greig et al. 2003) and at the sex-linked marker, *Oty3*, to determine sex (Brunelli et al. 2008). Loci were amplified using polymerase chain reaction (PCR), PCR products visualized on an ABI 3730xl DNA analyzer, and allele sizes scored in GeneMapper software (Applied Biosystems, Inc., Foster City, CA). Most samples (97-100%) collected from live fish were successfully genotyped (Table 1). However, as DNA degrades rapidly post-mortem in salmon (Copeland et al. 2009), we achieved relatively low genotyping success for carcass samples (Table 1). All molecular work was performed in the Marine Fisheries Genetics Lab at Hatfield Marine Sciences Center, Newport, Oregon.

The 12 microsatellite loci were highly polymorphic (Appendix, Table A1). For instance, among 2007-2009 salmon outplants, putative parents of 2010-2014 NOR salmon recruits, the loci provided a non-exclusion probability for a candidate parental pair of 2.20×10^{-15}, as estimated by CERVUS v. 3.0 (Kalinowski et al. 2007). Moreover, analyses in Genepop v. 4.2 (Raymond and Rousset 1995) indicated that heterozygosity (patterns of genetic variation) at most loci, in most years of our study, conformed to Hardy-Weinberg expectations (Appendix, Table A2). Only individuals with genotypes at >=7 loci were included in the parentage analysis, a threshold that was determined based on the non-exclusion probabilities observed across loci for assigning parentage to an individual parent or parent pair (see Appendix, Table A1).

Table 1. Summary of North Santiam River spring Chinook salmon considered in genetic parentage analysis. Indicated are the total number of salmon of natural (NOR), hatchery (HOR), or unknown (UK) -origin released above Detroit Dam, Minto fish collection facility, or that were sampled as carcasses below Big Cliff Dam, according to Oregon Department of Fish and Wildlife (ODFW) field records. Also indicated are the number of fin clips received by the lab for genetic analyses and the number of individuals repeatedly sampled, as determined from observations of identical genetic profiles.

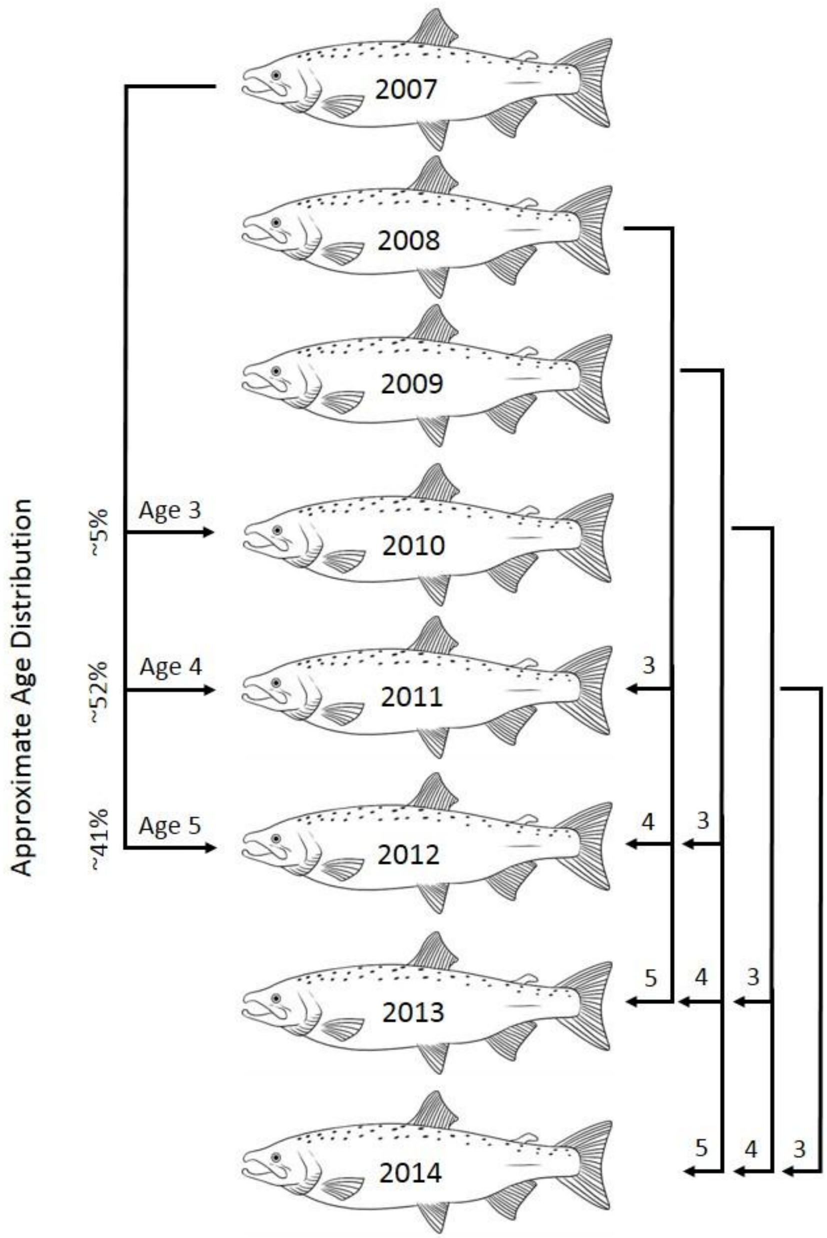
Year/sample	Release Location	Pedigree class	HOR	NOR	UK origin	Fin clips	Genotyped (7+ loci)	Repeat samples	Males	Females	UK Sex
2007 outplant	Detroit	parent	994	0	0	951	936	14	491	431	0
2008 outplant	Detroit	parent	129	0	0	129	125	5	110	10	0
2009 outplant[ǂ]	Detroit	parent	806	0	0	806	792	33	628	131	0
2010 outplant	Detroit	parent	1950	50	198	2198	2179	70	1146	963	0
2011 outplant	Detroit	parent	151	0	0	151	151	1	77	73	0
2011 carcass	-	parent/offspring	0	330	0	330	211	8	90	103	9
2011 dis. ch.[1]	-	offspring	0	74	0	74	74	0	38	36	0
2012 carcass	-	offspring	0	130	0	130	84	0	39	45	0
2013 carcass	-	offspring	0	61	0	58	54				
2013 outplant[*]	Minto	offspring	0	565	0	560	559				
2013 Total						*618*	*613*	*20*	*408*	*185*	*0*
2014 carcass	-	offspring	0	94	0	94	65				
2014 outplant	Minto	offspring	0	776	0	776	769				
2014 Total						*870*	*834*	*33*	*484*	*317*	*0*

ǂ Of salmon outplanted above Detroit, 269 were labeled "NOR" in outplant records, but hatchery records indicate that only HOR salmon were outplanted in this year, suggesting that some HOR outplants were mislabeled NOR; [1] In 2011, some NOR returns were used in a disease challenge experiment – these fish were collected at Bennett Dam and considered in the 2011 pedigree as possible progeny of previously outplanted parents (2007-2008) but were not considered as putative parents in later years as any released offspring were marked as HOR; [*] Salmon were batch-sampled in 2013, so individual phenotypic data cannot be associated to genetic sample.

To estimate the number of NOR salmon recruits that were progeny of outplanted salmon, we compared the microsatellite genotypes of putative progeny to the genotypes of outplanted adults, as indicated in Figure 2. The comparisons were conducted in the maximum-likelihood parentage assignment program CERVUS and assignments were made using a strict 95% confidence criterion. In addition, we used the PLS-FL likelihood algorithm implemented in COLONY v. 2.0 (Jones and Wang 2010) to reconstruct kinship groups based on 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 NOR salmon, i.e. from below dam spawners or strays from other systems, could therefore impact assignment accuracy using CERVUS. Moreover, simulation studies have suggested that COLONY's assignment protocol is the most accurate of current pedigree reconstruction methods (Harrison et al. 2013). COLONY was run using a medium run length and the polygamous male and female setting and allele dropout and general error rates were set to 1% each per locus. In the case of parentage assignment incongruence between the programs, we inspected putative parent-offspring matches by hand to ensure that the alleles conformed to the expectations of Mendelian inheritance and selected the best parent-offspring match (i.e. with the fewest allelic mismatches and no more than one locus mismatching between parent and offspring).

In COLONY, we also compared genotypes among individuals within each release year to identify salmon that may have been repeatedly sampled, e.g. during outplanting and a second time during spawning ground surveys. Duplicate genotypes could also reflect sampling errors in the field. Genotypes that were identical at all loci were assumed to represent a single individual and redundant genotypes were removed from the parentage analysis.

Figure 2. Framework used to reconstruct parent-offspring relationships for spring Chinook salmon from the North Santiam River, in Oregon. The majority (~98%) of UWR spring Chinook salmon mature as three, four, or five year olds. Thus, salmon returning to the North Santiam River during 2010-2014 represent possible progeny of salmon reintroduced above Detroit Dam during 2007-2011.



Fitness of reintroduced salmon

We estimated the fitness of outplanted salmon (i.e. above Detroit Dam) from the number of NOR adult progeny identified in subsequent cohorts/run years. For instance, the fitness of salmon from the 2007 outplant cohort was estimated from the number of three, four, and five year old progeny identified among NOR salmon sampled during 2010-2012 (Figure 2). Importantly, estimates of fitness for salmon from the 2007 and 2008 cohorts are likely to be downwardly biased due to the temporary closure of the Minto fish collection facility during 2011-2012. For the 2009 cohort, assignments to three year old progeny (sampled during 2012) will also be affected by Minto's closure, and therefore fitness estimates will predominantly reflect offspring returns during 2013 and 2014. We also calculated a preliminary estimate of fitness for 2010 salmon outplants based on three and four year old progeny returns (Figure 2).

Predictors of fitness

We used generalized linear models that incorporated a Poisson distribution and log link function to examine the influence of sex and release date, and the interaction between release date and sex on the fitness of outplanted spring Chinook salmon (2007-2010). While variable, we did not include release location as a factor in any of our models because location was typically confounded with release date or not recorded (Table 2). 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.

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 outplanted above Detroit Dam in 2009, for which estimates of four and five year old NOR offspring returns to the new Minto collection facility were available. In addition, parentage assignments to 2012 carcass samples provided an estimate of three year old progeny returns, albeit, as indicated above, a likely downwardly biased one. Our overall CRR estimate = total number of three, four, and five year old progeny produced by all outplanted salmon (males and females) in 2009 / total number of outplanted salmon in 2009.

In 2009, the sex ratio of salmon outplanted above Detroit Dam was extremely male-biased (~6:1 male:female; Table 1). The number and availability of females may have constrained overall reproductive opportunities above the dam. Therefore, we also calculated a female-only CRR = total number of three, four, and five year old female progeny produced by outplanted females / the total number of outplanted females.

Effective number of breeders

We estimated the effective number of breeders (N_b) among outplanted salmon in 2009 using the linkage disequilibrium (LD) method, as implemented in the program NeEstimator v.2 (Waples and Do 2008, Do et al. 2014). This method examines patterns of LD (nonrandom allelic associations, which are suggestive of common ancestry) among offspring of a cohort. N_b was calculated using a minimum allele frequency of 0.02. We report our estimate ± 95% confidence intervals, which was calculated using a jackknife re-sampling method (Waples and Do 2008).

Table 2. Summary of release dates and locations used during spring Chinook salmon outplanting on the North Santiam River during 2007-2010. In most years, the release location and number of salmon released was either not recorded or confounded with release date and thus, the influence of location on fitness could not be statistically examined.

Year	Date	Location	Number of Releases
2007	Aug. 21	*Location data was not recorded in this	173
	Aug. 28	year for majority of salmon*	104
	Sept. 4		59
	Sept. 10		68
	Sept. 12		125
	Sept. 13		53
	Sept. 18		75
	Sept. 24		186
2008	Sept. 2	Brietenbush, Cleator Bend	60
	Sept. 22	Brietenbush, Cleator Bend	1
		Cooper Ridge	33
	Sept. 29	Brietenbush, Cleator Bend	25
		Cooper Ridge	1
2009	Jul. 20	Cooper Ridge	159
	Aug. 11	Breitenbush, Cleater Bend	27
	Aug. 18	Cooper Ridge	38
	Aug. 31	Breitenbush, Cleater Bend	73
	Sept. 4	Cooper Ridge	57
	Sept. 9	Breitenbush, Cleater Bend	95
	Sept. 14	Breitenbush, Cleater Bend	153
	Sept. 18	Cooper Ridge	124
2010	Jul. 7	Cooper Ridge	49
	Jul. 14	Breitenbush, Rd. 096	25
		Cooper Ridge	25
	Jul. 16	Breitenbush, Cleater Bend	137
	Jul. 18	Cooper Ridge	260
	Jul. 20	Breitenbush, Cleater Bend	125
	Jul. 21	Cooper Ridge	159
	Aug. 2	Breitenbush, Cleater Bend	274
	Aug. 6	Breitenbush, Cleater Bend	126
	Aug. 16	Cooper Ridge	51
	Aug. 23	Cooper Ridge	130
	Aug. 30	Cooper Ridge	142
	Sept. 2	Cooper Ridge	148
	Sept. 6	Cooper Ridge	220
	Sept. 13	Detroit Reservoir, Mongold	95

RESULTS

Parentage assignments and inferred age at maturity

In all years considered by our study (2007-2014), we identified samples with identical genotypes, which were removed from further parentage analysis (Table 1).

A total of 6 of 50 (12%) NOR salmon outplanted above Detroit Dam during 2010 assigned as progeny of 2007 outplants (Table 3). Among salmon sampled as carcasses or used in the disease challenge experiment in 2011, 35% (96/276) were identified as progeny of outplanted salmon. The majority of assigned progeny were four year olds (i.e. assigned to parents from 2007; 91/96 or 95%); only five salmon assigned to parents from the 2008 cohort (Table 3). Among carcasses sampled in 2012 and included in our pedigree, 37% (31/84) assigned as progeny of outplanted salmon (Table 3). Most of the assigned progeny were five year olds that assigned to salmon outplanted above Detroit Dam during 2007 (27/31). Two salmon assigned to outplanted parents from each of the 2008 and 2009 outplant cohorts (Table 3). Assignment rates are likely affected by the incomplete sampling of outplanted adults in previous years. For example, at least 76, 194, and 537 salmon released above Detroit Dam were not sampled in 2008, 2009, and 2010, respectively.

Given that the new fish collection facility at Minto began operations in 2013, assignments to progeny in 2013 and 2014 provide the best estimates of outplant program contributions to subsequent NOR salmon recruitment to the system. In 2013, 59% (350/593) of NOR salmon were identified as progeny of outplanted salmon. Most progeny (74%) were four year olds (261/350), 21% (72/350) three year olds, and 5% (17/350) five year olds (Table 3). In 2014, 66% (529/801) of NOR salmon assigned as progeny of salmon outplanted above Detroit Dam during 2009-2010. As in the 2013 pedigree, most (71%) progeny were four year olds (377/529) and 27% (144/529) five year olds. A total of eight salmon assigned to parents from the 2011 outplant cohort (Table 3).

Fitness of reintroduced salmon

As estimated from three, four, and five year old adult offspring, the mean fitness of salmon outplanted above Detroit Dam during 2007 was ~0.20 offspring (Table 4) and most salmon produced no adult offspring that were detected in subsequent years (785/922 or 85%). We observed similar results for the 2008 cohort, with 102/120 (85%) salmon producing no adult offspring that were detected in subsequent genetic pedigree analyses. Again, as noted in the methods, these fitness estimates are likely downwardly biased given the limitations to sampling NOR salmon recruits to the North Santiam River during 2011-2012 when the Minto fish collection facility was closed.

For the 2009 cohort, 71% (541/759) of outplanted salmon produced no adult progeny. However, females performed better than males, with 64% (84/131) producing at least one adult offspring. Only 21% (134/628) of males produced adult progeny. Indeed, the mean fitness of females was 2.72 ± 3.53 progeny, whereas the mean fitness of males was 0.52 ± 1.62 progeny, a difference that was statistically significant (Table 5). In total, 358 adult progeny assigned to the 131 outplanted females in 2009. Of these progeny, 141 were females, resulting in a female CRR of 1.07. In contrast, when considering all outplanted salmon, the CRR was only 0.54 (409/759).

Fitness estimates for 2010 outplants are preliminary; however, current assignments to NOR offspring indicate that 22% (465/2109) of individuals produced at least one adult offspring. Of the 50 outplanted NOR salmon, only one produced adult offspring (N = 1) which was detected in 2013.

Across all outplant cohorts, except for 2007, release date was a significant predictor of variation in fitness, with a later release date generally associated with higher fitness (Table 5).

Effective number of breeders

The estimated N_b among salmon outplanted above Detroit Dam during 2009 was 130.7 (95% C.I. = 123.4-138.6). The ratio of the effective number of breeders to the census size of the outplanted cohort (N_b/N_c) was 131/759 = 0.17.

Table 3. Summary of adult offspring assigned to Chinook salmon outplants above Detroit Dam (2007-2011) on the North Santiam River, Oregon. Indicated are the total number of putative offspring considered in the pedigree analyses (N), summarized by year and sample type, and the number assigned to a parental pair (P), or to a male (M) or female (F) parent only.

		2007 parents			2008 parents			2009 parents			2010 parents			2011 parents			Assigned
Offspring	N	P	F	M	P	F	M	P	F	M	P	F	M	P	F	M	(%)
2010 Detroit outplant	50	0	3	3	-	-	-	-	-	-	-	-	-	-	-	-	6 (12%)
2011 total (carcass/disease challenge[1])	276	39	27	25	0	0	5	-	-	-	-	-	-	-	-	-	96 (35%)
2012 carcass	84	19	1	7	2	0	0	0	0	2	-	-	-	-	-	-	31 (37%)
2013 total (Minto outplant/carcass)	593	-	-	-	6	1	10	186	50	25	29	14	29	-	-	-	350 (59%)
2014 total (Minto outplant/carcass)	801	-	-	-	-	-	-	94	28	22	272	46	59	2	5	1	529 (66%)

[1] Disease challenge experiment fish

Table 4. Fitness estimates for spring Chinook salmon outplanted above Detroit Dam (2007-2010) on the North Santiam River, Oregon. See Figure 1 for an overview of assignment approach. Indicated are the total number of outplanted male and female salmon considered (N), and the mean, median, standard deviation (SD) and range of fitness values observed in each year.

Cohort		N	Mean	Median	SD	Minimum	Maximum
2007	Male	491	0.20	0	0.59	0	5
	Female	431	0.19	0	0.50	0	4
2008	Male	110	0.21	0	0.66	0	5
	Female	10	0.90	0	1.66	0	5
2009	Male	628	0.52	0	1.62	0	20
	Female	131	2.72	1	3.53	0	16
2010 (three and four	Male	1146	0.34	0	0.97	0	11
year old progeny)	Female	963	0.37	0	0.91	0	10

Table 5. Results of generalized linear models examining the influence of release date and sex on the fitness of outplanted spring Chinook salmon from the North Santiam River, Oregon. Separate models were run for each outplant cohort, 2007-2010, and results are summarized for each year. The hypothesis that each factor's (sex, release date) effect on fitness was zero was tested with the chi-square (χ^2) statistic. P-values falling below the critical α (0.05) are shown in boldface. Estimates (β) of effects on fitness are indicated when significant.

	2007				2008		
	χ^2 (df)	β	P		χ^2 (df)	β	P
Model	3.0 (2)		0.223	Model	15.2 (2)		<**0.001**
Sex	0.0 (1)		0.930	Sex	1.2 (1)		0.270
female		-0.01		*female*		0.31	
Date	2.9 (1)	-1.5×10^{-7}	0.088	Date	8.6 (1)	8.4×10^{-7}	**0.003**

	2009				2010		
	χ^2 (df)	β	P		χ^2 (df)	β	P
Model	100.6 (2)		**<0.001**	Model	12.1 (2)		**0.002**
Sex	81.4 (1)		**<0.001**	Sex	1.9 (1)		0.159
female		0.80	**<0.001**	*female*		0.09	
Date	14.2 (1)	1.8×10^{-7}	<**0.001**	Date	10.9 (1)	1.1×10^{-7}	**0.001**

Discussion

The main findings of our study are:

1. Most NOR salmon sampled at Minto fish collection facility or as carcasses on the spawning grounds during 2013 (59%) and 2014 (66%) were progeny of outplanted salmon. These are minimum estimates of outplant program contributions to NOR recruitment in these years due to incomplete sampling of parents in previous years (Table 1).
2. For the 2007 and 2008 cohorts, 15% of salmon outplants produced progeny that were detected using pedigree reconstruction. These are minimum estimates of fitness due to limited sampling of NOR adult recruits (i.e. putative progeny) in 2011-2012. By comparison, 29% of salmon outplants in 2009 produced at least one adult offspring, and among females, the limiting sex in 2009, 64% produced progeny.
3. For the 2009 cohort, female fitness was on average ~5× (2.72:0.52 progeny) that of males and fitness was highly variable among individuals (range: 0-20 progeny). Fitness estimates for other outplant cohorts are either heavily downwardly biased or preliminary due to incomplete sampling of progeny. In all years but 2007, there was a positive relationship between release date and fitness.
4. CRR, our index of the demographic viability of the outplant program, was 1.07 in 2009, as estimated from female replacement. However, when considering all outplanted salmon, the CRR was 0.54.
5. The N_b of the 2009 outplant cohort was 130.7 (95% C.I. = 123.4-138.6), leading to an N_b/N_c ratio of 0.17.

Outplant program contributions to NOR salmon recruitment to the North Santiam River

There were a number of issues that affected our ability to estimate outplant program contributions to NOR salmon production on the North Santiam River. First, in most years, some outplanted salmon were not tissue-sampled; for these individuals, we could not assign progeny. Second, Minto fish collection facility was not operational during 2011 and 2012. In these years, tissue samples from NOR salmon were collected primarily from carcasses and a small number of live salmon included in a disease challenge experiment. Carcasses represent only a subset of salmon recruits and are relatively difficult to genotype. Indeed, estimates of NOR salmon returns to Bennett Dam, located downstream of Minto (Figure 1), indicate that at least 1676 and 906 NOR salmon returned to the North Santiam River in 2011 and 2012, respectively (ODFW, unpublished data); ~200 (2011) and less than 100 (2012) NOR salmon were considered by our study as possible progeny.

Despite these limitations, our results indicate that most NOR spring Chinook salmon sampled in 2013 and 2014 were progeny of outplanted individuals. From these assignments, we were able to calculate an index of population productivity (CRR) for the 2009 cohort. This CRR, or the "number of spawners produced by a spawner", was less than one (0.54) when calculated for all outplants, indicating that adult offspring recruitment is not meeting population replacement. However, it is likely that the highly skewed male:female sex ratio (~6:1) limited reproductive opportunities for many outplanted males in 2009. Indeed, when calculated for females only, our CRR was almost twice that calculated for all salmon; 1.07.

The influence of skewed sex ratios on the reproductive success of male outplants was also apparent in our fitness estimates. The mean fitness of female outplants was more than 5× that of males, but the range of fitness values observed for male and female salmon was similar (males: 0-20 vs. females: 0-16 progeny), indicating that males who gained access to and spawned with females were as successful as the most successful females. Fitness estimates for salmon outplants in 2010 will provide some insight into reproductive performance and population productivity under a relatively even male:female sex ratio. While preliminary, estimates of fitness for the 2010 cohort already suggest that the sexes achieved similar fitness means, variances, and ranges. However, it will also be important to consider the influence of the higher breeding densities (i.e. larger outplant population) experienced by 2010 outplants, compared to in 2009, on population productivity.

Outplant program and spring Chinook salmon fitness

In addition to quantifying outplant contributions to subsequent NOR salmon recruitment to the North Santiam River, an objective of this study was to investigate how differing outplant protocols, including differences in release date and release location, influence fitness. Following a synthesis of data collected on spring Chinook salmon outplants, it was apparent that the release location was typically confounded by release date and/or not always recorded. Release date has previously been linked to fitness estimates in UWR spring Chinook salmon reintroduction programs (O'Malley et al. 2014). Thus, we had limited statistical ability to partition any effects of release location on fitness from date effects. Indeed, in this study, our analyses revealed a positive relationship between release date and fitness in all years but 2007. It is possible that this relationship is influenced by higher prespawn mortality (PSM) and consequent lower fitness of earlier compared to later outplants (Keefer et al. 2010) i.e. individuals outplanted at later dates represent a biased sample of a population that has already experienced a PSM "bottleneck".

Taken together, results from this study provide an important baseline for future investigations of the viability of salmon reintroductions above the Detroit-Big Cliff dam complex on the North Santiam River. With additional sampling in 2015, estimates of cohort replacement, total lifetime fitness, and N_b will be possible for the 2010 cohort, which comprised the largest release of HOR fish above Detroit Dam since tissue sampling of outplanted salmon was initiated.

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APPENDICES

Table A1. Polymorphism observed at 12 microsatellite loci used in genetic parentage analysis of spring Chinook salmon from the North Santiam River, Oregon. As a representation of the exclusion power of the loci, shown are the number of alleles (K) and polymorphic information criterion (PIC) observed per locus in salmon outplanted above Detroit Dam during 2007-2009, putative parents of salmon recruiting to the North Santiam in the subsequent years, 2010-2014. Non-exclusion probabilities (i.e. the probability of ambiguous assignments to parents) were calculated for the identification of individual parents (parent 1=NE-1P, parent 2=NE-2P) and parent pairs (NE-Pair), and the sequential cumulative (Cum.) non-exclusion probabilities across loci are shown, as calculated in CERVUS (Kalinowski et al. 2007).

Locus	K	PIC	NE-1P	Cum. NE-1P	NE-2P	Cum. NE-2P	NE-Pair	Cum NE-Pair
Ots211	24	0.912	0.283	0.283	0.165	0.165	0.044	0.044
OtsG409	51	0.945	0.190	0.053	0.106	0.017	0.019	0.001
Ots215	32	0.926	0.242	0.013	0.138	0.002	0.031	2.59E-05
Ots515	15	0.848	0.429	0.006	0.272	0.001	0.108	2.80E-06
Ots201	24	0.907	0.297	0.002	0.174	0.001	0.049	1.37E-07
Ogo2	15	0.785	0.542	0.001	0.367	4.19E-05	0.184	2.52E-08
Ssa408	27	0.906	0.298	0.001	0.175	7.34E-06	0.049	1.24E-09
OtsG249	36	0.942	0.200	5.36E-05	0.111	8.14E-07	0.021	2.60E-11
Ots212	21	0.873	0.379	2.03E-05	0.233	1.90E-07	0.084	2.18E-12
OtsG474	11	0.730	0.622	1.26E-05	0.441	8.37E-08	0.248	5.41E-13
Ogo4	13	0.662	0.698	8.81E-06	0.527	4.41E-08	0.34	1.84E-13
OtsG311	48	0.958	0.151	1.33E-06	0.082	3.62E-09	0.012	2.21E-15

Table A2. Heterozygosity (genetic variation) at 12 microsatellite loci used in genetic parentage analysis of spring Chinook salmon from the North Santiam River, Oregon. For each locus and year, the observed and expected proportion of heterozygotes (H_O and H_E, respectively) is indicated. Shown in bold are loci that exhibited significantly ($P < 0.05$) lower H_O than expected, according to Hardy-Weinberg exact tests conducted in Genepop v.4.2

	2007		2008		2009		2010		2011		2012		2013		2014	
Locus	H_O	H_E	H_O	H_E	H_O	H_E	H_O	H_E	H_O	H_E	H_O	H_E	H_O	H_E	H_O	H_E
Ots211	0.92	0.91	0.93	0.93	0.91	0.92	0.92	0.92	0.92	0.92	0.95	0.91	0.92	0.92	0.91	0.92
OtsG409	0.94	0.95	0.97	0.95	**0.94**	**0.95**	**0.94**	**0.95**	0.97	0.95	0.94	0.95	0.94	0.94	0.95	0.95
Ots215	0.93	0.93	0.92	0.94	0.91	0.93	0.93	0.93	**0.89**	**0.94**	0.92	0.94	0.91	0.94	0.94	0.94
Ots515	0.87	0.86	0.87	0.85	0.84	0.86	0.86	0.86	0.86	0.86	0.84	0.86	0.88	0.87	0.88	0.87
Ots201	0.91	0.91	0.89	0.91	0.91	0.92	0.90	0.91	0.93	0.92	0.89	0.90	0.93	0.91	0.92	0.92
Ogo2	0.82	0.82	0.72	0.77	0.85	0.81	0.82	0.82	0.80	0.81	0.82	0.81	**0.75**	**0.80**	0.81	0.81
Ssa408	0.91	0.91	0.90	0.91	0.92	0.90	0.91	0.91	0.86	0.91	0.89	0.90	0.92	0.91	0.92	0.91
OtsG249	0.93	0.95	0.97	0.95	0.94	0.94	0.94	0.95	0.95	0.94	0.92	0.95	0.94	0.94	0.95	0.95
Ots212	0.88	0.89	0.92	0.88	0.88	0.87	0.88	0.89	0.89	0.89	0.82	0.87	0.92	0.89	**0.87**	**0.89**
OtsG474	0.78	0.75	0.81	0.76	0.74	0.77	0.75	0.76	0.75	0.77	0.80	0.74	0.79	0.77	0.77	0.76
Ogo4	0.70	0.71	0.73	0.71	0.74	0.71	0.72	0.70	0.76	0.74	0.73	0.73	0.70	0.70	0.72	0.72
OtsG311	0.95	0.96	0.95	0.96	0.95	0.96	0.97	0.96	0.94	0.96	0.99	0.96	0.96	0.96	0.96	0.96