A genetics-based evaluation of the spring Chinook salmon reintroduction program above Cougar Dam, South Fork McKenzie River, 2007-2013

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List of Acronyms

- **AIC –** Akaike information criterion
- **CI –** Confidence interval
- **CRR –** Cohort replacement rate
- **LSDR –** Late season downstream release
- **ESA –** Endangered Species Act
- **FDR –** False discovery rate
- **GLM –** Generalized linear model
- **GLMM –** Generalized linear mixed-effects model
- **HCR –** Head of Cougar Reservoir
- **HOR –** Hatchery origin
- **HWE –** Hardy-Weinberg equilibrium
- **LE** – Linkage equilibrium
- **LOD –** Likelihood-odds ratio
- N_e **–** Effective population size
- **NOR –** Natural origin
- **ODFW –** Oregon Department of Fish and Wildlife
- **PCR –** Polymerase chain reaction
- **POPs –** Parent-offspring pairs
- **RET –** Reservoir entrance timing
- **RO –** Regulating outlet
- **RRS –** Relative reproductive success
- **RS –** Reproductive success
- **TLF –** Total lifetime fitness
- **TR –** Tail race

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Summary

Spring Chinook salmon (*Oncorhynchus tshawytscha*), hereafter Chinook, in the Upper Willamette River are listed as threatened under the U.S. Endangered Species Act. Dams have contributed to the species' decline because, in part, they block access to historical spawning habitat. Reintroduction of Chinook above Willamette River dams has been identified as a necessary step for population recovery.

On the South Fork McKenzie River, Chinook have been reintroduced above Cougar Dam since 1993. We have evaluated the efficacy of the reintroduction since 2007 using genetic techniques. From 2007-2009 only hatchery origin (HOR) Chinook were outplanted, but since 2010 natural origin (NOR) Chinook have also been collected at a trap and haul facility, hereafter Cougar Trap, and transported above the dam. We have genotyped nearly all Chinook released above Cougar Dam since 2007 at 11 highly variable microsatellites and used genetic pedigree methods to identify parent-offspring relationships between reintroduced Chinook with adult fish returning to the Cougar Trap, as well as juveniles emigrating to Cougar Reservoir.

We found that most of the NOR adult returns to the Cougar Trap in 2012 (64%) and 2013 (68%) were produced by fish previously released above the dam. Furthermore, the percentage of Chinook produced above Cougar Dam that returned before September 1st was high for both 2012 (85.2%) and 2013 (86.8%), whereas after that date it was relatively low (21.3% and 20.3%, respectively). Managers anticipated this result in 2013, and implemented a process we refer to as the late season downstream release (LSDR) method, which was intended to prevent transportation of NOR Chinook that were not produced above Cougar Dam. After September 1st, 2013 a total of 64 Chinook would have been released above the dam, of which 51 were not produced by adults previously reintroduced. The implementation of the LSDR method resulted in only 7 NOR Chinook being transported that were not produced above the dam after September 1st.

Our approach enabled us to evaluate management strategies associated with reproductive success (RS) and total lifetime fitness (TLF). We found that *release date* had a small negative relationship with TLF. However, we found a positive relationship between *release date* and RS for females. *Release location* did not significantly explained variation in RS or TLF. In both 2010 and 2011, we tested for RS differences between HOR and NOR Chinook. In 2010, we found that mean RS for NOR males was 2.1 times that of HOR males. However, we found no difference in RS between HOR and NOR females (p=0.16). In 2011, we found that mean RS for NOR Chinook was 1.4 times that of HOR Chinook. However, the effect of *origin* on RS was not significant (p=0.398) after accounting for variation explained by Chinook *length* in 2011. In 2008 we were able to compare RS and TLF estimates for the same adults, and we found that RS explained only 25.7% of the variation in TLF (p<0.001).

We estimated two demographic parameters, cohort replacement rate (CRR) and effective population size (N_e). We found that neither the 2007 or 2008 adult cohort replaced itself through adult recruitment to the Cougar Trap (CRR: 0.41 and 0.31, respectively). We found that N_e varied little between 2007 (185, CI_J: 169-203) and 2008 (184, CI_J: 169-204). Our estimates of N_e suggest that the risk of extinction from inbreeding depression was low for Chinook released above Cougar Dam.

Based on our findings we recommend that the LSDR method be used in future years because it effectively reduced the number of NOR Chinook that were not progeny of reintroduced adults from being released above the dam in 2013, while providing passage for most late-season adults produced above the dam. Because RS did not explain 74.3% of TLF variation, some conclusions regarding effects from alternate outplanting strategies may be subject to change in light of forthcoming TLF data. Thus, we recommend continued genetic analyses of NOR adults that return to the Cougar Trap, as this will be necessary to determine if HOR/NOR fitness differences exist as measured through adult returns. Such analyses would also provide CRR estimates for years in which both HOR and NOR Chinook were

reintroduced. Thus, adult-adult pedigree results in future years will provide managers with valuable information regarding the Chinook reintroduction.

Introduction

Upper Willamette River spring Chinook salmon (*Oncorhynchus tshawytscha*), hereafter Chinook, are listed as threatened under the U.S. Endangered Species Act (ESA)(NMFS 1999; NMFS 2005). The construction and operation of high-head dams on all major tributaries of the basin has contributed to the species' decline and subsequent ESA listing (NMFS 2008). These dams have impeded adult migration to most historical spawning habitat (ODFW 2005), as well as altered water temperature and flow regimes in the system (Sheer and Steel 2006). When the dams were initially built, hatcheries were viewed as a sufficient means to mitigate adverse effects on salmonid populations and maintain popular fisheries. However, recently mangers have begun to reintroduce Chinook to historical habitat above dams to aid in their recovery (NMFS 2008).

Among the major upper Willamette tributaries, the McKenzie River typically supports the highest proportion of unmarked Chinook returns (Johnson and Friesen 2010) despite the presence of several dams in the system, including Cougar Dam. Construction of this dam was completed in 1964 and it blocks access to 40 kilometers of historical spawning habitat. Following its construction, initial attempts to release Chinook above the dam were terminated because of poor numbers of adults returning to spawn. It wasn't until 1993 that hatchery origin (HOR) Chinook were released above the dam again to provide threatened bull trout (*Salvelinus confluentus*) with prey. Outplanting of sexually mature HOR Chinook has occurred annually since 1995. Anecdotal evidence suggested that some Chinook offspring successfully emigrated through Cougar Dam and returned as unmarked adults in subsequent years. Following the construction of a trap and haul facility at the base of the dam in 2010, hereafter Cougar Trap, natural origin (NOR) Chinook were also transported and released above the dam.

We have evaluated the reintroduction of Chinook above Cougar Dam since 2007 using genetic techniques because information derived from such data can be used to estimate many parameters relevant to mangers (De Barba et al. 2010; Schwartz et al. 2007; Vonholdt et al. 2008). We assembled pedigrees of naturally spawning fish using genetics-based parentage techniques, which enable us to estimate two measures of fitness: reproductive success (RS) assessed from juveniles and total lifetime fitness (TLF) assessed from adult returns. We measure RS through the number of fry, from a population sample, that assign to adults released above the dam in the previous year. We define TLF as the number of adult NOR Chinook returning to the Cougar Trap that assign to an adult released above the dam 3-6 years prior. We also used our data to estimate two demographic parameters, cohort replacement rate (CRR) and effective population size (N_e). Information produced by our research is relevant to several Reasonable and Prudent Alternatives identified in the Willamette Biological Opinion (NMFS 2008):

- 9.4.1 - Restoration of productivity by outplanting Chinook above dams
- 9.3 - Monitoring effectiveness of fish passage facilities
- 9.4.7 - Increase percent HOR that successfully spawn by developing new release locations
- 9.4.10 - Assess downstream juvenile fish passage through reservoir
- 9.9.5.1(4) - Estimate RS of HOR Chinook in wild
- 9.6.1.5 - Management of HOR Chinook upstream of Cougar Dam
- 9.6.2.3 - Continued adult Chinook outplanting, Willamette basin-wide

Here we report which factors associated with release strategies significantly explained variation in our estimates of fitness. We also tested for differences in RS between HOR and NOR Chinook, and evaluated the relationship between RS and TLF estimates for the 2008 adult cohort. Furthermore, we

assessed the efficacy of the late season downstream release (LSDR) method employed in 2013, which was intended to limit the number of NOR Chinook that were not produced above the dam, hereafter non-Cougar adult returns, from being transported above it. Finally, we assessed variation in CRR and N_e from 2007 to 2008 adult cohorts.

Methods

Study area

Construction of the 158 meter tall Cougar Dam was completed in 1964 on the South Fork McKenzie River, Oregon (Figure 1). Adult HOR Chinook that returned to the McKenzie River Hatchery, located on the mainstem McKenzie River (44°07),44"N 122°14'25"W have been released above Cougar Dam since 1993 (Figure 2). HOR Chinook (n=39) from Leaburg Hatchery (44° 8'8.63"N, 122°36'32.32"W) were also outplanted in 2009. HOR Chinook may have been held at one of these hatcheries for a period of time before release. Since July 28th, 2010, the Cougar Trap has been used to collect returning NOR Chinook at the base of the dam. These fish were subsequently released above the reservoir (Figure 2). Each year the Cougar Trap was operational throughout the Chinook spawning migration, however from July 19th to August 6th, 2011 it was closed due to technical issues.

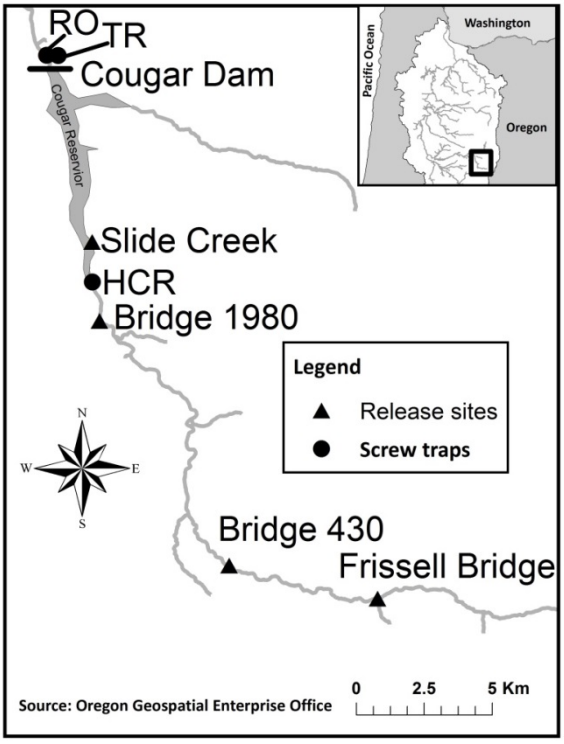

Figure 1. Cougar Dam, represented by the solid black horizontal line, is located on the South Fork McKenzie River, Oregon. Locations of adult Chinook release sites, as well as the head of Cougar Reservoir (HCR), regulating outlet (RO), and tailrace (TR) screw traps used to collect juveniles are indicated.

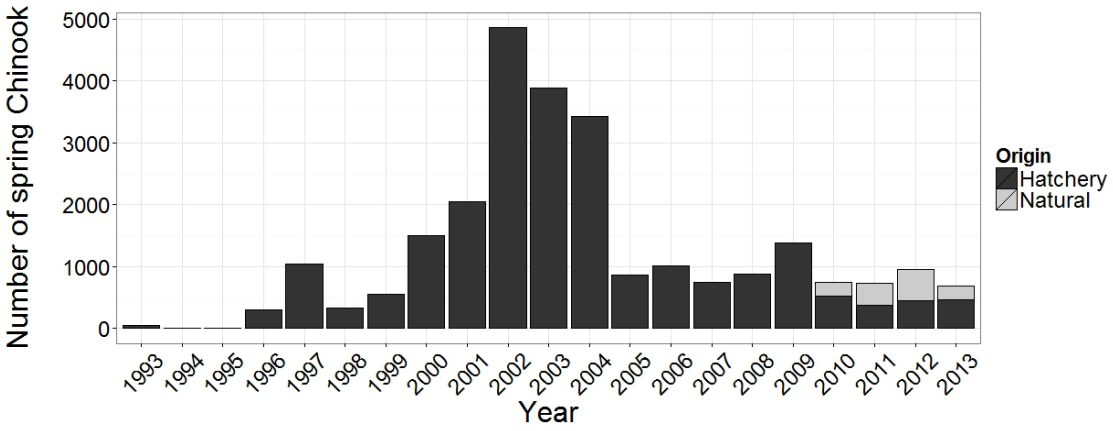

Figure 2. Number of Chinook released above Cougar Dam since 1993, origin is indicated in legend.

Data collection

Sampling for genetic analysis

Tissue samples intended for molecular parentage analysis have been collected from nearly all adult Chinook (99.95%) released above Cougar Dam since 2007. All samples were preserved in 95% ethanol prior to DNA extraction. The release location, release date, origin (HOR/NOR), and sex, determined by visual assessment of secondary sexual characteristics, were recorded for each adult. From 2011-2013, scales from NOR Chinook collected at the Cougar Trap were sampled, and fork length, hereafter length, (cm) recorded for both HOR and NOR Chinook.

From 2009-2012 unmarked fry were sampled in screw traps at the head of Cougar reservoir, the tailrace of Cougar Dam, and the regulating outlet spillway (HCR, TR, and RO, respectively; Figure 1). Each sampling day the date and number of juveniles collected were recorded. Up to 100 fry had tissue samples collected and stored on coffee filter paper each sampling day. Traps operated at 4% efficiency based on mark-recapture tests (M. Hogansen, unpublished data).

Genotyping

Total genomic DNA was isolated (Ivanova et al. 2006) from all adults, and a subset of juveniles each year. DNA samples were amplified at 11 highly polymorphic microsatellites using polymerase chain reaction (PCR): *Ots201, Ots208b, Ots209, Ots211, Ots212, Ots215, Ots249, Ots253, Ots311, Ots409,* and *Ots515* (Banks et al. 1999; Greig et al. 2003; Naish and Park 2002; Williamson et al. 2002). Brunelli et al. (2008) found that the sex-linked marker *Oty3* can correctly identify sex of Willamette River Chinook. Accordingly, we used this marker to determine the sex of adult Chinook and compared these results to those from phenotypic assessments. All PCR products were visualized on an ABI 3730XL DNA Analyzer (Applied Biosystems, Inc., Foster City, CA), and scored using GeneMapper software (Applied Biosystems, Inc., Foster City, CA).

We estimated genotyping error by repeating our genotyping procedure described above with adults and juveniles randomly sampled from each year (n=194). Re-processed genotypes were compared to original data, and error was calculated as the number of alleles that did not match divided by the total number rescored. We performed all genetic analyses in the Marine Fisheries Genetics Laboratory at the Hatfield Marine Science Center, Newport, Oregon.

Data analysis

Population genetics and parentage assignment power

Initially, we calculated the mean percent of individuals genotyped at each marker. Genetic variation was assessed by calculating the mean number of alleles per locus, as well as observed and expected heterozygosity (Nei 1987). We tested for deviations from Hardy-Weinberg Equilibrium (HWE) with exact tests, and linkage equilibrium (LE) in GENEPOP (Raymond and Rousset 1995; Rousset 2008) following Bonferroni corrections (α=0.05).

We assessed the power of our microsatellites to correctly infer parent-offspring pairs (POPs) by calculating average non-exclusion probabilities for a random single parent, a second parent, and a parent-pair assigning to any given offspring by chance (Jamieson and Taylor 1997), as well as the expected number of false POPs (Christie 2010) with 0, 1, or 2 mismatching loci.

Genetic pedigree assignments

Adults

NOR Chinook returning to the Cougar Trap in 2010-2013 were assigned to parents released in 2007-2010, because Willamette River Chinook typically spawn at age-4 and -5, with few age-3 and -6 returns. For each return year of adult NOR Chinook (2010-2013), we attempted to assign offspring to parents reintroduced 3-6 years prior (Figure 3). We performed separate parentage analyses for each potential pair of parent-offspring run years.

We identified POPs using CERVUS (Kalinowski et al. 2007; Marshall et al. 1998). CERVUS's likelihood approach simulates genetic data comparable to the given system when estimating log-likelihood statistics (LOD) and Δ scores, which are then used to assess confidence in assignments. Our simulations used the default setting for offspring (n=10,000), and the number of male and female adults in the actual datasets being analyzed. We set the proportion sampled for each sex to 98%, given that nearly all adults were sampled for genetic analysis. Finally, genotyping error was set to 2% as estimated using the procedure described above. We accepted all POPs with ≤1 genotypic mismatch based on our power analysis. Any adult offspring that were assigned to only a single parent using our assignment criteria were also included in pedigrees.

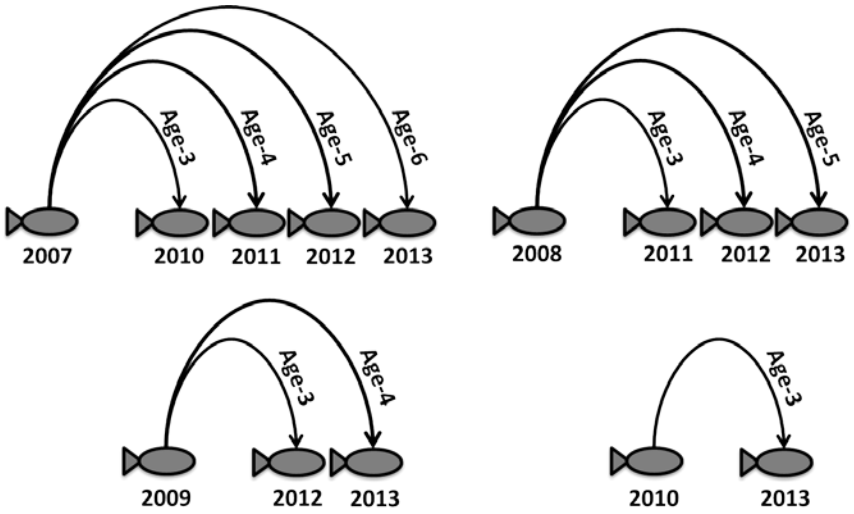

Figure 3. Reintroduced Chinook from 2007-2010 were assigned as parents to possible age-3 to -6 NOR adult offspring returning to the Cougar Trap. Return ages are indicated.

Juveniles

Most juvenile Chinook above Cougar Dam emigrate from headwater streams toward the reservoir as subyearlings (Romer et al. 2011). We therefore assigned reintroduced adults from 2008-2011 as parents to fry sampled in screw traps from 2009-2012 (Figure 4). Full- and half-sibling families are likely overrepresented in our samples of fry, due to a phenomenon known as the Allendorf-Phelps effect, because we sampled a small proportion of the juvenile cohort each year (Allendorf and Phelps 1981; Waples 1998). This effect often results in many loci deviating from HWE, which can affect parentage assignments. We therefore used the Bayes' method in SOLOMON to assign parents to juvenile offspring, because the only assumption of this method is that loci are unlinked (Christie et al. 2013). We assigned parents to offspring using the default settings - 1000 simulated datasets and 50,000,000 genotypes. In addition, we reduced the number of pairwise comparisons by assigning potential mothers and fathers to offspring separately.

Based on our power analysis, as well as Bayesian priors (Pr(Φ)) calculated for each run, we accepted all POPs with ≤1 genotypic mismatch. Among these POPs, we only accepted those that had a Bayes' posterior probability of assignment by chance <0.05 (Christie et al. 2013). Our preliminary analysis identified 11.9 ± 5.6% of offspring assigned to more than one parent of the same sex after parsing the data using criteria described above. With comparable simulated data (800 parents, 2000 offspring, and 11 microsatellites with 35 alleles per locus), we estimated that in 80% of these cases the true parent could be selected by choosing the POP with the lowest posterior probability. We therefore used this criterion when parsing SOLOMON output.

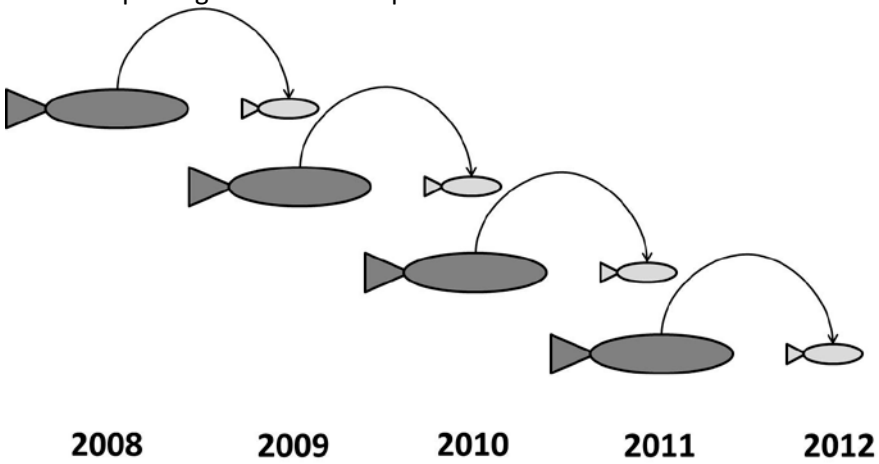

Figure 4. From 2008-2011 adults reintroduced above Cougar Dam were assigned as parents to juvenile fry sampled in the following year.

Biology of Reintroduced Chinook Offspring

Adults

We focused our analysis on 2012 and 2013 NOR returns, as we have sampled nearly every anadromous parent that could have produced Chinook above Cougar Dam. Initially, we tested if mean NOR *return date* differed between the sexes using an ANOVA to account for variation between years. We used *post-hoc t*-tests with False Discovery Rate (FDR) corrections (Benjamini and Hochberg 1995) to evaluate mean return time differences between males and females each year.

NOR Chinook typically return to the Cougar Trap bimodally, before and after September 1st (Cannon et al. 2010), hereafter referred to as early and late returns. We assessed if the proportion of early and late returns differed in assignment rates within each year (2012-2013) with Fisher Exact tests, after FDR corrections. In addition, we evaluated the relationship between NOR Chinook assigning to a

reintroduced parent (No- 0, Yes -1) and *return date* using logistic regression, after accounting for inter-annual variation. We also used Fisher Exact tests to determine if the proportion of NOR Chinook that assigned differed between males and females.

In 2013, managers attempted to limit the number of non-Cougar adult returns transported above the dam by double floy tagging all Chinook collected at the Cougar Trap after September 1st, then releasing these fish back into the McKenzie River below the confluence of the main stem and the south fork. All floy-tagged Chinook that returned to the Cougar trap were then transported above the dam. Collectively, we refer to these actions as the LSDR method.

Juveniles

For each adult-juvenile pedigree, we calculated the proportion of offspring that assigned to a mother and a father, only a mother, only a father, and no parents each year. Given the design of our study, we expected that most sampled fry would assign to reintroduced parents. We expected some fry would have missing fathers because precocial parr were not sampled. We tested if the proportion of offspring only assigning to a mother differed from those that assigned only to fathers, among years, using a Paired Wilcoxon Rank Sums test.

Fry were collected both above and below the dam. We tested whether the overall proportion of offspring that did or did not assign to a reintroduced adult differed between the three screw traps using Fisher's Exact tests (FDR corrected).

Juvenile Emigration timing

We used the sampling date (Julian date) of juvenile fry collected in the HCR screw trap as a proxy for reservoir entrance timing (RET). After accounting for interannual variation in 2010 and 2011, we evaluated differences in mean RET among juveniles produced by φ_{HOR}/ σ_{HOR}, φ_{HOR}/ σ_{NOR}, φ_{NOR}/ σ_{HOR}, and φ_{NOR}/ σ_{NOR} mate pairs using a repeated measures ANOVA in the R package *nlme* (Pinheiro et al. 2007). We accounted for variation among juveniles produced by the same mother, and therefore residing in the same redd, by using mother ID as a random effects variable. The scope of inference from our mate pair analysis was limited to offspring that assigned to both parents, though this will not affect the analysis as the majority of fry assigned to both parents. We used *post-hoc t*-tests with FDR corrections to evaluate mean RET differences among mate pair types within each year.

Release effects

Total lifetime fitness – Inference from adults

We estimated TLF by counting the number of NOR Chinook that assigned to adults released above Cougar Dam in 2007 and 2008. We included *release date* as a numeric predictor in our analysis. *Sex* and *year* were included as factors, whereby females and the year 2007 were treated as references. We also included *release location* as a factor, but collapsed our data to represent "lower" (≤18.5 river Kilometer, rKm) and "upper" (>18.5 rKm) river release site, because Chinook were not consistently released in the same locations in both years. We accounted for similarities among Chinook reintroduced on the same date and at the same location with a random effects variable, *release group*.

We tested for significant effects from each explanatory variable and all first-order interactions terms on TLF using a negative binomial regression that accounted for *release group* effects. We included all significant variables in a generalized linear mixed model (GLMM) in the R package *lme4* (Bates et al. 2013), and used backwards Akaike Information Criterion (AIC) model selection (Akaike 1974) to identify an adequate model to explain TLF variation.

Reproductive success – Inference from juveniles

We estimated RS by enumerating juveniles that assigned to adults released from 2008 to 2011. We evaluated effects from *release date*, *year*, and *release location* on RS with a GLMM approach similar to that used to assess TLF variation, except that in our analysis of RS, 2008 was treated as the reference year. We evaluated if *release location* significantly explained variation in RS for each year separately, because adults were not consistently released in the same locations throughout the study. In particular, Chinook were released in a single location in 2011, and therefore a simplification to "lower" and "upper" as we did for the TLF analysis could not resolve the issue because of inconsistent *release locations*.

In 2010 and 2011, both HOR and NOR Chinook were released above Cougar Dam. For each year, we evaluated the effect of *origin* (HOR/NOR) on RS using the same GLMM approach as used with the TLF estimates, with the addition of the predictor *origin*, whereby HOR was the reference. In the 2011 analysis we also included *length* for each reintroduced adult as a numeric predictor. However, we did not include the *release group* random effects variable because Chinook were released in a single location that year. As a result, the analysis was performed using generalized linear model (GLM) with a negative binomial distribution.

We tested if *length* differed among HOR and NOR reintroduced adults in 2011 using *a two-way ANOVA* because length has been shown to be important for RS in salmonids (Berejikian et al. 2000; Berejikian et al. 1997; Fleming and Gross 1993; Schroder et al. 2008). We evaluated if *origin*, *sex*, or the *sex*origin* interaction significantly explained variation in *length*. HOR Chinook and females were considered the references for *origin* and *sex*.

Araki and Blouin (2005) noted that assignment error can bias comparisons of RS between two groups using relative reproductive success (RRS) permutation tests. There are two general types of assignment errors: 1) not assigning an offspring to the true parent (Type A error) and 2) assigning an offspring to an incorrect parent (Type B error). Both of these errors can bias RRS to 1 when both are high, though Type A error more strongly affects RRS because it increases mean RS and decreases individual absolute fitness (Araki and Blouin 2005). To account for biases associated with Type A and B error, Araki and Blouin (2005) developed an unbiased RRS statistic. Therefore as an alternative to our regression approach above, we evaluated RRS between HOR and NOR Chinook using these methods described in Araki and Blouin (2005). Briefly, we used a permutation procedure to create 10,000 random RRS values based on our estimates of RS for each adult. We then compared the observed RRS value, after accounting for missing parents and assignment error (Araki and Blouin 2005) to the random RRS values. We determined significance by calculating the proportion of random RRS values less than that observed. We compared mean RS differences between HOR and NOR Chinook for each sex separately, and for the sexes combined in each year. We also evaluated HOR and NOR overall RS differences, independent of year, for each sex and sexes combined. All significance values were FDR corrected.

The RRS test requires RS estimates for individuals in each group, the total number of offspring, number of assigned offspring, and number of parents; Equation 14 from Araki and Blouin (2005). Type B error must also be estimated (Equation 1), which was defined as the rate a false parent assigned to offspring when the true parent was not present in the dataset (Araki and Blouin 2005). We empirically estimated type B error by assigning fry emigrating to the Cougar Reservoir to adults reintroduced in the same year, e.g. 2010 adults assigned to 2010 fry, because the adult cohort could not have produced those offspring. Type B error was calculated as the number of offspring that assigned to a parent divided by the total number of offspring.

$$RRS_{unbiased} = \frac{\widehat{W}_x - \left(\frac{N_{offspring} - N_{assigned}}{N_{parent}}\right)\left(\frac{\widehat{b}}{1-\widehat{b}}\right)}{\widehat{W}_y - \left(\frac{N_{offspring} - N_{assigned}}{N_{parent}}\right)\left(\frac{\widehat{b}}{1-\widehat{b}}\right)} \quad \text{(eqn 1)}$$

Equation 1. An estimator for unbiased relative reproductive success (RRS) (Araki and Blouin 2005).

Testing for a relationship between reproductive success and total lifetime fitness

We estimated both RS and TLF for 2008 adults, which enabled us to evaluate the relationship between them using negative binomial regression. We estimated D^2 (Guisan and Zimmermann 2000), which was used to describe the amount of TLF variation explained by RS using the output from the regression - null and residual deviance.

Demography

Population viability metrics

We estimated CRR and N_e from our genetic pedigrees. We defined CRR as the number of NOR progeny returning to the Cougar Trap divided by the total number of adults in the cohort that produced them. We estimated CRR for 2007 and 2008 adults, as the majority of their progeny have returned. In addition, we only used females in our calculations because the sex ratio was male biased in both years.

We employed methods developed by Waples and Do (2008) to estimate N_e for 2007 and 2008 adult cohorts with NeEstimator V2.0 (Do et al. 2014). We used genotypes from 2010-2013 progeny produced by 2007 and 2008 adults when estimating N_e. We report Jackknifed 95% confidence internals (CI_J), as parametric 95% confidence intervals were found to be too narrow when estimating this parameter based on simulation results (Waples and Do 2008).

Adult age estimates

We provided scale samples from 2011-2013 NOR Chinook returning the Cougar Trap to the Oregon Department of Fish and Wildlife (ODFW) Fish Life History Analysis Project to estimate the total age and juvenile life history (i.e. reservoir or river reared, and age at ocean entry) using standardized protocols (Clemens et al. *In prep*).We evaluated discordance between age estimates from scales and genetic pedigrees using logistic regression (0-agreement, 1-disagreement). We limited the scope of our analysis to only NOR Chinook that had age estimates from both scales and genetic pedigrees in 2012 and 2013. We tested if the odds of discordance could be explained by errors associated with genetic pedigree metrics, which included average number of mismatching loci (*avg.mm*), average LOD score for parent(s), (*avg.LOD*), and the number of parents that assigned,1 or 2 (*n.Parent*). Some scales were more difficult to score than others, coded as 0- acceptable, 1-diffciult (*scale.diff*), which we also evaluated in our analysis. We included year as a factor to account for variation between years. Finally, we tested if metrics associated with Chinook life history could explain variation in discordance. We included the age at ocean entry (*ocean.entry*), length (*length*), and the return date (*return.timing*). Each of the variables described above was tested individually to determine if it significantly explained the odds of discordance. We included all significant variables in a single logistic regression, and used backwards AIC model selection to determine an adequate model to explain discordance.

Sex identification

Before being released above Cougar Dam, adult Chinook from 2007-2013 were classified as male or female, based on secondary sexual (phenotypic) characteristics. In the laboratory we genotyped each adult at *Oty3* to determine the genetic sex of each individual. Chinook that arrive early to the Cougar Trap often do not present recognizable secondary sexual characteristics. We therefore used logistic regression to test if *release date* explained the odds of discordance, between the two methods, accounting for variation among years.

All analyses were performed using R unless otherwise stated (R Core Team 2014). General data analysis was aided by the use of *plyr* (Wickham 2011) and *reshape2* (Wickham 2007). Data were visualized using *ggplot2* (Wickham 2009).

Results

Data Summary

Adults

Since 2007 the number of Chinook passed above Cougar Dam averaged 811 ± 128 (± standard deviation), and in every year, except for 2013, the sex ratio (male/female) has been male biased (1.41 ± 0.38; Table 1). From 2010-2013 the number of NOR Chinook passed above the dam has ranged from 191 to 484 (Table 1). Some HOR Chinook (17-30) collected in the Cougar Trap have been released above the dam as well (Table 1).

Table 1. The number of Chinook that were collected at a hatchery or the Cougar Trap and released above Cougar Dam, 2007-2013. Sex ratio (male/female) is also indicated.

Year	Hatchery		Cougar Trap		Total	Sex ratio
	McKenzie	Leaburg	Hatchery	Natural origin		
2007	746	0	0	0	746	1.35
2008	873	0	0	0	873	2.03
2009	1347	39	0	0	1386	1.29
2010	527	0	30	191	748	1.81
2011	374	0	30	327	731	1.26
2012	447	0	17	484	948	1.16
2013	464	0	22	201	687	0.96

Juveniles

ODFW has trapped emigrating juveniles (11,548 ± 10,419) each year since 2009, and the annual number of fish sampled for genetics from this effort ranged from 3,841 to 4,870 (Figure 5). On average we genotyped 2,094 ± 112 juveniles each year to estimate RS for parents reintroduced the previous year (Figure 5).

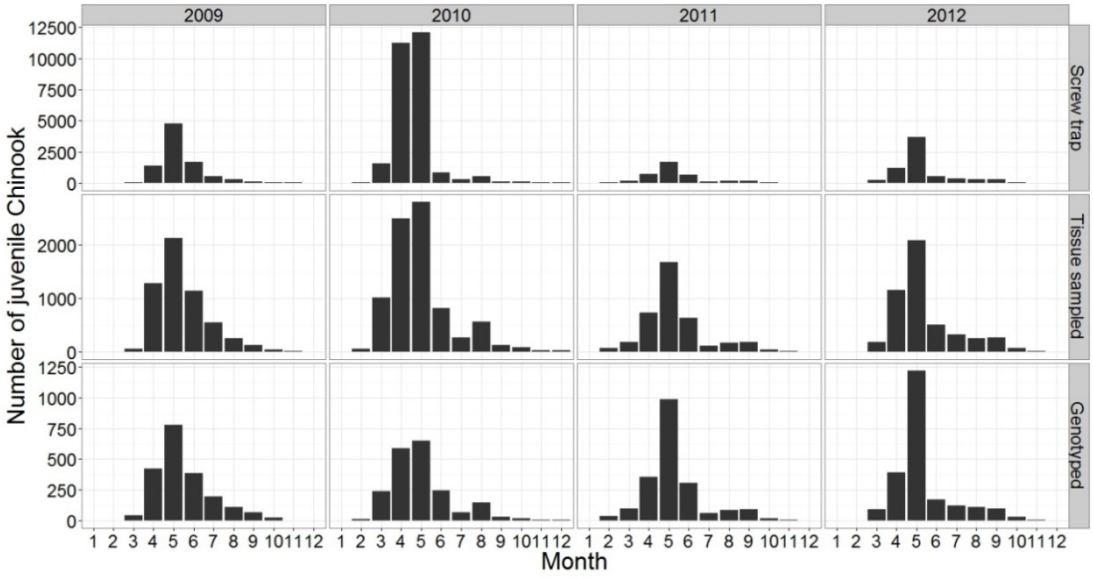

Figure 5. A summary of the number of juvenile Chinook collected by month in screw traps, sampled for genetic analysis, and genotyped, 2009-2012.

Population genetics and parentage assignment power

In total we genotyped 14,321 (n_{adults}=5,677; $n_{juveniles}$=8,644) Chinook for parentage analysis and had complete genotypes for 99.8 ± 0.24% of samples in each cohort (Table 2). We estimated our genotyping error at 2.3%. Our estimates for observed (0.92 ± 0.01) and expected heterozygosity (0.92 ± 0.01), as well as the mean number of alleles per locus (33 ± 1.79) were high and varied little among years (Table 2).

Table 2. Summary of genetic variation observed among adult and juvenile Chinook. The mean number of alleles per locus (K), observed heterozygosity (H_o), expected heterozygosity (H_e), and percent genotyped per locus are presented.

Year	Type	N	K	H_e	H_o	Percent genotyped
2007	Adult	746	33.6	0.93	0.91	99.7
2008	Adult	873	33.3	0.93	0.92	100.0
2009	Adult	1386	35.1	0.93	0.92	99.6
2010	Adult	748	34.3	0.93	0.93	99.4
2011	Adult	731	35.2	0.93	0.92	99.3
2012	Adult	948	36.2	0.93	0.92	99.9
2013	Adult[a]	245	29.7	0.93	0.92	100.0
2009	Juvenile	2056	31.7	0.92	0.91	100.0
2010	Juvenile	2246	34.8	0.92	0.92	99.8
2011	Juvenile	2077	34.4	0.92	0.92	100.0
2012	Juvenile	2265	33.5	0.92	0.91	99.8

[a] Only NOR adults sampled at the Cougar Trap are currently genotyped

The number of loci deviating from HWE was high for 2007-2009 adult cohorts. However, subsequent cohorts had fewer deviations (Figure 6). Additional investigation identified that the loci deviating from HWE were observed more often among HOR Chinook within each cohort (Figure 6, 7). We observed a similar trend in deviations from LE between HOR and NOR Chinook (Figure 6, 7). As expected, deviations from HWE and LE were high for all samples of juveniles (Figure 6), presumably due to family structure within our collection.

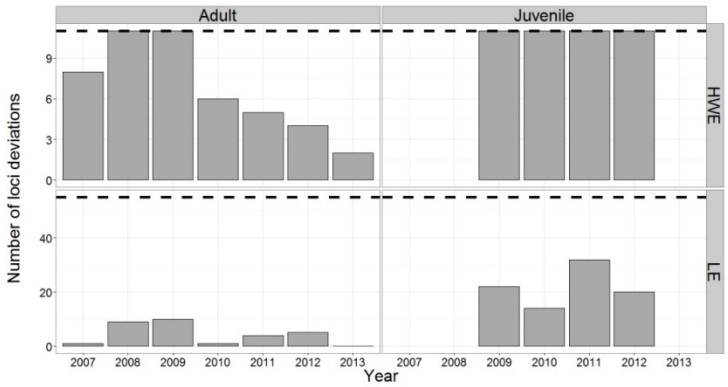

Figure 6. Number of loci deviating from Hardy-Weinberg Equilibrium (HWE) and pairwise comparisons among loci deviating from Linkage Equilibrium (LE) for adult and juvenile Chinook

sampled in 2007-2013. Juveniles were not sampled in 2007 and 2008. Horizontal dashed lines denote the maximum number of deviations possible for HWE (11) and LE (55) tests.

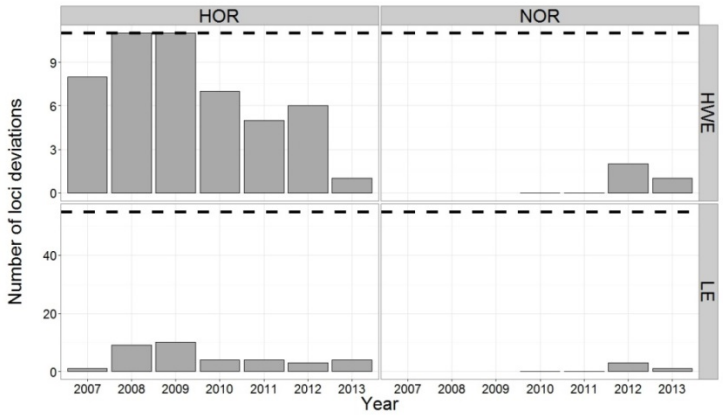

Figure 7. Number of loci deviating from Hardy-Weinberg Equilibrium (HWE) and pairwise comparisons among loci deviating from Linkage Equilibrium (LE) for hatchery and natural origin (HOR and NOR, respectively) adults sampled in 2007-2013. NOR adults were not sampled in 2007-2009. Horizontal dashed lines denote the maximum number of deviations possible for HWE (11) and LE (55) tests.

Overall we found that the microsatellites used in our study provided the high statistical power needed to correctly resolve parentage, as reflected in low non-exclusion probabilities for a single parent, a second parent, and a parent pair (Table 3). In addition, the expected number of false POPs was low when the parent and offspring matched all loci (0.21 ± 0.20) or mismatched at one locus (0.76 ± 0.68; Table 3), though in some years there was a considerable increase in false POPs when 2 mismatching loci were allowed (Table 3).

Table 3. Statistics describing power to resolve parent-offspring assignments correctly are represented for each parent-offspring dataset we evaluated.

Type[a]	Parent[b]	Offspring[b]	NE.1P[c]	NE.2P[c]	NE.PP[c]	EFP.0[d]	EFP.1[d]	EFP.2[d]
Adult-Adult	2007	2010	2.13E-07	4.95E-10	5.68E-17	0.10	0.23	1.79
		2011	2.24E-07	5.25E-10	6.36E-17	0.10	0.63	2.20
		2012	2.27E-07	5.27E-10	6.46E-17	0.15	0.35	3.45
		2013	2.39E-07	5.63E-10	7.18E-17	0.03	0.21	0.41
	2008	2011	2.04E-07	4.66E-10	5.32E-17	0.10	0.62	2.55
		2012	2.16E-07	4.93E-10	5.90E-17	0.16	0.60	2.94
		2013	2.38E-07	5.49E-10	7.23E-17	0.04	0.26	0.71
	2009	2012	2.18E-07	4.98E-10	5.86E-17	0.23	0.83	6.35
		2013	2.46E-07	5.71E-10	7.44E-17	0.07	0.32	0.83
	2010	2013	1.85E-07	4.22E-10	4.31E-17	0.03	0.14	0.40
Adult-Juvenile	2008	2009	3.49E-07	8.51E-10	1.62E-16	0.51	1.86	6.41
	2009	2010	2.48E-07	5.80E-10	7.71E-17	0.69	2.44	9.28
	2010	2011	2.81E-07	6.79E-10	9.91E-17	0.31	1.36	9.02
	2011	2012	3.07E-07	7.50E-10	1.22E-16	0.35	0.79	5.56

[a] Life stage the parent and offspring were when sampled, respectively

[b] The Parent and Offspring columns denote the year each was sampled

[c] Non-exclusion probabilities for a single parent (NE.1P), a second parent (NE.2P), and a parent pair (NE.PP)

[d] Expected number of false parent offspring pairs for zero (EFP.0), one (EFP.1), and two (EFP.2) genotypic mismatches

Biology of Reintroduced Chinook Offspring

Adults

We found that 64% of NOR Chinook returning to the Cougar Trap in 2012 were produced above the dam. We observed a similar result in 2013 (68%; Figure 8). The proportions of fish that were produced by previously reintroduced adults among the early and late returning Chinook differed in both 2012 (*Fisher's Exact Test*, $p<0.001$) and 2013 (*Fisher's Exact Test*, $p<0.001$; Figure 8). We also found that the likelihood that an adult fish had been produced above the dam decreased as NOR Chinook returned later in the spawning season ($b = -0.047 \pm 0.003$, $p<0.001$).

We found that, on average, NOR males returned to the Cougar Trap 7.54 ± 1.87 days later than females ($p<0.001$), after accounting for variation among years. The proportion of male and female NOR Chinook that assigned to reintroduced parents did not differ in 2012 (*Fisher's Exact Test*, $p=0.28$), but did in 2013 (*Fisher's Exact Test*, $p<0.02$). However, using logistic regression, we found overall *sex* did not significantly explain variation in the odds of being produced above the dam ($b = -0.202 \pm 0.163$, $p=0.21$).

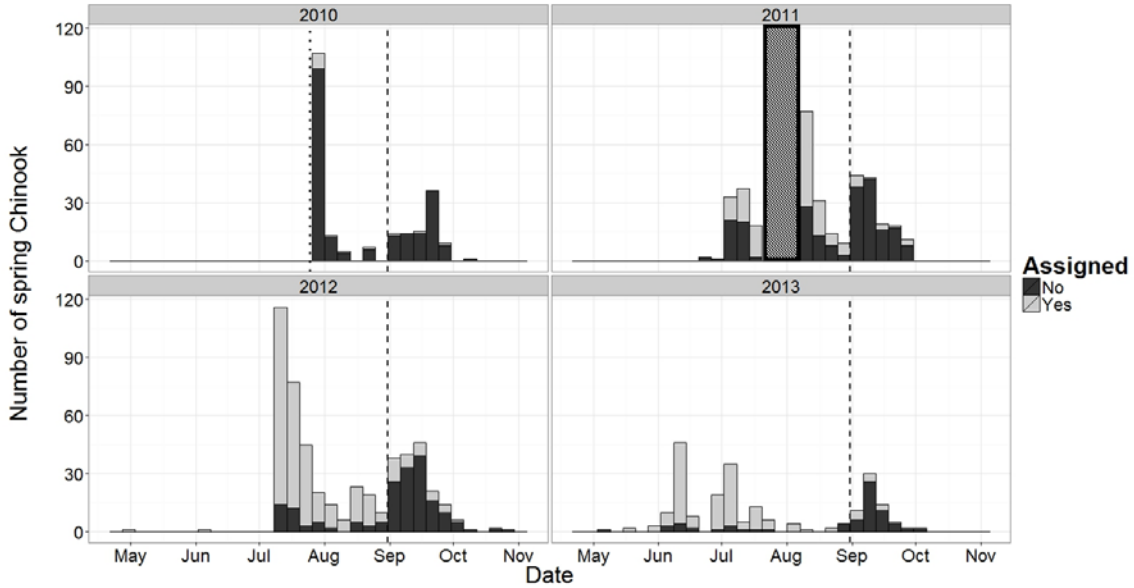

Figure 8. The number of Chinook collected at the Cougar Trap from 2010-2013 are represented. Black vertical dashed lines denote September 1st and Chinook that did (Yes) or did not (No) assign to reintroduced parents are indicated. The vertical dotted line in 2010 indicates delayed start date, and the striped box in 2011 denotes the Cougar Trap closure.

A total of 64 Chinook collected in the Cougar Trap in 2013 after September 1st were double floy tagged and released back into the mainstem McKenzie River. Among these fish 13 had been produced above Cougar Dam. If a double floy tagged Chinook entered the Cougar Trap a second time, it was transported above the dam. We found that among the 15 Chinook that returned to the Cougar Trap a second time, 8 were progeny from reintroduced parents, and of the 49 that did not return, 5 had been produced above Cougar Dam (Figure 9). The proportion of Chinook produced above the dam between those that did and did not return a second time was significantly different (*Fisher's Exact Test*, $p<0.001$)

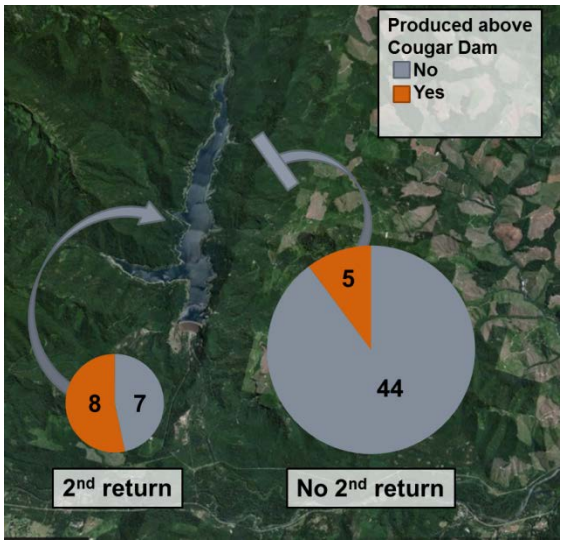

Figure 9. Pie charts denote the number of Chinook that did and did not return a second time to the Cougar Trap. The number of NOR returns that were and were not progeny of adults previously reintroduced above Cougar Dam is indicated.

Juveniles

From 2009-2012 the mean percent of juvenile offspring that we assigned to at least one parent was 98.3 ± 2.2% (Figure 10). Among the juveniles genotyped, 78.0 ± 7.3% were assigned to both parents, 7.0 ± 3.2% of offspring were missing a father assignment, and 13.3 ± 5.0% were missing a mother. From 2008-2011, the frequencies of offspring assigning to only a father and only a mother did not significantly differ (V=0, *p*=0.18).

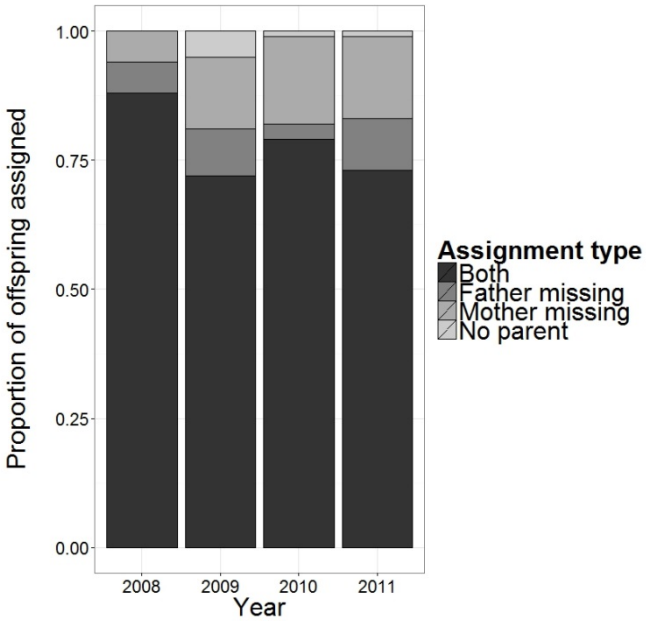

Figure 10. Proportion of parent-juvenile assignment types are indicated by shaded stacked bars for juvenile sampling years 2008-2011.

Most juveniles analyzed were captured in the HCR screw trap (96.3%, n=8,337), but among the four years of sampling we did process 307 juveniles captured in screw traps below the dam. Overall, 87.3% of the juveniles collected in below dam screw traps were produced above the dam. We compared the proportion of juveniles captured in the RO screw trap to that of the TR screw trap from 2010-2012 (Figure 11). We found that in 2010 the proportion of juveniles produced above the dam differed between the two screw traps (*Fisher's Exact Test*, $p<0.001$), but no difference was observed in 2011 (*Fisher's Exact Test*, $p=0.07$) or 2012 (*Fisher's Exact Test*, $p=1.0$). Most juveniles that did not assign in 2010 were captured in September and October of that year (Figure 11).

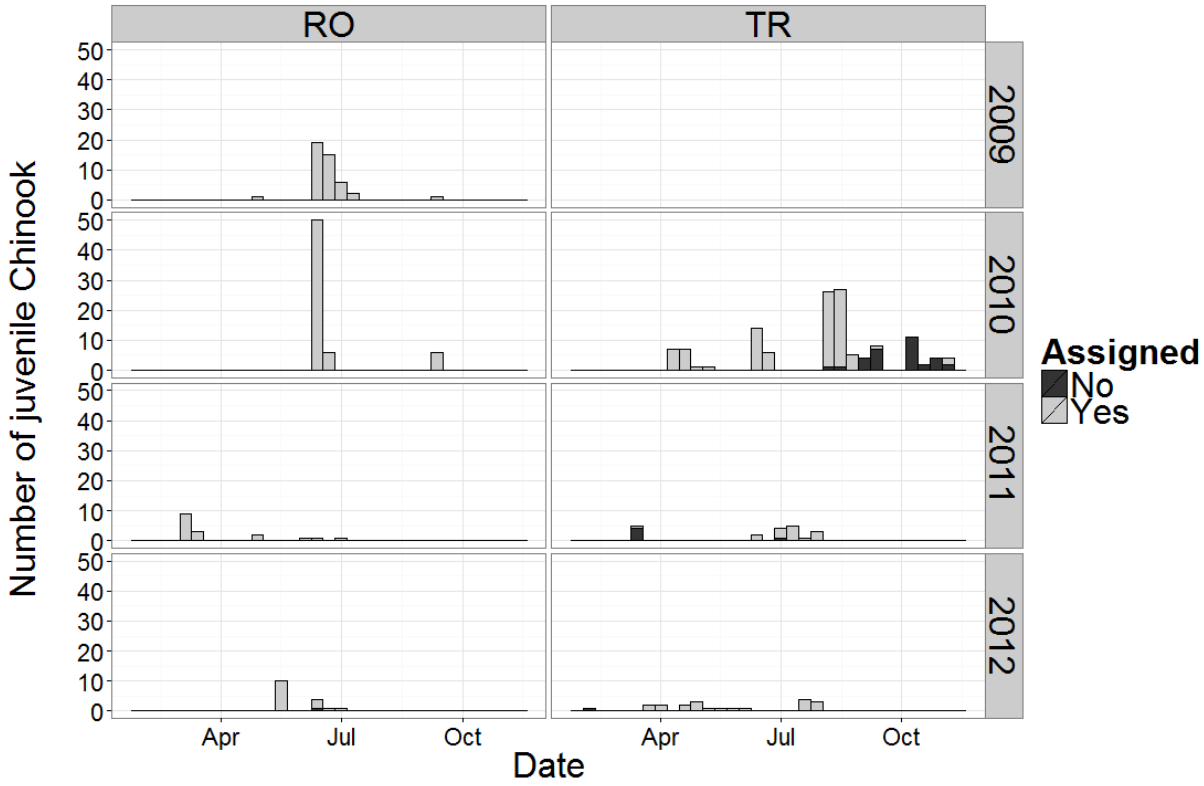

Figure 11. The number of juvenile Chinook captured in the regulating outlet (RO) and tailrace (TR) screw traps from 2009-2012, plotted by date. The number of juveniles sampled in RO and TR screw trap that assigned to a reintroduced parent is indicated.

Juvenile emigration timing

We found that mean RET differed among juveniles produced by different mate pairs ($F_3=6.44$, $p<0.001$), and that there was a significant *year*mate pair* effect ($F_3=3.94$, $p=0.008$). Our *post-hoc* analysis within each year revealed that in 2010, juveniles produced by ♀$_{HOR}$/ ♂$_{HOR}$ mate pairs entered the reservoir 30.75 ± 7.67 days after those produced by ♀$_{NOR}$/ ♂$_{NOR}$ mate pairs ($p<0.001$). In addition, we found that fry produced by ♀$_{HOR}$/ ♂$_{NOR}$ mate pairs entered the reservoir 19.30 ± 7.63 days after fry produced by ♀$_{NOR}$/ ♂$_{NOR}$ mate pairs ($p=0.012$) in 2010. However, we found no significant differences in mean RET among juveniles produced by different mate pairs in 2011 ($F_3=1.51$, $p=0.21$).

Release effects

Total lifetime fitness – Inference from adults

We estimated TLF for 1,619 Chinook released above Cougar Dam in 2007 and 2008. Of these, 29.7% were successful at producing offspring that returned as adults to the Cougar Trap. The maximum number of offspring produced by females and males were 17 and 11, respectively. We found that *release date*, *release location*, *sex*, and *year*, as well as the *year*sex* interaction term significantly explained variation in TLF individually. However, our AIC model selection procedure suggested that a model that included *sex*, *release date*, *year*, and *year*sex* adequately explained variation in TLF. We found that mean TLF decreased as a function of *release date* after accounting for variation explained by the other predictors (Table 4). We found that there was no difference in mean TLF between the sexes in 2007 (p=0.35), but the mean TLF for males was 45% lower than females in 2008 (p<0.001; Figure 12).

Table 4. Summary of the predictors included in the final generalized linear mixed-effect model used to identify factors that significantly explained total lifetime fitness in 2007 and 2008. Females and the year 2007 were used as the references for the predictors' *sex* and *year*, respectively.

Predictor	Estimate	Std. Error	z value	Pr(>|z|)
Sex-Male	-0.112	0.156	-0.72	0.473
Release Date	-0.006	0.002	-2.43	0.015
Year-2008	-0.011	0.205	-0.06	0.956
*Sex-Male*Year-2008*	-0.632	0.221	-2.86	0.004

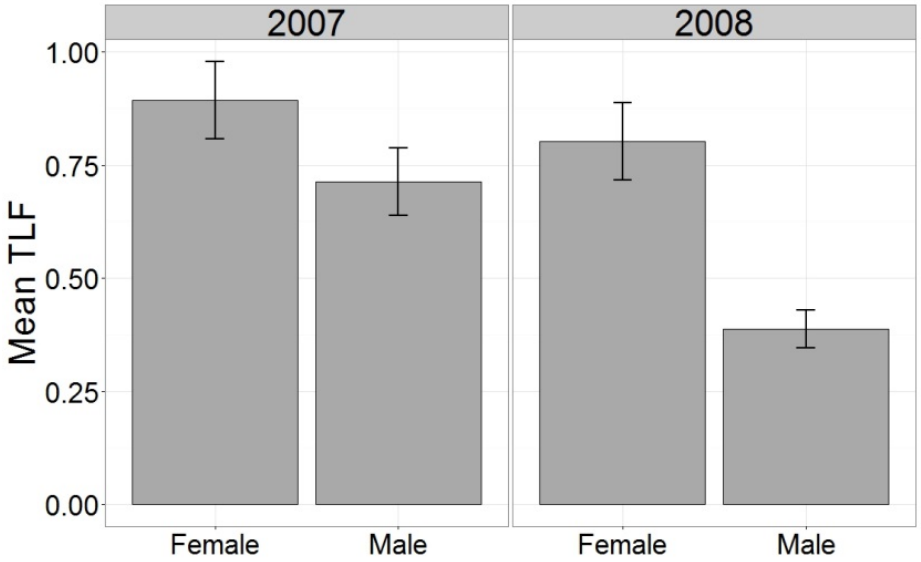

Figure 12. Mean total lifetime fitness (TLF) for female and male Chinook released above Cougar Dam in 2007 and 2008. Standard error is indicated by error bars.

Reproductive success – Inference from Juveniles

Of the 3,738 adult Chinook released above Cougar Dam from 2008-2011, we found evidence that 47% (n=1,764) were successful at producing juveniles. We also found that the highest mean RS for females was in 2010 and lowest in 2009 (Table 5). Mean RS for males was highest in 2011 and lowest in

2009. Variation in RS among the adults released above Cougar Dam when both HOR and NOR Chinook were reintroduced was high (Table 5). We observed the highest maximum RS estimates for females and males in 2010 (Table 5).

Table 5. A summary of reproductive success (RS) descriptive statistics for Chinook released above Cougar Dam from 2008-2011. Type describes hatchery origin (HOR) and natural origin (NOR). Standard deviation (SD) for mean RS estimates is indicated.

Year	Type	Sex	N	Mean RS	SD	Median RS	Max RS
2008	HOR	Female	288	6.68	8.29	4	40
		Male	585	3.27	6.89	0	54
2009	HOR	Female	604	2.68	4.25	0	37
		Male	782	2.23	4.55	0	42
2010	HOR	Female	209	6.90	12.78	0	85
		Male	318	2.98	7.59	0	47
	NOR	Female	57	4.56	10.5	0	54
		Male	164	6.29	14	0	107
2011	HOR	Female	179	5.50	9.81	0	42
		Male	195	3.31	6.94	0	44
	NOR	Female	145	6.06	10.32	0	45
		Male	212	6.44	13.36	2	93

We found that *release date, sex*, *year*, and the interaction terms *release date*sex*, *release date*year*, and *year*sex* were significantly associated with RS individually. However, the AIC model selection procedure identified a GLMM that included all of the predictors described above, except *year*sex* and *release date*year*, adequately explained variation in RS (Table 6). We found mean RS for males was 2.28 times that of females (Table 6). Mean RS increased as female Chinook were released later in the spawning season (p<0.001), though the effect was small. Finally, we found that *release location* did not significantly explain variation in RS within the four reintroduction years tested.

Table 6. Summary of predictors for final RS generalized linear mixed-effects model for Chinook released above Cougar Dam from 2008-2011. Females and 2008 were references for the indicator variables *sex* and *year*.

Predictor	Estimate	Std. Error	z value	Pr(>|z|)
Release Date	0.001	0.002	0.494	0.622
Sex-Males	0.824	0.399	2.064	0.039
Year-2009	-0.729	0.160	-4.548	<0.001
Year-2010	0.074	0.138	0.533	0.594
Year-2011	0.191	0.133	1.438	0.150
*Release Date*Sex-Males*	-0.006	0.002	-2.982	0.003

Our analysis of RS for fish released in 2010 suggested that *sex*, as well as the interaction terms *release date*sex* and *origin*sex* significantly explained variation in RS individually. We included all the variables except *release date*sex* in the final regression analysis based on AIC score. Mean RS for males

was 6.9 times that of females (p<0.001). After our *post-hoc* analysis of the *origin*sex* interaction term, we found that mean RS for NOR males was 2.1 times that of HOR males (p<0.001). However, we found no difference in RS between HOR and NOR females (p=0.16).

In 2011, we found that the predictors *length* and *origin* significantly explained variation in RS. Without accounting for variation in *length*, we found that on average RS for NOR Chinook was 1.4 times that of HOR Chinook (p=0.027). However based on AIC score, we included only *length* in the final GLMM. Overall we found on average a 1 cm increase in length resulted in a 6% increase in RS (p<0.001). The relationship between *length* and RS did not differ between HOR and NOR Chinook (p=0.25).
When evaluating *length* differences among HOR and NOR Chinook, we found that overall mean *length* for HOR Chinook was 1.97-4.02 cm (95% CI) less than NOR Chinook (p<0.001; Figure 13). On average males HOR Chinook were 1.28-3.34 cm shorter than females (p<0.001). But, the interaction between *origin* and *sex* was not significant (p=0.84).

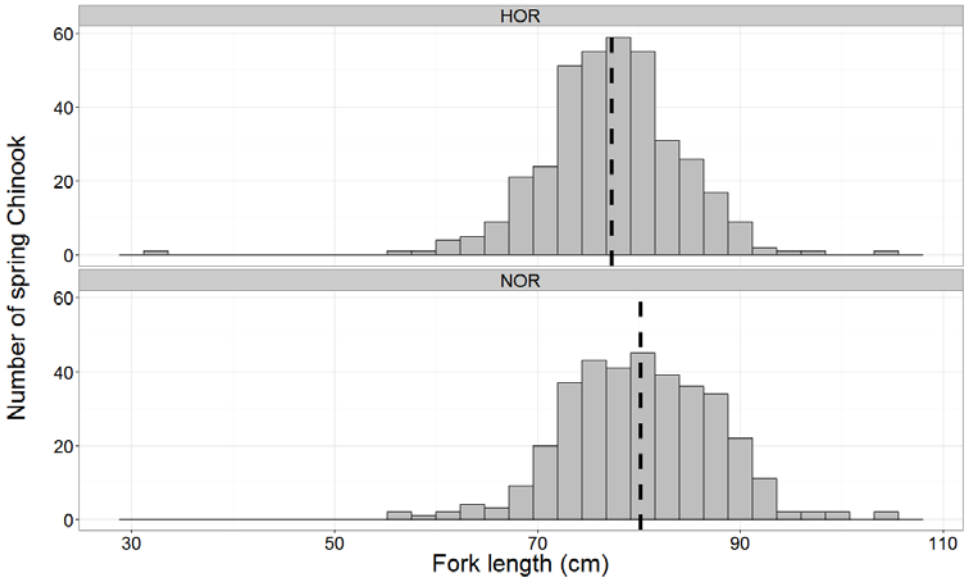

Figure 13. Distributions for fork-length for hatchery origin (HOR) and natural origin (NOR) Chinook. Vertical dashed lines represent mean fork length for each group.

We also evaluated RRS between HOR and NOR Chinook, which compared observed RRS to 10,000 RRS values created using a permutation procedure that required estimates of the rate at which a false parents assigned to offspring when the true parent was not present in the data set (type B error). Our type B error estimates were low for both 2010 and 2011 (0.001-0.010). RRS values greater than one denote that the mean RS for HOR Chinook was larger than mean RS for NOR Chinook, and values less than one indicate the opposite relationship. In general, our RRS tests corroborated our GLMM results. We found no differences among females for either year tested individually, or when years were combined (Figure 14). However, we found significant differences between HOR and NOR males for all three comparisons, in which mean RS for HOR males was less than NOR males (Figure 14). When we combined both sexes, we found that in 2010 there was no difference in RS between the two groups (p=0.38). However, in 2011 and when both years were combined mean HOR Chinook RS was significantly less than NOR Chinook (p=0.012 and p=0.008, respectively; Figure 14).

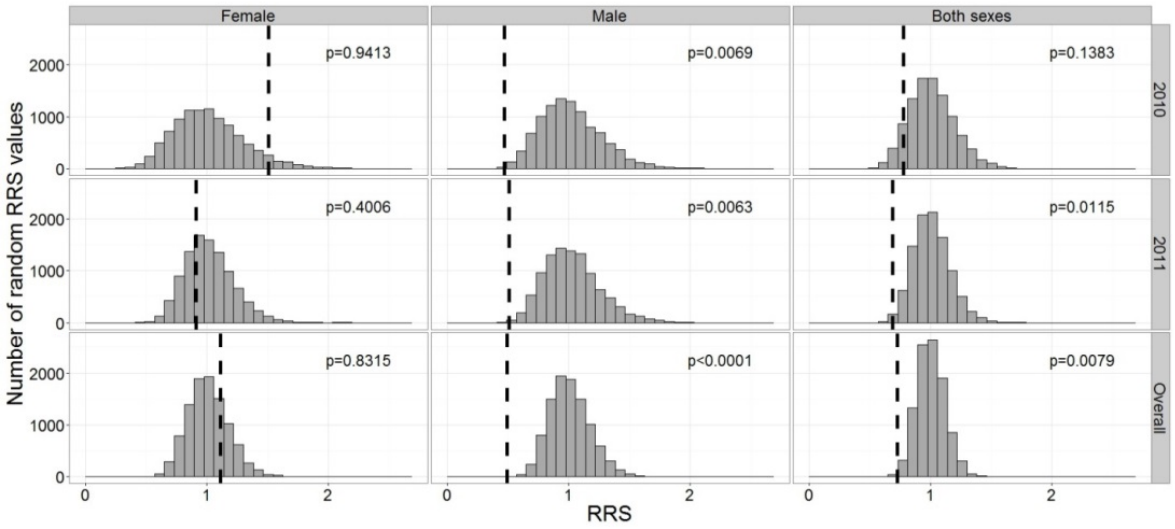

Figure 14. Relative reproductive success (RRS) values from 10,000 randomized comparisons between hatchery origin (HOR) and natural origin (NOR) Chinook are represented in each grid cell. Observed values for each category are represented by vertical dashed lines and p-values indicate statistical significance following FDR corrections. RRS values greater than one denoted mean RS for HOR Chinook was greater than that of NOR Chinook and values less than one represent the opposite relationship.

Testing for a relationship between reproductive success and total lifetime fitness

We compared RS and TLF estimates for the 2008 adult cohort (n=873) and found that 47.2% (n=412) had fitness estimates equal to zero. In addition, 23.7% (n=207) of adults had estimates of both RS and TLF greater than zero. However, we found that 27% (n=236) of adults that produced fry above Cougar Dam did not have any adult progeny return to the Cougar Trap. In total, 2.1% (n=18) of adults were not identified as successful breeders based on RS estimates, despite having adult progeny return to the Cougar Trap in subsequent years. Finally, we tested for a relationship between RS and TLF in 2008 and found that RS significantly explained only 25.7% of TLF variation (p<0.001) (Figure 15).

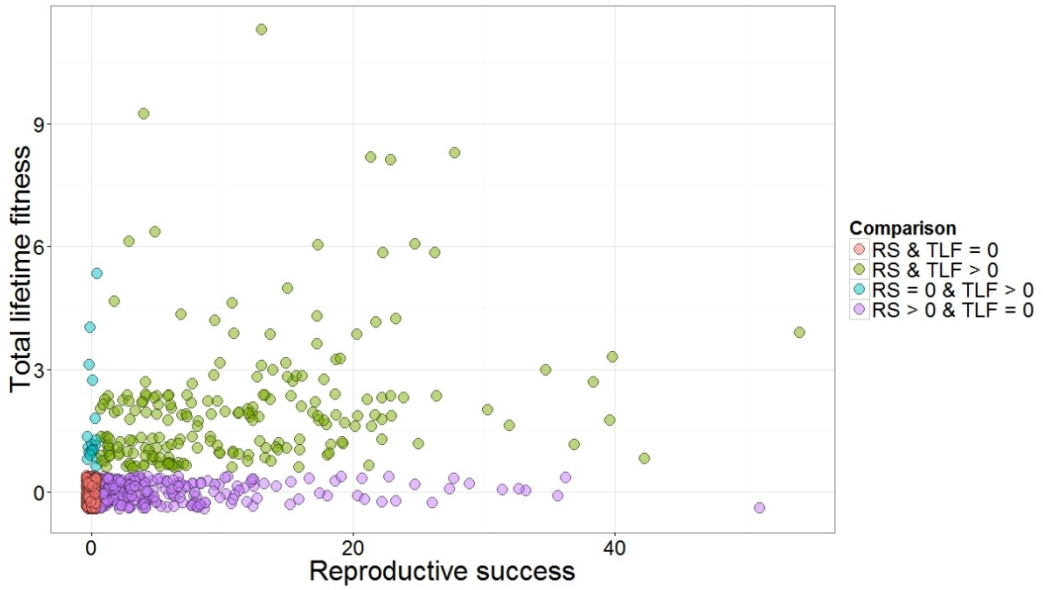

Figure 15. Scatterplot representing the significant (p<0.001) relationship between reproductive success (RS) and total lifetime fitness (TLF) – D^2=0.257. Color of the points indicated if estimates for only TLF, TLF and RS, or only RS were greater than zero, as well as if both were equal to zero. Points were jittered and made semi-transparent to better represent the number of individuals (n=873) being plotted.

Demography

Population viability metrics

We found that Chinook in 2007 and 2008 successfully produced 323 and 241 adult offspring that returned to the Cougar Trap from 2010-2013. However these returns were not sufficient to meet replacement for either cohort (CRR = 0.41 and 0.31 for 2007 and 2008, respectively). We observed little variation in N_e of Chinook reintroduced above Cougar Dam in 2007 (185, 95% CI_J: 169-203) and 2008 (184, 95% CI_J: 169-204).

Adult age analysis

A total of 403 NOR Chinook had age estimates from both scales and pedigree from 2012-2013. Among these Chinook, we found that concordance between the methods was 81.6% (Figure 16). Our logistic regression analysis found that for each 1 cm increase in *length* the odds of discordance decreased by 5.8% (Table 7). In addition, the odds of discordance increased by 1.7% for each day later in the spawning season a NOR Chinook returned to the Cougar Trap (Table 7). Finally, if a scale was difficult to read the odds of discordance was 4.12 times that of when a scale was not difficult to read (Table 7).

Table 6. Logistic regression predictors that significantly explained the odds of discordance because scale and pedigree age estimates.

Predictor	Estimate	Std. Error	z value	Pr(>|z|)
Length	-0.06	0.02	-3.50	< 0.001
Return timing	0.02	0.01	3.30	< 0.001
Scale read difficulty	1.42	0.62	2.29	0.022

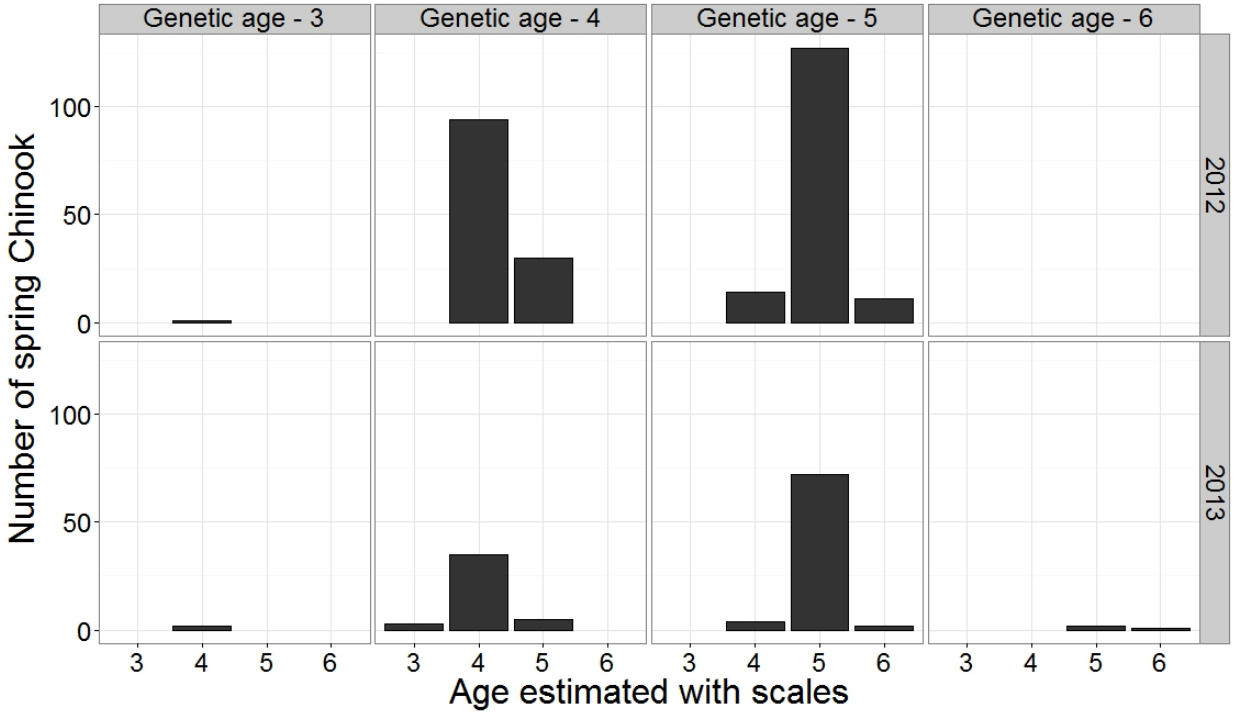

Figure 16. Summary of scale and pedigree age estimates in 2012 and 2013. Early freshwater life history is indicated.

Assessment of genotypic and phenotypic sex calls

We found that the mean concordance between phenotypic and genotypic sex calls was 90.1%, with the highest concordance in 2008 (95.0%) and the lowest in 2011 (83.2%) (Table 8). In total we identified 593 differences in phenotypic and genotypic sex calls among 5,656 adult Chinook released above Cougar Dam (Table 8). We lacked *Oty3* genotypes for 20 adult Chinook due to poor DNA quality and one lacked phenotypic sex identification. We observed adults that had been phenotypically identified as female, but were genotypically male more often (n=332) than phenotypically classified males that were genotypic females (n=261). In addition, we found that the odds of discordance decreased (b = -0.014 ± 0.002, p<0.001) as Chinook were sampled later in the spawning season. We used genotypic sex identification for all parentage analyses.

Table 8. Summary of concordance between phenotypic and genotypic sex identification for adult Chinook released above Cougar Dam from 2007-2013. Discordant sex call sub-categories describe changes from phenotypic sex to genotypic sex. HOR adult Chinook in 2013 have not been genotyped at *Oty3*.

Call type	2007	2008	2009	2010	2011	2012	2013
Concordant							
Female	268	265	522	245	267	405	92
Male	399	563	676	415	340	466	140
Discordant							
Female -> Male	27	22	105	64	66	41	7
Male -> Female	49	22	80	14	57	33	6
Percent Concordance	89.8	95.0	86.6	89.4	83.2	92.2	94.7

Discussion

In this report we used genetic techniques to evaluate the efficacy of the spring Chinook reintroduction program at Cougar Dam. Briefly, below are key results from our research:

Overview of results

Assignment rates

I. The percentage of Chinook returning early to the Cougar Trap was high for both 2012 (85.2%) and 2013 (86.8%), but was low (21.3% and 20.3%, respectively) among those returning late.
II. On average, males returned 7.54 ± 1.87 days later than females to the Cougar Trap (p<0.001).
III. Overall assignment rates did not differ between the sexes (p=0.21).
IV. Among the non-Cougar adults that returned after September 1st in 2013, only 7 (10.9% of the total number of Chinook that returned late) were transported above the dam. This result is a substantial reduction when compared to the 78.7% of non-Cougar adult late returns reintroduced in 2012.
V. On average, 78.0 ± 7.3% of fry sampled in 2009-2012 assigned to both a mother and father.
VI. Most fry (87.3%) collected in screw traps below Cougar Dam were produced by parents released above the dam. Among the fry collected below the dam, most that were missing parents (97.4%) were collected in the TR screw trap.

Release strategies

I. We found a negative relationship between *release date* and TLF (p<0.015). However, we found a positive relationship between *release date* and RS for females (p<0.001).
II. Release locations had no effect on either measure of fitness.

Origin effects

I. In 2010 NOR males were on average 2.1 times as fit as HOR males (p<0.001). However, we found no difference in RS between HOR and NOR females (p=0.16).
II. The overall mean RS for NOR Chinook was 1.4 times that of HOR Chinook (p=0.027) in 2011, though the effect of origin on RS was not significant (p=0.389) after we accounted for variation explained by length.
III. Unbiased methods comparing RS between HOR and NOR Chinook corroborated results from the GLMM analysis.

Assessing methodology

I. For the 2008 adult cohort, RS only explained 25.7% of the variation in TLF (p<0.001).
II. Concordance between genotypic and phenotypic sex identification methods was 90.1%, and the odds of discordance decreased as Chinook were sampled later in the year (p<0.001).
III. Scale and pedigree age estimates were 81.6% concordant. The odds of discordance were explained by Chinook length (p<0.001), returning timing (p<0.001), and if the scale was difficult to read (p<0.022).

Demography

I. Both the 2007 and 2008 adult cohorts did not meet replacement (CRR: 0.41 and 0.31, respectively).
II. N_e varied little between 2007 (185, CI_J: 169-203) and 2008 (184, CI_J: 169-204).

Assignment rates

Low non-exclusion probabilities and expected numbers of false POPs within our genetic pedigrees suggest that our methodology accurately resolved parent-offspring relationships. Furthermore, the statistical power obtained from the genetic markers we used, as well as our estimated genotyping error rate, are comparable to other recently published parentage studies on salmonids (DeHaan and Bernall 2013; Ford et al. 2012; Seamons et al. 2004; Serbezov et al. 2010; Williamson et al. 2010). We are therefore confident that we identified the majority of progeny produced by Chinook reintroduced above the dam that returned to the Cougar Trap.

We previously found that most Chinook returning early to the Cougar Trap were produced above the dam, yet a minority of those that returned late assigned (Banks et al. 2013). Managers anticipated the same pattern would occur in 2013, and therefore implemented the LSDR method to limit the number of non-Cougar adults from being released above the dam. As a result of the use of the LSDR method, we found that 7 non-Cougar adult returns were passed above the dam in 2013, which was 10.9% of the total number of Chinook returning after September 1st. Our results suggest that the LSDR method was effective at limiting the number of non-Cougar adult returns released above the dam, particularly when compared to 2012 in which 78.7% of transports after September 1st were not produced above the dam. We therefore recommend the continued use of the LSDR method in future years, together with genetic parentage analyses.

Among juveniles, we consistently found that most (98.3 ± 22%) assigned to at least one parent reintroduced above Cougar Dam, but we identified both parents for only 78.0 ± 7.3% of them. Three alternative hypotheses could explain why juveniles would be the missing parents. First, though low, our genotyping error may have resulted in a small number parents not assigning to offspring. Second, there could be a low error rate for sex identification made with the *Oty3* marker that would result in a parent not being assigned. For example, if both the parents for a given offspring were present in the data set, but the sex of the father was incorrectly identified as female, that male would not be present among potential fathers in our analyses. Subsequently, we would have incorporated both parents' genotypes into a single SOLOMON run to identify POPs. As a result, only one parent would assign to the offspring based on our methods. Third, there may be unsampled parents within the system, which could include adfluvial Chinook residing above Cougar Dam. We expect that some offspring will have missing fathers based on the precocial life history exhibited by some male Chinook (Taylor 1989). But what is perplexing is that in all four pedigrees some offspring are missing mothers. This could potentially be explained by the presence of adfluvial Chinook residing in the reservoir. Though no adfluvial Chinook have been found in Cougar Reservoir, they have been observed in other reservoirs in the Willamette River basin (Romer and Monzyk *In press*), as well as described in other systems in Washington (Quinn and Myers 2005). Newly developed methods that accurately identify unsampled parents using knowledge of grandparent and grandoffspring genotypes are a promising means to identify unsampled parents in this system (Christie et al. 2011). We intend to thoroughly evaluate these three hypotheses in forthcoming analyses.

In 2010 we found that some juveniles sampled in the TR screw trap did not assign to reintroduced adults. We believe there are two possible explanations for this anomaly. First, the juveniles may have emerged late because of the colder than normal waters flowing from the tailrace of the dam. Second, there was an unusually high flow event late in 2010 that may have altered typical emigration behavior of juveniles below the dam and resultant sampling of juveniles that were not produced above Cougar Dam. However, we did not observe similar findings in other years. In 2013, a total of 117 juveniles were sampled in the TR screw trap, which will enable us to determine if our 2010 finding is an anomaly, or a result present in multiple years that may require additional investigation.

Juvenile emigration

We found that juveniles produced by mate pairs involving by NOR females emigrated to the reservoir earlier than juveniles produced by other mate pair types. However, early emigration timing was only observed in 2010. This result may be explained by the presence of few NOR females above Cougar Dam that year, which may have resulted in poor representation of juveniles produced by $♀_{NOR}/♂_{NOR}$ and $♀_{NOR}/♂_{HOR}$ mate pairs. Alternatively, our results in 2010 may be the result of HOR Chinook were released later in the spawning season than NOR Chinook. Regardless, we will continue to evaluate juvenile emigration to the reservoir to determine if our finding is observed over multiple years. Alternatively, our results in 2010 may be driven by the fact that HOR Chinook were released later in the spawning season than NOR Chinook that year.

Release strategies

The effect of sex on our estimates of fitness varied depending on which measure (RS or TLF) was evaluated. With TLF as the response, we found that males in 2008 were on average less fit than females, which is likely due to the male-skewed sex ratio (2.03, male/female) that year. Milot et al. (2013) found similar results when studying the fitness of Atlantic salmon (*Salmo salar*). However, we found that males were on average more fit than females when RS was the response. Polygyny and greater fecundity of males, relative to females, may explain this result (Quinn 2011).

From our TLF analysis we found that Chinook that arrived later in the season to spawn were, on average, less fit. However, we found that mean RS for females released later in the season was higher than that of earlier releases. Two studies of Chinook in Washington found similar negative relationships between release date and fitness, though the effect was inconsistent among years evaluated (Anderson et al. 2013; Williamson et al. 2010). Similarly, Dickerson et al. (2005) found that early-arriving pink salmon (*Oncorhynchus gorbuscha*) males were more successful breeders. Our results in Chinook may be explained by a density dependent spawning process. Males that arrive to the spawning grounds earlier may experience less competition for mates, but as the season progresses the operational sex ratio increases. Therefore, it becomes more difficult to successfully mate because of increased competition among males (Neville et al. 2006; Quinn 2011). Our finding that female RS increased for later releases in the spawning season may also be influenced by superimposition or a consequence of pre-spawn mortality being observed in Chinook released earlier, but having little time to manifest in fish released later in the season (Keefer et al. 2010).

We found that *release location* did not significantly affect fitness. Our TLF analysis required the simplification of *release location* to a two level factor describing the lower and upper sections of the river above Cougar dam. This approach, as well as the incorporation of an additional year's data, may explain why current results contrast with previous findings, that indicated that *release location* significantly explained variation in TLF (Banks et al. 2013). Current results suggest that, at most, *release location* has inconsistent effects on fitness of Chinook reintroduced above Cougar Dam. Chinook that are released months or even weeks prior to peak spawning have ample time to travel throughout the river to find redd locations and mates. Alternatively, release locations may be close to suitable spawning habitat or near holding pools, where fish can rest and recover after transport. Preliminary results suggest that 47.2% of the mate pairs identified among adult-juvenile pedigrees mated with at least one Chinook that was released in another location. Forthcoming analyses will evaluate results specific to mate pairs in more detail.

HOR/NOR reproductive success

We used two different approaches, GLMM and an unbiased RRS permutation test, to evaluate fitness differences between HOR and NOR Chinook. We found that, on average, male HOR Chinook were consistently less fit than NOR Chinook. Any fitness effect of origin for females, however, was not evident

from our data. We found no fitness differences between HOR and NOR females released in 2010 using either approach, but GLMMs suggested that mean RS for NOR Chinook, was 1.4 times that of HOR Chinook in 2011 when differences between sexes were ignored. This origin effect in 2011 was not significant when we accounted for RS variation explained by *length*, which corroborates our finding that NOR Chinook were 1.97-4.02 cm (95% CI) larger than HOR Chinook in 2011. Together, these findings suggest that fitness differences observed between hatchery and wild spring Chinook released above Cougar dam are readily explained by mean fork length, which differs significantly according to origin.

Our results largely support the growing body of literature that suggest on average HOR salmon are less fit than NOR in the wild (Anderson et al. 2013; Araki et al. 2007; Milot et al. 2013; Theriault et al. 2011; Williamson et al. 2010). Theriault et al. (2011) hypothesized that fitness differences between HOR and NOR salmon are likely caused by differences in sexual selection on the spawning ground or differences in natural selection during juvenile early life stages. Our results provide evidence for their sexual selection hypothesis because length has been shown to be an important trait under sexual selection. However, larger females typically dig deeper redds and are less susceptible to superimposition (Hawke 1978; Quinn 2011). In addition, larger Chinook are on average more fecund (Healey and Heard 1984). Cumulatively, these factors would likely result in greater fitness as well.

Though we do not have knowledge of HOR Chinook parentage history, our results may be explained by a mechanism similar to that described by Ford et al. (2012), whereby low RS for HOR spring Chinook could be explained by the higher frequency of precocial (younger and smaller) males present among HOR spawners that significantly lowered the mean RS of the HOR spawners. The male precocial life history is not as prevalent in the Willamette River basin, but Johnson and Friesen (2013) found that HOR Chinook length has decreased over time. Thus, early returning HOR Chinook that are smaller may explain the fitness differences between HOR and NOR Chinook.

Numerous authors have reported positive relationships between size and reproductive success for both sexes in Pacific salmon (Berejikian et al. 2000; Berejikian et al. 1997; Berejikian et al. 2001b; Fleming and Gross 1992; Fleming and Gross 1994; Schroder et al. 2008). In our study, age and length are confounded, which warrants additional investigation of our 2011 finding that length explains HOR/NOR fitness differences. We would expect that age-5 Chinook will have higher average fitness than age-4 Chinook, because on average they will be larger (Johnson and Friesen 2013). Therefore, research evaluating fitness differences between HOR and NOR Chinook of the same age, would eliminate the fact that age and length are confounded. We recommend that scales be sampled from HOR Chinook if managers continue to reintroduce them above Cougar Dam because acquiring age data holds potential to resolve age, length, origin cause of fitness differences.

Our results suggest consistent fitness differences between HOR and NOR males, but not for females, which is particularly interesting because, based on 2012 and 2013 Cougar Trap assignment rates, roughly 65% of the NOR Chinook are likely F_1 ♀$_{HOR}$/ ♂$_{HOR}$ progeny. Though it is difficult to conclusively state exactly what percent of NOR Chinook are F_1 ♀$_{HOR}$/ ♂$_{HOR}$ progeny, because we lack genotypes for Chinook reintroduced in 2005 and 2006. Our findings corroborate those from other fitness studies of Chinook (Anderson et al. 2013; Williamson et al. 2010). Behavior studies suggest NOR males tend to outcompete HOR males for mates and are preferred by females (Berejikian et al. 1997; Berejikian et al. 2001a; Fleming and Gross 1992; Fleming and Gross 1993; Fleming et al. 1996; Schroder et al. 2008). It may, therefore, be prudent to limit the number of HOR males in the reintroduction program, as they may lower the RS of NOR females and population productivity is likely not constrained by male spawners. But we caution that RS did not explain 74.3% of the variation in TLF, and relative fitness for HOR and NOR Chinook may differ in light of forthcoming TLF estimates. For instance, Ford et al. (2012) found that the relationship between Chinook individual fitness in the wild and their parents' success in captivity was not significant when RS was evaluated, however fitness differences were found when TLF was evaluated. We think it is difficult to conclusively state how fitness differences will change

when HOR and NOR adults return to spawn, because mortality associated with dam passage (Beeman et al. 2014; Keefer et al. 2013), outmigration to the ocean (Kareiva 2000), foraging in the open seas (Parker 1962), and prior to spawning themselves (Keefer et al. 2010) are all factors that may affect TLF estimates. All of which may or may not differentially affect HOR and NOR Chinook. As a result, we cannot comment on how it would alter the management of the reintroduction. We recommend the continued evaluation of fitness differences between HOR and NOR Chinook using TLF estimates. These estimates will provide definitive evidence when evaluating fitness differences among HOR and NOR Chinook and a clearer view of NOR contributions to population productivity.

Assessing methodology

We found 90.1% concordance between phenotypic and genotypic sex identification methods and that the odds of discordance between the two methods decreased later in the spawning season. These findings are likely influenced by an increase in the accuracy of visual sex identification that occurs later in the season, when secondary sexual characteristics become more evident closer to the spawning season and therefore facilitating sex identification using secondary sexual characteristics.

Our results suggest that scale and pedigree age estimates are relatively accurate given that we found 81.6% concordance from 2012-2013. The odds of discordance decreased as Chinook *length* increased, which may suggest that older fish are easier to age because length is correlated with age. In addition, the odds of discordance increased with return date. Our results suggest that majority of Chinook returning after September 1st were not produced above Cougar dam, and thus some false assignments may be present among late returning Chinook. Finally, the odds of discordance increased when the scale itself was difficult to read. Thus, when scales are difficult to read the age estimates maybe unreliable.

Demography

We found little variation between our estimates of N_e or CRR in 2007 and 2008. Our estimates of CRR indicate that Chinook being reintroduced above Cougar Dam are not replacing themselves, which is likely the result of the low survival probabilities of juveniles passing Cougar Dam (Beeman et al. 2014). To date, we have produced CRR estimates for years in which only HOR Chinook were reintroduced above Cougar Dam. Given that the mean and variance in fitness estimates were highest in years in which both HOR and NOR Chinook were released above Cougar Dam, CRR estimates may increase for later years. In addition, altering dam operations to improve recruitment and survival of juvenile Chinook passing through dams may improve CRR in the future.

N_e is often used to assess the probability of extinction due to inbreeding depression and the long-term maintenance of genetic variation required for future adaptation (Frankham 1996). As a general rule of thumb, it is recommended that a population have a N_e greater than 50 to mitigate the negative effects of inbreeding depression (Jamieson and Allendorf 2012). Additionally, a population with a N_e of 500 or greater can sufficiently maintain genetic diversity necessary for future adaptation (Jamieson and Allendorf 2012). Our N_e estimates suggest that the population of Chinook above Cougar Dam will be minimally affected by inbreeding depression. Though, it is difficult to determine if genetic variation will be maintained for future adaption because it depends on one's definition of a population. Considering salmonids in general, the reintroduced adults above Cougar Dam are not likely a discrete population, but rather a part of the larger McKenzie River total population.

Conclusions

We have consistently found that Chinook are not replacing themselves above Cougar Dam when only HOR Chinook were reintroduced. These results may suggest the need for improved juvenile survival

through Cougar Dam. However, we have not evaluated CRR in years that both HOR and NOR Chinook have been reintroduced. These years may have higher CRR because we have found higher mean RS estimates among NOR Chinook in 2010 and 2011. However, we caution relying on the use of results made with RS estimates too heavily, because our results suggest that RS does not explain 74.3% of the variation in TLF. In this report, we also found that the LSDR method was effective at limiting the number of non-Cougar adult returns transported above Cougar Dam, and we recommend that managers continue to use this method. Results from adult-adult pedigrees in future years will provide valuable information regarding CRR rates and TLF estimates between HOR and NOR Chinook, which can be used to improve the Chinook reintroduction program above Cougar Dam.

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