

December 2022 Report

EVALUATING SPRING CHINOOK SALMON RELEASES ABOVE COUGAR DAM, ON
THE SOUTH FORK MCKENZIE RIVER, USING GENETIC PARENTAGE ANALYSIS

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Cougar Dam Genetic Parentage Analysis

Summary

Summary text.

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Objectives

1. Determine the number and proportion of unmarked, presumed natural-origin (NOR) adult Chinook salmon sampled at various locations in the South Fork McKenzie River (e.g., Cougar Trap and spawning grounds below Cougar Dam) in 2016 – 2020 that can be assigned as progeny of Chinook salmon previously released above Cougar Dam, South Fork McKenzie River in 2011 – 2017.
2. Estimate and report the annual abundance and age structure of adult Chinook salmon that return to the South Fork McKenzie River in 2016 – 2020 that can be confidently assigned to parents through genetic parentage analysis.
3. Estimate the total lifetime fitness (TLF) for Chinook salmon released above Cougar Dam in 2011 – 2015. These estimates include NOR adult offspring sampled at Cougar Dam, as well as NOR spawners encountered on spawning grounds below the dam in 2014 – 2019.
4. Estimate cohort replacement rate (CRR), or “the number of future spawners produced by a spawner” for spring Chinook salmon released above Cougar Dam in 2011 – 2015.
5. Estimate the effective number of breeders (N_b) for the adult salmon population released above Cougar Dam in 2011 – 2015.
6. Determine the effect of various aspects of release strategy on the TLF of adult spring Chinook salmon released above Cougar Dam in 2011 – 2015, including timing and location of releases, sex ratios, origin, and number of salmon released.
7. Evaluate fitness differences between hatchery-origin (HOR) and NOR Chinook salmon released above Cougar Dam in 2011 – 2015 through assignment of adult offspring returns in 2014 – 2020.

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Introduction

Spring Chinook salmon (*Oncorhynchus tshawytscha*) in the Upper Willamette River, Oregon (UWR) are listed as a threatened evolutionary significant unit (ESU) under the U.S. Endangered Species Act (ESA) (NMFS 1999). Construction and operation of multiple U.S. Army Corps of Engineers (USACE) high head dams throughout the UWR have contributed to declines in abundance of this ESU by preventing access to historical spawning habitats and modifying temperature and flow regimes (NMFS 2008). The McKenzie River is a tributary of the UWR and historically supported one of the largest populations of spring Chinook salmon in the Willamette Basin (McElhany et al. 2007). Unlike most tributaries of the UWR, the McKenzie River continues to produce a large proportion of natural-origin (NOR) spring Chinook salmon (Johnson and Friesen 2010). Access to historical spawning habitat on the McKenzie River is blocked by several high head dams. Construction of Cougar Dam in 1964 on the South Fork McKenzie River impeded access to approximately 40 river km of the historically most productive reaches on the river (NMFS 2008).

Since 1993, hatchery-origin (HOR) salmon have been released above Cougar Dam to re-establish historical ecosystem functions. Juveniles produced by adults released above the dam provide prey for ESA listed bull trout (*Salvelinus confluentus*), and decaying carcasses restore nutrient transport. Anecdotal evidence suggested that some juvenile salmon survived downstream passage through the dam and returned to the South Fork McKenzie River as adults to spawn. After construction of a trap and haul facility at the base of Cougar Dam (hereafter the Cougar Trap) in 2010, NOR salmon were also released above the dam. From 2010 – 2012, all NOR salmon collected at the Cougar Trap were released above the dam, but from 2013 onwards, some or all NOR salmon collected at the Cougar Trap were floy-tagged, released downstream and only released above the dam if they were collected a second time.

The reintroduction of spring Chinook salmon above Cougar Dam has been evaluated using genetic parentage analysis since 2007 (Banks et al. 2013; Banks et al. 2014; Sard et al. 2015; Banks et al. 2016; Sard et al. 2016b). Previous USACE reports have assigned potential offspring to candidate parents released or otherwise sampled above the dam and used the resulting pedigrees to evaluate release strategies and infer demographic parameters that describe the productivity of the above dam population. These reports found that the cohort replacement

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rate (CRR), or “the number of future spawners produced by a spawner” (Botsford and Brittnacher 1998), was less than one in the years from 2007 – 2010, indicating that the above dam population was not replacing itself. They also found that the likelihood a NOR salmon collected at the Cougar Trap did not assign to a salmon previously released above the dam (i.e. likely NOR immigrant) increased throughout the season. Importantly, later reports (Banks et al. 2014; Banks et al. 2016) also identified significant differences in the fitness of NOR vs. HOR male salmon using two metrics, reproductive success (RS) and total lifetime fitness (TLF). RS is defined as the number of age-0 juveniles that assigned to an adult released above the dam in the previous year, and TLF as the number of age-3 to age-6 returning adult offspring that assigned to a previously released adult. Based on these findings, previous reports recommended prioritizing NOR instead of HOR salmon above the dam, judiciously supplementing with HOR females to reach demographic targets, limiting the number of HOR males above the dam, and carefully weighing the demographic and genetic benefits of releasing NOR immigrants above the dam against the costs of releasing NOR salmon into a likely demographic sink.

However, these recommendations came with the caveat that observed fitness differences between NOR and HOR salmon were based primarily on RS, which explained just 25.7% and 17.4% of the variation in TLF in 2008 and 2009, respectively, while direct comparisons of TLF between NOR and HOR salmon were available for just a single parental cohort (2010)(Banks et al. 2014; Banks et al. 2016). Here, we extend the evaluation of spring Chinook salmon releases above Cougar Dam on the South Fork McKenzie River to address the Research, Monitoring & Evaluation (RM&E) needs of the Reasonable and Prudent Alternatives (RPAs) described in the Willamette Project Biological Opinion (NMFS 2008):

- RPA 4.1 (adult Chinook salmon outplanting above dams)
- RPA 4.3(2) (identify protocols for optimal handling, sorting, and release conditions for ESA listed fish collected at USACE-funded fish collection facilities)
- RPA 4.7 (adult fish release sites above dams)
- RPA 5.4 (Cougar Dam RM&E, including effectiveness of the trap-and-haul program)
- RPA 6.1.5 (management of hatchery-origin spring Chinook salmon upstream of Cougar Dam)
- RPA 6.2.3 (continue adult Chinook salmon outplanting, Willamette basin-wide)
- RPA 9.3 (effectiveness of rebuilt trap-and-haul facilities and strategies)

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- RPA 9.5.1(3) (abundance and survival of spawners above Cougar Dam)
- RPA 9.5.1(4) (reproductive success of hatchery fish in the wild)

This research also addresses the implementation and reporting requirements (IRR) for the spring Chinook salmon hatchery programs detailed in Section 2.9.4 of the 2019 Biological Opinion for Upper Willamette hatchery programs (NMFS 2019).

- IRR 3a (assess genetic pedigree of Chinook salmon)
- IRR 3c (adaptively manage hatchery salmon outplanting above federal dams)

Specifically, we evaluate potential offspring sampled in the South Fork McKenzie River from 2016 – 2020 and candidate parents released above Cougar Dam from 2010 – 2017. We present assignment rates, fitness and demographic metrics, and identify significant predictors of fitness using a modeling approach. Finally, we update the recommendations of previous reports with particular attention to future supplementation of the above dam population with NOR *vs.* HOR salmon.

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Methods

Study System and Tissue Sample Collection

Adult HOR spring Chinook salmon from the McKenzie River Hatchery and, infrequently, the Leaburg Hatchery have been released annually above Cougar Dam since 1996. We refer to these individuals as *hatchery outplants*. The Cougar Trap has been operational throughout the spawning migration each year since 2010, except for July 19th to August 6th, 2011 (Figure 1). Primarily NOR Chinook salmon have been collected at the trap, transported in trucks and released above Cougar Dam at one of five sites to spawn. The above dam population has continued to be supplemented with **hatchery outplants** from McKenzie or Leaburg Hatcheries. To date, there is no assisted downstream passage for juveniles produced above the dam. Instead, juvenile fish can exit the reservoir volitionally, either by passage through hydroelectric turbines or over a steep, 73 m ‘regulating outlet’ spillway.

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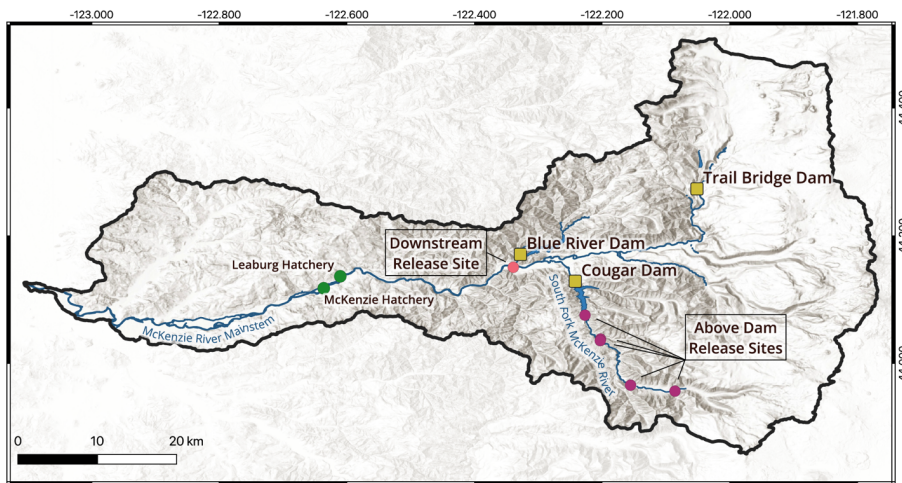


Figure. 1. Map of McKenzie River watershed, including major high head dams (gold squares), hatcheries (green circles), and release sites on the mainstem (pink circle) and on the South Fork McKenzie River, above Cougar Dam (purple circles). Data sources: ESRI World Hillshade, USGS NHDPlus HR

In 2013 and 2014, all NOR Chinook salmon collected at the Cougar Trap after September 1st were double floy-tagged and released into the mainstem McKenzie River, downstream of the

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confluence with the South Fork (Figure 1). After September 1st, only floy-tagged NOR Chinook salmon collected at the Cougar Trap were released above the dam. This program has been referred to as *late season downstream release* (LSDR) (Banks et al. 2014). Beginning in 2015, all NOR Chinook salmon collected at the Cougar Trap, regardless of date, were double floy-tagged and released into the mainstem, downstream of the confluence with the South Fork. Among NOR salmon collected at the Cougar Trap, only those with floy-tags were released above the dam. We refer to this program as *downstream recycling*. The downstream recycling program has been implemented each year since 2015. The small number of HOR salmon collected at the Cougar Trap were generally not recycled downstream but were released above the dam.

Previously published reports and papers evaluating the population above Cougar Dam (Banks et al. 2013; Banks et al. 2014; Sard et al. 2015; Banks et al. 2016; Sard et al. 2016b) presented results based on tissue samples collected from nearly all NOR Chinook salmon that entered the Cougar Trap from 2010 – 2015 and nearly all Chinook salmon released above the dam, regardless of origin, from 2007 – 2013. Here, we include tissue samples from nearly all NOR Chinook salmon that entered the Cougar Trap from 2010 – 2020 and nearly all Chinook salmon released above the dam, regardless of origin, from 2007 – 2017. Tissue samples were also collected from NOR Chinook salmon carcasses identified during spawning ground surveys (SGSs) on the South Fork McKenzie River from 2011 – 2019, including SGSs above the dam and SGSs between the confluence with the mainstem McKenzie River and the dam. Additionally, tissue samples were collected from precocial male Chinook salmon identified on spawning grounds above the dam during 2014.

Genotyping

Consistent with previously published reports (Banks et al. 2013; Banks et al. 2014; Banks et al. 2016; Sard et al. 2016b) all NOR Chinook salmon sampled from 2016 – 2020, and all sampled Chinook salmon released above Cougar Dam from 2014 – 2017 were genotyped at a panel of microsatellite loci. Whole genomic DNA was isolated from tissue samples using the protocol of Ivanova et al. (2006). Each DNA sample was then genotyped at 11 microsatellite loci: *Ots201*, *Ots208b*, *Ots209*, *Ots211*, *Ots212*, *Ots215*, *OtsG249*, *Ots253b*, *OtsG311*, *OtsG409*, *Ots515* (Banks et al. 1999; Naish and Park 2002; Williamson et al. 2002; Greig et al. 2003) and at the sex-linked marker, *Oty3*, to determine sex (Brunelli et al. 2008). Loci were amplified using

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polymerase chain reaction (PCR), PCR products were visualized on an ABI 3730xl DNA analyzer, and allele sizes scored using GENEMAPPER software (Version 5.0, Applied Biosystems, Inc., Foster City, CA). We also collated the unfiltered genotype data for all individuals that were genotyped in previous studies, including all NOR Chinook salmon sampled from 2010 – 2015, and all sampled Chinook salmon released above Cougar Dam from 2007 – 2013. These data were appended to those collected for the present study, before genotype quality filtering.

To produce a genetic dataset appropriate for parentage analysis, we conducted genotype quality filtering and removed potential duplicates. Salmon with successfully scored genotypes at less than seven loci were excluded, a threshold determined based on the sequential cumulative non-exclusion probabilities observed among loci. Different genotype quality filtering cutoffs were applied, therefore final sample sizes after filtering may vary from previous reports. Multilocus genotypes were then compared among individuals to identify salmon that could have been sampled more than once. For example, NOR Chinook salmon sampled at the Cougar Trap might be later sampled as carcasses. We considered individuals first collected at the Cougar Trap and later sampled as carcasses during SGSs as Cougar Trap individuals in all subsequent analyses. If individuals failed to genotype at the sex-linked marker *Oty3*, phenotypic information was used to infer sex.

Genetic Parentage Analysis

The primary objective of this report was to evaluate spring Chinook salmon releases above Cougar Dam, on the South Fork McKenzie River. Therefore, when inferring pedigrees, we defined *potential offspring* as NOR Chinook salmon sampled anywhere on the South Fork McKenzie River and *candidate parents* as any Chinook salmon, regardless of origin, released or otherwise sampled above Cougar Dam (Figure 2). Potential offspring that did not assign to at least a single candidate parent were assumed to be *NOR immigrants* descended from parents that spawned in the South Fork McKenzie River below the dam, in the mainstem McKenzie River, or elsewhere.

Previous reports and papers evaluating releases of Chinook salmon above Cougar Dam on the South Fork McKenzie River considered potential offspring from 2010 – 2015 and candidate parents from 2007 – 2012 (Banks et al. 2013; Banks et al. 2014; Banks et al. 2016;

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Sard et al. 2016b). Most Chinook salmon on the South Fork McKenzie River express an age at maturity of three to six years, with the majority being age-4 and age-5 (Banks et al. 2013; Banks et al. 2014; Sard et al. 2015; Banks et al. 2016; Sard et al. 2016b). Therefore, previous reports assigned offspring to all candidate parents from 2007 – 2009. Results based on the genetic parentage analysis of salmon released above Cougar Dam in 2010 were also provided along with the caveat that age-6 offspring were not yet evaluated.

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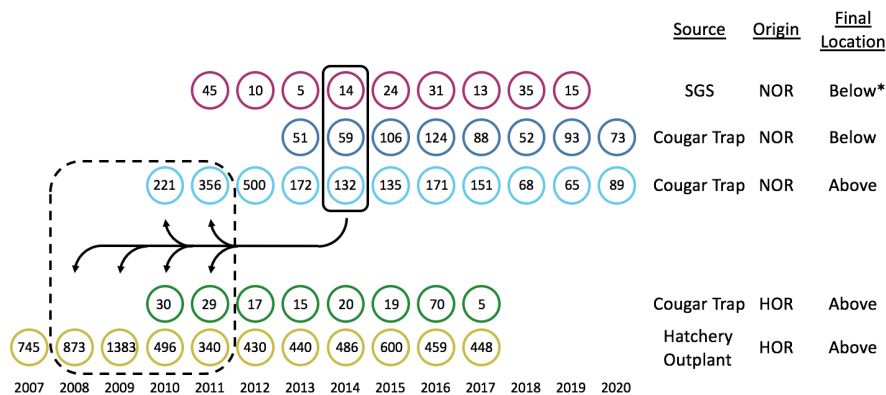


Figure 2. Illustration of genetic parentage analysis. Groups of individuals are organized into sets of potential offspring (solid rectangle) and candidate parents (dashed rectangle). Here, the 205 potential offspring that returned to the South Fork McKenzie in 2014 are assigned to 3,728 candidate parents released above Cougar Dam three to six years earlier (2008 – 2011). Source refers to where an individual was initially encountered: during a spawning ground survey on the South Fork McKenzie River (SGS), at the Cougar Trap (Cougar Trap) or at either the McKenzie or Leaburg Hatchery (Hatchery Outplant). Final location refers to whether a salmon was released above Cougar Dam (above) or not (below). Potential offspring include all NOR salmon, regardless of source or final location. Candidate parents include all salmon released above the dam, regardless of origin or source. * Note that 5 NOR SGS individuals and 12 NOR precocial males sampled above Cougar Dam are also included as both candidate parents and potential offspring and are not depicted in the figure.

We assigned potential offspring sampled on the South Fork McKenzie from 2016 – 2020 to candidate parents from 2010 – 2017. Using data collected for previous reports, we also re-assigned potential offspring sampled on the South Fork McKenzie from 2011 – 2015 to candidate parents from 2007 – 2012. Collectively, these assignments allow us to identify all offspring of salmon released above Cougar Dam from 2007 – 2014, most offspring of salmon released above Cougar Dam in 2015 and some offspring of salmon released above the dam from 2016 – 2017 (Figure 3).

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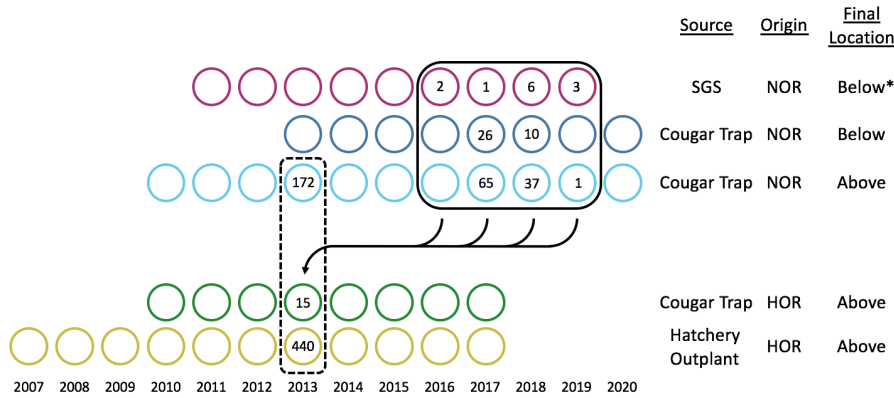


Figure 3. Illustration of how genetic parentage analysis results (Figure 2) are combined to make demographic inferences about parental cohorts. Here we demonstrate how inferences about the 2013 parental cohort are drawn. Assignments between offspring in 2016 – 2019 (solid rectangle) that assigned to parents in 2013 (dashed rectangle) are depicted as black arrows. Labels are as in Figure 2 except the values inside circles, which reflect the number of candidate parents and assigned offspring. For example, total cohort replacement rate is the sum of the values in the solid rectangle divided by the sum of the values in the dashed rectangle.

We inferred pedigrees by comparing microsatellite genotypes of potential offspring in each year to the genotypes of all candidate parents three, four, five and six years prior, as indicated in Figure 2. The comparisons were first conducted within the maximum-likelihood framework of the parentage assignment program CERVUS Version 3.07 (Kalinowski et al. 2007). Parent(s)-offspring assignments were made using a strict 95% confidence criterion, a minimum of seven loci, an assumed parent sampling rate of 95%, and a maximum of one mismatch between parent-offspring pairs (maximum of two mismatches for parent-offspring trios). We also estimated non-exclusion probabilities and expected number of false parent-offspring pairs (Christie 2010) (Appendix A). Parentage assignments from CERVUS were then verified using the combined PLS-FL algorithm implemented in COLONY Version 2.0.6.8 (Jones and Wang 2010). The second analysis was conducted because CERVUS's likelihood-based parentage assignment method requires an accurate estimate of the number of parents contributing to a cohort (Harrison et al. 2013), and previous work suggested that adfluvial females and precocial males may contribute to the productivity of the above dam population (Banks et al. 2016). Moreover, simulation studies have suggested that COLONY's assignment protocol is the most accurate of three alternate pedigree reconstruction methods (Harrison et al.

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2013). COLONY was run using the following parameters: medium run length, polygamous male and female setting, weak sibship prior of 1, allele dropout and miscalled allele rate prior of 2% per locus, and an assumed 95% rate of sampled parents. We also estimated the allele miscall rate and dropout rate in our dataset using COLONY (Wang 2018) (Appendix A).

Given the longitudinal nature of the South Fork McKenzie River spring Chinook salmon genetic parentage analysis, we developed an automated, reproducible procedure for choosing the best consensus pedigree from the outputs of CERVUS and COLONY that does not allow for technician bias. Other changes from previously reported parentage analysis methods include application of an updated version of COLONY. To evaluate how changes to parentage assignment procedure and the software may impact results, we compared results between pedigrees inferred using this approach and those in previous reports for the six years of overlap in assigned offspring (2010 – 2015). Ultimately, genetic pedigrees inferred with the modified parentage assignment procedure and updated software were used to identify long-term trends in the demographic and genetic characteristics of South Fork McKenzie River spring Chinook salmon.

Assignments

We summarized the number and proportion of unmarked adult Chinook salmon sampled at either the Cougar Trap or spawning grounds below Cougar Dam in 2010 – 2020 that can be assigned as offspring of Chinook salmon previously released above Cougar Dam in 2007 – 2017. To evaluate the effect of the LSDR and downstream recycling programs, we determined the number of both NOR salmon produced above the dam and NOR immigrants that were collected at the Cougar Trap each day. To better understand the relationship between arrival time and the probability that an individual collected at Cougar Trap was not produced above the dam, we fit a binomial generalized linear mixed model (GLMM_{immigrant}) using *sex*, and the *Julian day of sampling* at the Cougar Trap, for offspring years 2013 – 2020. Because the relationship varied strongly across years, we also included a random slope for *Julian day of sampling* across years and a random intercept for year. After model validation, effects of *sex* and *Julian day of sampling* were evaluated using likelihood ratio tests and Wald Tests.

Demography

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Age at Maturity

For each assigned progeny, we subtracted the return year (e.g., 2016) by each parent(s) release year (e.g., 2013) to infer age at maturity (e.g., age-3) and determined overall age structure among the adult returns from 2010 – 2020. Note that, because our candidate parents include salmon released above the dam from 2007 – 2017, we were able to identify age-3, age-4, age-5, and age-6 offspring in years 2013 – 2020.

Total Lifetime Fitness

Total lifetime fitness (TLF) is defined as the total number of adult offspring assigned to a candidate parent (Figure 2). Since most Chinook salmon on the South Fork McKenzie River express an age at maturity of three to six years, we estimated TLF for candidate parents if we sampled their potential offspring three, four, five, and six years after candidate parents were released above Cougar Dam (Figure 2). We also estimated partial TLF for candidate parents if at least a portion of their offspring are expected to have returned three, four, or five years after candidate parents were released above Cougar Dam. Candidate parents in our dataset include hatchery outplants from 2007 – 2017, NOR, HOR and unknown origin salmon released above Cougar Dam from the Cougar Trap from 2010 – 2017, precocial male salmon sampled above Cougar Dam in 2014, and NOR salmon sampled as carcasses during spawning ground surveys above the dam in 2014 and 2016.

We genotyped candidate parents from 2007 – 2017 and potential offspring from 2010 – 2020, therefore we present TLF for candidate parents from 2007 – 2014. We also present partial estimates of TLF for candidate parents in 2015, 2016 and 2017, but note that these partial values underestimate TLF. We always note these partial TLFs with an asterisk in figures and tables.

Cohort Replacement Rate

CRRs were estimated for each cohort of candidate parents released or observed above the Cougar Dam. We report CRR_{total} , defined as the total number of offspring produced by salmon released or observed above Cougar dam divided by the total number of salmon released or observed above Cougar dam. We also report both a female-only CRR_F and a male-only CRR_M . For example, CRR_F is the total number of age-3, age-4, age-5, and age-6 female offspring produced by females released or observed above Cougar Dam divided by the total number of

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females released or observed above Cougar Dam. We present CRR estimates for parental cohorts from 2007 – 2015, but note that the 2015 CRR is likely an underestimate given that it does not include age-6 offspring. This year is noted with asterisks in tables and figures.

Note that our definitions and estimation of CRR differ from those used in previous reports (Banks et al. 2013; Banks et al. 2014; Banks et al. 2016). For instance, CRR_F was reported as CRR in all previous reports and in the latter report both carcasses and unsampled offspring inferred from grandparentage analysis contributed to the CRR_F (Banks et al. 2016), whereas other estimates of CRR_F only considered offspring sampled at the Cougar Trap (Banks et al. 2013; Banks et al. 2014). CRR_F values might also vary due to changes in genotype quality filtering and assignment. To permit the identification of long-term trends, we present CRR for years previously reported (2007 – 2010), as well as CRR for 2011 – 2017 using a consistent, updated approach. We also distinguish between CRR_{total} , CRR_F , and CRR_M .

Effective Number of Breeders

The effective number of breeders (N_b) among cohorts of salmon released or observed above Cougar Dam was estimated using the linkage disequilibrium (LD) method, as implemented in the program NEESTIMATOR v2.1 (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 the genotypes of all offspring assigned to each parental cohort from 2007 – 2015, in which all or most offspring are expected to have returned. We excluded singletons and generated 95% confidence intervals using a jackknife re-sampling method (Waples and Do 2008). In each year, we calculate the ratio of N_b to the number of candidate parents (N_{cand}). N_{cand} potentially underrepresents the total number of salmon in the parental cohort above the dam due to incomplete sampling or incomplete genotyping. We also compare N_b to the number of candidate parents that produced one or more adult progeny (i.e. successful parents). Note that our methods to estimate N_b differs from methods used in previous reports. Previous reports used NEESTIMATOR v2.0, and excluded all alleles below a minor allele frequency of 0.02. To permit the identification of long-term trends in N_b in this report, we present N_b values for years previously reported (2007 – 2010), as well as N_b values for 2011 – 2015 using a consistent, updated approach.

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Predictors of Fitness

We fit a generalized linear mixed model (GLMM) to identify significant predictors of fitness in the above dam population. Specifically, we fit a single GLMM on TLF of candidate parents from 2007 – 2014 and partial TLF of candidate parents from 2015. Candidate parents in 2015 were included in addition to candidate parents from 2007 – 2014, because age-6 offspring are expected to contribute very little to TLF. We considered the influence of multiple potential predictors of fitness including *sex*, *origin*, *release day*, *release location*, *release group density*, *release group sex ratio*, *annual sex ratio*. In addition to fitting each of these predictors as a main fixed effect, we also examined three interaction terms, including *sex*release day*, *sex*origin*, and *sex*annual sex ratio* and two random effects, *release group*, and *year*. *Release day* is the Julian day that individuals were released and was modeled as a continuous fixed effect. *Release group* is defined as the individuals released at a single location during a single day. *Release group density* is the number of individuals in a release group. *Release group sex ratio* is the ratio of males to females in a release group. *Annual sex ratio* is the ratio of males to females in a year. Sex ratios were log-transformed before inclusion as predictors in a model.

Our modeling approach primarily followed the recommendations of Zuur et al. (2009) and Bolker (2015). We conducted an exploratory data analysis to identify the distribution and link function that provided the best fit to the data, calculated variance inflation factors of main effects to examine the data for multicollinearity and determined if non-linear effects of *release day*, *release group density*, *release group sex ratio*, or *annual sex ratio* improved the fit to the data. Model fit under different distributions were evaluated using AIC, BIC, rootograms and QQ-plots of randomized quantile residuals from the *COUNTREG* package in R, and simulated residuals produced by the *DHARMA* package in R. Non-linear effects were evaluated using AIC, BIC, and likelihood ratio tests.

After exploratory data analysis, we fit our models using the negative binomial distribution and a log link function using the *glmmTMB* function from the *glmmTMB* package in R. For model selection, we first identified the best random effects structure by fitting a fully saturated fixed effect model using restricted maximum likelihood and varying the random effects. Model selection of random effects was by AIC. After refitting the fully saturated fixed effects model with the final random effects structure using maximum likelihood, we conducted model selection for fixed effects based on both likelihood ratio tests for each predictor and

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backward stepwise selection using Wald tests for significant effects of each predictor. Where the two model selection criteria disagreed we chose to be conservative and only retained predictors selected by both approaches. After a final model was selected (hereafter GLMM_{TLF}), we conducted model validation by testing for goodness of fit, overdispersion and influence of outliers using residuals simulated by the *DHARMA* package in *R*. Effect plots of significant predictors in the GLMM_{TLF} were generated using the *effects* package in *R* and conditioned on the typical values of all other significant predictors in the final model.

We also fit a *post-hoc* GLMM on TLF for a subset of candidate parents with *size at maturity* measurements (hereafter GLMM_{size}). We defined *size at maturity* as the fork length in cm for candidate parents measured at the time of release. This GLMM_{size} used the final significant predictors from the GLMM on TLF using all parents (GLMM_{TLF}), but also included *size at maturity* as an additional fixed effect. Significance of the effect of *size at maturity* was tested using a likelihood ratio test. We also examined the relationship between *origin* and *size at maturity* using a linear mixed model that fit *size at maturity* as an effect of *origin*, *sex* and a random effect of year.

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Results

Sampling and Genotyping

After filtering, there were 9,839 individuals genotyped at an average of 10.86 microsatellite loci (Table 1). 99% of individuals in the filtered dataset were genotyped at nine or more loci. There were 6,700 salmon initially collected at McKenzie or Leaburg Hatcheries and transported above Cougar Dam (hatchery outplants), 2,930 NOR and HOR salmon initially encountered at the Cougar Trap and released above the dam, into the mainstem or immediately below the tailrace of the dam, 12 precocial males sampled on spawning grounds above the dam, 192 carcasses sampled during SGSs below the dam, and five carcasses sampled during SGSs above the dam (Table 2).

Table 1. Summary of genotype quality filtering. Individuals were removed from the analysis if they were genotyped at < 7 loci (missingness filtered), or if they represented a duplicate multilocus genotype (duplicate filtered).
* Indicates some or all individuals from this year genotyped in prior reports

Year	Tissue Samples	Missingness Filtered	Duplicate Filtered	N _{final}
2007*	746	1	0	745
2008*	873	0	0	873
2009*	1386	2	1	1383
2010*	748	1	0	747
2011*	791	20	1	770
2012*	962	3	2	957
2013*	695	4	1	690
2014*	744	16	2	726
2015*	917	28	5	884
2016	891	20	4	867
2017	718	9	2	707
2018	156	1	0	155
2019	192	18	1	173
2020	169	7	0	162

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Table 2. Sample sizes after genotype quality filtering of salmon initially encountered at McKenzie or Leaburg Hatcheries (Hatchery Outplant), at the Cougar Trap, during spawning ground surveys (SGS) above or below Cougar Dam, or as precocial males observed on the spawning grounds above Cougar Dam. Note that all hatchery outplants are HOR, Cougar Trap salmon include both NOR, HOR and unknown origin salmon, and all precocial males and SGS salmon are NOR.

Year	Hatchery Outplant	Cougar Trap			Precocial Male	SGS	
		HOR	NOR	Unknown		Below	Above
2007	745						
2008	873						
2009	1383						
2010	496	30	221				
2011	340	29	356			45	
2012	430	17	500			10	
2013	440	22	223			5	
2014	486	21	191	1	12	14	1
2015	600	19	241			24	
2016	459	74	295	4		31	4
2017	448	6	239	1		13	
2018			120			35	
2019			158			15	
2020			162				

Assignment

We attempted to assign 2915 potential offspring to 8985 candidate parents (Tables 4 and 3, respectively). Of these 2915 offspring, 1669 assigned to 1681 successful parents for an overall assignment rate of 57% (1669/2915) (Table 4). In the eight years when all candidate parents of potential offspring were sampled (2013 – 2020), 1183 of 1783 potential offspring assigned to at least one parent, for a total assignment rate of 67%. Within a year, the assignment rate varied from a low of 49% in 2019 to a high of 94% in 2020 (Table 4).

For the six offspring years when pedigrees were inferred in both this report and in previous reports, the average absolute difference in assignment rate was 0.7% (Table 4), indicating that changes to software versions, genotype quality filtering and assignment procedures had only a limited impact on the final pedigree.

Commented [OMKG11]: From a low of 49% in 2019 to a high of 94% in 2020

So the average across all years was 67%?

Commented [DD12R11]: Yes. I think “total” might be preferable to “average” here. That way we can avoid any confusion about weighted vs unweighted means between years.

The total number of offspring that assigned to a parent in 2013 – 2020 was 1183 (of 1783 potential offspring), for a *total* assignment rate of 67%. Within years, the assignment rate ranged from 49% to 94%.

Also made some minor changes in the section below that just covers Cougar Trap offspring.

Cougar Dam Genetic Parentage Analysis

Table 3. Number of individuals released or otherwise sampled above Cougar Dam retained in the final filtered dataset. These values correspond to candidate parents used in genetic parentage analysis. All hatchery outplants are HOR, all precocial males and SGS individuals are NOR.

Year	Hatchery Outplant	Cougar Trap			Precocial Male	SGS
		HOR	NOR	Unknown		
2007	745					
2008	873					
2009	1383					
2010	496	30	221			
2011	340	29	356			
2012	430	17	500			
2013	440	15	172			
2014	486	20	132	1	12	1
2015	600	19	135			
2016	459	70	171	1		4
2017	448	5	151	1		

Table 4. Number of NOR Chinook salmon sampled in the South Fork McKenzie River and retained after genotype quality filtering ($n_{\text{potential offspring}}$) in each year and the number (n_{assigned}) and percent (% Assigned) assigned to candidate parents. Results for the full set of potential offspring including those sampled at the Cougar Trap, during spawning ground surveys or as precocial males above the dam (Overall), and potential offspring initially sampled at the Cougar Trap only (Cougar Trap) are presented separately. The previously reported assignment rate (Previous % Assigned) (for Cougar Trap only) is also presented. Note that the percent of NOR immigrants is equal to (1 - % assigned) for the Cougar Trap in 2013 – 2020.

* Note that for potential offspring that returned in 2010 – 2012, not all potential parents are included as candidate parents in the genetic parentage analysis.

Year	Overall			Cougar Trap			
	$n_{\text{potential offspring}}$	n_{assigned}	% Assigned	$n_{\text{potential offspring}}$	n_{assigned}	% Assigned	Previous % Assigned
2010*	221	14	6%	221	14	6%	6%
2011*	401	140	35%	356	138	39%	38%
2012*	510	328	64%	500	326	65%	64%
2013	228	153	67%	223	153	69%	68%
2014	218	118	54%	191	117	61%	61%
2015	265	179	68%	241	176	73%	72%
2016	330	228	69%	295	212	72%	
2017	252	173	69%	239	169	71%	
2018	155	100	65%	120	92	77%	
2019	173	84	49%	158	80	51%	
2020	162	152	94%	162	152	94%	

Commented [OMKG13]: We discussed this briefly at lab meeting. Unlike the North Santiam which saw a large increase in the number of returns and assignment rate in 2020, here we just see an increase in the assignment rate. Based on Figure 4, it looks like all of these fish were collected before or close to Julian Day 245 which may help explain this result?

Commented [DD14R13]: Yes, I think the sampling explains the results, but only in part.

The high overall rate is certainly driven in part by the period in which sampling occurred. Something to keep in mind here is that USACE chooses to close the trap at different times in each year. From the logs it looks like USACE closed the trap for the season in 2020 after two weeks of zero Chinook salmon returns. It's certainly possible that more salmon might have arrived at the trap later and it is likely that many of these would be NOR immigrants.

I don't think the sampling period tells the entire story, though. The assignment rate was unusually high in 2020 BEFORE the trap was closed (figure 4), which also contributes to the very high assignment rate in that year. Contrast 2020 with 2018, when the trap was closed even earlier, but the assignment rate before trap closure is similar to the "typical" pattern (heavy black line figure 4). The overall assignment rate in this year is high (77%), but not as high as 2020 (94%).

I was concerned that the pattern here may be spurious and stem from differences in genotyping between Dave and I. 2020 and their candidate parents were all genotyped by me, but the same applies to 2019 and that year saw the lowest assignment rate, so I doubt changes to genotyping are the cause of the high assignment rate we observe in 2020.

Cougar Dam Genetic Parentage Analysis

Considering only offspring years when all candidate parents that returned three to six years prior were sampled (2013 – 2020), 1629 potential offspring were sampled at the Cougar Trap. Of these 1629, 1151 assigned to at least one parent above Cougar Dam, for a total assignment rate of 71%. Assuming individuals that did not assign to at least one parent above the dam were not produced above the dam, this suggests 29% of NOR salmon collected at the Cougar Trap from 2013 – 2020 were NOR immigrants. We found that the proportion of NOR immigrants collected at the Cougar Trap increased throughout the season (Table 5, Figure 4). In our model (GLMM_{immigrant}), the proportion of NOR immigrants collected at the Cougar Trap was estimated to increase from less than 5% early in the season to ~50% by September 1st. However, there was substantial variation among years in the relationship between time and the proportion of NOR immigrants collected at the Cougar Trap. The 95% confidence interval of the predicted proportion of NOR immigrants on September 1st spanned from ~38% – 63%.

Table 5. GLMM_{immigrant} model fit. Results of generalized linear mixed model examining the influence of *sex*, *Julian day of sampling* on whether or not a NOR salmon sampled at the Cougar Trap was assigned to at least one parent from above the dam. Only the first observation of an individual is used. Estimated effect (β) and standard error (s.e.) of each fixed predictor on the link (logit) scale for predictors that were retained in the final model are presented. Variance (σ^2) and standard deviation (s.d.) for random intercepts for year and random slope *Julian day of sampling* per year and their correlation (ρ) are also presented. The null hypothesis that each predictor did not significantly improve the model effect was tested with a likelihood ratio test (LRT p-value). The null hypothesis that each predictor has an effect significantly different than zero was evaluated with the Wald test (Wald p-value). Significant p-values are in bold.

Fixed effects	β	s.e	LRT p-value	Wald p-value
(Intercept)	7.130	0.930		1.7 x 10⁻¹⁴
<i>Julian day of sampling</i>	-0.029	0.004	4.7 x 10⁻⁵	1.3 x 10⁻¹²
<i>Sex</i> [Male]	-0.261	0.135	0.053	0.054
Random effects	σ^2	s.d.	ρ	
<i>year</i> (Intercept)	4.883	2.209	-0.95	
<i>year</i> * <i>Julian day of sampling</i>	8.5 x 10 ⁻⁵	0.009		

Cougar Dam Genetic Parentage Analysis

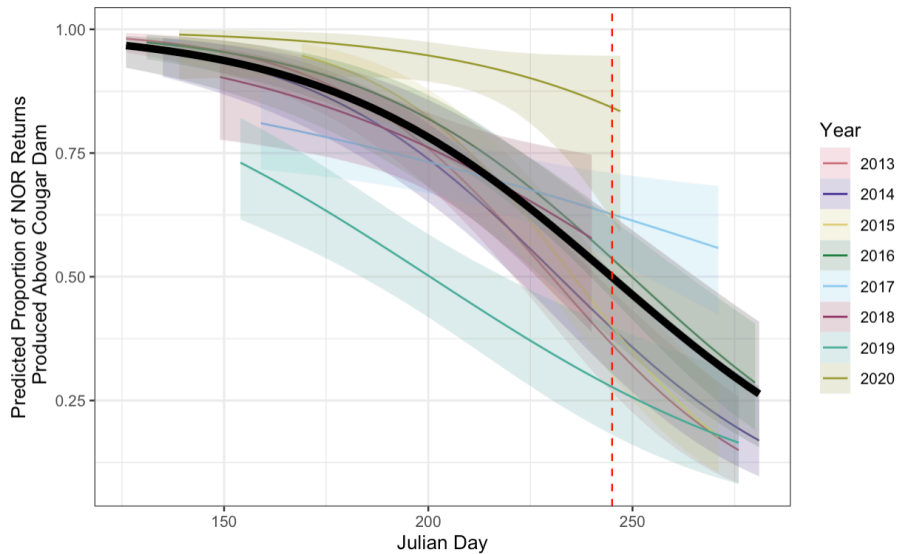


Figure 4. Effect of *Julian day of sampling* on the predicted proportion of NOR salmon collected at the Cougar Trap was produced above the dam (thick black line) as predicted by GLMM_{immigrant}. Only the first observation of a salmon at the Cougar Trap was used. Vertical dashed red line indicates Julian Day 245, which corresponds to either September 1st or October 31st, depending on the year. Light colored lines show predicted effect of *Julian day of sampling* in from binomial GLMs fit to data from each year.

In 2015 – 2020, when downstream recycling was implemented, 875 NOR salmon collected at the Cougar Trap were produced above the dam in 2009 – 2016. Of these 875 NOR salmon that were recycled downstream, 275 (31%) did not return to the trap, and 600 (69%) returned a second time. The mean interval between first and second collection at the Cougar Trap for these NOR salmon was 30.9 days (s.d. = 28.3). During the same period from 2015 – 2020, 334 NOR immigrants were collected at the trap. Of these, 252 (75%) did not return to the trap a second time, and 82 (25%) returned a second time. In summary, NOR salmon produced above the dam were significantly more likely to return a second time than NOR immigrants (odds ratio = 6.7, Fisher’s exact test, $p = 2.2 \times 10^{-16}$). If LSDR using a September 1st cutoff date had been implemented during these years instead of downstream recycling, 834 (95%) NOR salmon produced above the dam and 212 (63%) NOR immigrants would have been released above the dam.

Commented [DD15]: Is this confusing? We attempt to assign 2015 – 2020 potential offspring to candidate parents in 2009 – 2017, but of the 875 we describe here, none are assigned to a parent from 2017. Should the range include 2017?

Cougar Dam Genetic Parentage Analysis

Demography

Age at Maturity

Most salmon were age-4 or age-5 (54.6% and 42.0%, respectively), with few returning at age-3 or age-6 (1.6% and 1.8%, respectively). This pattern was consistent across all years when we could identify age-3, age-4, age-5, and age-6 salmon (2013 – 2020). However, there was substantial variation in the proportion of age-4 and age-5 returns from year to year (Figure 5).

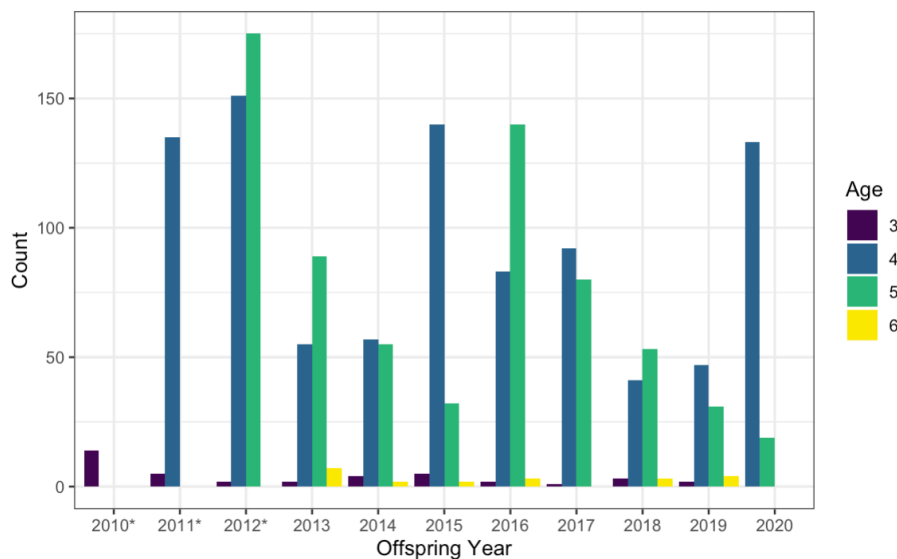


Figure 5. Inferred age at maturity for NOR salmon sampled in South Fork McKenzie River from 2010 – 2020.

* Parents prior to 2007 are not included as candidate parents in the genetic parentage analysis. Therefore, offspring in years 2010, 2011, and 2012 cannot be identified across the full range of potential ages.

Total Lifetime Fitness

We present the mean TLF for candidate parents as well as its range and standard deviation by year, sex, and origin in Table 6. From 2007 – 2015, there were 7,453 candidate parents, and only 1,511 (20%) produced at least one offspring that returned to the Cougar Trap or was sampled as a carcass below the dam. For parental cohort years when all (2007 – 2014), or most (2015) offspring are expected to have returned, the overall mean TLF was 0.36 and ranged from 0 – 17. However, there was substantial variation in TLF among parental cohort years. Mean

Commented [OMKG16]: Based on these results, 2011 and to some extent 2013 appear to be good years when considering age-4 and age-5 proportions. Might be worth including in the text.

Commented [DD17R16]: Yes, I thought about mentioning that too, but realized it's redundant with table 6, figure 6 and results/discussion pertaining to year as a random effect in the model. It's much easier to determine which parent years are better directly these tables and figures than infer it from the age structure.

Cougar Dam Genetic Parentage Analysis

TLF was greater for NOR than HOR salmon (0.49 vs. 0.32, respectively) and for females than males (0.38 vs. 0.34).

Table 6. Mean TLF, standard deviation and range per parent year, sex, and origin.

* Note that 2015 estimates do not include potential age-6 offspring. However, we expect these offspring to contribute very little to TLF (< 2%).

** Note that 2016 and 2017 estimates do not include age-5 and age-6 offspring, and age-4, age-5 and age-6 offspring, respectively, which are expected to substantially contribute to TLF for these parents' years.

Year	Sex	HOR				NOR			
		n	Mean	s.d.	Range	n	Mean	s.d.	range
2007	F	318	0.89	1.49	0 - 11				
	M	427	0.72	1.56	0 - 17				
2008	F	288	0.80	1.46	0 - 12				
	M	585	0.40	1.03	0 - 9				
2009	F	603	0.16	0.47	0 - 4				
	M	780	0.13	0.43	0 - 3				
2010	F	206	0.29	0.73	0 - 5	57	0.25	0.63	0 - 3
	M	320	0.13	0.52	0 - 6	164	0.29	0.69	0 - 4
2011	F	176	0.76	1.57	0 - 9	144	0.68	1.33	0 - 7
	M	193	0.27	0.69	0 - 4	212	0.86	1.74	0 - 9
2012	F	256	0.25	0.58	0 - 3	183	0.41	0.77	0 - 5
	M	191	0.18	0.46	0 - 2	317	0.37	0.78	0 - 5
2013	F	248	0.28	0.7	0 - 5	77	0.75	1.25	0 - 6
	M	207	0.21	0.56	0 - 3	95	0.85	1.41	0 - 8
2014	F	334	0.14	0.45	0 - 3	52	0.27	0.79	0 - 4
	M	172	0.23	0.57	0 - 3	80	0.30	0.72	0 - 3
2015*	F	417	0.12	0.35	0 - 2	48	0.31	0.95	0 - 6
	M	202	0.17	0.50	0 - 4	87	0.31	0.58	0 - 3
2016**	F	336	0.3	0.64	0 - 5	64	0.39	0.63	0 - 2
	M	193	0.35	0.84	0 - 6	107	0.54	1.16	0 - 8
2017**	F	328	0	0	0 - 0	42	0	0	0 - 0
	M	125	0	0	0 - 0	109	0	0	0 - 0

Cougar Dam Genetic Parentage Analysis

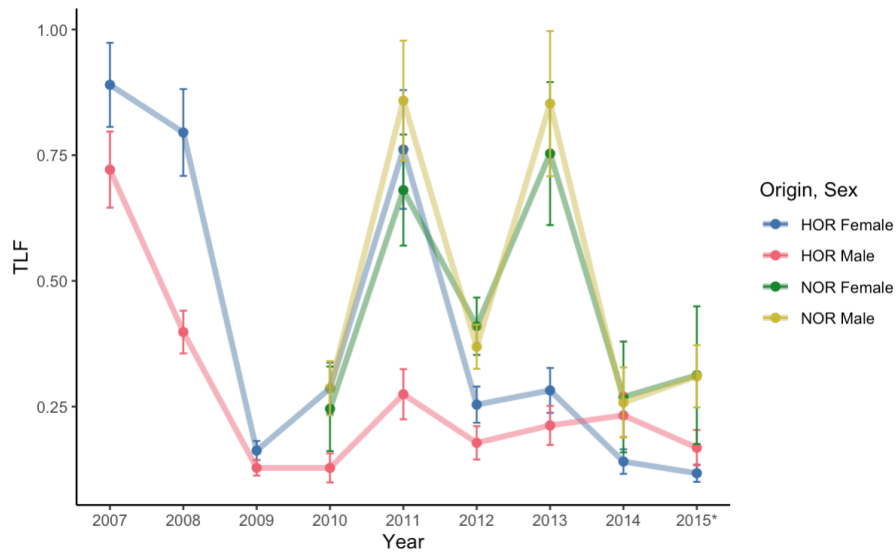


Figure 6. Mean TLF and standard deviation from 2007 to 2015, by sex and origin.

* Note that 2015 TLF estimates do not include potential age-6 offspring. However, we expect these offspring to contribute very little to TLF (~2%).

Cohort Replacement Rate

The total cohort replacement rate (CRR_{total}) was less than one in all years from 2007 – 2015, indicating that the population above Cougar Dam is not replacing itself (Table 7). Maximum CRR_{total} (0.44) was observed in 2007, and minimum CRR_{total} (0.08) was observed in 2009, both years when only HOR hatchery outplants were released above the dam. In most years (2007 – 2012), females were the limiting sex. CRR_F was less than one in these years. In the three years when males were the limiting sex (2013 – 2015), CRR_M was also less than one.

Cougar Dam Genetic Parentage Analysis

Table 7. Cohort Replacement Rate (CRR_{total}) per parent year. CRR_{total} is defined as the number of spawners produced by a spawner estimated as number offspring successfully assigned to at least one parent in a given year ($n_{offspring}$), divided by the number of candidate parents (n_{cand}) in that year. We also present CRR_F : the number female offspring successfully assigned to at least one female parent in a given year, divided by the number of female candidate parents ($n_{cand\ female}$) in that year. CRR_M is the equivalent value for males.

* Note that 2015 estimates do not include potential age-6 offspring. However, we expect these offspring to contribute very little to TLF (~2%).

** Previous reports present CRR_F as “CRR”.

Year	$n_{offspring}$	n_{cand}	$n_{cand\ male}$	$n_{cand\ female}$	Sex Ratio (male:female)	CRR_{total}	CRR_F^{**}	CRR_M
2007	331	745	427	318	1.3 : 1	0.44	0.36	0.43
2008	247	873	585	288	2.0 : 1	0.28	0.30	0.26
2009	114	1383	780	603	1.3 : 1	0.08	0.06	0.08
2010	94	747	484	263	1.8 : 1	0.13	0.12	0.11
2011	284	725	405	320	1.3 : 1	0.39	0.34	0.32
2012	171	947	508	439	1.2 : 1	0.18	0.11	0.19
2013	151	627	302	325	1 : 1.1	0.24	0.14	0.26
2014	73	652	266	386	1 : 1.5	0.11	0.08	0.11
2015*	69	754	289	465	1 : 1.6	0.09	0.06	0.12

Effective Number of Breeders

The effective number of breeders (N_b), ranged from 139.8 to 368.8 (Table 8), indicating that there is likely sufficient genetic diversity within a cohort to avoid inbreeding depression.

The ratio between N_b and the number of candidate parents ranged from 0.22 to 0.36.

Commented [OMKG18]: Columns shifted here

Commented [DD19R18]: This lines up on my end (on the colon), so it's probably a word version issue. I manually changed the kerning to fixed-width for this part of the table, so hopefully this should line up perfectly on the colon now, regardless of word version. If not, it'll be fixed when we export to a final pdf for distribution.

If we don't like this approach (center on colon, set the less common sex to 1), we can change sex ratio to the proportion of females expressed as a percent (e.g. 2007 is 43%, 2015 is 62%).

I don't recommend presenting ratios less than one as people have a hard time comparing them to ratios over 1. For example, (0.8 : 1) and (1.2 : 1) are not equivalently biased sex ratios, but people tend to misinterpret them as such. This is why the sex ratio is plotted on the log scale in figure 8 (sex ratio 0.5 : 1 and sex ratio 2 : 1 are equidistant from sex ratio 1 : 1)

Cougar Dam Genetic Parentage Analysis

Table 8. Effective number of breeders (N_b) per parent year as estimated by NeEstimator v2.1. Number of candidate parents (n_{cand}) is the number of salmon released above the Cougar Dam in a given year that were sampled, and successfully genotyped, $n_{success}$ is the number of candidate parents with one or more offspring in the pedigree. $n_{offspring}$ is the number of offspring assigned to candidate parents released above the dam that parent year. Upper and lower 95% confidence intervals based on jack-knife are provided. The $N_b : n_{cand}$ ratio is the N_b estimate divided by the number of candidate parents.

* Note that 2015 estimates do not include potential age-6 offspring. However, we expect these offspring to contribute very little to TLF (~2%)

Year	n_{cand}	$n_{success}$	$n_{offspring}$	N_b	CI _{lower}	CI _{upper}	$N_b : n_{cand}$ ratio
2007	745	261	331	265.5	222.7	322.8	0.36
2008	873	229	247	247.5	203.7	308.8	0.28
2009	1383	156	114	368.6	228.1	848.6	0.27
2010	747	105	94	169.8	116.6	288	0.23
2011	725	209	284	220.1	181.7	272.7	0.30
2012	947	206	171	297.2	216.5	451.4	0.31
2013	627	152	151	139.8	104.3	199.7	0.22
2014	652	90	73	167.5	104.7	361.6	0.26
2015*	754	103	69	211.9	122.1	627.5	0.28

Predictors of Fitness

Generalized Linear Mixed Modeling

We did not find evidence of strong multicollinearity among the evaluated predictors of TLF and included all predictors at the start of model selection. Modeling the effect of *release group density* as a second order polynomial provided a marginally better fit to the data than modeling *release group density* as a linear predictor, but all other predictors were modeled as linear effects. The best random effects structure according to AIC included random intercepts for both *year* and *release group*. After model selection of fixed effects, four predictors and two interactions were included in the final model: *sex*, *origin*, *Julian day of release*, *annual sex ratio*, *sex*origin* and *sex*annual sex ratio*. Parameter estimates and their standard errors, as well as significance testing for each predictor retained in the final model are presented in Table 9.

Cougar Dam Genetic Parentage Analysis

Table 9. Results of generalized linear mixed model examining the influence of *sex*, *origin*, *release day*, *release location*, *release group density*, *release group sex ratio*, *annual sex ratio*, *sex*release group density*, *sex*release day*, *sex*origin*, and *sex*annual sex ratio* on the total lifetime fitness of spring Chinook salmon released above Cougar Dam from 2007 – 2015. *Year* and *release group* are included as random effects. Estimated effect (β) and standard error (s.e.) of each fixed predictor on the link (log) scale for predictors that were retained in the final model are presented above. The null hypothesis that each predictor did not significantly improve the model effect was tested with a likelihood ratio test (LRT p-value). The null hypothesis that each predictor has an effect significantly different than zero was evaluated with the Wald test (Wald p-value). Estimated variance (σ^2) and standard deviation (s.d.) are presented for random effects. Significant p-values are in bold.

Fixed effects	β	s.e	LRT p-value	Wald p-value
(Intercept)	-1.343	0.208		
<i>sex</i> [male]	-0.150	0.082		0.066
<i>origin</i> [NOR]	0.446	0.132		0.001
<i>Julian Day of release</i>	-0.004	0.001	0.004	0.003
<i>annual sex ratio</i>	1.042	0.501		0.038
<i>sex</i> [male] * <i>origin</i> [NOR]	0.293	0.142	0.039	0.039
<i>sex</i> [male] * <i>annual sex ratio</i>	-0.750	0.177	<0.001	<0.001
Random effects	σ^2	s.d.		
<i>year</i>	0.306	0.553		
<i>release group</i>	0.085	0.292		

Predicted Effects of Significant Predictors of TLF

To aid in interpretation of the parameters estimated in the final model (Table 9), we also estimated effects of each significant predictor on the response scale (TLF) after accounting for variation at all other significant predictors (Figures 7 to 9). NOR salmon have substantially higher predicted fitness than HOR salmon and this effect is somewhat stronger for males than females, but this interaction is only marginally significant and has a limited effect size (Figure 7). NOR males are predicted to be 2.1-fold more fit than HOR males, and NOR females are predicted to be 1.6-fold more fit than HOR females.

Cougar Dam Genetic Parentage Analysis

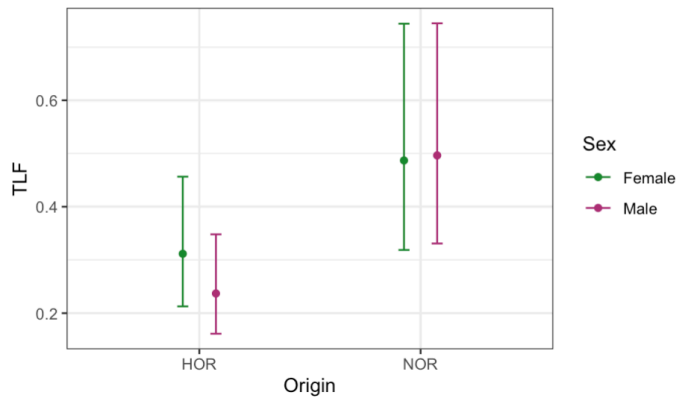


Fig 7. Predicted effects of *origin* (NOR vs. HOR) and *sex* on TLF from GLMM_{TLF}. Predicted values are conditioned on the typical values of all other predictors in the final model (*Julian day of release*, *annual sex ratio*). Error bars depict 95% confidence intervals for the estimates.

Overall, the *annual sex ratio* has a small, and marginally significant effect on TLF, with male-biased sex ratios producing somewhat higher fitness than female-biased sex ratios, however this effect was much stronger for females than males. When viewed on response scale (TLF) (Figure 8), changes in *annual sex ratio* affects fitness mostly through females, who perform worse when the sex ratio is female-biased. Using the most extreme values observed in any years (male:female ratio 0.6 and 2.0), female fitness is predicted to vary 3.5-fold, whereas male fitness is expected to vary 1.4-fold.

Cougar Dam Genetic Parentage Analysis

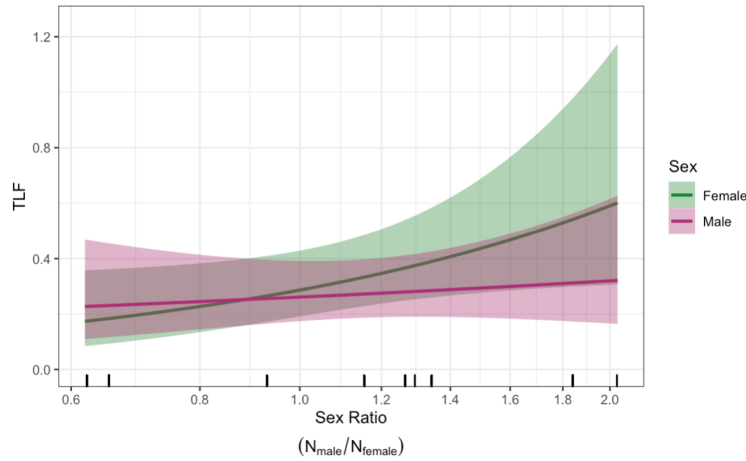


Figure 8. Predicted effects of *annual sex ratio* and *sex* on TLF from GLMM_{TLF}. Predicted values are conditioned on the typical values of all other predictors in the final model (*Julian day of release*, *origin*). Rug plot at bottom of the figure highlights the observed *annual sex ratios* used to fit the model. Bands represent 95% confidence intervals for the estimates.

Finally, salmon released above Cougar Dam earlier in the season are predicted to have greater fitness than those released later (Figure 9). Individuals released on the earliest day in the dataset are predicted to have 1.7-fold greater fitness than the latest release day.

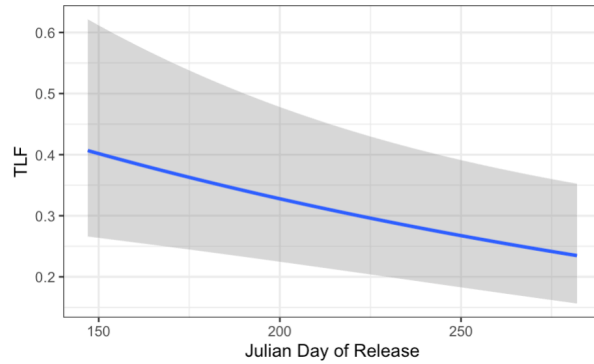


Figure 9. Predicted effects of *Julian day of release* on TLF from GLMM_{TLF}. Predicted values are conditioned on the typical values of all other predictors in the final model (*Julian sex*, *origin*, *annual sex ratio*). Grey band represents 95% confidence intervals for the estimates.

Cougar Dam Genetic Parentage Analysis

The random effects of *year* and *release group* also contribute substantially to the variation in TLF among individuals (Table 9). Variation in TLF attributed to differences among years or release groups, as measured by standard deviation of the *year* and *release group* random effects, was similar in scale to the fixed effect of *origin* presented above.

Size at Maturity

Our dataset included *size at maturity* for approximately one half of the candidate parents released above the dam from 2007 – 2015 used to fit GLMM_{TLF}. NOR salmon released above the dam were significantly larger than their HOR counterparts after controlling for size differences owing to *sex* and *year* (linear mixed model, $\beta_{\text{origin [NOR]}} = 2.92$ cm, s.e. = 0.26, p-value likelihood ratio test $< 2.2 \times 10^{-16}$). To evaluate the relationship between *size at maturity*, *origin* and TLF, we fit a GLMM on TLF for the 3,781 candidate parents with a *size at maturity* measurement, using the significant predictors of fitness from the final model and *size at maturity* as an additional predictor (GLMM_{size}). Size had a significant positive effect on TLF ($\beta_{\text{size}} = 0.069$, s.e. = 0.006, p-value likelihood ratio test $< 2.0 \times 10^{-16}$), but the estimated effect of origin was reduced to 44% of its estimated effect when *size at maturity* was not included in the model, confirming that these two variables are highly confounded.

Cougar Dam Genetic Parentage Analysis

Discussion

Main Findings

Assignments

1. Most (71%) NOR salmon collected at the Cougar Trap from 2013 – 2020 were produced above Cougar Dam. Leaving 29% remaining as likely immigrants.
2. The proportion of NOR immigrants collected at the Cougar Trap varied among years. As few as 6% and as many as 49% of NOR salmon collected at the Cougar Trap were immigrants in 2020 and 2019, respectively.
3. The proportion of NOR immigrants collected at the Cougar Trap was estimated to increase from less than 5% early in the season to ~50% by September 1st.
4. From 2015 – 2020, a salmon produced above the dam was more likely to return a second time after being recycled downstream than an NOR immigrant. Recycling all salmon collected at the Cougar Trap downstream during this period prevented above dam transport of 75% of NOR immigrants and 31% of NOR salmon produced above the dam.
5. LSDR during the same period (2015 – 2020) would have prevented above dam transport of only 37% of NOR immigrants and 5% of NOR salmon produced above the dam.

Commented [OMKG20]: 94% of salmon sampled at the Cougar Trap assigned so how can 49% be immigrants?

Sorry, I'm just diving back into this again after a break and may be missing the obvious?

Commented [DD21R20]: You got it right, the years are swapped. Fixed here and in the discussion.

Demography

1. Most salmon produced above Cougar Dam from 2007 – 2015 returned at age-4 (55%) or age-5 (42%), with few returning at age-3 (2%) or age-6 (2%).
2. From 2007 – 2015, 20% of candidate parents above Cougar Dam produced one or more adult offspring (TLF ≥ 1) that returned to the Cougar Trap, or was sampled as a carcass below the dam.
3. Mean TLF for all candidate parents from 2007 – 2015 was 0.36. TLF was highly variable at the individual level and ranged 0 - 17.
4. Mean TLF was greater for NOR than HOR salmon (0.49 vs. 0.32, respectively) and for females than males (0.38 vs. 0.34).
5. In the nine years when we sampled nearly all potential offspring of parental cohorts above Cougar Dam, CRR_{total} never approached one, indicating that population above the dam is not replacing itself. The maximum CRR_{total} was 0.44 (2007) and the minimum was 0.08 (2009).

Commented [OMKG22]: So these are averages? Might be good to state that.

Commented [DD23R22]: I don't think of these as averages. Of all of the NOR salmon we sampled that assigned to at least one parent from 2007 – 2015 (i.e. that we can infer their age) 55% are age-4, 42% are age-5 etc.

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6. In most years females were the limiting sex. CRR_F was less than one in these years. In years when males were the limiting sex, CRR_M was also less than one.
7. N_b ranged from 139.8 to 368.8, indicating that there is likely sufficient genetic diversity within a parental cohort to avoid inbreeding depression.

Predictors of Fitness

1. Three variables and two interactions were predictive of TLF: *origin*, *Julian day of release*, *annual sex ratio*, *sex*origin* and *sex*annual sex ratio*.
2. NOR males are predicted to be 2.1-fold more fit than HOR males, and NOR females are predicted to be 1.6-fold more fit than HOR females.
3. Both males and females are predicted to have higher TLF when the sex ratio is male-biased, but this effect is much stronger for females than males. Using the most extreme values observed in any years (male:female ratio 0.6 and 2.0), female fitness is predicted to vary 3.5-fold, whereas male fitness is expected to vary 1.4-fold.
4. Individuals released on the earliest release day in the dataset are predicted to have 1.7-fold greater fitness than the latest release day.
5. Variance in TLF among both years and release groups was substantial after accounting for the significant predictors, suggesting that unmeasured variables within years and release groups have a large effect on TLF.
6. NOR salmon are larger than HOR salmon, and larger size at maturity is associated with higher TLF, indicating that fitness differences between NOR and HOR salmon may be due, in part, to differences in size at maturity.

Assignment Rates

Changes to software versions, data filtering and methods of inferring a consensus pedigree had only a minor effect on the overall assignment rate compared to the approaches employed in previous reports. This suggests that our genetic parentage approach is robust to small changes in methods and increases our confidence that the final pedigree accurately reflects true parent-offspring relationships. Our confidence in the pedigree is further bolstered by the high genetic diversity and attendant low non-exclusion probabilities given the genetic data, and the low estimated genotyping error rates (Appendix A).

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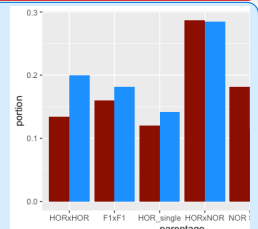
The majority of spring Chinook salmon collected at the Cougar Trap assign to at least one parent released or otherwise sampled above the dam. Among the years that we can assign potential offspring sampled at the Cougar Trap to all of their candidate parents (i.e. 2013 – 2020), 29% of NOR salmon collected at the Cougar Trap were unassigned and inferred to be NOR immigrants produced below the dam or elsewhere. However, we found significant variation in the proportion of NOR immigrants among years, with as few as 6% in 2020 and as many as 49% in 2019.

Previous reports found that the LSDR program implemented in 2013 and 2014 selectively limited above dam transport of NOR immigrants relative to NOR salmon produced above the dam. From 2015 onwards, managers transitioned to recycling all NOR salmon downstream, regardless of the date they were collected at the Cougar Trap. To evaluate the impact of downstream recycling on the disposition of NOR salmon, we determined how many NOR salmon produced above the dam and how many NOR immigrants would have been released above the dam if no downstream recycling program was implemented during the period from 2015 – 2020, or if LSDR was implemented in its place.

NOR salmon produced above the dam are significantly more likely to return a second time after being recycled downstream than NOR immigrants. Consequently, from 2015 – 2020, recycling all NOR salmon collected at the Cougar Trap downstream prevented above dam transport of 75% of the 334 NOR immigrants and 31% of the 875 NOR salmon produced above the dam. We also confirmed the tendency for NOR immigrants to arrive at the trap later than NOR salmon produced above the dam. Consequently, implementing LSDR with a September 1st cutoff in place of downstream recycling during the same period (2015 – 2020), would have resulted in preventing above dam transport of fewer (37% of 334) NOR immigrants and very few (5% of 875) NOR salmon produced above the dam.

Future changes to the downstream recycling program that result in the release of greater numbers of NOR salmon are expected to provide demographic and genetic benefits to the reintroduction program above Cougar Dam. First, NOR salmon produced above the dam provide a direct demographic benefit to the above dam population when they are released above the dam. Second, we found that NOR salmon are more fit than their HOR counterparts above the dam. Therefore, decreasing the proportion of HOR spawners above the dam is expected to improve productivity per salmon released. Finally, there may be adaptive genetic variation among NOR

Commented [OMKG24]: How many of these are offspring of HOR? NOR?



Commented [DD25R24]: Here's a plot of the parentage (female x male) of these 875 NORs, split according to the number of times they return. An F1 here is defined as NOR offspring of HOR parents, so the second set of columns (F1xF1 parents) represents F2s. There doesn't seem to be any strong differences in parentage between fish that return once and those that return twice.

Commented [OMKG26]: But if we know CRR and TLF are low, so is this really true? They have the potential but how many do?

Commented [DD27R26]: Maybe this was a little unclear. It is much simpler than that. They necessarily increase productivity, because their mean fitness is greater than 0.

This result is not in the text, but it makes my point clear: Known F1s (NOR offspring of two HOR parents) released above the dam produced 290 offspring that were sampled at the trap. If these F1s were not transported above the dam, those 290 offspring would not contribute to the above dam population. They may have been more productive below the dam, but this productivity does not accrue to the above dam population, so it's not relevant to this paragraph which is articulating how NORs benefit the above dam population.

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immigrants that is absent from or rare among hatchery outplants and their NOR descendants. Therefore, above dam transport of NOR immigrants in particular may promote the adaptive potential and long-term productivity of the above dam **population**. Implementing downstream recycling is also associated with two costs for the reintroduction program. First, for the NOR salmon ultimately released above the dam, downstream recycling delays release by ~31 days which is associated with a 12% reduction in fitness as quantified by the $GLMM_{TLF}$. Second, downstream recycling imposes additional handling stress which may be associated with further unquantified reductions to fitness.

However, these proposed demographic and genetic benefits provided to the reintroduction program by above dam transport NOR salmon must be weighed against its costs. Above dam transport subjects the offspring of NOR salmon to the high mortality associated with downstream passage through Cougar Dam (Romer et al. 2013; Beeman et al. 2014). Above dam transport of NOR salmon, regardless of whether they are produced above the dam or not, presumably negatively influences NOR production basin wide, because the above dam habitat is a net demographic sink, with a CRR less than one in all years from 2007 – 2015. Therefore, by influencing the disposition of NOR salmon, changes to downstream recycling presents different arrays of costs and benefits for salmon above Cougar Dam than for NOR salmon below the dam, and more broadly throughout the McKenzie basin.

Demography

Previous reports have found that spring Chinook salmon released above Cougar Dam are not replacing themselves (Banks et al. 2013; Banks et al. 2014; Banks et al. 2016). The CRR was substantially less than one from 2007 – 2010. These reports attributed this finding to low survival of juveniles through Cougar Dam (Romer et al. 2013; Beeman et al. 2014), but shared a **hopeful outlook** for future years given the greater fitness of NOR relative HOR salmon released above the dam (Banks et al. 2014). Our analysis extended estimates of the CRR to include 2011 – 2015. We found that the above dam population is not replacing itself in these years. The CRR has remained below one from 2007 – 2015, regardless of whether cohort replacement rate is estimated using all individuals (CRR_{total}), only females (CRR_F) or only males (CRR_M).

N_b was high in all years, suggesting that inbreeding depression is unlikely to negatively affect the above dam population. However, this perspective depends on the definition of a

Commented [OMKG28]: That's assuming they successfully reproduce AND offspring survive passage through the dam. But the data indicate that few produce offspring and few survive to return as adults to spawn.

Commented [DD29R28]: Yes, these are these expected benefits of releasing NORs above the dam. In the case of NOR immigrants, they provide adaptive *potential*, but it is unlikely that potential will be realized until the downstream passage mortality is reduced, which is discussed in the next paragraph.

I tried to make it clear that these are potential benefits and costs and restructured the paragraphs so that the presentation of our results are integrated into the discussion of costs and benefits.

Commented [DD30]: Here's one of the passages I'm referring to here:

"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 30 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."

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population. Given the population genetic structure of Chinook salmon generally and the ongoing supplementation above the dam with both hatchery outplants and a small number of NOR immigrants, spring Chinook salmon above Cougar Dam are more appropriately considered a component of the larger McKenzie River total population. The genetic diversity above the dam, and hence N_b , reflects the collective genetic diversity of the NOR descendants of hatchery outplants, hatchery outplants themselves and NOR immigrants that successfully spawn above the dam. It is not known if inbreeding depression will represent a risk to above dam population without supplementation with either hatchery outplants or NOR immigrants.

Banks *et al* (2016) and Sard *et al* (2016a) assigned offspring to grandparents to infer that unsampled adfluvial females and precocial males likely make a small contribution to productivity above the dam. While we did not conduct a similar grandparentage analysis, we attempted to confirm that either precocial males or adfluvial females may contribute to above dam productivity by assigning potential offspring to a small number of precocial males and NOR carcass samples of unknown provenance sampled above the dam. We found that that these salmon were not parents of any salmon that returned to the Cougar Trap or were sampled as carcasses below the dam in later years. Therefore, while precocial males and adfluvial females may contribute to above dam productivity, we were unable to confirm this finding by assigning offspring directly to sampled parents.

Predictors of Fitness

Due to the availability of a complete pedigree for only four parental cohort years, previous modeling approaches to identify aspects of release strategies or other variables that significantly explained variation in TLF were forced to examine each parental cohort year separately. Release date, release location, and origin by sex interactions were all identified as significant predictors of TLF in some years, but not others. By combining data for all candidate parents released above Cougar Dam from over nine years into a single model, we were able to improve statistical power to identify variables that are consistently predictive of TLF across years. We found that variation in TLF can be predicted by origin, release day, annual sex ratio, an origin by sex interaction and an annual sex ratio by sex interaction. We also found that there was much variation in TLF among years and release groups after accounting for the effects of the

Commented [OMKG31]: Not sure I follow here? If you don't supplement with those two groups there is no above dam population?

Commented [DD32R31]: The above dam population consists of three groups: salmon produced above the dam, HORs and NOR immigrants.

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significant predictors and residual variation, suggesting that other unmeasured variables that operate at the level of year or release group likely influence TLF.

Origin had a strong effect on TLF of salmon released above the dam. NOR males were predicted to be 2.1-fold more fit than the HOR males, and NOR females were predicted to be 1.6-fold more fit than HOR females. However, consistent with previous reports, we found a relationship between size and origin among candidate parents in *post-hoc* analyses. NOR candidate parents were significantly larger than their HOR counterparts, and size was a significant predictor of TLF when included in a *post-hoc* model, indicating that the effect of origin on fitness is potentially due, in part, to the different sizes of NOR and HOR salmon.

Salmon released above Cougar Dam earlier in the season were predicted to have greater TLF than those released later. Previous genetic parentage analyses of UWR spring Chinook salmon reintroduction programs have found inconsistent effects of release day on fitness, with opposite patterns detected year to year in the same river (Banks et al. 2014; Banks et al. 2016; Evans et al. 2016; Sard et al. 2016b). Early release has also been associated with high pre-spawn mortality among hatchery outplants above dams in the UWR (Keefer et al. 2010). These authors attributed inconsistent findings between years in the same river to interannual variation in the proportion of HOR spawners, the operational sex ratio, and environmental variables that affect the rate of pre-spawn mortality (Banks et al. 2014; Banks et al. 2016; Evans et al. 2016; Sard et al. 2016b). We also found that there was variation among years in the effect of release day on TLF, however the overall effect of later release over nine years was negative.

We found that the annual sex ratio likely influences TLF. This effect was mostly driven by females which were predicted to have greater fitness when the sex ratio is male-biased. These findings contradict those from a recent report evaluating releases of spring Chinook salmon above Detroit Dam on the North Santiam River that found lower TLF for both sexes when the sex ratio was strongly male biased (O'Malley et al. 2022). While the range of sex ratios in both rivers was similar, and similar numbers of salmon were released above both dams, we note that many ecological processes may mediate the relationship between sex ratio and TLF, and these processes may vary between the two rivers. For example, the proportion of hatchery-origin spawners (pHOS) above Detroit Dam on the North Santiam River was 100% for most years evaluated, while pHOS above Cougar Dam on the South Fork McKenzie River averaged 65% after construction of the Cougar Trap in 2010. It is possible that the presence of larger NOR

Commented [OMKG33]: Is this true? Comparing 2011 to 2015, the number of salmon released above Detroit and Cougar are not that similar.

Commented [DD34R33]: The average number of candidate parents are within about 10% of one another across rivers.

Mean candidate parents MCKR: 741 (2011 – 2015)
Mean candidate parents NSNT: 687 (2011 – 2015)

But I'm happy to remove this idea given the small releases in NSNT in 2011 and 2012 (149 and 258).

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males in the South Fork McKenzie River reduces the deleterious effects of strongly male-biased sex ratios that we observed in the North Santiam River, by providing the opportunity for mate choice (Auld et al. 2019) and reducing the tendency for females to delay spawning in the presence of a high proportion of smaller, HOR males (Berejikian 2000).

We evaluated additional predictors of TLF that were not retained in the final model. These predictors are unlikely to substantially or consistently contribute to variation in TLF. We did not find that release location had a significant effect on TLF. We also defined release group as the set of salmon released above the dam at a single location on a single day. While there was much variation in TLF among release groups, we did not find that this variation was explained by either the number of salmon in a release group or the sex ratio of a release group.

Conclusion

Previous reports found that the population above Cougar Dam was not reaching replacement when only HOR salmon were released. However, early evidence suggested that NOR fitness was greater than HOR fitness above the dam, suggesting that productivity may increase in later years. In this report, we evaluated five additional years of releases above Cougar Dam that included both HOR and NOR salmon. While NOR salmon indeed demonstrated substantially greater fitness than the relatively smaller HOR salmon, the cohort replacement rate never approached one in any year.

We also confirmed that the proportion of NOR immigrants at the Cougar Trap increases throughout the season and that NOR salmon produced above the dam are more likely to return to the Cougar Trap a second time after downstream recycling than their NOR immigrant counterparts. Therefore, while implementation of either LSDR or downstream recycling reduces the number of NOR salmon released above the dam, both programs selectively limit above dam transport of NOR immigrants relative to NOR salmon produced above the dam. When evaluating these programs, managers must weigh the expected demographic and genetic benefits of above dam transport of NOR salmon to the above dam population against its expected costs to NOR productivity basin wide.

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APPENDIX A: ASSIGNMENT POWER

Table A1. Cumulative non-exclusion probabilities based on 11 microsatellite loci for the identification of the first parent (NE.1P), second parent (NE.2P), and parent pairs (NE.PP) for each offspring year and its set of candidate parents. The expected number of false parent-offspring pairs for each offspring year given zero (EFP.0), one (EFP.1) and two (EFP.2) genotype mismatches is also presented.

Parent Years	Offspring Year	NE.1P	NE.2P	NE.PP	EFP.0	EFP.1	EFP.2
2007	2010	2.54E-07	6.12E-10	7.83E-17	0.02	0.12	0.70
2007 – 2008	2011	2.24E-07	5.27E-10	6.72E-17	0.07	0.43	2.47
2007 – 2009	2012	2.19E-07	5.07E-10	5.94E-17	0.17	0.98	5.63
2007 – 2010	2013	2.07E-07	4.71E-10	5.39E-17	0.09	0.52	3.01
2008 – 2011	2014	1.94E-07	4.43E-10	4.54E-17	0.08	0.46	2.71
2009 – 2012	2015	1.96E-07	4.44E-10	4.89E-17	0.10	0.59	3.40
2010 – 2013	2016	1.94E-07	4.43E-10	4.72E-17	0.10	0.58	3.39
2011 – 2014	2017	1.89E-07	4.28E-10	4.40E-17	0.07	0.43	2.51
2012 – 2015	2018	1.96E-07	4.40E-10	4.75E-17	0.05	0.27	1.53
2013 – 2016	2019	2.00E-07	4.57E-10	4.93E-17	0.05	0.28	1.57
2014 – 2020	2020	1.77E-07	4.01E-10	3.83E-17	0.04	0.23	1.34

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Table A2. Summary of variation and genotyping error rates of microsatellite markers for each offspring year and its set of candidate parents. PIC (Polymorphic information content), k (Number of alleles), H_o (observed heterozygosity), H_E (expected heterozygosity), and HW (test of significance for a significant departure from Hardy Weinberg proportions) were calculated in CERVUS. ADO rate (allele dropout rate), and miscall rate were estimated in COLONY.

Offspring Year	Marker	PIC	k	H_o	H_E	HW	ADO Rate	Miscall Rate
2010	Ot201	0.909	21	0.931	0.916	NS	0.001	0.021
2010	Ot209	0.938	55	0.927	0.941	NS	0.011	0.022
2010	Ot249	0.932	37	0.934	0.936	NS	0.000	0.025
2010	Ot253	0.915	25	0.894	0.92	***	0.016	0.026
2010	Ot215	0.933	32	0.923	0.936	*	0.000	0.012
2010	Ot311	0.95	46	0.941	0.952	NS	0.011	0.014
2010	Ot409	0.951	60	0.961	0.954	NS	0.002	0.026
2010	Ot211	0.906	21	0.895	0.912	NS	0.006	0.007
2010	Ot208	0.945	36	0.87	0.948	***	0.040	0.023
2010	Ot212	0.869	22	0.883	0.881	NS	0.002	0.022
2010	Ot515	0.843	18	0.86	0.858	NS	0.007	0.011
2011	Ot201	0.912	23	0.921	0.918	NS	0.002	0.008
2011	Ot209	0.935	59	0.921	0.938	NS	0.013	0.013
2011	Ot249	0.935	37	0.94	0.939	NS	0.002	0.028
2011	Ot253	0.913	30	0.897	0.919	***	0.011	0.007
2011	Ot215	0.933	35	0.931	0.937	NS	0.002	0.007
2011	Ot311	0.951	51	0.952	0.953	NS	0.004	0.018
2011	Ot409	0.951	66	0.963	0.953	*	0.001	0.008
2011	Ot211	0.913	26	0.914	0.918	*	0.005	0.010
2011	Ot208	0.943	36	0.893	0.946	***	0.027	0.016
2011	Ot212	0.875	23	0.882	0.886	NS	0.004	0.010
2011	Ot515	0.847	19	0.858	0.861	NS	0.007	0.008
2012	Ot201	0.911	26	0.921	0.917	*	0.005	0.003
2012	Ot209	0.934	64	0.912	0.937	***	0.016	0.017
2012	Ot249	0.936	37	0.932	0.939	**	0.002	0.007
2012	Ot253	0.914	31	0.895	0.919	***	0.012	0.004
2012	Ot215	0.933	39	0.936	0.936	NS	0.000	0.007
2012	Ot311	0.95	58	0.953	0.952	***	0.004	0.008
2012	Ot409	0.951	68	0.947	0.953	**	0.004	0.011
2012	Ot211	0.913	25	0.919	0.919	**	0.003	0.001
2012	Ot208	0.941	39	0.907	0.944	***	0.018	0.008
2012	Ot212	0.881	24	0.886	0.891	*	0.002	0.012
2012	Ot515	0.856	21	0.862	0.869	**	0.008	0.004
2013	Ot201	0.91	27	0.924	0.916	**	0.004	0.002
2013	Ot209	0.936	68	0.919	0.939	***	0.014	0.007
2013	Ot249	0.936	37	0.937	0.94	**	0.001	0.007
2013	Ot253	0.914	31	0.902	0.92	***	0.010	0.000
2013	Ot215	0.936	37	0.936	0.94	NS	0.004	0.002
2013	Ot311	0.951	55	0.952	0.953	***	0.003	0.008

Cougar Dam Genetic Parentage Analysis

Offspring Year	Marker	PIC	k	H _o	H _E	HW	ADO Rate	Miscall Rate
2013	Ot409	0.952	68	0.95	0.954	***	0.003	0.010
2013	Ot211	0.911	25	0.916	0.917	**	0.001	0.003
2013	Ot208	0.94	38	0.905	0.943	***	0.019	0.002
2013	Ot212	0.884	25	0.894	0.894	NS	0.001	0.002
2013	Ot515	0.852	21	0.859	0.865	*	0.003	0.002
2014	Ot201	0.91	28	0.919	0.916	***	0.005	0.005
2014	Ot209	0.937	69	0.923	0.94	***	0.013	0.008
2014	Ot249	0.937	37	0.939	0.94	*	0.003	0.007
2014	Ot253	0.914	36	0.907	0.92	***	0.006	0.002
2014	Ot215	0.937	37	0.938	0.941	NS	0.003	0.009
2014	Ot311	0.951	54	0.956	0.953	***	0.001	0.007
2014	Ot409	0.951	66	0.948	0.953	***	0.002	0.005
2014	Ot211	0.911	26	0.92	0.916	*	0.000	0.004
2014	Ot208	0.94	39	0.92	0.943	***	0.012	0.003
2014	Ot212	0.886	25	0.895	0.895	NS	0.003	0.005
2014	Ot515	0.853	21	0.859	0.866	NS	0.003	0.002
2015	Ot201	0.911	29	0.919	0.917	*	0.005	0.001
2015	Ot209	0.938	71	0.923	0.941	***	0.014	0.004
2015	Ot249	0.936	37	0.931	0.939	***	0.004	0.008
2015	Ot253	0.914	34	0.904	0.92	***	0.007	0.002
2015	Ot215	0.937	41	0.941	0.94	**	0.002	0.003
2015	Ot311	0.951	57	0.953	0.953	NS	0.002	0.005
2015	Ot409	0.952	67	0.944	0.954	***	0.004	0.010
2015	Ot211	0.91	25	0.92	0.916	**	0.000	0.003
2015	Ot208	0.941	39	0.927	0.944	***	0.010	0.000
2015	Ot212	0.883	23	0.881	0.893	NS	0.004	0.005
2015	Ot515	0.854	21	0.858	0.867	NS	0.004	0.003
2016	Ot201	0.912	28	0.918	0.918	NS	0.004	0.002
2016	Ot209	0.938	67	0.928	0.941	***	0.010	0.009
2016	Ot249	0.936	37	0.933	0.939	NS	0.004	0.011
2016	Ot253	0.915	36	0.908	0.92	***	0.007	0.002
2016	Ot215	0.937	42	0.94	0.941	NS	0.002	0.005
2016	Ot311	0.951	54	0.952	0.953	NS	0.003	0.008
2016	Ot409	0.952	67	0.953	0.954	NS	0.003	0.010
2016	Ot211	0.908	23	0.911	0.914	NS	0.003	0.004
2016	Ot208	0.942	39	0.928	0.945	NS	0.010	0.008
2016	Ot212	0.882	23	0.885	0.892	NS	0.001	0.004
2016	Ot515	0.848	19	0.86	0.862	NS	0.000	0.005
2017	Ot201	0.913	28	0.916	0.919	*	0.003	0.002
2017	Ot209	0.938	64	0.925	0.941	***	0.011	0.008
2017	Ot249	0.937	37	0.929	0.94	NS	0.006	0.007
2017	Ot253	0.914	34	0.908	0.92	***	0.007	0.002
2017	Ot215	0.937	44	0.942	0.94	NS	0.000	0.005

Cougar Dam Genetic Parentage Analysis

Offspring Year	Marker	PIC	k	H _o	H _E	HW	ADO Rate	Miscall Rate
2017	Ot311	0.951	55	0.95	0.953	*	0.004	0.005
2017	Ot409	0.954	66	0.949	0.956	NS	0.003	0.006
2017	Ot211	0.908	23	0.916	0.914	NS	0.001	0.002
2017	Ot208	0.942	39	0.927	0.945	**	0.009	0.002
2017	Ot212	0.882	22	0.88	0.892	NS	0.003	0.004
2017	Ot515	0.851	19	0.865	0.864	NS	0.002	0.002
2018	Ot201	0.912	26	0.914	0.918	***	0.003	0.001
2018	Ot209	0.939	65	0.924	0.942	***	0.010	0.004
2018	Ot249	0.936	36	0.922	0.939	NS	0.009	0.003
2018	Ot253	0.915	29	0.914	0.921	***	0.005	0.000
2018	Ot215	0.937	45	0.938	0.94	NS	0.004	0.003
2018	Ot311	0.949	56	0.943	0.951	***	0.007	0.005
2018	Ot409	0.953	66	0.949	0.955	NS	0.004	0.003
2018	Ot211	0.909	25	0.912	0.915	*	0.000	0.000
2018	Ot208	0.941	38	0.933	0.944	***	0.008	0.000
2018	Ot212	0.885	22	0.878	0.895	NS	0.006	0.007
2018	Ot515	0.85	21	0.866	0.864	NS	0.002	0.000
2019	Ot201	0.91	24	0.905	0.916	***	0.005	0.002
2019	Ot209	0.94	60	0.913	0.942	***	0.015	0.012
2019	Ot249	0.937	36	0.927	0.94	NS	0.008	0.000
2019	Ot253	0.916	31	0.918	0.921	***	0.003	0.004
2019	Ot215	0.938	40	0.929	0.941	NS	0.007	0.006
2019	Ot311	0.949	53	0.926	0.952	***	0.017	0.009
2019	Ot409	0.951	63	0.931	0.953	***	0.009	0.008
2019	Ot211	0.906	25	0.908	0.912	NS	0.002	0.000
2019	Ot208	0.94	42	0.921	0.943	***	0.012	0.000
2019	Ot212	0.889	25	0.893	0.898	NS	0.002	0.003
2019	Ot515	0.848	21	0.873	0.862	**	0.002	0.000
2020	Ot201	0.909	22	0.898	0.916	**	0.006	0.002
2020	Ot209	0.94	60	0.911	0.943	***	0.018	0.004
2020	Ot249	0.937	37	0.936	0.94	*	0.004	0.004
2020	Ot253	0.916	29	0.916	0.921	**	0.004	0.004
2020	Ot215	0.939	39	0.931	0.942	NS	0.003	0.003
2020	Ot311	0.951	51	0.933	0.953	***	0.014	0.009
2020	Ot409	0.951	64	0.927	0.953	***	0.011	0.006
2020	Ot211	0.909	25	0.906	0.915	NS	0.004	0.000
2020	Ot208	0.941	38	0.929	0.944	NS	0.010	0.000
2020	Ot212	0.888	24	0.895	0.897	NS	0.003	0.001
2020	Ot515	0.852	21	0.883	0.866	***	0.001	0.006