December 2022 Report

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

Prepared for:

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**Glossary**

* Assignment – Offspring are *assigned to* parents.
* Candidate Parent – Salmon released above Cougar Dam included in our parentage analysis as a potential parent (i.e in the filtered dataset)
* Cohort – Set of salmon that could potentially spawn together. Not set of offspring descended from a set of parents that spawned together.
* CRR (Cohort Replacement Rate) – Number of offspring produced by a cohort of parents, divided by the number of parents in the cohort.
* Fitness – Number of offspring that return as an adult
* Hatchery Outplant – HOR salmon initially collected at a hatchery and outplanted above Cougar Dam. NOT HOR salmon collected at Cougar Trap and released above Cougar Dam.
* HOR (hatchery-origin) –
* LSDR (late season downstream release) - Double floy tag and release salmon at Forest Glen (in mainstem, below confluence with South Fork) after September 1st. Only release above Cougar Dam if collected a second time at trap.
* *Nb* (Effective Number of Breeders) -
* NOR (natural-origin) –
* Offspring Year – Calendar year an individual returns the South Fork McKenzie River to spawn
* Origin –
* Outplant – release HOR individual into inaccessible habitat (as verb, not noun) DON’T USE.
* Parent Year – Calendar year an individual returns to the South Fork McKenzie River to spawn
* Potential Offspring – Any NOR individual sampled in the South Fork McKenzie that remains in the dataset after genotype quality filtering
* Progeny – sometimes used in place of offspring in NSNT report. DON’T USE.
* Recycle – double floy tag and all release salmon at Forest Glen (in mainstem, below confluence with South Fork). Only release above Cougar Dam if collected a second time at trap.
* Reintroduce – previously defined release NOR individual into inaccessible habitat (as verb, not noun). DON’T USE.
* Release – trap and haul salmon from below the dam to above the dam (use as verb, not noun)
* Source – Where was a fish initially encountered for this study? This can be one of hatchery outplant (initially encountered at a hatchery), at the Cougar Trap, as a carcass sample or as a precocial male above the dam. Note th
* TLF (Total Lifetime Fitness) – total number of offspring assigned to a candidate parent

**Summary**

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Report with hatchery outplant before 2007 available here: https://odfw.forestry.oregonstate.edu/willamettesalmonidrme/sites/default/files/hatchery-research/Johnson\_and\_Friesen\_2010.pdf

**Objectives**

1. Determine the number and proportion of unmarked, presumed 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 that can be confidently assigned to parents through genetic pedigree in 2016-2020.
3. Estimate the 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 (Nb) for the adult salmon population reintroduced above Cougar Dam in 2011-2015.
6. Estimate the effects of release date and release site on the total lifetime fitness of adult spring Chinook salmon released above Cougar Dam in 2011 - 2015.
7. Evaluate fitness differences between HOR and NOR Chinook salmon released above Cougar Dam in 2011-2015 through assignment of adult offspring returns in 2014-2020.

**Introduction**

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**Methods**

Study System and Sample Collection

Adult hatchery-origin (HOR) 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 construction of a trap and transport facility near the base of Cougar Dam, hereafter the Cougar trap, was completed in July 2010 (Fig. 1). Since that time, both natural-origin (NOR) and HOR Chinook salmon collected at the Cougar trap have been released above Cougar Dam, while the population has continued to be supplemented with hatchery outplants. The Cougar trap has been operational throughout the spawning migration each year since 2010, with the exception of August 6th to July 19th 2011. At both the hatcheries and the Cougar trap, adults are collected using small fish ladders that end in holding tanks. Adults are transported above the dam in trucks and released at one of six sites to spawn. 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 (Duncan, 2011).

Diagram

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**Figure. 1:** Map of the study system.

Beginning in 2013, all NOR Chinook salmon collected at the Cougar trap after September 1st were double floy-tagged and released into the mainstem McKenzie River, beneath the confluence with the South Fork (Fig. 1). After September 1st, only floy-tagged NOR Chinook salmon collected at the Cougar trap were released above the dam. We refer to this program as *late-season downstream release* (LSDR). The motivation of the LSDR program was to limit transportation above the dam of NOR Chinook salmon that were not produced in the above the dam. LSDR was implemented in 2013 and 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, beneath 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 *recycling*. The recycling program has been implemented each year since 2015. HOR salmon collected at the Cougar trap were generally not recycled downstream, but were released above the dam after their first capture at the trap.

Previously published reports and manuscripts evaluating the population above Cougar Dam (Banks et al. 2013; Banks et al. 2014; Banks et al. 2016; Sard et al. 2016) 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. We continued this work in the present report by extending tissue sample collection to include 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. 2016) 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* (Olsen *et al.* 1998, Cairney *et al.* 2000, Naish and Park 2002, Williamson *et al.* 2002, Greig *et al.* 2003 reformat and confirm cites for this panel) and at the sex-linked marker, *Oty3*, to determine sex (Brunelli et al. 2008). Loci were amplified using 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.

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 (Appendix A). Different genotype quality filtering cutoffs were applied in previous reports, 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 Cougar Trap might be later sampled as carcasses. We considered individuals first encountered at 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 on the South Fork McKenzie River above Cougar Dam (Fig. 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 manuscripts evaluating the reintroduction 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. 2014; Banks et al. 2016; Sard et al. 2016). Most Chinook salmon on the South Fork McKenzie River express an age at maturity of 3 - 6 years (cite). Therefore, previous reports assigned offspring to all candidate parents salmon 2007 – 2009. Results based on the pedigree 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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**Fig. 2:** Illustration of parentage analysis. Groups of individuals are organized into sets of potential offspring (solid rectangle) and candidate parents (dashed rectangle) for parentage analysis. Here, the 205 potential offspring that returned to the South Fork McKenzie in 2014 are assigned to 3,151 candidate parents released above Cougar Dam in 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). Note that while all individuals initially encountered during SGS are NOR, and all individuals initially encountered at a Hatchery are HOR, individuals initially encountered at Cougar Trap are both NOR and HOR. Final location refers to whether a salmon was eventually released above the dam and determines whether it is considered a candidate parent.

\* 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.

Continuing this work, 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 (Fig. 3).

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**Fig. 3:** Illustration of how results from genetic parentage analysis (Fig. 2) are combined to make demographic inferences about parental cohorts. Here we demonstrate how inferences about the 2013 parental cohort are drawn. Assignments between 2013 candidate parents (dashed rectangle) and their offspring in 2014 – 2017 (solid 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 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 3, 4, 5 and 6 years prior, as indicated in Fig. 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). Parentage assignments from CERVUS were then verified using the combined PLS - FL algorithm implemented in COLONY Version 2.0.6.8 (Jones & 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. 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).

Given the longitudinal nature of the genetic parentage analysis of South Fork McKenzie River spring Chinook salmon, we developed an automated, reproducible procedure for choosing the best consensus parentage 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 these changes to software versions and parentage assignment procedure may impact results, we compared results between pedigrees inferred using the approach used in this report and those inferred in previous reports for the six years of overlap in assigned offspring (2010 – 2015). To facilitate the identification of long term trends in the demographic and genetic characteristics of South Fork McKenzie River spring Chinook salmon, we conducted all analyses using the pedigree inferred using the new methods. All results presented are based on the new pedigrees.

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 progeny of Chinook salmon previously released above Cougar Dam, South Fork McKenzie River in 2007 - 2017.

To evaluate the efficacy of the LSDR and recycling programs, we also determined the number of NOR immigrants 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 (GLMMimmigrant) using *sex*, and the *Julian day of sampling* at the Cougar trap, across the years in our combined pedigree where we evaluate all possible parentages of potential offspring (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

*Age at Maturity*

For each assigned progeny, we subtracted the year potential offspring returned (e.g., 2016) by each parent(s) release year (e.g., 2013) to infer the age at maturity of progeny (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 onwards, we were able to identify age 3, 4, 5, and 6 offspring in return years 2013 – 2020. For example, we cannot identify age 5 salmon returning in 2010, because we did not examine candidate parents from 2005.

*Total Lifetime Fitness*

We defined total lifetime fitness (TLF) as the total number of offspring assigned to a candidate parent (Fig. 2). We estimated TLF for all candidate parents in our dataset, including HOR 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.

Most Chinook salmon on the South Fork McKenzie River express an age at maturity of 3 - 6 years. Therefore, we estimated TLF for candidate parents only if we sampled their potential offspring 3, 4, 5, and 6 years after candidate parents were released above Cougar Dam (Fig. 2). 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 and the severity of the underestimation depends on the age structure of Chinook salmon in this river. We always note these partial TLFs with an asterisk in figures and tables.

*Cohort Replacement Rate*

Cohort replacement rate (CRR), or “the number of future spawners produced by a spawner” (Botsford & Brittnacher 1998) was estimated for each cohort of candidate parents released or observed above the Cougar Dam. We also report both a female-only CRRF and a male-only CRRM. These sex specific CRRs were calculated by summing the assigned same-sex progeny and dividing this sum by the total number of released females or males. For example, a CRRF = total number of age-3, age-4 and age-5 female progeny produced by females released or observed above Cougar Dam divided by the total number of females released or observed above Cougar Dam. Similar to our TLF results, the age structure of Chinook salmon in the McKenzie River precludes us from estimating an accurate CRR until age 6 offspring of candidate parents have returned and are sampled. Therefore, we present CRR estimates for parental cohorts from 2007 – 2017 but note that these likely underestimate the true CRR in 2015, 2016 and 2017. These are noted by asterisks in tables and figures.

Note that our definition and estimation of CRR differs from those used in previous reports. Only the CRRF (presented as CRR) was presented in previous reports, and in some reports, both carcasses and unsampled offspring inferred from grandparentage analysis contributed to the CRRF, whereas others only considered the contribution to CRRF made by offspring sampled at the Cougar trap. CRR values might also vary due to changes in genotype quality filtering and assignment. To permit the identification of long term trends in CRR in this report, we present CRR values for years previously reported (2007 – 2010), as well as CRR values for 2011 - 2017 using the same approach.

*Effective Number of Breeders*

The effective number of breeders (*Nb*) among cohorts of salmon released or observed above Cougar Dam from 2007 - 2017 was estimated using the linkage disequilibrium (LD) method, as implemented in the program NEESTIMATOR v2.1 (Waples & 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. *Nb* was calculated using the genotypes of all offspring assigned to each cohort. 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 *Nb* to the number of candidate parents (*Ncand*). *Ncand* potentially underrepresents the total number of salmon in the parental cohort above the dam due to incomplete sampling or incomplete genotyping. We also compare *Nb* to the number of candidate parents that produced one or more adult progeny (i.e. successful parents). Note that our methods to estimate *Nb* 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 *Nb* in this report, we present CRR values for years previously reported (2007 – 2010), as well as CRR values for 2011 - 2017 using the same approach.

Predictors of Fitness

We applied a generalized linear mixed model (GLMM) to identify predictors of TLF of all candidate parents from 2007 - 2015. We fit a single GLMM using data from candidate parents from 2007 - 2015. 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 after centering and scaling. *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 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 retained by both approaches. After a final model was selected, 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 retained in the final model were generated using the *effects* package in *R* and conditioned on the typical values of all other significant predictors in the final model.

**Results**

Sampling and Genotyping

After genotype quality filtering, there were 9,839 individuals genotyped at an average of 10.86 microsatellite loci (Table 1). 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 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 5 carcasses sampled during SGSs above the dam (Table 2).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Year** | **Tissue Samples** | **Missingness Filtered** | **Duplicate Filtered** | **Nfinal** |
| 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 |

**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 multi-locus genotype (duplicate filtered).

\* Indicates some or all individuals from this year genotyped in prior reports (cites)

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **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 |  |  |  |  |

**Table 2:** Sample sizes after genotype quality filtering of salmon initially encountered at McKenzie or Leaburg Hatcheries (Hatchery Outplant), at 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.

Parentage Assignment

We attempted to assign 2,915 potential offspring to 8,985 candidate parents (Tables 3 and 4, respectively). Of these 2,915 offspring, 1,669 assigned to 1,681 successful parents for an overall assignment rate of potential offspring of 57% (1,669 / 2,915) (Table 4). In the eight years when all candidate parents of potential offspring are sampled (2013 - 2020), the assignment rate was 67% (1,183 / 1783) and varied across years from 51% in 2019 to 94% in 2020 (Table 4, Fig. 6)).

For the six offspring years when pedigrees were inferred in both this report and in previous reports, the average absolute difference in assignment rate for was 0.7% (Table 3), indicating that changes to software versions, genotype quality filtering and assignment procedures had only a limited impact on the final pedigree.

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | **Overall** | | |  | **Cougar Trap** | | | | | |
| **Year** | ***npotential offspring*** | ***nassigned*** | **% Assigned** |  | | ***npotential offspring*** | | ***nassigned*** | **% 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% |  |

**Table 3:** Number of NOR Chinook salmon sampled in the South Fork McKenzie River and retained after genotype quality filtering (*npotential offspring*) in each year and the number (*nassigne****d***) and percent (% Assigned) assigned to candidate parents. Results for the full set of potential offspring (Overall) and potential offspring initially sampled at Cougar Trap (Cougar Trap) are presented separately. The previously reported assignment rate (Previous % Assigned) (for Cougar Trap only) is also presented.

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

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **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 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.

Considering only years where all potential parents were include in the genetic parentage analysis as candidate parents (2013 - 2020), the average proportion of individuals assigned to at least one parent above Cougar Dam was 71%. Assuming individuals that do not assign to at least one parent above the dam were not produced above the dam, this suggests 29% of NOR salmon collected at Cougar dam are NOR immigrants. We found that the probability of collecting NOR immigrants at the Cougar Trap increased throughout the season, and that males were more likely to be NOR immigrants than females (Table 5, Fig. 4). In our model, the proportion of NOR immigrants collected at Cougar Trap was estimated to increase from less than 10% early in the season to ~40% by September 1st. However, there was substantial variation among years in the relationship between time and the proportion of NOR immigrants collected at Cougar Trap. The 95% confidence interval of the estimate on September 1st spanned from ~ 25% – 50% NOR immigrants.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Fixed effects** | **β** | **s.e** | **LRT**  **p-value** | **Wald**  **p-value** |
| (Intercept) | 5.040 | 0.923 |  | **<0.001** |
| *Julian day of sampling* | -0.018 | 0.004 | **0.004** | **<0.001** |
| *Sex*[Male] | -0.351 | 0.127 | **0.006** | **<0.001** |
| **Random effects** | **σ2** | **s.d.** | **ρ** |  |
| *year*(Intercept) | 4.623 | 2.150 | -0.95 |  |
| *year \* Julian day of sampling* | 0.0001 | 0.010 |  |  |

**Table 5:** Results of generalized linear mixed model examining the influence of *sex, Julian day of sampling* on whether or not a NOR salmon sampled at Cougar Trap was assigned to at least one parent from above the dam. 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 (σ2) 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).

Chart

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**Figure 4:** Effect of *Julian day of sampling* on the predicted proportion of NOR salmon collected at Cougar Trap was produced above the dam (heavy black line) as predicted by GLMMimmigrant. Vertical dashed red line is 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.

Demography

*Age at Maturity*

The average age at maturity for NOR Chinook salmon that we were able to successfully assign to a parent was 4.4 years. Most salmon were ages 4 or 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 offspring years when we are able to identify all of age 3, 4, 5, and 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).

Chart

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**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. There was substantial variation in TLF among years. For years when all (2007 – 2014), or most (2015) offspring are expected to have returned and TLF is likely to be accurate, the mean TLF for all candidate parents was 0.36 and ranged from 0 - 17. 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).

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **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 |

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

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

\*\* Note that 2016 and 2017 offspring do not include potential year 5 and 6 offspring, and potential year 4 5 and 6 offspring, which are expected to substantially contribute to TLF for these parents years

Chart, line chart

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**Figure 6:** Mean Total lifetime Fitness and standard deviation from 2007 to 2015, by sex and origin.

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

*Cohort Replacement Rate*

The cohort replacement rate was less than 1 in all years from 2007 – 2015, indicating that the population above Cougar Dam is not replacing itself (Table 7). Maximum CRR (0.44) was observed in 2007, and minimum CRR (0.08) was observed in 2009, both years where only HOR hatchery outplants were released above the dam. In most years (2007 – 2012) females were the limiting sex. CRRF was less than one in these years. In the three years when males were the limiting sex (2013 - 2015), CRRM was also less than one.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Year** | ***noffspring*** | ***ncand*** | ***ncand female*** | ***ncand male*** | **CRR** | **CRRF\*\*\*** | **CRRM** |
| 2007 | 331 | 745 | 318 | 427 | 0.44 | 0.36 | 0.43 |
| 2008 | 247 | 873 | 288 | 585 | 0.28 | 0.30 | 0.26 |
| 2009 | 114 | 1383 | 603 | 780 | 0.08 | 0.06 | 0.08 |
| 2010 | 94 | 747 | 263 | 484 | 0.13 | 0.12 | 0.11 |
| 2011 | 284 | 725 | 320 | 405 | 0.39 | 0.34 | 0.32 |
| 2012 | 171 | 947 | 439 | 508 | 0.18 | 0.11 | 0.19 |
| 2013 | 151 | 627 | 325 | 302 | 0.24 | 0.14 | 0.26 |
| 2014 | 73 | 652 | 386 | 266 | 0.11 | 0.08 | 0.11 |
| 2015\* | 69 | 754 | 465 | 289 | 0.09 | 0.06 | 0.12 |
| 2016\*\* | 135 | 705 | 403 | 302 | 0.19 | 0.10 | 0.29 |
| 2017\*\* | 0 | 605 | 370 | 235 | 0.00 | 0.00 | 0.00 |

**Table 7:** Cohort Replacement Rate (CRR) per parent year. CRR 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 (noffspring), divided by the number of candidate parents (ncand) in that year. We also present CRRF: the number female offspring successfully assigned to at least one female parent in a given year, divided by the number of female candidate parents (ncand female) in that year. CRRM is the equivalent value for males.  
\* Note that 2015 estimates do not include potential year 6 offspring. However we expect these offspring to contribute very little to TLF (~2%)  
\*\* Note that 2016 and 2017 offspring do not include potential year 5 and 6 offspring, and potential year 4 5 and 6 offspring, which are expected to substantially contribute to TLF for these parents years

**\*\*\* Previous reports present CRRF as CRR.**

*Effective Number of Breeders*

The effective number of breeders (*Nb*), 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 relationship between *Nb* and the number of successful parents in our pedigree is influenced by the genetic characteristics of the parental cohorts, the completeness of our sampling and the accuracy of our inferred pedigrees. An *Nb* estimate much greater than the number of successful parents in the pedigree may be due to disassortative mating, unsampled parents, or underassignment of offspring to parents (e.g. offspring assigns does not assign to a parent because the parent was not sampled or was incorrectly excluded during assignment). In contrast, an *Nb* estimate much less than the number of successful parents in the estimated pedigree may be due to unbalanced sex ratios, fluctuations in *Nb* over time, assortative mating, or spurious assignments of offspring to parents. *Nb* and the ratio between *Nb* and the number of successful parents in our pedigree for each parent cohort is presented in table 8. The ratio was substantially greater than one (1.5x) in four of the nine years that we considered, however estimates of *Nb*in these years were associated with smaller datasets (*noffspring*) and larger confidence intervals than other years.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Year** | ***ncand*** | *nsuccess* | ***noffspring*** | ***Nb*** | **CIlower** | **CIupper** | **Nb nsuccess ratio** |
| 2007 | 745 | 261 | 331 | 265.5 | 222.7 | 322.8 | 1.02 |
| 2008 | 873 | 229 | 247 | 247.5 | 203.7 | 308.8 | 1.08 |
| 2009 | 1383 | 156 | 114 | 368.6 | 228.1 | 848.6 | 2.36 |
| 2010 | 747 | 105 | 94 | 169.8 | 116.6 | 288 | 1.62 |
| 2011 | 725 | 209 | 284 | 220.1 | 181.7 | 272.7 | 1.05 |
| 2012 | 947 | 206 | 171 | 297.2 | 216.5 | 451.4 | 1.44 |
| 2013 | 627 | 152 | 151 | 139.8 | 104.3 | 199.7 | 0.92 |
| 2014 | 652 | 90 | 73 | 167.5 | 104.7 | 361.6 | 1.86 |
| 2015\* | 754 | 103 | 69 | 211.9 | 122.1 | 627.5 | 2.06 |

**Table 8:** Effective number of breeders (*Nb*) per parent year as estimated by NeEstimator v2.1. Number of candidate parents (*ncand*) is the number of salmon released above the Cougar Dam in a given year that were sampled, and successfully genotyped, *nsuccess* is the number of candidate parents with one or more offspring in the pedigree. *noffspring* 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. Finally the Nb : *nsucces* ratio is the Nb estimate divided by the number of successful breeders.

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

Predictors of Fitness

*Generalized Linear Mixed Modeling*

We did not find evidence of strong multicollinearity among the evaluated predictors, 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 is presentedin Table 9*.*

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Fixed effects** | **β** | **s.e** | **LRT**  **p-value** | **Wald**  **p-value** |
| (Intercept) | -1.343 | 0.208 |  |  |
| *sex*[male] | -0.150 | 0.082 |  | 0.066 |
| *origin*[NOR] | 0.446 | 0.132 |  | **0.001** |
| *Julian Day of release* | -0.004 | 0.001 | **0.004** | **0.003** |
| *annual sex ratio* | 1.042 | 0.501 |  | **0.038** |
| *sex*[male] \* *origin*[NOR] | 0.293 | 0.142 | **0.039** | **0.039** |
| *sex*[male] \* *annual sex ratio* | -0.750 | 0.177 | **<0.001** | **<0.001** |
| **Random effects** | **σ2** | **s.d.** |  |  |
| *year* | 0.306 | 0.553 |  |  |
| *release group* | 0.085 | 0.292 |  |  |

**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 (σ2) and standard deviation (s.d.) are presented for random effects.

*Predicted Effects of Significant Predictors of TLF*

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

Chart, box and whisker chart

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**Fig 7:** Predicted effects of *origin* (NOR *vs.* HOR) and *sex* on TLF from the final GLMM. 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 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 considered on response scale (TLF) (Fig. 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 in 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.

Chart, histogram

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**Fig. 8:** Predicted effects of *annual sex ratio* and *sex* on TLF from the final GLMM. 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 (Fig. 9). Individuals released on the earliest day in the dataset are predicted to have 1.7 fold greater fitness than the latest release day.

Chart, line chart

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**Fig. 9:** Predicted effects of *Julian day of release* on TLF from the final GLMM. 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.

Other results

**Discussion**

Main Findings

1. Main findings presented in same order as objectives
2. Main Finding 2
3. Main Finding 3
4. Main Finding 4
5. Main Finding 5
6. Main Finding 6
7. Main Finding 7

Assignment Rates

Discussion of any important results from the assignments. Including discussion of the rate of NOR immigrants arriving at the trap.

Predictors of Fitness

Discussion paragraphs about the what drives variation in fitness among individuals, including environmental/release strategy variables and origin.

* Age length and origin are confounded. something previously noted in this system and fitting with the general observation that relative reproductive success of HOR and NOR salmon is at least partly mediated by differences in growth rates and AAM. I might conduct variance partitioning on the GLMM using commonality analysis to see how much we can tease apart this multicollinearity into shared and unique contributions of size and origin to TLF, but in any case, we should note how these variables are confounded in the discussion.

Demography

Discussion of whether or not the population is reaching replacement.

* Unsampled parents?
  + Nb:Nsuccess ratio often greater than 1. Does this suggest unsampled parents? Reference discussions in previous paragraphs about nb:nsuccessful. We didn’t do the grandparentage analysis conducted in previous studies, but we were able to assess the reproductive success of some precocial males and some carcass samples above the dam (n = 17). None produced offspring observed at Cougar trap or in subsequent SGS. This doesn’t mean there aren’t precocial males or adfluvials above the dam contributing to the returns, but we didn’t find direct evidence of this from these additional samples.

Conclusion

Example conclusion from 2016 report: 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.

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APPENDIX A: ASSIGNMENT POWER

This appendix will hold all the tables describing allele frequencies and variation, marker information content, non-exclusion probabilities, expected false parentages, and estimated genotype error rates for each offspring year and their set of candidate parents. I plan to generally follow the approach to presenting these values as Evans 2016, with a few changes. Most importantly, I will estimate a worst case scenario NEP, which assumes each parent offspring pair is evaluated at only the 7 markers with the largest (i.e. least powerful) NEPs.