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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 adult offspring produced by a cohort of parents, divided by the number of parents in the cohort.
* 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.
* 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.
* Offspring Year – Calendar year an individual returns the South Fork McKenzie River to spawn
* Outplant – release HOR individual into inaccessible habitat (as verb, not noun) DON’T USE, use release instead.
* 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.
* Downstream 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 in NSNT as release NOR individual into inaccessible habitat (as verb, not noun). DON’T USE, use release instead.
* Release – trap and haul salmon from below the dam to above the dam (use as verb, not noun)
* TLF (Total Lifetime Fitness) – total number of adult offspring assigned to a candidate parent

**Summary**

Summary text.

**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 that can be confidently assigned to parents through genetic pedigrees in 2016 – 2020.
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 (Nb) for the adult salmon population reintroduced 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.

**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 contributed to declines in abundance of this ESU by preventing passage to and from historical spawning habitats and by 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 & Friesen 2010). Access to historical spawning habitats 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 South Fork McKenzie 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. Following anecdotal evidence, genetic parentage assignments confirmed that some juvenile salmon survived downstream passage through the dam and returned to the South Fork McKenzie River as adults to spawn (Banks et al. 2013). After construction of a trap and haul facility at the base of Cougar Dam (hereafter the Cougar Trap) in 2010, natural-origin (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 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 rate (CRR – the number of future spawners produced by a spawner) was less than one in the years from 2007 – 2010, indicating that the above dam population is not replacing itself. They also found that the likelihood that 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 of the above dam population with HOR females where necessary 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 are 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). In the present report, 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). Results of the present report address the following RPAs:

* 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 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 strateies)
* 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)

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.

**Methods**

Study System and Sample Collection

Adult hatchery-origin (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 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, primarily natural-origin (NOR) Chinook salmon collected at the Cougar Trap have been released above Cougar Dam, while the population has continued to be supplemented with hatchery outplants from McKenzie or Leaburg Hatcheries. The Cougar Trap has been operational throughout the spawning migration each year since 2010, with the exception of July 19th to August 6th 2011. At both the hatcheries and the Cougar Trap, adults are collected using fish ladders that end in holding ponds. 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.

Map

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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, 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). 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 *downstream recycling.* The downstream 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; 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 & 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 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 (Appendix A). 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 Cougar Trap might be later sampled as carcasses. We considered individuals first collected 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. 2016b). Most Chinook salmon on the South Fork McKenzie River express an age at maturity of 3 – 6 years, with the majority being age 4 and 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 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). Final location refers to whether a salmon was eventually released. 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 (Fig. 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 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, 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 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 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 constructed 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 progeny 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 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 (GLMMimmigrant) 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

*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, age-4, age-5, and age-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*

Total lifetime fitness (TLF) is defined as the total number of adult offspring assigned to a candidate parent (Fig. 2). Since most Chinook salmon on the South Fork McKenzie River express an age at maturity of 3 – 6 years, 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). 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 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 (CRRtotal), 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, CRRF is the 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 – 2015 but note that these likely underestimate the true CRR in 2015. This year is noted with asterisks in tables and figures.

Note that our definitions and estimation of CRR values differ from those used in previous reports. CRRF (previously 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 other estimates of CRRF only considered offspring sampled at the Cougar Trap. CRRF 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. We also clearly distinguish between CRRtotal, CRRF, and CRRM.

*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 parental 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 *Nb* values for years previously reported (2007 – 2010), as well as *Nb* values for 2011 – 2017 using the same, updated 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 (hereafter GLMMTLF), 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 GLMMTLF 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 TLFfor a subset of candidate parents with *size at maturity* measurements (hereafter GLMMsize). We defined *size at maturity* as the fork length in cm for candidate parents measured at the time of release. This GLMMsize used the final significant predictors from the GLMM on TLF using all parents (GLMMTLF), 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.

**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

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

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 57% (1,669 / 2,915) (Table 4). In the eight years when all candidate parents of potential offspring were 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 the percent of NOR immigrants is equal to (1 - % assigned) for the Cougar Trap in 2013 – 2020.

\* 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 when all potential parents were included 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 the Cougar Trap are NOR immigrants. We found that the proportion of NOR immigrants collected at the Cougar Trap increased throughout the season (Table 5, Fig. 4). In our model (GLMMimmigrant), the proportion of NOR immigrants collected at 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 Cougar Trap. The 95% confidence interval of the estimated proportion of NOR immigrants on September 1st spanned from ~ 38% – 63%.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Fixed effects** | **β** | **s.e** | **LRT**  **p-value** | **Wald**  **p-value** |
| (Intercept) | 7.130 | 0.930 |  | **1.7 x 10-14** |
| *Julian day of sampling* | -0.029 | 0.004 | **4.7 x 10-5** | **1.3 x 10-12** |
| *Sex*[Male] | -0.261 | 0.135 | 0.053 | 0.054 |
| **Random effects** | **σ2** | **s.d.** | **ρ** |  |
| *year*(Intercept) | 4.883 | 2.209 | -0.95 |  |
| *year \* Julian day of sampling* | 8.5 x 10-5 | 0.009 |  |  |

**Table 5.** GLMMimmigrant 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 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 (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, line 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. Only the first observation of an salmon at the Cougar Trap is used. 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.

In 2015 – 2020, when downstream recycling was implemented, 875 NOR salmon produced above the dam were collected at the trap. The mean interval between first and second collection at the Cougar Trap for NOR salmon produced above the dam was 30.9 days (s.d. = 28.3). Of the 875 NOR salmon produced above the dam that were recycled downstream, 275 (31%) did not return to the trap, and 600 (69%) returned a second time. 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 x 10-16). During the same period, 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.

Had LSDR been implemented during these years in place of downstream recycling, more of both NOR salmon produced above the dam and NOR immigrants would have been released above the dam. Of the 875 NOR salmon produced above the dam that were collected at the trap, 834 (95%) would have been released above the dam. Of the 334 NOR immigrants, 212 (63%) would have been released above the dam.

Demography

*Age at Maturity*

Most salmon were age-4 or age-5 (55% and 42%, respectively), with few returning at age-3 or age-6 (2% and 2%, respectively). This pattern was consistent across all offspring years when we could identify all 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 (Fig. 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 parental cohort years. For parental cohort years when all (2007 – 2014), or most (2015) offspring are expected to have returned and TLF is likely to be accurate, the overall mean TLF 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). 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.

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **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 age-6 offspring. However, we expect these offspring to contribute very little to TLF (< 2%)

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

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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 age-6 offspring. However, we expect these offspring to contribute very little to TLF (~2%)

*Cohort Replacement Rate*

The total cohort replacement rate (CRRtotal) was less than 1 in all years from 2007 – 2015, indicating that the population above Cougar Dam is not replacing itself (Table 7). Maximum CRRtotal (0.44) was observed in 2007, and minimum CRRtotal (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. 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*** | **Sex Ratio (female:male)** | **CRRtotal** | **CRRF\*\*** | **CRRM** |
| 2007 | 331 | 745 | 318 | 427 | 1 : 1.3 | 0.44 | 0.36 | 0.43 |
| 2008 | 247 | 873 | 288 | 585 | 1 : 2.0 | 0.28 | 0.30 | 0.26 |
| 2009 | 114 | 1383 | 603 | 780 | 1 : 1.3 | 0.08 | 0.06 | 0.08 |
| 2010 | 94 | 747 | 263 | 484 | 1 : 1.8 | 0.13 | 0.12 | 0.11 |
| 2011 | 284 | 725 | 320 | 405 | 1 : 1.3 | 0.39 | 0.34 | 0.32 |
| 2012 | 171 | 947 | 439 | 508 | 1: 1.2 | 0.18 | 0.11 | 0.19 |
| 2013 | 151 | 627 | 325 | 302 | 1.1 : 1 | 0.24 | 0.14 | 0.26 |
| 2014 | 73 | 652 | 386 | 266 | 1.5 : 1 | 0.11 | 0.08 | 0.11 |
| 2015\* | 69 | 754 | 465 | 289 | 1.6 : 1 | 0.09 | 0.06 | 0.12 |

**Table 7.** Cohort Replacement Rate (CRRtotal) per parent year. CRRtotal 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 age-6 offspring. However, we expect these offspring to contribute very little to TLF (~2%)

**\*\* 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. The ratio between *Nb* and the number of successful parents was substantially greater than one (1.5x) in four of the nine years that we considered (Table 8). 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). However, estimates of *Nb*in these years were associated with smaller datasets (*noffspring*) and larger confidence intervals than other years. 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. No *Nb* estimates were substantially (1.5x) lower than the number of successful parents.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **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 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 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 than 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 GLMMTLF. 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) (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 GLMMTLF. 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 GLMMTLF. 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.

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 GLMMTLF. 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, βorigin [NOR] = 2.92 cm, s.e. = 0.26, p-value likelihood ratio test < 2.2 x 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 (GLMMsize). Size had a significant positive effect on TLF (βsize = 0.069, s.e. = 0.006, p-value likelihood ratio test < 2.0 x 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.

**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 many as 49% and as few as 6% of NOR salmon collected at the Cougar Trap were immigrants in 2019 and 2020, respectively.
3. The proportion of NOR immigrants collected at 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 47% of NOR immigrants and 5% of NOR salmon produced above the dam.

*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. Most (80%) candidate parents from 2007 – 2015 did not produce a single offspring (TLF = 0) that returned to the Cougar Trap as an adult, or was sampled as a carcass,
3. Mean TLF 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 where we sampled nearly all potential offspring of parental cohorts above Cougar Dam, CRRtotal never approached one, indicating that population above the dam is not replacing itself. Maximum CRRtotal was 0.44 and minimum was 0.08.
6. In most years females were the limiting sex. CRRF was less than one in these years. In years when males were the limiting sex, CRRM was also less than one.
7. *Nb* 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 the 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 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.
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 that are nested within year and release group have a large effect on TLF.
6. NOR salmon are larger than HOR salmon, 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.

Our assignment results broadly corroborate those presented in previous reports. 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 are able to assign potential offspring sampled at the Cougar Trap to all of their candidate parents (offspring sampled from 2013 – 2020), 29% of NOR salmon collected at the Cougar Trap did not assign to any candidate parent and were inferred to be NOR immigrants produced below the dam or elsewhere. However, we found significant variation in assignment rate throughout a season and among years.

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. We corroborated previous findings that NOR fitness is greater than HOR fitness and that CRR for the above dam population is substantially below one in all years (discussed further in relevant sections below). Given these findings, by influencing the disposition of NOR salmon, 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. Specifically, above dam transport of NOR salmon may provide several benefits to the reintroduction program above Cougar Dam. First, NOR salmon produced above the dam are able to contribute to the future productivity of their source population. Second, 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 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 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 which is associated with reduced fitness as quantified by the GLMMTLF. 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, CRR less than one in all years from 2007 – 2015.

We recommend managers carefully consider the following findings in light of the costs and benefits outlined above. NOR salmon produced above the dam are significantly more likely to return a second time after being recycled downstream than NOR immigrants. As a consequence, 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 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. Finally, the interval between the first collection of an NOR salmon at the Cougar Trap and its eventual release above the dam was ~31 days. Release day was significantly predictive of fitness in the GLMMTLF, and the delay in release associated with recycling is predicted to reduce fitness of NOR salmon above the dam by 12%.

Demography

Previous reports have found that spring Chinook released above Cougar Dam are not replacing themselves (Banks et al. 2013; Banks et al. 2014; Banks et al. 2016). The cohort replacement rate was substantially less than one from 2007 – 2010. These reports attributed the low productivity of the above dam population to the 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 increased fitness of NOR salmon released above the dam and possible implementation of measures to increase downstream passage survival. Our analysis extended estimates of the cohort replacement rate to include 2011 – 2015. We found that the above dam population is not replacing itself in these years. The cohort replacement rate has remained below one from 2007 – 2015, regardless of whether cohort replacement rate is estimated using all individuals (CRRtotal), only females (CRRF) or only males (CRRM).

Nb 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 population. Given the population genetic structure of Chinook salmon generally, spring Chinook salmon released above Cougar dam are more appropriately considered a component of the larger McKenzie River total population. Genetic diversity among salmon released above the dam depends on the genetic diversity among hatchery outplants and NOR immigrants, and so long as the above dam population continues to be supplemented with hatchery outplants or NOR immigrants there is no reason to believe inbreeding depression represents a risk to future productivity.

Banks *et al* (2016) and Sard *et al* (2016a) assigned offspring to grandparents to infer that unsampled adfluvial females and precocial males very likely contribute to productivity above the dam. We found that our estimate of Nb was substantially greater than the number of successful parents in the pedigree for four of the nine years that we analyzed, a result potentially explained by unsampled parents above the dam. While we did not conduct a similar grandparentage analysis, we attempted to confirm that either precocial males or adfuvial 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 used 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 improve statistical power to identify significant predictors of fitness. 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 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 the HOR males, and NOR females were predicted to be 1.6 fold more fit than HOR females. 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 mediated by 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 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). Later 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 hatchery-origin 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). While we also found that there was some variation among years in the effect of release day on TLF, the overall effect of later release over 9 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 (format endnote cite for O’Malley 2022). While the range of sex ratios used 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.

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 above dam population was not reaching replacement when only HOR salmon were released. However, early evidence suggested that NOR fitness was greater than HOR fitness above Cougar Dam, suggesting that productivity may increase in later years. In this report, we extended previous results by evaluating five additional years of releases above Cougar Dam that include both HOR and NOR salmon. While NOR salmon indeed demonstrated substantially greater fitness than 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

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

**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.

| **Offspring Year** | **Marker** | **PIC** | **k** | **HO** | **HE** | **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 |
| 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 |
| 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 |

**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), HO (observed heterozygosity), HE (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.