**Introduction**

The evolutionary history of Pacific salmon (*Oncorhynchus spp*.) is defined by a dynamic balance between disturbance, population connectivity and local adaptation (Fraser *et al.* 2011; Waples *et al.* 2008). Shifts in climate, marine productivity, sea level and geology have led to repeated extirpations, but also produced a mosaic of habitats and accompanying selective regimes on different temporal and spatial scales (Waples *et al.* 2008). Pacific salmon have evolved extensive life-history diversity under these conditions and successfully utilize a wide array of freshwater habitats throughout their range (Taylor 1991). Because productivity at broad scales (e.g. species, metapopulations, stocks) integrates asynchronous benefits and risks at fine scales (e.g. life-history variants, habitats), this diversity promotes stability and resilience in Pacific salmon (Brennan *et al.* 2019; Greene *et al.* 2010; Schindler *et al.* 2010). However, parallel impacts at broad temporal and spatial scales threaten the ability of this portfolio effect to buffer negative effects on Pacific salmon (Crozier *et al.* 2019; Waples *et al.* 2009).

For example, parallel effects of warming rivers caused by broad scale climate forcing, and reduced habitat connectivity caused by construction of passage barriers interact to reduce the resiliency of Chinook salmon (*Oncorhynchus tshawytscha*) (Cordoleani *et al.* 2021; FitzGerald *et al.* 2021; McClure *et al.* 2008; Munsch *et al.* 2022). Large dams (>15 m) have directly contributed to declines of Pacific salmon throughout their range by altering downstream temperature and flow regimes (Angilletta Jr *et al.* 2008; Crozier *et al.* 2020; Ligon *et al.* 1995; USAR 2021), creating reservoirs that delay migration and increase susceptibility to predation (High *et al.* 2006; Monzyk *et al.* 2015; Murphy *et al.* 2021; Schreck *et al.* 2006), and truncating available freshwater habitat (Nehlsen *et al.* 1991). While, a variety of mechanisms have been employed to promote volitional upstream and downstream passage around dams, many dams are too large. For example, impassible dams currently block access to more than half of stream habitat in the Upper Willamette and Lower Columbia River basins (Sheer & Steel 2011). Importantly, the habitat types beyond impassable dams are not evenly distributed, but are biased towards high-elevation tributaries (Sheer & Steel 2011), that may serve as cold-water refugia during warm years (Ebersole *et al.* 2020; Myers *et al.* 2018), and are associated with particular life-history variants (Beechie *et al.* 2006). Furthermore, salmon life-history variation often has a heritable genetic basis (Carlson & Seamons 2008), and loss of the underlying genetic variation may hinder the evolutionary rescue of Chinook salmon (McClure *et al.* 2008; Pess *et al.* 2014; Waples *et al.* 2022). Therefore, while mitigation strategies, such as hatchery propagation below dams, may offset the direct impacts of dams by supplementing productivity, they cannot restore connectivity to the diverse habitats that is may be necessary for long term survival and abundance of Chinook salmon in a changing climate (Cordoleani *et al.* 2021; FitzGerald *et al.* 2021; Herbold *et al.* 2018).

These constraints leave two options for communities wishing to benefit from the predicted benefits of restored connectivity: dam removal or trapping salmon and transporting them around dams using trucks or other means (hereafter trap-and-haul) (Lusardi & Moyle 2017). In the United States, the intersection of many large dams reaching the end of their operational lifespans, increasing recognition of their ecological costs, and reconsideration of their social and economic benefits has led to an rising perception that dam removal is both feasible and necessary (Doyle *et al.* 2008; Foley *et al.* 2017; O'Connor *et al.* 2015). Indeed, multiple recent dam removals have been successful in restoring connectivity and establishing nascent populations through natural recolonization (Allen *et al.* 2016; Duda *et al.* 2021; Hill *et al.* 2019). However, dam removal faces many socio-political hurdles, and is associated with significant costs and ecological tradeoffs (Fox *et al.* 2016; Stanley & Doyle 2003; Vahedifard *et al.* 2021). Consequently, dam removal on conservation relevant time scales is often undesirable or impossible, leaving trap-and-haul based reintroduction as the best tool to reestablish connectivity.

Despite intensive research to optimize trap-and-haul practices (Kock *et al.* 2020), there are also significant challenges and uncertainties associated with trap-and-haul based reintroduction (Anderson *et al.* 2014; Kock *et al.* 2020; Lusardi & Moyle 2017). These challenges and uncertainties include risks of inbreeding and outbreeding depression (Huff *et al.* 2011; Huff *et al.* 2010), fitness costs of delayed migration (Dickerson *et al.* 2005; Marschall *et al.* 2011), phenotype-environment mismatches and imposition of artificial selection regimes (Burger *et al.* 2000; Evans *et al.* 2019; Tillotson *et al.* 2019), increased risks of pre-spawn mortality or disease susceptibility following handling and transport stress (Bowerman *et al.* 2018; Colvin *et al.* 2018; Keefer *et al.* 2010), and conflicts with extant populations, particularly source-sink dynamics (Pess *et al.* 2012; Sard *et al.* 2016b). Therefore, trap-and-haul programs must be frequently evaluated and adjusted using clearly defined metrics in an adaptive management framework (Anderson *et al.* 2014; Kock *et al.* 2020; Lusardi & Moyle 2017).

Trap-and-haul based reintroduction of spring Chinook salmon and steelhead (*Oncorhynchus mykiss*) above impassible dams on several tributaries of the Upper Willamette River (Oregon, United States) has been ongoing for nearly three decades with varied motivations and metrics for success (cite NMFS 2008?). These reintroductions have been subject to ongoing evaluation using multigenerational pedigrees inferred with genetic parentage analysis, permitting adaptive management (Banks *et al.* 2013; Banks *et al.* 2016; Banks *et al.* 2014; Evans *et al.* 2016; O’Malley *et al.* 2017; O’Malley *et al.* 2022; O’Malley *et al.* 2014; Sard *et al.* 2016b; Sard *et al.* 2015; Weigel *et al.* 2019). Importantly, inference of multigenerational pedigrees allows for adult recruits to be parsed into offspring of salmon previously released above the dam and immigrants produced elsewhere. This allows for the calculation of a cohort replacement rate (CRR), defined as “the number of future spawners produced by a spawner” (Botsford & Brittnacher 1998). A CRR greater than one suggests demographic viability without immigration, and net source dynamics for the reintroduced population, while a CRR less than one suggests the population is not demographically viable and is a net sink. Evaluations provide additional important insights into the reintroduction including estimates of genetic diversity, and the identification of management strategies that promote or reduce fitness.

In this study, we use genetic parentage analysis to evaluate a trap-and-haul based reintroduction above the Cougar Dam on the South Fork McKenzie River. Summary of previous results. We extend previous pedigrees to include insights into x years of adult returns and y years of reintroduced cohorts. We provide demographic information including estimates of productivity and fitness. The additional years of data improves the statistical power of our modeling approach used to evaluate trap-and-haul practices and identify significant predictors of fitness, with a particular focus on the relative reproductive success of hatchery-origin (HOR) *vs.* natural-origin (NOR) salmon reintroduced above the dam. We also examine a tag and release program used to manage the disposition of NOR salmon produced above or below the dam. Finally, we discuss how our results can be used in to inform the adaptive management of the reintroduction program and attempt to place our results into context with the current salmon reintroduction literature.

**Methods**

Study System

Spring Chinook salmon in the Upper Willamette River are listed as a threatened evolutionary significant unit (ESU) under the U.S. Endangered Species Act (ESA) (NMFS 1999). Construction and operation of multiple impassible dams throughout the Upper Willamette River have contributed to declines of this ESU (NMFS 2008). The McKenzie River, a tributary of the Upper Willamette River, historically supported one of the largest populations of spring Chinook salmon in the Willamette Basin (McElhany *et al.* 2007). Unlike most Upper Willamette River tributaries, the McKenzie River continues to produce a large proportion of natural-origin (NOR) spring Chinook salmon (Bowerman *et al.* 2018; Johnson & Friesen 2010). Access to historical spawning habitat on the McKenzie River is blocked by several dams. Construction of Cougar Dam (158m) in 1964 on the South Fork McKenzie River impeded access to approximately 40 river km of the historically most productive reaches on the river (NMFS 2008)(Figure 1).

Adult hatchery-origin (HOR) salmon collected from the McKenzie and Leaburg hatcheries on the McKenzie River have been released above Cougar Dam since 1993 (Figure 1). We refer to these individuals as *hatchery outplants*. The initial motivation for these releases was to re-establish historical ecosystem functions, including production of prey for ESA listed bull trout (*Salvelinus confluentus*) and transport of marine nutrients. However, anecdotal evidence suggested that offspring of hatchery outplants survived passage through Cougar Dam and returned to the South Fork McKenzie River as adults. A trap and haul facility was constructed at the base of Cougar Dam in 2010 (hereafter *the Cougar Trap*). The Cougar Trap has been operational throughout the spawning migration each year since 2010, except for July 19 to August 6,2011. The Cougar Trap collects NOR salmon produced above the dam and a small number of HOR salmon. Importantly, NOR salmon that are not produced above the dam also volitionally enter the Cougar Trap and are collected (hereafter *NOR immigrants*) (Banks *et al.* 2013; Banks *et al.* 2016; Banks *et al.* 2014; Sard *et al.* 2016b). Salmon collected at the trap are loaded in trucks and released above Cougar Dam at one of five sites to spawn (Figure 1). Supplementation of the above dam population with hatchery outplants from the McKenzie or Leaburg Hatcheries has continued since construction of the Cougar Trap. Genetic evidence has also confirmed that precocial resident males and adfluvial females make a small contribution to the productivity of the above dam population (Sard *et al.* 2016a). Therefore, spawners above Cougar dam are known to come from six sources: hatchery outplants, HOR salmon collected at the Cougar Trap, NOR salmon produced above the dam, NOR immigrants, precocial resident males, and adfluvial females.

Two programs have been implemented to manage the disposition of NOR salmon collected at the Cougar Trap, late-season downstream release (LSDR) and downstream recycling. Under LSDR all NOR Chinook salmon collected at the Cougar Trap after September 1 were double floy-tagged and released on the mainstem McKenzie River, downstream of the confluence with the South Fork McKenzie River (Figure 1). After September 1, only floy-tagged NOR Chinook salmon collected at the Cougar Trap were released above the dam. The LSDR program was implemented in 2013 and 2014 and reduced above dam transport of NOR immigrants relative to NOR salmon produced above the dam (Banks *et al.* 2016; Banks *et al.* 2014; Sard *et al.* 2016b). Downstream recycling has been implemented each year since 2015. Under downstream recycling, all NOR Chinook salmon collected at the Cougar Trap, regardless of date, are double floy-tagged and released into the mainstem, downstream of the confluence with the South Fork McKenzie River. Among NOR salmon collected at the Cougar Trap, only those with floy-tags are released above the dam.

To date, there is no assisted downstream passage for juveniles produced above the dam. Instead, juvenile fish must navigate through the reservoir and volitionally pass the dam, either by passage through hydroelectric turbines or over a steep, 73 m regulating outlet spillway. Downstream passage of outmigrants through Cougar Reservoir and Dam is associated with high mortality (Beeman *et al.* 2014; Duncan 2011; Monzyk *et al.* 2015; Romer *et al.* 2016).

Sampling

Fin clips were taken 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 and used in previous evaluations of the reintroduction efforts above Cougar Dam (Banks *et al.* 2013; Banks *et al.* 2016; Banks *et al.* 2014; Sard *et al.* 2016b; Sard *et al.* 2015). We extended sampling to include fin clips 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. We also include fin clips 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, we include fin clips collected from precocial male Chinook salmon identified on spawning grounds above the dam during 2014.

Genetic Data

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 fin clips 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; Greig *et al.* 2003; Naish & Park 2002; Williamson *et al.* 2002) 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 evaluations at the same microsatellite loci (Banks *et al.* 2013; Banks *et al.* 2016; Banks *et al.* 2014; Sard *et al.* 2016b; Sard *et al.* 2015), 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.

After genotype data collection and collation, we conducted genotype quality filtering and removed potential duplicates. Salmon with genotypes at less than seven loci were excluded, a threshold determined based on the sequential cumulative non-exclusion probabilities observed among loci. Multilocus genotypes were then compared among individuals to identify salmon that could have been sampled more than once. For example, NOR Chinook salmon sampled at the Cougar Trap might be later sampled as carcasses. We considered individuals first collected at the Cougar Trap and later sampled as carcasses during SGSs as Cougar Trap individuals in all subsequent analyses. If individuals failed to genotype at the sex-linked marker *Oty3*, phenotypic information was used to infer sex.

Genetic Parentage Analysis

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

Most Chinook salmon on the South Fork McKenzie River express an age at maturity of three to six years, with the majority being age-4 and age-5, and less than 2% age-6 (Banks *et al.* 2016). Therefore, we assigned potential offspring sampled on the South Fork McKenzie to candidate parents released above Cougar Dam three to six years prior. We assigned potential offspring that returned to the South Fork McKenzie River 2010 – 2020 to candidate parents released, or otherwise observed above the dam from 2007 – 2017 (Figure 2). Given the known age structure of returning adults, these assignments allow us to identify all offspring of salmon released above Cougar Dam from 2007 – 2014, most (likely >98%) offspring of salmon released above Cougar Dam in 2015, and some offspring of salmon released above the dam in 2016 and 2017 (Figure 3).

Genetic parentage analysis followed the approach used in previous studies evaluating spring Chinook salmon reintroductions throughout the Upper Willamette River (Banks *et al.* 2013; Banks *et al.* 2016; Banks *et al.* 2014; Evans *et al.* 2019; Evans *et al.* 2016; O’Malley *et al.* 2014; O’Malley *et al.* 2015; Sard *et al.* 2016b; Sard *et al.* 2015). Assignment of offspring to parents was first conducted within the maximum-likelihood framework of CERVUS v3.07 (Kalinowski *et al.* 2007). Then, we assigned parentage using the PLS-FL algorithm implemented in COLONY v2.0.6.8 (Jones & Wang 2010). We combined the outputs CERVUS and COLONY to generate a consensus pedigree used in all downstream analyses. Further detail of pedigree inference is available in the supplemental methods. We estimated non-exclusion probabilities and expected number of false parent-offspring pairs (Christie 2010) (supplemental table 1). We also estimated the allele miscall rate and dropout rate using COLONY (Wang 2018) (supplemental table 2).

Assignments

We summarized the number and proportion of unmarked adult Chinook salmon sampled at either the Cougar Trap or spawning grounds below Cougar Dam in 2010 – 2020 that can be assigned as offspring of Chinook salmon previously released above Cougar Dam in 2007 – 2017. To evaluate the effect of the LSDR and downstream recycling programs, we determined the number of both NOR salmon produced above the dam and NOR immigrants that were collected at the Cougar Trap each day. To better understand the relationship between arrival time at the Cougar Trap and the probability that a salmon was produced above the dam for offspring years 2013 – 2020 (when nearly all candidate parents are sampled), we fit a binomial generalized linear mixed model (GLMMimmigrant) using *sex*, the *Julian day of sampling* at the Cougar Trap, and their interaction as predictors, and a random slope among years for *Julian day of sampling*. Further detail of model selection, validation and hypothesis testing are provided in the supplemental methods.

Demography

We defined total lifetime fitness (TLF) as the total number of adult offspring assigned to a candidate parent (Figure 2). We analyzed 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 (based on age-3, age-4, age-5 offspring only), 2016 (based on age-3, age-4, offspring only), and 2017 (based on age-3 offspring only) but note that these partial values underestimate TLF.

CRRswere estimated for each cohort of candidate parents released or observed above the Cougar Dam. We report CRRtotal, defined as the total number of offspring produced by salmon released or observed above Cougar Dam divided by the total number of salmon released or observed above Cougar Dam. We also report both a female-only CRRF and a male-only CRRM. For example, CRRF is the total number of female offspring produced by females released or observed above Cougar Dam divided by the total number of females released or observed above Cougar Dam. We present CRR estimates for parental cohorts from 2007 – 2015, but note that the 2015 CRR is likely an underestimate given that it does not include age-6 offspring.

The effective number of breeders (*Nb*) among cohorts of salmon released or observed above Cougar Dam was estimated using the linkage disequilibrium (LD) method, as implemented in the program NEESTIMATOR v2.1 (Do *et al.* 2014; Waples & Do 2008). 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 from 2007 – 2015. We excluded singletons and generated 95% confidence intervals using a jackknife re-sampling method (Waples and Do 2008).

Predictors of Fitness

We fit a generalized linear mixed model (GLMM) to identify significant predictors of fitness in the above dam population. Specifically, we fit a single GLMM on TLF of candidate parents from 2007 – 2014 and partial TLF of candidate parents from 2015, because age-6 offspring are expected to contribute very little to TLF (<2%) (hereafter GLMMTLF). We considered the influence of multiple potential predictors of fitness including *sex, origin, release day, release location, release group density, release group sex ratio, annual sex ratio.* In addition to fitting each of these predictors as a main fixed effect, we also examined three interaction terms, including *sex\*release day, sex\*origin,* and *sex\*annual sex ratio* and two random effects, *release group*, and *year. Release day* is the Julian day that individuals were released and was modeled as a continuous fixed effect. *Release group* is defined as the individuals released at a single location during a single day. *Release group density* is the number of individuals in a release group. *Release group sex ratio* is the ratio of males to females in a release group. *Annual sex ratio* is the ratio of males to females in a year. Sex ratios were log-transformed before inclusion as predictors in a model. Our modeling approach primarily followed the recommendations of Zuur et al. (2009) and Bolker (2015). Details of our modeling approach can be found in the supplemental methods.

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 filtering, there were 9839 individuals genotyped at an average of 10.86 microsatellite loci (Table 1). Ninety-nine percent of individuals in the filtered dataset were genotyped at nine or more loci. There were 6700 salmon initially collected at McKenzie or Leaburg Hatcheries and transported above Cougar Dam (hatchery outplants), 2930 NOR and HOR salmon initially encountered at the Cougar Trap and released above the dam or downstream, 12 precocial males sampled on spawning grounds above the dam, 192 carcasses sampled during SGSs below the dam, and five carcasses sampled during SGSs above the dam (Table 2).

Assignment

We attempted to assign 2915 potential offspring to 8985 candidate parents (Tables 4 and 3, respectively). Considering only the eight offspring years when all candidate parents that returned three to six years prior were sampled (2013 – 2020), 1183 of 1783 potential offspring assigned to at least one parent, for a total assignment rate of 67%. 1629 potential offspring were sampled at the Cougar Trap in this period. Of these 1629, 1151 assigned to at least one parent above Cougar Dam, for an assignment rate of 71%. Assuming individuals that did not assign to at least one parent above the dam were not produced above the dam, this suggests 29% of NOR salmon collected at the Cougar Trap were NOR immigrants. We found that the proportion of NOR immigrants collected at the Cougar Trap increased throughout the season (Table 5, Figure 4). During model selection, we found that the sex by Julian day of sampling interaction did not improve the fit to the data. Including sex only marginally improved the fit (Table 5, delta AIC = 1.7), but we chose to retain it in the final model (GLMMimmigrant). Using GLMMimmigrant, the proportion of NOR immigrants collected at the Cougar Trap was estimated to increase from less than 5% early in the season to ~50% by September 1. However, there was substantial variation among years in the relationship between time and the proportion of NOR immigrants collected at the Cougar Trap. The 95% confidence interval of the predicted proportion of NOR immigrants on September 1 spanned from ~ 38% – 63%.

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

Demography

*Age at Maturity*

Among the parental cohort years when we could identify age-3 through age-6 salmon (2007 – 2014), most assigned offspring were age-4 or age-5 (51.5% and 44.7%, respectively), with few returning at age-3 or age-6 (2.4% and 1.4%, respectively). This pattern was consistent across all years (Figure 5). However, there was weak but significant trend towards younger offspring in later years (linear model, -0.014 year offspring age, per parent cohort year, p = 0.014).

*Total Lifetime Fitness*

We present the mean TLF for candidate parents as well as its range and standard deviation by year, sex, and origin in Table 6. From 2007 – 2015, there were 7453 candidate parents, and only 1511 (20%) produced at least one offspring that returned to the Cougar Trap or was sampled as a carcass below the dam. For the parental cohort years when all (2007 – 2014) or most (2015) offspring are expected to have returned, the overall mean TLF was 0.36 and ranged from 0 – 17. For the subset of these years when both NOR and HOR salmon were released above the dam (2010 – 2015), mean TLF was greater for NOR than HOR salmon (0.49 *vs.* 0.23, respectively).

*Cohort Replacement Rate*

The total cohort replacement rate (CRRtotal) was less than one 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. The overall weighted mean CRR was 0.21.

*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 ratio of *Nb* to the number of candidate parents ranged from 0.22 to 0.36.

Predictors of Fitness

*Generalized Linear Mixed Modeling*

We did not find evidence of strong multicollinearity among the evaluated predictors of TLF (GVIF1/2\*df < 2), and included all predictors at the start of model selection. Modeling the effect of *release group density* as a second order polynomial provided a marginally better fit to the data than modeling *release group density* as a linear predictor, but all other predictors were modeled as linear effects. The best random effects structure according to AIC included random intercepts for both *year* and *release group.* After model selection of fixed effects, four predictors and two interactions were included in the final model: *sex, origin, Julian day of release, annual sex ratio*, *sex\*origin* and *sex\*annual sex ratio.* Parameter estimates and their standard errors, as well as significance testing for each predictor retained in the final model are presentedin Table 9*.*

*Effects of Significant Predictors of TLF*

To aid in interpretation of the parameters estimated in the final model (Table 9), we also estimated effects of each significant predictor on the response scale (TLF) after accounting for variation at all other significant predictors (Figures 7 – 9). NOR salmon have substantially higher predicted fitness than HOR salmon and this effect is somewhat stronger for males than females, but this interaction is only marginally significant and has a limited effect size (Figure 7). NOR males are predicted to be 2.1-fold more fit than HOR males, and NOR females are predicted to be 1.6-fold more fit than HOR females. Overall, the *annual sex ratio* has a small, and marginally significant effect on TLF, with male-biased sex ratios producing somewhat higher fitness than female-biased sex ratios, however this effect was much stronger for females than males. When viewed on response scale (TLF) (Figure 8), changes in *annual sex ratio* affects fitness mostly through females, who perform worse when the sex ratio is female-biased. Using the most extreme values observed in any years (male:female ratio 0.6 and 2.0), female fitness is predicted to vary 3.5-fold, whereas male fitness is expected to vary 1.4-fold. Finally, salmon released above Cougar Dam earlier in the season are predicted to have greater fitness than those released later (Figure 9). Individuals released on the earliest day in the dataset are predicted to have 1.7-fold greater fitness than the latest release day.

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 3781 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), and 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**

*Genetic Parentage Analysis Provides Crucial Demographic Information*

Previous evaluations of the reintroduction effort above Cougar Dam found that none of the four cohorts of salmon reintroduced from 2007 – 2010 replaced themselves (i.e. CRR was less than one) (cites), even after accounting for productivity of precocial males and adfluvial females (cite). We also found that the CRR did not exceed one from 2011 – 2015, regardless of whether cohort replacement rate was estimated using all individuals (CRRtotal), only females (CRRF), or only males (CRRM). Together these results indicate that no cohorts of reintroduced salmon have reached replacement in any year from 2007 – 2015. Overall, from 2007 – 2015, approximately one adult offspring returned for every five salmon released above the dam.

We found that multiple aspects of upstream (adult) trap-and-haul likely influence fitness at the individual level (TLF). Incorporating these findings into the adaptive management of the reintroduction may improve productivity (see *Mixed Modeling Provides Insights into Trap-and-Haul Practices* and *Origin Effects* discussion below). However, our estimate of fitness integrates productivity and mortality at multiple life-stages across both parents and their offspring (Wolf & Wade 2001). Bottlenecks at any stage may assert a large influence on TLF, and therefore CRR. For example, downstream passage through the Cougar Dam and reservoir is associated with high mortality among outmigrating juveniles (Beeman *et al.* 2014; Duncan 2011; Monzyk *et al.* 2015; Romer *et al.* 2016), and is likely a significant impediment to sustained demographic viability of the reintroduced population (i.e. CRR greater than one). Indeed, genetic parentage analysis by Evans et al (2016) found that CRR was greater than one for three consecutive cohorts of Chinook salmon reintroduced above Foster Dam on the nearby Upper Willamette River tributary, the South Santiam River. The higher productivity of this program has been attributed, in part, to greater downstream passage survival at Foster Dam (38m) compared to Cougar Dam (158m) (Evans *et al.* 2016; Hughes *et al.* 2016; Kock *et al.* 2020). To date, no assisted downstream passage measures are in place at Cougar Dam. Fortunately, substantial variation in downstream passage survival with dam operating conditions (Beeman et al. 2014) suggests that interim measures may improve downstream passage survival. We suggest that our findings on the effects of trap-and-haul practices, such as the effect of origin, be combined with other results from this reintroduced population (e.g. production of age-0 offspring (Banks *et al.* 2016; Banks *et al.* 2014; Sard *et al.* 2015), downstream passage survival (Beeman *et al.* 2014; Duncan 2011; Romer *et al.* 2016), and prespawn mortality (Keefer *et al.* 2010)) in a life-cycle model that integrates productivity and survival across multiple life-stages (Pess & Jordan 2019). This life-cycle model will be a powerful tool in the adaptive management of the reintroduction, because it can predict how simultaneous changes to the reintroduction program may effect CRR.

The effective number of breeders (Nb) is a population genetic parameter used to account for overlapping age classes in the estimation of effective population size. A threshold of fifty to one hundred is commonly used to determine when a population is facing extinction risk due to inbreeding depression (Waples 1990). We found that the effective number of breeders was greater than this threshold in all parental cohorts above Cougar Dam. However, these values need to be placed into the context of the greater metapopulation structure of McKenzie River Chinook salmon. The population of salmon above Cougar Dam is not an isolated population composed solely of salmon produced above the dam. Instead, it is supplemented with hatchery outplants that represent the majority of potential spawners in all years, and a small number of NOR immigrants. Therefore, genetic diversity above the dam, and hence *Nb*, reflects the collective genetic diversity of the NOR descendants of hatchery outplants, hatchery outplants themselves and NOR immigrants that successfully spawn above the dam. Assuming measures to improve downstream survival are implemented, managers may wish to reduce the level of future supplementation to benefit from the increased productivity of natural origin spawners (see *Origin Effects* discussion), and to facilitate local adaption (Campbell *et al.* 2017; Galbreath *et al.* 2014). However, it is not known how changes to the level of supplementation will influence Nb, and the risk of inbreeding depression to above dam population. Continued genetic monitoring will be critical for guiding such changes.

*Mixed Modeling Provides Insights into Trap-and-Haul Practices*

We were able to identify aspects of trap-and-haul practices that significantly explained variation in individual fitness across nine cohorts of Chinook salmon released above Cougar Dam using a mixed modeling approach. We found that fitness 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 much fitness variation was distributed among the random effects of year and release group.

First, we found that Chinook salmon released above Cougar Dam earlier in the season were predicted to have greater fitness than those released later. Attempts to directly characterize patterns of selection on arrival timing find substantial variation from year to year, including directional, stabilizing, disruptive selection (Anderson *et al.* 2013; Dickerson *et al.* 2005; Evans *et al.* 2019; Seamons *et al.* 2007). These inconsistent patterns can be attributed to interannual variation in competition, and the environment encountered by adult salmon returning to spawn and emerging offspring. Indeed, previous genetic parentage analyses of UWR spring Chinook salmon reintroduction programs have found inconsistent effects of release day on fitness, with opposite patterns detected year to year in the same river (Banks *et al.* 2016; Banks *et al.* 2014; Evans *et al.* 2016; Sard *et al.* 2016b). Early release has also been associated with greater risk of pre-spawn mortality among hatchery outplants above dams in the UWR (Keefer *et al.* 2010). Our modeling efforts were focused on identifying consistent relationships between predictors and fitness among nearly nine thousand salmon released over nine years. We did not conduct year-by-year modeling, nor did we allow the relationships between predictors and fitness to vary among years (i.e. a random slopes model). Using this approach, we found that the overall pattern favored early release. However, we also found that there was variation among years in the effect of release during exploratory data analysis, including two years when the early release was associated with reduced fitness. Taken together, we believe these results from multiple reintroductions and years highlight how phenotypic variation may buffer populations in the face of unpredictable environmental variation, and emphasize that trap-and-haul practitioners should attempt to schedule releases to match the distribution of migration timing that would be observed among volitionally migrating salmon.

We also found that the annual sex ratio and its interaction with sex were predictive of fitness. This effect was stronger among females, which were predicted to have greater fitness when the sex ratio is male biased. Interestingly, this pattern in inconsistent with the pattern observed on the nearby North Santiam that found lower fitness for both sexes of reintroduced spring Chinook salmon when the sex ratio was male biased (O’Malley *et al.* 2022). Many ecological processes may mediate the relationship between sex ratio and fitness, and these processes may vary between the two rivers. For example, the proportion of hatchery-origin spawners (pHOS) above Detroit Dam on the North Santiam River was 100% for most years evaluated, while pHOS above Cougar Dam on the South Fork McKenzie River averaged 65% after construction of the Cougar Trap. It is possible that the presence of larger NOR males in the South Fork McKenzie River ameliorate the deleterious effect of strongly male-biased sex ratios like that observed in the North Santiam River, by providing the opportunity for female mate choice (Fleming & Gross 1994; Seamons *et al.* 2007), or by reducing the tendency for females to delay spawning in the presence of a high proportion of smaller, HOR males (Berejikian 2000). Alternatively, there may be differences in the strength of density-dependent processes between the rivers, altering the relationship between sex ratio and fitness for each sex (Seamons *et al.* 2007) (other seamons 2004 cite???). Ultimately, identifying the mechanisms responsible for producing the relationship between sex ratio and fitness is beyond the scope of this study. The conflicting patterns between the North Santiam and McKenzie Rivers highlight the complexity inherent to trap-and-haul based reintroduction and the need for genetic monitoring. In the absence of genetic monitoring, for example in the early stages of reintroductions, we recommend that practitioners exercise the precautionary principle and attempt to reproduce the operational sex ratios expected among volitionally migrating salmon.

Decades of experience and research into trap-and-haul has allowed practitioners to minimize stress and improve outcomes for salmon after they are released (Kock *et al.* 2020). Consequently, it is not surprising that we did not observe significant fitness effects of some variables related to trap-and-haul practices. For example, we did not find that the number or sex ratio of salmon in a release group, or the release location impacted fitness, suggesting these variables may already be optimized, or do not affect fitness in the current ranges in which they are applied. Importantly, we observed substantial variation that could be attributed to the random effect of release group. This finding suggests that other, unmeasured variables nested within release group might impact fitness. Similarly, we found that there was much fitness variation among years after accounting for the effects of the significant, suggesting that other unmeasured variables that operate at the level of year likely influence fitness.

*Origin Effects*

A large body of literature has demonstrated that captive-reared salmon and steelhead released into the wild are less fit than their natural-origin counterparts (Christie *et al.* 2014)(build out a few good representative papers here). The hatchery outplants released above Cougar Dam stem from the McKenzie River spring Chinook hatchery program. This program has a complex history (Johnson & Friesen 2010; ODFW & USACE 2019). Since 1990, only McKenzie River salmon have been used as broodstock with varying levels of NOR salmon integrated into the broodstock in each year. However, the extent to which hatchery production and within basin stock transfers have eliminated local adaptation prior to that time is not known (Johnson & Friesen 2010; Johnson & Friesen 2014). Integrating local and NOR individuals into hatchery broodstock may reduce the effects of successive generations of domestication selection (Araki *et al.* 2007a; Hayes *et al.* 2013; Janowitz-Koch *et al.* 2019), however, even a single generation in captivity is associated with a substantial reduction in fitness in the wild (Araki *et al.* 2007b; Christie *et al.* 2012).

“At one extreme, all of the spawners in

captivity every generation may consist of wild fish. Several

studies have found that in this case the reproductive performance

in nature of the returning hatchery-produced fish is

increased, and genetic divergence between the hatchery and

natural components of supplemented population decreased,

compared to segregated programs (Araki et al. 2007 ; Waters

et al. 2015 ; Ford et al. 2016 ).”

We found that our estimates of the relative reproductive success of HOR relative to NOR salmon in the wild (RRS), and the interaction between origin and sex were both consistent with findings from other local-origin broodstocks (Christie *et al.* 2014). NOR males were predicted to be 2.1-fold more fit than HOR males, and NOR females were predicted to be 1.6-fold more fit than HOR females, after controlling for other variables. Importantly, RRS may be mediated by a variety of processes (cite), and many studies have pointed to the role of both heritable and plastic differences in body size between HORs and NORs in mediating RRS (fix redundancy). Indeed, for the subset of individuals with both size and fitness estimates in our study, we found that both larger size and natural origin were predicted to improve fitness, but that size and origin were strongly confounded. This leads one to suspect that selecting among HOR returns at McKenzie and Leaburg Hatcheries to increase the size of hatchery outplants may ameliorate some of the fitness differences between NOR and HOR salmon above the dam. However, this choice must be weighed against the benefit of including these larger individuals into the broodstock, and must comply with guidelines set forth in the HGMP. Similarly, the finding that NOR salmon, generally, are more fit than HOR salmon above the dam, suggests that the number of adult returns per salmon released (e.g. mean TLF or CRR) can be expected to improve with reductions in pHOS, but this may come at the cost of reducing absolute productivity more broadly (see source sink dynamics discussion). Importantly, our estimate of relative reproductive success do not attempt to parse the fitness of NOR salmon produced above the dam from NOR immigrants. Future analyses using this pedigree will examine origin effects in greater detail, including potential reduction of fitness among NOR salmon owing to spawning with HORs (fix wording), and evidence of re-adaptation to natural conditions among descendants of captive reared salmon.

*Genetic Monitoring Informs Complex Risk-Benefit Tradeoffs Inherent to Reintroduction Programs*

Most salmon populations are organized into a larger metapopulation structure, with the level of connectivity between populations determined by the balance between philopatry and dispersal (does this even need a citation?). Reintroductions fundamentally alter this metapopulation connectivity by design. Examining the consequences of these changes to connectivity on both metapopulation source-sink dynamics and the potential for local adaptation is an important aspect of adaptive management of reintroduced populations (Anderson *et al.* 2014). Local populations with persistent negative growth rates (i.e. sinks), provide both benefits and risks at the metapopulation level. For example, sinks can increase connectivity between source populations and allow individuals to avoid negative density dependent effects within sources, or they may rescue source populations during periods of local disturbance, thereby stabilizing or increasing productivity at the metapopulation scale (Heinrichs *et al.* 2015; Matthews & Gonzalez 2007). Alternatively, sinks may reduce net metapopulation productivity by serving as ecological traps and increase the metapopulation extinction risk (Gundersen *et al.* 2001). Since the construction of the Cougar Trap in 2010, the reintroduction program has released hatchery outplants as well as NOR salmon collected at the trap above the dam. Importantly, these NOR salmon include both NOR salmon produced above the dam, and NOR immigrants produced below the dam or elsewhere. Recognizing the benefits and risks that these potential source-sink dynamics pose to natural production at the metapopulation level, managers implemented two programs to control the disposition of NOR salmon in the South Fork McKenzie: LSDR and downstream recycling. In the discussion below, we apply a metapopulation framework to provide an example of how genetic monitoring can intervene to reduce uncertainties when balancing the complex suite of risks and benefits inherent to reintroduction programs.

Increasing the number or proportion of NOR salmon, regardless of source, is expected to provide demographic and genetic benefits to the reintroduced population above Cougar Dam (i.e. provide local benefits). First, NOR salmon produced above the dam provide a direct demographic benefit to the above dam population when they are released above the dam. Second, we found that NOR salmon are more fit than their smaller HOR counterparts above the dam, and consequently, decreasing pHOS may improve productivity per salmon released. ( <-this is an example of how to weave results into the context, either take this out to make consistent or follow suit with other empirical results that inform each of these general ideas) Finally, allowing successive generations of NOR salmon produced above the dam to return to their natal habitat may permit local adaptation (Nuetzel *et al.* 2022), and 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 salmon may promote the adaptive potential and long-term productivity of the above dam population. Indeed, in the Wenatchee river, a Coho salmon reintroduction seeded with out-of-basin HOR salmon, transitioned to natural production, and saw population growth and evidence of local adaptation (Campbell *et al.* 2017; Galbreath *et al.* 2014; Murdoch 2015)(this obscures the role of broodstock selection to (a) generate environment-phenotype match and (b) maintain SGV in the Wenatchee Coho, but this is outside the scope of the desired statement in the paragraph, think about how to fix). Implementing downstream recycling is also associated with two costs incurred by reintroduced population: delayed migration and additional handling stress.

However, these proposed demographic and genetic benefits provided to the reintroduced population by above dam transport NOR salmon must be evaluated in light of costs and benefit expected to accrue at the metapopulation level. For example, if the natural produced population below the dam demonstrates net positive or neutral growth rates, and is not limited by density dependent effects, then the impact of above dam transport of NOR on natural productivity at the metapopulation will depend on whether net source or net sink dynamics are in place for the above dam population. Increased connectivity is also expected to provide benefits at the metapopulation level by promoting the diversity-stability relationship, and allowing for local adaptation.

We found that approximately one adult recruit returned to the South Fork McKenzie River for every five parents released or otherwise sampled above the dam, indicating that the above dam population is a strong sink. While the relative-costs and benefits of a sink population depends on the dynamics of source populations (cites), it is likely that such a strong sink produces net deleterious effects at the metapopulation level (cite). Furthermore it is unlikely that locally adapted variants can accrue in the face of such strong selection, without continued supplementation. However, as planned downstream passage improvements increase survival, managers may wish to increase the number or proportion of NOR salmon to allow metapopulation benefits to accrue, such as diversity-stability relationship, and local adaptation. Our results indicate that modification to downstream recycling empowers managers to selectively control the disposition of NOR immigrants and NORs produced above the dam.

Among the years where we are able to confidently parse NOR immigrants from NOR salmon produced above the dam, we found that that 29% are NOR immigrants. We also found significant variation in the proportion of NOR immigrants among years, with as few as 6% and as many as 49% in consecutive years (this underscores how source-sink dynamics are largely driven by source demography). The LSDR program implemented in 2013 and 2014 selectively limited above dam transport of NOR immigrants relative to NOR salmon that were produced above the dam (Banks *et al.* 2016; Banks *et al.* 2014). From 2015 onwards, managers transitioned to recycling all NOR salmon downstream, regardless of the date they were collected at the Cougar Trap. We found that for the NOR salmon ultimately released above the dam, downstream recycling delays release by ~31 days which is associated with a 12% reduction in fitness as quantified by the GLMMTLF. We also found that NOR salmon produced above the dam were significantly more likely to return a second time after being recycled downstream than NOR immigrants. Consequently, recycling all NOR salmon collected at the Cougar Trap from 2015 – 2020 prevented above dam transport of 31% of the NOR salmon produced above the dam and 75% of the NOR immigrants. We also confirmed the tendency for NOR immigrants to arrive at the Cougar Trap later than NOR salmon produced above the dam (Banks *et al.* 2016; Banks *et al.* 2014). Consequently, implementing LSDR with a September 1 cutoff in place of downstream recycling during the same period (2015 – 2020), would have prevented the above dam transport of very few (5%) NOR salmon produced above the dam and fewer (37%) NOR immigrants. These results indicate that modification to downstream recycling empowers managers to selectively control the disposition of NOR immigrants and NORs produced above the dam (arrived at literally the exact same wording here, fix this).

Notes/thoughts consider while taking time away from this section:

(1) It would be easy to use the data at hand to describe exactly how the disposition of NOR immigrants and NOR descendants would change given an arbitrary LSDR cutoff, provide this as a model that incorporates interannual variation and therefore uncertainty, that would give managers a direct mechanism to choose a given disposition under future passage conditions, but I still haven’t found the time to do this.

*(2) Currently this feels like a dump of all these concepts and results. Too long and a lot of redundancy. The style here needs to change to elegantly and simultaneously weave our results (currently presented at the end) into the context (currently front loaded). Alternatively, we can share context first and propose specific questions that are addressed with the results. Either case would make this more engaging and do a better job of delivering on the promise to “*apply a metapopulation framework to provide an example of how genetic monitoring can intervene to reduce uncertainties when balancing the complex suite of risks and benefits inherent to reintroduction programs.”

*(3) I also think getting Ryan’s input on the below dam population productivity, or thinking more about carcass survey results*

*(e.g.*

https://odfw.forestry.oregonstate.edu/willamettesalmonidrme/sites/default/files/hatchery-research/zymonashogansen2013-sfmckenziechsspawning-projrpt2011-finalrw.docx )

*would be great here. The cost-benefit analysis depends critically on whether or not there’s evidence of density dependence in productivity below the dam, and while the current discussion leaves this open, there’s data to address it. Also look for the report associated with this presentation https://pweb.crohms.org/tmt/documents/FPOM/2010/Willamette\_Coordination/WFSR/Day%202\_1315\_Lindsey\_Spawning%20Ground%20Surveys\_WFSR%202020.pdf*

*that suggests that habitat restoration has increased redd counts.*

*Alternatively, we can cite to the extensive restoration work done downstream of the dam (Hinshaw et al. 2022) and simply say that it is doubtful that the below dam population is at carrying capacity, given that the purpose of recent restoration work is primarily to increase lateral connectivity and therefore capacity.*

(4) an option to color the benefits of a net sink population with an example from this river can come from the 2011 finding that increased outplanting above the dam is correlated with increased redd counts BELOW the dam, as articulated here: https://odfw.forestry.oregonstate.edu/willamettesalmonidrme/sites/default/files/hatchery-research/zymonashogansen2013-sfmckenziechsspawning-projrpt2011-finalrw.docx) “Results of correlation analyses suggested that higher proportions of redds were located in the upstream section of the lower SFMR in years with higher adult returns to the upper McKenzie Basin, higher proportions of hatchery-origin salmon, and higher abundance of adult females out-planted in the upper SFMR 3-6 years earlier.”), also see this quote “Correlation analyses indicated that proportion wild-origin spawners in the lower SFMR was negatively associated with adult abundance at Leaburg Dam and positively associated with abundance of adult females out-planted 3–6 years earlier in the upper SFMR. “

**Tables**

**Table 1.** Summary of genotype quality filtering. Individuals were removed from the analysis if they were genotyped at < 7 loci (missingness filtered), or if they represented a duplicate multilocus genotype (duplicate filtered).

\* Indicates some or all individuals from this year were genotyped in prior reports

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

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

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

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

**Table 4.** Number of NOR Chinook salmon sampled in the South Fork McKenzie River and retained after genotype quality filtering (*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 including those sampled at the Cougar Trap, during spawning ground surveys or as precocial males above the dam (Overall), and potential offspring initially sampled at the Cougar Trap only (Cougar Trap) are presented separately. Note that the percent of NOR immigrants is equal to (1 - % assigned) for the Cougar Trap in 2013 – 2020.

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

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | **Overall** | | |  | **Cougar Trap** | | | |
| **Year** | ***npotential offspring*** | ***nassigned*** | **% Assigned** |  | ***npotential offspring*** | | ***nassigned*** | **% Assigned** |
| 2010\* | 221 | 14 | 6% |  | 221 | 14 | | 6% |
| 2011\* | 401 | 140 | 35% |  | 356 | 138 | | 39% |
| 2012\* | 510 | 328 | 64% |  | 500 | 326 | | 65% |
| 2013 | 228 | 153 | 67% |  | 223 | 153 | | 69% |
| 2014 | 218 | 118 | 54% |  | 191 | 117 | | 61% |
| 2015 | 265 | 179 | 68% |  | 241 | 176 | | 73% |
| 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 5.** GLMMimmigrant model fit. Results of generalized linear mixed model examining the influence of *sex, Julian day of sampling* on whether an NOR salmon sampled at the Cougar Trap was assigned to at least one parent from above the dam. Only the first observation of an individual is used. Estimated effect (β) and standard error (s.e.) of each fixed predictor on the link (logit) scale for predictors that were retained in the final model are presented. Variance (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). Significant p-values are in bold.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Fixed Effects** | **β** | **s.e.** | **LRT**  **p-value** | **Wald**  **p-value** |
| (Intercept) | 7.130 | 0.930 |  | **1.7 x 10-14** |
| *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 7.** Cohort Replacement Rate (CRRtotal) per parent year. CRRtotal was estimated by determining the number of offspring successfully assigned to at least one parent in a given year (noffspring) and dividing it 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%).

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Year** | ***noffspring*** | ***ncand*** | ***ncand male*** | ***ncand female*** | **Sex Ratio (male:female)** | **CRRtotal** | **CRRF** | **CRRM** |
| 2007 | 331 | 745 | 427 | 318 | 1.3 : 1.0 | 0.44 | 0.36 | 0.43 |
| 2008 | 247 | 873 | 585 | 288 | 2.0 : 1.0 | 0.28 | 0.30 | 0.26 |
| 2009 | 114 | 1383 | 780 | 603 | 1.3 : 1.0 | 0.08 | 0.06 | 0.08 |
| 2010 | 94 | 747 | 484 | 263 | 1.8 : 1.0 | 0.13 | 0.12 | 0.11 |
| 2011 | 284 | 725 | 405 | 320 | 1.3 : 1.0 | 0.39 | 0.34 | 0.32 |
| 2012 | 171 | 947 | 508 | 439 | 1.2 : 1.0 | 0.18 | 0.11 | 0.19 |
| 2013 | 151 | 627 | 302 | 325 | 1.0 : 1.1 | 0.24 | 0.14 | 0.26 |
| 2014 | 73 | 652 | 266 | 386 | 1.0 : 1.5 | 0.11 | 0.08 | 0.11 |
| 2015\* | 69 | 754 | 289 | 465 | 1.0 : 1.6 | 0.09 | 0.06 | 0.12 |

**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 sampled, released above the Cougar Dam in a given year 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. The *Nb* : *ncand* ratiois provided for each year.

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

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Year** | ***ncand*** | *nsuccess* | ***noffspring*** | ***Nb*** | **CIlower** | **CIupper** | ***Nb* : ncand ratio** |
| 2007 | 745 | 261 | 331 | 265.5 | 222.7 | 322.8 | 0.36 |
| 2008 | 873 | 229 | 247 | 247.5 | 203.7 | 308.8 | 0.28 |
| 2009 | 1383 | 156 | 114 | 368.6 | 228.1 | 848.6 | 0.27 |
| 2010 | 747 | 105 | 94 | 169.8 | 116.6 | 288 | 0.23 |
| 2011 | 725 | 209 | 284 | 220.1 | 181.7 | 272.7 | 0.30 |
| 2012 | 947 | 206 | 171 | 297.2 | 216.5 | 451.4 | 0.31 |
| 2013 | 627 | 152 | 151 | 139.8 | 104.3 | 199.7 | 0.22 |
| 2014 | 652 | 90 | 73 | 167.5 | 104.7 | 361.6 | 0.26 |
| 2015\* | 754 | 103 | 69 | 211.9 | 122.1 | 627.5 | 0.28 |

**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. Significant p-values are in bold.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **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 6.** Mean TLF, standard deviation (s.d.) and range per parent year, sex, and origin.

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

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

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

**Figures**

Map

Description automatically generated

**Figure. 1.** Map of McKenzie River watershed, including major 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

A picture containing diagram

Description automatically generated

**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 3728 candidate parents released above Cougar Dam three to six years earlier (2008 – 2011). Source refers to where an individual was initially encountered: during a spawning ground survey on the South Fork McKenzie River (SGS), at the Cougar Trap (Cougar Trap) or at either the McKenzie Hatchery or Leaburg Hatchery (hatchery outplant). Final location refers to whether a salmon was released above Cougar Dam (above) or not (below). Potential offspring include all NOR salmon, regardless of source or final location. Candidate parents include all salmon released above the dam, regardless of origin or source.

\* Note that five 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.

A picture containing graphical user interface

Description automatically generated

**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 of offspring in 2016 – 2019 (solid rectangle) to parents in 2013 (dashed rectangle) are depicted as black arrows. Labels are as in Figure 2 except the values inside circles which now 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.

Chart, line chart

Description automatically generated

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

Chart

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**Figure 5.** Number of offspring of candidate parents released above Cougar Dam from 2007 – 2017, by inferred age-at-maturity of offspring.

\* Note that offspring of salmon released above the dam in 2015 do not include potential age-6 offspring that have not been sampled.

\*\* Note that offspring of salmon released above the dam in 2016 do not include potential age-5 and age-6 offspring that have not been sampled.

Chart, line chart

Description automatically generated

**Figure 6.** Mean Total Lifetime Fitness (TLF) and standard deviation from 2007 – 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%).

Chart, box and whisker chart

Description automatically generated

**Figure 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.

Chart, histogram

Description automatically generated

**Figure 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.

Chart, line chart

Description automatically generated

**Figure 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.

Allen MB, Engle RO, Zendt JS*, et al.* (2016) Salmon and steelhead in the white salmon river after the removal of condit dam–planning efforts and recolonization results. *Fisheries* **41**, 190-203.

Anderson JH, Faulds PL, Atlas WI, Quinn TP (2013) Reproductive success of captively bred and naturally spawned chinook salmon colonizing newly accessible habitat. *Evol Appl* **6**, 165-179.

Anderson JH, Pess GR, Carmichael RW*, et al.* (2014) Planning pacific salmon and steelhead reintroductions aimed at long-term viability and recovery. *North American Journal of Fisheries Management* **34**, 72-93.

Angilletta Jr MJ, Ashley Steel E, Bartz KK*, et al.* (2008) Big dams and salmon evolution: Changes in thermal regimes and their potential evolutionary consequences. *Evolutionary Applications* **1**, 286-299.

Araki H, Ardren WR, Olsen E, Cooper B, Blouin MS (2007a) Reproductive success of captive-bred steelhead trout in the wild: Evaluation of three hatchery programs in the hood river. *Conserv Biol* **21**, 181-190.

Araki H, Cooper B, Blouin MS (2007b) Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. *Science* **318**, 100-103.

Banks M, Blouin M, Baldwin B*, et al.* (1999) Isolation and inheritance of novel microsatellites in chinook salmon (oncorhynchus tschawytscha). *Journal of Heredity* **90**, 281-288.

Banks MA, O’Malley KG, Sard NM*, et al.* (2013) Genetic pedigree analysis of spring chinook salmon outplanted above cougar dam, south fork mckenzie river. *U.S. Army Corps of Engineers*.

Banks MA, Sard NM, O’Malley KG*, et al.* (2016) A genetics-based evaluation of the spring chinook salmon reintroduction program above cougar dam, south fork mckenzie river, 2013-2015. *U.S. Army Corps of Engineers*.

Banks MA, Sard NM, O’Malley KG*, et al.* (2014) A genetics-based evaluation of the spring chinook salmon reintroduction program above cougar dam, south fork mckenzie river, 2007- 2013. *U.S. Army Corps of Engineers.*

Beechie T, Buhle E, Ruckelshaus M, Fullerton A, Holsinger L (2006) Hydrologic regime and the conservation of salmon life history diversity. *Biological Conservation* **130**, 560-572.

Beeman JW, Evans SD, Haner PV*, et al.* (2014) Passage and survival probabilities of juvenile chinook salmon at cougar dam, oregon, 2012. US Geological Survey.

Berejikian B (2000) Female mate choice and spawning behaviour of chinook salmon under experimental conditions. *Journal of Fish Biology* **57**, 647-661.

Bolker BM (2015) Linear and generalized linear mixed models. *Ecological statistics: contemporary theory and application*, 309-333.

Botsford LW, Brittnacher JG (1998) Viability of sacramento river winter‐run chinook salmon. *Conservation Biology* **12**, 65-79.

Bowerman T, Roumasset A, Keefer ML, Sharpe CS, Caudill CC (2018) Prespawn mortality of female chinook salmon increases with water temperature and percent hatchery origin. *Transactions of the American Fisheries Society* **147**, 31-42.

Brennan SR, Schindler DE, Cline TJ*, et al.* (2019) Shifting habitat mosaics and fish production across river basins. *Science* **364**, 783-786.

Brunelli JP, Wertzler KJ, Sundin K, Thorgaard GH (2008) Y-specific sequences and polymorphisms in rainbow trout and chinook salmon. *Genome* **51**, 739-748.

Burger CV, Scribner KT, Spearman WJ, Swanton CO, Campton DE (2000) Genetic contribution of three introduced life history forms of sockeye salmon to colonization of frazer lake, alaska. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 2096-2111.

Campbell NR, Kamphaus C, Murdoch K, Narum SR (2017) Patterns of genomic variation in coho salmon following reintroduction to the interior columbia river. *Ecol Evol* **7**, 10350-10360.

Carlson SM, Seamons TR (2008) A review of quantitative genetic components of fitness in salmonids: Implications for adaptation to future change. *Evol Appl* **1**, 222-238.

Christie MR (2010) Parentage in natural populations: Novel methods to detect parent-offspring pairs in large data sets. *Mol Ecol Resour* **10**, 115-128.

Christie MR, Ford MJ, Blouin MS (2014) On the reproductive success of early-generation hatchery fish in the wild. *Evol Appl* **7**, 883-896.

Christie MR, Marine ML, French RA, Blouin MS (2012) Genetic adaptation to captivity can occur in a single generation. *Proc Natl Acad Sci U S A* **109**, 238-242.

Colvin ME, Peterson JT, Sharpe C, Kent ML, Schreck CB (2018) Identifying optimal hauling densities for adult chinook salmon trap and haul operations. *River Research and Applications* **34**, 1158-1167.

Cordoleani F, Phillis CC, Sturrock AM*, et al.* (2021) Threatened salmon rely on a rare life history strategy in a warming landscape. *Nature Climate Change* **11**, 982-988.

Crozier LG, McClure MM, Beechie T*, et al.* (2019) Climate vulnerability assessment for pacific salmon and steelhead in the california current large marine ecosystem. *PLoS One* **14**, e0217711.

Crozier LG, Siegel JE, Wiesebron LE*, et al.* (2020) Snake river sockeye and chinook salmon in a changing climate: Implications for upstream migration survival during recent extreme and future climates. *PLoS One* **15**, e0238886.

Dickerson B, Brinck K, Willson M, Bentzen P, Quinn T (2005) Relative importance of salmon body size and arrival time at breeding grounds to reproductive success. *Ecology* **86**, 347-352.

Do C, Waples RS, Peel D*, et al.* (2014) Neestimator v2: Re‐implementation of software for the estimation of contemporary effective population size (ne) from genetic data. *Molecular Ecology Resources* **14**, 209-214.

Doyle MW, Stanley EH, Havlick DG*, et al.* (2008) Aging infrastructure and ecosystem restoration. *Science* **319**, 286-287.

Duda JJ, Torgersen CE, Brenkman SJ*, et al.* (2021) Reconnecting the elwha river: Spatial patterns of fish response to dam removal. *Frontiers in Ecology and Evolution*, 811.

Duncan JP (2011) Characterization of fish passage conditions through a francis turbine and regulating outlet at cougar dam, oregon, using sensor fish, 2009–2010. Pacific Northwest National Lab.(PNNL), Richland, WA (United States).

Ebersole JL, Quiñones RM, Clements S, Letcher BH (2020) Managing climate refugia for freshwater fishes under an expanding human footprint. *Frontiers in Ecology and the Environment* **18**, 271-280.

Evans ML, Hard JJ, Black AN, Sard NM, O’Malley KG (2019) A quantitative genetic analysis of life-history traits and lifetime reproductive success in reintroduced chinook salmon. *Conservation Genetics* **20**, 781-799.

Evans ML, Johnson MA, Jacobson D*, et al.* (2016) Evaluating a multi-generational reintroduction program for threatened salmon using genetic parentage analysis. *Canadian Journal of Fisheries and Aquatic Sciences* **73**, 844-852.

FitzGerald AM, John SN, Apgar TM, Mantua NJ, Martin BT (2021) Quantifying thermal exposure for migratory riverine species: Phenology of chinook salmon populations predicts thermal stress. *Glob Chang Biol* **27**, 536-549.

Fleming IA, Gross MR (1994) Breeding competition in a pacific salmon (coho: Oncorhynchus kisutch): Measures of natural and sexual selection. *Evolution* **48**, 637-657.

Foley MM, Bellmore JR, O'Connor JE*, et al.* (2017) Dam removal: Listening in. *Water Resources Research* **53**, 5229-5246.

Fox CA, Magilligan FJ, Sneddon CS (2016) “You kill the dam, you are killing a part of me”: Dam removal and the environmental politics of river restoration. *Geoforum* **70**, 93-104.

Fraser DJ, Weir LK, Bernatchez L, Hansen MM, Taylor EB (2011) Extent and scale of local adaptation in salmonid fishes: Review and meta-analysis. *Heredity* **106**, 404-420.

Galbreath PF, Bisbee MA, Dompier DW, Kamphaus CM, Newsome TH (2014) Extirpation and tribal reintroduction of coho salmon to the interior columbia river basin. *Fisheries* **39**, 77-87.

Greene CM, Hall JE, Guilbault KR, Quinn TP (2010) Improved viability of populations with diverse life-history portfolios. *Biology letters* **6**, 382-386.

Greig C, Jacobson DP, Banks MA (2003) New tetranucleotide microsatellites for fine‐scale discrimination among endangered chinook salmon (oncorhynchus tshawytscha). *Molecular Ecology Notes* **3**, 376-379.

Gundersen G, Johannesen E, Andreassen H, Ims R (2001) Source–sink dynamics: How sinks affect demography of sources. *Ecology Letters* **4**, 14-21.

Hayes MC, Reisenbichler RR, Rubin SP*, et al.* (2013) Effectiveness of an integrated hatchery program: Can genetic-based performance differences between hatchery and wild chinook salmon be avoided? *Canadian Journal of Fisheries and Aquatic Sciences* **70**, 147-158.

Heinrichs JA, Lawler JJ, Schumaker NH, Wilsey CB, Bender DJ (2015) Divergence in sink contributions to population persistence. *Conservation Biology* **29**, 1674-1683.

Herbold B, Carlson SM, Henery R (2018) Managing for salmon resilience in california’s variable and changing climate. *San Francisco Estuary and Watershed Science* **16**.

High B, Peery CA, Bennett DH (2006) Temporary staging of columbia river summer steelhead in coolwater areas and its effect on migration rates. *Transactions of the American Fisheries Society* **135**, 519-528.

Hill NL, Trueman JR, Prévost AD*, et al.* (2019) Effect of dam removal on habitat use by spawning atlantic salmon. *Journal of Great Lakes Research* **45**, 394-399.

Hinshaw S, Wohl E, Burnett JD, Wondzell S (2022) Development of a geomorphic monitoring strategy for stage 0 restoration in the south fork mckenzie river, oregon, USA. *Earth Surface Processes and Landforms* **47**, 1937-1951.

Huff DD, Miller LM, Chizinski CJ, Vondracek B (2011) Mixed‐source reintroductions lead to outbreeding depression in second‐generation descendents of a native north american fish. *Molecular Ecology* **20**, 4246-4258.

Huff DD, Miller LM, Vondracek B (2010) Patterns of ancestry and genetic diversity in reintroduced populations of the slimy sculpin: Implications for conservation. *Conservation Genetics* **11**, 2379-2391.

Hughes J, Bellgraph B, Kim J*, et al.* (2016) Evaluation of juvenile salmonid passage and behavior at foster dam using radio telemetry, 2015. *PNNL-25253. Final report submitted by the Pacific Northwest National Laboratory to the US Army Corps of Engineers, Portland, Oregon*.

Ivanova NV, Dewaard JR, Hebert PDN (2006) An inexpensive, automation-friendly protocol for recovering high-quality DNA. *Molecular Ecology Notes* **6**, 998-1002.

Janowitz-Koch I, Rabe C, Kinzer R*, et al.* (2019) Long-term evaluation of fitness and demographic effects of a chinook salmon supplementation program. *Evol Appl* **12**, 456-469.

Johnson MA, Friesen TA (2010) Spring chinook salmon hatcheries in the willamette basin: Existing data, discernable patterns and information gaps. *US Army Corps of Engineers Task Order NWPPM-09-FH-05* **88**.

Johnson MA, Friesen TA (2014) Genetic diversity and population structure of spring chinook salmon from the upper willamette river, oregon. *North American Journal of Fisheries Management* **34**, 853-862.

Jones OR, Wang J (2010) Colony: A program for parentage and sibship inference from multilocus genotype data. *Molecular Ecology Resources* **10**, 551-555.

Kalinowski ST, Taper ML, Marshall TC (2007) Revising how the computer program cervus accommodates genotyping error increases success in paternity assignment. *Molecular Ecology* **16**, 1099-1106.

Keefer M, Taylor G, Garletts D*, et al.* (2010) Prespawn mortality in adult spring chinook salmon outplanted above barrier dams. *Ecology of Freshwater Fish* **19**, 361-372.

Kock TJ, Ferguson JW, Keefer ML, Schreck CB (2020) Review of trap-and-haul for managing pacific salmonids (oncorhynchus spp.) in impounded river systems. *Reviews in Fish Biology and Fisheries* **31**, 53-94.

Ligon FK, Dietrich WE, Trush WJ (1995) Downstream ecological effects of dams. *BioScience* **45**, 183-192.

Lusardi RA, Moyle PB (2017) Two-way trap and haul as a conservation strategy for anadromous salmonids. *Fisheries* **42**, 478-487.

Marschall EA, Mather ME, Parrish DL, Allison GW, McMenemy JR (2011) Migration delays caused by anthropogenic barriers: Modeling dams, temperature, and success of migrating salmon smolts. *Ecological Applications* **21**, 3014-3031.

Matthews DP, Gonzalez A (2007) The inflationary effects of environmental fluctuations ensure the persistence of sink metapopulations. *Ecology* **88**, 2848-2856.

McClure MM, Carlson SM, Beechie TJ*, et al.* (2008) Evolutionary consequences of habitat loss for pacific anadromous salmonids. *Evol Appl* **1**, 300-318.

McElhany P, Chilcote M, Myers J, Beamesderfer R (2007) Viability status of oregon salmon and steelhead populations in the willamette and lower columbia basins part 7: Upper willamette steelhead. *Prepared for Oregon Department of Fish and Wildlife and National Marine Fisheries Service*.

Monzyk FR, Friesen TA, Romer JD (2015) Infection of juvenile salmonids by salmincola californiensis (copepoda: Lernaeopodidae) in reservoirs and streams of the willamette river basin, oregon. *Transactions of the American Fisheries Society* **144**, 891-902.

Munsch SH, Greene CM, Mantua NJ, Satterthwaite WH (2022) One hundred-seventy years of stressors erode salmon fishery climate resilience in california's warming landscape. *Glob Chang Biol* **28**, 2183-2201.

Murdoch KJ, T. (2015) Factors affecting migratory success within the wenatchee river in a population of reintroduced coho salmon. . *Yakama Nation Fisheries Resource Management*.

Murphy CA, Romer JD, Stertz K*, et al.* (2021) Damming salmon fry: Evidence for predation by non‐native warmwater fishes in reservoirs. *Ecosphere* **12**, e03757.

Myers J, Jorgensen J, Sorel M*, et al.* (2018) Upper willamette river life cycle modeling and the potential effects of climate change. *US Dep Commerce, NOAA Fisheries Northwest Fisheries Science Center, Seattle, Washington*.

Naish KA, Park LK (2002) Linkage relationships for 35 new microsatellite loci in chinook salmon oncorhynchus tshawytscha.

Nehlsen W, Williams JE, Lichatowich JA (1991) Pacific salmon at the crossroads: Stocks at risk from california, oregon, idaho, and washington. *Fisheries* **16**, 4-21.

NMFS (1999) Endangered and threatened species: Threatened status for three chinook salmon evolutionarily significant units (esus) in washington and oregon, and endangered status for one chinook salmon esu in washington. *Federal Register* **64**, 14308-14328.

NMFS (2008) Endangered species act section 7 (a)(2) consultation biological opinion and magnuson‐stevens fishery conservation and management act essential fish habitat consultation: Consultation on the “willamette river basin flood control project.”. NMFS Portland, Oregon.

Nuetzel HM, Galbreath PF, Staton BA*, et al.* (2022) Improved productivity of naturalized spring chinook salmon following reintroduction from a hatchery stock in lookingglass creek, oregon. *Canadian Journal of Fisheries and Aquatic Sciences*.

O'Connor JE, Duda JJ, Grant GE (2015) Ecology. 1000 dams down and counting. *Science* **348**, 496-497.

O’Malley KG, Black AN, Johnson MA, Jacobson D (2017) Evaluating spring chinook salmon reintroductions above detroit dam, on the north santiam river, using genetic parentage analysis. *U.S. Army Corps of Engineers*.

O’Malley KG, Dayan DI, Fitzpatrick CK, Bohn S, Grenbemer GA (2022) Evaluating spring chinook salmon releases above detroit dam and below big cliff dam, on the north santiam river, using genetic parentage analysis. *U.S. Army Corps of Engineers*.

O’Malley KG, Evans ML, Johnson MA*, et al.* (2014) Genetic parentage analysis of spring chinook salmon on the south santiam river: Insights into population productivity and reintroduction strategies. Oregon state department of fish and wildlife. *US Army Corps of Engineers, Portland District*.

O’Malley KG, Evans ML, Johnson MA, Jacobson D, Hogansen M (2015) An evaluation of spring chinook salmon reintroductions above detroit dam, north santiam river, using genetic pedigree analysis. *Report to the US Army Corps of Engineers, Portland District, Portland, Oregon*.

ODFW, USACE (2019) Hatchery and genetic management plan: Mckenzie river spring chinook salmon.

Pess GR, Hilborn R, Kloehn K, Quinn TP, Bradford M (2012) The influence of population dynamics and environmental conditions on pink salmon (oncorhynchus gorbuscha) recolonization after barrier removal in the fraser river, british columbia, canada. *Canadian Journal of Fisheries and Aquatic Sciences* **69**, 970-982.

Pess GR, Jordan CE (2019) Characterizing watershed-scale effects of habitat restoration actions to inform life cycle models: Case studies using data-rich vs. Data-poor approaches.

Pess GR, Quinn TP, Gephard SR, Saunders R (2014) Re-colonization of atlantic and pacific rivers by anadromous fishes: Linkages between life history and the benefits of barrier removal. *Reviews in Fish Biology and Fisheries* **24**, 881-900.

Romer JD, Monzyk FR, Emig R, Friesen TA (2016) Juvenile salmonid outmigration monitoring at willamette valley project reservoirs. *Annual Report of Oregon Department of Fish and Wildlife (ODFW) to US Army Corps of Engineers, Portland, Oregon*.

Sard NM, Jacobson DP, Banks MA (2016a) Grandparentage assignments identify unexpected adfluvial life history tactic contributing offspring to a reintroduced population. *Ecology and Evolution* **6**, 6773-6783.

Sard NM, Johnson MA, Jacobson DP*, et al.* (2016b) Genetic monitoring guides adaptive management of a migratory fish reintroduction program. *Animal Conservation* **19**, 570-577.

Sard NM, O’Malley KG, Jacobson DP*, et al.* (2015) Factors influencing spawner success in a spring chinook salmon (oncorhynchus tshawytscha) reintroduction program. *Canadian Journal of Fisheries and Aquatic Sciences* **72**, 1390-1397.

Schindler DE, Hilborn R, Chasco B*, et al.* (2010) Population diversity and the portfolio effect in an exploited species. *Nature* **465**, 609-612.

Schreck CB, Stahl TP, Davis LE, Roby DD, Clemens BJ (2006) Mortality estimates of juvenile spring–summer chinook salmon in the lower columbia river and estuary, 1992–1998: Evidence for delayed mortality? *Transactions of the American Fisheries Society* **135**, 457-475.

Seamons TR, Bentzen P, Quinn TP (2007) DNA parentage analysis reveals inter-annual variation in selection: Results from 19 consecutive brood years in steelhead trout. *Evolutionary Ecology Research* **9**, 409-431.

Sheer MB, Steel EA (2011) Lost watersheds: Barriers, aquatic habitat connectivity, and salmon persistence in the willamette and lower columbia river basins. *Transactions of the American Fisheries Society* **135**, 1654-1669.

Stanley EH, Doyle MW (2003) Trading off: The ecological effects of dam removal. *Frontiers in Ecology and the Environment* **1**, 15-22.

Taylor EB (1991) A review of local adaptation in salmonidac, with particular reference to pacific and atlantic salmon. *Aquaculture* **98**, 185-207.

Tillotson MD, Barnett HK, Bhuthimethee M, Koehler ME, Quinn TP (2019) Artificial selection on reproductive timing in hatchery salmon drives a phenological shift and potential maladaptation to climate change. *Evolutionary Applications* **12**, 1344-1359.

USAR EPA (2021) Total maximum daily load (tmdl) for temperature in the columbia and lower snake rivers.

Vahedifard F, Madani K, AghaKouchak A, Thota SK (2021) Are we ready for more dam removals in the united states? *Environmental Research: Infrastructure and Sustainability* **1**, 013001.

Wang J (2018) Estimating genotyping errors from genotype and reconstructed pedigree data. *Methods in Ecology and Evolution* **9**, 109-120.

Waples RS (1990) Conservation genetics of pacific salmon. Ii. Effective population size and the rate of loss of genetic variability. *Journal of Heredity* **81**, 267-276.

Waples RS, Beechie T, Pess GR (2009) Evolutionary history, habitat disturbance regimes, and anthropogenic changes

what do these mean for resilience of pacific salmon populations? *Ecology and Society* **14**.

Waples RS, Do C (2008) Ldne: A program for estimating effective population size from data on linkage disequilibrium. *Molecular Ecology Resources* **8**, 753-756.

Waples RS, Ford MJ, Nichols K*, et al.* (2022) Implications of large-effect loci for conservation: A review and case study with pacific salmon. *Journal of Heredity* **113**, 121-144.

Waples RS, Pess GR, Beechie T (2008) Evolutionary history of pacific salmon in dynamic environments. *Evol Appl* **1**, 189-206.

Weigel D, Koch I, Monzyk F*, et al.* (2019) Evaluation of a trap-and-transport program for a threatened population of steelhead (oncorhynchus mykiss). *Conservation Genetics* **20**, 1195-1199.

Williamson KS, Cordes JF, May B (2002) Characterization of microsatellite loci in chinook salmon (oncorhynchus tshawytscha) and cross‐species amplification in other salmonids. *Molecular Ecology Notes* **2**, 17-19.

Wolf JB, Wade MJ (2001) On the assignment of fitness to parents and offspring: Whose fitness is it and when does it matter? *Journal of Evolutionary Biology* **14**, 347-356.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with r* Springer.