**A single generation in the wild increases fitness for descendants of hatchery Chinook salmon (*Oncorhynchus tshawytscha*)**

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# Abstract

Reintroduction is an important tool for salmon recovery. These programs often use hatchery salmon from a nearby source to re-establish populations in vacant, historically occupied habitat. However, this approach is challenged by the relatively low reproductive success that hatchery-origin (HOR) salmon experience when they spawn in the wild, relative to their natural-origin (NOR) counterparts. In this study, we used genetic parentage analysis to compare the reproductive success of three groups of Chinook salmon (*Oncorhynchus tshawytscha*) reintroduced above the Cougar Dam on the South Fork McKenzie River, Oregon: HOR salmon from an integrated stock; their first generation of wild-born offspring (hereafter F1s); and NOR salmon that were born elsewhere. We found that F1s produced nearly as many adult offspring as NOR salmon, and 1.8-fold more adult offspring than their hatchery parents. This result suggests that, for the South Fork McKenzie reintroduction program, a single generation in the wild increases fitness for the descendants of hatchery salmon. However, even with elevated fitness, successful reintroduction remains demographically constrained by extrinsic factors.

# Introduction

Reintroduction is a critical component in the recovery of Pacific salmon (*Oncorhynchus spp.*). Pacific salmon have been extirpated from much of their historical range (Gustafson et al. 2007), including more than half of historical habitat in the Upper Willamette and Lower Columbia River basins (Sheer and Steel 2011). Reintroduction promotes species persistence directly by increasing demographic productivity, and indirectly by adding to habitat and life-history diversity (Anderson et al. 2014; Lusardi and Moyle 2017; Kock et al. 2020). In cases where natural recolonization by volitional dispersal is unfeasible, or when risks to extant natural populations are unacceptable, reintroductions are seeded with hatchery salmon from nearby stocks (Anderson 2014). These hatchery salmon produce offspring in the wild that subsequently return to the target habitat as adults to spawn. Reintroductions often seek to establish productive, self-sustaining natural populations (Anderson et al. 2014). However, potentially low relative reproductive success (RRS) of hatchery salmon when spawning in the wild compared to their wild-born counterparts (Ford 2002; Kostow et al. 2003; Araki et al. 2007a; Araki et al. 2007b; Theriault et al. 2011; Christie et al. 2014; Koch and Narum 2021) presents a challenge to achieving this goal. Similarly, low RRS challenges supplementation programs that seek to provide demographic benefits to natural populations by spawning wild-born salmon in the hatchery and allowing their offspring to reproduce in the wild as adults (Berntson et al. 2011; Christie et al. 2012; Ford et al. 2012).

Following more than two decades of research, there are many point estimates of RRS across species, hatchery programs, and river basins (reviewed in Christie et al. 2014; Koch and Narum 2021). These studies have revealed important trends and suggested areas where more research is needed. In general, RRS is less than one across species, but RRS also depends on habitat and hatchery broodstock characteristics, as well as the age, size, and sex of individual spawners (Christie et al. 2014; Koch and Narum 2021). In Chinook salmon (*Oncorhynchus tshawytscha*), there is evidence that integrating 100% wild-born spawners into the broodstock may ameliorate the fitness impacts of captive rearing. Using a completely integrated broodstock reduces fitness differences between wild-born and hatchery Chinook salmon spawning in the (Hess et al. 2012; Janowitz-Koch et al. 2019), although this result is not observed consistently across populations (Koch et al. 2022). In contrast, RRS of Chinook salmon is consistently less than one when the broodstock is segregated, or only partially integrated (Williamson et al. 2010; Anderson et al. 2013; Banks et al. 2016; Evans et al. 2016; O’Malley et al. 2023). The focus of the body of RRS literature to date has primarily been documenting potential fitness differences between hatchery and wild-born salmon spawning in the wild, the pace at which these fitness differences, if present accrue, and the role of contributing factors. Yet, overcoming the challenge posed to reintroduction and supplementation by low RRS of hatchery salmon depends on whether or not there is a transgenerational increase in fitness among their wild born offspring.

To our knowledge this question has only been explicitly addressed in three populations. Araki *et al.* (2009) found that wild-born descendants of hatchery Hood River steelhead had lower reproductive success than their wild counterparts, but a re-analysis of these data to account for variance and bias in the population of RRS point estimates could not reject the null hypothesis that RRS was equal to one (Kitada et al. 2011). In McKenzie River Chinook salmon, we previously observed that first-generation wild born hatchery descendants produced more age-0 offspring than hatchery salmon from a partially integrated stock, and similar numbers to other wild-born salmon in the same habitat across two years, but did not account for bias from fitness associated covariates, or estimate fitness using adult offspring (Banks et al. 2016). Finally, Nuetzel *et al.* (2023) found that early generation descendants from a partially integrated stock of Chinook salmon reintroduced to Lookingglass Creek in the Grande Ronde Basin produce more juvenile offspring, adult offspring, and juvenile grand-offspring than hatchery salmon spawning in the same habitat. This finding was consistent across multiple years and after accounting for fitness associated covariates. However, only hatchery salmon and their descendants were reintroduced in this system, and the reproductive success relative to wild-born salmon from natural populations could not be evaluated.

In this study, we rely on a Chinook salmon pedigree that spans 14 years and includes up to four generations to characterize the RRS of wild-born hatchery descendants relative to both hatchery salmon and wild-born salmon from a natural population. Hatchery spring Chinook salmon have been reintroduced into historical habitat above the Cougar Dam on the South Fork McKenzie river since 1993, and wild-born salmon have been released alongside them since 2010. This reintroduction effort has been continuously evaluated using genetic parentage analysis since 2007. Chinook salmon released above Cougar Dam include not only hatchery salmon and their wild-born descendents, but also wild-born salmon produced below the dam or elsewhere (hereafter NORs). NORs volitionally enter the trap at the base of Cougar Dam and therefore are representative of natural colonizers that might act to re-establish the population in absence of the dam. First, we compare the fitness of hatchery salmon to that of their first-generation wild-born offspring (hereafter F1s) to assess if fitness increases after a single generation in the wild. Second, we compare the fitness of F1s to NORs. Finally, we compare the fitness of hatchery salmon and NORs. We also examine two ecologically relevant phenotypes of the offspring of each of the three groups.

# Methods

## Reproducible Research

Detailed logs and all data needed to replicate this study are available at a github repository, <https://github.com/david-dayan/mckenzie_naturalization> and archived at zenodo with a stable identifier ([DOI:10.5281/zenodo.7946956](https://zenodo.org/badge/latestdoi/633996942)). An R notebook containing narrative logs of all analyses with integrated code, results and commentary are available as supplementary files.

## Study System

Spring Chinook salmon in the Upper Willamette River are listed as a threatened evolutionarily significant unit (ESU) under the U.S. Endangered Species Act (ESA) (NMFS 1999). The McKenzie River, a tributary of the Upper Willamette River, historically supported one of the largest populations of spring Chinook salmon and currently supports a large proportion of the natural production of spring Chinook salmon in the Willamette Basin, with proportion of hatchery origin spawners ranging from 27% in the upper reaches of the mainstem to 77% in lower reaches (McElhany et al. 2007; Johnson and Friesen 2010; Bowerman et al. 2018). Since hatchery operations began in the late 19th century, incorporation of non-Willamette basin salmon into broodstock is thought to be rare, but there have been frequent stock transfers within the Willamette Basin that likely reduced differentiation among sub-basins (Myers 2006; Johnson and Friesen 2010). For much of the 20th century, hatchery operations on the McKenzie used a mixed broodstock consisting of Middle Fork Willamette and McKenzie stocks (Johnson and Friesen 2010). Since 1990, only McKenzie basin fish have been used as broodstock. The proportion of wild-born salmon integrated into broodstock has varied between years, with a target rate of 10-30% (Johnson and Friesen 2014; ODFW and USACE 2019). Within the Willamette basin, hatchery stocks are most similar to within sub-basin wild fish (Johnson and Friesen 2014).

The 158m tall Cougar Dam was constructed in 1964 on the South Fork McKenzie River and blocks access to approximately 40 river km of the historically most productive reaches in the McKenzie sub-basin (NMFS 2008)(Fig. 1). Adult HOR salmon from the McKenzie Hatchery have been released above Cougar Dam since 1993 until the present (Fig. 1). We refer to these individuals as hatchery outplants. A trap-and-haul facility was constructed at the base of Cougar Dam in 2010 (hereafter the Cougar Trap). The Cougar Trap collects wild-born salmon and a small number of HOR salmon that volitionally enter the trap. Importantly, the wild-born salmon collected at the Cougar Trap include offspring of individuals previously released above the dam in addition to salmon that are produced below the dam, on the mainstem or elsewhere (Banks et al. 2013; Banks et al. 2016; Banks et al. 2014; Sard et al. 2016b, O’Malley 2023). Adfluvial females and precocial resident males also make a small contribution to the productivity of the above-dam population (Sard et al. 2016a). Therefore, the above-dam spawning population is composed six sources: hatchery outplants, HOR salmon collected at the Cougar Trap, wild-born salmon produced above the dam, wild-born salmon produced below the dam, on the mainstem, or elsewhere, precocial resident males, and adfluvial females.

There is no assisted downstream passage for juveniles produced above the dam. 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), and is likely a key factor limiting recovery (ODFW & NMFS 2011). Productivity of the reintroduced population has been continuously evaluated since 2007 using genetic parentage analysis. These studies have found that productivity has not reached replacement in a single year from 2007 – 2015 (cites).

## Sample collection

Mass marking of hatchery salmon in the Willamette Basin began in 1997, and in the McKenzie the proportion of unmarked hatchery salmon is < 2% (McLaughlin et al. 2008), so we consider all unmarked salmon to be wild-born. Fin clips were taken from nearly all wild-born 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 (Banks et al. 2013; Banks et al. 2014; Banks et al. 2016; Sard et al. 2016). We also include fin clips collected from wild-born 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 a small number of precocial male Chinook salmon identified on spawning grounds above the dam during 2014.

## Genetic Data, Parentage Analysis, and Focal Groups

We used genetic data and the pedigree inferred from previous evaluations of the reintroduction effort (Banks et al. 2013; Banks et al. 2014; Banks et al. 2016; Sard et al. 2016; O’Malley et al. 2023). Methods detailing collection of genetic data and inference of the pedigree can be found in the previous evaluation (O’Malley et al. 2023). In brief, we isolated genomic DNA from fin clips, genotyped each sample at 11 microsatellite loci, and performed genotype quality filtering to remove individuals genotyped at fewer than 7 microsatellite loci and individuals that could have been sampled more than once. When inferring pedigree we defined *potential offspring* as any wild-born individual sampled anywhere on the South Fork McKenzie, and *candidate parents* as any individual, regardless of origin, released or otherwise sampled above the dam. We assigned potential offspring to candidate parents using CERVUS v3.07 (Kalinowski et al. 2007) and COLONY v2.0.6.8 (Jones and Wang 2010). We combined results from CERVUS and COLONY to generate a consensus pedigree used in all downstream analyses.

Nearly all (98%) Chinook salmon on the South Fork McKenzie express an age at maturity of 4 – 5 years, with approximately 2% returning at age 3 or age 6 (O’Malley et al. 2023), and 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. Therefore, our data allowed us to identify all offspring of salmon released above Cougar Dam in 2010 – 2014, and nearly all (~98%) offspring of salmon released above Cougar Dam in 2015. From the perspective of returning potential offspring, we sample all possible parents of potential offspring that returned from 2013 – 2020, and nearly all (98%) parents of potential offspring that returned in 2012. Taken together, the pedigree identifies both the parents and offspring of candidate parents released above the dam from 2012 – 2015. Our results are focused on candidate parents from these four years.

We consider three focal groups of candidate parents released above the dam from 2012 – 2015 based on the identity of their parents: hatchery, F1 and NOR. We refer to this variable as *generation*. Hatchery salmon are captive-reared salmon from the McKenzie spring Chinook salmon hatchery program, that are collected at the hatchery trap on the mainstem or at the Cougar Trap, and released above the dam. F1s are the first generation, wild-born offspring of hatchery salmon released above the dam. Both parents of F1s must be inferred in the pedigree and both must be HOR. Finally, NORs are any wild-born salmon released above the dam that do not assign to a parent previously released above the dam. These salmon are presumed to be produced below the dam, on the mainstem, or elsewhere. We do not consider other candidate parents from 2012 – 2015 that do not fall into one of these three groups. For example, individuals that assign to a single parent, or individuals from mixed mate pairs are not analyzed.

## Body Length

Spawning ground surveys were conducted on the South Fork McKenzie River below the dam and the mainstem McKenzie River. Body length and sex were recorded for each carcass observed in 2012 – 2015. To understand if body length of hatchery salmon, F1s, and NORs differed from one another or from the natural McKenzie River spring Chinook salmon population in 2012 we fit a linear model on body length with three fixed effects, *year, sex,* and *generation* (including carcass samples as an additional level)*,* and the *generation*\**sex* interaction. We validated the model using Pearson residuals and evaluated significance with an F-test and type II sums of squares. We used the *emmeans* package in R to conduct *post-hoc* estimation of marginal mean lengths and hypothesis testing.

## Relative Reproductive Success

For each candidate parent (any salmon released above the dam), we estimated total lifetime fitness (TLF) as the number of adult offspring produced by an individual candidate parent. To address if there was a fitness differences between HORs, F1s and NORs (*generation*), we first estimated relative reproductive success (RRS) using a model based approach. This approach permits parsing of the effect of *generation* from covariates such as *body length* and *year*. In a complementary approach, we estimated RRS by simple division of mean TLF of HORs by mean TLF of either F1s or NORs. To distinguish between RRS estimated with each approach, we refer to estimates as modelRRS and ΔRRS, respectively.

In the model based approach, we began by fitting a generalized linear mixed model on TLF using the *glmmTMB* package in *R*. In addition to the effect of *generation* on TLF, we considered the influence of multiple potential covariates including *sex, body length, release day*, and *year* and two interaction terms, including *sex\*release day* and *sex\*generation*. We also included a random effect of *release group*. *Release day* was the Julian calendar day that individuals were released and was modeled as a continuous fixed effect. Previous work suggested that non-linear effects for *release day* such as disruptive or stabilizing selection were not necessary (O’Malley et al. 2023). *Release group* was the set of individuals released at a single location during a single day. Our modeling followed the recommendations of Zuur et al. (2009) and Bolker (2015). We conducted an exploratory data analysis to understand the relationship among predictors and compared model fit under negative binomial and zero-inflated negative binomial distributions. Model fit under different distributions was evaluated using AIC, BIC, rootograms and QQ-plots of randomized quantile residuals from the *COUNTREG* package in *R*. To quantify multicollinearity among categorical and continuous predictors we used the generalized variance inflation factor (GVIF^(1/(2\*df)) (Fox and Monette 1992), and a conservative cutoff of 2.0.

After exploratory data analysis, we fit models using the negative binomial distribution and a log link function. For model selection, we first identified the best random effects structure by fitting a fully saturated fixed effect model using restricted maximum likelihood and varying the random effects. Model selection of random effects was by AIC. After refitting the fully saturated fixed effects model with the final random effects structure using maximum likelihood, we conducted backwards stepwise model selection for fixed effects based on likelihood ratio tests for each predictor. Once a final model was selected (hereafter GLMMTLF), we conducted model validation by testing for goodness of fit, overdispersion, and influence of outliers using residuals simulated by the *DHARMa* package in *R*. Effect plots of significant predictors retained in the GLMMTLF were generated using the *effects* package in *R* and conditioned on the typical values of all other significant predictors in the final model. We used the *emmeans* package in R to conduct *post-hoc* estimation of modelRRS and hypothesis testing. We estimated modelRRS by contrasting the marginal mean fitness for each level of generation after controlling for other significant predictors in the final model. We used cell-based weighting during estimation of marginal means to accommodate the unbalanced sample sizes across *generation* and *year*. We considered modelRRS to be significantly different than one if the Tukey adjusted p-values for these *post-hoc* contrasts were less than 0.05.

In the second approach to determine if RRS was different than one, we defined ΔRRS as the ratio between mean TLF of all pairwise comparisons of HORs, F1s and NORs, within years. We conducted an additional analysis within both years and sexes. Confidence intervals of for relative reproductive success were estimated using a maximum likelihood approach following (Kalinowski). ΔRRS was considered different than one of the confidence interval did not include one.

## Offspring Characteristics

We also examined if the offspring produced by HOR, F1 and NOR salmon released above the Cougar Dam differed in age at maturity (AAM) or body length. We chose to model offspring age using a binomial generalized linear model with the proportion of age-5 offspring vs. age-4 offspring as the response variable, because nearly all (98%) spring Chinook salmon in the McKenzie River return at either age 4 or at age 5. We used three fixed explanatory variables, generation of parents, year of parents, and sex. We also included the interaction generation\*sex. Model validation, effect plotting and post-hoc analysis followed the approach used with GLMMTLF. We examined offspring body length using the same fixed effects structure, but a linear model. We validated the model using Pearson residuals and evaluated significance with an F-test and type II sums of squares.

# Results

## Parentage and Focal Group Sample Size

Our pedigree included 9,839 individuals sampled from 2007 – 2020. Of these individuals, 2,027 hatchery salmon and 952 wild-born salmon were released above the dam during the four focal years where we can confidently identify both the parents and offspring of individuals. Among the 952 wild-born salmon released above the dam in this period, 465 were identified as F1s and 237 were identified as NORs (Table 1). 250 wild-born salmon were assigned to a single parent or to a mixed mate pair and excluded from further analysis. 15 individuals with no body length measurements were also excluded.

## Body Length

Body length was significantly explained by *year*, and the *sex\*generation* interaction (F-test p-value < 2e-16, type II sums of squares). In our *post-hoc* analyses, we conditioned marginal mean length on *sex* and averaged across all levels of *year*, and therefore present results separately for males and females. For females, only pairwise contrasts that included HORs were significant. HOR females were smaller than each other group of females (Supplemental Fig. 1, Tukey p-value < 0.001). For males, every pairwise contrast was significant (Tukey p-value < 0.01). HORs males had the shortest body length, followed by F1s, NORs, and finally, wild-born salmon sampled as carcasses below the dam or on the mainstem (Supplemental Fig. 1).

## Relative Reproductive Success

Several predictors in the generalized linear mixed model of TLF were correlated with *generation*. HOR salmon were smaller on average and included more females than both F1s and NORs (Supplemental Figs. 1 and Supplemental Table 1, also see Body Length section above). F1s tended to be released above the dam earlier than both HORs and NORs (Supplemental Fig. 2). However, we did not find evidence of strong multicollinearity among the predictors as assessed with the generalized variance inflation factor, indicating that despite the relationships between predictors, there is sufficient information in the dataset to parse their individual effects.

After model selection, the final model (GLMMTLF) included *generation, length,* and *year* as fixed predictors and release group as a random effect. We did not find that *sex* or a *sex\*generation* interaction improved the model fit to the data and therefore present modelRRS for both sexes together. Parameter estimates and standard errors, as well as significance testing for each predictor retained in GLMMTLF are presented in Table 2. Predicted F1 and NOR fitness was greater than HOR fitness (Wald-test p-value 7.75e-5 and 9.85e-5, respectively, Table 2, Supplemental Fig. 3). modelRRS for HOR *vs.* F1 and for HOR *vs*. NOR contrasts were significantly different than one (0.56 and 0.57 respectively, Fig. 2, Table 3) modelRRS for the F1 *vs.* NOR contrast was not significantly different than one (Fig. 2, Table 3).

Relative to GLMMTLF, a model that also included the effect of *release day* marginally improved the fit to the data (ΔAIC = 1.8, likelihood ratio test p-value = 0.053). Because *release day* varies across the levels of generation, and potentially influences our estimate of modelRRS, we also considered this model and provide the model fit and *post-hoc* analysis as supplements (Supplemental Tables 2 and 3). We note that both parameter estimates and *post-hoc* significance testing were qualitatively similar to those from GLMMTLF.

We found similar patterns for ΔRRS to modelRRS for both HOR *vs.* F1 and HOR *vs*. NOR contrasts. ΔRRS for the HOR *vs.* F1 contrast (ΔRRS = TLFHOR / TLFF1) was less than one all years (Fig. 3). ΔRRS for the HOR *vs.* NOR contrast (ΔRRS = TLFHOR / TLFNOR) was significantly less than one in three of the four years (Fig. 3). Similar to our model-based approach, we did not find strong differences in these ΔRRS contrasts between sexes, but ΔRRS was significantly less than 1 in fewer years for males than females. Specifically, when we split the data by sex, ΔRRS for both HOR *vs.* F1 and HOR *vs*. NOR contrasts was significantly less than one for males in two of four years and for females in three of four years (Supplemental Fig. 4). There was one notable difference between ΔRRS and modelRRS results: ΔRRS for the F1 *vs* NOR contrast (ΔRRS = TLFF1 / TLFNOR) was significantly less than one in 2012 (Fig. 3). When we split the data by sex, we found ΔRRS for this contrast was less than one in 2012 for males, but not females (Supplemental Fig. 4).

## Offspring Characteristics

Model fit to the proportion of *age-5* vs. *age-4* offspring produced by candidate parents released above the dam was not significantly improved by inclusion *year* of parents or the interaction between *year* and *generation* (ΔAIC < 1, likelihood ratio test p-value > 0.05), so the data was pooled across years. Parameter estimates and standard errors, as well as significance testing for the effects of *generation* of parents, *sex* and their interaction on the age at maturity of their offspring are presented in Table 4. We found that F1s and NORs produced a significantly greater proportion of age-5 *vs.* age-4 female offspring compared to HORs, but similarly aged offspring to each other (Fig. 4). For male offspring, we found a different pattern. F1s produced a significantly greater proportion of age-5 *vs.* age-4 female offspring compared to both HORs and NORs. We found similar trends in body length between the levels of *generation* and *sex,* but only one *post-hoc* contrast was significant, possibly due to a smaller number of individuals with length measurements than AAM estimates. Male F1swere larger than male NORs.

# Discussion

## Relative Reproductive Success

Low reproductive success of hatchery relative to wild-born salmon challenges reintroduction and supplementation programs and prompts an important question: does lower fitness of hatchery salmon in the wild persist among their wild-born descendants? To our knowledge, only one other study has explicitly addressed this question in Chinook salmon (Nuetzel et al. 2023), and no study has compared fitness of wild-born hatchery descendants to Chinook salmon with no known recent hatchery ancestry. We found that the first generation, wild-born offspring of hatchery salmon produced significantly more adult offspring than hatchery salmon when spawning in the wild. The strongest evidence of this fitness advantage comes from our model-based estimates of relative reproductive success, which reduce bias by accounting for interannual variation and for potential fitness covariates such as sex, release strategies, and body length. However, this finding is also supported by directly contrasting mean fitness between F1s and hatchery salmon in each year.

We found only weak evidence of fitness differences between F1s and wild-born salmon of unknown parentage (NORs). Direct contrasts of mean TLF suggest that NORs produced more adult offspring than F1s in one of four years. Importantly this year had the highest sample size, suggesting that there may be limited power to identify significant differences in mean fitness within years using this method. Also, by not accounting for increased fitness among F1s associated with earlier release day, these direct contrasts may overestimate fitness differences directly attributable to *generation*. Our model-based estimates suggest that F1s and NORs produce equal numbers of adult offspring after accounting for covariates. We conclude that fitness differences between these two groups, if present, are minor relative to the differences between either group and hatchery salmon. Our results corroborate the observation that F1s produced more age-0 offspring than hatchery salmon, but a similar number of age-0 offspring to NORs in 2012 and 2013 (Banks et al. 2016). Together, our two central findings that F1 fitness is greater than hatchery fitness, but not NOR fitness, suggest that a single generation in the wild increases fitness for descendants of hatchery Chinook salmon, such that they may be comparable to wild-born salmon that might naturally colonize newly available habitat through dispersal if the passage barrier was removed. Our findings encourage the continued use of hatchery Chinook salmon to initially re-establish naturally spawning populations in habitats where they have been extirpated (but see *Limitations* section below).

Our study also provides an estimate of the relative reproductive success of hatchery and wild-born salmon. Among Chinook salmon, relative reproductive success in the wild tends to be lower for hatchery than wild-born individuals, but there is substantial variation among studied populations attributed to broodstock integration, inclusion of precocial males, sex, body size, interannual variation and release strategies (reviewed in Koch and Narum, 2021). We previously found that hatchery salmon produced fewer adult offspring than wild-born salmon in the reintroduced South Fork McKenzie population (Banks et al. 2016; O’Malley et al. 2023). However, in this population, wild-born spawners include descendants of hatchery salmon and wild-born salmon released above the dam in previous years, as well as salmon that do not assign to parents previously released above the dam. This latter group, which refer to as NORs, are presumably produced elsewhere and may be representative of the natural McKenzie River spring Chinook salmon population. After accounting for other variables associated with fitness, we found NORs produce about ~1.7 fold more adult offspring than hatchery salmon (modelRRS = 0.568).

## Offspring Characteristics

In addition to the number of returning adult offspring produced by salmon released above the dam, we also considered two ecologically relevant phenotypes of their offspring, age at maturity and body length. We found that F1s and NORs produced female offspring that returned at an older age than female offspring produced by hatchery salmon. F1s produced male offspring that returned at an older age than male offspring produced by both hatchery salmon and NORs. We found similar trends in body length, which is consistent with the strong genetic correlation between these two traits (Reed et al. 2019). One interpretation of these patterns is that while all groups demonstrated differences in size and age at maturity of offspring between sexes, these differences were weakest among offspring of hatchery salmon, and greatest in NORs, with F1s intermediate.

Age at maturity and fitness are positively associated in Pacific salmon (Ohlberger et al. 2020). The observation that F1s produced older offspring than hatchery salmon across both sexes suggests that subsequent generations of wild-born hatchery descendants (e.g. F2s) may have greater fitness. Interestingly, differences between the offspring of F1s and NORs depended on offspring sex. Trade-offs between survival to maturity and size or age at maturity are commonly observed among salmon species, and result in sexually antagonistic selection, with earlier maturation favored in males than females (Berejikian et al. 2010; Seitz et al. 2019). This sexually antagonistic selection may be responsible for the maintenance of diversity in age at maturity, and therefore increased fishery and population resilience (Greene et al. 2010; Schindler et al. 2010). Sexually antagonistic selection for age at maturity may be resolved in Atlantic salmon *via* sex dependent dominance (Barson et al. 2015), and in Chinook salmon *via* sex specific haplotypes (McKinney et al. 2021). However, sex dependent dominance for large-effect loci underpinning variation in age at maturity has been lost in aquacultured Atlantic salmon, potentially due to relaxed selection (Sinclair-Waters et al. 2020). In Chinook salmon the effects male-specific age at maturity associated haplotypes are reduced in the hatchery relative to natural environment, and this conditional neutrality may lead to evolved changes in the genetic architecture of this trait among hatchery descendants (McKinney et al. 2021). Our finding of reduced sex dependence in age at maturity phenotypes in offspring of F1s relative to NORs highlights the risks of ignoring the crucial role of diversity in long term persistence. Specifically, hatchery descendants may reach similar fitness levels over short periods, but may differ in diversity and the associated benefits to evolutionary potential and resilience against short term disturbance. Ultimately, we do not know if there is reduced genetic variation at age at maturity associated genetic loci among hatchery descendants, and further investigation is required to address this concern.

## Limitations

There are important limitations to our findings that must be considered before applying our conclusions to other reintroductions, or to hatchery supplementation in general.

The first limitation is related to the reciprocal influences of integrating wild-born salmon into the hatchery broodstock, and interbreeding between hatchery and wild-born salmon in the wild. Low relative reproductive success of hatchery Chinook salmon in the wild may be ameliorated by integrating local-origin, wild-born salmon into the hatchery broodstock (Waters et al. 2015; Waters et al. 2018; Janowitz-Koch et al. 2019), but see Koch et al. (2022). It is possible that sustained natural production and limited non-local origin stock transfers in the Upper Willamette Basin, coupled with integration of the McKenzie hatchery broodstock has maintained adaptive genetic diversity and the capacity for increased fitness among the wild-born descendants of hatchery salmon. Similar findings by Nuetzel *et al* (2023) also stem from early generation, wild-born offspring of hatchery Chinook salmon from an integrated broodstock. Therefore, our finding that a single generation in the wild increases fitness among hatchery descendants may not be generalizable to non-local origin or segregated broodstocks. Reciprocally, interbreeding between hatchery and wild-born salmon in the wild may reduce genetic diversity and fitness of natural populations (Ryman and Laikre 1991; Ford 2002; Baskett and Waples 2013; Willoughby and Christie 2019). Our finding that F1 fitness is comparable to that of NORs is potentially mediated by the extent to which hatchery production has influenced the natural population in the McKenzie River. Fitness differences between F1s and NORs may be greater in populations with less hatchery influence on the natural population.

A second limitation to the generalizability of our conclusions is the possibility that NOR salmon in our study are not reflective of a hypothetical natural and locally-adapted above dam population. NORs released above the dam must volitionally enter the Cougar Trap. Most NORs tend to arrive at the Cougar Trap later than salmon produced above Cougar Dam. While this difference may reflect a heritable variation in migration timing between hatchery descendants and individuals from the natural McKenzie river population, it is also possible that NORs represent late-season dispersers from below the dam and the mainstem, or strays from another river. Studies in other Pacific Salmon species suggest that late-season dispersers previously homed to their natal habitat (Peterson et al. 2016), and have lower fitness than successfully homing individuals in the same environment (Peterson et al. 2014; Mobley et al. 2019). We also found that NOR males were smaller than other wild-born salmon encountered during spawning ground surveys below the dam and on the mainstem. Therefore, while F1 fitness was substantially greater than hatchery fitness and similar to NOR fitness, NOR fitness may not represent that reached by putatively locally-adapted individuals returning to their natal habitat to spawn.

However, in a reintroduction context, there are no locally-adapted natal-origin individuals against which to contrast F1 fitness. Salmon reintroduction programs generally seek to re-establish highly productive, self-sustaining populations, but face substantial uncertainty (Anderson et al. 2014; Lusardi and Moyle 2017). Therefore, reintroduction practitioners must choose between seeding a reintroduced population with hatchery salmon, wild-born salmon collected from a natural populations, volitional dispersers, or a mix to balance risks to extant natural populations with the goal of maximizing productivity and growth rate of the reintroduced population. Contrasts between F1 and NOR fitness allow evaluation of alternative reintroduction management strategies. Absence of fitness differences between F1s and NORs suggest that F1s may be as productive as volitional dispersers allowed to naturally recolonize the above dam habitat.

## Conclusion and Future Directions

We found that fitness of hatchery descendants increases after a single generation in the wild. These improvements make them indistinguishable from wild-born salmon produced elsewhere that volitionally migrate to and spawn in the same habitat. We also found that a trait positively associated with fitness, AAM, is increased among second generation relative to first generation hatchery descendants, suggesting that fitness increases may continue in subsequent generations. However, our findings likely depend of patterns of gene flow between the hatchery broodstock and the natural population in the McKenzie River and care must be taken before generalizing to other populations.

Our data do not directly address the mechanistic basis of the observed differences in fitness. If reduced reproductive success among hatchery salmon is driven by domestication selection (Christie et al. 2012; Christie et al. 2016), and domestication has severely reduced genetic variance for traits under selection in the wild, the pace of adaptation to natural conditions may be too slow to be ecologically important on conservation relevant timescales. Our findings suggest either that low relative reproductive success is driven by plastic responses to the hatchery environment, or that despite domestication selection, improved hatchery practices and integration of wild-born salmon into the broodstock has maintained sufficient genetic variance on which selection to natural conditions can act. Our data do not allow us to parse these alternative explanations for the patterns we observe, and we encourage continued research into the mechanisms underlying low RRS of hatchery salmon.

# Tables

**Table 1** Number of candidate parents by generation and year collected from 2012 – 2015 and released above Cougar Dam. HOR are any captive-reared salmon collected at either the hatchery or Cougar Trap. F1s are first generation, wild-born offspring of two HOR parents previously released above the dam. NOR are wild-born salmon that do not assign to a parent previously released above the dam and are presumed to be produced below the dam, on the mainstem, or elsewhere.

|  |  |  |  |
| --- | --- | --- | --- |
| **Year** | **HOR** | **F1** | **NOR** |
| 2012 | 446 | 275 | 174 |
| 2013 | 454 | 127 | 26 |
| 2014 | 506 | 48 | 25 |
| 2015 | 619 | 15 | 12 |

**Table 2** GLMMTLF model fit. Generalized linear mixed model examining the influence of *generation, sex, body length, release day, year,* *sex\*generation* and *release day\*generation* on total lifetime fitness. *Release group* included as random effects. Estimated effect (β) and standard error (s.e.) of each fixed predictor on the link scale (log) for predictors that were retained in the final model are presented. The null hypothesis that each predictor did not significantly improve the model fit was tested with a likelihood ratio test (LRT p-value). The null hypothesis that each predictor has an effect significantly different from zero for continuous predictors and different from the focal level for categorical variables was evaluated with the Wald test (Wald p-value). Focal level for *generation* was HOR, and *year* was 2012. 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 | -6.942 | 0.590 |  |  |
|  |  |  |  |  |
| Generation [F1] | 0.527 | 0.133 | **4.3e-05** | **7.8e-05** |
| Generation [NOR] | 0.635 | 0.163 |  | **9.9e-05** |
|  |  |  |  |  |
| Body Length | 0.067 | 0.007 | **5.1e-21** | **2.0e-16** |
|  |  |  |  |  |
| Year [2013] | 0.708 | 0.141 | **3.6e-6** | **5.4e-07** |
| Year [2014] | -0.028 | 0.161 |  | 0.86 |
| Year [2015] | -0.033 | 0.184 |  | 0.86 |
|  |  |  |  |  |
| **Random Effects** | **σ2** | **s.d.** |  |  |
| Release Group | 0.040 | 0.200 |  |  |

**Table 3** modelRRS. *Post-hoc* contrasts of marginal mean TLF between different levels of *generation* in GLMMTLF after controlling for effects of *body length* and *year*. S.E. is the standard error of the modelRRS estimate. P-values are Tukey-adjusted for three pairwise comparisons.

|  |  |  |  |
| --- | --- | --- | --- |
| **Contrast** | **modelRRS** | **s.e.** | **P-value** |
| HOR / F1 | 0.563 | 0.073 | < 0.0001 |
| HOR / NOR | 0.568 | 0.089 | 0.0009 |
| F1 / NOR | 1.009 | 0.1625 | 0.9985 |

**Table 4** OffspringAAM model fit. Binomial generalized linear model examining the influence of *generation, sex* and their interactionon proportion of age-5 vs age-4 offspring produced by candidate parents. Estimated effect (β) and standard error (s.e.) of each fixed predictor on the link scale (log odds ratio) for predictors that were retained in the final model are presented. The null hypothesis that each predictor did not significantly improve the model fit was tested with a likelihood ratio test (LRT p-value). The null hypothesis that each predictor has an effect significantly different from the focal level of the predictor was evaluated with the Wald test (Wald p-value). Focal level for *generation* is hatchery, and sex is female .

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Predictor** | **β** | **s.e.** | **LRT**  **p-value** | **Wald**  **p-value** |
| (Intercept) | -0.097 | 0.166 |  |  |
|  |  |  |  |  |
| Generation [F1] | 1.037 | 0.289 |  | **3.3E-04** |
| Generation [NOR] | 1.013 | 0.380 |  | **7.8E-03** |
|  |  |  |  |  |
| Sex [Male] | -0.945 | 0.224 |  | **2.5E-05** |
|  |  |  |  |  |
| Generation\*Sex [F1\*Male] | -0.354 | 0.373 | 0.05 | 0.34 |
| Generation\*Sex [NOR\*Male] | -1.175 | 0.504 |  | **0.02** |

# Figures

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**Fig. 1** Map of Study System. This is a placeholder, I will make a cleaner map before submission.

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**Fig. 2** modelRRS. *Post-hoc* contrasts of marginal mean TLF between different levels of *generation* in GLMMTLF after controlling for effects of *body length* and *year*. Error bars is the standard error of the modelRRS estimate. Horizontal line at RRS = 1 indicated equal fitness between the two groups.

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**Fig. 3** ΔRRS. Mean TLF of HOR salmon divided by mean TLF of either F1s or NORs. Error bars are maximum likelihood based 95% confidence intervals. The confidence interval for the F1 *vs* NOR contrast extends beyond the plot extent.

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**Fig. 4** Estimated proportion of age-5 *vs.* age-4 female (left panel) and male (right panel) offspring produced by hatchery salmon, F1s and NORs. Error bars are 95% confidence limits of the estimates.

# Supplemental Tables

**Supplemental Table 1** Sex ratios by generation.

|  |  |  |  |
| --- | --- | --- | --- |
| **Generation** | **nmale** | **nfemale** | **proportion female** |
| HOR | 771 | 1254 | 0.62 |
| F1 | 278 | 187 | 0.40 |
| NOR | 153 | 84 | 0.35 |

**Supplemental Table 2** GLMMmodel fit with final predictors from GLMMTLF and *release day*. Estimated effect (β) and standard error (s.e.) of each fixed predictor on the link scale (log) for predictors. The null hypothesis that each predictor did not significantly improve the model fit was tested with a likelihood ratio test (LRT p-value). The null hypothesis that each predictor has an effect significantly different from zero for continuous predictors and different from the focal level for categorical variables was evaluated with the Wald test (Wald p-value). Focal level for *generation* was HOR, and *year* was 2012. 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 | -6.846 | 0.589 |  |  |
|  |  |  |  |  |
| Generation [F1] | 0.363 | 0.158 | **1.7e-03** | **2.2e-02** |
| Generation [NOR] | 0.593 | 0.165 |  | **3.2e-04** |
|  |  |  |  |  |
| Body Length | 0.067 | 0.007 | **2.2e-16** | **2.0e-16** |
|  |  |  |  |  |
| Release Day | -0.004 | 0.002 | 5.2e-02 | 5.5e-02 |
|  |  |  |  |  |
| Year [2013] | 0.688 | 0.142 | **8.7e-06** | **1.3e-06** |
| Year [2014] | -0.040 | 0.161 |  | 8.0e-01 |
| Year [2015] | -0.099 | 0.188 |  | 6.0e-01 |
| **Random Effects** | **σ2** | **s.d.** |  |  |
| Release Group | 0.040 | 0.200 |  |  |

**Supplemental Table 3** modelRRS from GLMM with *release day*. *Post-hoc* contrasts of marginal mean TLF between different levels of *generation* after controlling for effects of *release day, body length* and *year*. S.E. is the standard error of the modelRRS estimate. P-values are Tukey-adjusted for three pairwise comparisons.

|  |  |  |  |
| --- | --- | --- | --- |
| **Contrast** | **modelRRS** | **s.e.** | **P-value** |
| HOR / F1 | 0.651 | 0.098 | 0.0120 |
| HOR / NOR | 0.580 | 0.091 | 0.0015 |
| F1 / NOR | 0.890 | 0.155 | 0.7818 |

# Supplemental Figures

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**Supplemental Figure 1** Estimated marginal mean body length averaged over years for female (left panel) and male (right panel) HORs, F1s, NORs and Carcasses. Carcass refers to a wild-born individuals encountered during spawning ground surveys conducted on the South Fork McKenzie River below Cougar Dam or on the mainstem McKenzie River. Error bars are the 95% confidence interval of the estimated marginal mean.

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**Supplemental Figure 2** Density plot of Julian Calendar day of release for HORs, F1s, and NORs.

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**Supplemental Fig. 3** Predicted effect of *generation* on TLF from the GLMMTLF at typical levels of *length* and *year.* Error bars are standard errors of the predicted TLF.

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**Supplemental Fig. 4** ΔRRS by sex and year. Male ΔRRS is in top panel. Female ΔRRS is in bottom panel. Mean TLF of HOR salmon divided by mean TLF of either F1s or NORs. Error bars are maximum likelihood based 95% confidence intervals. Error bars extend beyond plot extent in some contrasts.

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