**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 1.7-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

800 – 1000 word target

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 & Steel 2011). Reintroduction promotes species persistence by increasing productivity and promoting habitat and life-history diversity (just an outline for this sentence currently cites).

* Necessity and goals of reintroduction
* However RRS less than one is a challenge
  + RRS review, following Koch and Narum framework
  + ~~In Chinook salmon, there is evidence that a completely integrated broodstock may ameliorate the fitness impacts of captive rearing such that fitness differences between wild-born and hatchery salmon spawning in the wild are reduced (hess 2012 and Koch 2019), although this result is not consistent (Koch 2022). In contrast, relative reproductive success is consistently less than one when the broodstock is segregated, or only partially integrated (Williamson, Anderson, Banks 2016, O’Malley 2023).~~
* Following ~two decades of research, there are many point estimates of RRS across species, hatchery programs (integrated vs segregated), and river basins. These studies have revealed important trends and suggested areas where more research is needed. However, the focus of this body of literature has primarily been documenting potential fitness differences between HOR and wild born salmon spawning in the wild, the pace at which these fitness differences (if present) accrue, and the underlying mechanisms. (put in here somewhere)
* Overcoming this challenge to reintroduction efforts depends critically on whether or not there is a transgenerational increase in fitness among the wild born offspring of hatchery origin salmon.
* However, this rapid re-adaptation is not assured, because it depends on the availability of beneficial variants in the standing genetic variation among HOR salmon used to seed the reintroduced population/ and or plasticity.
* To date, there is little empirical evidence to suggest that adaptation to natural conditions among wild-born descendants of HOR salmon occurs as rapidly as domestication. This information gap stems from multiple logistical and analytical challenges: (1) inferences require accurate pedigree data, necessitating sampling of a large portion of possible parents in the target habitat, (2) the variable of interest, fitness, has a negative binomial distribution and large variance, requiring large sample sizes to detect ecologically relevant difference in fitness, (3) the pedigree must include three or more generations, in the case of Chinook salmon this may require longitudinal sampling efforts spanning 10 or more years, and (4) confounding signals of adaptive phenotypic plasticity and genetic adaptation present experimental design challenges.
* Nuetzel and juvenile RS from Banks 2016
* For nearly three decades, HOR spring Chinook salmon (latin) have been released above Cougar Dam on the South Fork McKenzie River to restore ecosystem functions and access to historically productive spawning grounds above the dam (NMFS 2008). Since 2010, NOR salmon have also been released above the dam. Genetic parentage analysis has been used to evaluate this reintroduction effort (Banks et al. 2013; Banks et al. 2014; Sard et al. 2015; Banks et al. 2016; Sard et al. 2016). The resulting pedigree includes nearly all candidate parents released above Cougar Dam from 2007-2015 and nearly all returning adult potential offspring from 2010-2020, spans 14 years and includes up to four generations. Importantly, releases of Chinook salmon above Cougar Dam include not only HOR salmon and their NOR descendents, but also NOR salmon that are produced elsewhere (hereafter NOR immigrants).
* Set up questions
* Compare this RRS estimate to other Chinook salmon RRS estimates (Anderson *et al.* 2013; Hess *et al.* 2012; Koch *et al.* 2022; Nuetzel *et al.* 2022; Williamson *et al.* 2010)

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# 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 (Bowerman et al. 2018; Johnson & Friesen 2010) (McElhany et al. 2007). 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 unmarked salmon and a small number of HOR salmon that volitionally enter the trap. Importantly, the unmarked 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, unmarked salmon produced above the dam, unmarked 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

Fin clips were taken 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 (Banks *et al.* 2013; Banks *et al.* 2016; Banks *et al.* 2014; Sard *et al.* 2016b; Sard *et al.* 2015). 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, Parentage Analysis, and Focal Groups

We used genetic data and the pedigree inferred from a previous evaluation of the reintroduction effort (O’Malley 2023). Methods detailing collection of genetic data and inference of the pedigree can be found in the previous evaluation (O’Malley 2023). In brief, we isolated genomic DNA from fin clips according to (Ivanova cite), 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 unmarked 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 & 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 (Banks et al 2016; O’Malley 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 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 provides information regarding both parentage (i.e. who are the parents of an individual) and fitness estimates (i.e. how many returning adult offspring were produced by that individual) for 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: 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 must be HOR. Finally, NORs are any wild-born salmon 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.

## 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* function from the *glmmTMB* package in *R*. In addition to the effect of *generation*, 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. *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 & 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 model selection for fixed effects based on both 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 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 relative reproductive success 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 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 two fixed explanatory variables, generation and year. Model validation, effect plotting and post-hoc analysis followed the approach used with GLMMTLF. We examined offspring body length using a linear model with two fixed effects, generation and year. 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 parentage and TLF. Among the 952 wild-born salmon released above the dam in this period, 465 were identified as F1s and 237 were identified as NORs that did not assign to a candidate parent previously released above the dam (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.

## Relative Reproductive Success

Several predictors in the generalized linear mixed model of TLF were correlated with generation. HOR salmon tended to be smaller and include more females than both F1s and NORs (Supplemental Figs. 1 and Supplemental Table 1). F1s tended to be released above the dam earlier than both HORs and NORs (Supplemental Fig. 2). However, we did not find evidence of 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. 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). We also considered this model and provide the model fit and *post-hoc* analysis as supplements (Supplemental Tables 2 and 3), and note that both parameter estimates and *post-hoc* significance testing were qualitatively similar to those from GLMMTLF.

We found that including *generation* significantly improved the fit to the data (likelihood ratio test p-value = 4.29e-5, Table 2), and 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 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).

We found similar patterns for ΔRRS 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 also 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

The proportion of *age-5* vs. *age-4* offspring produced by candidate parents released above the dam was significantly explained by *generation* of parents, but not *year* of parents (ΔAIC = 0.6, likelihood ratio test p-value = 0.14). Parameter estimates and standard errors, as well as significance testing for the effects of *generation* of parents on the age at maturity of their offspring are presented in Table 4. We found that F1s produced a significantly greater proportion of age-5 *vs.* age-4 offspring compared to HORs, but no other pairwise comparison was significant. The parameter estimates presented in Table 4 were equivalent to producing 34%, 54% and 42% age-5 offspring for HORs, F1s, and NORs respectively. Despite this difference in age at maturity among offspring, we did not find that offspring varied in body length after accounting for the effect of *year* (F-test for ­*generation* p-value = 0.44, type II sums of squares).

# Discussion

## Relative Reproductive Success

Low reproductive success of hatchery relative to wild-born salmon challenges reintroduction 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 (Nuetzel). We found that the first generation, wild-born offspring of hatchery salmon (F1s) 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.

In contrast, we found little evidence of fitness differences between F1s and wild-born salmon of unknown parentage (NORs). Our model-based estimates suggest that F1s and NORs produce equal numbers of adult offspring after accounting for covariates, but direct contrasts of mean TLF suggest that NORs produced more adult offspring 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. 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 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 in the McKenzie basin more broadly. 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).

In addition to these important findings, we estimate 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). We previously found that hatchery salmon produced fewer adult offspring than wild-born salmon in the reintroduced South Fork McKenzie population (Banks 2016)(O’Malley *et al* 2023). However, in this population, wild-born spawners include both descendants of hatchery 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 examining the number of returning adult offspring produced by salmon released above the dam, we also examined two ecologically relevant phenotypes of offspring, age at maturity and body length. We found that F1s produced significantly more age-5 *vs.* age-4 offspring than hatchery salmon. Despite this age difference, we did not observe a similar pattern in body length, suggesting that first generation offspring of hatchery salmon exhibited faster growth rates than offspring of F1s, despite rearing in the same environment. Age at maturity and fitness are positively associated in Pacific salmon (cites). Indeed in the subset of individuals in our dataset with both age at maturity and TLF estimates, we observed a strong effect of age at maturity on fitness, with age-5 wild-born parents estimated to produce approximately twice the returning adult offspring than age-4 wild-born parents. The observation that F1s produced older offspring the hatchery salmon suggests that subsequent generations of wild-born hatchery descendants (e.g. F2s) may have greater fitness.

Let’s try to explore this collection of observations below:

1. Faster growth associated with younger AAM
2. Hatchery salmon tend return at younger ages than wild-born salmon.
   1. Because larger size at smoltification results in faster growth rates and younger AAM
   2. But is this relevant for explaining this finding, both sets of offspring spent their entire life cycles in the wild
3. Relaxed selection for large egg size in the hatchery tends to result in fecundity selection and rapid decrease in egg size.
4. Age at maturity is highly heritable, but also plastic.

pointing to heritable genetic or epigenetic effects hatchery rearing on life-history expression?

## 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 2015, waters 2018, Koch 2019, but see Koch 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. Therefore, our finding that a single generation in the wild increases fitness ~~for descendants of hatchery Chinook salmon~~ 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 Laikre 1991, Ford 2002, Basket et al 2013, Willoughby 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 the broader natural McKenzie River spring Chinook salmon population, or 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 hillborn hauser 2016), and have lower fitness in non-natal habitats than individuals that successfully homed (mobley 2019). We also found that NORs also tended to be smaller than other wild-born salmon encountered during spawning ground surveys below the dam ~~and on the mainstem~~, although this trend was not significant. Therefore, while F1 fitness was substantially greater than hatchery fitness and similar to NOR fitness, NOR fitness may not represent fitness that may be reached by a hypothetical locally-adapted above dam population.

Despite this limitation, it is important to remember that contrasts between F1 and NOR fitness is still relevant in a reintroduction context. Salmon reintroduction programs generally seek to re-establish highly productive, self-sustaining populations, but face many uncertainties (Anderson and Lusardi cites). 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. There is no locally-adapted above dam population against which to contrast fitness.

 Conclusion

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. ~~which may be representative of NOR salmon in the McKenzie basin more broadly.~~ 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 be ongoing.

* We found
  + Both fitness and a fitness related trait (AAM of offspring) improve after just a single generation in the wild
  + These improvements make them indistinguishable from NORs that spawned above the dam (with respect to these traits), which may be representative of NOR salmon in the McKenzie basin more broadly.
* If RRS < 1 is due to domestication selection, the pace of adaptation to natural conditions may be too slow to be materially important on conservation relevant timescales, especially if domestication selection has severely reduced genetic variance in the wild. Alternatively, if RRS < 1 may be driven by plastic responses to the hatchery environment. Even in the case of plasticity, reduced genetic diversity among hatchery stocks might lead to canalization of reaction norms. Therefore hatchery associated, maladaptive phenotypes may continue to be expressed in the wild despite the absence of the environmental cues that initially produced them.

# 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* and *year* on 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* was HOR.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Predictor** | **β** | **s.e.** | **LRT**  **p-value** | **Wald**  **p-value** |
| Intercept | -0.646 | 0.109 |  |  |
|  |  |  |  |  |
| Generation[F1] | 0.806 | 0.175 | **2.25e-05** | **4.31e-06** |
| Generation[NOR] | 0.325 | 0.224 |  | 0.15 |

# Figures

Fig. 1 Map of Study System.

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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.

# Supplemental Tables

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

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

# Supplemental Figures

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**Supplemental Figure 1** Density plot of body length in cm for HORs F1s and NORs

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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.

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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.