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

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# **Abstract**

Reintroduction is an important tool for the recovery of imperiled species. For threatened salmon species, hatchery-origin (HOR) salmon from a nearby source are often used to reestablish populations in vacant, historically occupied habitat. However, this approach is challenged by the relatively low reproductive success that 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; first generation, wild-born descendants (hereafter F1s) of fish produced at the same hatchery; and NOR salmon that were born elsewhere and volitionally entered a trap below Cougar Dam. We found that F1s produced nearly as many adult offspring as NOR salmon, and 1.8-fold more adult offspring than HOR salmon. This result suggests that, for the South Fork McKenzie reintroduction program, a single generation in the wild increases fitness for the descendants of hatchery-origin salmon. Care must be taken before extrapolating our results to other systems.

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# **Introduction**

Reintroducing organisms into habitats from which they have been extirpated is a common strategy used to aid in the recovery of threatened and endangered taxa (Seddon et al. 2007; Seddon et al. 2014). Reintroduction programs often seek to establish productive, self-sustaining natural populations (IUCN/SSC 2013). However, they frequently fail to achieve their recovery and conservation objectives (Fischer and Lindenmayer 2000; Godefroid et al. 2011; Bellis et al. 2019; Bubac et al. 2019). Many factors contribute to reintroduction success, or failure, including suitability of the source population (Cochran-Biederman et al. 2015; Bubac et al. 2019). Source populations must express appropriate phenotypes in the new habitat, and possess sufficient genetic and phenotypic diversity to avoid short term extinction risk and promote the adaptive potential of the reintroduced population (Miller et al. 2009; Weeks et al. 2011; Malone et al. 2018; Furlan et al. 2020).

Pacific salmon (*Oncorhynchus spp.*) 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). Reintroducing populations into these habitats has the potential to provide tremendous benefits to Pacific salmon, especially in areas where access can be provided to functional habitat that is currently blocked. Such reintroductions reduce extinction risk directly by providing additional abundance and productivity, and indirectly by promoting habitat, life history and genetic diversity (Anderson et al. 2014; Lusardi and Moyle 2017; McClure et al. 2018; Kock et al. 2020). However, selecting the appropriate source population for Pacific salmon reintroductions is challenging. Managers must choose between transplanting individuals from extant natural populations, promoting natural colonization by volitional dispersal through passage barrier removal, or releasing hatchery-origin (HOR) salmon (Anderson et al. 2014; McClure et al. 2018). Extensive transplanting from extant natural populations often poses unacceptable risks to threatened or endangered populations (Anderson et al. 2014; McClure et al. 2018), and removal of passage barriers is often not feasible, precluding natural colonization by volitional dispersal. Consequently, Pacific salmon reintroductions are frequently seeded with HOR salmon from nearby stocks (Anderson et al. 2014). These HOR salmon produce offspring in the wild that subsequently return to the target habitat as adults to spawn. However, potentially low reproductive success of HOR salmon, as compared to that of natural-origin (NOR) salmon (i.e. relative reproductive success; RRS) (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) can thwart efforts to establish self-sustaining populations. Similarly, low RRS challenges supplementation programs that seek to provide demographic benefits to extant natural populations by spawning NOR salmon in the hatchery and allowing their offspring to reproduce in the wild as adults (Berntson et al. 2011; Christie et al. 2012; Hess et al. 2012).

Following more than two decades of research, there are many point estimates of RRS across salmonid species, hatchery programs, and river basins (reviewed in Christie et al. 2014; Koch and Narum 2021). These studies have revealed important patterns and suggested areas where more research is needed. In general, RRS of HOR salmon tends to be 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 (*O. tshawytscha*), there is evidence that integrating 100% wild-born spawners into the broodstock may ameliorate the fitness impacts of captive rearing (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 broodstocks are segregated, or only partially integrated (Williamson et al. 2010; Anderson et al. 2013; Sard et al. 2015; Evans et al. 2016; Sard et al. 2016b; O’Malley et al. 2023). To date, the literature has primarily focused on documenting potential fitness differences between HOR and NOR 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 HOR salmon depends on whether 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 of salmonids. Araki et al. (2009) found that early generation, wild-born descendants of HOR steelhead (*O. mykiss*) in the Hood River, Oregon had lower reproductive success in the wild than wild-born steelhead with no recent hatchery ancestry, but a re-analysis of these data to account for variance and bias in RRS estimates could not reject the null hypothesis that RRS was equal to one (Kitada et al. 2011). In Chinook salmon from the McKenzie River, Oregon, we previously observed that first-generation, wild-born hatchery descendants produced more age-0 offspring than HOR salmon from a partially integrated stock, and similar numbers to other wild-born salmon in the same habitat across two years. But, we 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, Oregon produced more juvenile offspring, adult offspring, and juvenile grand-offspring than HOR salmon spawning in the same habitat. This finding was consistent across multiple years and after accounting for fitness-associated covariates (e.g., release day, body length, and sex). However, only HOR salmon and their descendants were reintroduced in this system, and the reproductive success relative to wild-born salmon from a local natural population could not be evaluated.

In this study, we examine a Chinook salmon pedigree from a reintroduction program above the Cougar Dam on the South Fork McKenzie River, Oregon to evaluate how the source of reintroduced individuals influences reproductive success. Specifically, we test whether lower reproductive success of HOR salmon in the wild persists among wild-born descendants of HOR salmon. We also compare the reproductive success of these wild-born hatchery descendants to that of NOR salmon in the McKenzie River that volitionally enter the trap at the base of Cougar Dam. This latter group is representative of natural colonizers that might act to reestablish the population in absence of the dam, and provides important context for our results. Finally, we examine two ecologically relevant phenotypic characteristics of the adult offspring of reintroduced salmon, age and size at maturity. We conclude by highlighting that care must be taken before extrapolating our results to other systems.

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# **Methods**

## Reproducible Research

Detailed logs and all data from 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.8097487](https://doi.org/10.5281/zenodo.8097487)). 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 naturally produced spring Chinook salmon in the upper Willamette Basin (McElhany et al. 2007; Johnson and Friesen 2010). In recent years, spring Chinook salmon recorded in the McKenzie River have included a proportion of hatchery-origin spawners (pHOS) ranging from 16 – 31% in the upper reaches of the mainstem, and consistently greater than 67% in lower reaches (Bowerman et al. 2018; Whitman 2022). Since hatchery operations began in the late 19th century, incorporation of non-Willamette basin salmon into the McKenzie River broodstock is thought to be very rare, but frequent stock transfers within the Willamette Basin 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, but only McKenzie Basin fish have been used as broodstock since 1990 (Johnson and Friesen 2010). The proportion of NOR salmon integrated into broodstock has varied between years, with an average of 5% between 2006 and 2012 and a current target rate of 10-30% (Johnson and Friesen 2014; ODFW and USACE 2019). Within the Willamette Basin, HOR spring Chinook salmon are most similar to NOR conspecifics from the same sub-basin (Johnson and Friesen 2014).

Construction on the 158m tall Cougar Dam was completed 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 and nearby Leaburg Hatchery (4.5 river km upstream) have been released above Cougar Dam since 1993 until the present (Fig. 1). A trap-and-haul facility was constructed at the base of Cougar Dam in 2010 (hereafter the Cougar Trap). The Cougar Trap collects adult salmon that volitionally enter, with a relatively small percentage (~8%) of these being HOR salmon. Importantly, 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, in the mainstem McKenzie River, or elsewhere (Banks et al. 2013; Banks et al. 2014; Sard et al. 2015; Banks et al. 2016; Sard et al. 2016b; O’Malley et al. 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 of three sources: (1) HOR salmon collected at the McKenzie Hatchery, Leaburg Hatchery, and the Cougar Trap, (2) wild-born salmon collected at the Cougar Trap, and (3) resident salmon above the dam.

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 (Duncan 2011; Beeman et al. 2014; Monzyk et al. 2015; Romer et al. 2016), and is likely a key factor limiting recovery (ODFW and 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 any year from 2007 – 2015 (Banks et al. 2013; Banks et al. 2014; Sard et al. 2015; Banks et al. 2016; Sard et al. 2016b; O’Malley et al. 2023).

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## Sample Collection for Genetic Analysis

Mass marking of HOR salmon (i.e., adipose fin removed) in the Willamette Basin began in 1997, and the proportion of unmarked HOR salmon in the McKenzie River is estimated at < 2% (McLaughlin et al. 2008), so we consider all unmarked salmon to be wild-born. Fin clips for genetic analysis were collected 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; Sard et al. 2015; Banks et al. 2016; Sard et al. 2016b; O’Malley et al. 2023). Fin clips were also collected from wild-born Chinook salmon carcasses identified during spawning ground surveys (SGSs) on the South Fork McKenzie River from 2011 – 2019, including above the dam and below the dam to the confluence with the mainstem McKenzie River. Additionally, we include fin clips collected from a small number of precocial male Chinook salmon encountered during SGSs above the dam in 2014.

## Genetic Data, Parentage Analysis, and Focal Groups

We used genetic data from previous evaluations of the reintroduction effort (Banks et al. 2013; Banks et al. 2014; Sard et al. 2015; Banks et al. 2016; Sard et al. 2016b; O’Malley et al. 2023). Methods detailing collection of genetic data and inference of the pedigree can be found in O’Malley et al. (2023). In brief, we isolated genomic DNA from fin clips, genotyped each sample at 11 microsatellite loci and a sex-linked marker, and performed genotype quality filtering to remove individuals genotyped at fewer than seven microsatellite loci and individuals that could have been sampled more than once. When inferring the pedigree, we defined *potential offspring* as any wild-born individual sampled 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). We assigned potential offspring that returned to the South Fork McKenzie in 2010 – 2020 to candidate parents released above Cougar Dam from 2007 – 2017. Therefore, our data allowed us to identify age-3 to age-6 offspring of salmon released above Cougar Dam in 2007 – 2014, and age-3 to age-5 offspring (98%) of salmon released above Cougar Dam in 2015. From the perspective of returning adult offspring, we sampled nearly all possible parents of salmon that returned from 2013 – 2020, and nearly all (98%) parents of salmon 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 considered three focal groups of candidate parents released above the Cougar Dam from 2012 – 2015: HOR, F1 and NOR. We refer to this variable as *origin.* HORs are hatchery-produced salmon that were spawned and reared to the smolt stage in the hatchery and then collected as returning adults at the hatcheries on the mainstem or at the Cougar Trap. F1s are the first generation, wild-born descendants of two HOR salmon released above the dam in previous years. 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 have been produced below the dam, on the mainstem McKenzie River, or elsewhere. NORs possess an unknown level of hatchery ancestry. We did not consider other candidate parents from 2012 – 2015 that do not fall into one of these three groups. For example, individuals that assigned to a single parent, or individuals that are offspring of mixed (i.e., HOR x NOR) mate pairs were not analyzed.

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## Body Length

We compared body lengths of HORs, F1s, and NORs released above the dam from 2012 – 2015 with body lengths of wild-born individuals encountered as carcasses on the mainstem McKenzie River, and on the South Fork McKenzie River below Cougar Dam. Body length was measured for HORs, F1s, and NORs at the Cougar Trap prior to release above the dam. Body length was measured for carcass samples during spawning ground surveys conducted on the mainstem and South Fork McKenzie River from 2012 – 2015 (*n* = 610). We fit a linear model on body length with three fixed effects, *year, sex,* and *group* (HOR, F1, NOR, Carcass)*,* and the *group*\**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

We defined total lifetime fitness (TLF) as the number of adult offspring produced by each candidate parent released above the dam (O’Malley et al. 2023). To address if there were fitness differences among HORs, F1s and NORs, we first estimated relative reproductive success (RRS) using a model-based approach that permits parsing of the effect of *origin* from covariates such as *body length* and *year*. In a complementary approach, we estimated RRS by calculating simple ratios of mean TLF between all pairwise comparisons of HORs, F1s, and NORs. To distinguish between the two approaches, we refer to RRS 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 *origin* on TLF, we considered the influence of multiple potential covariates including *sex, body length, release day*, and *year* and two interaction terms, *sex\*release day* and *sex\*origin*. We also included *release group* as a random effect. *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, and there was insufficient evidence to support a *year*\**release day* interaction (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 (GVIF1/(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, and a p-value cutoff of 0.05. We also considered alternative models with marginal differences in support from the final model (ΔAIC < 2). 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 *origin* 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 *origin* 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 for ΔRRS were estimated using a maximum likelihood approach following (Kalinowski and Taper 2005). ΔRRS was considered different from one if 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: *origin* of parents, *year* of parents, and *sex*. We also included the interaction *origin*\**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.

*Hatchery and Transport Effects*

Hatchery staff may select for larger and more fecund individuals for inclusion in the broodstock, thereby biasing the remaining individuals available for release above the Cougar Dam. Also, HOR salmon collected at the hatcheries on the mainstem experience more time in transit before release than individuals collected at the Cougar Trap. Both factors may contribute to fitness differences between HORs, F1s, and NORs salmon in our study, because the majority of HOR salmon in the study are collected at the hatcheries on the mainstem, whereas all F1s and NORs are collected at the Cougar Trap. To address these concerns, we examined if there were differences in TLF or body length between HORs collected at the hatcheries and HORs collected at the Cougar Trap. We used a generalized linear model to test for differences in TLF using *collection location* (mainstem hatchery *vs.* Cougar Trap) as an explanatory variable in addition to *sex, body length, release day*, and *year*. We did not include the random effect of *release group*. Model selection and validation followed the approach used with GLMMTLF. Effect of *collection location* was evaluated using a likelihood-ratio test. We examined body length using the same predictors and a linear model. We validated the model using Pearson residuals and evaluated significance with an F-test and type II sums of squares.

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# **Results**

## Parentage and Focal Group Sample Size

Our pedigree included 9,839 individuals sampled from 2007 – 2020 (O’Malley et al. 2023). Of these individuals, 2,027 HOR salmon and 952 wild-born salmon were released above the dam during 2012 – 2015, when we could 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). The remaining 250 wild-born salmon assigned to a single parent or to a mixed mate pair and were excluded from further analysis. Also, 15 individuals with no body length measurements were excluded.

## Body Length

Body length was significantly explained by *year*, and the *sex\*group* 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 every other group of females (Supplemental Fig. 1, Tukey p-value < 0.001). For males, every pairwise contrast was significant (Tukey p-value < 0.01). HOR males had the shortest body length, followed by F1s, NORs, and finally, Carcasses (Supplemental Fig. 1).

## Relative Reproductive Success

Several predictors used in the generalized linear mixed model of TLF were correlated with *origin*. HOR salmon were smaller on average and included more females than both F1s and NORs (Supplemental Fig. 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 *origin, length,* and *year* as fixed predictors and *release group* as a random effect. We did not find that *sex* or a *sex\*origin* 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 (modelRRS = 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 *origin*, 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 evaluated (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 one 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 were 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).

## Adult 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 including *year* of parents or the interaction between *year* and *origin* (ΔAIC < 1, likelihood ratio test p-value > 0.05), so the data were pooled across years. Parameter estimates and standard errors, as well as significance testing for the effects of *origin* of parents, *sex* of offspring and their interaction on the age at maturity of their offspring are presented in Table 4. Female adult offspring of F1s and NORs returned at an older age than female adult offspring of HOR salmon (Fig. 4). Male adult offspring of F1s returned at an older age than male adult offspring of both HORs and NORs (Fig. 4). We found similar trends in body length between the levels of *origin* and *sex,* but only one *post-hoc* contrast was significant, possibly due to a smaller number of individuals with length measurements than AAM estimates (Supplemental Table 4). Adult male offspring of F1swere larger than adult male offspring of NORs.

*Hatchery and Transport Effects*

We did not observe any significant differences in fitness or body length between HOR salmon collected at the hatcheries on the mainstem and the HOR salmon collected at the Cougar Trap. Mean fitness of HORs collected at the Cougar Trap was slightly higher among HOR salmon collected at the trap relative to HOR salmon collected at Cougar Trap (mean TLF 0.19 and 0.14, respectively). Collection location was not a significant predictor of TLF (ΔAIC < 1, likelihood ratio test p-value = 0.36), or body length among HOR salmon (F-test p-value 0.81, type II sums of squares). These results suggest that selection of larger and more fecund fish for broodstock at the hatchery does not strongly bias the remaining individuals released above the Cougar Dam towards smaller or less fit individuals.

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# **Discussion**

## Relative Reproductive Success

Low relative reproductive success of HOR salmon challenges reintroduction and supplementation programs and prompts an important question: does lower fitness of HOR salmon in the wild persist among their wild-born descendants? We found that F1s (i.e., first-generation, wild-born descendants of HOR salmon) produced significantly more adult offspring than HOR salmon that spawned alongside them in the wild. The strongest evidence of this generational fitness advantage comes from our model-based estimates of RRS, 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 HORs in each year.

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 only weak evidence of fitness differences between F1s and NORs (i.e., wild-born salmon of unknown parentage), with direct contrasts of mean TLF suggesting that NORs produced more adult offspring than F1s in one (2012) 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 in the other three years using this method. However, by not accounting for increased fitness among F1s associated with *body length*, these direct contrasts may overestimate fitness differences directly attributable to *origin*. 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 F1s and NORs, if present, are minor relative to the differences between either group and HORs. Our results corroborate the observation that F1s produced more juvenile offspring (age-0) than HORs, but a similar number of juvenile offspring to NORs in 2012 and 2013 (Banks et al. 2016). Together, our two central findings that F1 fitness is greater than HOR fitness, but not greater than NOR fitness, suggest that a single generation in the wild increases fitness for descendants of HOR Chinook salmon, such that they may be comparable to wild-born salmon that might naturally colonize available habitat through dispersal if the passage barrier was not present. Our findings offer support for the continued use of HOR Chinook salmon to initially reestablish naturally spawning populations in habitats where they have been extirpated (but see *Limitations* section below).

## Offspring Characteristics

In addition to evaluating the RS of the three groups of salmon released above the dam, we also considered two ecologically relevant phenotypes of their adult offspring, AAM and body length. We found that female adult offspring of F1s and NORs returned at an older age than female adult offspring of HOR salmon, whereas male adult offspring of F1s returned at an older age than male adult offspring of both HORs 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 there were differences in age and size at maturity of offspring between sexes, these sex differences were weakest among offspring of HOR salmon and F1s, and greatest among offspring of NORs. This framing prompts two questions, why might there be less age and size variation across sexes within salmon with recent, known hatchery ancestry, and what are the evolutionary and conservation implications of this reduction in variation?

AAM and fitness are positively associated in salmonids (Ohlberger et al. 2020). The observation that F1s produced older offspring than HOR salmon across both sexes suggests that subsequent generations of wild-born hatchery descendants (e.g., F2s) may have greater fitness. However, 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 AAM, and therefore increased fishery and population resilience (Greene et al. 2010; Schindler et al. 2010). Sexually antagonistic selection for AAM may be resolved in Atlantic salmon (*Salmo salar*) *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 AAM has been lost in aquacultured Atlantic salmon, potentially due to relaxed selection (Sinclair-Waters et al. 2020). In Chinook salmon, the effects of male-specific AAM associated haplotypes are reduced in the hatchery relative to the natural environment (McKinney et al. 2021), and this conditional neutrality may lead to evolved changes in the genetic architecture of this trait among hatchery descendants (Van Dyken and Wade 2010). Our finding of reduced sex dependence in AAM phenotypes among offspring of HOR salmon and their descendants relative to salmon with no known recent hatchery ancestry highlights the risks of ignoring the crucial role of diversity for long term species persistence. Specifically, hatchery descendants may reach similar fitness levels over short periods, but may differ in genetic and phenotypic 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 in AAM 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, hatchery supplementation programs, or hatchery risk evaluations, in general.

The first limitation is related to the reciprocal influences of integrating wild-born salmon into the hatchery broodstock, and interbreeding between HOR and wild-born salmon in the wild. Low RRS of HOR Chinook salmon in the wild may be ameliorated by integrating local-origin, wild-born salmon into a hatchery broodstock (Hess et al. 2012; 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, and other hatchery practices (e.g., random selection of individuals for broodstock, brood collected throughout the run period, number of breeders per cohort, etc.) have maintained adaptive genetic diversity and the capacity for increased fitness among the wild-born descendants of HOR salmon. Similar findings by Nuetzel et al. (2023) also stem from early generation, wild-born descendants of HOR 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. In short, pHOS is not zero in the McKenzie River and NORs may have some degree of hatchery ancestry. Fitness differences between F1s and NORs may be greater in populations with less hatchery influence on the natural population.

A second limitation that must be considered before generalizing our results to other systems is the possibility that NOR salmon in our study are not reflective of a hypothetical natural and locally adapted 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 of sockeye (*O. nerka*) and Atlantic salmon 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 HOR 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. This limitation is particularly important in a supplementation context.

However, in a reintroduction context, there are no locally adapted individuals against which to contrast F1 fitness. Salmon reintroduction programs generally seek to reestablish highly productive, self-sustaining populations, but face substantial uncertainty (Anderson et al. 2014; Lusardi and Moyle 2017; McClure et al. 2018). Therefore, managers must choose between seeding a reintroduction with hatchery salmon, wild-born salmon collected from 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, namely, the choice between using hatchery salmon and their descendants, or relying on natural colonization. Absence of fitness differences between F1s and NORs suggest that descendants of hatchery salmon may be as productive as volitional dispersers allowed to naturally colonize vacant habitats.

Finally, we caution that our findings do not negate prior evidence that has demonstrated low RRS of HOR salmon (Christie et al. 2014; Koch and Narum 2021), and the risk that chronically elevated hatchery influence can pose to the genetic integrity and productivity of natural populations (McMillan et al. 2023). This caution is particularly salient to hatchery augmentation programs. There are important differences between these programs and reintroduction or supplementation programs. Most notably, augmentation programs are typically located in areas with relatively healthy, self-sustaining natural populations. While our results offer evidence that naturally spawning salmon populations can be established with HOR salmon and hope that reestablished populations may experience generational increases in mean fitness, they also demonstrate the relatively low parental contribution to population productivity from HOR salmon spawning in the wild. This limited contribution to population productivity from HOR salmon should be carefully weighed against the potential risks HOR salmon pose to the fitness of NOR spawners. Repeated interbreeding between HOR and NOR salmon may result in a decline in fitness of NOR salmon unless the level of interbreeding is managed to a low level.

## Conclusion and Future Directions

We found that the fitness of hatchery descendants (F1s) increases after a single generation in the wild, such that the fitness of F1s is indistinguishable from that of other wild-born salmon released into the same habitat to spawn. 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 on the pattern 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 identify the mechanistic basis of the observed differences in fitness. If reduced reproductive success among hatchery salmonids is driven by domestication selection (Christie et al. 2012; Christie et al. 2016; Waters et al. 2018), 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 that either low RRS is driven by plastic responses to the hatchery environment (e.g., growth, behavior, etc.), or that despite domestication selection, improved hatchery practices (e.g., the proportion of wild-born salmon into broodstock, the effective number of breeders per cohort, etc.) may maintain sufficient genetic variance on which selection to natural conditions can act, and adaptation is rapid. Our data do not allow us to parse these alternative explanations for the patterns we observe, and underscore the need for continued research into the mechanisms that drive low RRS of HOR salmon.

# **Tables**

**Table 1** Number of candidate parents by origin and year collected from 2012 – 2015 released above Cougar Dam. HOR are any hatchery-produced salmon collected at either the hatchery or Cougar Trap. F1s are first generation, wild-born descendants of two HOR parents that were released above the dam in previous years. 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 |

\* Wild-born salmon released above the dam beginning in 2010. Modifications to trap-and-haul operations reduced the number of wild-born salmon released above the dam in 2013 and subsequent years (Sard et al. 2015; O’Malley et al. 2023).

**Table 2** GLMMTLF model fit. Generalized linear mixed model examining the influence of *origin, sex, body length, release day, year,* *sex\*origin* and *release day\*origin* on total lifetime fitness. *Release group* included as random effect. 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 *origin* 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 |  |  |
|  |  |  |  |  |
| Origin [F1] | 0.527 | 0.133 | **4.3e-05** | **7.8e-05** |
| Origin [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 *origin* 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.

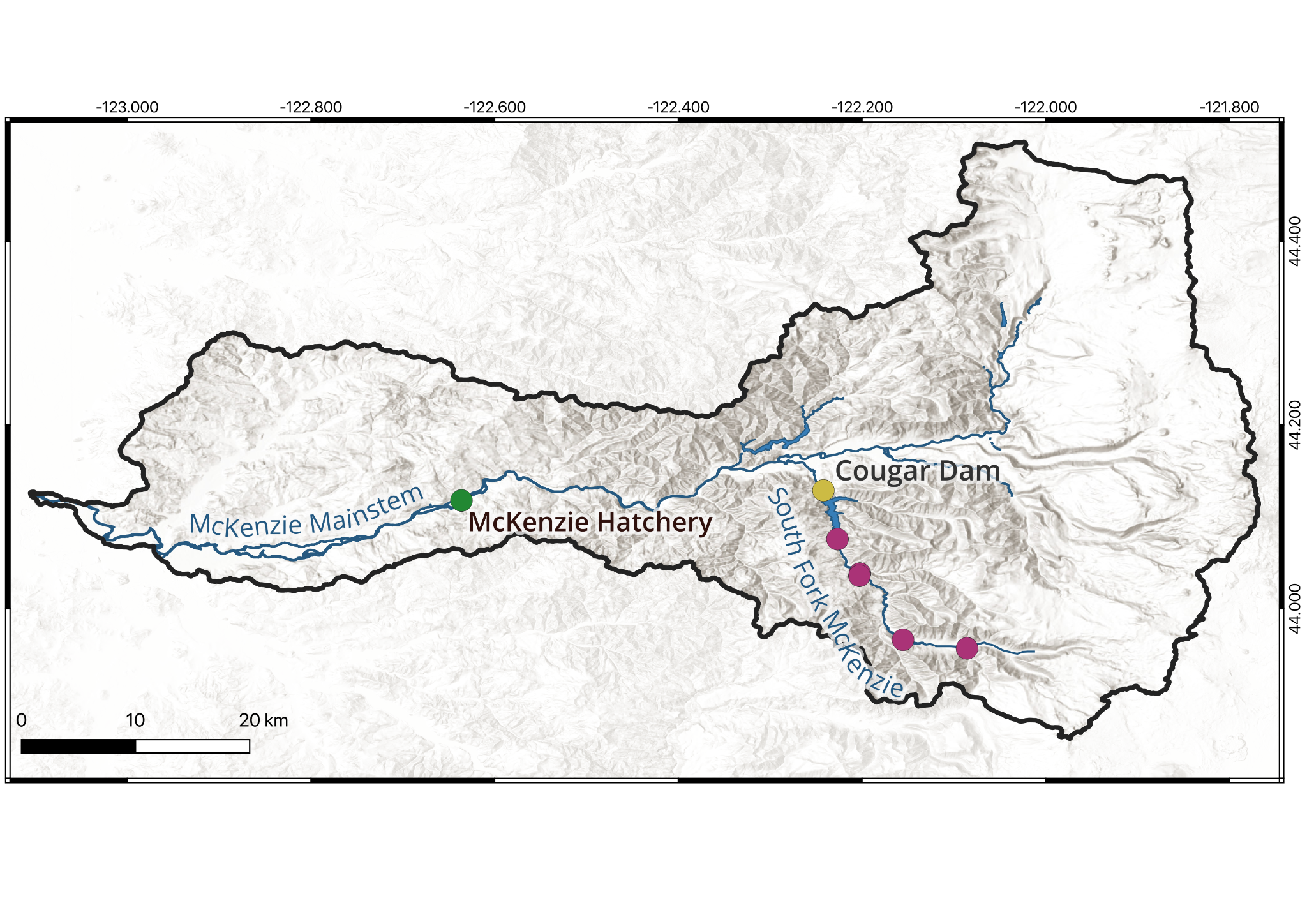
|  |  |  |  |
| --- | --- | --- | --- |
| **Contrast** | **modelRRS** | **s.e.** | **p-value** |
| HOR /F1 | 0.563 | 0.073 | < 0.0001 |
| HOR / NOR | 0.568 | 0.089 | 0.001 |
| F1 / NOR | 1.009 | 0.162 | 0.999 |

**Table 4** OffspringAAM model fit. Binomial generalized linear model examining the influence of *origin, 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 *origin* is hatchery, and sex is female.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Predictor** | **β** | **s.e.** | **LRT p-value** | **Wald p-value** |
| Intercept | -0.097 | 0.166 |  |  |
|  |  |  |  |  |
| Origin [F1] | 1.037 | 0.289 |  | **3.3e-04** |
| Origin [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**



**Fig. 1** Map of McKenzie River sub-basin including Cougar Dam (gold point), McKenzie Hatchery (green point) and release sites on South Fork McKenzie River, above Cougar Dam (magenta circles). Data sources: ESRI World Hillshade, USGS NHDPlus HR

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**Fig. 2** modelRRS. *Post-hoc* contrasts of marginal mean TLF between different levels of *origin* in GLMMTLF after controlling for effects of *body length* and *year*. Error bars are 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. 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 HORs, F1s and NORs. Error bars are 95% confidence limits of the estimates.

# 

# **Supplemental Tables**

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

|  |  |  |  |
| --- | --- | --- | --- |
| **Origin** | **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 *origin* 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 |  |  |
|  |  |  |  |  |
| Origin [F1] | 0.363 | 0.158 | **1.7e-03** | **2.2e-02** |
| Origin [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 | 0.041 | 0.201 |  |  |

**Supplemental Table 3** modelRRS from GLMM with *release day*. *Post-hoc* contrasts of marginal mean TLF between different levels of *origin* 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 | 0.012 |
| HOR / NOR | 0.580 | 0.091 | 0.002 |
| F1 / NOR | 0.890 | 0.155 | 0.782 |

**Supplemental Table 4** Number of adult offspring assigned to HOR, F1, and NOR parents, used to fit the offspring AAM model (**offspring** **nAAM**), and with body length measurements (**Offspring** **nlength**)

|  |  |  |
| --- | --- | --- |
| **Parent Origin** | **Offspring nAAM** | **Offspring nlength** |
| HOR | 383 | 231 |
| F1 | 216 | 147 |
| NOR | 114 | 91 |

# 

# **Supplemental Figures**

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**Suppl. Fig. 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 individual 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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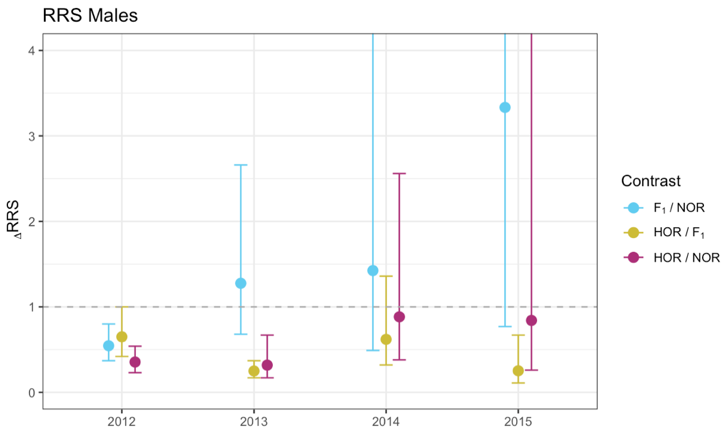
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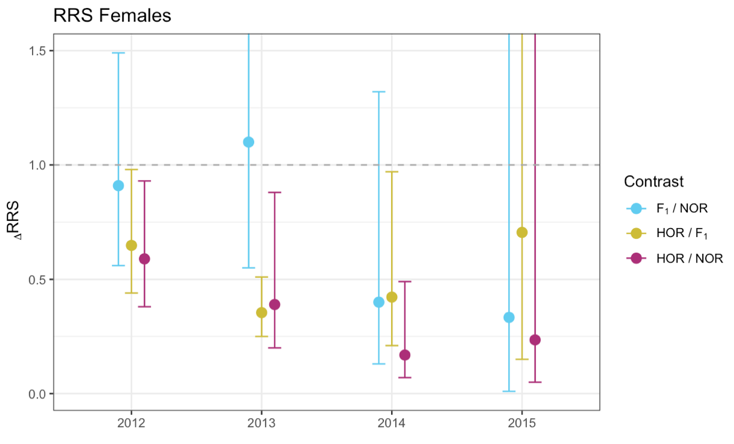
**Suppl. Fig. 2** Density plot of Julian Calendar day of release for HORs, F1s, and NORs.

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**Suppl. Fig. 3** Predicted effect of *origin* 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 the top panel. Female ΔRRS is in the bottom panel. Mean TLF of HORs 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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