Improved productivity of naturalized spring Chinook salmon following reintroduction from a hatchery stock in Lookingglass Creek, Oregon

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[A] *Abstract*

Supplementation of depressed salmonid populations with hatchery production has been questioned due to domestication effects, which may reduce reproductive fitness. However, for extirpated populations, reintroduction typically requires use of hatchery stocks. We evaluated this strategy by monitoring the naturalization of spring Chinook salmon reintroduced to Lookingglass Creek, OR (Grande Ronde Basin) from a captive brood, hatchery stock. We compared the reproductive success (RS) of naturally spawning natural-origin (NOR) relative to hatchery-origin (HOR) adults across nine brood years. Individual RS (the number of progeny produced) was estimated by pedigree reconstruction analyses, and then analyzed by generalized linear models to estimate the effect of parental origin, while controlling for potentially confounding covariates. When evaluating RS by juvenile progeny, NOR spawners were more likely to be reproductively successful, and when successful, produced more progeny on average than successful HOR counterparts. We found a similar advantage when evaluating RS by adult progeny, although the origin effect was not as important among successful spawners. Results suggest fish reintroduced from a hatchery stock possess the adaptive capacity to positively contribute to natural productivity and recovery goals.

Keywords: reintroduction, origin, Chinook, reproductive success

[A] *Introduction*

Populations of anadromous salmonids (*Oncorhynchus* spp.) have been dramatically reduced in abundance across their historic range in the Pacific Northwest (e.g., see reviews by Nehlsen et al. 1991; Gustafson et al. 2007). In the Columbia River Basin, where extensive and dramatic alterations to the migratory corridor have occurred, an estimated 117 of 333 historical populations have been extirpated (CBP 2020). When the central cause of extirpation involved a physical barrier to migration that was subsequently removed, instances of reintroduction or range expansion via the natural exploratory behaviors of migrating adults have occurred (Pess et al. 2014; Anderson et al. 2015; Allen et al. 2016; Brewitt 2016; Brenkman et al. 2019). However, when barrier removal or habitat restoration actions are not feasible or when extant source populations are distant, natural recolonization via straying may be impractical or insufficient to establish a self-sustaining population, thereby necessitating active reintroduction efforts (Deredec and Courchamp 2007; Anderson et al. 2014). Such efforts generally rely on hatchery stocks and presume that fish of the chosen stock possess the phenotypic and genotypic diversity upon which natural selective forces may act over generations to affect population-level adaptations to the introduced habitat (Narum et al. 2007; Anderson et al. 2014; Liermann et al. 2017; Evans et al. 2019).

The ability of a hatchery stock to successfully adapt and positively contribute to a reintroduction effort, however, may have been compromised by domestication effects associated with hatchery rearing. Several studies involving hatchery supplementation of depressed populations have shown that domestication selection, or selection for traits that are beneficial under conditions of captivity, may negatively impact the reproductive success (i.e., fitness) of hatchery-origin (HOR) transplants when spawning in nature, as well as that of the natural-origin

(NOR) fish with which they may interbreed (Lynch and O'Hely 2001; Ford 2002; Frankham et al. 2002; Araki et al. 2007a; Frankham 2008; McClure et al. 2008; Berntson et al. 2011; Christie et al. 2012; Ford et al. 2012). Similar to these evaluations of supplementation programs for depressed populations, it is possible to monitor the naturalization of reintroduced fish by comparing the reproductive success (RS) of NOR fish (i.e., those that are one or more generations removed from the hatchery) relative to HOR fish (i.e., incubated and reared in a hatchery). If natural selective forces select against maladaptive domestication effects, naturally spawning NOR adults should demonstrate higher RS than their HOR counterparts, and therefore present relative reproductive success (RRS) ratios greater than one within a given brood year (RRS ratio expressed as NOR:HOR since RS of the HOR fish is the baseline value for a reintroduced population). A reintroduction program for spring Chinook salmon in Lookingglass Creek, a tributary to the Grande Ronde River (rkm 138 from its confluence with the Snake River) in northeastern Oregon (Figure 1), provided an opportunity to test this hypothesis.

Since the reintroduction program began in 2001, the Confederated Tribes of the Umatilla Indian Reservation (CTUIR) have conducted a systematic monitoring program including tissue sampling and collection of biological data from all adult spring Chinook salmon intercepted at the Lookingglass Hatchery weir each year, as well as from a sample of juvenile outmigrants captured in a rotary screw trap located between the weir and hatchery (Figure 1). We used these samples and associated datasets to conduct a multi-generational parentage analysis to evaluate the naturalization of spring Chinook salmon reintroduced to Lookingglass Creek upstream of the weir, by comparing the RS of naturally spawning NOR fish relative to HOR fish within brood years. We estimated individual RS as average recruits-per-spawner, where recruits were expressed as either juvenile outmigrants, returning adults, or grand-progeny (both juvenile and adult life stages), and then estimated relative reproductive success (RRS) ratios between origins using generalized linear models. We hypothesized that the NOR spawners, which hatched and reared in the stream, would demonstrate higher RS than their HOR counterparts, which hatched and reared in the hatchery, within each brood year.

[A]*Methods*

[B] *Study Area and sample collection* – The native population of spring Chinook salmon in Lookingglass Creek suffered drastic declines in abundance in the late-1900s, largely due to increased migration mortality associated with the construction of the four lower Snake River dams (ODFW 1990; Tranquilli et al. 2004). To mitigate for these losses, Lookingglass Hatchery was constructed on Lookingglass Creek (rkm 3.7; Figure 1) in 1982 under the federally mandated Lower Snake River Compensation Plan (LSRCP; COE 1975; Herrig 1990; Marshall 2010). To meet the hatchery's abundance and harvest goals, broodstock was initially sourced from Carson National Fish Hatchery (located on the Wind River; Carson, Washington) and later from Rapid River Hatchery (located on the Salmon River; Riggins, Idaho) (Olsen et al. 1992). However, in 1992, Snake River spring/summer Chinook salmon were listed under the Endangered Species Act (ESA), obligating managers to reconcile goals outlined in the LSRCP with stipulations of the ESA (NMFS 1992). As a result, the reliance on out-of-basin stocks in the Grande Ronde basin was terminated after the 1999 brood year, and managers instead sourced broodstock from in-basin returning adults or fish which were raised under one of three, in-basin, captive broodstock programs (Catherine Creek, Lostine River, Upper Grande Ronde; see Figure 1) (Hesse et al. 2006; Carmichael et al. 2011).

For Lookingglass Creek, however, by the time these practices were initiated in 2000, the native population was functionally extirpated due to excessive removal of returning adults for hatchery broodstock and significant introgression by out-of-basin hatchery stocks (ICBTRT 2003; Van Doornik et al. 2013). Managers therefore sought to reestablish a Lookingglass Creek spring Chinook salmon population by reintroducing fish derived from the Catherine Creek captive broodstock program (Hesse et al. 2006). The first Catherine Creek stock juveniles were released from the hatchery into Lookingglass Creek in 2001 (brood year 2000), and the first year of substantial returns from this cohort occurred in 2004 (age-4 is the dominant age at maturity for Grande Ronde spring Chinook salmon; Burck 1994; Boe et al. 2010). A proportion of the hatchery-origin (HOR) adults returning to Lookingglass Creek in 2004 were collected for broodstock to create a local, Lookingglass Hatchery stock. The remainder were passed upstream of the weir for natural spawning, thereby initiating the reintroduction of spring Chinook salmon to the upper reaches of Lookingglass Creek (Boe et al. 2010). The first age-4 natural-origin (NOR) progeny from the BY2004 natural spawners returned to the Lookingglass weir in 2008. Since 2008, the upstream spawning population of spring Chinook salmon in Lookingglass Creek has consisted of a mix of NOR and HOR adults (Figure 2).

To monitor productivity of the reintroduced spring Chinook salmon population and collect fish for hatchery broodstock, the Confederated Tribes of the Umatilla Indian Reservation (CTUIR) and Oregon Department of Fish and Wildlife (ODFW) operate a weir on Lookingglass Creek, approximately 400m upstream of the Lookingglass Hatchery (Figure 1). The weir presents an essentially impassable barrier to upstream migration and operated with an estimated efficiency of 99.2% during the study years (2008-2020; C. Crump personal communication, 2022). From 2008 through 2020, adults intercepted at the weir were measured for fork length (mm), tissue sampled (opercular punch), sexed by visual assessment of external morphology and identified to origin, where an adipose-intact fish with no coded wire tag was designated as NOR (Crump et al. 2021). A portion of the intercepted fish were transferred to the hatchery for use as broodstock, with the remainder passed upstream of the weir for natural spawning each year (except for some or all of the age-3 HOR jacks, which were donated to the CTUIR foodbank or transported back downstream for fisheries) (Boe et al. 2010; ODFW 2011). A limited number of tissue samples were also collected from post-spawned adults that escaped handling at the weir (identifiable by lack of an opercular punch) during spawning ground surveys conducted above the Lookingglass Creek weir.

To monitor juvenile production from natural spawning, CTUIR captures out-migrating juveniles year-round in a rotary screw trap (RST) located 200 meters downstream of the weir (Figure 1). The RST operated with an estimated average sampling efficiency of 35% during the study years (C. Crump, personal communication, 2022). From 2009 through 2018, tissue samples (fin clips) were randomly collected from a portion of the captured juveniles for genetic analysis, along with individual fork length (mm), weight (g) and sample date. Juvenile spring Chinook salmon out-migrate from Lookingglass Creek primarily as age-0+ parr (fork length range 39-118mm, mean 74.6mm) from June through December. These fish overwinter within the mainstem of the Grande Ronde River prior to continuing their migration to the ocean the following spring. A smaller proportion of juveniles over-winter in Lookingglass Creek, and are captured out-migrating in February through May as age-1+ smolts (fork length range 56-197mm, mean 89.6mm; Burck 1994; Crump et al. 2017).

[C] *Ethics Approval*

Sampling and handling of both juvenile and adult spring Chinook salmon is authorized via appropriate ESA permits and consultations, as outlined in Section 2.1 of the Lookingglass Hatchery Genetic Management Plan (ODFW 2011).

[B]*Genetic sample preparation and parentage analysis* − DNA was extracted from tissue initially using a standard Qiagen DNeasy protocol (Qiagen Inc., Valencia, CA) and subsequently a custom Chelex 100 protocol (Sigma-Alrich, St Louis, MO). Genotyping was performed for a panel of single nucleotide polymorphism (SNP) markers (Hess et al. 2015), plus an additional sex marker (Brunelli et al. 2008; Yano et al. 2013) developed for spring Chinook salmon using the genotyping-in-thousands by sequencing approach (GTseq; Campbell et al. 2015). All parentage analyses were performed using a panel of 93 markers that were shared and informative across relevant collection years (2008-2020; marker list detailed in Nuetzel 2022). Individual genotype data was then quality filtered such that any individual missing ≥10% genotypic data, or which represented a duplicate sample of the same individual, was removed from the analytical data set.

Parentage analysis was performed for each progeny collection separately, with a collection being defined by a unique combination of life stage and collection year (see Nuetzel 2022). We used two pedigree reconstruction programs, both of which use likelihood-based methods to assign parentage for each progeny collection. Genotype data were first analyzed in the program SNPPIT (Anderson 2010; Anderson 2012) to identify parent-progeny trios (i.e., a progeny and both its mother and father). Each SNPPIT run considered parent spawn year and assumed a genotyping per locus error rate of 0.5%, which was guided by author recommendations and our preliminary assessment of per locus error rates across collection years (from 0.00014 to 0.0053;

Anderson 2010). We did not include parental sex data due to inconsistency between sex identity based on genetic sex markers versus phenotypic sex indicated in the field data, particularly in the earliest collection years. All resulting trios were filtered for false discovery rate (FDR) ≤0.010, and no more than two Mendelian incompatible loci. The parent-progeny trio assignments passing these filtration criteria were then compared to recorded genetic and phenotypic sex data to resolve sex identity for those individuals assigned as parents. Any trios in which parents were ultimately presumed to be the same sex were not retained.

Each progeny collection was then analyzed in the program COLONY (v2.0.6.6; Jones and Wang 2010) to identify single-parent progeny pairs and additional trios. As with SNPPIT, each COLONY run was performed naïve of parent sex; however, we used the quality-filtered parent-progeny trios identified by SNPPIT to construct known paternity and maternity matrices for each run in COLONY. This effectively informed COLONY of sex for individuals attributed progeny by SNPPIT. Run parameters for each progeny collection were as follows: both parents polygamous, medium run length and precision, and full-likelihood analysis method. Additionally, we identified the probability of either mother or father having been sampled as 0.90 – an estimate which considered weir efficiency data, as well as computational risks of overestimating sampling probability. All resulting single-parent progeny pairs and novel trios were filtered for probability ≥ 0.90.

Lastly, all quality-filtered trio and single-parent assignments from SNPPIT and COLONY were combined, and then reviewed alongside individual biodata to ensure plausibility. Non-plausible assignments included those for which: 1) the inferred age of the progeny given parental assignment did not align with recorded life stage and/or fork length, 2) instances of implausible precocious female spawning, and 3) trios in which the parental dispositions (i.e., natural spawner, broodstock spawner, etc.) did not align. Assignments which failed any of these three plausibility checks were removed from the analysis; this amounted to a relatively small proportion (1.3%) of total trio and single-parent assignments across all progeny collections.

[B]*Relative Reproductive Success Analyses* – We summarized finalized parentage assignments to tally the total number of parr, smolt, and adult progeny assigned to adult (age-4 and age-5) female and male fish that spawned naturally in Lookingglass Creek upstream of the weir during brood years 2008-2016. We then estimated the number of juvenile and adult grand-progeny attributed to adult spawners in brood years 2008-2012 by summing across generations. For example, if 2008 is the F0 generation, its adult progeny (F1) largely returned in 2012, and its adult grand-progeny (F2) largely returned in 2016. We therefore tallied the number of grand-progeny attributed to a given spawner from 2008-2012 by summing all progeny assigned to its adult, naturally spawning progeny in the F1 generation. If an adult spawner from BY2008-2012 was assigned zero F1 offspring, then it was assumed to produce zero grand-progeny. If an adult spawner from BY2008-2012 was assigned an adult F1 progeny that was taken for broodstock, we did not consider this individual in our grand-progeny analyses as we were explicitly interested in stream spawners and therefore would not have analyzed the progeny of any broodstock spawners. We did not perform any progeny or grand-progeny summations for naturally spawning jacks (age-3 males) because returning hatchery-origin (HOR) jacks were not passed above the weir starting in 2012. We also conducted a sensitivity analysis by excluding single-parent assignments from the tallies of individual reproductive success, and thereby the relative reproductive success (RRS) estimates. We found that we would have drawn the same qualitative conclusions regardless of whether single-parent assignments were included or excluded, and therefore chose to include the single-parent assignments in our subsequent analyses.

We initially considered parr and smolt progeny separately in reproductive success (RS) comparisons to account for possible differences in the propensity of juvenile offspring to emigrate as a parr or smolt according to parental origin. Given the geographic differences in over-wintering by juvenile emigration type, and knowing that the overwintering period is associated with significant mortality (Huusko et al. 2007; Brown et al. 2011; Favrot and Jonasson 2020), the number of progeny per spawner would appear higher if enumerated at the parr versus smolt stage. This could bias estimates of individual reproductive success if one parental origin is more likely to produce juvenile offspring that emigrate as parr. We therefore assessed whether NOR and HOR spawners were assigned parr at relatively equal proportions of their total juvenile assignments within brood years. While the proportion of all assignments that indicated parr progeny varied among years, the difference between NOR and HOR spawners within years was statistically significant in only a single year (2009, 0.77 for HOR vs 0.65 for NOR; all other years had smaller differences), leading us to conclude that we could combine the number of parr and smolt progeny assigned per adult into a single measure of RS without concern of a juvenile progeny type bias (Supp. Material – Section 5; Figure S9[1]). As an additional sensitivity analysis to verify that this summation did not bias our inference, we replicated some RRS analyses on parr and smolt progeny separately and found that we would have drawn similar conclusions had we not combined them (Supp. Material – Section 6).

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[1] Supplementary material are available with the article at 10.1139/cjfas-2022-0114

The summed juvenile and adult progeny per spawner assignment data were then analyzed to address four questions that comprehensively evaluated origin-specific differences in RS when spawning naturally:

(1) *Relative Reproductive Success – Parent to Progeny*: Is expected RS a function of variables such as origin, sex, body size, arrival day, and year of spawning?

(2) *Relative Reproductive Success – Grand-Parent to Grand-Progeny:* Do any RS differences identified in question (1) carry through to later generations?

(3) *Relative Reproductive Success by Parental Cross Type:* Does expected RS vary depending on the origin of the spawners involved; e.g., does a spawning pair involving 1 or 2 NOR spawners have a different RS expectation than a spawning pair involving two HOR spawners?

(4) *Reproductive Success Comparison given Progeny Age:* To what extent does evaluation of RS based on juvenile progeny predict RS based on adult progeny?

To quantify statistical evidence for answers to these questions, we required a model to estimate the expected progeny production by spawners of specific characteristics, from which we could then build a ratio (with an accompanying confidence interval) to represent RRS between origins. Among various analytical options, several aspects of our data set required special care and ultimately dictated our analytical design. First, RS may be influenced by factors aside from, or in addition to, the origin of the spawner and we sought to both quantify the effects of sex, size, return timing and inter-annual variability, and to control for any potential confounding impact they may have on our estimates of RRS (Anderson et al. 2010; Williamson et al. 2010; Berntson et al. 2011; Schroder et al. 2012; Anderson et al. 2013; Evans et al. 2016; Janowitz-Koch et al.

2019). While spawn location (Hoffnagle et al. 2008; Williamson et al. 2010; Hughes and Murdoch 2017) and the incidence of pre-spawn mortality (Bowerman et al. 2018) have been identified as factors that may interact with origin to affect reproductive success, carcass recovery is quite low in Lookingglass Creek due to high predation (Crump et al. 2021), precluding the consideration of either for this dataset. Second, the data set contained many spawners with zero progeny assigned to them. This follows observations from several other naturally spawning anadromous salmonid populations (Seamons et al. 2004; Ford et al. 2006; Williamson et al. 2010; Hess et al. 2012; Janowitz-Koch et al. 2019). These individuals are hereafter referred to as "unsuccessful" spawners, whereas those with ≥1 progeny assigned are termed "successful" spawners (Supp. Material – Sections 1 & 2). The frequency of zero values would violate the assumptions of many statistical models, and thus required specific treatment (note, however, that the analyses for questions 3 and 4 used only successful spawners or spawning pairs which removed this feature of the data set). It is important to acknowledge, however, that the designation of "successful spawner" in this study and others (e.g., Hess et al. 2012; Janowitz-Koch et al. 2019; Koch et al. 2022) is a product of sampling and analytical design. Except in circumstances where sampling of potential spawners and progeny is essentially complete, progeny-per-spawner estimates are best treated as indices of RS rather than true RS. Third, there was high variability in progeny numbers among successful spawners (Supp. Material – Section 2) even for spawners with similar attributes such as brood year, sex, and origin. This indicated the data would likely be over-dispersed relative to count models that cannot accommodate this level of variability for low values of the expected count (e.g., the Poisson distribution). And fourth, we considered two life stages of progeny for characterizing the RS of a given spawner in a given brood year: (*a*) total juveniles detected migrating out of and (*b*) total adults returning to

Lookingglass Creek. We chose to replicate identical analyses for both response variables separately for all questions except question (4), which compared adult and juvenile progeny assigned to individual spawners.

Based on these considerations, we opted to use the generalized linear modeling (GLM) framework (Nelder and Wedderburn 1972) with outcomes assumed to follow a negative binomial distribution for each of our analyses. For analyses involving excessive zeros (i.e., those for questions 1 and 2), we employed a negative binomial hurdle model (described below; Zeileis et al. 2008). For analyses involving successful spawners only (i.e., those for questions 3 and 4), we removed the hurdle and employed standard negative binomial GLMs. Except for the analysis for question (4), we chose to use solely fixed effects for modeling heterogeneity in RS. For each progeny life stage, we performed an all subsets analysis of a global model where models were ranked by AIC corrected for small sample size (AIC_c) (Burnham and Anderson 2002) and selected the model with the fewest parameters that was within 2 AIC_c units of the lowest AIC_c model for inference; we considered only models that converged successfully in these selections. From this model, we then calculated the ratio (NOR:HOR) as a measure of RRS while controlling for spawner attributes like sex, size, and return day.

[C] Statistical Models – We used maximum likelihood methods to fit models to data in program R (R Core Team 2020) using the 'glmmTMB' package (Brooks et al. 2017) and checked the consistency of the data with the statistical assumptions of the model using the 'DHARMa' R package (Hartig 2020). The assumption checks indicated that the data conformed well with the assumptions of the top models for each analysis (Supp. Material – Section 4). We used parametric bootstrapping to quantify the uncertainty in quantities derived from model

coefficients, e.g., for ratios of two model-predicted RS values. The parametric bootstrap (implemented via R package 'lme4', Bates et al. 2015) involved simulating 1,000 data sets from the best model, refitting the model to each simulated data set, and summarizing the variability in the predicted quantity of interest across refitted models. We fitted all models to data from multiple brood years, and we used model selection to determine whether among-year variability in parameters (e.g., an origin × year interaction) was justified. The specific code and data files to reproduce all GLM analyses can be found in Staton (2022).

[D] Q1: Relative Reproductive Success – Parent to Progeny & Q2: Relative Reproductive Success – Grand-Parent to Grand-Progeny

[E] GLMs with Hurdle – The hurdle model is a GLM with two components: (*a*) the "conditional" model to describe counts that have a non-zero expected value and (*b*) the "zero" model to describe the probability that observations will be zero. Unlike the related class of zero-inflated count models, the hurdle model allows zero-valued outcomes to occur only from the zero model, and never from the conditional model (Zeileis et al. 2008). Thus, we chose the hurdle approach for addressing questions (1) and (2) because it enabled modeling covariate effects on outcomes of successful and unsuccessful spawners separately but within the same model (an advancement of prior RRS analyses of successful and total spawners). This approach allowed us to quantify three primary metrics of interest based on varying characteristics of each spawner (e.g., origin, size, etc.): (*a*) the expected number of progeny produced by successful spawners, (*b*) the expected probability that spawners will be successful and (*c*) the expected number of progeny produced by each spawner, which combines metrics (*a*) and (*b*).

We denote the observed number of progeny (juvenile or adult progeny analyzed separately) assigned to spawner i by y_i, where $i \in \{1,2,...,n\}$. Both the conditional and zero components of the hurdle model may be influenced by covariates in an attempt to explain among-spawner variability in y_i; we denote the design matrices for these models by $\mathbf{X}$ and $\mathbf{Z}$ (and row vectors for spawner i by $\mathbf{x}_i$ and $\mathbf{z}_i$), respectively, and note that some covariates may be shared by both models. Thus, the conditional model took the form:

$$\log(\mu_i) = \mathbf{x}_i^{\top}\boldsymbol{\beta}, \qquad (1)$$

where $\boldsymbol{\beta}$ is a vector of coefficients that quantify the additive effect of each covariate on $\log(\mu)$; multiplication of two bold terms (i.e., vectors or matrices) implies matrix multiplication. The zero component of the hurdle model predicts the expected probability that spawner i was unsuccessful (π_i):

$$\operatorname{logit}(\pi_i) = \mathbf{z}_i^{\top}\boldsymbol{\gamma}, \qquad (2)$$

where $\boldsymbol{\gamma}$ is a vector of coefficients (estimated in addition to the $\boldsymbol{\beta}$ vector) that quantify the additive effect of each covariate on $\operatorname{logit}(\pi)$.

The negative binomial distribution includes an additional parameter to capture extra-Poisson variability (ϕ). There are two expressions of the negative binomial distribution (Hardin and Hilbe 2007), and we used the (most common) version where the variance increases as a quadratic function of the expected count ($V(y_i) = \mu_i + \frac{\mu_i^2}{\phi}$); we denote the negative binomial probability mass function by $f(y_i;\mu_i,\phi)$. The expected number of progeny for spawner i ($\hat{y}_i$) was:

$$\hat{y}_i = (1-\pi_i)\sum_{m=1}^{M}\frac{f(m;\mu_i,\phi)}{1-f(0;\mu_i,\phi)}m, \qquad (3)$$

where M is some arbitrarily large number where the probability mass $f(M,\mu_i,\phi)$ is effectively zero (we used M=1000 in all calculations). The term $(1-\pi_i)$ in eq. (3) is the expected probability that spawner i was successful, and the remaining portion is the expected number of progeny for spawner i if it was definitely successful.

Candidate models were distinguished from one another by the inclusion or exclusion of particular variables in the $\mathbf{X}$ and $\mathbf{Z}$ design (i.e., covariate) matrices. The simplest (i.e., null) models we evaluated had only the intercept terms included in the $\boldsymbol{\beta}$ and $\boldsymbol{\gamma}$ coefficient vectors, which produced identical expected values for μ and π, respectively, for all spawners. Hence, this model assumed RS of NOR and HOR spawners was identical and that no other covariates influenced expected RS.

The conditional component of the global models for the question (1) analysis included a three-way interaction for sex × origin × year and two-way interactions for arrival day × origin and spawner size (length, mm) × origin. Arrival day was rescaled each year so day 0 corresponded to April 20 (the earliest date a spawner arrived across all years) prior to model fitting. The zero component of the global models for question (1) included only the three-way interaction for sex × origin × year and all associated main effects and two-way interactions. The purpose of the three-way interaction was to allow the most complex models we fitted to have unique expectations (for both μ and π) for spawners of each sex/origin in every year. We also explored including a quadratic term for arrival day (identified as significant in Koch et al. 2022), however, nearly all models with this term failed to converge so it was removed from consideration. The analysis for question (2) was nearly identical to that as for question (1), but the global conditional and zero models included only origin × year. We used the R package ‘MuMIn’ (Bartoń 2022) to carry out model selection tasks.

[D] Q3: Relative Reproductive Success by Parental Cross Type & Q4: Reproductive Success Comparison given Progeny Age

[E] GLMs without Hurdle – For analyses that only considered successful spawners (i.e., those for questions 3 and 4), the negative binomial GLMs we employed quantified variability in the expected progeny count for spawner $\boldsymbol{i}$ as explained by spawner-level attributes (i.e., covariates). That is, the GLM was made only of the conditional component of eq. (1) and did not include a separate model component to explain zero-valued $\boldsymbol{y_i}$.

Note that in the analysis for question (3), the individual observations were progeny produced by a specific pair of spawners, unlike all other analyses which treated progeny produced by individual spawners as the response variable. The only effects evaluated in the question (3) analysis were cross type (e.g., NOR male × NOR female – N × N; NOR male × HOR female – N × H; HOR male × NOR female – H × N; HOR male × HOR female – H × H), year of spawning, and their interaction. For such a pair of spawners to have been detected it must have been successful; we used GLMs with a zero-truncated negative binomial distribution to account for this fact that no observations were zero. The expected number of progeny (y_i) in this case was identical to that of eq. (3), except with the term $(1-\pi_i)$ removed (or, equivalently, with $\pi_i = 0$).

[E] Mixed-Effects Model – To evaluate if there was a relationship between juvenile ($y_{i,\text{juvenile}}$) and adult production ($y_{i,\text{adult}}$) by any given spawner (regardless of sex, origin, size, etc.) in any given year (question 4) we used a negative binomial generalized linear mixed-effects model, where the slope and intercept terms included random effects for year of spawning. Thus, the

expected number of adult progeny produced by spawner i ($\hat{y}_{i,\text{adult}} = \mu_{i,\text{adult}}$ due to no zero-truncation) was:

$$\begin{aligned} \log(\mu_{i,\text{adult}}) = (\beta_0 + \varepsilon_{0,j(i)}) + (\beta_1 + \varepsilon_{1,j(i)})y_{i,\text{juvenile}} \\ \varepsilon_{0,j} \sim \mathcal{N}(0,\sigma_0^2) \\ \varepsilon_{1,j} \sim \mathcal{N}(0,\sigma_1^2) \end{aligned} \qquad (4)$$

where β_0 and β_1 are the fixed-effect intercept and slope terms and $\varepsilon_{0,j(i)}$ and $\varepsilon_{1,j(i)}$ are year-specific (j) random effects with variances σ_0^2 and σ_1^2, respectively (the notation $j(i)$ denotes the year j in which spawner i returned). All spawners that were unsuccessful according to juvenile production (i.e., $y_{i,\text{juvenile}} = 0$) were discarded prior to analysis and the resulting model showed no evidence of zero-inflation.

[A]*Results*

[B]*Parentage analyses* – After removing individuals with duplicate genotypes or which failed to genotype at nine or more loci (7.0% of analyzed samples), we estimated the assignment rate for each progeny collection, where the collection was defined by collection year and life stage. For adults sampled between 2012-2020, and which were interrogated as progeny, an average of 65.6% of individuals were successfully assigned at least one parent from brood years 2008-2016. For juveniles (smolt + parr) sampled from 2009-2018, and which were interrogated as progeny, an average of 83.6% of individuals were successfully assigned to at least one parent from brood years 2008-2016. These observed differences in assignment rates by progeny life stage are associated with spatial distribution patterns of spawning adults in Lookingglass Creek, such that adult progeny were more likely to have been the descendants of fish that spawned below the weir, which were not included in the analysis (Crump et al. 2021). Parent-offspring trios identified by SNPPIT (Anderson 2012) had an average FDR of 0.00075, and trios or single-parent offspring pairs identified by COLONY (Jones and Wang 2010) had an average assignment probability of 0.99.

These assignments were then summarized to reflect raw, brood year specific, reproductive success (RS) estimates for naturally spawning natural-origin (NOR) and hatchery-origin (HOR) adults. Across brood years 2008-2016, a total of 41.8% of HOR spawners and 53.8% of NOR spawners were assigned at least one juvenile progeny, while 23.0% of HOR spawners and 21.8% of NOR spawners were assigned at least one adult progeny (Supp. Material – Section 1). For grand-progeny, across brood years 2008-2012, a total of 19.6% of HOR spawners and 28.7% of NOR spawners were attributed at least one juvenile grand-progeny, while 6.5% of HOR spawners and 12.0% of NOR spawners were attributed at least one adult grand-progeny (Supp. Material – Section 1).

[B]*Relative Reproductive Success analyses*

[C] *Q1: Relative Reproductive Success – Parent to Progeny*

[D] *Model Selection Results* – For juvenile progeny, the best model included the terms *day + length + origin + sex + year* in the conditional model and the terms *origin + year* in the zero model (Table 1). There was considerable model uncertainty, evidenced by 14 models with $\Delta\mathrm{AIC}_c$ values less than 2, however all of these top models included main effects for day, length, origin, and year in the conditional model – differences in the 14 models came in the form of the complexity of the zero model or whether interactions by origin or by year were included in the conditional model. All of these models included effects for origin and year for the zero model as well, but only one included the interaction between origin and year.

For adult progeny, the best model included the terms *sex + year + sex:year* in the conditional model and the terms *origin + year* in the zero model (Table 1). There was less model uncertainty for total adult progeny than for total juvenile progeny, with only 6 models with Δ AIC_c values less than 2. None of the top models included an origin effect in the conditional model, but all included effects for sex, year, and their interaction. Conversely, the zero component of all top models included origin and year effects.

[D] *Reproductive Success Patterns* – Expected juvenile progeny per female spawner varied widely among years: female NOR spawners produced from 2.05 to 8.42 (mean: 3.40) and HOR spawners produced from 1.19 to 7.19 (mean: 2.36) (Figure 3c). The high inter-annual variability was attributed to both the number of progeny produced by successful spawners (Figure 3a) and the probability of being successful (Figure 3b). Successful males were estimated to produce 1.12 (95% CI: 0.99 – 1.26) times as many juvenile progeny as successful females and model selection concluded that there was insufficient evidence to suggest that this varied among years or origin types (Supp. Material, Figure S2a,b). The two continuous covariates we assessed (arrival day and spawner length) were retained in the top conditional model for juvenile progeny (although neither included an interaction with origin type) and were estimated to have opposite effects. Successful spawners were estimated to have 1.19 (95% CI: 1.12 – 1.27) times as many juvenile progeny for every 1 standard deviation (~50 mm) increase in length (Supp. Material, Figure S3) and 0.994 (95% CI: 0.991 – 0.997) times as many juvenile progeny for every one day increase in their arrival day (Supp. Material, Figure S4).

Adult progeny produced per female spawner also varied widely among years, but unlike for juvenile progeny, it showed a marked decreasing trend over the years evaluated in this study (Figure 3f). This trend was attributed somewhat to progeny per successful spawner (Figure 3d) but primarily to the probability of being successful (Figure 3e); this finding was true of both NOR and HOR spawners and the patterns were estimated to be similar for male spawners (Supp. Material, Figure S2b). The top model for adult progeny included a sex × year interaction (but not by origin) in the conditional model (Table 1). Male successful spawners were estimated to have produced fewer adult progeny than female successful spawners in only two years: 2009 (0.61 times as many; 95% CI: 0.46 – 0.81) and 2013 (0.95 times as many; 95% CI: 0.64 – 1.36). The average effect of all other years suggested that successful males produced 1.18 times as many adult progeny as successful females, which ranged from 1.06 (in 2014; 95% CI: 0.90 – 1.25) to 1.35 (in 2012; 95% CI: 1.16 – 1.58).

[D] *Relative Reproductive Success* – All else equal (e.g., arrival day and spawner size), successful NOR spawners were estimated to have 1.34 (95% CI: 1.17 – 1.53) times as many juvenile progeny as were successful HOR spawners. Additionally, NOR spawners were estimated to be 1.63 (95% CI: 1.4 – 1.92) times as likely to be successful at producing juvenile progeny as were HOR spawners. Similar patterns (i.e., relative reproductive success (RRS) ratios generally > 1.0) were found when inter-annual variability in arrival day and spawner size by sex, origin, and year were accounted for (Figure 4a,b,c). In particular, we interpret the highly consistent RRS ratios > 1.0, alongside 95% confidence intervals that did not overlap the 1.0 dashed line (Figures 4a,b,c), as evidence that NOR spawners exhibited greater RS than their HOR counterparts when evaluating by juvenile progeny.

Unlike for juvenile progeny, the top model for adult progeny did not include an origin effect in the conditional model component (Table 1), which resulted in equal expected RS estimates among HOR and NOR successful spawners and a RRS ratio equal to 1.0 (seen in Figure 4d). However, the top model did include an origin effect in the zero model such that NOR spawners were 1.29 (95% CI: 1.03 – 1.58) times as likely to be successful at producing adult progeny than HOR spawners (Figure 4e) – as a result, NOR spawners were estimated to have overall higher RS when considering adult progeny (Figure 4f).

[C] *Q2: Relative Reproductive Success – Grand-Parent to Grand-Progeny*

[D] *Model Selection Results* – For juvenile grand-progeny, the best model included the intercept only in the conditional model and the terms *origin* + *year* in the zero model (Table 2). The best model for adult grand-progeny included only the *year* term in the conditional but both *year* and *origin* effects in the zero model (Table 2).

[D] *Relative Reproductive Success* – Similar to the results from the RRS analyses of question (1), we found that RS when considering juvenile grand-progeny was, on average, higher (by a factor of 1.39; 95% CI: 1.11 – 1.69) for NOR spawners than for HOR spawners. The best model did not include a year × origin interaction which indicates this ratio was relatively constant over the five brood years (2008 – 2012) included in this analysis. In contrast to the RRS analyses of question (1), spawners that were successful at producing juvenile grand-progeny were estimated to produce equal numbers of juvenile grand-progeny among origin types, so the difference in overall RS was explained by a difference in the frequency of success: NOR spawners were estimated to be 1.57 (95% CI: 1.16 – 2.08) times as likely to be successful at producing juvenile grand-progeny than were HOR spawners. We found similar inferences for spawners producing adult grand-progeny: successful spawners produced equal numbers on average, but NOR spawners were 1.64 (95% CI: 1.05 – 2.46) times as likely to be successful than HOR spawners, leading to an estimated RRS ratio (NOR:HOR) of 1.52 (95% CI: 1.04 – 2.15) when considering all spawners.

[C] *Q3: Relative Reproductive Success by Parental Cross Type*

[D] *Model Selection Results* – The top model for both juvenile and adult progeny suggested that the expected progeny production from a spawning pair varied depending on the origins of the spawners involved (e.g., N × N vs. N × H vs. H × N vs. H × H) and by year, but neither included an interaction between spawning pair type and year. Because a spawning pair could only be detected if it had at least one offspring, the models for this analysis were zero-truncated negative binomial GLMs as there was no model component to explain the presence of zeros.

[D] *Relative Reproductive Success* – Since the year interaction was not included in the top model, RRS ratios were estimated to be identical for all brood years. In calculating the RRS ratio among pair types, we treated H × H as the reference (i.e., denominator). N × N spawn pairs produced, on average, 1.25 (95% CI: 1.04 – 1.54) times as many juvenile progeny as did H × H pairs. In contrast, RRS ratio confidence intervals for H × N and N × H spawn pairs encompassed 1.0, suggesting spawning pairs involving only one natural-origin parent produce comparable numbers of juvenile progeny as spawn pairs involving two hatchery-origin parents (Figure 5). Relative reproductive success ratios when considering adult progeny were near 1.0 for all pair types and all confidence intervals encompassed 1.0 (Figure 5), suggesting no substantial difference in RS between crosses involving 1 or 2 NOR parent(s) and crosses with two HOR parents.

[C] *Q4: Reproductive Success Comparison given Progeny Age*

In any given year, successful spawners were expected to have 1.05 (95% CI: 1.02 – 1.07) times as many adult progeny assigned for every one additional juvenile progeny assigned to them, although there was much inter-spawner variability even within a year (Figure 6). The mixed-effects model quantified variability in this value across brood years, and we found that it varied moderately over the 9 study years (range of year-specific values: 1.01 – 1.08). This finding is seen graphically in Figure 6: some years showed a noticeable increasing trend (e.g., 2008, 2010, 2011), whereas in other years the relationship appeared nearly flat (e.g., 2009, 2013, 2015).

[A] *Discussion*

[B] *Progression of Naturalization* – Our estimates of relative reproductive success (RRS) largely suggest a reproductive advantage for natural-origin (NOR) adults, which were derived from the reintroduced hatchery stock, relative to hatchery-origin (HOR) adults when spawning naturally in Lookingglass Creek. This advantage was most evident in the RRS estimates when considering juvenile progeny across one generation (parent to progeny; Figures 4a,b,c). Successful NOR spawners of both sexes consistently produced more juvenile progeny across brood years (with the exception of female spawners in 2009; Figure 4a) and were more likely to be reproductively successful across all brood years (Figures 4b). When considering adult progeny, NOR spawners of both sexes were more likely to be reproductively successful (Figure 4e); however, when comparing successful spawners only, the reproductive success (RS) of HOR spawners was comparable to that of NOR spawners (RRS = 1.0; Figure 4d). The synthesis of these model outputs ultimately predicted more progeny per NOR adult spawner of both sexes across all brood years when considering both juvenile and adult progeny (Figures 4c and 4f, respectively).

This apparent RS advantage becomes slightly less pronounced when estimates are made across two generations (i.e., grand-parent to grand-progeny). For example, successful HOR spawners were attributed similar numbers of juvenile and adult grand-progeny as successful NOR spawners. However, NOR adults did demonstrate a higher likelihood of successfully producing both juvenile and adult grand-progeny and thus had a higher overall average RS than HOR adults across all five brood years. While we were still able to detect patterns in RS by parental origin when considering grand-progeny, the low variation across brood years and seemingly imperceptible effect of sex – both of which were identified as significant in the juvenile and adult progeny models – may be due to reduced counts of assigned grand-progeny relative to the number of assigned F1 progeny. We identified grand-progeny (F2 generation) by tracing through the F1 generation to the grand-parents (F0 generation), which essentially required the F1 generation was thoroughly sampled, that the F1 progeny survived to maturity and were allowed to spawn naturally rather than being taken for broodstock, and that progeny assignments to the F1 generation met probability thresholds. While adult sampling is comprehensive in this study system (weir efficiency avg. 99.2%), this feature of the analytical approach, alongside accumulation of mortality risks to adulthood across multiple generations, necessarily reduces the number of F2 grand-progeny that can be analyzed (see Supp. Material Table S1e & S1f). The lower counts of identified F2 grand-progeny (i.e., the response variable) likely reduced our analytical resolution for disentangling contributing factors (i.e., sex or interannual variability) when performing estimations across two generations.

Consistent with our observation that individual NOR spawners demonstrate higher estimates of RS when considering both juvenile progeny (Figure 4c) and juvenile grand-progeny, parental crosses involving two, naturally spawning NOR parents (NxN) produce more juvenile progeny than crosses involving two HOR parents (Figure 5). However, the RS of the crosses involving one NOR parent (either HxN or NxH) were not detectably different from that estimated for HxH crosses. Similarly, when considering adult progeny, the estimated RS values for parental crosses involving 1 or 2 NOR parents (i.e., NxN or HxN or NxH) were not detectably different than that estimated for HxH crosses (Figure 5). This result reflects model outcomes when considering adult progeny of individual spawners as this cross type analysis could only consider successful spawners, for which origin was not an important factor in explaining RS (conditional model component, Table 1; Figure 4d).

Taken together, our results support the presumption that natural selective forces can diminish deleterious fitness effects associated with hatchery rearing, ultimately facilitating adaptation as reflected by improved fitness over generations of fish derived from a hatchery stock and reintroduced to a novel natural environment. In Lookingglass Creek, it appears that adaptation occurred and fitness improved relatively quickly. The NOR progeny from the first Catherine Creek stock HOR adults reintroduced into upper Lookingglass Creek largely returned in 2008. Thus, we know the NOR spawners in 2008 were only one generation removed from the hatchery, and yet we observed a consistent RS advantage among NOR fish as early as 2008 across progeny types (Figure 4). We may therefore expect the RS of NOR adults spawning amongst themselves to increasingly track upwards through time. However, many of the impediments to survival that contributed to the original extirpation of the native Lookingglass Creek spring Chinook salmon stock remain, as illustrated by the high variability in return rate (Figure 2). This necessitates the continued supplementation of the spawning population with HOR adults each year (Figure 2), which invariably spawn with NOR fish, and thereby reduce the likelihood of developing a lineage composed solely of NOR x NOR crosses. Nonetheless, the consistent RS advantage observed for NOR spawners, and the fact that this was observed in the first generation of NOR adult returns, indicates fish derived from a hatchery stock can respond to natural selective pressures fairly rapidly and naturalize to a novel natural environment.

[B] *Inferring productivity from juvenile versus adult progeny* – Obtaining adult-to-adult parentage assignment data for a reintroduction program, from which it is possible to accurately compare RS by origin, requires thorough, moderate to long-term monitoring to maximize the sample size of potential adult spawners and their returning adult progeny. These circumstances require operation of a highly efficient trap (capture rate approaching 100% of returning adults) over several consecutive years to accommodate for variability in annual escapement. However, even in systems with such sampling infrastructure, achieving sample sizes that permit reliable inference is increasingly difficult as many Columbia River Basin salmon populations continue to decline from historical levels, and annual return rates are highly variable (McClure et al. 2003; CBP 2020).

In contrast, out-migrating juveniles captured before subjection to various downstream migration stressors are many times more numerous than returning adults, and sampling infrastructure for juveniles (e.g., rotary screw traps) exists in many systems. Reproductive success estimates based on juvenile-to-adult assignments may therefore be logistically preferable for many salmonid programs throughout the Basin, and this approach has been utilized in several studies seeking to evaluate fitness (reviewed in Koch and Narum 2021). However, very few studies have included both adult-to-juvenile and adult-to-adult RS estimates within the same system (Kostow et al. 2003; Ford et al. 2006; Berntson et al. 2011; Ford et al. 2012), and none to our knowledge have directly compared the number of adult and juvenile progeny produced per individual spawner. This Lookingglass Creek dataset provided an opportunity to perform such individual-level comparisons and to more directly assess the validity of extending RS estimates given juvenile progeny to later life stages. While we did identify some relationship between adult and juvenile progeny assigned, specifically the average spawner in the average year was assigned 1.05 times as many adult progeny for every juvenile progeny assigned, this relationship was not consistent across brood years (Figure 6). Additionally, in some years the expected patterns did not hold, e.g., spawners in BY2012 with the highest number of adult progeny had some of the lowest numbers of juvenile progeny. Despite the lack of a strong and consistent relationship, the qualitative inference gained from adult-to-juvenile and adult-to-adult RS estimates was identical – NOR spawners experience higher RS than their HOR counterparts when spawning naturally (Figure 4).

The generalized linear model analyses based on adult-to-juvenile assignments also identified two covariates – return day and fork length – that were important in predicting RS, and which were not identified when considering adult-to-adult assignments (Table 1). Return day and fork length have been commonly identified as significant variables in predicting RS, with the positive relationship between fork length and RS being particularly well-documented (see Supp. Material, Figure S3a,b; Anderson et al. 2010; Williamson et al. 2010; Berntson et al. 2011; Schroder et al. 2012; Anderson et al. 2013; Evans et al. 2016; Janowitz-Koch et al. 2019; Koch et al. 2022). While we did not identify a significant difference in the average length of NOR and HOR adult spawners when combined across all study years (sexes analyzed separately), we did identify a significant difference in the average day of return, with HOR adults of both sexes returning three days later on average (data not shown). A propensity to return later may have contributed to the lower observed RS of HOR spawners, as model outputs based on juvenile progeny generally demonstrated a negative correlation between return day and RS – a trend that has been observed in other systems (Supp. Material S4a,b; Dickerson et al. 2005; Anderson et al. 2013; Janowitz-Koch et al. 2019). Thus, estimation of RS based on juvenile progeny provided more insight regarding metrics that may interact with origin to affect individual RS, which was likely due to the higher counts of juvenile progeny and resulting finer-scale resolution in RS outcomes to identify interacting effects. Therefore, while assessing RS by adult progeny obviously provides the most direct insight into spawner characteristics that produce progeny best equipped to survive system-specific stressors through a full life cycle, assessments by juvenile progeny can provide valid inference, especially when adequate sampling of adults is constrained.

[B] *Conclusions and Management Implications* – Ultimately, our analyses of RS across two generations, and based on both adult and juvenile progeny, indicated increased fitness among NOR adults relative to HOR adults when spawning naturally. These NOR fish were derived from an in-basin, captive broodstock hatchery program (Catherine Creek stock), which was used to initiate the reintroduction of spring Chinook salmon to the upper basin of Lookingglass Creek in 2001. This supports our initial hypothesis that natural selective forces can counteract maladaptive traits associated with hatchery rearing and suggests reliance on hatchery stocks to reintroduce extirpated salmon populations, as well as to supplement depressed extant populations, can be an impactful mechanism for achieving recovery. Of course, the magnitude of annual HOR stocking relative to NOR escapement, and the management strategies employed at the donor hatchery (e.g., the level of integration of NOR fish in the broodstock, juvenile rearing, acclimation and release protocols, etc.; Naish et al. 2007) are factors that will influence adaptive capacity, and the amount of time before naturalization becomes evident. In Lookingglass Creek, managers implement an integrated broodstock model, with up to 30% of the broodstock being NOR fish each year. Such integration reduces accumulation of domestication effects across successive generations, and likely contributes to the positive RS outcomes observed here, as well as those documented in other systems supplemented by integrated hatchery programs (Araki et al. 2007b; Hess et al. 2012; Ford et al. 2016; Janowitz-Koch et al. 2019).

As anthropogenic modifications and climate change interact to amplify mortality risks moving forward, hatchery programs that adaptively manage and implement informed strategies may provide important demographic buffers. In Lookingglass Creek, the downward trend in adult-to-adult RS since BY2011 (Figure 3f), while juvenile-to-adult RS demonstrated no obvious trend (Figure 3c) suggest these mortality risks are particularly pronounced post-emigration from the natal stream. In fact, downstream survival of emigrants from Lookingglass Creek to Lower Granite Dam has been trending downward through time, with summer and fall emigrants demonstrating the lowest survival estimates (Crump et al. 2021). These elevated stressors and reduced juvenile survival have undoubtedly contributed to the declining escapement to

Lookingglass Creek in recent years (Figure 2), mirroring population abundance trends observed throughout the Columbia River Basin (McClure et al. 2003; Gustafson et al. 2007), as well as those that have been predicted under future climate scenarios (Crozier et al. 2021). These trends highlight the importance of holistic habitat restoration actions that address all components of the salmonid life cycle, but which are unfortunately quite challenging given the expense, the need for extensive collaboration and coordination among various stakeholders, and the difficulty of reconciling diverse socioeconomic objectives across the riverscape (Hand et al. 2018). Until such efforts are supported and enacted at necessary levels, well-managed reintroduction and supplementation hatchery programs can act as conservation tools. While this evaluation of the reintroduction of spring Chinook salmon to Lookingglass Creek is a single case study, these results – namely, the apparent and fairly rapid naturalization from a captive, hatchery stock – suggest fish sourced from hatchery stocks have the capacity to naturalize to a reintroduced system and may therefore contribute to long-term recovery goals.

[A] *Data availability*

The step-by-step guides for completing the parentage analyses are available at the following GitHub repository: https://github.com/hnuetzel/Lookingglass-Creek-spring-Chinook-RRS. The code for performing the generalized linear model analyses is available at the following: https://doi.org/10.5281/zenodo.6621724. If you wish to use the dataset detailed in this manuscript to execute the scripts in the aforementioned repositories, please contact the following individuals: Hayley Nuetzel at hnuetzel@critfc.org, Gene Shippentower at geneshippentower@ctuir.org, Carrie Crump at carriecrump@ctuir.org and Leslie Naylor at lesnaylor@ctuir.org.

[A] *Competing interests*

The authors declare there are no competing interests.

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Table 1. All hurdle models ranked by AIC_c that fell within 2 AIC_c units of the lowest AIC_c model for each progeny type. The models selected for inference (i.e., fewest parameters with <2 ΔAIC_c units, K) for each progeny type are highlighted in bold. The linear predictors for the two hurdle model components are shown: the conditional model captures variability in the expected count for successful spawners (i.e., assigned progeny > 0) and the zero model captures variability in the expected probability that a spawner will be unsuccessful (i.e., assigned progeny = 0). The notation var1:var2 indicates a two-way interaction, i.e., where the effect of var1 depends on the value of var2. Model weights were rescaled to sum to 1 within each progeny type for presentation.

Progeny Type	Hurdle Model Component		AIC$_c$ Output		
	Conditional	**Zero**	**K**	**ΔAIC$_c$**	**Weight**
Juvenile	day + length + origin + sex + year	origin + sex + year + sex:year	33	0.00	0.13
	day + length + origin + sex + year + length:origin	origin + sex + year + sex:year	34	0.68	0.10
	day + length + origin + sex + year + sex:year	origin + sex + year + sex:year	41	0.78	0.09
	day + length + origin + year	origin + sex + year + sex:year	32	1.07	0.08
	day + length + origin + sex + year	**origin + year**	**24**	**1.23**	**0.07**
	day + length + origin + sex + year + length:origin + sex:year	origin + sex + year + sex:year	42	1.34	0.07
	day + length + origin + sex + year + day:origin	origin + sex + year + sex:year	34	1.36	0.07
	day + length + origin + sex + year	origin + sex + year + origin:year + sex:year	41	1.53	0.06
	day + length + origin + year + length:origin	origin + sex + year + sex:year	33	1.61	0.06
	day + length + origin + sex + year	origin + sex + year	25	1.71	0.06
	day + length + origin + sex + year + day:origin + length:origin	origin + sex + year + sex:year	35	1.76	0.06
	day + length + origin + sex + year + length:origin	origin + year	25	1.90	0.05
	day + length + origin + sex + year + sex:year	origin + year	32	1.94	0.05
	day + length + origin + sex + year	origin + sex + year + origin:sex + sex:year	34	1.98	0.05
Adult	length + sex + year + sex:year	origin + year	30	0.00	0.25
	sex + year + sex:year	**origin + year**	**29**	**0.50**	**0.20**
	day + length + sex + year + sex:year	origin + year	31	0.76	0.17
	day + sex + year + sex:year	origin + year	30	1.10	0.15
	length + sex + year + sex:year	origin + sex + year	31	1.34	0.13
	sex + year + sex:year	origin + sex + year	30	1.84	0.10

Table 2. All hurdle models ranked by AIC$_c$ that fell within 2 AIC$_c$ units of the lowest AIC$_c$ model for each grand-progeny type. The models selected for inference (i.e., fewest parameters with <2 ΔAIC$_c$ units, K) for each grand-progeny type are highlighted in bold. The linear predictors for the two hurdle model components are shown: the conditional model captures variability in the expected count for successful spawners (i.e., assigned grand-progeny > 0) and the zero model captures variability in the expected probability that a spawner will be unsuccessful (i.e., assigned grand-progeny = 0). The notation var1:var2 indicates a two-way interaction, i.e., where the effect of var1 depends on the value of var2. Model weights were rescaled to sum to 1 within each progeny type for presentation. "Intercept only" indicates no effects of any covariates were included, i.e., that the expected value was constant for all spawners.

Grand-Progeny Type	**Hurdle Model Component**		**AIC$_c$ Output**		
	Conditional	**Zero**	**K**	**ΔAIC$_c$**	**Weight**
Juvenile	**Intercept only**	**origin + year**	**8**	**0.00**	**0.62**
	origin	origin + year	9	0.99	0.38
Adult	**year**	**origin + year**	**11**	**0.00**	**0.50**
	origin + year + origin:year	origin + year	16	0.90	0.32
	origin + year	origin + year	12	1.99	0.18

Figure 1. Map of the Grande Ronde River basin in northeast Oregon, with the inset on the bottom right framing its location within the larger Columbia River Basin. The inset on the top left highlights Lookingglass Creek, the weir and the hatchery. The rotary screw trap is located 200m downstream of the weir, between the weir and hatchery. Data sourced from StreamNet (2012). Map projection: Lambert Conformal Conic, NAD 1983.

Figure 2. Spring Chinook salmon adult escapement above Lookingglass Creek weir from 2000 to 2020, the final year of sampling for this study. From 2000-2003, no adult fish returning to the Lookingglass Creek weir were permitted passage above the weir to remove any Rapid River ancestry fish from the upper reaches of Lookingglass Creek. The BY2000 Catherine Creek fish that had been outplanted to Lookingglass Creek in 2001 largely returned in 2004, and the first NOR offspring of these fish returned in 2007 as age-3 jacks, but predominately as age-4 adults in 2008. The return years that were interrogated as potential parents in this study are highlighted by the grey rectangle.

Figure 3. Expected reproductive success based on juvenile (panels a, b, and c) and adult (panels d, e, and f) progeny for the average female spawner of each origin type spawning in each brood year as quantified by the top negative binomial hurdle model for each progeny type. “Progeny per Spawner” (panels c and f) accounts for the number of progeny produced by successful spawners (panels a and d) and the probability of being successful at all (panels b and e). Expected values were obtained at the average value of the arrival day and length variables for each year by origin for juvenile progeny only (these variables were not in the top model for adult

progeny, Table 1). Error bars represent 95% confidence intervals obtained via parametric bootstrap.

Figure 4. Relative reproductive success based on juvenile (panels a, b, and c) and adult (panels d, e, and f) progeny for the average spawner by sex in each brood year according to three measures estimated by the top hurdle models. The ratio is expressed as NOR to HOR such that values greater than 1.0 indicate higher success for NOR spawners. Error bars represent 95% confidence intervals obtained via parametric bootstrap. Panel (d) demonstrates no difference in RRS between NOR and HOR spawners because origin was not an important factor in the conditional model for adult progeny (see Table 1), and no error bars are needed given that the ratio of expected counts is equal with no uncertainty. For panels (b) and (e), while we did identify year as a significant variable in the zero model for both juvenile and adult progeny (Table 1), it did not include an interaction with origin. This lack of interaction, in combination with the observation that the ratio of progeny produced by HOR and NOR spawners of each sex did not vary across years (see Figure 2b,e for females; Supp. Figure S2b for males), explains the equal RRS ratios across years and sexes.

Figure 5. Relative reproductive success ratios based on the juvenile and adult progeny produced by spawning pairs comprised of different origins. Spawning pair types are: N × N = NOR male and NOR female; H × N = HOR male and NOR female; N × H = NOR male and HOR female; H × H = HOR male and HOR female. Ratios are expressed with H × H in the denominator such that values greater than one indicate that pairs of the corresponding type (denoted by the bar color) had higher expected reproductive success than pairs of type H × H. All calculations

involved only successful spawning pairs, i.e., those pairs with at least one offspring assigned. Although ratios were calculated for each year, the top model did not include an interaction between pair type and year so the estimated ratios were identical for all years. Error bars represent 95% confidence intervals obtained via parametric bootstrap.

Figure 6. Brood year-specific relationships between the number of adult and juvenile progeny assigned to individual spawners. Fitted curves were obtained using a negative binomial generalized linear mixed effects model with random slopes and intercepts for each year. The shaded region represents the 95% confidence interval around the year-specific curve.

Figure 1.

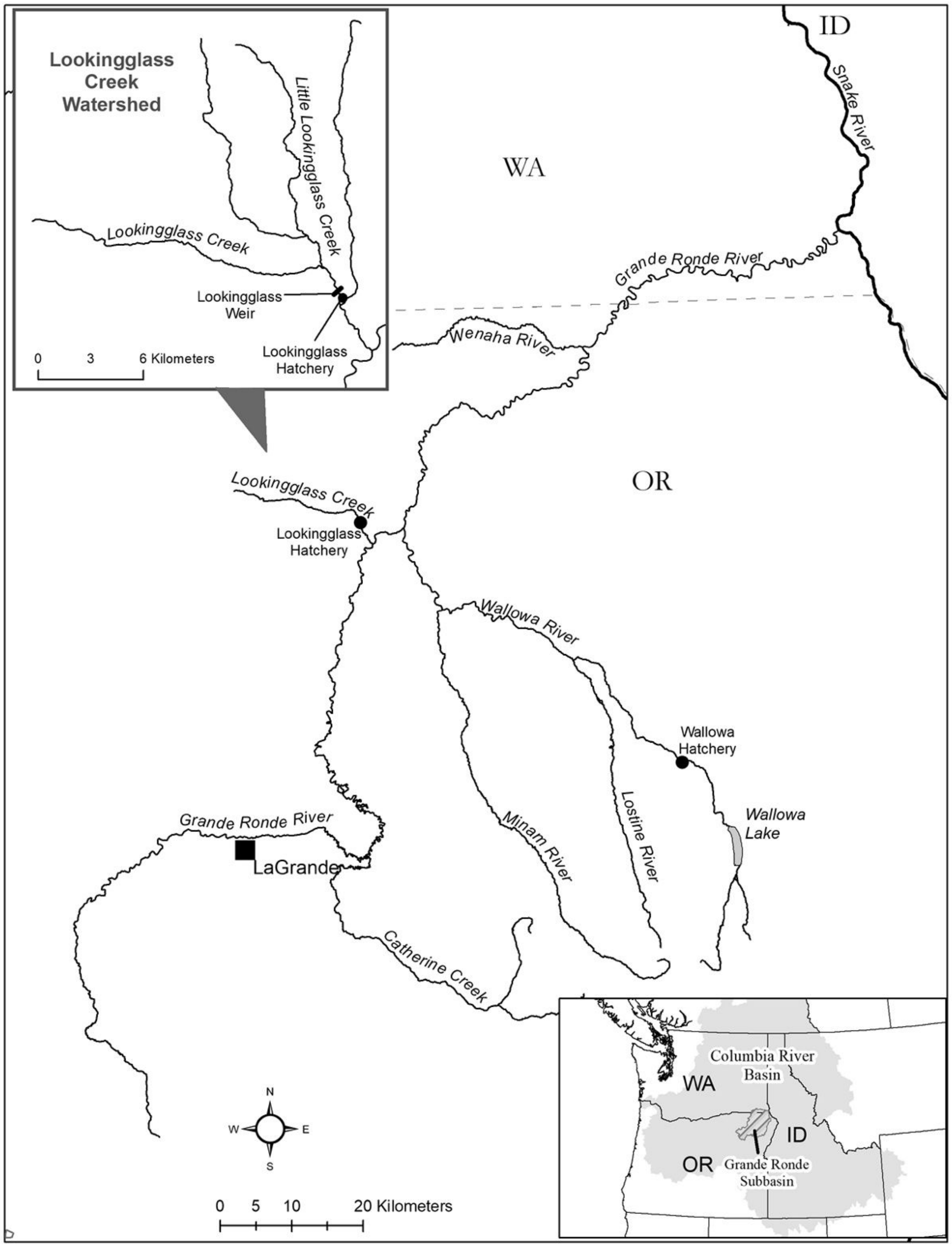

Lookingglass
Creek
Watershed
Little Lookingglass Creek
Lookingglass Creek
Lookingglass
Weir
Lookingglass
Hatchery
0 3 6 Kilometers
ID
Snake River
WA
Grande Ronde River
Wenaha River
OR
Lookingglass Creek
Lookingglass
Hatchery
Wallowa River
Wallowa
Hatchery
Wallowa
Lake
Lostine River
Minam River
Grande Ronde River
LaGrande
Catherine Creek
N
W
E
S
0 5 10 20 Kilometers
Columbia River
Basin
WA
ID
OR
Grande Ronde
Subbasin

Figure 2.

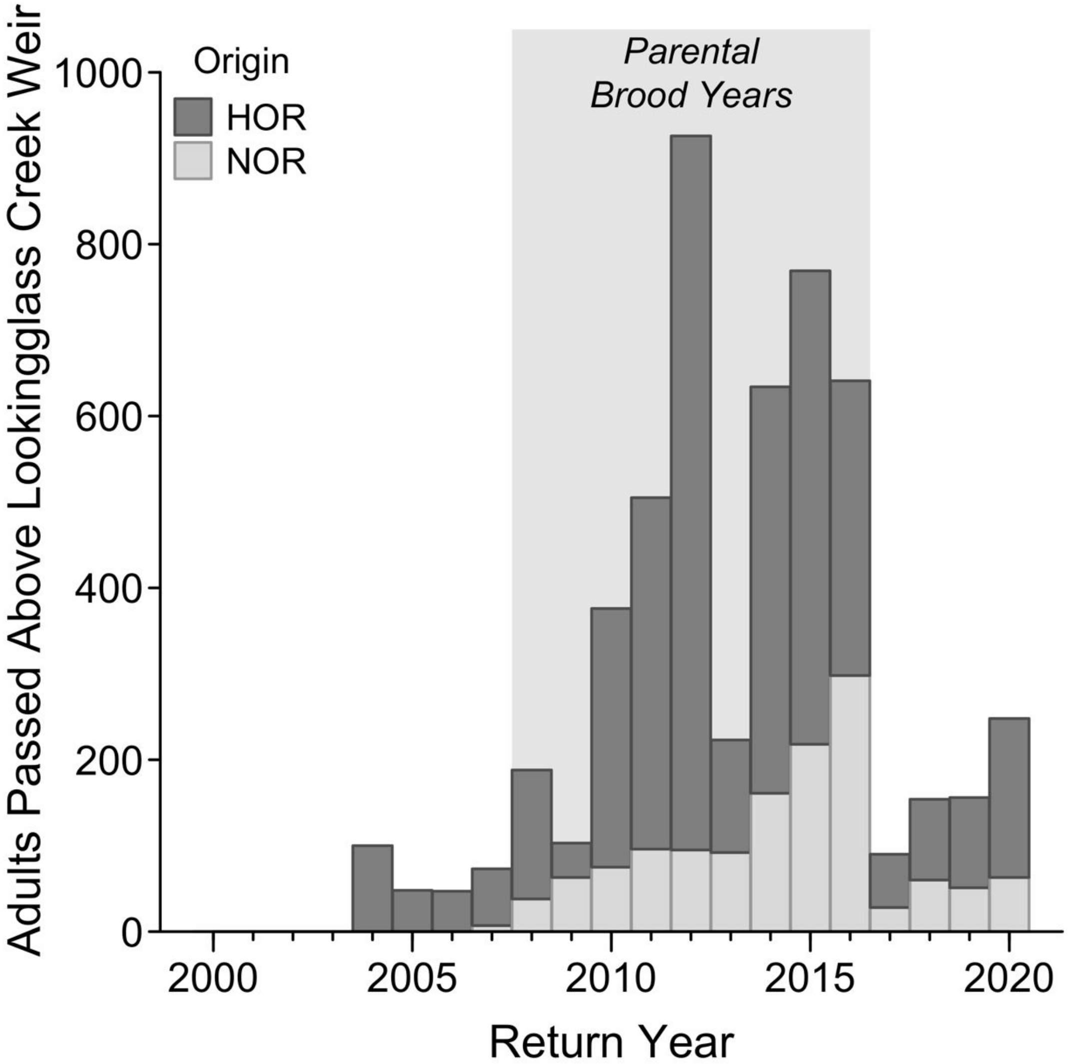

Parental
Brood Years
Origin
HOR
NOR
Adults Passed Above Lookingglass Creek Weir
1000
800
600
400
200
0
2000
2005
2010
2015
2020
Return Year

Figure 3.

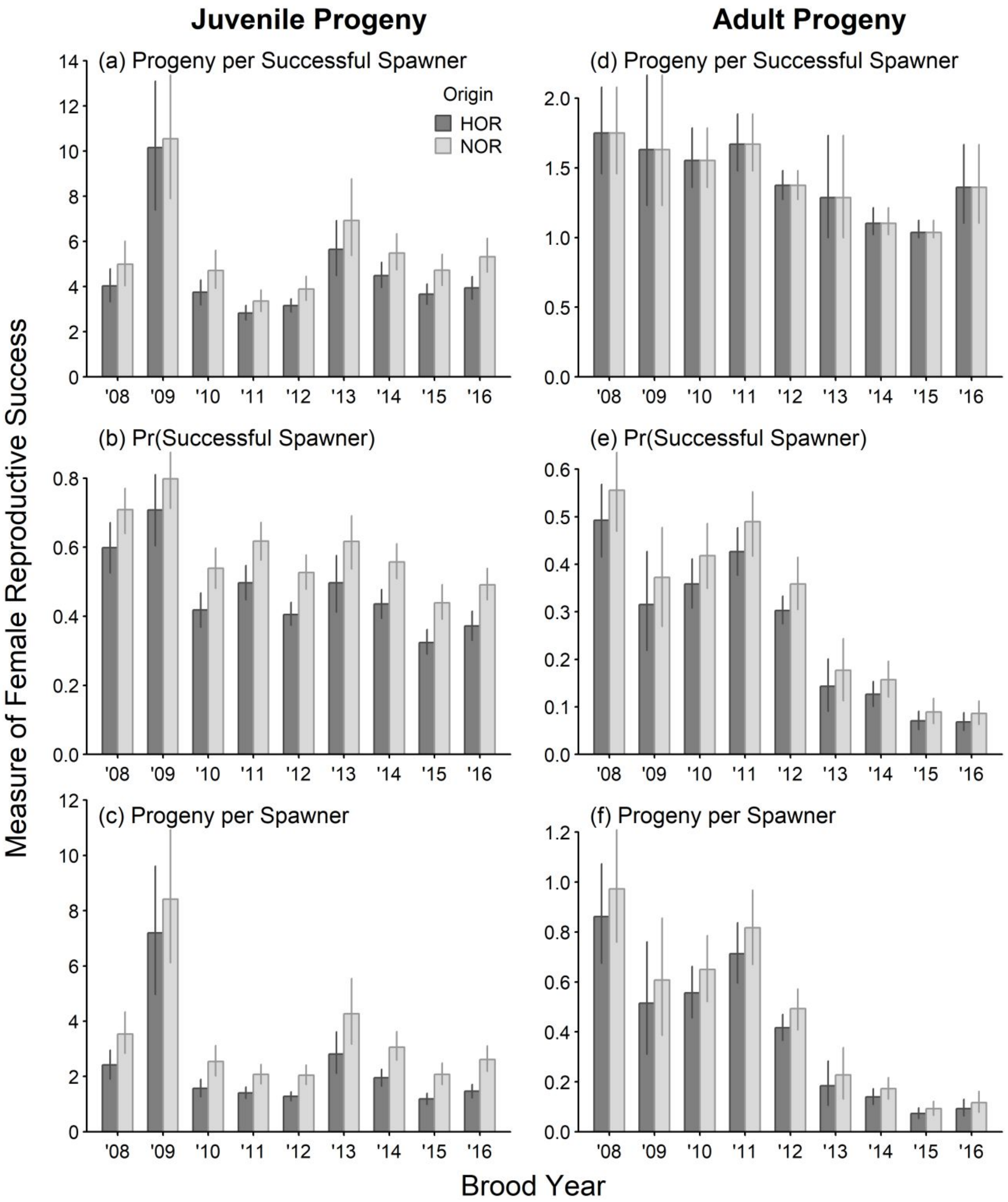

Juvenile Progeny
Adult Progeny
(a) Progeny per Successful Spawner
(b) Pr(Successful Spawner)
(c) Progeny per Spawner
(d) Progeny per Successful Spawner
(e) Pr(Successful Spawner)
(f) Progeny per Spawner
Origin
HOR
NOR
Measure of Female Reproductive Success
Brood Year
'08
'09
'10
'11
'12
'13
'14
'15
'16
0
2
4
6
8
10
12
14
0.0
0.2
0.4
0.6
0.8
0.5
1.0
1.5
2.0
0.1
0.3
0.5
0.6
1.2

Figure 4.

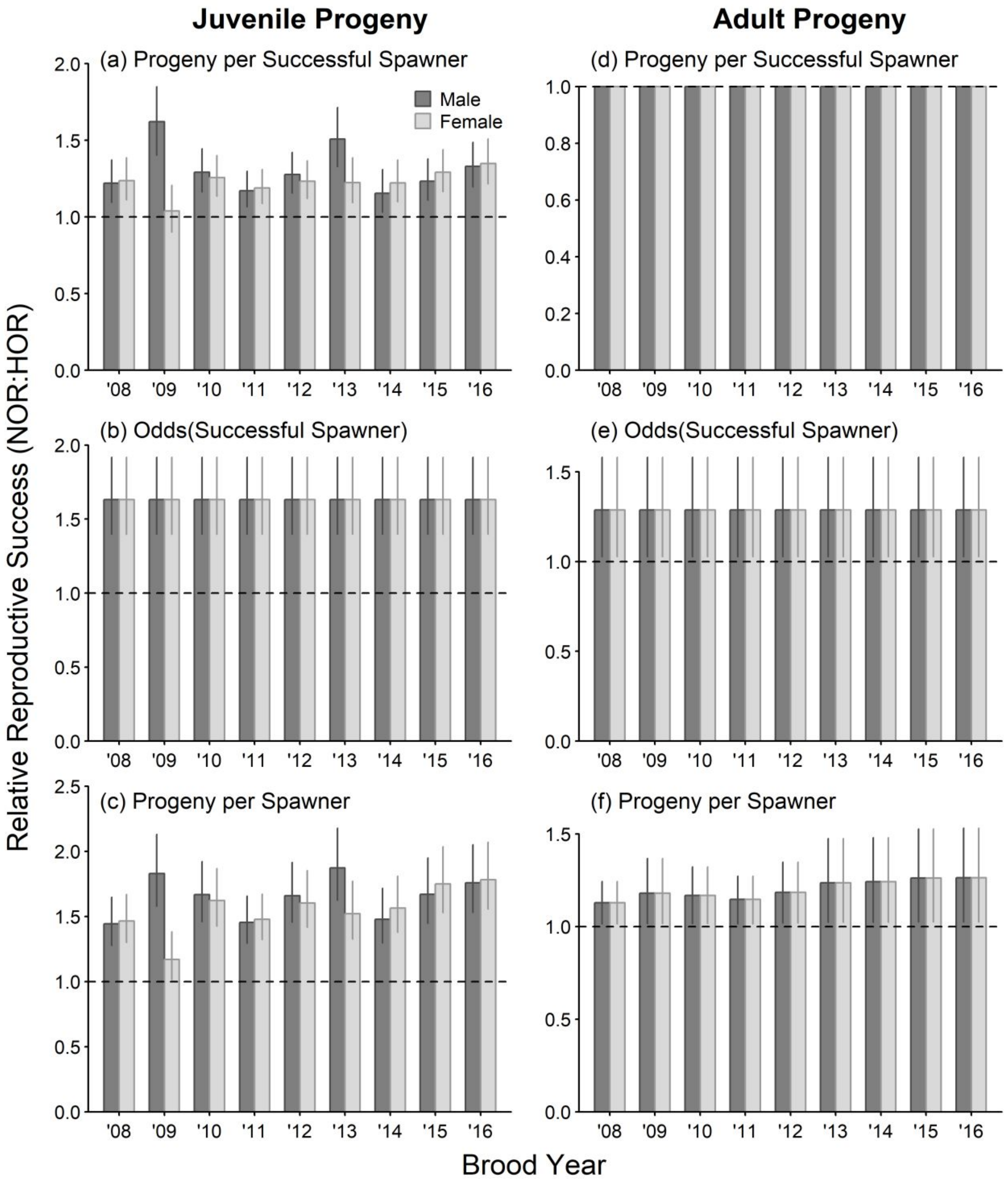
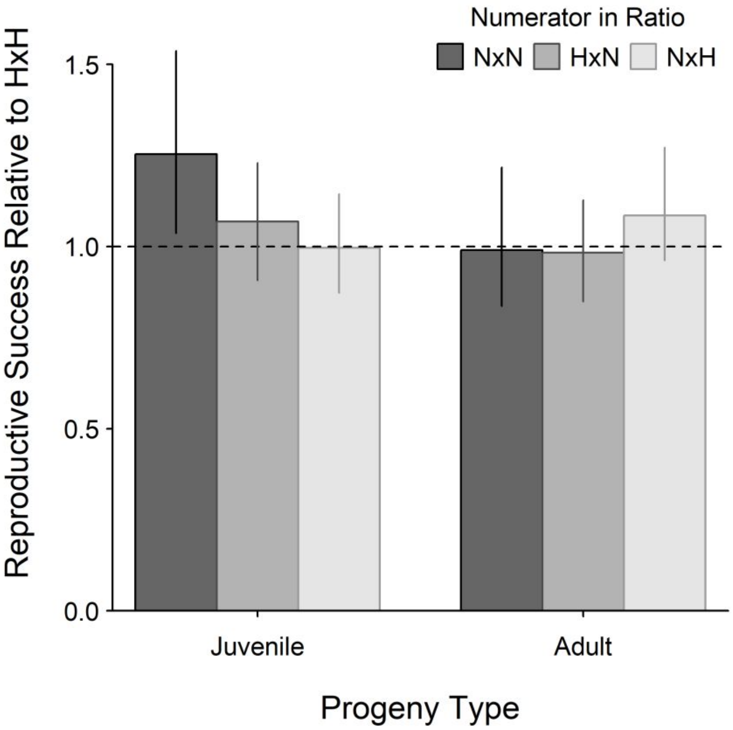
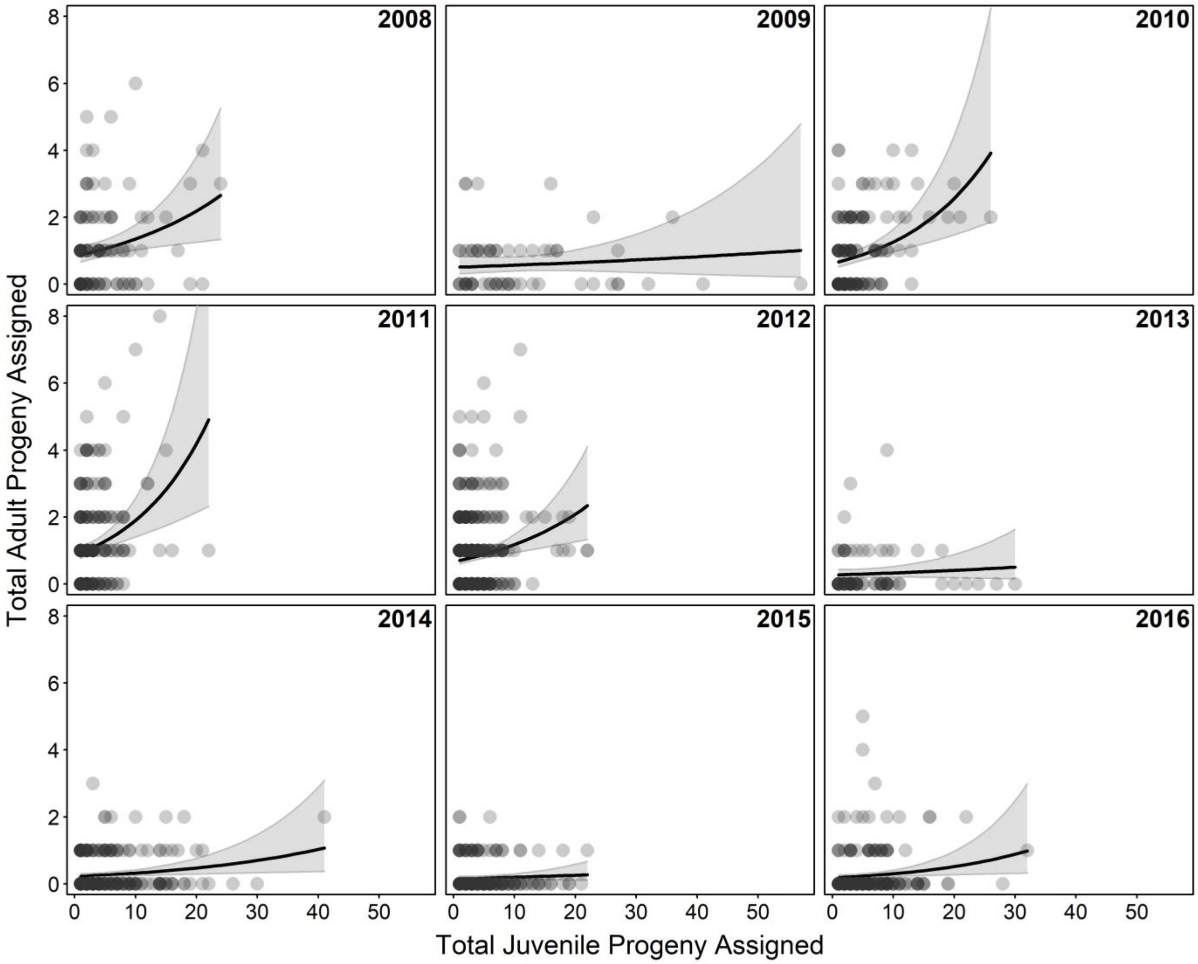

Juvenile Progeny
Adult Progeny
(a) Progeny per Successful Spawner
Male
Female
(d) Progeny per Successful Spawner
(b) Odds(Successful Spawner)
(e) Odds(Successful Spawner)
(c) Progeny per Spawner
(f) Progeny per Spawner
Relative Reproductive Success (NOR:HOR)
Brood Year
0.0
0.5
1.0
1.5
2.0
2.5
0.2
0.4
0.6
0.8
'08
'09
'10
'11
'12
'13
'14
'15
'16

Figure 5.


Numerator in Ratio
NxN
HxN
NxH
Reproductive Success Relative to HxH
1.5
1.0
0.5
0.0
Juvenile
Adult
Progeny Type

1193 **Figure 6.**

1194



1195