

Factors influencing spawner success in a spring Chinook salmon (*Oncorhynchus tshawytscha*)
reintroduction program

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1 **Abstract**

2 Dams have contributed to the decline of migratory fishes by blocking access to historical habitat.
3 The active transport (trap and haul) of migratory fish species above existing dams can sometimes
4 support population recovery when the use of fish ladders or dam removal is infeasible. However, little is
5 known about the efficacy of trap and haul conservation strategies. Here we used genetic parentage
6 assignments to evaluate the efficacy of reintroducing adult Chinook salmon above Cougar Dam on the
7 South Fork McKenzie River, Oregon, USA from 2008-2011. We found that mean reproductive success
8 (RS) declined as adults were released later in the spawning season in 2009 and 2010; however release
9 location did not affect RS. In 2010 and 2011, we tested for RS differences between hatchery and natural
10 origin (HOR and NOR) adults. HOR males were consistently less fit than NOR males, but little evidence
11 for fitness differences was apparent between HOR and NOR females. Interestingly, the effect of origin
12 on RS was not significant after accounting for variation explained by body length. Our results indicate
13 that release date and location have inconsistent or no effect on the reproductive success of
14 reintroduced adults when active transport strategies are employed for migratory fishes.

15
16 Key words: reintroduction, active transport, genetic parentage, reproductive success, hatchery and
17 natural origin

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21 **Introduction**

22 Reintroduction programs attempt to re-establish locally extirpated species to their historical
23 habitat (IUCN 2013) and can serve to restore a species' distribution when access to habitat has simply
24 been blocked. However, few reintroduction programs have been successful to date (Fischer and
25 Lindenmayer 2000; Wolf et al. 1996), and most research on reintroductions has focused on mammals
26 and birds (Seddon et al. 2005), rather than fish (but see George et al. 2009). There are many migratory
27 fish species (see Brönmark et al. 2014; Lucas et al. 2001) whose access to critical habitat has been
28 negatively affected by dams. Therefore, an understanding of factors that affect the success of fish
29 reintroductions is greatly needed.

30 Reintroduction efforts have become an increasingly common management strategy to aid in the
31 recovery of threatened salmonid populations, often through the decommissioning of dams or the
32 construction of fish ladders (reviewed by Pess et al. 2014). In Chinook salmon (*Oncorhynchus*
33 *tshawytscha*), reintroductions following dam removal or fish ladder construction have been evaluated
34 through studies of juvenile production and subsequent adult returns (Anderson et al. 2013; Baumsteiger
35 et al. 2008). However, habitat connectivity cannot always be restored through dam removal or fish
36 ladder construction, as with the case of high-head flood control dams (see example projects in Anderson
37 et al. 2014). In such scenarios, the collection and active transport of migratory salmonids provides an
38 alternative approach that has received little attention in the literature (but see Evans et al. *In Review*).

39 Spring Chinook salmon, in the upper Willamette River, Oregon, are listed as a threatened
40 Evolutionary Significant Unit (ESU) under the U.S. Endangered Species Act (ESA) (NMFS 1999; 2005;
41 2008). Dams impede migration to 32% of Chinook salmon historical habitat, and alter water
42 temperature and flow regimes (ODFW 2005; Sheer and Steel 2006). In addition, it has been estimated
43 that natural juvenile production has been reduced by up to 95% (ODFW and NMFS 2010) as a result of
44 dam construction and operation in most tributaries within the basin. In the mid-1990s, state and federal

45 fisheries managers began to trap Chinook salmon for transport and release into historical spawning and
46 rearing habitat above upper Willamette River dams to increase natural production and facilitate the
47 species' recovery. Because habitat quality (Groves and Chandler 1999; Kondolf and Wolman 1993) and
48 return timing (Anderson et al. 2013; Dickerson et al. 2002; Williamson et al. 2010) can influence salmon
49 reproductive success, it is important to determine whether release location and date affect the success
50 of reintroduction efforts.

51 Salmon often mature at various ages (Quinn 2011), including male mini-jacks and jacks that
52 mature prior to the youngest age class of sexually mature females (Heath et al. 1994). Because matings
53 by early maturing males can increase the effective size of a population (e.g. Araki et al. 2007; Perrier et
54 al. 2014), it may be beneficial to include jacks during reintroductions. Yet this topic has received scarce
55 attention in the literature.

56 Chinook salmon adults produced in hatcheries may also play an important role in reintroduction
57 programs involving threatened or endangered ESUs. Hatchery origin (HOR) Chinook salmon may be used
58 to found a wild-spawning population and quantify important viability parameters when little is known
59 about the demographic risks associated with a reintroduction (e.g. juvenile survivorship through a
60 reservoir and dam, effects from active transport stress, etc.). HOR fish may also be used to supplement
61 reintroduction programs that use natural origin (NOR) adults, particularly when cohorts return in low
62 numbers, which may help to sustain natural production at a desired level. Anderson et al. (2013)
63 described the reproductive success of HOR Chinook salmon naturally colonizing habitat above a dam
64 accessible following fish ladder construction, but the active transport of HOR salmon when founding and
65 supplementing a reintroduction has not been thoroughly evaluated.

66 By reintroducing both HOR and NOR adults, more may be learned about fitness differences that
67 often exist between hatchery and wild salmon. There is growing evidence that, on average, HOR salmon
68 are less fit in the wild than NOR salmon, and the effect is stronger among males (reviewed by Christie et

69 al. 2014). Differences between the size of eggs from HOR and NOR females may affect fitness (Heath et
70 al. 2003), and sperm competition may play a role as well (Flannery et al. 2013; Lehnert et al. 2012).
71 However, no study to date has clearly identified causal mechanisms for these fitness differences
72 (Christie et al. 2014), though Theriault et al. (2011) hypothesized that two general processes may be
73 relevant: sexual selection on the spawning grounds and/or natural selection early in the life cycle of
74 salmon (i.e. before smoltification). When adult salmon are actively released during a reintroduction
75 program, some phenotypic traits associated with greater fitness can be measured, which may be
76 important for either natural or sexual selection (Milot et al. 2013; Theriault et al. 2011). Thus, recording
77 phenotypic variation and evaluating the effects of that variation on fitness may provide insight into the
78 mechanisms resulting in HOR and NOR fitness differences.

79 In this study we measured the reproductive success of adult Chinook salmon reintroduced to
80 habitat above Cougar Dam, located on the South Fork McKenzie River, Oregon, USA. We used genetic
81 parentage methods to test for and estimate effects from factors associated with adult reintroductions
82 on their subsequent juvenile production (i.e. reproductive success). Our four main objectives were to 1)
83 test if release date and release location affected the reproductive success (RS) of reintroduced adults; 2)
84 describe RS for jacks among reintroduced cohorts; 3) test if mean RS differed between HOR and NOR
85 Chinook salmon reintroduced in 2010-2011 and; 4) test if adult fork length explained variation in RS.

86 **Methods**

87 *Study area*

88 Of all Upper Willamette River tributaries, the McKenzie River typically supports the highest
89 proportion of unmarked Chinook salmon returns (Johnson and Friesen 2010), despite the presence of
90 several dams, including the 158 meter tall Cougar Dam. Construction of Cougar Dam was completed in
91 1964, blocking access to 40 kilometers of Chinook salmon spawning habitat (Figure 1). Following

92 construction, attempts to release Chinook salmon above the dam were terminated because of low
93 numbers of adults returning to spawn. In 1993, HOR Chinook salmon were released above the dam, and
94 adults have been released annually since 1995. Most or all of these HOR Chinook salmon were likely
95 produced by the McKenzie River Hatchery (44°07'44"N, 122°14'25"W), where 99% were collected.
96 However, in 2009, a small number (N=39) of adults were collected at the nearby Leaburg Hatchery
97 (44°8'8.63"N, 122°36'32.32"W), which does not produce salmon. We found no evidence of fitness
98 differences between adults collected at these two hatcheries, so we treat them equally in our analyses
99 (data not shown). More recently, NOR Chinook salmon were reintroduced above Cougar Dam, following
100 the construction of a trap and haul facility (hereafter Cougar Trap) completed in 2010. Adults have been
101 collected each year throughout the duration of the spawning migration at the Cougar Trap, with the
102 exception of July 19th-August 6th, 2011, when it was closed due to repairs. Since 2007, adults were
103 released in four locations above Cougar Reservoir. However, the number of release locations (range: 2-
104 4), and number of release dates varied (range: 11-32) between years. (Figure1, Table S1). In addition,
105 the sex ratio (number of males / number of females) was male skewed in all reintroduction years
106 evaluated (Table 1).

107

108 *Sample collection*

109 The number of adults Chinook salmon reintroduced each year ranged from 731 to 1,386 (Table
110 1). From 2008-2011, tissue samples were collected from nearly all adults (99%) passed above Cougar
111 Dam (Table 1). All tissue samples were stored in 95% ethanol. Release location, date, and origin (HOR or
112 NOR) were recorded for all adults reintroduced above the dam. Sex was determined by visual
113 assessment of secondary sexual characteristics and recorded. Males were classified as jacks if they were
114 less than 610 millimeters in total length in accordance with Oregon Department of Fish and Wildlife
115 policy. In addition, the sex of jacks was verified using a sex linked marker (see below, 98% concordance

116 Table S2). From 2008-2011, 131 jacks were reintroduced. The number of jacks each year ranged from 5-
117 107 jacks (Table 2). Fork length was measured for all adults reintroduced above Cougar Dam in 2011.

118 Reintroduced adults spawned naturally above Cougar Dam each fall, and subyearling juveniles,
119 i.e. fish that were less than one year in age, were sampled with a screw trap at the head of the reservoir
120 in each following year (2009-2012). For each sampling day, the date and total number of juveniles
121 collected in the screw trap were recorded. Overall, the number of juveniles collected (96 ± 197 , mean \pm
122 1 standard deviation), tissue sampled (44 ± 52), and genotyped (15 ± 21) varied by day (Table S3). On
123 average, juveniles were collected on 132 ± 22 days per year (Table S3). In all four years, we evaluated
124 the proportion of juveniles genotyped per month and found no difference from the portion of juveniles
125 collected in the screw trap (paired Wilcoxon signed-rank tests, $p > 0.05$). Mark-recapture studies
126 indicated that the screw trap operated at a mean efficiency of 5% (Zymonas et al. 2010).

127

128 *Genotyping*

129 We isolated total genomic DNA (Ivanova et al. 2006) from reintroduced adults and a sample of
130 juveniles (range: 1,826-2,220) collected in each year of our study (Table 1). We used the polymerase
131 chain reaction (PCR) to amplify 11 highly polymorphic microsatellites from each fish: *Ots201*, *Ots208b*,
132 *Ots209*, *Ots211*, *Ots212*, *Ots215*, *Ots249*, *Ots253*, *Ots311*, *Ots409*, and *Ots515* (Banks et al. 1999; Greig
133 et al. 2003; Naish and Park 2002; Williamson et al. 2002). We also amplified *Oty3* to determine the
134 genotypic sex of reintroduced adults because accuracy has been proven 100% correct among Chinook
135 salmon sampled in the Willamette River (Brunelli et al. 2008). We visualized PCR products on an ABI
136 3730XL DNA analyzer (Applied Biosystems, Inc., Foster City, CA) and scored genotypes using
137 GeneMapper software (Applied Biosystems, Inc.).

138 We estimated genotyping error by repeating the genotyping procedure described above on a
139 random sample ($n=159$, 1% of total dataset) of adults and juveniles collected each year. We compared

140 re-processed genotypes with originals and estimated error by dividing the number of discordant allele
141 calls by the total number scored. Genetic analyses were performed at the Coastal Oregon Marine
142 Experiment Station, Marine Fisheries Genetics Laboratory, Hatfield Marine Science Center in Newport,
143 Oregon.

144

145 *Microsatellite characterization and assignment power*

146 We calculated observed and expected heterozygosity (Nei 1987) for each adult cohort and
147 sample of juveniles to characterize genetic variation among loci genotyped. We then tested for
148 deviations from Hardy-Weinberg Equilibrium (HWE), and Linkage Disequilibrium (LD) using GENEPOP
149 (Raymond and Rousset 1995; Rousset 2008) for adult and juvenile year classes separately. This
150 informed our choice of parent-offspring assignment program (see below: *Parent-offspring assignments*).
151 We assessed the power of our suite of microsatellite loci by calculating average non-exclusionary
152 probabilities for a random single parent, a second parent, and a parent-pair to assign to any given
153 offspring by chance (Jamieson and Taylor 1997). In addition, we calculated the expected number of false
154 parent-offspring pairs mismatching at 0, 1, or 2 loci (Christie 2010).

155

156 *Parent-offspring assignments*

157 We assigned reintroduced adults from 2008-2011 as parents of subyearling juveniles captured in
158 the screw trap the following year (e.g. 2008 adults were assigned to 2009 juveniles), because most
159 juveniles typically emigrate from natal streams as subyearlings in this system (Romer et al. 2011).
160 Deviations from HWE may occur when sampling large numbers of juveniles because some families, and
161 therefore genotypes, are overrepresented in the sample, known as the Allendorf-Phelps Effect
162 (Allendorf and Phelps 1981; Waples 1998). We accounted for these deviations by using SOLOMON's

163 Bayes method for no known parents, hereafter referred to as SOLOMON, because it carries no
164 assumption with regard to HWE (Christie et al. 2013).

165 We assigned potential mothers and fathers to juveniles separately to reduce the number of
166 pairwise comparisons. For each run we used the default SOLOMON settings – 1000 simulated data sets
167 and 50,000,000 genotypes because the posterior probabilities for each parent-offspring pair differed by
168 < 0.001 when running the analysis a second time with the same dataset, as recommended by the
169 SOLOMON manual. We accepted all parent-offspring pairs with ≤ 1 genotypic mismatch that had
170 posterior probabilities < 0.05 based on our power analysis (Table S4). On average $76 \pm 4\%$ of juveniles
171 assigned to one parent of each sex after parsing the data based on criteria described above. However,
172 on average $12 \pm 6\%$ of juveniles were assigned to multiple parents of the same sex. We simulated
173 comparable data (e.g. 800 parents, 2,000 offspring, and 11 microsatellites with 35 alleles per locus)
174 using SOLOMON, and found that in 80% of these cases the true parent could be identified by choosing
175 the parent-offspring pair with the lowest posterior probability. We therefore used this criterion when
176 parsing SOLOMON output. However, SOLOMON assigned a single parent to an offspring without
177 accounting for the second parent's genotypes. Thus, we could not initially account for both of the
178 putative parents' genotypes at the same time. We verified that the genotypes of the offspring assigning
179 to both a mother and father were in accordance with Mendelian inheritance, using a function developed
180 by N.S. in R (Supplemental File 1).

181

182 *Assignment rates*

183 For each juvenile cohort, we calculated the proportion of offspring that assigned to 1) both a
184 mother and a father, 2) only a mother, 3) only a father, and 4) no parent. The reintroduction of Chinook
185 salmon above Cougar Dam began over a decade before the first tissue samples were collected from
186 adults in 2007. Accordingly, we expected that unsampled, residualized or precocial males could be

187 present in the system. We expected that female Chinook salmon would be less likely to residualize
188 because this life history has rarely been observed in small freshwater systems (but see Romer and
189 Monzyk 2014). Therefore, we expected that some juveniles would have “missing” fathers and few or no
190 juveniles would have missing mothers in our genetic pedigrees.

191

192 *Release effects*

193 We estimated RS by counting the number of subyearling juveniles within a population sample
194 that were assigned to adults released above Cougar Dam in the previous year. From 2008-2011, we
195 examined factors associated with RS using a negative binomial generalized linear mixed-effect model
196 (GLMM) using the R library *lme4* (Bates et al. 2013). We evaluated each year separately because of the
197 variability in release location and release date, as well as variation in the number of juveniles used in
198 parentage assignment among years. For each year, we included *sex* as a factor, with females reported as
199 the reference. We also included *release date* as a covariate. We were unable to evaluate the effect of
200 *release location* across years on RS, as adults were not consistently released in the same locations in
201 different years. In 2011, adults were released at a single location. Thus, we tested for *release location*
202 effects only in 2008 to 2010. We accounted for similarities among Chinook salmon released on the same
203 date and location with a *release group* random effects variable. For each reintroduction year, all
204 variables and first order interaction terms were tested individually to determine if they significantly
205 explained variation in RS. We included all significant variables in a single GLMM and used backwards AIC
206 model selection to determine an adequate model to explain variation in RS.

207 Since 2010, both HOR and NOR Chinook salmon were reintroduced above Cougar Dam. We
208 tested for a difference in mean RS between HOR and NOR Chinook salmon by including an *origin* (HOR
209 or NOR) predictor, whereby HOR was the reference, when repeating the same GLMM approach
210 described above. In addition, 2011 was the only reintroduction year that had length measurements for

211 all reintroduced Chinook salmon. Thus, we included length as a covariate in 2011. Finally, we did not
212 include the *release group* random effects variable in 2011 because adults were released in a single
213 location. We therefore applied a generalized linear model (GLM) with a negative binomial distribution
214 using the R package MASS (Venables and Ripley 2002).

215 Spawner length has been shown to be positively related to greater fitness. We therefore tested
216 if *sex*, *origin*, or *sex*origin* significantly explained variation in *length* in 2011 using an ANOVA.

217

218 *Relative reproductive success*

219 As an alternative to our GLMM approach, we also tested for potential RS differences between
220 HOR and NOR adults using methods described in Araki and Blouin (2005), because these methods
221 account for biases associated with Type A and B error (see Araki and Blouin (2005) for more detail).
222 Briefly, we permuted 10,000 random relative reproductive success (RRS) values using our estimates of
223 individual RS for HOR and NOR Chinook salmon in R (Supplemental file 1). Equation 14 in Araki and
224 Blouin (2005) requires that Type B error is calculated, which is defined as the rate at which a false
225 parent assigns to an offspring when the true parent is not in the dataset. We estimated Type B error by
226 assigning subyearling juveniles to adults reintroduced after the juveniles were spawned – e.g. 2010
227 adults assigned to juveniles emigrating from head waters in 2010. We calculated observed RRS, after
228 accounting for errors in assignments and potential missing parents (Araki and Blouin 2005). We
229 determined significance by calculating the frequency of random RRS values less than our observed
230 value. Within each year we compared NOR and HOR Chinook salmon RS differences for the sexes
231 separately, as well as combined years for each sex individually. All critical values were false discovery
232 rate corrected (Benjamini and Hochberg 1995).

233 All analyses were performed using R version 3.1.1 (R Core Team 2014). Means were reported
234 with ± 1 standard deviation, except for *post-hoc* tests of first order interaction terms. In these cases, we

235 report effect estimates \pm standard errors. General data analysis was aided by *plyr* (Wickham 2011) and
236 *reshape2* (Wickham 2007) packages in R.

237

238 **Results**

239 *Microsatellite characterization and assignment power*

240 We included a total of 11,819 Chinook salmon in our genetic parentage analysis, and we
241 genotyped 99% (3709/3738) of adults and 100% (8081/8081) of juveniles at ≥ 10 loci (Table 1). We
242 estimated a $2 \pm 1\%$ genotyping error rate for both adults and juveniles, and we observed variation in
243 genotyping error among loci ($2 \pm 2\%$) likely due to mis-scoring and allele dropout. We found that all loci
244 were out of HWE for the 2008 and 2009 adult cohorts. However, only 6 and 5 loci deviated from HWE in
245 2010 and 2011, respectively. Similarly, the number of locus pairs in LD was higher in 2008 and 2009,
246 though average number of locus pairs in LD among years was low (4 ± 3). As expected, we observed all
247 loci out of HWE and many locus pairs in LD among juvenile samples (21 ± 7). Deviations from HWE were
248 likely due to large samples sizes because F_{IS} values were small (0.005 ± 0.014 , Table S5). We found that
249 observed (0.92 ± 0.01) and expected (0.92 ± 0.01) heterozygosity, as well as the average number of
250 alleles per locus (34 ± 1) were high and varied little among adult and juvenile datasets used in genetic
251 parentage analyses (Table 1).

252 For the four reintroduction years evaluated, we assigned most ($99 \pm 2\%$) juveniles to at least one
253 parent and an average of $79 \pm 7\%$ juveniles to both a mother and a father (Figure S1). We found the
254 average frequency of juveniles that were missing a mother ($14 \pm 5\%$) was nearly twice that of those
255 missing a father ($7 \pm 3\%$).

256

257

258

259 *Reproductive success variation*

260 We observed positively skewed RS distributions in all four adult cohorts (Figure S2-S5). Means
261 and standard deviations varied between years and sexes, at least in part, due to variation in number of
262 adults reintroduced each year and the number of juveniles genotyped (Table S6). We found evidence
263 that jacks contributed to juvenile production in all years except 2011 (Table 2). However, because we
264 did not genotype all juveniles produced in the system, production by jacks may simply have gone
265 undetected by our study in that year.

266

267 *Release effects*

268 The factors that were significantly associated with RS varied among the four reintroduction
269 years we evaluated. Regression analysis suggested that in 2008 the mean RS for males was 49% that of
270 females ($p < 0.001$, Table 3). In 2009, we only found a small negative relationship between *release date*
271 and RS ($p < 0.001$, Table 3). Overall, from 2008-2010, we found that *release location* did not significantly
272 explain variation in RS (Table S7).

273 In 2010, we included an *origin* term in our analysis because both NOR and HOR Chinook salmon
274 were released in that year and thereafter. We found that *sex*, as well as the interaction terms *origin*sex*
275 and *origin*release date* significantly explained variation of individual RS. All variables were included in
276 the final GLMM based on AIC scores. We found that mean RS for males was 0.43 times that of females
277 ($p < 0.001$, Table 3), after accounting for variation explained by other predictors. Our results indicated
278 that the effect of *origin* on RS was different between the sexes. Accordingly, we tested for the effect of
279 *origin* on RS for each sex separately. We found that the mean RS for NOR males was 2.2 times that of
280 HOR males ($e^{0.776 \pm 0.237}$, $p = 0.001$), whereas mean RS for NOR and HOR females did not differ ($p = 0.160$).
281 We also evaluated the effects that *release date* had on RS of HOR and NOR Chinook salmon separately,
282 because the *origin*release date* term was significant ($p = 0.016$, Table 3). Mean RS of NOR Chinook

283 salmon decreased ($e^{0.018 \pm 0.006}$, $p=0.003$) each day of the release season. However, *release date* did not
284 significantly explain variation in RS for HOR Chinook salmon ($p=0.606$).

285 The predictors *origin* and *length* significantly explained variation in RS in 2011. In contrast to
286 results from 2010, we found no significant interaction between *origin* and *sex* ($p=0.096$) in 2011. We
287 also found no significant interaction between *length* and *origin* that year ($p=0.241$). We found that mean
288 RS for NOR Chinook salmon was 1.5 times that of HOR Chinook salmon when variation in *length* was not
289 accounted for in the GLM ($p=0.023$). However, we found that *origin* was not a significant predictor of RS
290 ($p=0.352$) when *length* was accounted for in the same GLM. Based on AIC scores, we included only
291 *length* in the final GLM. We found that for each centimeter (cm) increase in *length*, mean RS increased
292 by 6% ($p<0.001$, Table 3).

293 We found that mean *length* for NOR Chinook salmon was 2.0-4.0 cm (95% CI) greater than HOR
294 Chinook salmon ($F_1=58.4$, $p<0.001$) and that males were 1.3-3.3 cm (95% CI) shorter than females
295 ($F_1=9.58$, $p<0.001$). The interaction term *sex*origin* was not significant ($F_1=0.04$, $p=0.788$), suggesting
296 that the effect of *origin* on *length* did not differ between the sexes.

297

298 *Relative reproductive success*

299 Results from permutation tests provided corroborative evidence for RS differences between
300 HOR and NOR male Chinook salmon. Mean RS for HOR males was significantly less than that of NOR
301 males in 2010 (RRS= 0.46, $p=0.004$), 2011 (RRS= 0.51, $p=0.003$), and when both years were combined
302 (RRS= 0.48, $p<0.001$). We found no significant differences between RS of NOR and HOR females in 2010
303 (RRS= 1.51, $p=0.938$), 2011 (RRS= 0.89, $p=0.434$), or when both years were combined (RRS= 1.10,
304 $p=0.869$).

305 **Discussion**

306 We examined the effects of factors associated with an active trap and haul strategy on the
307 reproductive success (RS) of Chinook salmon reintroduced above an existing dam on the South Fork
308 McKenzie River, Oregon. We used RS as a measure of success for each Chinook salmon reintroduced
309 above the dam, because RS is a prerequisite to total lifetime fitness, based on adult returns, in future
310 years. Our results are consistent with findings from other studies, which have demonstrated that
311 reintroduction of sexually mature adult salmonids can contribute to overall production of juveniles
312 (Baumsteiger et al. 2008; DeHaan and Bernall 2013). To our knowledge, this is one of two (see Evans et
313 al. *In Review*) studies that provide insight on effects from release strategies associated with active
314 transport. We found inconsistent evidence that release date affected the success of reintroduced adults
315 and release location did not affect RS in any year evaluated. We are also the first to evaluate the RS of
316 reintroduced jacks and found that jacks contributed to overall juvenile production, thereby mediating
317 gene flow among generations for the reintroduced population. Overall, we consistently found fitness
318 differences between HOR and NOR males, which corroborates findings from other HOR/NOR fitness
319 studies. Finally, we found that length may partially explain why HOR Chinook salmon are less fit than
320 NOR Chinook salmon, which is consistent with hypotheses that fitness differences between HOR and
321 NOR salmon are the result of sexual selection on the spawning ground and/or natural selection in the
322 early life stages of juvenile salmon.

323

324 *Estimating RS from a sample of juveniles*

325 For Chinook salmon, as with many fishes, estimating mean RS is difficult, particularly during
326 early offspring life stages because hundreds of thousands of juveniles can be produced within a system.
327 In such scenarios, sampling every juvenile is not practical and in many cases, not possible. One
328 alternative is to wait for adult progeny to return in subsequent years, but this approach requires

329 sampling for many years, and sometimes decades. When management action is required within a
330 shorter time frame, sampling of early-stage juveniles can answer important questions relevant
331 conservation. Anderson et al. (2011) evaluated the accuracy of such an approach and provided some
332 guidance when estimating mean RS in salmonids using assignments made with adults and juveniles.
333 They noted that three important parameters to control for Type I error are: 1) the number of parents, 2)
334 variance in RS, and 3) the number of offspring that assigned to a parent. Anderson et al. (2011) suggest
335 sampling enough offspring such that estimated mean RS is >6.2 . We exceeded a mean RS >6.2 in 4 of the
336 12 cases in our study (Table S6). Type I error rate may exceed 0.05 in the remaining 8 cases. We note,
337 however, Ford et al. (2012) previously used both adult-juvenile and adult-adult assignments in a
338 salmonid fitness study, and results were consistent between both approaches in all but one comparison.
339 Moreover, our preliminary (unpublished) findings from parentage assignments for returning adult
340 salmon thus far are consistent with adult-to-juvenile results presented here. Nevertheless, a
341 conservative approach would be to interpret our results in light of potential elevated Type I error rates.

342 There are other factors that could potentially bias results. First the location of the screw trap
343 relative to redds could potentially bias RS estimates. Indeed Anderson et al. (2011) noted that the
344 probability of collecting juveniles likely decreases as the distance between a given redd and the screw
345 trap increases. Similarly, juveniles will not likely be collected if they were produced in a redd located
346 below the screw trap. Finally, juveniles are increasingly able to avoid a screw trap with greater size,
347 though we do not believe this was a significant factor in our study because ongoing life history studies
348 indicate that most juvenile Chinook salmon migrate to Cougar Reservoir as subyearlings.

349

350 *Release effects*

351 Factors that explained variability in RS were inconsistent across years evaluated. Males were on
352 average less fit than females in 2008, which was likely driven by the male-skewed sex ratio (2 males:1

353 female) in that year. In 2009, we only found that mean RS decreased slightly as Chinook salmon were
354 released later in the season. Similarly, a small negative relationship between *release date* and RS was
355 evident in 2010, though it was only for NOR Chinook salmon. Our results corroborate findings from two
356 previous studies of Chinook salmon that reported a negative relationship between fitness and timing of
357 entry to spawning grounds. Similar to our findings, release date effects observed in those studies were
358 inconsistent among years (Anderson et al. 2013; Williamson et al. 2010). Dickerson et al. (2005) found
359 that early-arriving pink salmon (*O. gorbuscha*) males were also more successful, which may be explained
360 by a density-dependent process. Males that arrive to the spawning grounds earlier may experience less
361 competition for mates, but as the season progresses the operational sex ratio increases. Individual
362 mating success therefore decreases because of increased competition among males (Quinn 2011).
363 Results observed here and by others suggest that; overall, *release date* is a weak and inconsistent
364 predictor of RS.

365 Water velocity and depth, as well as gravel size are important factors for Chinook salmon redd
366 site selection (Groves and Chandler 1999; Kondolf and Wolman 1993). Moreover, spawning habitat
367 quality can also affect the early survival of juvenile salmonids (Quinn 2011). However, we found no
368 significant effect from *release location* on RS. This is likely because Chinook salmon disperse throughout
369 the river after release, and do not necessarily spawn near their release sites. A telemetry study of
370 female Chinook salmon reintroduced above Cougar Dam in 2010 found that females moved a minimum
371 distance of between 4.2 -17.1 kilometers (Zymonas et al. 2010). Males were not evaluated by Zymonas
372 et al. (2010) and males are likely to move more than females on spawning grounds, because they are
373 not anchored by the construction and defense of a redd.

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377 *Jacks*

378 Our results show that the reintroduction of jacks can help contribute to juvenile production and,
379 more importantly, contribute to gene flow among cohorts of Chinook salmon reintroduced above
380 Cougar Dam. Gene flow among cohorts will help to increase and/or buffer effective population size of
381 the population over time (e.g. Araki et al. 2007; Perrier et al. 2014). In our study system, gene flow is
382 already achieved by overlapping age-4 and age-5 Chinook salmon adults returning to spawn. But, jacks
383 are likely more important to gene flow between generations in coho (*Oncorhynchus kisutch*) and other
384 migratory fishes with more constrained age at maturity.

385

386 *HOR and NOR Fitness*

387 Our findings generally support the growing body of evidence that HOR salmon are less fit in the
388 wild than NOR salmon (reviewed by Christie et al. 2014). We found that male HOR Chinook salmon
389 were less fit than NOR Chinook salmon using two different approaches: GLMM/GLM and an unbiased
390 RRS permutation test. However, no consistent fitness differences were found between HOR and NOR
391 females. In particular, we found no fitness differences between HOR and NOR females released in 2010
392 using either approach, but results from 2011 indicated that mean RS for NOR Chinook salmon (both
393 males and females, combined) was 1.5 times greater than HOR Chinook salmon. Interestingly, this origin
394 effect in 2011 was not significant when we accounted for RS variation explained by *length*. Indeed, NOR
395 adults had a mean length that was 2.0-4.0 cm (95% CI) greater than HOR adults. Together, these results
396 suggest that fitness differences observed between HOR and NOR Chinook salmon released above
397 Cougar Dam may be explained by mean fork length, which differs significantly according to *origin*.

398 We did not directly test the hypotheses posited by Theriault et al. (2011), that fitness
399 differences between HOR and NOR salmon are likely caused by 1) effects from sexual selection on the
400 spawning ground and/or 2) natural selection during juvenile early life stages. However, our results are

401 consistent with both hypotheses. First, *length* has been shown to be an important trait under sexual
402 selection. In particular, female Chinook salmon will delay spawning with smaller males, which likely
403 indicates that they prefer to mate with larger males (Berejikian et al. 2000). Second, larger females
404 typically dig deeper redds, are less susceptible to superimposition, and are more fecund than smaller
405 females (Hawke 1978; Healey and Heard 1984; Quinn 2011). Cumulatively, larger females may have
406 greater fitness because their progeny may experience less mortality associated with the location and
407 quality of the redd where they were reared.

408 Some have suggested that hatchery practices relax selection for larger individuals (Hankin et al.
409 1993; Ricker 1981). In addition, numerous authors have reported positive relationships between body
410 size and RS for both sexes in Pacific salmon (Berejikian et al. 2001; Fleming and Gross 1992; Schroder et
411 al. 2008). Therefore, HOR salmon are likely to be less fit compared to NOR salmon because, on average,
412 they are smaller in size. Indeed, Ford et al. (2012) found that low RS for HOR Chinook salmon could be
413 explained by a higher frequency of precocial (younger and smaller) males present among HOR spawners,
414 relative to the NOR population. In addition, Milot et al. (2013) found that HOR Atlantic salmon (*Salmo*
415 *salar*) returned earlier than NOR Atlantic salmon, and that the difference in the number of years at sea
416 contributed to lower HOR fitness. Although precocial male life history is relatively rare in the Willamette
417 River basin, Johnson and Friesen (2013) found that HOR Chinook salmon length has decreased over time
418 within the basin. Our results therefore corroborate findings from Ford et al. (2012) and Milot et al.
419 (2013) because we found that HOR Chinook salmon were on average smaller than NOR Chinook salmon,
420 which resulted in an overall reduction in fitness. However, the relationship between size and RS that we
421 report warrants further investigation because it is based upon data from a single reintroduction year,
422 and we do not have age information for all reintroduced adults.

423 Based on our HOR/NOR findings, it may be prudent to limit the number of HOR males in the
424 reintroduction program, because HOR males may be maladapted to the “wild” environment (e.g.

425 Christie et al. 2012) and therefore may lower the RS of NOR females. Moreover, juvenile production is
426 not typically constrained by the number of male spawners, in terms of gametes, such that a reduction in
427 the number of HOR males used for reintroduction would not likely limit population productivity.
428 However, research that evaluates potential differences in mate pair reproductive success and that
429 manipulates the number of HOR males to determine its effect on overall productivity is warranted
430 before such management decisions could be made.

431 Successful reintroduction programs above dams will likely prove important to the recovery of
432 many migratory fishes, as they can increase the spawning distributions and natural production. In our
433 study area, reintroduction provided Chinook salmon the opportunity to spawn and rear in headwater
434 reaches of the McKenzie River for the first time in 50 years. We demonstrated that reintroduction of
435 Chinook salmon above dams by active transport can increase natural production. This reintroduction
436 strategy may be effective for the conservation of other migratory fishes (but see Pelicice et al. 2014).
437 Our study found that sex, origin, as well as release date can be important factors influencing the RS of
438 reintroduced Chinook salmon and, therefore, overall population productivity. Observed fitness
439 differences between HOR and NOR male Chinook salmon can likely be explained, at least in part, by the
440 smaller size of HOR fish. Further research on the relationships between age at maturity, length, and
441 fitness of HOR and NOR salmon is need to better understand HOR and NOR fitness differences. Overall,
442 our results provide information on factors that are important for the reintroduction of a migratory fish
443 species into historical habitat despite the continued presence of a dam.

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445

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656 Table 1. Summary of the number of adult and juvenile Chinook salmon genotyped at ≥ 10 and < 10 loci,
 657 the number of adults missing a tissue sample (Missing Tissue Sample), and genetic variation observed
 658 among cohorts sampled. The sex ratio (number of males / number of females), mean number of alleles
 659 per locus (A), mean observed heterozygosity (H_o), and mean expected heterozygosity (H_e) are described.
 660

Year	Type	Loci genotyped		Missing tissue sample	Sex ratio	A	H_o	H_e
		≥ 10	< 10					
2008	Adult	873	0	0	2	33.3	0.92	0.92
2009	Adult	1373	12	1	1.3	35.1	0.91	0.93
2010	Adult	738	9	1	1.8	34.3	0.93	0.92
2011	Adult	725	5	1	1.3	35.2	0.92	0.92
2009	Juvenile	2001	0	-	-	31.5	0.91	0.92
2010	Juvenile	1826	0	-	-	33.8	0.92	0.92
2011	Juvenile	2034	0	-	-	33.6	0.92	0.92
2012	Juvenile	2220	0	-	-	33.1	0.91	0.92

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663 Table 2. Summary of the number (N) and mean (\pm one standard deviation) reproductive success (RS)
 664 estimates for Chinook salmon jacks released above Cougar Dam from 2008-2011.

Year	N	RS
2008	13	2.0 \pm 2.6
2009	107	0.8 \pm 1.6
2010	5	0.0 \pm 0.0
2011	6	6.8 \pm 9.1

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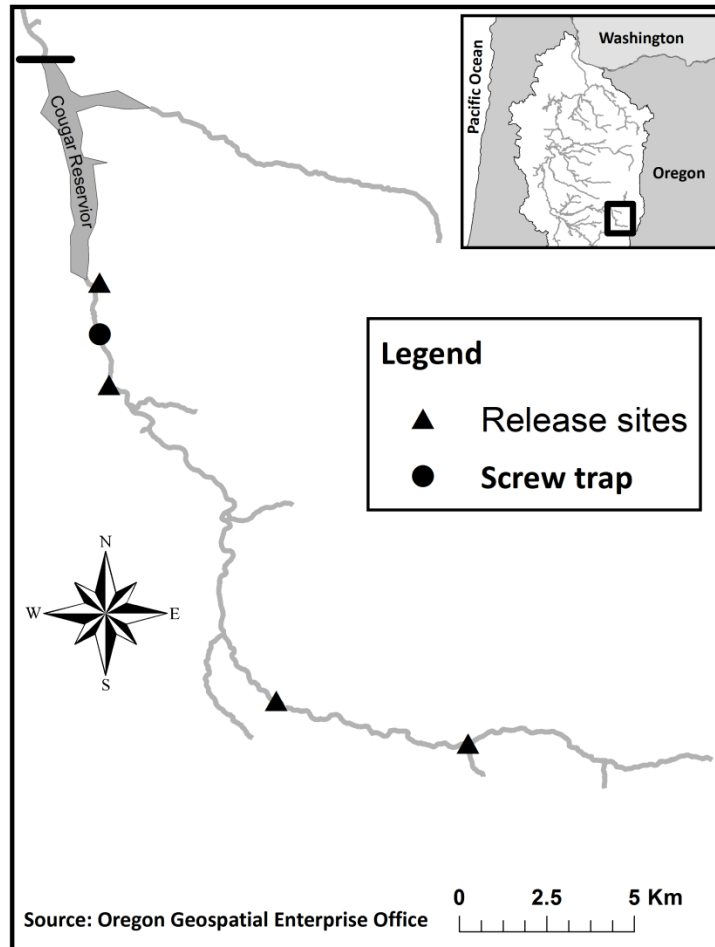
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671 Table 3. Summary of predictors for final reproductive success generalized linear mixed-effects
 672 model/generalized linear model for Chinook salmon released above Cougar Dam from 2008-2011. We
 673 used hatchery origin Chinook salmon and females as references for *origin* and *sex*, respectively. Results
 674 are described for each year separately.

Year	Predictor	Estimate	Std. Error	z value	Pr(> z)
2008	<i>Sex</i>	-0.718	0.135	-5.329	< 0.001
2009	<i>Release date</i>	-0.018	0.004	-4.442	< 0.001
2010	<i>Sex</i>	-0.844	0.202	-4.178	< 0.001
	<i>Origin</i>	3.787	1.781	2.126	0.033
	<i>Release date</i>	0.001	0.004	0.240	0.810
	<i>Sex*Origin</i>	1.119	0.404	2.769	0.006
	<i>Origin*Release date</i>	-0.018	0.008	-2.402	0.016
2011	<i>Length</i>	0.055	0.012	4.757	< 0.001

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690 Figure 1. Cougar Dam (solid black horizontal line) is located on the South Fork McKenzie River, Oregon.

691 Locations of adult Chinook salmon release sites and screw trap used to collect juveniles are indicated.