GENETIC PEDIGREE ANALYSIS OF SPRING CHINOOK SALMON OUTPLANTED ABOVE COUGAR DAM, SOUTH FORK MCKENZIE RIVER

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Summary

Cougar Dam is a high-head dam on the South Fork McKenzie River, Oregon, that impedes passage of spring Chinook to and from historically productive spawning grounds. Recent efforts have aimed to re-establish spring Chinook above Cougar Dam by transporting and releasing adults above the reservoir. Tissue samples have been collected from all adult Chinook released above the dam since 2007 and in this study we used genetic pedigree to infer parent-offspring relationships between outplanted adults and juvenile Chinook collected above and below the reservoir. We then used pedigree information to estimate the reproductive success (RS) of each outplanted adult.

In 2010, the Cougar Dam trap and haul facility became operational, facilitating the collection of natural origin spring Chinook for transport and release above the dam. We used parentage assignments of natural origin (NOR) adults collected at the trap in 2010-2012 to estimate total lifetime fitness (TLF) of 2007 outplants. We observed that on average adult Chinook outplanted earlier in the season of 2007 were more successful at producing adult returns. A similar relationship was only observed for males with respect to the production of juveniles. We also observed that the mean TLF of spring Chinook outplanted at Slide Creek in 2007 was higher than at other outplant sites.

We found that in 2010 the mean RS of NOR males was greater than that of hatchery origin (HOR) males, but that the mean RS of NOR females was less than that of HOR females. Using adult to adult assignments we estimated the female cohort replacement rate (CRR) at 0.38 and the effective population size (N_e) at 184 (95% CI: 166-204). These estimates suggested that the spring Chinook population above Cougar Dam is not replacing itself, but short-term negative effects associated with genetic drift on the population are unlikely to occur. In future years, assessing trends in TLF, RS, CRR, and N_e will be important to ensure the long term viability of spring Chinook above Cougar Dam.

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Introduction

High-head dams have impacted the viability of native spring-run Chinook salmon (*Oncorhynchus tshawytscha*) and winter steelhead (*O. mykiss*) populations in the upper Willamette River (UWR), Oregon (NMFS 2008). Notably, Willamette Project dams represent significant barriers for migratory fish species and restrict volitional access to historical spawning grounds. Adult fish outplanting programs, originally intended to provide supplemental forage for isolated populations of native bull trout (*Salvelinus confluentus*), were adopted by the Willamette Project Biological Opinion (NMFS 2008) as necessary actions for the recovery of wild spring Chinook salmon (hereafter, Chinook) and steelhead in the UWR basin.

Although winter steelheads are rarely observed in the McKenzie River, this subbasin supports the largest natural origin (NOR) Chinook population of the UWR Evolutionarily Significant Unit (ESU). To provide forage for bull trout and to re-establish a viable Chinook population in the upper South Fork McKenzie River, adult hatchery origin (HOR) Chinook have been outplanted at multiple sites above Cougar Dam (Figure 1). In 2010 completion of the Cougar Dam trap and haul facility (hereafter "Cougar Trap") allowed adult NOR Chinook to be collected at the base of the dam and released above Cougar Reservoir. The (parental) source of these adult NOR Chinook and the reproductive success of Chinook outplanted above Cougar Dam are the subjects of our investigation.

We used a genetic pedigree approach to determine the proportion of NOR Chinook collected at the Cougar Trap that probabilistically assigned as progeny of adult Chinook previously released above the dam. We used multiple sampling strategies to estimate the reproductive success (RS) for adult outplanted in 2008-2010 and total lifetime fitness (TLF) of 2007 adult Chinook outplanted above Cougar Dam in past years and we relate our findings to key cohort replacement rate and effective population size. Here we define RS as the number of juvenile offspring sampled at the head and tail of Cougar Dam that assigned to an adult Chinook outplanted above Cougar. TLF is defined as the number of returning adult offspring to the

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Cougar Trap that assign to an adult outplanted in a previous year. This work serves to address information needs identified by Reasonable and Prudent Alternative (RPA) 9.5.1(4) of the Willamette Project Biological Opinion (NMFS 2008), as it provides estimates the RS of hatchery fish in the wild. Our results also address RPAs 4.1 (restoration of productivity by outplanting Chinook above dams), RPA 4.7 (increase the percent of outplanted adults that successfully spawn through development of new release locations), RPA 6.1.5 (management of hatchery-origin spring Chinook upstream of Cougar Dam), and RPA 9.3 (monitoring the effectiveness of fish passage facilities and strategies at Project dams).

Our study carried the following research objectives:

1. Estimate the percentage of unmarked adult Chinook captured at the Cougar Trap that can be confidently assigned as progeny of Chinook outplanted above Cougar Dam, South Fork McKenzie River, Oregon.

2. Estimate the effects of handling and transport protocols, release date and release location on the RS of adult hatchery Chinook salmon outplanted above Cougar Dam on the South Fork McKenzie River, Oregon.

3. Estimate the effects of handling and transport protocols, release date and release location on the TLF of adult Chinook salmon outplanted above Cougar Dam on the South Fork McKenzie River, Oregon.

Results from this study provide insight on the genetic and demographic viability of a Chinook population reintroduced above Cougar Dam, South Fork McKenzie River. Our analyses provide estimates of the cohort replacement rate and effective population size of adult Chinook outplants. Findings from this study also offer some indication of best practices for adult Chinook releases that aim to maximize RS. Results from our study provide managers with information that can directly be used to guide future actions.

Methods

Study Area

Cougar Dam and its associated trap and haul facility are located on the South Fork McKenzie River, Oregon, at 44°07'44"N 122°14'25"W. The dam was completed in 1964, stands 158 m high and has a capacity of 0.270 km^3. The Cougar Trap was completed and operations began on July 28th, 2010. It has been used since that time to collect adult NOR Chinook for release above the dam. In 2011, the Cougar Trap was closed from July 19th to August 6th due to technical issues (Figure 4).

McKenzie River Hatchery is located on the mainstem McKenzie River at 44°07'00"N 122°38'10"W and was originally constructed in 1938. This facility was completely rebuilt in 1975. Most adult HOR Chinook outplanted above Cougar Dam have been collected at this facility or at the nearby Leaburg Hatchery.
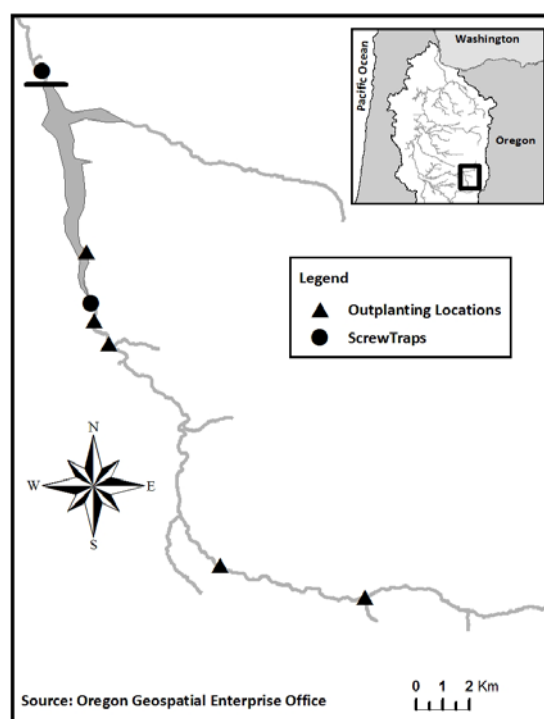

Figure 1. The South Fork McKenzie River subbasin of the Willamette River, Oregon. Locations of outplanting sites, and screw traps are indicated. Cougar Dam is represented by the solid black line.

Data Collection

Sampling for Genetic Analyses

Since 2007, nearly all adult Chinook released above Cougar Dam have been sampled for genetic analyses. For each fish, the sex, origin[1], outplant location, and outplant date were recorded. A small sample of fin tissue was collected from each Chinook and stored in a labeled vial filled with 95% ethanol. Scale samples were taken from Chinook collected at Cougar Trap in 2011 and 2012. The outplant date approximates the fish collection date for Chinook trapped at Cougar Dam and therefore can be used to a proxy for return time. Fish collected at McKenzie River Hatchery were in some cases held for a period at that facility prior to release.

Because UWR spring Chinook typically return to spawn as age-4 and age-5 adults, with few age-3 or age-6 spawners, Chinook that spawned in 2007 and 2008 can be expected to represent the potential parents for most adult fish sampled in 2012 (Figure 2). Samples collected from adult NOR Chinook in 2010-2012 were expected to include all major age classes from the 2007 cohort, lacking only those Chinook that might return as age-6 adults.
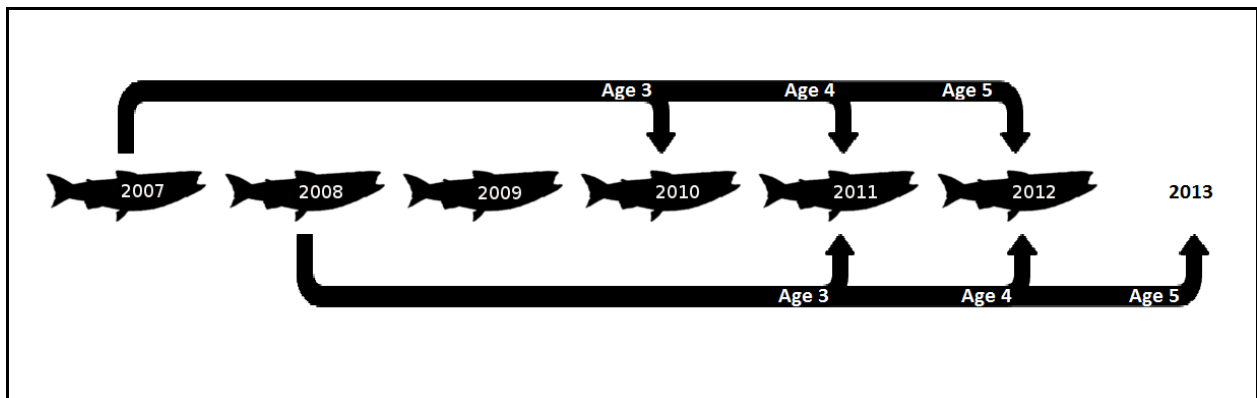
Figure 2. Representation of adult return years for two cohorts of UWR spring Chinook produced in 2007 and 2008. Three adult age classes are depicted, though a small percentage of adults could return at age 6.

In addition to adult Chinook, we collected tissue from unmarked juvenile Chinook sampled from the tailrace and head of Cougar Dam reservoir from 2009-2011. We used a rotary

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[1] NOR or HOR, as determined by adipose fin presence or absence

screw trap to collect juvenile samples from the river at each location. Traps operated at 4% juvenile sampling efficiency based on mark-recapture studies (M. Hogansen, unpublished data).

Our analyses focused on assessing parent-offspring relationships among the unmarked adult Chinook that returned to the Cougar Trap from 2010-2012. We used parent-offspring assignments to estimate TLF for 2007 outplants. In addition, we have applied similar methods to assess the RS using parent offspring relationships between adults outplanted in 2008-2010 and outmigrating juveniles sampled in screws traps present at head and tail of the reservoir in 2009-2011. Finally, we investigated HOR/NOR RS differences of Chinook outplanted in 2010.

Genotyping

We used a glass fiber filtration-elution protocol (Ivanova et al. 2006) to isolate whole genomic DNA from Chinook tissue samples. Each DNA sample was amplified at a suite of 11 microsatellite loci using PCR: *Ots201, Ots208b, Ots209, Ots211, Ots212, Ots215, Ots249, Ots253, Ots311, Ots409,* and *Ots515* (Banks et al. 1999, Greig et al. 2003, Naish and Park 2002). We used the genetic sex marker, *Oty3*, to genotype all adult Chinook passed above Cougar Dam to determine sex (Brunelli et al. 2008). *Oty3* is a minisatellite located on the Chinook Y chromosome and it has been verified to correctly identify sex among a variety of samples tested, including Chinook from the Willamette River (Brunelli et al. 2008). All PCR products and a DNA size standard were visualized on an ABI 3730XL DNA Analyzer (Applied Biosystems, Inc., Foster City, CA).   Microsatellite alleles were scored by size with GeneMapper software (Applied Biosystems, Inc., Foster City, CA). All molecular genetic work was performed at the Marine Fisheries Genetics Laboratory of the Coastal Oregon Marine Experiment Station, Oregon State University.

Genetic Pedigree Assignments - Adults

We used maximum likelihood methods to identify parents of returning adult offspring in our analysis as implemented in CERVUS (Marshall et al. 1998, Kalinowski et al. 2007). CERVUS requires an allele frequency analysis prior to conducting simulations of parent offspring relationships, which were used to calculate the confidence of each assignment. As a final step, actual parent offspring assignments are made and given 95% confidence, if applicable based on

the simulations. From this analysis we obtained the mean number of alleles per locus, observed and expected heterozygosities, non-exclusion parent pair probability and the percent of individuals genotyped at each marker. We also tested for Hardy-Weinberg Equilibrium (HWE) deviations with exact tests in GENEPOP (Rousset and Raymond 1997) following Bonferroni corrections (α=0.05).

CERVUS uses a likelihood ratio approach that calculates the natural log of the likelihood-odds ratio (LOD) scores for assignments to each potential parent (Marshall et al. 1998). The difference between LOD scores for the two most likely parents of the same sex is defined as Δ. We allowed a genotyping error of 0.01 and set the proportion of males and females sampled to 0.98 to generate Δ in CERVUS simulations. Based on CERVUS simulations, we applied a 95% confidence criterion for acceptance of parental assignments (parental-offspring pairs; POPs). In addition, we required that all assignments had no more than one genotype mismatch. Any adult offspring that were confidently assigned to only one parent were included in the pedigree.

Genetic Pedigree Assignments - Juveniles

When sampling a small proportion of juveniles produced in a population, over-representation of closely related half- and full-siblings individuals within the dataset can alter allele frequencies; referred to as the Allendorf and Phelps effect (Waples 1998; Allendorf and Phelps 1981). Datasets that exhibit the Allendorf and Phelps effect often contain loci that are out of HWE, which can affect parentage assignments. Accordingly, we used the Bayes' Method in SOLOMON (Christie et al. 2013; hereafter referred to as SOLOMON) to assign parents to juvenile offspring, as this method's only assumption is that loci are unlinked. Initially, the prior probability of a dyad sharing alleles by chance across all possible number of mismatches (Pr(Φ)) was calculated using 1000 simulated datasets and 50,000,000 genotypes. We reduced the number of pairwise comparisons made by assigning potential parents of each sex to juveniles in separate SOLOMON analyses.

Christie et al. (2013) recommended analyzing all POPs with Bayes' posterior probabilities < 0.05. We included all POPs that had posterior probabilities <0.05 and included all

dyads with a Pr(Φ) < 0.05. Preliminary analysis revealed that a small proportion of the offspring could be assigned to more than one parent of the same sex after parsing the data using the criteria described above. Using simulated data comparable to ours (800 parents, 2000 offspring, and 11 microsatellites with 35 alleles per locus) we determined that the true parent had the lowest posterior probability in 80% of the cases when an offspring had more than one parent of the same sex assign. Therefore we included the parent with the lowest posterior probability in our analysis in all instances when an offspring could be assigned to more than one parent of the same sex.

Data Analysis

Parentage Assignment Rates for Adult Chinook

We estimated the number of male and female adult Chinook collected at the Cougar Trap in 2012 that could be confidently assigned as offspring of Chinook outplanted in 2007-2009. The ratio between this number and the total number of NOR Chinook collected at the Cougar Trap in 2012 provided an estimate for the parentage assignment rate for adult returns to Cougar Dam. Observed upstream passage of Chinook is bimodal at some UWR locations (Cannon et al. 2010, 2011, 2012), whereby the majority of adult fish that arrive between June-August are typically followed by a second, smaller influx of spawners after September 1st. To investigate possible differences between the composition of spawners in these two groups we estimated the proportion of Chinook that assigned to outplanted parents before and after September 1st, then compared these proportions with a Fisher's exact test ($\alpha = 0.05$). We also assessed if the proportions of early and late arrivals were different between the sexes or ages using Fisher's exact tests ($\alpha = 0.05$).

Outplanting Effects on Adult Returns

We estimated TLF for adult Chinook outplanted in 2007 from the number of progeny sampled as adults in 2010-2012 at the Cougar Trap. We included *outplant date* as a numeric predictor and included *outplant location* and *sex* as factors, whereby Slide Creek and female served as the reference values. Each unique combination of *outplant location* and *outplant date* were considered as an *outplant group* and these groups were included as a random effects

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variable. The random effects variable was used to account for any similarities Chinook experienced as outplant groups. We initially tested each variable separately and all first order interaction terms using Poisson regression accounting for the random effects of each *outplant group*. We then included all significant variables in generalized linear mixed model (GLMM) and used backwards Akaike information criterion (AIC) model selection to determine the most adequate model to explain variation in TLF.

We evaluated the effects of the late Cougar Trap start date in 2010 and the 12 day closure in 2011 using Fisher's exact tests, which determined if the proportion of fish caught in the Cougar Trap that genetically assigned as age-3 and -4 returning adults differed among 2010-2012 samples. We tested age classes separately because direct year comparisons would be flawed due to the lack of genotypes of Chinook outplanted before 2007. If the Cougar Trap late and closure operational issues resulted in a significant number of Chinook strays we would expect the proportions Chinook that assigned in those years to be less than 2012 assignments, which was a year that lacked operational issues.

Parentage Assignment Rates for Juvenile Chinook

We evaluated the frequency of each assignment type (both parents, father only, mother only, and no parent assigned) from 2008-2010 in order to assess interannual variance in assignment rates. The ratio between the frequency of each assignment type and the total number of offspring genotyped each year provided estimates of assignment rates. In addition, we assessed the number of juveniles produced by each type of mate pair between HOR, NOR, and Chinook of unknown origin in 2010.

Outplanting Effects on Juvenile Production

We evaluated outplanting effects on RS with the same approach used to assess TLF, whereby we included both male and female RS into a single dataset*.* The predictors were the same as those used TLF regression analysis. We also included *year* as a factor to account for possible differences among years, with 2008 as the reference. From 2008-2010, Chinook were not consistently outplanted at each location. This limited our ability to develop inferences about the effects of *outplant location* on RS. We addressed this issue by simplifying *outplant*

location into two categories, "upper" and "lower". We define all outplant locations at or below rkm 18.5 as lower and all above rkm 18.5 as upper. We then conducted regression analyses with each predictor separately and all first order interaction terms to determine which variables to include in the full model. We used backwards AIC model selection to choose the best explanatory model for RS.

Using the same analysis approach as described for the TLF analysis, we investigated HOR and NOR differences with just the 2010 adult-2011 juvenile dataset. In this GLMM we also included origin as a factor, whereby HOR was the reference. All analyses were conducted in R (The R Development Team 2011).

Demography

Population Viability Metrics – CRR and Ne
Using the results from our pedigree analyses, we estimated two demographic parameters: 1) the Cohort Replacement Rate (CRR) and 2) the genetic effective population size (N_e). To avoid potentially misleading effects from the male-biased sex ratio of adult Chinook outplanted in 2007, we estimated CRR from female data only, whereby female CRR was defined as the number of adult females that returned to the Cougar Trap in 2010-2012 that assigned as progeny of females outplanted in 2007, divided by the number of adult females outplanted in 2007.

Waples and Do (2010) demonstrated that information from linkage disequilibrium among microsatellite loci can be used to estimate the effective population size (N_e) of natural populations. We used the approach of Waples and Do (2010), implemented in the software LDNE (Waples and Do 2008) to estimate N_e from the microsatellite data for adult Chinook (2010-2012 returns) that assigned as progeny of 2007 outplants. We report jackknifed 95% CIs for N_e to address the parametric CI bias identified in Waples and Do (2008).

Adult Age Estimates – Agreement between Scale and Pedigree Results
We provided scale samples from Chinook collected at the adult trap in 2010-2012 to the ODFW Fish Life History Analysis Project to estimate the total age and juvenile life history (i.e. reservoir v. river reared) using standardized protocols (Clemens et al. *In prep*). We compared

the ages of adult spring Chinook as estimated from scale and pedigree analyses to determine percent concordance between these methods. These exploratory analyses provided valuable comparisons that may be used to calibrate future estimates, but in absence of known-age individuals, could not be used to estimate error for either method.

Results

Data Summary

Adult Chinook Sampled for Genetic Pedigree Analyses

From 2007 to 2012 the number of adult Chinook released above Cougar Dam ranged from 746 to 1387 individuals (Figure 3). In all years the sex ratio of outplants was male skewed (male:female = 1.48±0.14). The proportion of NOR Chinook among outplants was 0.34 in 2010 and increased to 0.53 in 2011 and 2012. The increase in the proportion of NOR fish among outplants reflected a steady increase in the number of NOR fish collected at the Cougar Trap from 2010-2012.
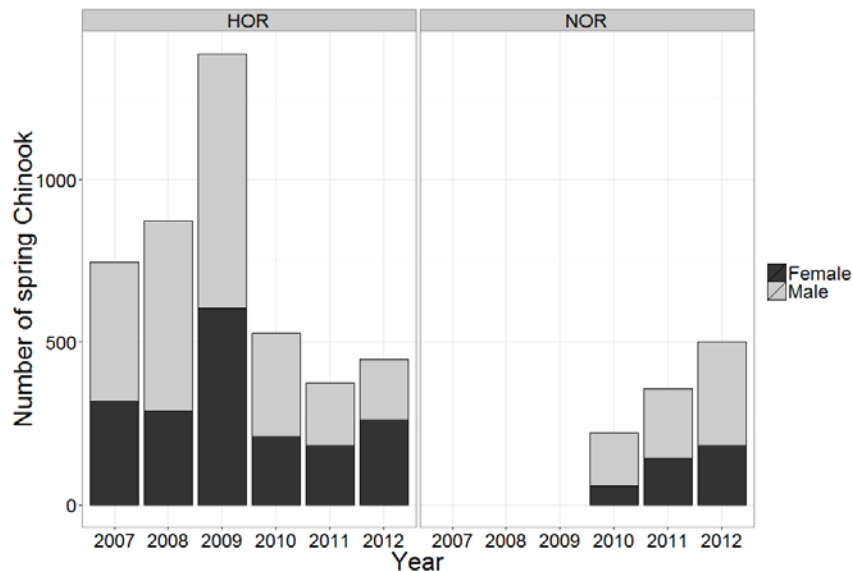

Figure 3. Number of adult Chinook released above Cougar Dam, 2007-2012. (HOR – hatchery origin; NOR – natural origin)

The total number of adult Chinook collected at the Cougar Trap increased from 250 in 2010 to 517 in 2012 (Table 1), the majority of which were unmarked, presumably NOR fish (Table 1). The date of sample collection at the Cougar Trap (2010-2012) provided some indication for the timing of upstream migration of Chinook in the South Fork McKenzie River. The arrival of adult Chinook at the Cougar Trap appeared to be temporally bimodal, similar to patterns observed at Leaburg Dam (mainstem McKenzie River; Cannon et al. 2010, 2011, 2012). Although the timing of the first influx of spawners was somewhat obscured by variable trap

start dates and operation, the second influx appeared to begin in the first week of September (Figure 4). We hereafter refer to these migratory groups as "early" and "late" arriving Chinook, defined by collection at Cougar Dam before and after September 1st.

Figure 4. The number of Chinook collected at the Cougar Trap from 2010-2012. Solid black vertical line represents September 1ST. Dashed black line represents delayed start date in 2010 and the stripped black box represents when the trap was closed due to technical issues.
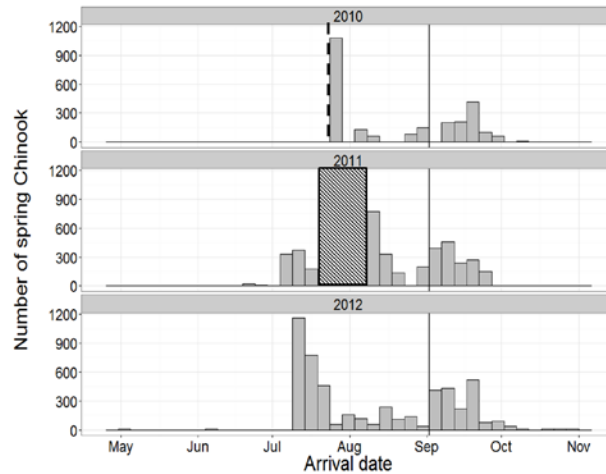

Table 1. Summary of the number of hatchery supplementation, Cougar Trap – (HOR), and Cougar Trap – Natural origin (NOR) Chinook passed above Cougar Dam 2007-2012.

Year	Hatchery Supplementation	Cougar Trap - HOR	Cougar Trap - NOR
2007	746	0	0
2008	873	0	0
2009	1386	0	0
2010	497	30	220
2011	375	30	356
2012	447	17	500

Juvenile Chinook Sampled for Genetic Pedigree Analyses

From 2009-2011, we collected a total of 39,575 juvenile Chinook in screw traps at the head and tail of Cougar Reservoir and tailrace of Cougar Dam. We sampled juveniles in screw traps for 94, 169, and 182 days in 2009, 2010 and 2011 and collected a total of 17,752 caudal fin clips (Figure 5). We genotyped 6,117 of these juveniles at 11 microsatellite loci. The number

of juveniles sampled in screw traps varied widely among years (13,191 ± 12,108); however the peak of juvenile outmigration was May for all years (Figure 5).
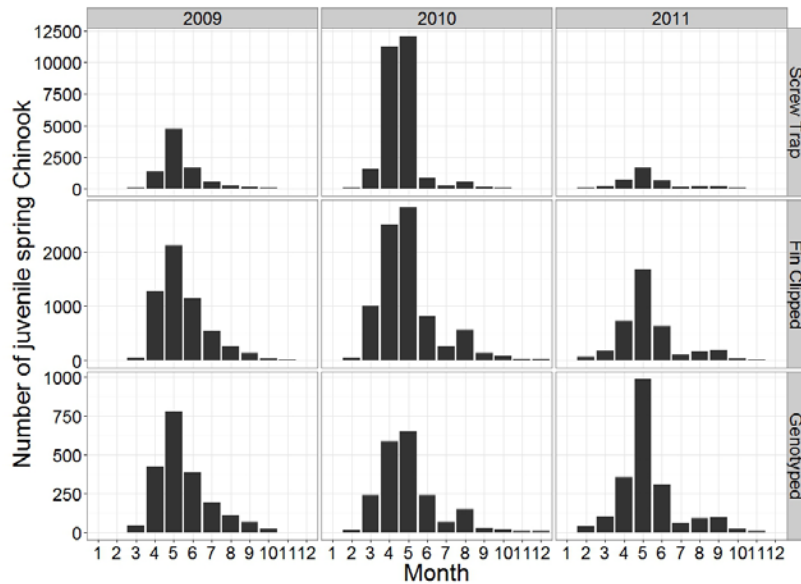

Figure 5. The number of juvenile Chinook sampled in screw traps, fin clips collected, and genotyped from 2009-2011.

Genetic Data Quality and Parentage Assignment Power

We successfully genotyped 99% of the 10,620 adult and juvenile Chinook at all 11 microsatellite loci (Table 1). The mean number of alleles per locus was 33.8 (range 16-74) and the mean non-exclusion probability per locus for one parent was 0.26 (Table 2). From our set of 11 microsatellites we established that the probability for false assignment, $Pr(\Phi)$, was <0.05 when the number of mismatches between parent and offspring was ≤1. Observed and expected heterozygosities were greater than 84% for all loci, with a maximum observed heterozygosity of 96% (Table 2). Among juvenile samples, we found all loci to be out of HWE and that the observed heterozygosity was less than expected for 70% of loci. We also observed significant deviations from HWE for 8-11 loci among adults passed above Cougar Dam prior to the implementation of the Cougar Trap (Figure 6). In 2010 deviations from HWE began to decrease and in 2012 only three loci were out of HWE (Figure 6).
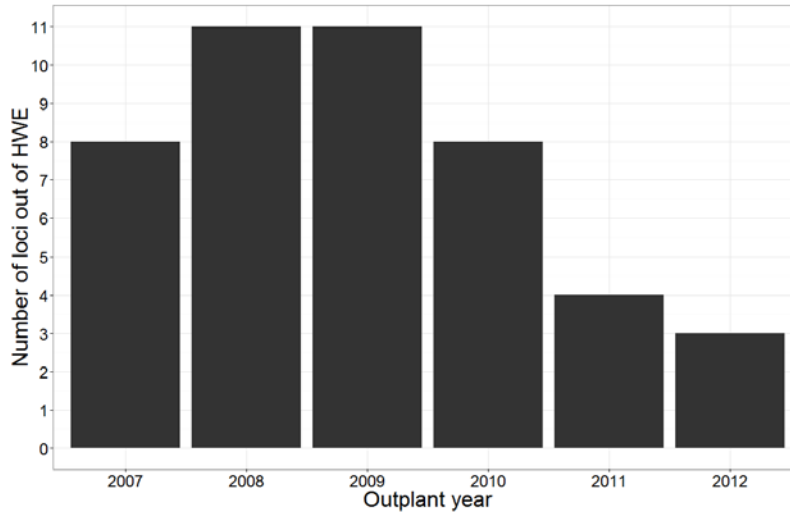
Figure 6. The number of loci out of Hardy-Weinberg Equilibrium (HWE) following Bonferroni corrections (α=0.05) for adult Chinook outplanted above Cougar Dam (2007-2012)

Table 2. Summary of genetic variation observed among both 2007-2012 adults and 2009-2011 juveniles at each microsatellite locus used in our analysis. The mean number of alleles per locus (K), mean observed heterozygosity (H_O), mean expected heterozygosity (H_E), mean non-exclusion one parent power (NE.1P), and mean percent of individuals genotyped (Per.GT) are described for each locus.

Locus	K	H_O	H_E	NE.1P	Per.GT
Ots201b	22.1	0.92	0.91	0.30	1.00
Ots209	51.5	0.92	0.94	0.22	0.99
Ots249	34.3	0.94	0.94	0.22	1.00
Ots253b	27.4	0.90	0.92	0.29	1.00
Ots215	32.6	0.93	0.94	0.22	1.00
OtsG311	47.6	0.95	0.95	0.18	1.00
OtsG409	58.8	0.95	0.95	0.17	1.00
Ots211	26.6	0.91	0.92	0.28	1.00
Ots208b	32.4	0.91	0.94	0.22	1.00
Ots212	21.8	0.89	0.89	0.36	1.00
Ots515	16.8	0.86	0.86	0.43	1.00

Assessment of genotypic and phenotypic sex calls

We found that the mean concordance between phenotypic and genotypic sex calls was 89.1%, with the highest concordance in 2008 (95%) and the lowest in 2011 (81%) (Table 3). We found a total of 599 differences in sex calls among the 5,416 adult Chinook genotyped at Oty3 (Table

3) and observed that adults that were phenotypically male, but genotypically female were observed more frequently than phenotypic males that were genotypically female. We used the genotypic sex calls when assigning adult outplants to NOR adults returning to the Cougar trap.

Table 3.Summary of concordance between phenotypic[2] and genotypic sex calls for adult Chinook outplanted above Cougar Dam from 2007-2012. Different sex call sub-categories describe changes from phenotypic sex to genotypic sex.

	2007	2008	2009	2010	2011	2012
Concordant sex call						
Female	268	265	522	249	256	405
Male	399	563	676	416	332	466
Discordant sex call						
Female -> Male	27	22	105	63	77	41
Male -> Female	49	22	80	15	65	33

Parentage Assignment Rates

Adult-Adult Assignments

A total of 500 adult NOR Chinook were captured at the Cougar Trap in 2012. These fish consisted of 182 females and 318 males. We estimated that 112 females and 204 males were progeny of at least one parent from outplant years 2007-2009. Among the 316 returns that assigned, we estimated that 165 were age-5 and 149 were age-4, as inferred from the parental outplant year to which they assigned. Eighty-four percent (281 of 331) of NOR Chinook passed above Cougar Dam before September 1st, 2012 assigned to at least one parent outplanted in 2007-2009, whereas only 21% (35 of 169) collected after September 1st assigned as progeny of a previous outplant; presenting different assignment rates for early and late arriving Chinook at Cougar Trap (Figure 7; Fisher's exact test, $p < 0.001$). The proportions of males and females, as well as, age-4 and age-5 Chinook were not different between early and late returning fish (Fisher's exact test, *p> 0.05*).

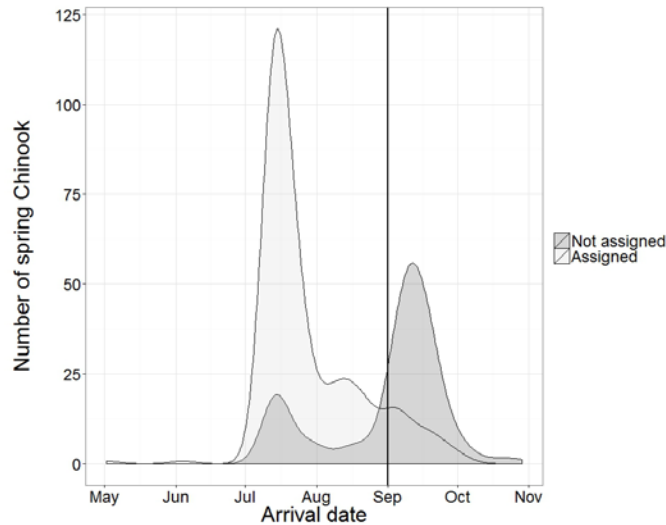[2] Phenotypic sex as determined from secondary sexual characteristics

Figure 7. The number of natural origin Chinook collected at the Cougar Trap from 2010-2012. Solid black vertical line represents September 1ST.

We found that the proportions of age-4 fish caught in 2011 and 2012 were not different (p= 0.14). The proportions age-3 fish caught in 2010 compared to 2012 age-3 fish were different (p= 0.008). However this result does not support the hypothesis that potential increased straying during trap closure times decreased assignment rates because the proportion of 2010 age-3 Chinook (0.03) was actually larger than the proportion in 2012 (0.004). We also found that the proportions of age-3 Cougar trap adults in 2011 compared 2012 were no different (p= 0.41). Cumulatively, these results provide no evidence that operational issues in 2010 and 2011 significantly affected assignment rates.

Adult to Juvenile Assignments

Of the juvenile Chinook that we collected in 2009, 2010, and 2011 and subsequently genotyped, we assigned 99%, 95% and 84% to at least one parent (Figure 8). We also found the frequency of juveniles with no parents that assigned in our genetic pedigrees increased from 0.2% in 2008 to 16.1% in 2010. Among single parent assignments, we observed more juveniles were assigned to only a mother in 2009; however, in both 2010 and 2011 there were more juveniles that assigned to only a father (Figure 8).
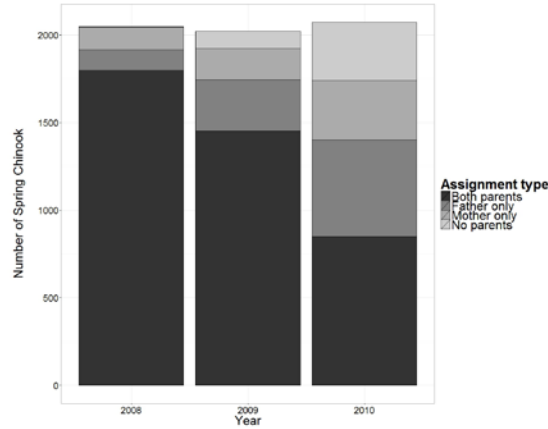
Figure 8. Summary of assignment rates for each type of assignment made among the adult-juvenile pedigrees from 2008-2010.

We investigated the number of juveniles that were produced by different types of mating pairs in 2010 because both HOR and NOR Chinook were passed above Cougar Dam. We observed that most juveniles produced were progeny of the HOR-HOR Chinook mating events. Interestingly, HOR females mated with NOR males to produce 333 juveniles, yet HOR males mated with NOR females to produce 21 juveniles (Table 4). In addition, we found a large number of juveniles that were produced by parents of unknown origin (Table 4). Finally, we observed more juveniles that were produced by unassigned mothers than unassigned fathers (Table 4).

Table 4. The number juveniles produced by each type of mate pairs that were observed in the 2010 adult -2011 juvenile pedigree. (HOR – hatchery origin; NOR – natural origin)

Mother Origin	Father Origin		
	HOR	NOR	Unassigned
HOR	357	333	306
NOR	21	138	33
Unassigned	311	240	333

Total Lifetime Fitness – Inference from Adults

We found that both *outplant date* and *outplant location* had significant relationships with TLF. Neither *sex* nor any first order interaction term significantly explained variance in TLF.

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Based on AIC scores, we found that a model that included *outplant date* and *outplant location* best explained variance in TLF (Table 5). After accounting for effects from *outplant location*, we found that mean TLF decreased in function of *outplant* date and that mean TLF of Chinook outplanted at Slide Creek was greater than at other locations (Table 5).

Table 5. Predictors included in the final GLMM of TLF for Chinook outplanted above Cougar Dam in 2007 are described. Slide Creek was used as the reference for the *outplanting location*.

Predictor	Estimate	Std. Error	Z value	Pr(>|z|)
Outplant date	-0.008	0.002	-3.892	<0.001
Outplant location-Bridge 1980	-0.450	0.214	-2.101	0.036
Outplant location-Bridge 430	-0.434	0.133	-3.270	0.001
Outplant location-Hard Rock	-0.462	0.127	-3.643	<0.001

Reproductive Success – Inference from Juveniles

We found that 1,322 of the 3,006 adult Chinook outplanted above Cougar Dam from 2008-2010 were successful at producing juveniles. We observed that 2008 females had the highest mean and median RS values and that the lowest mean RS values were observed in 2009 for males and females (Table 6). We also found that the 2010 outplants had the highest variance in RS for both sexes and the lowest variances were observed in 2009. In agreement with these results, we found the highest RS values for all three years and between the sexes were present among the 2010 outplants. The maximum RS was 85 offspring for females and 105 offspring for males. These values were roughly twice the maximum RS for both sexes in other years (Table 6).

Table 6. A summary of reproductive success descriptive statistics for Chinook outplanted above Cougar Dam from 2008-2010. (HOR – hatchery origin; NOR – natural origin)

Year	Origin	Sex	N	Mean	Standard Deviation	Median	Max
2008	HOR	*Females*	288	6.7	8.3	4	40
		Males	585	3.3	6.9	0	54
2009	HOR	*Females*	604	2.7	4.3	0	37
		Males	782	2.2	4.6	0	42
2010	HOR	*Females*	202	4.9	11.3	0	85
		Males	295	2.3	7.2	0	47
	NOR	*Females*	64	3.0	8.8	0	54
		Males	186	3.7	12.2	0	105

We found that *outplant date*, *sex*, *year*, and the interaction terms *outplant date*sex*, *sex*outplant location*, *outplant date*year*, and *sex*year* were significantly associated with RS. Based on AIC scores, we determined that a GLMM that included these predictors, except for *sex*outplant location* and *outplant date*year*, best explained variance in RS (Table 7). The mean RS for males decreased by 0.3 percent per outplant date and the mean RS for males outplanted in 2009 and 2010 was 1.4 times that of males outplanted in 2008 (Table 7).

Table 7. Predictors included in the final GLMM of RS for Chinook outplanted above Cougar Dam from 2009-2010 are described. Slide Creek was used as the reference for the *outplanting location*, 2008 was used as the reference *year*, and females were used as the reference for *sex*.

Predictor	Estimate	Std. Error	Z value	Pr(>|z|)
Outplant date	-0.009	0.006	-1.613	0.107
Sex-male	0.154	0.216	0.714	0.475
Year-2009	-1.336	0.473	-2.823	0.005
Year-2010	-1.374	0.356	-3.860	<0.001
Outplant date*Sex-male	-0.004	0.001	-3.947	<0.001
Sex-male*Year-2009	0.366	0.072	5.057	<0.001
Sex-male*Year-2010	0.325	0.055	5.865	<0.001

In 2010 we investigated differences in RS between HOR and NOR Chinook. *Outplant date*, *sex*, and *sex*origin* all had significant relationships with RS in 2010. However following the AIC model selection procedure, only *sex*, *origin*, and *sex*origin* were included in the final GLMM. After accounting for *origin* and *sex*origin*, the mean RS for male Chinook was 0.56 times that of female RS (Table 8). The mean RS of NOR Chinook was less than that of HOR Chinook (Table 8), though we also observed a significant interaction between *sex* and *origin*. An interaction plot indicated that the mean RS for NOR males was greater than HOR males, whereas the mean RS for HOR females was greater than NOR females (Figure 8).

Table 8. RS predictors included in the final GLMM for Chinook outplanted above Cougar Dam in 2010 are described. Slide Creek was used as the reference for outplanting location, females were used as the reference for the *sex* predictor and HOR were used as the reference in the Origin predictor. (HOR – hatchery origin; NOR – natural origin)

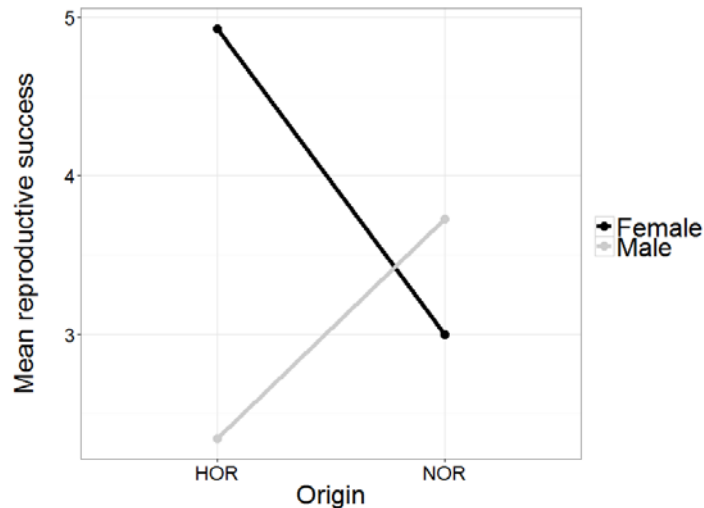| Predictor	Estimate	Std. Error	Z value	Pr(>|z|)
Sex-male	-0.579	0.055	-10.595	<0.001
Origin-NOR	-1.718	0.741	-2.319	0.020
*Sex-male*Origin-NOR*	0.971	0.111	8.749	<0.001

Figure 8. Interaction plot describing the differences in mean reproductive success between HOR and NOR for each sex. (HOR – hatchery origin; NOR – natural origin)

Demography

Population Viability Metrics

We estimated that 119 females and 123 males outplanted in 2007 successfully produced 305 adult offspring that returned in 2010 (n = 7), 2011 (n = 133) and 2012 (n = 165). However, the sex ratio for spring Chinook outplanted above Cougar Dam in 2007 was heavily male biased. We therefore calculated the CRR based on females only, as Chinook population productivity is typically not limited by males (Anderson et al. 2012) and excessive male outplants could result in an unrealistically low CRR if estimated from both sexes. From our analyses we inferred that the 318 females outplanted in 2007 produced only 122 females that returned to the Cougar Trap as 3-, 4-, and 5-year old adults in 2010-2012, resulting in a CRR of 0.38. We estimated the genetic N_e of Chinook outplanted above Cougar Dam was 184 (95% CI: 166-206).

Adult Age Estimates – Scale Analyses

A total of 275 Chinook passed above Cougar Dam had both age estimates from scale readings and from genetic pedigree assignment information. Among these Chinook concordance between scale and genetic estimates for age-4 returns was 75% and 84% for age-5 returns (Figure 9). Notably 31% of the Chinook determined to be age-4 from genetic pedigree exhibited a scale pattern indicative of reservoir rearing, known as pattern "X". In contrast, only 5% of the age-5 adult returns provided pattern X scales (Figure 9).
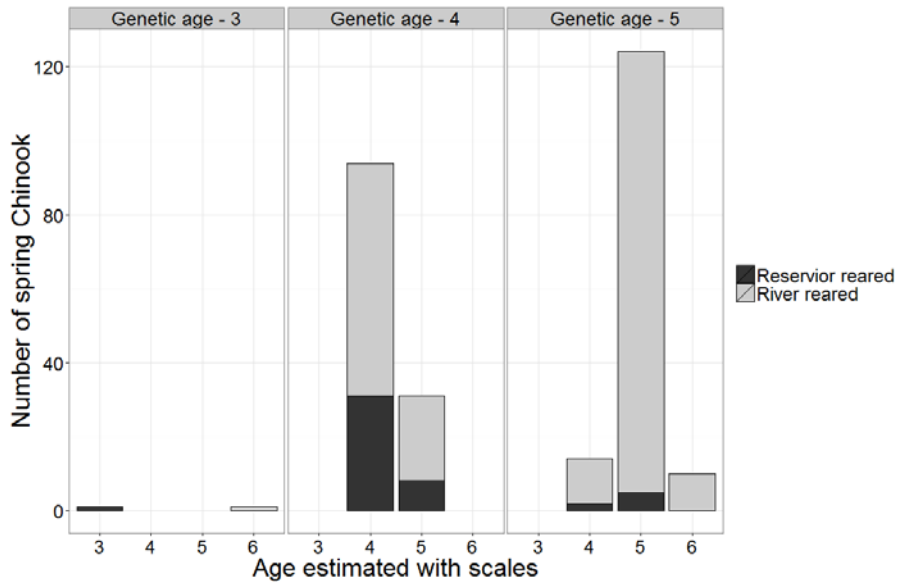

Figure 9. Ages of Chinook passed above Cougar Dam, as estimated from scale and genetic pedigree analyses.

Discussion

In this study, we used a genetic pedigree approach to estimate total lifetime fitness (TLF)of adult hatchery-origin (HOR) Chinook outplanted above Cougar Dam in 2007. We also estimated reproductive success (RS) for 3,006 hatchery- and natural-origin (NOR) adults outplanted in 2008-2010, then tested for effects of origin, outplant date and outplant location on TLF and RS for male and female spring Chinook. We evaluated parent-offspring assignment rates and the age of adult return for South Fork McKenzie River spring Chinook. Finally we estimated values for two important demographic metrics, cohort replacement rate (CRR) and genetic effective population size (N_e).

Overview of Results

In brief, our analyses provided the following results:

Assignment rates – Sixty-three percent of the 500 NOR Chinook collected at the Cougar Trap in 2012 were progeny of 2007-2009 outplants.

I.   Eighty-four percent of Chinook collected at the Cougar Trap before September 1ST were assigned to outplants from 2007-2009, whereas only 21% assigned to outplant parents after that date.

II.   From both 2008 and 2009 adult-juvenile datasets, we assigned >95% of all juveniles to at least one parent. This assignment rate fell to84%in 2010.

III. We identified 503 differences between genotypic and phenotypic sex calls made for 2007-2012 NOR adults (HOR 2011 and 2012 have yet to be scored at *Oty3*).

Outplanting strategies – We identified significant relationships between TLF and both *outplant location* and *outplant date*.

I.   Mean TLF decreased in function of *outplant date* and was highest for adult Chinook released at Slide Creek.

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II.   We identified a similar negative relationship between *outplant date* and RS for male Chinook.

III.   Mean RS for 2009 male outplants was 1.47 times greater than male outplants in 2008. Mean RS for 2010 male outplants was 1.40 times greater than for 2008 male outplants.

HOR/NOR reproductive success – We observed contrasting effects of *origin* on RS between the sexes. The mean RS for NOR males was greater than that of HOR males; whereas, the mean RS for HOR females was greater than that of NOR females.

Demography– The N_e for 2007 outplants was 184 (95% CI: 166-206).

I.   The female CRR for Chinook passed above Cougar Dam in 2007 was 0.38.

II.   Concordance between age estimates using genetic pedigree and scale analyses were 75% for age-4 and 84% for age-5 Chinook. Notably, the reservoir rearing scale pattern was more frequent among for age-4 returns (31%) than age-5 returns (5%).

Assignment rates

Our 11 microsatellite loci had sufficient power to resolve parentage, as evidenced by two statistics. First, we estimated that the mean probability for single parent non-exclusion was 2.47×10^{-7}. Second, the mean probability of POP being false if they matched at every locus was 2.02×10^{-7} and if they matched at all but one locus, the mean probability was 2.82×10^{-6}. Moreover, >99% of all Chinook analyzed in our study were successfully genotyped at all 11 microsatellites and our estimated genotyping error rate was 1%. These results suggest that our methods were rigorous and that we have accurately identified the majority of parent-progeny pairs among our samples.

By sampling and analyzing nearly all Chinook outplanted above Cougar Dam and collected at the Cougar Trap, we found that 63% (316/500) of the adult NOR Chinook collected

at the Cougar Trap in 2012 were progeny of previous outplants. We found that the parent-offspring assignment rate was 84% prior to September 1st and 21% after that date. These results suggest that the majority of Chinook that returned after September 1st were not F1 progeny of Chinook that had been sampled and outplanted above Cougar Dam.

Adult Chinook that home to natal streams are more likely to find favorable spawning habitat and mates (Quinn 2005). However, salmon display variability in the spatial scale to which they home (Connor and Garcia 2006, Dittman et al. 2010). This variability can safeguard them against environmental stochasticity that can make spawning conditions in natal streams unfavorable (Quinn 2005). Therefore, prior to spawning adult Chinook may explore areas near their natal stream because of tradeoffs between homing and habitat quality (Keefer and Caudill 2012; Cram et al. 2012). Given the inferential power that we have demonstrated for microsatellite-based pedigree analyses and the pre-spawn searching behavior just described, we recommend that adult Chinook samples collected from the McKenzie River below Cougar Dam be used to identify progeny of outplants that may have returned to the subbasin without entering the Cougar Trap. Information from such analyses could improve the accuracy of N_e and CRR estimates, and could possibly elucidate source-sink population dynamics in the subbasin.

Male Chinook can become sexually mature at ages 1-6 (Beckman et al. 2003, Larson et al. 2004, Quinn 2005). Diversity among life history strategies may account for some of the progeny without fathers in our pedigree, because some of the unassigned males may be precocious offspring from outplants earlier than 2007 that were not DNA sampled. However, such a life history scenario does not explain observed lack of assignment for mothers in early pedigree because precocious maturation is not commonly observed among Chinook females. Lack of assignment of juveniles to outplant mothers among three adult-juvenile genetic pedigrees (2008-2010) is particularly interesting because almost all outplant parents were DNA sampled. Anecdotal reports suggest that some female Chinook above Willamette Valley Projects may present an adfluvial life history (F. Monzyk, personal comm.), whereby the entire lifecycle occurs in freshwater. It is possible that juveniles with 'unassigned' mothers may in part result from the production of adfluvial offspring from previous outplants. Sampling

adfluvial and precocial male Chinook might serve to resolve additional parental assignments and provide valuable insight into the prevalence of these enigmatic life histories.

The 2010 adult-2011 juvenile pedigree presented a much lower parent-offspring assignment rate (84%). As described above precocial males and adfluvial Chinook that are not accounted for in our genetic pedigree may explain some of the unknown parents in our pedigree. Additionally, the lower assignment rate may be related to the effect of small sample size on variance in family structure observed. In 2011 the total number of juvenile samples captured (3,864) in screw traps was small compared to 2009 (26,876) and 2010 (8,835), despite a comparatively longer sampling effort (182 days). As noted earlier, full- and half-sib family structure is pervasive in juvenile samples. The variance in family structure present within the 2010 adult-2011 juvenile pedigree may be disproportionately large compared to other years because of the smaller sample size in 2011. We observed the highest maximum RS and for both males and females in 2010, which were nearly double the maximum RS values for either sex in any other year. Similarly we observed the highest variance in RS for both sexes in 2010. These results may provide some indication that variance associated with the small sample of juveniles could have inflated the apparent effects that unsampled adfluvial parents have on assignment rates.

We genotyped 4,627 adult Chinook passed above Cougar at *Oty3* and found that 503 differed between phenotypic and genotypic sex calls. Among the 503 sex call differences, we observed that adult Chinook that were phenotypically female, but were genotypically male occurred most frequently (284/503). Correct sex identification is essential because sex is used when assigning parents to offspring. We recommend that sex of all adult Chinook being passed above Cougar Dam be verified using *Oty3* in future years.

Outplanting strategies

Our results for 2007 outplants suggested an adults outplanted earlier in the year had greater TLF than those outplanted later. We observed a similar result when testing the relationship between *outplant date* and RS for 2008-2010 outplants. However, the relationship was only present for male Chinook. Similarly, Williamson et al. (2010) reported significant

negative relationship between run timing and reproductive success for Chinook spawning in the Wenatchee River, Washington. These results may be explained by spawning behavior of Chinook. The higher RS of early arriving Chinook may be related to advantages gained during the establishment of spawning territories. Females that return earlier to spawning grounds may select redd sites with limited intraspecific competition (Quinn 2005). As for male Chinook, more time on the spawning grounds may afford additional opportunities to search for and mate with a greater number of females (Quinn 2005; Neville et al. 2006). We acknowledge that our TLF results are limited to a single cohort HOR Chinook. Nevertheless, our results suggest that RS of Chinook above Cougar Dam could be maximized by releasing outplants as early in the season as possible.

We found that mean TLF was higher at Slide Creek than other sites. However, no relationship between *outplant location* and RS was observed for 2007 outplants. Outplant locations can vary with respect to water depth, temperature and distance to quality spawning habitats. These differences may explain some variance in TLF and RS of Chinook outplanted at different locations. Other researchers have used radio telemetry to track the movement of female Chinook passed above Cougar Dam (Zymonas et al. *In prep*) and forthcoming data syntheses may reveal additional relationships between *outplant location,* adult movements and RS.

HOR/NOR reproductive success

In recent years, numerous studies have investigated differences between the RS of HOR and NOR salmonids (Araki et al. 2007a; Araki et al. 2007b; Williamson et al. 2010; Thériault et al. 2011; Thériault et al. 2011; Hess et al. 2012; Anderson et al. 2012; Milot et al. 2013). These studies have informed the debate over the use of hatcheries in supplementation programs. Using parentage assignment data for 250 NOR and 497 HOR Chinook passed above Cougar Dam in 2010, we found the effect of HOR on RS was different for males and females. Specifically, the mean RS for NOR males was greater than for HOR males, but the mean RS for NOR females was less than that of HOR females. Anderson et al. (2012) reported the mean RS for NOR male was greater than that of HOR males for three consecutive years. They found no consistent effect of

origin on RS for female Chinook (Anderson et al. 2012). Williamson et al. (2010) reported negative effects of HOR on RS for both males and females in two consecutive years. Our observation that HOR males had a mean RS lower than that of NOR males is consistent with these findings and further suggests that the value of male HOR Chinook in supplementation and reintroduction programs should be carefully considered by managers. Our results also suggest that the relatively high RS of female HOR Chinook may provide significant demographic benefits to the reintroduction program above Cougar Dam.

Prior to 2010 the only Chinook passed above Cougar Dam were HOR, which likely means that some of the 2010 NOR Chinook are F_1 progeny of a two HOR parents. Several studies have shown that F_1 hatchery fish that are reared in the wild do not do as well as NOR fish including Araki et al. (2009) and Theriault et al. (2011). Therefore the F_1 fish in our study would likely not do as well. However, we lack tissue samples from HOR Chinook passed above Cougar Dam prior to 2007 and therefore are unable to determine age-4 and -5 NOR Chinook were actually F_1 progeny of HOR parents.

Demography

We estimated two demographic metrics in our study, N_e and CRR. N_e is defined as the size of the ideal population that will result in the same amount of genetic drift as in the actually population being considered (Allendorf and Luikart 2007). Currently N_e is used when assessing population viability (Jamieson and Allendorf 2012). N_e served as the basis for the 50/500 rule (Frankham 1980), which provides guidelines to avoid the short term risks posed by rapid genetic drift that occurs in small populations and secure the long term adaptive benefits of genetic diversity that can only be maintained in larger populations. In brief, this rule suggests that a population should have a N_e of no less than 50 for short term persistence and no less than 500 over the long term. Some suggest that the 50/500 rule should only be used as a general guideline for genetic management of populations (Allendorf and Luikart 2007). In this context, we estimated N_e for the 2007 year class was 184 (95% CI: 166-206). An Ne of this size should be sufficient to avoid immediate impacts from inbreeding depression and random

genetic drift. Future estimates of N_e will be useful for assessing long-term genetic integrity of Chinook passed above Cougar Dam.

We estimated the female CRR for 2007 outplants to be 0.38, which is well below one. This result indicates that the population above Cougar Dam is not replacing itself. There are many factors that may affect spawner success and survivorship to adulthood including pre-spawn mortality (Keefer et al. 2010), availability of spawning habitat, dam passage (Muir et al. 2001), availability of juvenile rearing habitat (Quinn and Peterson 1996), estuary conditions (Magnusson and Hilborn 2003), and ocean conditions (Peterson and Schwing 2003). Understanding how these factors affect spring Chinook returns to the headwaters of the South Fork McKenzie River will provide direction to improve replacement rates. Because current estimates of genetic effective population size are closer to 50 than 500 and the first estimated cohort replacement rate is well below one, it remains important to monitor trends in this population to ensure successful reintroduction of Chinook into the historically important habitat above Cougar Dam.

Acknowledgments

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