Relative Reproductive Success of Supplemented Upper Yakima River Spring Chinook - Preliminary Report for Broodyear 2007

P.F. Galbreath, I.J. Koch, S.R. Narum, K.I. Warheit, T.R. Seamons, T.W. Kassler, D.E. Fast, W.J. Bosch, M.V. Johnston, and C.R. Strom
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Peter F. Galbreath, Ilana J. Koch, and Shawn R. Narum

1 Columbia River Inter-Tribal Fish Commission (CRITFC), Fish Science Department, 700 NE Multnomah Street, Portland, OR, 97232

Kenneth I. Warheit, Todd R. Seamons, and Todd W. Kassler

Molecular Genetics Laboratory, Washington Department of Fish and Wildlife, 600 Capitol Way N., Olympia, WA 98501

David E. Fast, William J. Bosch, Mark V. Johnston, and Charles R. Strom

Yakama Nation Fisheries, Post Office Box 151, Toppenish, Washington 98948, USA

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Abstract

The Cle Elum Supplementation and Research Facility (CESRF) operates integrated hatchery program for Yakima River spring Chinook Salmon *Oncorhynchus tshawytscha*, designed to test whether artificial propagation can increase natural production and harvest opportunities while keeping ecological and genetic impacts within acceptable limits. Among the original goals for the CESRF monitoring program is performance of a population-scale productivity assessment. Recent advances in molecular genetic technologies have made such an assessment feasible, and a collaborative (CRITFC and WDFW) 5-broodyear (2007-2011) study was designed and initiated. The study will not be complete until 2019, although an initial analysis for broodyear 2007 was recently performed. Results for this analysis include: a) the proportion of adults passed upstream for natural spawning that were identified as having produced one or more adult progeny was relatively high: 82% and 80% for natural and hatchery origin females, 73% and 75% for natural and hatchery origin males, and 47% and 35% for natural and hatchery origin age 3 jack males; b) natural origin adults (sexes combined) used as hatchery broodstock produced on average 2.15 times more returning adult progeny than natural origin fish passed upstream for natural spawning; c) the average number of adult recruits-per-spawner within females and adult males, was similar for hatchery origin and natural origin fish spawning naturally, though average natural productivity of age 3 hatchery origin jack males was lower than for natural origin jacks. Within hatchery origin fish that spawned naturally, average productivity differed depending on which of the 3 acclimation sites the fish were released from as smolts, though these differences were not statistically significant.

I.   Introduction

Returns of anadromous salmon and steelhead *Oncorhynchus* spp. to rivers throughout the Columbia River basin decreased dramatically over the 20th century, largely due to passage impediments and other effects associated with the development of the Columbia River system for hydroelectric power (NPPC 1987). In response, numerous hatchery programs were established to produce fish as mitigation for the loss of natural freshwater smolt production. These hatchery programs were financed in large part through the Mitchell Act (1938), the Grand Coulee Fish Maintenance Project (1939) and the Lower Snake River Compensation Plan (1975), and in additional agreements with the Bonneville Power Administration (BPA), public utility districts and other hydroelectric companies.

While the hatchery programs led to increased adult escapement, returns of naturally produced salmonids continued to decline, reaching all-time lows in the mid-1990s. Status reviews of Columbia basin salmonid populations conducted in that period led to the designation of several of the evolutionarily significant units (ESUs) of salmonid species in the basin as Threatened or Endangered under the Endangered Species Act

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(http://www.westcoast.fisheries.noaa.gov/publications/status_reviews/salmon_steelhead/salmon_steelhead_esa_status_reviews.html).

Until that time, the overriding objective of the hatchery programs was to augment the number of returning adults available for sport and commercial fisheries. The hatcheries were located largely in lower mainstem areas of the Columbia River and its tributaries, and smolts were commonly released directly from their hatchery of origin. Returns of the fish as mature adults were, therefore, to the vicinity of their natal hatcheries. Also, the hatcheries practiced segregated broodstock management - returning hatchery origin adults were used as broodstock each successive generation, resulting in selection for fish increasingly adapted to the hatchery environment (domestication selection). While unintended, varying numbers of returning adults from these harvest augmentation programs did escape to natural spawning areas and successfully interbred with fish of the wild populations. The likely result was a reduction of the overall fitness of the affected natural populations, which further threatened their viability.

An alternative strategy for hatchery management was therefore proposed for programs associated with depressed natural populations. Supplementation, as this approach was termed, was defined as "the use of artificial production in the attempt to maintain or increase natural production while maintaining the long term fitness of the target population, and keeping the ecological and genetic impacts on non-target populations within specified biological limits" (RASP 1992). To achieve these goals, the supplementation model recommended use of integrated broodstock management - incorporation of natural origin fish (up to 100%, if possible) into the hatchery broodstock, and that the program be scaled relative to each subbasin's estimated current and historic capacity for natural smolt production. Additionally, following rearing to the smolt stage the juveniles were to be transported to upstream areas for release in proximity to the natural spawning grounds within the system, preferably from holding facilities where the smolts would be acclimated for a period of time prior to release. Following this approach, supplementation fish are not subjected to domestication selection to the extent experienced under conventional hatchery management, and returning supplementation adults will imprint and home to the spawning areas to augment the natural population (SRG 1991; RASP 1992; Cuenco et al. 1993). However, as described in these reports, the ability of a supplementation program to achieve these goals had been largely untested.

In the 1987 Columbia River Basin Fish and Wildlife Program of the Northwest Power and Planning Council (NPPC 1987), the Yakima River Basin was identified as one in which to focus efforts for off-site enhancement as mitigation for hydropower development in the Columbia basin, with funding from BPA. In response, the Yakima Fisheries Project was developed (later expanded to the Yakima Klickitat Fisheries Project; YKFP). In addition to proposing actions to improve water management and fish passage within the Yakima subbasin, the project called for construction of a spring Chinook salmon *O. tshawytscha* hatchery facility, for production of fish to increase abundance of the depressed population in the upper Yakima River basin. The hatchery program was designed with the additional objective of assessing utility of the supplementation model. To this end, an extensive monitoring program was included to "provide resource managers with knowledge" regarding survival of hatchery reared fish, competitive interactions with wild populations, and long-term fitness of fish stocks, and "to

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identify and apply improved methods for carrying out hatchery production and supplementation of a natural production" (BPA et al. 1996; Busack et al. 1997).

Construction of the Cle Elum Supplementation and Research Facility (CESRF), Cle Elum WA, was completed in 1997 (Figure 1). Each year since then a proportion of the natural-origin (NOR) migrating adult spring Chinook salmon intercepted in the Roza Adult Monitoring Facility (RAMF; rkm 206) located adjacent to the Roza irrigation diversion dam (Figure 1), are selected and transported to CESRF for holding until the spawning season. NOR fish not selected for broodstock and all hatchery-origin (HOR) adults are immediately released to continue their upstream migration for natural spawning in the upper Yakima River basin.
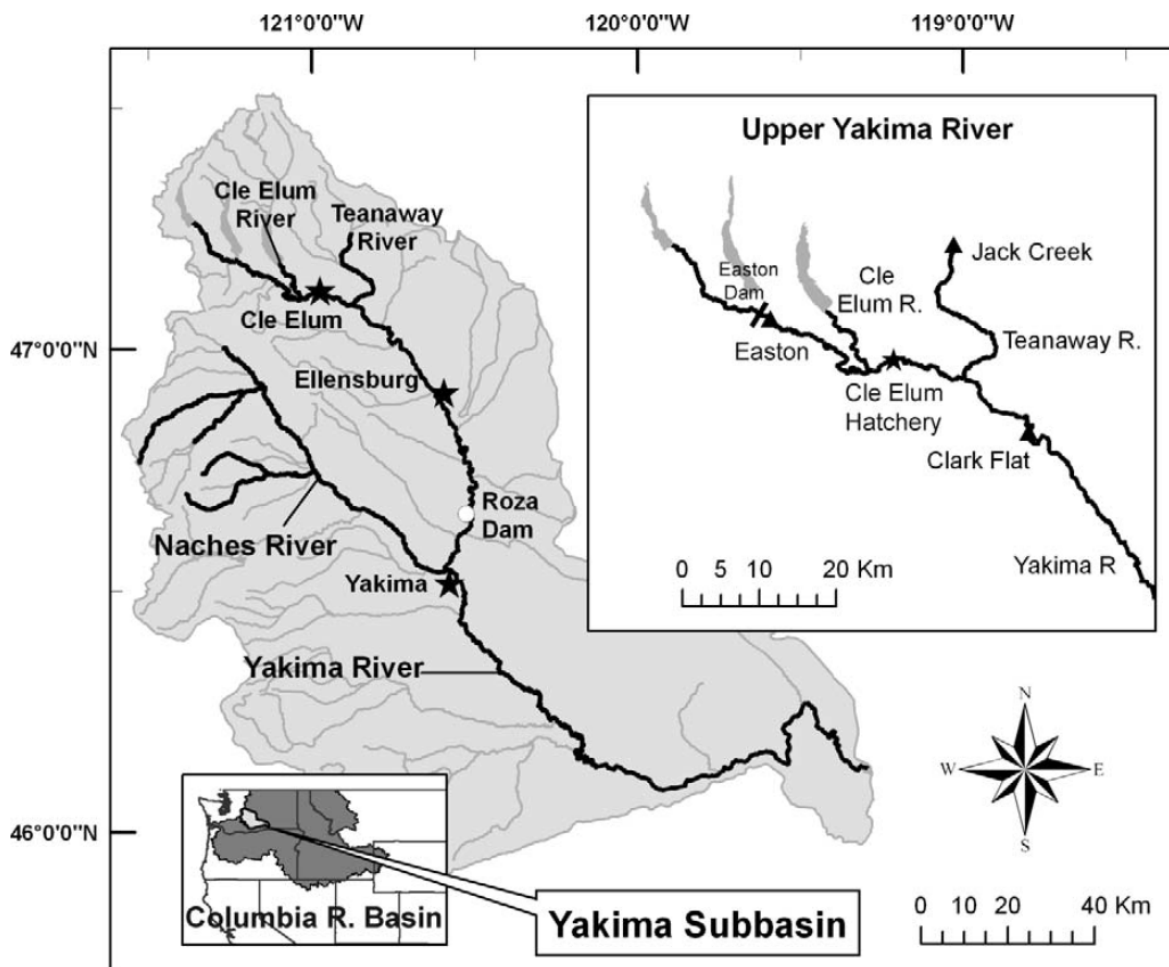

Figure 1. Map of the Yakima River basin, Washington, including location of Roza Dam (site of the Roza Adult Monitoring Facility, RAMF) and the town of Cle Elum, adjacent to which is located the Cle Elum Supplementation Research Facility. The upper inset illustrates location of the Cle Elum hatchery, and of the three acclimation sites (black triangles) - Easton, Jack Creek, and Clark Flat. The lower inset shows the location of the Yakima River subbasin within the Columbia River basin (figure copied from Dittman et al. 2010).

The NOR broodstock transferred to CESRF (generally 400 to 500) are spawned in September-October each year. Their HOR progeny are reared to the smolt stage (age 1+; approximately 720,000 per broodyear; BY). The fish are then transferred, typically in March, to one of three satellite acclimation facilities located in the upper Yakima basin – Easton, Clark Flats and Jack Creek (Figure 1). Prior to transfer, the smolts are coded wire tagged (CWT) and marked by injection with one of three colors of fluorescent elastomer into the clear adipose eyelid tissue, with each color specific to the acclimation site to which the fish were transferred. After acclimation for 4-6 weeks, the smolts are released into the river, and the fish proceed to out-migrate. To date, adult returns from these HOR fish consist of age 3 jack males, a majority of females and males returning as age 4 adults, and a limited number of age 5 females and males (YN 2010; Fast et al. 2015).

Monitoring information gathered since initiation of the program has been used to evaluate and report differences among NOR and HOR fish for: a) life history traits of smolts and returning adults (e.g., size, age, sex ratio, external morphometrics; Busack et al. 2007, Knudsen et al. 2006, 2008), b) relative rates of precocious male maturation and environmental and management factors influencing maturation rate (Larsen et al. 2004, 2006, 2010, 2013, and Pearsons et al. 2009), c) homing and spatial distribution of naturally spawning adults (Dittman et al. 2010), d) aggression and competition characteristics (Pearsons et al. 2007), and e) ecological interactions of the HOR fish with other fish taxa in the basin (Fritts et al. 2007, Fritts and Pearsons 2008, Pearsons and Temple 2007, 2010). Additionally, the extent to which the supplementation program has been able to boost NOR returns has been assessed by a comparison of return number to the upper Yakima basin relative to the adjacent Naches River, which has remained unsupplemented (Fast et al. 2015).

One aspect of supplementation that has been difficult to test, however, is the effect of supplementation on naturally-spawning population fitness. The original monitoring and evaluation plan for the program proposed a "macro level" genetic assessment of relative productivity, involving DNA fingerprinting and pedigree analysis of the entire supplemented upper Yakima River population (Busack et al. 1997; 2006). Results of the parentage analyses were to be examined to estimate individual productivity (number of returning adult progeny per natural spawner), average productivity of NOR and HOR adults within sexes, and relative reproductive success (RRS) – the ratio of average productivity for HOR/NOR. A finding of similar productivity (RRS≈1) would indicate that hatchery rearing had little or no deleterious effect on reproductive success of the supplementation fish, while a finding of RRS<1 would indicate reduced success and the possibility of supplementation causing a progressive reduction in fitness of the integrated population. However, the technologies for screening with the proposed microsatellite DNA markers were still under development in regional fisheries genetics laboratories. Also, with annual adult returns numbering in the thousands, the cost for such an extensive study were well beyond available Project funds. In lieu of a full population study, smaller "micro level" scale studies to assess RRS of NOR and HOR fish were conducted in a semi-natural spawning channel constructed adjacent to the CESRF hatchery raceways (Schroder et al. 2008 and 2010). These studies were conducted over several years involving combinations of fish of differing sizes and ages within sexes and origins. While results indicated

minimal differences in spawning behaviors and productivity between NOR and HOR spawners in the artificial channel, performance of a productivity assessment of the natural spawning population in the upper basin remained a goal for project co-managers.

In recent years, technologies for performance of molecular genetic analyses and application of these technologies to questions concerning population genetics and fisheries management have expanded dramatically. These advances have facilitated evaluation of genetic divergence in HOR fish from the Cle Elum program (Waters et al. 2015). Additionally, development of a large array of single nucleotide polymorphism (SNP) DNA markers (replacing microsatellites as the marker type of choice in most cases) for Chinook salmon and application of new high throughput genotyping techniques (Campbell et al. 2015) has led to a dramatic decrease in per-sample genotyping cost, and a "macro level" genetic assessment of relative productivity in the Cle Elum supplementation program is now technically and financially feasible. In 2014, discussions between YN, WDFW, and CRITFC led to an agreement to perform a RRS study of naturally spawning NOR and HOR fish in the upper Yakima River, covering five consecutive broodyears (2007-2011). The study involves genotyping a total of approximately 46,000 samples, involving the NOR and HOR adults passed upstream of Roza Diversion Dam for natural spawning in those five years, plus their NOR adult progeny that returned in years 2012 through 2016 (Table 1).

Table 1. Sample numbers per return year involved in the five broodyear relative reproductive success study of the upper Yakima River spring Chinook salmon supplementation program.

	Adults Sampled for Genotyping		
Year	Natural Origin	Hatchery Origin	Unknown Origin
2007	1,282	1,498	na
2008	1,677	3,240	191
2009	2,544	4,462	175
2010	3,186	5,514	157
2011	3,925	4,819	232
2012	2,927	na	160
2013	2,784	na	na
2014	3,761	na	na
2015	3,386	na	14
2016	500*	na	na
Sub-Totals	25,972	19,533	929

(* estimated)

The genotyping and subsequent parentage and productivity analyses are being performed collaboratively between the CRITFC molecular genetics laboratory at the Hagerman Fish Culture Experiment Station, Hagerman ID, and the WDFW Molecular Genetics Laboratory, Olympia WA. Funding for work performed by CRITFC is provided through the Basinwide Supplementation Evaluation project (BPA Project No. 2009-009-00), and by WDFW through the YKFP (BPA Project

No. 995-063-25). While completion of analyses for all five broodyears is not anticipated until 2019, genotyping and a preliminary relative productivity analysis was performed for the initial broodyear (BY 2007). A description of the methodologies and results from this preliminary analysis are described in the present report.

II.   Methods

Biodata has been recorded each year for all returning adult spring Chinook salmon collected in the RAMF during their migration to the upper Yakima River basin. These data include collection date, origin, sex, length and weight, and presence of a CWT, passive integrated transponder (PIT) tag, and/or elastomer tag for each individual, plus a tissue (fin clip) and scale sample were collected from a representative sample of the fish. Finally, note was made whether a fish was passed upstream for natural spawning, or diverted to the Cle Elum hatchery for use as broodstock. Beginning in 2007, tissue sampling was expanded to 100% of the adults interrogated at RAMF, and the retrospective RRS study was therefore designed to begin with BY 2007.

This preliminary assessment of productivity for BY 2007 adults involved extraction of DNA from the tissue samples collected from all of the NOR and HOR adults released upstream for natural spawning, along with all NOR adults that returned to the RAMF in 2010, 2011 and 2012 as potential age 3, age 4 and age 5 progeny from BY 2007, respectively. DNA was extracted from the fin tissue using two separate methods over the course of the study: a standard Qiagen DNeasy protocol paired with a Qiagen 3000 robotic pipetting system (Qiagen Inc., Valencia, CA) and the Chelex 100 method (Sigma-Alrich, St Louis, MO). Genotyping was then performed for a standardized suite of 189 SNP markers, which included one marker that identifies genetic sex (Hess et al. 2014). Among the 189 markers, 6 failed to produce a genotype for ≥10% of the samples analyzed; these 6 markers were therefore deleted, leaving 183 markers in the panel for use in the parentage analyses. The package idfgen in R (RCore 2016) was then used to trim individuals with ≥10% missing genotypes for the panel, along with any samples that had duplicate genotypes (https://github.com/mackerman44/idfgen). The remaining data were then entered into SNPPIT (Anderson 2010), a public domain likelihood-based software package for performing parentage inference – identification of the most likely parent pair for each progeny - based on SNP genotypes (https://swfsc.noaa.gov/textblock.aspx?Division=FED&ParentMenuId=54&id=16021). The parentage analyses were conducted with the following parameter settings:

- assume a genotyping error rate of <0.005% (1% per locus)
- removal of any trios (progeny and parent pair combinations) with >2 SNP marker mismatches
- False Discovery Rate (a measure of confidence of parentage assignment) <0.05

The resulting data were analyzed to determine the number of adult progeny assigned to each of the BY 2007 individuals. Average individual productivity was estimated within parent origin

(HOR versus NOR) for females, males and jacks separately. RRS ratios were then estimated for all adults passed upstream for natural spawning, and for just successful parents – adults for which one or more progeny were assigned with high certainty.

III.   Results and Discussion

Of the 2,314 tissue samples collected in 2007 from the NOR and HOR adults that were passed upstream of RAMF for natural spawning, 2,291 (99%) were successfully genotyped. Parentage analyses for these individuals identified a total of 2,516 trio assignments with adults among the returns in 2010, 2011 and 2012. Average productivity was estimated within parent origin (HOR versus NOR) for females, age 4 and 5 males, and age 3 jack males, and the resulting RRS ratios are provided in Table 2.

Table 2 – Average productivity (recruits-per-spawner; R/S) and relative reproductive success (RRS) of natural origin (NOR) and hatchery origin (HOR) spring Chinook salmon released for natural spawning in the upper Yakima River in 2007.

Sex/Age	Origin	Number Adults Genotyped	Number (Proportion) Successful Adults	Number Adult Offspring	All Adults Genotyped		Successful Adults	
					Average R/S	RRS (HOR/NOR)	Average R/S	RRS (HOR/NOR)
Females	HOR	400	318 (0.80)	1,215	3.04	0.90	3.82	0.94
(age 4&5)	NOR	386	318 (0.82)	1,297	3.36		4.08	
				2,512				
Males	HOR	319	238 (0.75)	920	2.88	0.95	3.87	0.93
(age 4&5)	NOR	260	190 (0.73)	787	3.03		4.14	
				1,707				
Jacks	HOR	767	272 (0.35)	632	0.82	0.72	2.32	0.95
(age 3)	NOR	159	74 (0.47)	181	1.14		2.45	
		2,291		813				

Among the adult females and males of both origins, a large majority (73% to 82%) were identified as having produced one or more adult progeny (Table 2). This rate of successful adult offspring production is high relative to that observed in other studies of supplemented spring Chinook salmon populations. For example, spawning success averaged across multiple broodyears was approximately 40% in both the Wenatchee River (Williamson et al. 2010) and in Johnson Creek (Hess et al. 2012, Supplemental Data).

The proportion of BY 2007 jacks that were assigned one or more progeny was only half that of adult males within origins (Table 2). Reduced reproductive success of spring Chinook salmon jacks was also observed by Williamson et al. (2010) and Hess et al. (2012), and conforms with observations for early maturing males among salmon species in general. The smaller size of

early maturing males reduces their competitive abilities on the spawning grounds relative to older larger adult males (Foote 1997; Esteve 2005; Berejikian et al. 2010; Schroder et al. 2012).

The proportion of females, males and jacks (origins combined) assigned 0, 1, 2, etc. offspring is illustrated in Figure 2. The relatively linear decline in frequency among female and male parents as family size (number of progeny per parent) increases contrasts substantially with the exponentially declining distribution for jacks. The rapid decline observed for jacks is an effect both of the lower success rate for jacks (i.e., a large proportion were assigned zero progeny), and of the lower productivity among successful jacks relative to age 4 and 5 adults. In fact, the highly skewed frequency observed for the BY 2007 jacks resembles more closely the family size distributions observed for spring Chinook salmon by Williamson et al. (2010) and Hess et al. (2012). In both studies, success rate was low, as was average productivity among successful spawners, relative to the Yakima BY 2007 females and males. It remains to be seen whether these frequency distributions for females and males in the remaining four broodyears (2008-2011) planned for this study - broodyears where the number of adult progeny relative to the number of potential spawners is likely much lower - will more closely resemble the skewed distribution observed for BY 2007 jacks.
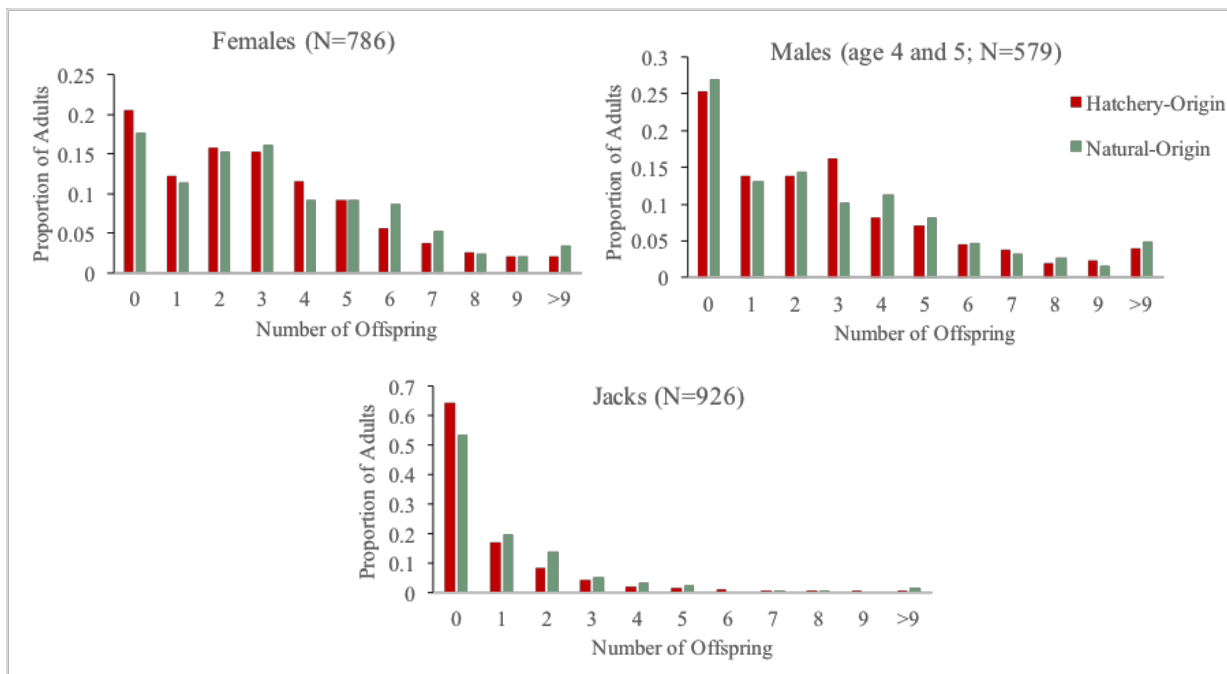

Figure 2. Frequency distribution for family size (number of progeny per parent) for BY 2007 females, males and jacks (NOR and HOR presented separately).

To meet the objective of a hatchery supplementation program to increase natural production, the number of adult recruits produced by fish taken into the hatchery broodstock must exceed the number they would have produced had they been left in the river to spawn naturally. To assess the extent to which the Cle Elum hatchery supplementation program provided this demographic boost, we calculated the number of HOR adult recruits (n=1,123) assigned to NOR

fish used as broodstock in 2007 (n=365; adult females and males, and jacks combined), which yields an overall average of 3.08 recruits-per-spawner (1,123 / 365 = 3.08). To estimate the average number of NOR recruits attributable to the 805 NOR fish released for natural spawning in BY 2007, we multiplied the total number of NOR adult recruits (n=2,520) by the sum of the proportion of these fish produced by two NOR parents (0.206) plus one half the proportion produced by a NOR and a HOR parent (0.500/2): 2,520 x (0.206 + 0.500/2) = 1,149. The estimate for average productivity of a NOR natural spawner was therefore 1,149 / 805 = 1.43, and the estimate for the demographic boost from taking a NOR fish into the broodstock was therefore 3.08 / 1.43 = 2.15.

Average productivity for all adult females and adult males, within origins, that were passed upstream for natural spawning was approximately three adult recruits-per-spawner (range = 3.03 to 3.36). As regards only successful spawners - fish for which one or more adult progeny were identified – average productivity was approximately four recruits-per-successful spawner (range = 3.82 to 4.14). These levels of productivity are well above replacement (Table 2). However, it should be noted that BY 2007 was exceptional in that adult returns that year were low and competition for spawning and juvenile rearing habitat would have been minimal. Additionally, the years when BY 2007 progeny returned as mature adults were years of relatively high return numbers for BY 2007 cohorts of salmon across the Columbia River basin, reflecting generally favorable ocean conditions for these cohorts. The high average productivity observed in BY 2007 is unlikely to be observed in the remaining broodyears to be assessed in this study (2008-2011). These subsequent broodyears were characterized by much higher adult escapement, with the likelihood of proportionally lower average NOR recruits-per-spawner.

Relative productivity of HOR females spawning naturally in 2007 was numerically lower than for NOR females, though these values were not significantly different (p>0.05), both when compared for all adults passed upstream (RRS=0.90) and when limited to successful spawners (RRS=0.94). Likewise, productivity of NOR and HOR age 4 and 5 males was numerically lower but not significantly different (p>0.05); RRS for all males = 0.95, and RRS for successful males = 0.93. In contrast, productivity of age 3 jack males calculated for all fish passed upstream was significantly lower for HOR jacks (RRS=0.72; p=0.042), though when considering only successful jacks productivity was similar for NOR and HOR fish (RRS=0.95; p>0.05; Figure 3).

Relative productivity of naturally spawning NOR and HOR adults was also assessed by comparing average recruits-per-spawner for crosses between two NOR fish to that of: a) crosses between two HOR fish, and b) crosses between a HOR and a NOR fish. In both cases relative fitness did not differ significantly from 1.0 (Figure 4).
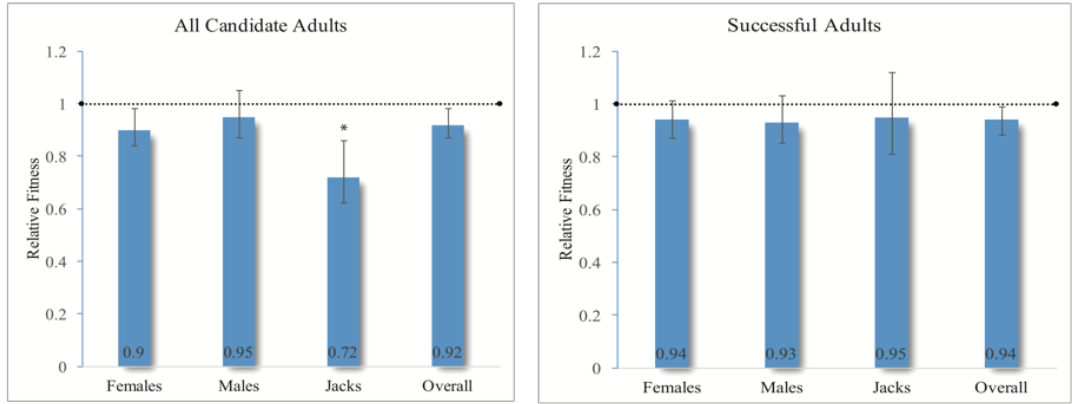
Figure 3. Relative fitness of BY 2007 females, males and jacks, calculated as the ratio of the average number of recruits-per-spawner of HOR fish divided by NOR fish.
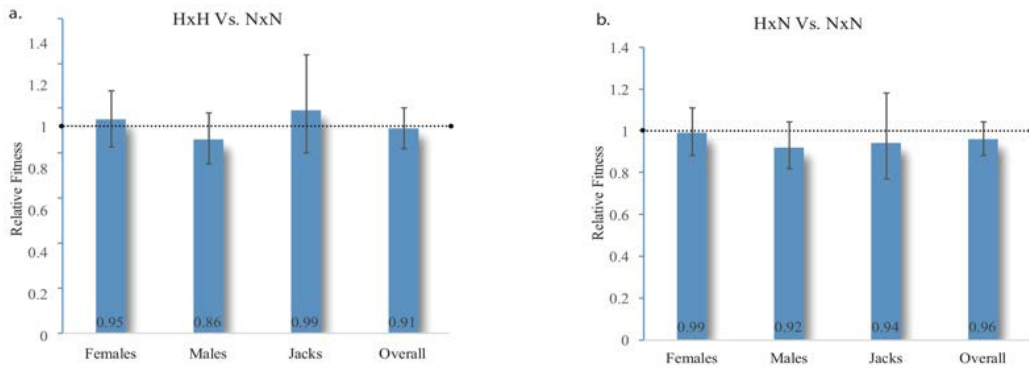

Figure 4. Relative fitness of BY 2007 HOR females, males and jacks involved in a.) crosses with a second HOR parent (HxH), and b.) crosses with a NOR parent (HxN), standardized to fitness of NOR females, males and jacks that spawned with a second NOR parent (NxN). Error bars represent 95% confidence intervals; ANOVA results for each comparison indicated no significant differences from RRS=1.0.

Productivity was further assessed for differences associated with acclimation release site. Among the 1,498 HOR fish released upstream for natural spawning in 2007, 1192 (80%) were identifiable to their acclimation site (the elastomer tag was unreadable for the remaining 20%). Relative reproductive success of the HOR fish was then calculated by estimating the average productivity for females, males and jacks within acclimation site, and dividing by the overall average productivity of NOR fish in the basin. Numerically, productivity of females and males was consistently greatest for HOR fish released from Easton and lowest for fish released from Clark Flat, although these differences were not statistically significant (Table 3). Curiously, jacks exhibited the opposite trend; jacks released from Clark Flat demonstrated the highest average productivity and those released from Easton the lowest, though again the differences were not statistically significant. Likewise, none of the RRS estimates were statistically significant (Table 3).

Table 3. Average productivity of successful HOR spawners relative to acclimation site of release, and relative reproductive success (RRS) estimates (in parentheses) standardized to overall NOR reproductive success.

Acclimation Site	Recruits per Successful HOR Spawner (RRS)		
	Clark Flat	Jack Creek	Easton
Females	3.46 (0.85)	3.83 (0.94)	4.00 (0.98)
Males	3.33 (0.80)	3.73 (0.90)	3.96 (0.96)
Jacks	2.34 (0.96)	2.29 (0.94)	2.06 (0.84)

The Yakima River supplementation program was designed with three different acclimation sites in order to encourage widespread use of available spawning and juvenile rearing habitat in the upper basin. Quality of the habitat for spawning and juvenile rearing in proximity to the different acclimation site varies, and it was suspected that differences in relative productivity of fish released from one site versus another might be observed. As indicated above, however, average productivity was generally similar.

Dittman et al. (2010) observed that the majority of spawning by NOR spring Chinook salmon in the upper Yakima River basin occurs in an approximately 20 km stretch of the river that happens to also be centered around the location of the CESRF. This reach is well upstream of Clark Flat, and downstream of Easton – the two mainstem release sites for the HOR smolts. Presumably, this stretch where the NOR fish concentrate represents the higher quality spawning habitat within the upper basin. Returning HOR adults released from Easton and Clark Flat in the mainstem Yakima River also tend to concentrate in this area for spawning, though distribution of HOR fish released from Easton extends further upstream, while those released from Clark Flat have a distribution that extends further downstream. Among fish released from Jack Creek, only a minority of the returning adults were observed to have spawned in the Teanaway River or Jack Creek itself. This is likely due to habitat and low flow conditions in the lower Teanaway which may impede or discourage adult passage. Instead, the majority of these fish were observed to have spawned in the same general area as the NOR fish. Dittman et al. (2010) concluded that while a homing response to the general area of their respective release site was evident among the three groups of HOR spring Chinook salmon, the final spawning location appeared to be based on favorable characteristics of the spawning habitat – which coincided largely with habitat chosen by NOR fish in the basin.

This preliminary RRS assessment for BY 2007 was based on genotypes for individuals with a standardized panel of 183 SNP markers, followed by parentage analyses with SNPPIT. Since 2015 when sample genotyping was initiated, the standardized SNP panel for Chinook salmon has been expanded to 298 SNP markers, to provide additional resolving power. Currently, all samples associated with the RRS study are being genotyped in the CRITFC and WDFW laboratories for the expanded panel, and supplemental genotyping is being performed on those samples analyzed previously for 183 markers, so that all individuals in the study will have genotypes for the full panel. Additionally, since the preliminary assessment described here, the decision was made to switch software programs for performance of the parentage analyses, from SNPPIT to Colony (https://www.zsl.org/science/software/colony; Jones and Wang 2010).

Colony utilizes a maximum likelihood approach with multilocus genotypes to assign sibship and parentage jointly. The program will identify not just parent pairs, but also single parent assignments (unlike SNPPIT) when one parent is missing from the database or cannot be distinguished with sufficient certainty. Inclusion of single parent assignments should increase the power to test for differences in productivity. It will also allow for evaluation of spawning success of non-migratory male Chinook salmon, and should the study be extended for additional years, grandparentage analysis will permit evaluation of the RRS of non-migratory HOR and NOR male Chinook salmon as well as help in parsing out heritable from environmental effects on productivity in HOR fish (e.g., Christie et al. 2011; Ford et al. 2015; Sard et al. 2016). Genotyping is ongoing, and analyses using Colony for all five broodyears is anticipated to be complete in 2019. Additionally, analyses of the parentage and productivity results will be expanded to include tests for differences in size and arrival date at RAMF, to assess whether these factors might have interacting effects on relative productivity with respect to origin within sex/age groups.

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