Comprehensive Evaluation of Grant County Public Utility District's Fall Chinook Salmon Hatchery Program

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Executive Summary

The three Public Utility Districts (PUD) of the middle Columbia River strive to achieve no net impact of Salmon and steelhead as a result of construction and operation of five Columbia River dams. One of the three components the PUDs use to achieve no net impact is the production of hatchery fish to replace juvenile fish lost through the project areas. A comprehensive monitoring and evaluation plan is implemented to determine if the performance of the hatchery programs is achieving the goals described in the plan (Hillman et al. 2019). This report is a synthesis of the analyses and results from data collected for the Grant County PUD fall Chinook Salmon hatchery program through 2018. Other covered species (e.g., spring and summer Chinook, Sockeye Salmon, and steelhead) are presented in other reports. Authorship, titles, and abstracts of each of the report chapters are presented below.

1) Pearsons, T. N., A. H. Haukenes and S. P. Richards. The effects of a harvest augmentation hatchery on the abundance and productivity of fall Chinook Salmon in the Hanford Reach of the Columbia River.

We evaluated a large integrated harvest augmentation hatchery program to determine if it could meet the dual goals of harvest augmentation and minimizing negative impacts to a naturally spawning population in the Hanford Reach of the Columbia River. Adult escapement to the Hanford Reach and the peak abundance of redds before (1948–1984 redds; 1964-1984 escapement) and during (1985-2018) the full supplementation program were compared. The mean peak redd count, adult natural-origin escapement, and total adult escapement to the Hanford Reach before supplementation were 2,067, 26,311 and 26,525, respectively. During the supplementation period the mean peak redd abundance, 8,024, adult natural-origin escapement, 65,785, and total adult escapement, 73,526, were significantly larger than the pre-supplementation period ($P<0.001$). During the supplementation period we compared return rates for hatchery-origin fish (HRR) to those of natural-origin fish (NRR) between 1993 and 2018; these values included adult fish that contributed to harvest. The mean HRR (16.7) was significantly larger ($P<0.001$) and over five times greater than the mean NRR (3.1). From brood years 1993 to 2012 the relationship for HRR across time was positive while no significant change was observed in NRR. The proportion of hatchery-origin fish on the spawning grounds did not affect the density-corrected freshwater productivity of the natural-origin population for brood years 1979-2009. It is clear the hatchery program has contributed to harvest, but the effect of the hatchery on the natural spawning population is less clear because of limitations in evaluation options and variation in many factors influencing productivity within and between treatment periods. Despite the low ability to detect negative effects on the natural-origin population, there is minimal evidence that negative impacts occurred, and the population is among the largest and most productive Chinook Salmon populations in the United States.

2) Pearsons, T. N., A. H. Haukenes, P. A. Hoffarth, and S. P. Richards. Expanding partnerships and innovations to implement reform of a large Columbia River hatchery program.

Recent reviews of salmon and steelhead hatchery programs have led to recommendations to reform hatchery practices and produce better supplementation outcomes. Of particular concern were reductions in performance of supplemented populations due to domestication selection attributed to hatchery production. One key recommendation was to achieve an index of domestication selection termed Proportionate Natural Influence (PNI) of 0.67 or higher. The Priest Rapids Hatchery, located adjacent to the Columbia River below Priest Rapids Dam, was one of the hatcheries included in this review. Data gathered from the hatchery and from the population being supplemented before implementation of reform measures indicated that the program was falling short of this goal. In this case study, we describe the influence of various partnerships and practices implemented in the Priest Rapids Hatchery program to achieve the recommended PNI for the program. The program exceeded the PNI goal in each of the last five years and since 2012 has averaged 0.72. The success in reaching the recommended benchmark was the result of generating creative solutions and building diverse decisional and operational partnerships that could achieve goals of hatchery reform in a cost-effective and broadly supported manner.

3) Pearsons, T. N., S. P. Richards, and A. H. Haukenes. Distribution of hatchery- and natural-origin adult Chinook Salmon carcasses in the Hanford Reach and the influence of carcass drift.

Adult carcasses are frequently used in long-term monitoring to index the spawning distribution of hatchery- and natural-origin Salmon. We show that hatchery- and natural-origin Chinook Salmon carcasses were well distributed throughout the Hanford Reach of the Columbia River and that the proportion of hatchery-origin carcasses generally matched that of natural-origin. In addition, we found that the sex ratios of carcasses were different in different sections (14-21 km long) of the Hanford Reach, and the number of redds in a section were associated with higher proportions of females. This suggested that carcasses may drift between sections. We tagged approximately 1,000 aged 2-6 Chinook Salmon carcasses annually between 2012 and 2018 and recovered carcasses during annual carcass surveys approximate 1-30 days later to evaluate carcass drift. We found that carcasses could drift the full length of Hanford Reach (94 km), it was common for carcasses to drift over 40 km, and that males were more likely to be found in downstream sections than females. This suggested that female carcasses were likely to be a better index of spawning location than male carcasses. It was likely that the deep water, low structural complexity, and variable flows of the Columbia River were partly responsible for the large drift distances we observed. Despite large amounts of drift in the Hanford Reach, carcasses were useful for assessing spawner distribution at large spatial scales and decreased in reliability with decreasing spatial scale. Furthermore, it is important to understand the scale of resolution of carcass surveys relative to evaluating management objectives.

4) Pearsons, T. N., S. P. Richards, and A. H. Haukenes. A comparison of run and spawn timing of hatchery- and natural-origin fall Chinook Salmon.

Hatcheries have the potential to alter run and spawn time of adult Chinook Salmon which has the potential to affect natural production goals. We sought to evaluate whether adult run and spawn timing differed in hatchery- and natural-origin fall Chinook Salmon that spawn in the Hanford Reach of the Columbia River. Run timing was evaluated using PIT tag detections of adults ascending Bonneville Dam between 2010 and 2018. Spawn time was evaluated by comparing the proportion of hatchery- and natural-origin carcasses that were collected at different times after spawning between 2012 and 2018. Run times were similar between hatchery- and natural-origin fish; no significant differences were detected between natural- and hatchery-origin adults arriving at Bonneville Dam at 10^{th} percentile (df = 8, t = 1.5, P = 0.1618), 50^{th} percentile (df = 8, t = 0.7, P = 0.5334) or 90^{th} percentile (df = 8, t = -2.1, P = 0.0668) of the day of year. In contrast, there were significant differences detected between natural- and hatchery-origin fish for the recovery timing of female carcasses at the 10^{th} (df = 7, t = 4.8, P = 0.0031), 50^{th} (df = 7, t = 01.9, P = 0.0090) and 90^{th} percentile (df = 7, t = 2.5, P = 0.0465) with natural-origin fish recovery day of year being later at all percentiles than their hatchery-origin counterpart. However, the time differences were typically 2-4 days. There was no evidence of a trend in female carcass recovery time between 2005 and 2018 (r^2 <0.1, P >0.05). The similarity of run and spawn timing of hatchery- and natural-origin salmon suggests that these factors are unlikely to contribute to large differences in natural production if they exist.

5) Pearsons, T. N. and R. R. O'Connor. Stray rates of natural-origin Chinook Salmon and steelhead in the upper Columbia Watershed.

Despite the importance of straying in understanding the ecology of salmon and steelhead, most of what is known about salmon and steelhead straying comes from tagged hatchery fish. We provide donor estimates of natural-origin spring, summer, and fall Chinook Salmon *Oncorhynchus tshawytscha* and steelhead *Oncorhynchus mykiss* straying at three spatial scales in the upper Columbia watershed using Passive Integrated Transponder (PIT) tags. A total of 823,770 natural-origin spring, summer, and fall Chinook Salmon and summer steelhead were PIT-tagged as juveniles in the Wenatchee, Entiat, Methow, and Okanogan River subbasins and tributaries and the upper Columbia River between 2002 and 2017. Anadromous adults with PIT tags were detected at a variety of antenna arrays in the Columbia River Basin between 2004 and 2018 (n=2,611). Mean donor stray rates of each population were less than 1% at the basin scale (range 0.0%-0.7%), less than 10% at the subbasin scale (range 0.0%-9.8%) and less than 15% at the tributary scale (range 0.0%-14.3%). Many of the populations (11 of 28) that were evaluated across all spatial scales did not have any strays detected, and the mean of means of all species stray rates at all spatial scales was generally less than 5% (range 0.2%-4.0%). Chinook Salmon and steelhead strayed at similar rates when originating from the same subbasins and tributaries. Most straying occurred in an upstream direction at the subbasin (84%) and tributary scales (94%). Variation in stray rates was most consistently associated with spatial scale and location and was less than 15% for all species at all spatial scales.

6) Pearsons, T. N. and R. R. O'Connor. Comparisons of donor stray percentages between hatchery- and natural-origin Chinook Salmon and steelhead in the upper Columbia Watershed

Artificial propagation of salmon *Oncorhynchus* spp. and steelhead *O. mykiss* is a common strategy that is used to achieve conservation and harvest goals. However, unintended effects of artificial propagation, such as high donor stray percentages, can reduce the number of adults that return to target areas and also contribute spawners to different populations where they are not desired. Until recently, it was difficult to assess if hatchery-origin fish stray rates were atypical because few estimates of stray rates of natural-origin fish were available. We used last PIT-tag detections to estimate and compare donor stray percentages of hatchery-origin and natural-origin Chinook Salmon *O. tshawytscha* and steelhead in the upper Columbia River watershed between 2002-2018. Donor stray percentages of hatchery-origin spring, summer, and fall Chinook Salmon and steelhead were <0.3% at the upper-Columbia basin scale and generally not higher than natural-origin donor stray percentages at larger spatial scales but were higher (up to 62%) at smaller spatial scales. Returning hatchery-origin Chinook Salmon and steelhead generally strayed in an upstream direction and the proportions of fish that strayed upstream were not significantly higher than natural-origin fish. Juvenile spring Chinook Salmon that were moved 14 to 389 river kilometers from centralized hatcheries to tributaries for overwintering or final acclimation, strayed at a much higher rate than those that completed their incubation, rearing, and acclimation at a single location. In contrast, steelhead that were moved for acclimation, including direct releases from trucks, did not stray at higher rates than those that completed their incubation, rearing, and acclimation at a single location. Other adaptive management actions that were implemented to reduce straying produced mixed results. A variety of approaches can be considered to reduce undesirable production of strays, but most of them involve difficult trade-offs.

7) Pearsons, T. N., and M. D. Miller. Stray compositions of hatchery-origin Chinook Salmon *Oncorhynchus tshawytscha* and steelhead *O. mykiss* in recipient natural populations of the upper Columbia Watershed.

One of the biggest concerns of operating hatchery Salmon and steelhead programs is high straying of returning adults into non-target populations and the possible homogenization of genetic diversity among populations caused by spawning of stray fish. The composition of hatchery-origin stray Chinook Salmon *Oncorhynchus tshawytscha* and steelhead *O. mykiss* relative to the natural spawning populations, termed recipient population stray rate, was evaluated in the Upper Columbia Basin. Chinook Salmon carcasses were collected from 1999-2018 in spawning areas shortly after spawning and carcasses were examined to determine origin. Adipose fin clips and coded-wire-tags were used to distinguish non-target hatchery, target hatchery, and natural-origin fish; coded-wire-tags were read in the lab to determine the origin of hatchery-origin fish. Steelhead strays and spawning escapement were evaluated using passive-integrated transponder (PIT) tags between 2013-2018. The recipient population stray rates ranged between 0.02-87.35% and increased with decreasing spatial scale. Recipient stray rates of all taxa at the basin scale were <3%, and summer Chinook and fall Chinook salmon were

<0.5%. Stray rates in subbasins for all taxa ranged between 0.07-33.04%; spring and summer Chinook Salmon exceeded 5% in some 10 year periods in the Entiat and Methow subbasins, but stray rates for all Chinook Salmon were <5% in the Wenatchee, Okanogan, and Hanford Reach for all periods. All steelhead stray rates exceeded 5% except for those in the Wenatchee subbasin. Stray rates of spring Chinook Salmon in tributaries (the only taxa that met the tributary criteria) ranged between 0.61%-87.35% and only the Chiwawa, Icicle, and Twisp rivers were consistently below 10%; the Chiwawa River was consistently below 5%. In cases where recipient stray management targets were exceeded, some were the result of single hatchery contributions, but others were the result of cumulative contributions from multiple hatcheries. Options to achieve recipient stray management targets include reducing donor stray rates, reducing hatchery program size, removing hatchery-origin adults prior to spawning in the natural environment, and increasing the natural-origin population. It is likely that balancing trade-offs among hatchery program size and recipient population stray rate will be necessary in order to achieve management targets in some locations.

8) McKinney, G., S. Brown, A. Louden, M. P. Small, T. R. Seamons, C. C. Willard, T. N. Pearsons, T. H. Kahler, and G. Mackey. Examining the genetic structure of upper Columbia Summer/Fall Chinook Salmon and evaluating the effects of the supplementation program.

We examined baseline (1982-1994) and contemporary (2017-2018) summer and fall Chinook Salmon (*Oncorhynchus tshawytscha*) from the Upper Columbia River Watershed to determine if hatchery supplementation programs have had any impacts on the genetic diversity and structure of these populations. Baseline collections included both hatchery- and natural- origin samples where available. Contemporary collections exclusively consisted of samples collected at broodstock collection facilities; their origin (hatchery or natural) was only sometimes known. Summer Chinook Salmon populations with paired baseline and contemporary samples included the Methow River, the Wenatchee River, and the Okanogan River. Populations with only contemporary samples included Chelan Falls, Entiat National Fish Hatchery, and Wells Fish Hatchery. Fall Chinook Salmon were represented by collections from the Hanford Reach spawning grounds and Priest Rapids Hatchery. Measures of genetic diversity (allelic richness, heterozygosity, linkage disequilibrium, and effective number of breeders) showed little differentiation among baseline and contemporary populations for either summer or fall Chinook, suggesting that hatchery programs have not led to a decrease in genetic diversity. There was a general pattern where F_{ST} was higher among baseline than contemporary collections suggesting that genetic drift and homogenization among stocks has occurred over time. Despite these patterns, pairwise comparisons of F_{ST} were generally statistically non-significant both for baseline and contemporary collections. Similar to previous evaluations, there appears to be little evidence for neutral genetic divergence between contemporary hatchery programs in the upper Columbia watershed and baseline samples collected in the late 1980s and early 1990s. The large population sizes of summer and fall Chinook Salmon relative to the hatchery program sizes in the upper Columbia basin, low recipient population stray rates in natural populations, and the management strategies that were implemented to reduce genetic risk all likely contribute to the

lack of neutral genetic change. This evaluation did face two limitations: first, we were not able to evaluate potential differentiation among contemporary hatchery and natural origin individuals due to lack of data on individual origin; second, we were not able to evaluate potential shifts in adaptive genetic diversity using genetic techniques and it is possible for adaptive genetic diversity (i.e., run-timing, age at maturity) to change in response to selection (i.e., domestication) while neutral genetic diversity remains the same. While adaptive genetic variation was not directly monitored, phenotypic metrics measured as part of other portions of the monitoring plan can serve as a proxy for adaptive genetic variation.

9) Pearsons, T. N., A. H. Haukenes and S. P. Richards. Comparison of age at maturity, size-at-age, and sex ratio between hatchery- and natural-origin fall Chinook Salmon in the Hanford Reach of the Columbia River.

We characterized differences in age-at-maturity, size-at-age, and sex ratio between hatchery- and natural-origin adult fall Chinook Salmon carcasses collected during surveys of the Hanford Reach of the Columbia River during brood years 2007-2013. A shift to younger adult fish was observed in hatchery-origin fish in both males and females. The majority of adult natural-origin males and females and from brood years were age 4; whereas, increases in age 3 fish were observed in both hatchery-origin males and females with the majority of hatchery-origin males returning as age 3. A significant difference ($P < 0.0001$) in the relative frequencies of males and females was observed between natural-and hatchery-origin carcasses recovered in the Hanford Reach for all brood years; the M:F ratios of hatchery-origin fish were lower than natural-origin males were 0.67 and 1.04, respectively. Hatchery-origin fish were slightly larger than natural-origin at age 3 but not significantly ($P = 0.1420$) and natural-origin fish were significantly ($P < 0.0001$) larger than hatchery-origin fish at ages 4 and 5 regardless of fish sex. The interaction between fish age and fish sex was also significant ($P < 0.0001$) and the post-hoc Tuckey tests for fish age and fish sex revealed that females were significantly ($P < 0.0001$) larger than males at age 3, while males were significantly ($P<0.0001$) larger than females at ages 4 and 5. A carcass recovery bias for larger, older, male fish likely contributes to these results, particularly sex ratio. However, patterns of differences between origins for age and size are accurate even after accounting for carcass recovery bias.

10) Pearsons, T. N., S. P. Richards, and A. H. Haukenes. Egg production and deposition between hatchery- and natural- origin fall Chinook Salmon in the Hanford Reach of the Columbia River

The reproductive potential of hatchery- and natural-origin fish is an important performance characteristic to compare when evaluating impact of supplementation hatchery programs and this was studied for fall Chinook Salmon that spawn in the Hanford Reach of the Columbia River. Hatchery- and natural-origin adults and carcasses were collected between 2004 and 2018 and reproductive traits were compared. Fecundity, individual egg weights, and total egg mass ranged from 1,356 – 6,385 eggs/female, 0.15 – 0.46 g/egg, and 255 – 2,205 g/female, respectively. All three reproductive characteristics increased significantly with fork length ($P < 0.0001$). Multiple

linear regressions revealed significant differences between hatchery- and natural-origin fish for fecundity (P = 0.0393) and individual egg weight (P = 0.0002) although each result was confounded by a significant interaction between fork length and origin indicating heterogeneity of slope for these two populations. Multiple linear regression for total egg mass revealed no difference between hatchery- and natural-origin fish (P = 0.3277) and no interaction between origin and the fork length (P = 0.2876). At the extreme values of fork length, the relative outcomes for fecundity and individual egg mass for hatchery- and natural-origin fish change. Fecundities of the smallest natural-origin fish sampled were less than that observed among hatchery-origin fish while at the largest fork lengths the opposite was observed. For individual egg mass, greater values were observed among the smallest natural-origin fish than hatchery-origin fish while at the largest sizes the opposite was observed. No such inversion in the relative rank order was apparent for the total egg mass of hatchery- and natural-origin fish at the extremes of fork length. The mean fork length of hatchery-origin fish found on the Hanford Reach was significantly smaller than natural-origin females leading to hatchery-origin females with significantly lower fecundity, individual egg weight, and total egg mass weight than natural-origin females (P<0.05). The annual index of egg retention based on visual estimates of egg retention for years 2004 – 2018 ranged from 0.5 – 9.9% and with a mean of 2.1%. Over this same period there was not a significant change in the egg retention index over time (df = 14, t = 0.559 P = 0.5855). There was a significant difference in percentage of eggs retained with mean egg retention indices of 9% and 2% for hatchery- and natural-origin females, respectively (X^2_{MH} = 370.76, df = 6, P = <0.0001). Egg retention for hatchery-origin females were notably high during years 2013 and 2014. Recent changes to broodstock collection and adult management may decrease the disparity in allocation of reproductive investments between hatchery- and natural-origin females, however it is likely that younger maturation age of hatchery-origin fish will continue to result in differences in fecundity from natural-origin fish.

11) Pearsons, T. N., and S. P. Richards. Juvenile release numbers and size metrics at the Priest Rapids Hatchery.

Objective 9 of the Grant County Public Utility District's (GPUD) hatchery monitoring and evaluation plan is to determine if hatchery fish were released at the programmed size and number at the Priest Rapids Hatchery (PRH). The subyearling fall Chinook Salmon released from the Priest Rapids Hatchery were produced as part of two mitigation programs: GPUDs mitigation and the Army Corp of Engineers mitigation. This report is focused on GPUDs mitigation. Prior to 2014, GPUDs mitigation was 5 million subyearling fall Chinook Salmon smolts with a target size of 50 fish per pound. Beginning in 2014, GPUDs mitigation was increased to 5,599,504 with a target weight of 50 fish per pound and a target coefficient of variation in length of <10 mm. Releases from 2014-2018 were within 10% of the release number target and ranged from 5,374,566 to 6,129,355. The mean annual weight of fish was between 49-52 fish per pound and the coefficient of variation was <10 mm for all years (annual range = 6.1-8.4 mm). The range in annual condition factor (K) was 1.2-1.3. In summary, GPUD met its fall Chinook Salmon hatchery mitigation target every year between 2014-2018.

12) O'Connor, R. R., and T. N. Pearsons. Harvest of Chinook Salmon and steelhead originating from Upper Columbia River hatchery programs.

The objective of this evaluation was to determine if a diversity of upper Columbia Basin Chinook Salmon and steelhead hatchery programs contributed to harvest. More specifically, we were interested in evaluating whether harvest rates were consistent with management objectives and where fish were harvested. Harvest rates were lowest on endangered spring Chinook Salmon with annual brood year means of 5-6% for Methow, Chewuch, and Twisp spawning aggregates (annual range 0 to 59%) and 26% for the Chiwawa spawning aggregate (annual range 0 to 95%). The percent of the population harvested was not correlated with spawning escapement ($P>0.05$) and the total number of fish harvested was correlated with spawning escapement ($P<0.05$) in the Chiwawa and Twisp rivers but not in the Methow or Chewuch rivers. Most harvest of spring Chinook Salmon occurred in freshwater. Harvest rates were much higher for the more abundant summer and fall Chinook Salmon programs with annual brood year averages around 53-75% and annual ranges of 14 to 91%. Percent harvest increased with increasing spawning escapement for summer Chinook in the Methow ($P=0.01$) and Okanogan ($P=0.0002$) rivers but not for summer Chinook in the Wenatchee River ($P=0.49$), Chelan Falls/Turtle Rock program ($P=0.43$), and Hanford Reach fall Chinook ($P=0.28$). The total number fish harvested was not correlated with spawning escapement ($P>0.05$) for the Wenatchee River, Wells subyearling, Methow River, or Okanogan River programs, but significant correlations were detected ($P<0.05$) for the Chelan Falls/Turtle Rock yearling and Wells yearling programs and for fall Chinook Salmon from Priest Rapids Hatchery. Most of the harvest of summer Chinook Salmon occurred in the ocean and harvest of fall Chinook Salmon occurred evenly between freshwater and the ocean. Harvest rates averaged 16% (range 0-54%) for threatened hatchery-origin steelhead and less than 5% (range 0 to 4%) for natural-origin steelhead. The percent of steelhead harvested increased with increasing escapement in the Okanogan River ($P=0.006$) but was not significantly correlated in the Methow ($P=0.29$) and Wenatchee rivers ($P=0.85$). Total harvest of hatchery steelhead was not significantly correlated with spawning escapement in the Methow or Wenatchee rivers ($P>0.05$) but was correlated in the Okanogan River ($P=0.006$). Every hatchery program that was evaluated contributed to harvest and sometimes substantially. The magnitude of harvest generally corresponded to the status of the population: the lowest harvest occurred on the most imperiled stocks and the highest harvest occurred on the healthiest stocks. However, harvest sometimes hindered meeting broodstock collection goals and harvest management of endangered or threatened species could impede conservation objectives and might be improved by tailoring harvest to abundance, weak stocks, and weak broodyears.

13) Pearsons, T. N., S. P. Richards, and A. H. Haukenes. Evaluation of fall Chinook Salmon carcass recovery bias in the Columbia River.

A common way to inventory the characteristics of a Chinook Salmon (*Oncorhynchus tshawytscha*) spawning population is to collect their carcasses after spawning. However, this method can produce biased results. Two approaches to characterize bias in carcass samples when examining population demographics were evaluated with fall-run Chinook Salmon from the Hanford Reach of the Columbia River. A mark recapture approach and a comparison of hatchery-origin carcasses collected in river versus those recruited to a hatchery trap. In each instance the post-orbital hypural lengths and sex ratios were compared to determine differences in the characteristics of each sample. In the mark recapture study, the recaptured carcasses had similar lengths and sex ratios as the original marked group. In the evaluation of carcass and trap populations, the hatchery-origin carcasses found in the river contained lower proportions of smaller fish sampled and a lower relative frequency of male fish than were collected at the hatchery trap. Taken together the results illustrate that younger male salmon may be under-represented in carcass samples; a phenomenon commonly reported. This feature of carcass sampling contributes to a weakness in the design of mark recapture study as the original marked fish may be weighted towards larger animals that were subsequently recaptured at similar sizes and sex ratios. Furthermore, carcass recovery bias should be considered when interpreting data collected from salmon carcasses.

14) Pearsons, T. N., S. P. Richards, and A. H. Haukenes. Examination of sources of error in estimating abundance of adult Chinook Salmon derived from expansion of juvenile mark and tag rates.

Marks and tags such as adipose fin clips (Ad-Clip) and coded-wire-tags (CWT) are applied at most salmon and steelhead hatcheries in the Pacific Northwest to identify origin and characterize abundance, survival, and other important population parameters. Error and/or bias associated with these estimates are infrequently evaluated. We compared estimates of adult abundance returning to the Priest Rapids Hatchery (PRH) between 2012 and 2018 using juvenile expansions of tagging rates for Ad-Clip and CWTs to estimates generated from a subsample of fish with a 100% mark rate (thermally marked otoliths). The average estimates derived from the otolith mark (90±12%), the CWT (80±13%), the adipose clipped and CWT (77±11%), and Ad-Clip (86±12) were highly variable but not significant over the time period of the study. We also evaluated possible systematic sources of these errors that may have occurred either before release or as adults were returning: 1) we compared proportions of tagged animals in pre-release sampling efforts to values reported from hatchery inventory, 2) we evaluated our methods of detection of CWT, and 3) we examined error rates attributed to aging scales. Each of these sources of error may contribute to underestimation, but none of the data gathered provide an explanation for the magnitude of underestimation derived from the partially tagged population in earlier years (e.g., 2012-2013). However, the size of underestimation has been diminished over the course of the study suggesting that quality control steps are providing better estimates.

Please read the full chapters for more detail about each of the topics in the abstracts presented above. All data in this report should be considered preliminary until published in a peer-reviewed journal.

Monitoring and Evaluation Program Reporting Structure and Schedule

The three Public Utility Districts (PUD) of the middle Columbia River strive to achieve no net impact of Salmon and steelhead as a result of construction and operation of five Columbia River dams. This report describes one of the main ways the PUDs achieve no net impact; the production of hatchery fish to replace those lost through the project areas. A comprehensive monitoring plan is implemented to determine the performance of the hatchery programs at achieving their goals (Hillman et al. 2019). This report is a synthesis of the data collected for Grant PUD's fall Chinook Salmon hatchery program through 2018. Other covered species/taxa (e.g., summer Chinook, spring Chinook, Sockeye Salmon, and steelhead) are presented in other reports.

The Douglas and Chelan PUDs' Habitat Conservation Plans (HCPs), Grant PUD's Settlement Agreement, and the 2008 NMFS Biological Opinion (Biop) for Grant PUD (hereafter referred to collectively as the Agreements) specify certain reporting dates or intervals for hatchery monitoring and evaluation (M&E). The Endangered Species Act (ESA) incidental take permits and the Monitoring and Evaluation Plan for PUD Hatchery Programs (Hillman et al. 2019) also have reporting requirements. These reporting date requirements were designed to provide timely information to operators and managers and fulfill permitting requirements. Additionally, the reports are used to inform other activities such as updating M&E plans, recalculation of hatchery production, evaluation of meeting M&E objectives, status of meeting permit requirements, and adaptive management actions. Past reporting timing has not necessarily met the intent of the Agreements, and has not been orchestrated to align with the various actions that the Hatchery Committees and NMFS require. Subsequently, we have designed a reporting schedule that is consistent with the Agreements, meets reporting requirements under the M&E Plan, meets ESA Section 10 permit requirements, and optimizes the sequence of reporting and the actions that rely on M&E information.

Three levels of M&E reporting have been and will be implemented (Table 1). These reports are consistent with past reporting and the M&E Plan, but have been restructured to streamline transfer of information and meet the requirements of the Agreements.

Table 1. Monitoring and evaluation report types, frequency, content and function.

Report type	Frequency	Content	Function
Data	Annual	Cumulative description of data (raw and derived) and field methods. Basic statics reported.	Informs annual M&E implementation plans
Statistical	5 year	Presentation of statistical analyses and description of statistical methods. Addressed in the Program Review when the two would occur in the same year.	Informs 5 year M&E plan and provides in depth data analysis
Program Review	10 year	Integrates and interprets information from data and statistical reports and also includes integration from other programs and studies. Written in scientific manuscript format. Fulfills HCP "Program Review" requirements. Addresses Statistical Report requirements.	Informs recalculation and adaptive management. Determines if programs are meeting objectives.

The Data Report will be produced annually and will provide data collected in the most recent field year. The report will provide tables of cumulative data, including the most recently collected, and provide summary statistics where appropriate (e.g., mean, standard deviation, etc.). The report will provide a concise description of the field methods that could be used in a scientific publication and describe deviations from previous sampling, standard field practices or sampling plans. This report will provide up to date information for managers and operators, fulfill incidental take reporting requirements, and inform annual adjustments to the implementation of the M&E plan.

The Statistical Report will be produced every ten years on the five year intervals between the Program Review (a.k.a Comprehensive Report; see below). The report will provide a concise description of the analytical methods used (e.g., similar to a scientific journal article) and the results of the statistical analyses for each objective as described in the M&E plan. The report will also provide the assumptions of the statistical analyses and note any deviations in expected performance of a given analysis (e.g., issues related to normality, dependency, non-constant variance; etc.). The report is not intended to provide interpretation of the results, but will provide the outcomes of the statistical tests. This will provide managers and operators a periodic update of the performance of the hatchery programs.

The Program Review, otherwise know as the Comprehensive Report, will be produced every ten years and will meet the Program Review as described in the HCPs (Section 8.8 of the Wells HCP, Section 8.7 of the Rocky Reach/Rock Island HCPs) and will address the information reported in the Statistical Report. The report will provide the results of any natural population/hatchery interaction studies (as needed), and determine if the hatchery programs are operating consistent with the goals as outlined in the relevant M&E Plan. The review will determine if hatchery program goals and objectives, as defined in the Hatchery Plan (HCPs Section 8), Section 10 permits, as further defined in the HCPs, have been met or sufficient progress is being made toward their achievement; and determine if hatchery production objectives are being achieved.

The M&E reporting schedule is designed to be consistent with the Agreements. However, it also has been designed to provide a logical sequence of information based on significant milestones in the HCPs as well as consistency with Grant PUDs settlement agreement and NMFS Biological Opinion. Reporting was designed to provide the Program Review (ten year interval) prior to recalculation in order to have the most up to date data vetted and organized prior to recalculation. The Statistical Report will be produced every ten years. On the five year intervals between the ten year intervals, the Statistical Report material will be addressed in the Program Review. The Data Report will be produced annually. The PUDs also require advanced knowledge of M&E and reporting requirements to facilitate timely contracting. The Agreements terminate in 2052.

Summary

Annual reports have been conducted for decades (e.g., Hillman et al. 2020, Snow et al. 2020, Richards and Pearsons 2019), but there has only been one comprehensive analysis of PUD programs and this did not integrate data from all of the PUD programs nor with relevant literature from other locations (Hillman et al. 2012; Murdoch et al. 2012). Furthermore, many of the data sets were not mature enough to make robust conclusions. The current evaluation attempts to improve upon previous evaluations by: 1) including more data, 2) improving analytical techniques, 3) including all PUD programs together, and 4) integration of findings relative to other published work.

We attempted to generate relevant chapter topics that encompassed all of the monitoring and evaluation plan objectives (Hillman et al. 2019). The objectives of the M&E plan and the associated chapter numbers are in Table 2. Finally, we conducted more analyses than were identified in the plan in order to provide a more comprehensive evaluation of the programs.

Table 2. Hatchery monitoring and evaluation plan objectives contained in Hillman et al. 2019 and the associated chapter numbers in this report that address them.

Objective	Objective Description	Report Chapter
1	Determine if conservation programs have increased the number of naturally spawning and naturally produced adults of the target population and if the program has reduced the natural replacement rate (NRR) of the supplemented population.	1, 14
2	Determine if the proportion of hatchery fish on the spawning grounds affects the freshwater productivity of supplemented stocks.	1
3	Determine if the hatchery adult-to-adult survival (i.e., hatchery replacement rate, HRR) is greater than the natural adult-to-adult survival (i.e., natural replacement rate, NRR) and the target hatchery survival rate.	1
4	Determine if the proportion of hatchery-origin spawners (pHOS or PNI) is meeting the management target.	2
5	Determine if the run timing, spawn timing, and spawning distribution of the hatchery component is similar to the natural component of the target population or is meeting program-specific objectives.	3, 4
6	Determine if the stray rate of hatchery fish is below the acceptable levels to maintain genetic variation among stocks.	5, 6, 7
7	Determine if genetic diversity, population structure, and effective population size have changed in natural spawning populations as a result of the hatchery program.	8
8	Determine if hatchery programs have caused changes in phenotypic characteristics of natural populations.	9, 10, 13
9	Determine if hatchery fish were released at the programmed size and number.	11
10	Determine if appropriate harvest rates have been applied to conservation, safety-net, and segregated harvest augmentation programs to meet the HCP/SSSA goal of providing harvest opportunities while also contributing to population management and minimizing risk to natural populations.	12

Some of the topics identified for the hatchery program review have already been published in peer-review journals, the highest standard of the profession. The citations of the publications are provided below.

Pearsons, T. N. and R. R. O'Connor. 2020. Stray rates of natural-origin Chinook Salmon and Steelhead in the Upper Columbia Watershed. Transactions of the American Fisheries Society 149:147–158. DOI: 10.1002/tafs.10220

Pearsons, T. N., A. H. Haukenes, P. A. Hoffarth, and S. P. Richards. 2020. Expanding partnerships and innovations to implement reform of a large Columbia River hatchery program. Fisheries 45(9):484-491. DOI: 10.1002/fsh.10437

There has been extensive review and adaptation of both the PUD hatchery and monitoring and evaluation programs. The PUD hatchery programs have been reviewed by the PUD Hatchery Committees and the Hatchery Science and Review Group (HSRG). In addition, the PUD hatchery monitoring and evaluation plan has been reviewed by a number of different groups including the PUD Hatchery Committees, the Independent Scientific Advisory Board (ISAB) in 2018, and an expert genetics panel that was assembled in 2019. These reviews and associated adaptations have resulted in high quality hatchery and monitoring and evaluation programs.

The hatchery programs have undergone many operational and in some cases facility changes during the time of monitoring and implementation. This poses challenges to evaluate the many changes that have occurred. For example, hatchery programs were resized in 2013 and will be resized every 10 years based upon mitigation requirements and hatchery programs were revised consistent with hatchery reform principles such as PNI management. In many cases, the programs were not held constant for enough years to statistically evaluate changes such as those associated with resizing the hatchery programs that began with smolt releases in 2014. Therefore, we evaluated the programs as the outcome of adaptive management to achieve long-term program goals, which generally did not change. This is appropriate because, the programs are continually evolving in attempts to improve the probability of achieving overarching management goals.

In addition to changes in hatchery programs, other actions occurred during the span of this evaluation. For example, building of dams, harvest, and changes in flow management in the Hanford Reach undoubtedly influenced the performance of hatchery and natural-origin fall Chinook Salmon. These changes pose challenges to making definitive conclusions about some of the metrics contained in this report. Where possible, we attempted to account for methodological biases and also described the limitations of our findings.

The committees had an extended period of time to review the chapters contained in this report and their comments are presented as a separate document. The authors' responses to those comments are also presented in that document.

This report will help inform a future committee authored summary report. The summary report will include committee approved recommendations that will inform a revision of the monitoring and evaluation plan as well as program operation. The recommendations that are

provided in this report are those of the authors and do not necessarily reflect the views of the hatchery committees.

Acknowledgments

We thank the many people who have contributed to the collection, analysis, and presentation of the data contained in this report. Specific contributions are mentioned at the end of each chapter of this report. We also thank the PUDs and other funding entities such as the Bonneville Power Administration who have invested in understanding the fishes in the Upper Columbia. Finally, we thank the HCP Hatchery Committees and the PRCC Hatchery Subcommittee for their input and review of the hatchery and M&E program.

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The Effects of a Harvest Augmentation Hatchery on the Abundance and Productivity of Fall Chinook Salmon in the Hanford Reach of the Columbia River

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Abstract

We evaluated a large integrated harvest augmentation hatchery program to determine if it could meet the dual goals of harvest augmentation and minimizing negative impacts to a naturally spawning population in the Hanford Reach of the Columbia River. Adult escapement to the Hanford Reach and the peak abundance of redds before (1948–1984 redds; 1964-1984 escapement) and during (1985-2018) the full supplementation program were compared. The mean peak redd count, adult natural-origin escapement, and total adult escapement to the Hanford Reach before supplementation were 2,067, 26,311 and 26,525, respectively. During the supplementation period the mean peak redd abundance, 8,024, adult natural-origin escapement, 65,785, and total adult escapement, 73,526, were significantly larger than the pre-supplementation period ($P<0.001$). During the supplementation period we compared return rates for hatchery-origin fish (HRR) to those of natural-origin fish (NRR) between 1993 and 2018; these values included adult fish that contributed to harvest. The mean HRR (16.7) was significantly larger ($P<0.001$) and over five times greater than the mean NRR (3.1). From brood years 1993 to 2012 the relationship for HRR across time was positive while no significant change was observed in NRR. The proportion of hatchery-origin fish on the spawning grounds did not affect the density-corrected freshwater productivity of the natural-origin population for brood years 1979-2009. It is clear the hatchery program has contributed to harvest, but the effect of the hatchery on the natural spawning population is less clear because of limitations in evaluation options and variation in many factors influencing productivity within and between treatment periods such as dam construction and changes in upstream dam operations. Despite the low ability to detect negative effects on the natural-origin population, there is minimal evidence that negative impacts occurred, and the population is among the largest and most productive Chinook Salmon populations in the United States.

Introduction

One of the key uncertainties about supplementation hatcheries with the primary aim of increasing harvest is whether it can be done without negatively impacting natural-origin populations (Pearsons and Hopley 1999; Pearsons 2002; Fast et al. 2015). Well-run hatcheries can be used to support increased harvest because they can produce more adults-per-spawner than the natural environment can (Fast et al. 2015). However, it is less clear whether hatcheries can be used to provide harvest benefits while keeping genetic and ecological impacts within acceptable limits (Ham and Pearsons 2001; Williamson et al. 2010; Chilcote et al. 2011). There are two strategies that have been proposed to attempt to contain risks to natural-origin populations while contributing to harvest (Mobrand et al. 2005, Paquet et al. 2011). The first strategy is to keep the gene pools of hatchery- and natural-origin populations separate. This strategy is termed "segregated" and guidelines suggest that hatchery-origin fish should make up less than 5% of the natural spawning population (Mobrand et al. 2005, Paquet et al. 2011). The second strategy, and the subject of this article, is to mix the gene pools of the hatchery- and natural-origin populations. This strategy is termed "integrated."

In cases where it was not possible to achieve the guidelines of a segregated program (e.g., gene flow >5%), integrated hatchery strategies were selected or were used by default prior to identification of a particular strategy. Many hatcheries have been in operation for decades before risk containment strategies had been identified and established. The guidelines of operating an integrated hatchery program are to mix the gene pools sufficiently so that the dominant selection pressures are from the natural environment, not the hatchery environment (Mobrand et al. 2005, Paquet et al. 2011). Selection pressures from the hatchery environment is referred to as domestication selection and it has been indexed as Proportionate Natural Influence (PNI). The relatively recent standard for reducing genetic risks of domestication is to exceed a PNI of 0.66 (Mobrand et al. 2005, Paquet et al. 2011; Pearsons et al. 2020). Domestication selection can reduce survival in the natural environment (Araki et al. 2008; Fritts et al. 2007; Pearsons et al. 2007). Other unintentional effects of integrated harvest augmentation hatcheries can also include demographic changes (Knudsen et al 2006; Larsen et al 2013; Ford et al. 2015), undesirable ecological interactions (Pearsons et al. 2007; Pearsons et al. 2012; Temple and Pearsons 2012), and straying (Pearsons and O'Connor 2020, Keefer and Caudill 2014), and it can be challenging to disentangle the genetic and ecological mechanisms leading to these impacts (Chilcote et al. 2011).

Most evaluations of the effects of hatchery supplementation on Chinook Salmon have focused on spring run Chinook Salmon that spawn in small river systems (Williamson et al 2010; Fast et al. 2015; Venditti et al. 2018). Populations that spawn in small rivers are much easier to evaluate than those in large rivers. For example, Chinook Salmon that spawn in large rivers can be more difficult to enumerate because of the difficulty in working in such large, deep, and often turbid environments. In addition, it is often challenging to achieve sufficient sample sizes to reduce sampling error. Furthermore, there are fewer populations of Chinook Salmon that spawn in large rivers to serve as reference populations for making comparisons between supplemented and non-supplemented populations. Without the ability to compare supplemented populations to non-supplemented populations, conclusions about supplementation effects are limited (Venditti et al. 2018). However, even suboptimal evaluations can be useful in data limited situations if there is not better information available for an important topic.

The goal of this work is to determine if a hatchery augmentation hatchery, Priest Rapids Hatchery (PRH), has produced high harvest while keeping negative impacts within acceptable limits. More specifically, the purpose of this report is to use the best available data to determine if Priest Rapids Hatchery has: 1) negatively impacted abundance of redds and total and natural-origin escapement in the Hanford Reach of the Columbia River 2) effected the productivity rates of hatchery- and natural-origin fish, and 3) effects of the proportion of hatchery-origin fish on the spawning grounds on the density-corrected freshwater productivity of the natural-origin component of the population. The contribution of Priest Rapids Hatchery production to harvest is presented in O'Connor and Pearsons (this report).

Methods

Study area

The Hanford Reach is one of the last non-impounded reaches of the Columbia River and the location of the largest and most productive natural spawning fall Chinook Salmon population in the United States (Harnish et al. 2014, Langshaw et al. 2015, Harnish 2017, Langshaw et al. 2017). The Hanford Reach extends 82 km from the city of Richland to the base of Priest Rapids Dam. Natural-origin fall Chinook Salmon produced in the Hanford Reach emerge from the substrate in the spring and rear there until outmigration in the summer. Egg-to-fry survival and egg-to-pre smolt survival of natural production within the Hanford Reach have been estimated to be ~71% and 40.2-63.4%, respectively (Oldenburg et al. 2012; Harnish et al. 2012; Harnish 2017). The Hanford Reach population of fall Chinook Salmon is unique, and no suitable reference population not influenced by hatchery production is available to evaluate the effects of supplementation.

The Priest Rapids Hatchery (PRH) was constructed at the upstream end of the Hanford Reach to mitigate for losses associated with the inundation of the portions of the Columbia River caused by the construction of Priest Rapids (1959) and Wanapum dams (1963). The PRH has evolved from a spawning channel initially constructed downstream from Priest Rapids Dam in 1963 to a state-of-the-art hatchery facility completed in 2014. While operating as a spawning channel from 1963 through 1971, summer/fall Chinook salmon adults trapped in the east ladder of Priest Rapids Dam were used as broodstock. This practice was generally ineffective at producing juveniles because of a variety of factors leading to mortality of both adult broodstock and in eggs deposited in redds. Artificial propagation of fall Chinook salmon at the site began in 1972 with the collection and spawning of broodstock derived from adults returning to the spawning channel. In 1978, use of the spawning channel was terminated and all fish released from PRH were derived from artificial production at that facility (Chapman et al. 1994). A major rebuild of the facility was completed in 2014 including a renovated trapping facility, new adult holding ponds, new adult sorting capabilities, a new incubation building, 30 new raceways, and five renovated acclimation ponds.

The annual release of fall Chinook salmon smolts from PRH has ranged considerably since the initial release of roughly 150,625 million smolts from the 1977 brood year to over roughly 10.30 million from the 1982 brood year (Table 1). From 1977 to 2013 the release goal of the PRH program was 5 million subyearling smolts and additional production was produced

Table 1. Annual number of juvenile fall Chinook Salmon marked and released from Priest Rapids Hatchery during years 1978 – 2018.

Release Year	Non Marked or Tagged	Adipose Clipped	Adipose Clipped and Coded Wire Tagged	Non Marked and Coded Wire Tagged	Total Released
1978	0	3,287	147,338	0	150,625
1979	0	1,308	152,532	0	153,840
1980	2,858,509	0	147,145	0	3,005,654
1981	4,581,054	0	251,537	0	4,832,591
1982	5,198,365	0	310,876	0	5,509,241
1983	9,888,989	0	407,711	0	10,296,700
1984	9,517,263	3,382	222,055	0	9,742,700
1985	6,253,240	2,800	106,960	0	6,363,000
1986	5,843,176	1,290	203,534	0	6,048,000
1987	7,506,142	1,015	201,843	0	7,709,000
1988	7,501,578	11,201	196,221	0	7,709,000
1989	5,200,080	2,862	201,608	0	5,404,550
1990	6,224,770	11,800	194,530	0	6,431,100
1991	5,134,031	0	199,469	0	5,333,500
1992	6,798,453	0	201,647	0	7,000,100
1993	6,939,537	0	194,622	0	7,134,159
1994	6,520,153	0	185,683	0	6,705,836
1995	6,526,120	0	175,880	0	6,702,000
1996	6,503,811	0	196,189	0	6,700,000
1997	6,450,885	0	193,215	0	6,644,100
1998	6,541,351	0	196,249	0	6,737,600
1999	6,311,140	0	193,660	0	6,504,800
2000	6,651,664	0	204,336	0	6,856,000
2001	6,661,771	0	200,779	0	6,862,550
2002	6,559,109	0	219,926	0	6,779,035
2003	6,422,232	0	355,373	0	6,777,605
2004	6,415,444	0	399,116	0	6,814,560
2005	6,399,766	0	200,072	0	6,599,838
2006	6,676,845	0	199,445	0	6,876,290
2007	4,912,487	1,628,614	202,000	0	6,743,101
2008	4,344,926	813	202,568	0	4,548,307
2009	4,850,844	1,719,388	218,082	0	6,788,314
2010	3,413,334	1,717,188	619,568	1,026,561	6,776,651
2011	3,383,859	1,702,961	602,580	1,108,990	6,798,390
2012	3,094,666	2,768,643	595,608	598,031	7,056,948
2013	2,905,694	2,712,228	603,930	601,009	6,822,861
2014	3,347,417	2,712,975	603,417	603,439	7,267,248
2015	3,125,734	2,712,392	600,688	600,730	7,039,544
2016	3,317,992	2,720,176	602,116	601,770	7,242,054
2017	3,088,547	2,710,302	603,539	603,864	7,006,252
2018	4,067,088	2,710,121	602,725	607,287	7,987,221
				Mean	6,401,485
				Median	6,777,605

Table 2. Annual number of juvenile fall Chinook Salmon marked and released from Ringold Springs Hatchery during years 1994 – 2018.

Release Year	Non Marked or Tagged	Adipose Clipped	Adipose Clipped and Coded Wire Tagged	Total Released
1994	3,817,491	0	217,184	4,034,675
1995	3,324,895	0	200,000	3,524,895
1996	3,156,127	0	200,000	3,356,127
1997	3,186,173	0	199,771	3,385,944
1998	3,039,407	0	220,800	3,260,207
1999	3,064,112	0	212,048	3,276,160
2000	3,223,221	0	213,676	3,436,897
2001	2,575,659	0	181,722	2,757,381
2002	2,063,589	0	219,431	2,283,020
2003	3,128,066	0	194,880	3,322,946
2004	2,795,278	0	212,038	3,007,316
2005	2,577,855	0	222,200	2,800,055
2006	65,386	27	4,489	69,902
2007	3,179,824	0	222,706	3,402,530
2008	28,859	2,857,071	211,519	3,097,449
2009	59,882	3,305,684	137,509	3,503,075
2010	44,365	3,151,170	203,024	3,398,559
2011	22,094	3,231,944	222,916	3,476,954
2012	22,569	3,111,479	194,871	3,328,919
2013	72,518	2,960,342	214,873	3,247,733
2014	46,907	3,116,672	198,800	3,362,379
2015	5,610	3,351,763	227,869	3,585,242
2016	7,995	3,133,410	469,673	3,611,078
2017	5,757	2,603,051	437,647	3,046,455
2018	5,355	3,065,065	451,058	3,521,478
			Mean	3,163,895
			Median	3,356,127

for USACE. In 2013, the target number of fish to release at PRH was revised to 7,299,504 (5,599,504 combined with the ongoing USACE's John Day mitigation of 1,700,000 smolts).

In addition to production released by PRH, the United States Army Corps of Engineers (USACE) also released subyearling fall Chinook Salmon from Ringold Springs Hatchery (RSH) into the lower end of the Hanford Reach beginning in 1994 (Table 2). The smolts released by RSH were derived from adult salmon returning to Bonneville Hatchery prior to 2009 and PRH during years afterwards to collect eggs sufficient to release 3.5 million subyearling smolts. Thus, a total annual release goal of 10,799,504 hatchery reared subyearling smolts was planned for the Hanford Reach from 2014 to present.

The age at maturity for naturally produced fish in the Hanford Reach varies between age-1 mini-jack and age-6 adults: albeit recoveries of age-1 and 6 fish are generally rare. The abundance of mini-jacks maturing as age-1 males is currently not known. Age-2 male fall Chinook Salmon (jacks) return to the Hanford Reach after spending roughly one year in the

ocean. The majority of the natural-origin adults return after spending three to four years in the ocean (age-4 and 5). A small portion, typically less than 2%, will spend up to five years in the ocean and return as age-6. The ocean distribution of natural- and hatchery-origin Hanford Reach fall run Chinook Salmon are similar and range from the northern California coast to the Gulf of Alaska (Norris et al. 2000, Weitkamp 2010). The majority of the adults migrate north of the Columbia River with the harvest primarily occurring in non-selective ocean and freshwater fisheries (Norris et al, 2000). Adults return to the mouth of the Columbia River between August and October and spawn in large cobble substrate between October and December (Langshaw et al. 2017; Richards and Pearsons 2019).

Release Numbers and Marking

Various mark types and rates have occurred at PRH over the years for both the Grant PUD and USACE mitigation fish to determine contributions to ocean and river fisheries (Table 1 and 2). The tagging and marking approach has recently been described in Pearsons et al. (2020). In 1976, PRH staff began adipose fin clipping and coded-wire tagging a portion of the juvenile fall Chinook released to determine PRH contributions to ocean and river fisheries. The smolt production at PRH associated with the USACE mitigation increased the number of adipose clipped smolts released by ~1.7 million starting with brood year 2006. The number of coded-wire tagged fish released from PRH increased to >1.2 million fish starting with brood year 2009 of which ~600,000 were adipose clipped. An additional 1 million adipose clipped smolts were included in the release since brood year 2011.

All PRH releases for both mitigation programs were 100% otolith marked beginning with the 2008 release to distinguish them from natural-origin fish resulting in all hatchery-origin fish being marked from brood year 2010 to the present. Fish released from RSH were also initially otolith marked but the marking program was discontinued beginning with the 2017 brood year. Fish released by RSH are 100% marked with adipose clips with ~6 – 12% receiving a coded-wire tag (CWT).

Since 1987, the U.S. Section of the Pacific Salmon Commission (PSC) has supported a coordinated project which seeks to capture and apply a CWT to 200,000 naturally produced juvenile fall Chinook Salmon in the Hanford Reach (Fryer 2017). Fish (40-80 mm length) are collected with seines over a ten-day period between late May and early June. Recoveries from these tagged fish are used to estimate harvest exploitation rates and interception rates for Hanford Reach natural-origin fall Chinook salmon. These data have also more recently been used to estimate the number of natural-origin juveniles produced in the Hanford Reach (Harnish et al. 2014, Harnish 2017).

Redd counts

Redd counts in the Hanford Reach were conducted from 1948 to 2018. Redd surveys were performed from a fixed wing airplane during the peak period of spawning (USDOE In Press). Redds were identified by the presence of clean substrate and stream bed morphology resembling redds. These annual redd counts serve as an index value for the Hanford Reach and not a total census because they were not conducted throughout the entire spawn time and because all redds were presumably not visible during flights due to wind, turbidity, ambient light, and

depth. A significant linear relationship between redd counts and total escapement was detected, suggesting that the redd counts were a good index of abundance (Figure 1).

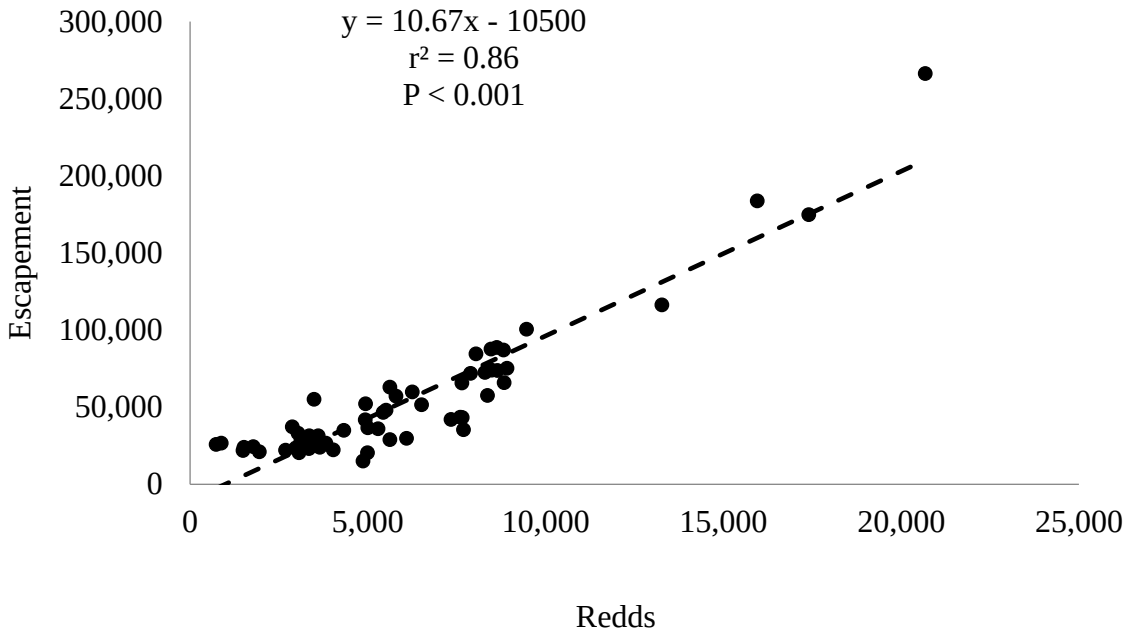

Figure 1. Linear relationships between the numbers of redds and the escapement to the Hanford Reach for years 1948 – 2018.

Escapement of fish to the Hanford Reach (E_{HR}) was estimated by subtracting the sources of fish that did not stay in the Hanford Reach from the total count at McNary Dam. The following equation was used to estimate abundance:

$E_{HR} = E_{McN} – E_{ICH}-E_{PRD}-E_{YAK}-HR_{PRH}-HR_{RGH}$ - Catch

Where: E_{McN} = Counts of adult Chinook Salmon passing McNary dam between August 9 to October 31.

E_{ICH} = Counts of adult Chinook Salmon passing Ice Harbor dam (the lowest dam on the Snake River) between August 12 to October 31.

E_{PRD} = Counts of adult Chinook Salmon passing Priest Rapids dam between August 14 to October 31.

E_{YAK} = Counts at Prosser Dam in the Yakima River

HR_{PRH} = Counts of fish collected by the Priest Rapids Hatchery volunteer trap

HR_{RSH} = Counts of fish collected Ringold Springs Hatchery trap

Catch = reflects the number of fish harvested in this portion of the Columbia River and the Yakima River

The estimated annual escapements to the Hanford Reach were not adjusted for pre-spawn mortality.

Carcass surveys

Salmon carcasses were sampled after spawning to evaluate the characteristics of the spawning population. Prior to 2010, the carcass surveys in the Hanford Reach were generally performed by two boat crews of two staff operating seven days a week. Beginning in 2010 the effort was increased to three boats with a three-person crew operating seven days per week. The sampling goal for obtaining a sufficient number of CWT was 10% of the escapement which was achieved in 17 of 35 years and the mean percentage of the escapement sampled was 10.3%. Carcass surveys covering all portions of the Hanford Reach were performed during all of November through mid-December. All recovered carcasses were screened for the presence of a CWT and the CWT were removed and later read in the laboratory. The population of carcasses collected was also subsampled to collect information on fish sex, fish length, egg retention, and scale and otolith samples to characterize demographic information. The subsample rate has ranged from 10-50% of the fish collected and varied as the result of collection goals and as escapements changed.

We used CWT recoveries from the adult carcasses in the Hanford Reach to estimate hatchery-origin fish in the escapement and the proportion of hatchery-origin fish in the spawning population of the Hanford Reach (pHOS). The recovered CWTs were expanded by sample rate of the survey and then by the juvenile tag rate. These estimates were supported by estimates generated using otolith marks Pearsons et al. (2020). The CWTs recovered from natural-origin adult salmon (NOR) originating from the Hanford Reach are difficult to expand accurately because the juvenile tag rates were unknown. Therefore, an assumption was made that returns not accounted for by hatchery-origin recruits and marked otolith recoveries were of natural-origin fish. Recent data indicates that CWT data may underestimate the true number of hatchery-origin recruits and may result in overestimates of NOR (See otolith bias chapter in this report).

The number of hatchery-origin recruits for each brood year (1993 to 2018) were estimated from the expansion of CWT recoveries. As age class cohorts for specific brood years returned to PRH and the Hanford Reach they were summed by brood year. Hatchery replacement rates (HRR) were calculated as the ratio between brood year specific hatchery-origin recruits and parent broodstock used at PRH during that brood year. Natural replacement rates (NRR) for the Hanford Reach URB fall Chinook salmon were calculated as the ratio of the sum of all NOR from a particular brood year divided by the number of the spawning population estimated in the Hanford Reach using the escapement estimates for specific brood years. Harvest of hatchery-origin recruits were estimated by expanding CWT recoveries in the fisheries, stream surveys, and hatchery traps. Since there is not a CWT mark rate for NOR, the harvest rates for PRH origin returns were used to estimate harvest of similar brood years of NOR. The data gathered allowed for a continuous data series for brood years 1993 - 2012.

Analysis

A before-after supplementation comparison was made to evaluate the effects of supplementation on the redd counts, total spawning escapement and natural-origin spawning

escapement in the Hanford Reach. The periods of analysis were selected by maximizing the number of years where data were available. The availability of salmon origin data limited the years that could be used for some analyses and therefore some of the evaluations consisted of different years. The supplementation treatment period was set as 1985 – 2018 (corresponds to brood years 1979-2012) and the pre period was represented by the years 1948 – 1984. The start of the supplementation treatment period was selected based upon hatchery release numbers (Table 1) and associated life-stages of adult returns. A t-test assuming unequal variance was performed to determine any difference between the treatment periods. A similar analysis was performed for the total and natural-origin spawning escapement for the Hanford Reach where the treatment period was similar to analysis of redds but the pre period represented the years of 1964 to 1984. A paired t-test was used to compare the numbers of natural- and hatchery-origin spawners during the treatment period. A paired t-test was also used to compare HRR and NRR for the brood years 1993-2012. Trends in HRR and NRR were evaluated with linear regression (1993-2012). Thresholds for statistical significance were set at $P = 0.05$.

The influence of pHOS on the density corrected presmolt productivity was evaluated by comparing pHOS estimates described above and data from Harnish 2017 (brood years1979-2009). Residuals were estimated from a Linearized Ricker Model Fit to the Hanford Reach Fall Chinook Salmon Pre-Smolts/Egg Stock–Recruit Data, brood years 1975–2009 (Harnish 2017). An examination of the relationship between pHOS and the annual residuals around a spawner-recruit curve was conducted to determine if there was evidence that hatchery-origin fish were affecting freshwater productivity of the naturally spawning population. The number of natural-origin juveniles produced in the Hanford Reach was estimated using methods described by Harnish et al. (2014), and Harnish (2017). Briefly, the estimated number of adults produced from a particular brood year were expanded by the annual survival among years to generate an estimate of presmolts in the Hanford Reach. CWTs were placed in natural-origin presmolts annually beginning in 1987, except 2002 and 2006, and then CWTs from harvest and escapement were used to estimate survival. A lack of a significant correlation between pHOS and residuals would suggest that hatchery fish did not have a strong influence on density corrected survival.

Results

The mean number of redds counted during the treatment period were 3.9 times greater and significantly more numerous than observed in the pre period (Figure 2; df = 46, t = -8.322, P <0.001). Similarly, Hanford Reach total spawning escapement was 2.8 times greater and significantly larger in the treatment period than the pre period (Figure 2; df = 35, t= -5.496, P < 0.001). Contributions of hatchery-origin fish in the spawning escapement during the treatment period ranged from 0.2% to 37.1% with a median value of 7.8%. The total number of natural-origin fish in the Hanford Reach escapement during the treatment period were significantly larger than hatchery-origin fish (df= 35, t= -5.496, $P < 0.001$) with the highest recorded values for natural-origin fish recorded from 2013-2016 (Figure 3). The mean abundance of natural-origin spawners during the treatment period 65,785 (SD = 44,484) was 2.5 times greater than that observed during the reference period. From brood year 1993 to 2012, the mean HRR for the Hanford Reach was 16.7 and significantly larger than that for NRR, 3.1 (Figure 4; df=19, t= 4.189, $P < 0.001$). Over this same time period a significant increase in HRR occurred (Figure 5; df =19, t = 2.313, $P = 0.033$) but not in NRR (Figure 5; df = 19, t = 1.801, $P = 0.089$). The

density-corrected relationship between pHOS and juvenile productivity was not significantly different from zero (Figure 6).

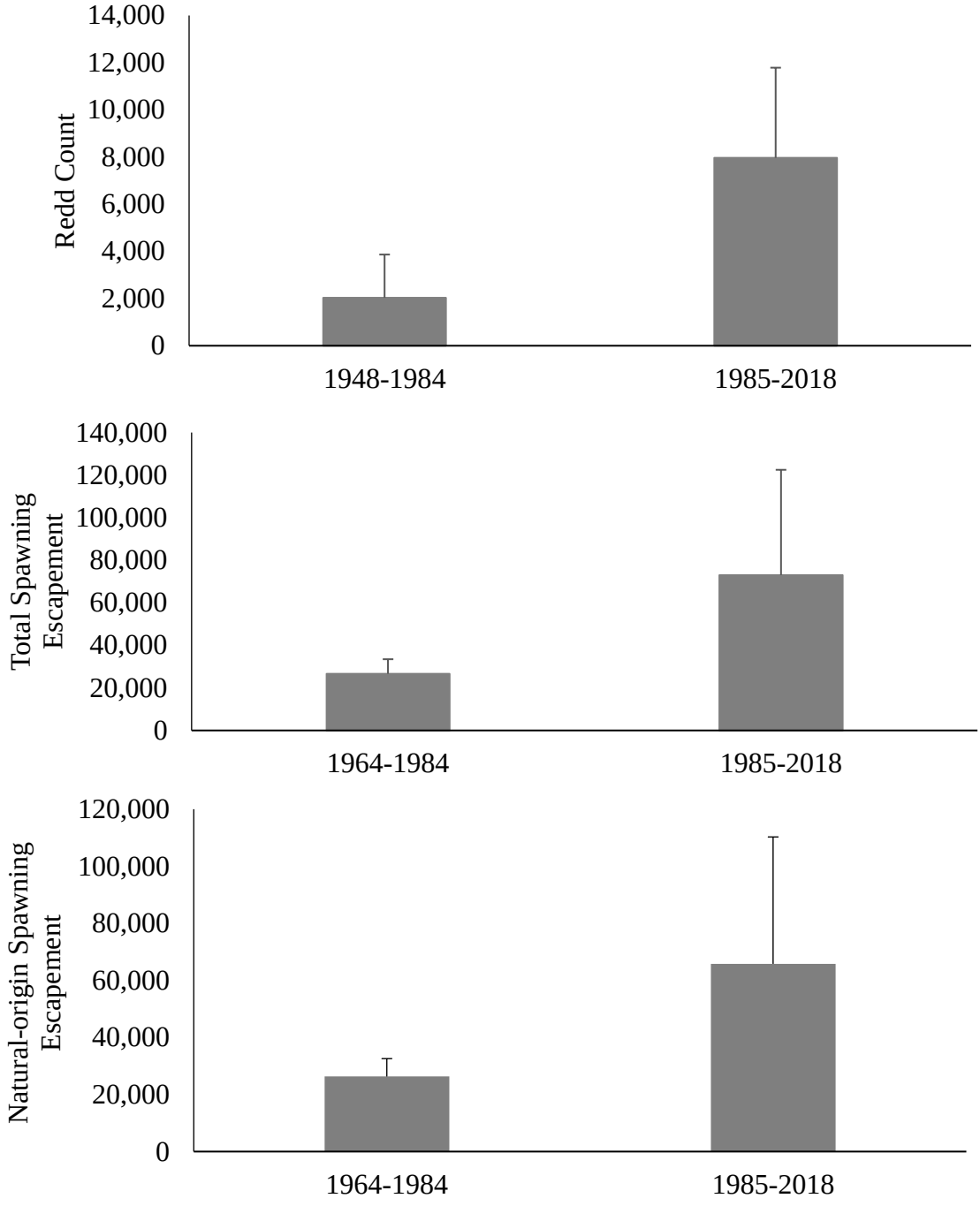

Figure 2. The average number (± 1 SD) of redds and spawning escapements before (pre 1985) and during the full implementation of the Priest Rapids Hatchery program.

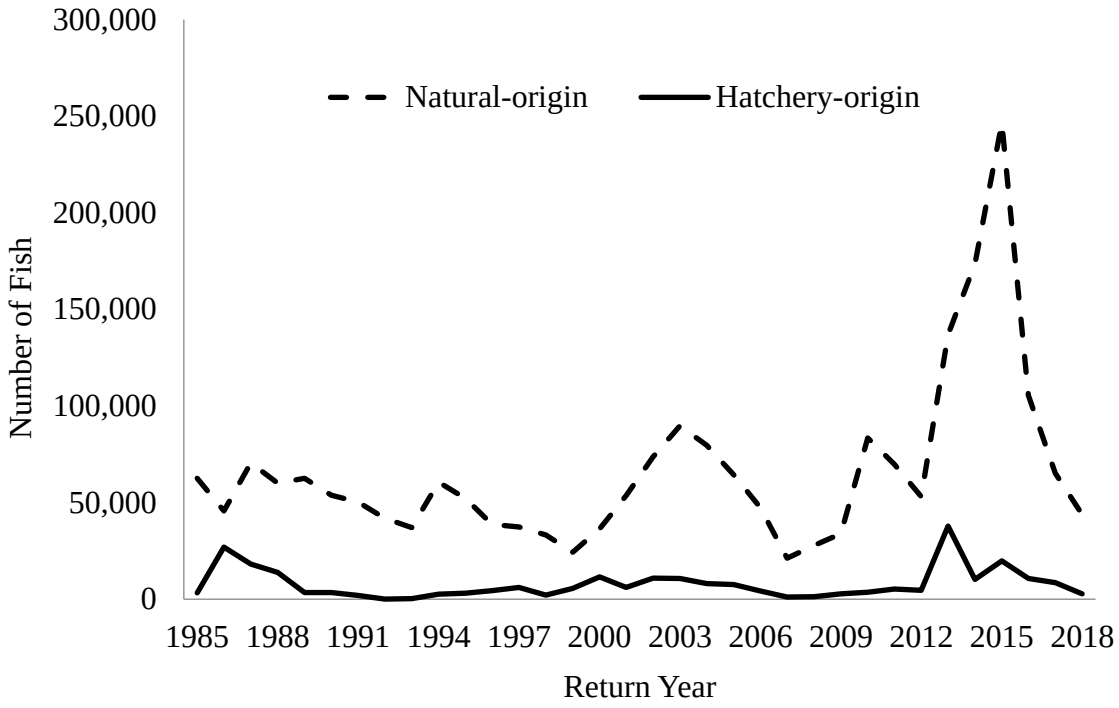

Figure 3. Contributions of hatchery- and natural-origin spawners to the spawning escapement in the Hanford Reach (Return Years, 1985-2018).

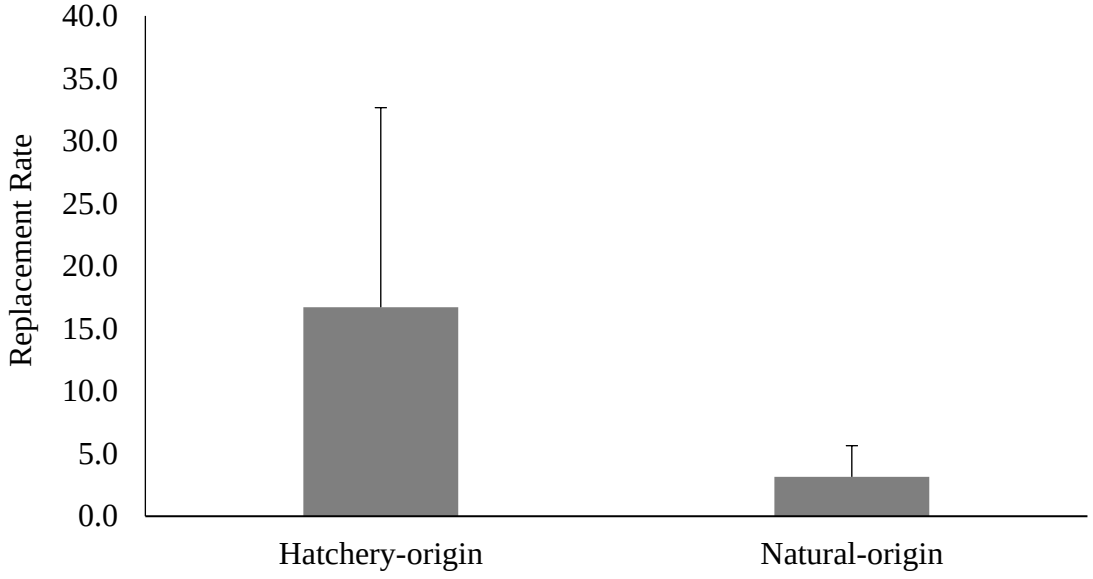

Figure 4. The average adult replacement rates (±1 SD) for hatchery- and natural-origin Chinook Salmon in the Hanford Reach (Brood Years 1993 – 2012).

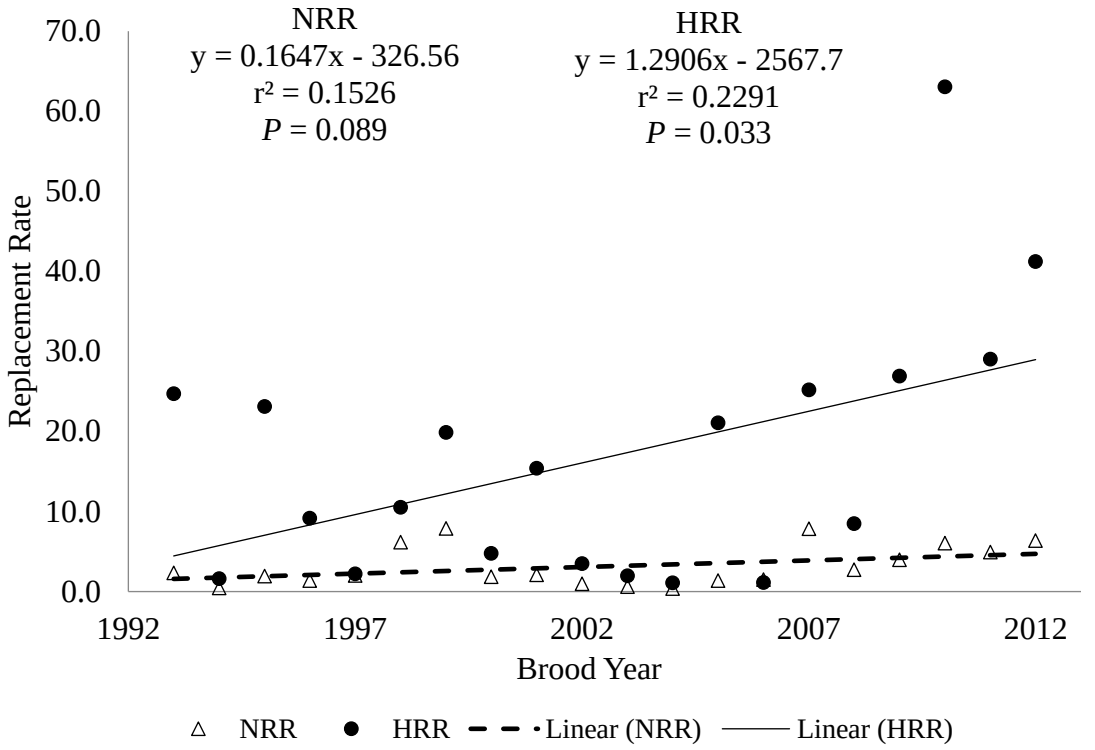

Figure 5. Replacement rates for hatchery- (HRR) and natural- (NRR) origin fall Chinook Salmon within the Hanford Reach (Brood Years 1993-2012**).**

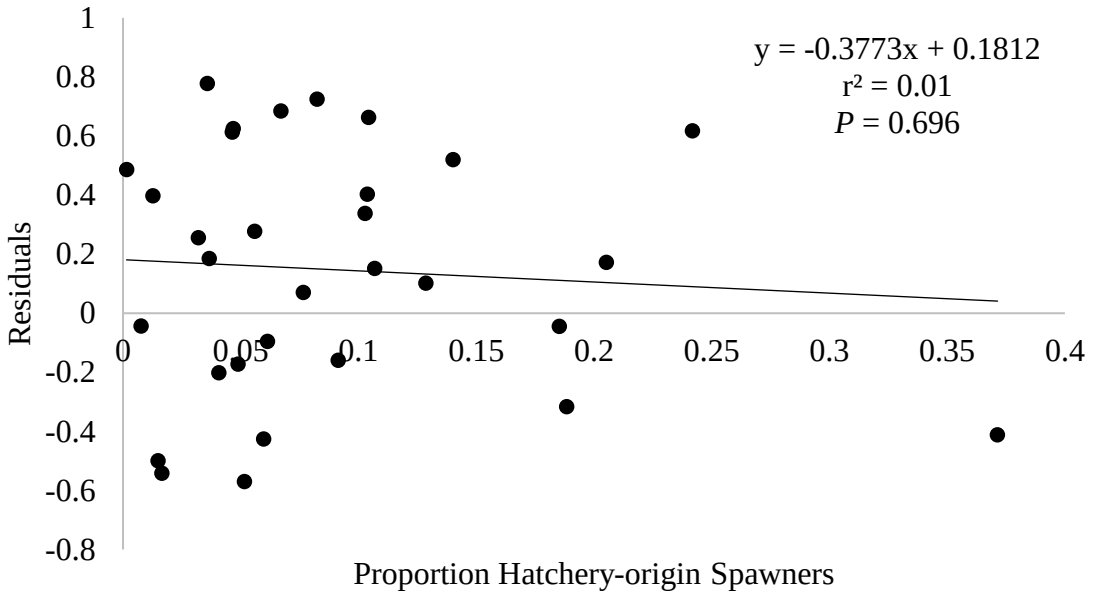

Figure 6. The relationship between the proportion of hatchery-origin spawners and residuals of juvenile abundance from a stock-recruitment relationship (BY 1979-2009). Residuals were

estimated from a Linearized Ricker Model Fit to the Hanford Reach Fall Chinook Salmon Pre-Smolts/Egg Stock–Recruit Data, BY 1975–2009 and sourced from Harnish (2017).

Discussion

The twofold goal of harvest augmentation and minimizing impact to the natural-origin population was likely achieved for the hatchery programs in the Hanford Reach. The first of the two goals was relatively easy to evaluate: the PRH has produced significantly more adults than if there was not a hatchery. The productivity of the hatchery in producing adults for harvest was over five times higher than that of the natural production of the Columbia River. This feature has contributed to some of the highest harvest rates from populations in the Columbia Basin with harvest occurring in Alaska, Canada, Washington and the Columbia River (Norris et al. 2000, Weitkamp 2010, Richards and Pearsons 2019). Harvest rates have been around 60-70% of the adult population (Richards and Pearsons 2019) and yet the population in the Hanford Reach continues to be abundant and productive. The productivity and abundance are some of the highest recorded for Chinook Salmon populations in the United States and Canada, even with many dams above and below the spawning population (Harnish et al. 2014, Langshaw et al. 2017).

Effects on natural production

Hatchery supplementation effects on the naturally spawning population was more difficult to evaluate than increases in harvest. There was no evidence that the PRH has depressed the abundance or productivity of the naturally spawning population in the Hanford Reach. There were significant increases in the number of redds and adults after supplementation was started and pHOS appeared to have little effect on density-corrected juvenile productivity. In addition, egg to fry survival produced from hatchery-origin fish in egg tubes in the Hanford Reach exceeded 70% which is within the range of natural-origin survival (McMichael et al. 2005; Oldenburg et al. 2012). It is possible that our evaluation of redds was conservative because we included years that were before the construction of Wanapum and Priest Rapids dams which may have impacted redd abundance. Because increases in abundance occurred during supplementation, any negative effects of supplementation, if they occurred, would have reduced the increase of abundance that we observed (e.g., Pearsons and Temple 2007; 2010; Temple and Pearsons 2012). However, the absence of a suitable non-supplemented population for comparison over this time period makes it difficult to assess the effect of supplementation as many features of the Hanford Reach contribute to abundance and productivity. The effects of hydropower management (Harnish et al. 2014, Langshaw et al., 2017, Harnish 2017), changing ocean conditions (Mantua et al. 1997), density dependence (Harnish et al. 2014, Harnish 2017), fisheries affects (Ohlberger et al. 2018), climate change (Goniea et al. 2006), and alteration of food webs from non-native species (Fritts and Pearsons 2004, 2006, 2008; Naiman et al. 2012) are also likely contributors to changes in abundance and productivity during the time of this evaluation. In addition, to the different factors that influence the productivity of the population, the statistical power to detect changes is low even when optimal designs are available (Ham and Pearsons 2000; 2001; Pearsons 2012). In short, the many limitations of our study limit our ability to draw firm conclusions about the effects of supplementation on abundance and

productivity, but if effects occurred that we could not detect, they were likely small and clearly outweighed by the many other factors influencing this population.

In contrast to the weaknesses described above, one of the strengths of this study was the long time series that was available for analysis. In some of our analyses we had 37 years (1948-1984) of pretreatment data and 34 years (1985-2018) of treatment data, a robust sample size that few hatchery evaluations have available. This long time-frame allowed for evaluation across the full life-span of supplementation and allowed for manifestation of the accumulation of genetic effects in the population (Pearsons 2002). Our data do not support the hypothesis that a genetic load decreased productivity because we did not observe a decline in NRR over the course of this study. Since 2010, the PRH program has been adapted to reduce genetic and ecological risks to the Hanford Reach population. This has included increased attention on increasing pNOB and reducing pHOS to achieve Hatchery Scientific Review Group recommendations (Mobrand et al. 2005, Paquet et al. 2011; Pearsons et al. 2020). These efforts have improved PNI substantially, exceeding recommendations, and reduced the risk of domestication selection to the Hanford Reach population (Pearsons et al. 2020). This reduction in genetic risk should decrease the likelihood that hatchery production will reduce the abundance and productivity of the Hanford Reach population in the future. In addition, beginning in 2016 hatchery smolts were released at night, in part, to reduce ecological interactions with naturally produced juveniles rearing in the Hanford Reach and reduce ecological risks of impacts to naturally rearing juveniles (Pearsons and Hopley 1999). Night releases may reduce risks of ecological interactions by reducing short term competitive interactions through visual isolation of competitors, however despite releasing fish at night, many of the fish released from PRH enter the Columbia River during the day.

Despite the high productivity of PRH, the pHOS remains relatively low because of the large natural population and the management of hatchery-origin adults in the terminal area. The abundance of natural-origin adults was considerably higher than hatchery-origin adults. The low pHOS reduces the potential to detect effects on productivity, even when estimation of productivity is restricted to freshwater. The volunteer trap at PRH has been used to remove around 75% of the PRH fish that return to the Hanford Reach (Pearsons et al. 2020). The low pHOS reduces the risk that PRH negatively influences the productivity of the naturally spawning population. Recent changes in hydropower operations to increase fall Chinook Salmon productivity (Harnish et al. 2014, Langshaw et al. 2015, Harnish 2017, Langshaw et al. 2017) and increased focus on pHOS management (Pearsons 2020) will likely continue to result in higher productivity compared to pre-hatchery performance.

Conclusion

In summary, we found that HRRs were approximately five times higher than NRRs which have contributed substantially to harvest from Alaska to the Columbia River (O'Connor and Pearsons, this report). We also found no evidence of negative impacts to juvenile or adult productivity or abundance associated with the supplementation program. However, the findings are not robust because of limited availability of non-supplemented reference populations, the presence of many factors that influence productivity and abundance that changed within and between pre and post treatment periods, and the low variation in pHOS. Despite the weaknesses of the analyses, recent observations of productivity and abundance of fall Chinook Salmon in the Hanford Reach are among the highest that have been observed, including those populations that have not been the target of hatchery supplementation (Harnish et al. 2014, Harnish 2017,

Langshaw et al. 2017). Given this result, and the recent improvements in hatchery operations (Pearsons et al. 2020), it is likely that undesirable impacts of hatchery-origin fish on abundance and productivity will continue to be low or absent and sustainable looking forward to the future.

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Expanding Partnerships and Innovations to Implement Reform of a Large Columbia River Hatchery Program

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Abstract

Recent reviews of salmon and steelhead hatchery programs have led to recommendations to reform hatchery practices and produce better supplementation outcomes. Of particular concern were reductions in performance of supplemented populations due to domestication selection attributed to hatchery production. One key recommendation was to achieve an index of domestication selection termed Proportionate Natural Influence (PNI) of 0.67 or higher. The Priest Rapids Hatchery, located adjacent to the Columbia River below Priest Rapids Dam, was one of the hatcheries included in this review. Data gathered from the hatchery and from the population being supplemented before implementation of reform measures indicated that the program was falling short of this goal. In this case study, we describe the influence of various partnerships and practices implemented in the Priest Rapids Hatchery program to achieve the recommended PNI for the program. The program exceeded the PNI goal in each of the last five years and since 2012 has averaged 0.72. The success in reaching the recommended benchmark was the result of generating creative solutions and building diverse decisional and operational partnerships that could achieve goals of hatchery reform in a cost-effective and broadly supported manner.

The Priest Rapids Hatchery, located adjacent to the Columbia River below Priest Rapids Dam, has long been considered a successful hatchery program. This large hatchery was built to mitigate the effects of two Columbia River dams (Priest Rapids and Wanapum dams) and has produced and released at least 4.5 million (range 4,548,307 to 10,296,700) sub yearling fall Chinook Salmon *Oncorhynchus tshawytscha* smolts annually to the Columbia River since 1981 that have contributed to hundreds-of-thousands of fish harvested (annual brood year mean=26,179**)** from Alaska to the Columbia River (Richards and Pearsons 2019). The Priest Rapids Hatchery is operated as an integrated hatchery program with a goal of supplementing harvest and limiting impacts to the naturally spawning population and non-target taxa of concern (Pearsons et al. 2012). Historically, the success of this hatchery was measured by adult contributions to ocean and in-river harvest. However, definitions for 'hatchery success' have evolved (Flagg 2015) and been redefined for most salmon and steelhead hatcheries in Washington and other areas as a result of large-scale hatchery reform recommendations provided by the Hatchery Scientific Review Group (HSRG 2009).

The United States Congress established the HSRG in 1999 to review hatcheries in the Pacific Northwest with the goal of continuing to provide fish for harvest while at the same time reducing risks to natural populations and contributing to achieving conservation goals for Pacific salmon and steelhead trout (Paquet et al. 2011). The recommended improvements to hatchery practices were designed to be more consistent with societal goals and recent science (Mobrand et al. 2005, Paquet et al. 2011) and included protections to the fall Chinook Salmon population in the Hanford Reach of the Columbia River, the largest naturally spawning Chinook Salmon population in the Columbia River, and the original broodstock source for Priest Rapids Hatchery (HSRG 2009, Paquet et al. 2011, Langshaw et al. 2017). A key element of hatchery reform is the reduction in the impact of domestication selection imposed by the hatchery environment on fish released to supplement natural production (Mobrand et al. 2005, Paquet et al. 2011). Domestication selection can reduce the productivity of natural spawning populations by contributing hatchery-origin fish to the spawning population that are not adapted to produce offspring that reproduce and survive in the natural environment (Ford 2002, Fritts et al. 2007, Pearsons et al. 2007). Offspring of natural-origin fish are assumed to possess traits that are well adapted for survival in their natural environment, and so should be strongly represented in hatchery broodstock.

The imposition of domestication selection by a hatchery program can be characterized by a metric termed proportionate natural influence (PNI), which represents the fitness of an integrated population of hatchery and natural spawners by an estimate of the equilibrium point of the relative degree of adaptation to natural conditions. PNI is calculated, using the proportion of natural-origin fish in hatchery broodstock (pNOB) and the proportion of hatchery-origin spawners in the naturally spawning population (pHOS), as: pNOB / (pNOB + pHOS) (Mobrand et al. 2005, Paquet et al. 2011). More recently, in recognition that multiple hatchery programs supplement some populations, an enhanced model was developed to estimate PNI (Busack, 2016). This model involves solving systems of complicated simultaneous equations to find equilibrium points and is calculated in a spreadsheet and run to equilibrium. Regardless of the method used, when PNI is greater than 0.5, selection pressures imposed by the natural environment are assumed to be stronger than those imposed by the hatchery environment, whereas when PNI is less than 0.5 the opposite is assumed to be true. HSRG recommendations for "core/critical" Columbia River populations, such as Hanford Reach fall Chinook Salmon,

were to maintain PNI values greater than or equal to 0.67. This would hypothetically allow for 67% of selection pressures to be exerted by natural processes. The average proportion of natural-origin returns (2012-2016) to the Priest Rapids Hatchery trap was 0.052 and the average proportion of hatchery-origin spawners in Hanford Reach over the same period was 0.14 (Richards and Pearsons 2019). This resulted in a PNI value of 0.27, which was far less than the HSRG recommendation.

To address this concern, partnerships were expanded and innovations were implemented in an attempt to increase PNI within the Priest Rapids Hatchery program. These actions represented a major change in hatchery operating procedures and required the existing partners, Grant County Public Utility District and Washington Department of Fish and Wildlife (WDFW), to develop new methods and collaborations guided by hatchery reform goals. The Priest Rapids Hatchery program obtained four additional partners when the United States Fish and Wildlife Service, National Marine Fisheries Service, Yakama Nation, and Confederated Tribes of the Colville Reservation, joined with Grant County Public Utility District and the WDFW as co-signers on the 2006 Priest Rapids Project Salmon and Steelhead Settlement Agreement. This agreement formed the Priest Rapids Coordinating Committee's Hatchery Subcommittee that was tasked with making unanimous decisions on Priest Rapids Hatchery operations. This expanded set of decisional partners created challenges in reconciling the different cultural, financial, and biological interests represented by these six organizations. For example, different objectives associated with marking and tagging required creative solutions to achieving PNI goals. It also required an increased number of participating individuals within and among different organizations to achieve committee goals. In addition, a new agreement between the Grant County Public Utility District, WDFW, and Army Corps of Engineers to produce fish at Priest Rapids Hatchery for the Army Corps of Engineers mitigation program was formalized in 2011. We document implementation of these efforts and their relative impact in increasing PNI.

Improvements to marking and tagging and monitoring and evaluation. Estimates of pNOB and pHOS, required to calculate PNI, are derived from demographic samples collected systematically from Priest Rapids Hatchery broodstock during spawning operations and from carcasses recovered during spawning ground surveys of Hanford Reach (Richards and Pearsons 2019). Hatchery-origin fish are identified by tags and marks applied to fish as juveniles. Scales, coded wire tags (CWT), and otoliths collected from fish at the hatchery and carcasses during spawning ground surveys provide information on fish age and origin. Additional data gathered on fish size and sex are used to characterize any phenotypic differences between hatchery- and natural-origin fish. Sample data are expanded by survey and mark rates to estimate the numbers of hatchery- and natural-origin fish within the survey population (e.g. Priest Rapids Hatchery broodstock, Hanford Reach population).

Increased investment in marking and tagging has led to improvements in monitoring and evaluation for the Priest Rapids Hatchery program. In 1977, the hatchery began clipping adipose fins and applying CWTs to a portion of released juvenile fall Chinook Salmon to determine contributions to ocean and river fisheries. In 1982, the hatchery began marking ~200,000 juveniles annually with an adipose clip and CWT. In 2008, an otolith-marking program was initiated that enabled marking of all juveniles released from the hatchery by altering water temperatures during incubation. Compared to other marking approaches, this technique was considered to be less stressful on fish and more cost-effective for both placing and recovering marks. Since all fish produced by the hatchery are marked, more precise estimates of pNOB,

pHOS, and PNI should be obtained. Juvenile fish released from the hatchery in 2008 (2007 brood year) began returning as three-year olds in 2010. Increases in the number of CWT and adipose fin clipped fish were prompted by a desire to enhance the precision of estimated numbers of hatchery- and natural-origin fish as well as the possibility of a mark-selective fishery. In release year 2010 and 2011, 600,000 fish received an adipose clip and CWT and 1.0 to 1.1 million fish were tagged only with CWT. From 2012 to the present, the number of fish tagged only with CWT has been set at 600,000. Also in 2012, WDFW funded marking an additional 1 million fish with adipose clips. Additional adipose clipping and coded wire tagging has not been universally supported by all of the decisional partners of the program, and program objectives needed to be accomplished within the boundaries set by the partners. By 2012, nearly all hatchery origin-fish could be identified effectively because most hatchery-origin fish return at two to five years of age (Richards and Pearsons 2019).

Increased use of CWTs and otolith marking of all produced fish led to greater costs associated with Priest Rapids Hatchery monitoring and evaluation and expanded the operational partnerships with WDFW (e.g., otolith laboratory). Grant County Public Utility District and WDFW revised the monitoring and evaluation plan (Pearsons and Langshaw 2009) and increased funding for WDFW staff to process greater numbers of CWTs and analyze otolith. Increased investments in tagging, collection and analysis have led to greater confidence in estimates for pNOB, pHOS, and PNI relative to those determined before return year 2012, which resulted in broader support of the tagging program by decisional partners.

Targeted removal of hatchery-origin adults at the hatchery trap. Hatchery-origin adult salmon returning to Priest Rapids Hatchery are removed from the Hanford Reach spawning population at the hatchery trap. Total broodstock requirements to meet program goals are typically less than 6,000, while the total number of fish returning to the trap has routinely been greater than three times this value. Recent collections at this trap indicated that over 90% of the fish entering the trap are of hatchery origin (Richards and Pearsons 2019). If these fish were not removed, they would increase pHOS and decrease PNI for the integrated Hanford Reach population. The HSRG recommends maintaining pHOS at less than 0.30 for the Hanford Reach population.

A trapping program with a goal of 24 hours/day and 7 days/week throughout the spawning migration (Sep-Dec) has been a consistent component of recent Priest Rapids Hatchery protocols. Operating this trap in this manner, along with sport harvest and trapping at Ringold Springs Hatchery can remove over 80% of Priest Rapids Hatchery-origin fish returning to Hanford Reach (Figure 1). Conversely, natural-origin fish dominate the fall Chinook Salmon population found in Hanford Reach, and the HSRG recommendation for maintaining pHOS below 0.30 have routinely been met in recent years. The importance of the trap to achieving low pHOS can be seen in instances when trap efficiency was compromised. For example, difficulties in maintaining continuous trap operation in 2013 (G. Pearson, WDFW, personal communication) led to the lowest percentage of hatchery fish captured (Figure 1) since 2012, an increase in hatchery-origin fish remaining in Hanford Reach, and the highest pHOS (0.28) recorded since 2012.

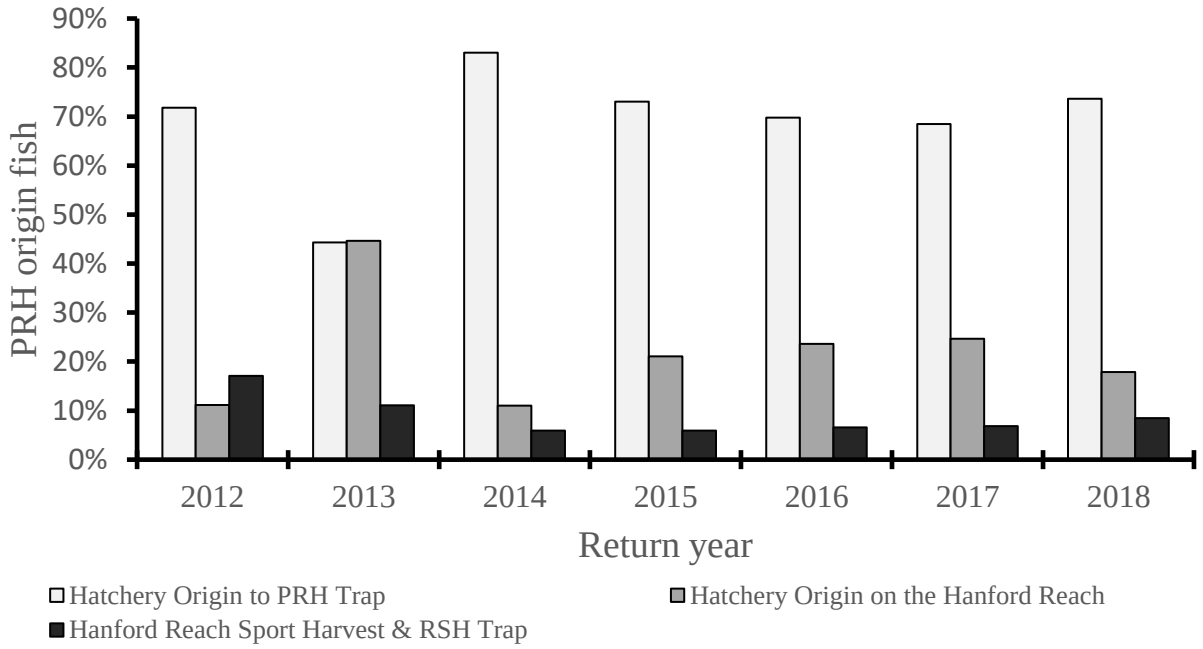

Figure 1. The percentages Priest Rapids Hatchery (PRH) origin fish removed from the Hanford Reach at the PRH trap (lightest colored bar); and those occurring in the following locations: Hanford Reach spawning population (grey bar); and Hanford Reach sport harvest and Ringold Springs Hatchery (RSH) trap (black bar).

Surplus Priest Rapids Hatchery fish removed by the trap make positive contributions elsewhere. While most surplus fish trapped between 2010 and 2018 (>200,000) were donated to local food banks (Figure 2), some are distributed to other groups, including tribes and educational groups that teach school students about salmon life history and ecology. In 2017 and 2018, at the request of other parties, surplus fish were used for other hatchery programs whose broodstock needs were not met by their usual sources.

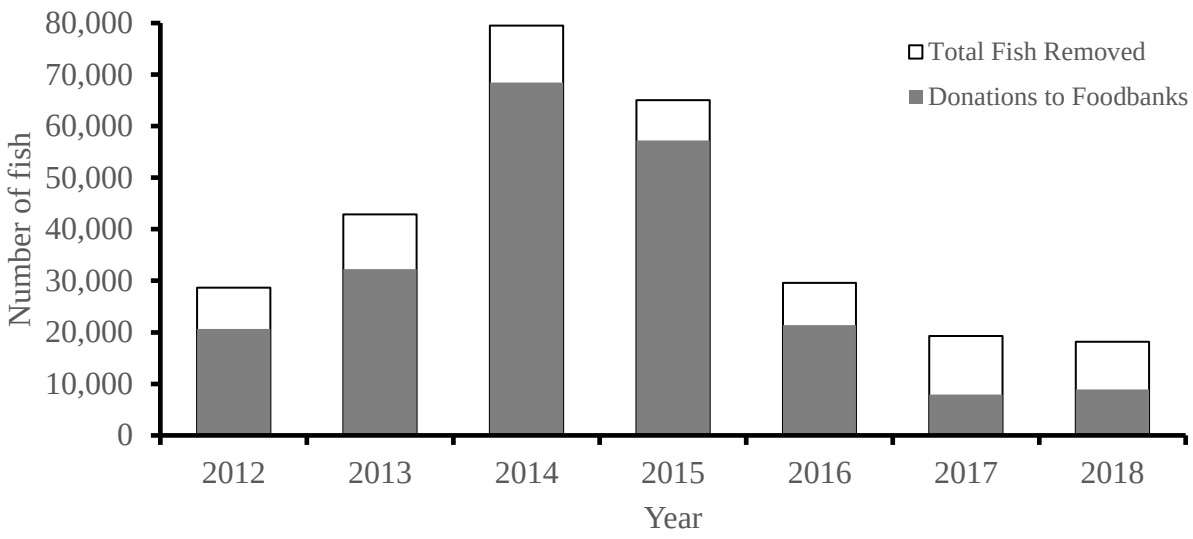

Figure 2. The numbers of Chinook Salmon removed from the Columbia River at the Priest Rapids Hatchery trap and the numbers donated to food banks during return years 2012 - 2018.

Prioritizing collection of unknown-origin fish at the hatchery trap. Most broodstock used for the Priest Rapids Hatchery program are collected from the hatchery trap (Figure 3), and strategies to increase the probability of securing natural-origin fish as broodstock continue to be developed and evaluated. Fish with intact adipose fins and without CWTs are prioritized for broodstock collection and spawning as they are more likely to be of natural origin. However, since only a portion of hatchery-origin fish returning to the hatchery trap have an adipose clip and CWT, this practice cannot screen for all hatchery-origin broodstock. Additional broodstock selection criteria, including targeting larger fish or specific temporal portions of returns to the hatchery trap, have the potential of improving PNI. However, use of such measures has only led to a small increase in pNOBs of broodstock sourced from the hatchery trap (Table 1), which have been insufficient in maintaining PNI above the 0.67 goal.

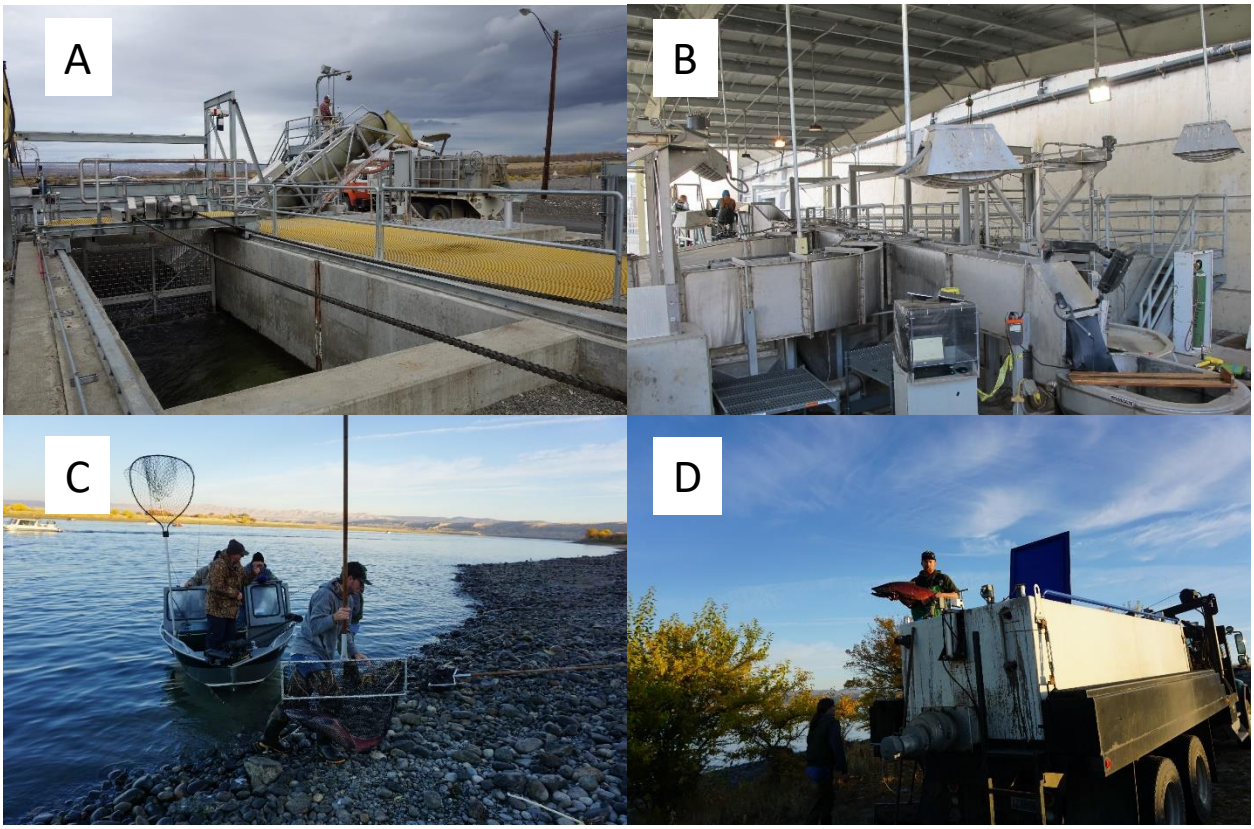

Figure 3. Broodstock sources that have evolved as a result of the goals of hatchery reform: A) Priest Rapids Hatchery trap; B) Priest Rapids Dam adult collection facility; C and D) Capture and transport of fish from the Hanford Reach of the Columbia River to Priest Rapids Hatchery by the Angler Broodstock Collection program.

Table 1. Number of fall Chinook Salmon used as broodstock for Priest Rapids Hatchery production that were collected from the hatchery trap, the adult fish trap at Priest Rapids Dam, and the King of the Reach Tournament (Angler Broodstock Collection) during return years 2012-2018. Numbers in parentheses are pNOB for each group.

Return Year	Priest Rapids Hatchery Trap	Priest Rapids Dam Adult Fish Trap	Angler Broodstock Collection
2012	4,408 (0.06)	471 (0.56)	67 (0.91)
2013	4,476 (0.02)	658 (0.55)	308 (0.81)
2014	4,427 (0.04)	825 (0.83)	221 (0.92)
2015	4,875 (0.08)	348 (0.87)	301 (0.96)
2016	4,324 (0.06)	366 (0.73)	247 (0.96)
2017	4,511 (0.09)	809 (0.87)	348 (0.91)
2018	4,028 (0.13)	711 (0.88)	1,085 (0.93)
Mean	**4,436 (0.07)**	**598 (0.76)**	**368 (0.91)**

Collecting fish from a mainstem river trap. A fish trap located on the mainstem Columbia River at Priest Rapids Dam adjacent to the Priest Rapids Hatchery complex has also been used to collect broodstock in an attempt to increase pNOB (Figure 3). Beginning in 2010, annual collection up to 1,000 fish without adipose marks or CWTs were made for use as hatchery broodstock. From 2012-2018, the number of broodstock fish collected from the mainstem fish trap each year (348-825) represented a smaller component of the total broodstock than those collected at the hatchery trap (4,028 to 4,875). However, the proportion of natural-origin fish from the mainstem trap has been much higher than at the hatchery trap (Table 1) and provides an important contribution to achieving the PNI goal.

Teaming with anglers to collect fish in the natural environment: Hanford Reach, the free-flowing portion of the Columbia River between Priest Rapids Dam and Richland WA, contains the highest proportion of natural-origin fish suitable for Priest Rapids Hatchery broodstock. Estimates for the proportion of natural-origin fish collected from Hanford Reach are frequently above 0.9 (Richards and Pearsons 2019). Both seining and trapping have been considered as methods to collect broodstock from Hanford Reach, but neither were thought to have the potential to be as successful and cost effective as angling due to challenges such as variable river depths, fast water flows, limited access, and impacts on federally listed species. Thus, angling was chosen as the best method for broodstock collection, even though it required the establishment of new partnerships to capture enough fish to substantially increase pNOB.

To effectively develop the angling method, given the popularity of the Hanford Reach Chinook Salmon sport fishery, a post-season fishing derby was initiated in 2012 as a means to increase pNOB without impacting the regular sport fishing season. Anglers are now drawn to Hanford Reach following the sport fishing season to participate in the ‘King of the Reach’

tournament. Fish caught by anglers during this effort provide the Angler Broodstock Collection (ABC) component of the broodstock for Priest Rapids Hatchery. The incentives for anglers to participate were opportunities to: 1) compete and win prizes, 2) contribute to fish conservation, and 3) fish in quality waters with lower number of anglers following the sport season closure. Anglers registered for the event are issued guidelines for collection and handling of live adult Chinook Salmon and provided equipment for holding live fish on their boats. When fish are caught, anglers either transport the fish to one of two locations where a hatchery transport truck is positioned or call WDFW and Grant County Public Utility District personnel who will pick up the fish with another boat and transport them to a hatchery transport truck (Figure 3). The angler catching the most fish is crowned 'King of the Reach', which is a source of pride among recreational anglers in the area that support the Priest Rapids Hatchery program. The effort started small, and the first year provided only 68 fish (Table 2). However, the local chapter of the Coastal Conservation Association, a large nationwide sport fishing group, assumed a larger responsibility and promoted the event nationally, leading to participation of greater numbers of anglers from around the country. Greatest participation and harvest occurred in 2018, when 85 boats (195 boats days) and 277 anglers (582 angler days) harvested 1,221 fish for broodstock. Currently, broodstock collection by the 'King of the Reach' tournament is sustained by collaborative efforts of three organizations. Grant County Public Utility District provides funds and equipment, the Coastal Conservation Association and WDFW promote and advertise the event, and all three organizations work together to manage the three-day tournament in late October. Pre-spawning mortality of harvested fish is generally low. For example, only one of 68 fish harvested in 2012 died (1.5%) before being spawned at the hatchery, and 136 of 1,221 fish died (11.1%) before being spawned in 2018.

Table 2. Annual angler participation and harvest for the 'King of the Reach' tournament held to collect Chinook Salmon broodstock for Priest Rapids Hatchery during return years 2012–2018.

Year	Number of Anglers	Number of Boats	Number of Chinook Salmon Harvested		
			Males	Females	Total
2012	57	21	42	26	68
2013	101	41	291	121	412
2014	65	25	164	132	296
2015	77	25	216	304	520
2016	115	38	132	202	334
2017	177	57	180	296	476
2018	277	85	614	607	1,221
Mean	**124**	**42**	**234**	**241**	**475**

Real time otolith reading and spawning protocol adjustments: Currently, identifying Priest Rapids Hatchery-origin fall Chinook Salmon without CWTs and adipose fin clips requires screening their otoliths for unique hatchery marks. Fish without otolith marks, adipose clips or CWTs are considered to be of natural origin. Otolith reading typically occurs offsite in a laboratory and results are not available for several months. However, in 2014, we initiated a

program of ‘real-time otolith reading’ so that otoliths could be read and fish origin identified prior to combining gametes (Figure 4). This was accomplished by transporting WDFW otolith reading equipment and personnel to Priest Rapids Hatchery. During the first year of this program, otoliths from both males and females were screened, but this slowed the spawning process. Since identification of female origin was less consequential for pNOB than male origin (see spawning protocols below), only males are now screened. Milt from males identified as natural origin is used to fertilize eggs from females with highest probability of being natural origin (e.g. ABC, Priest Rapids Dam, no CWT or adipose clip) during the peak spawning week.

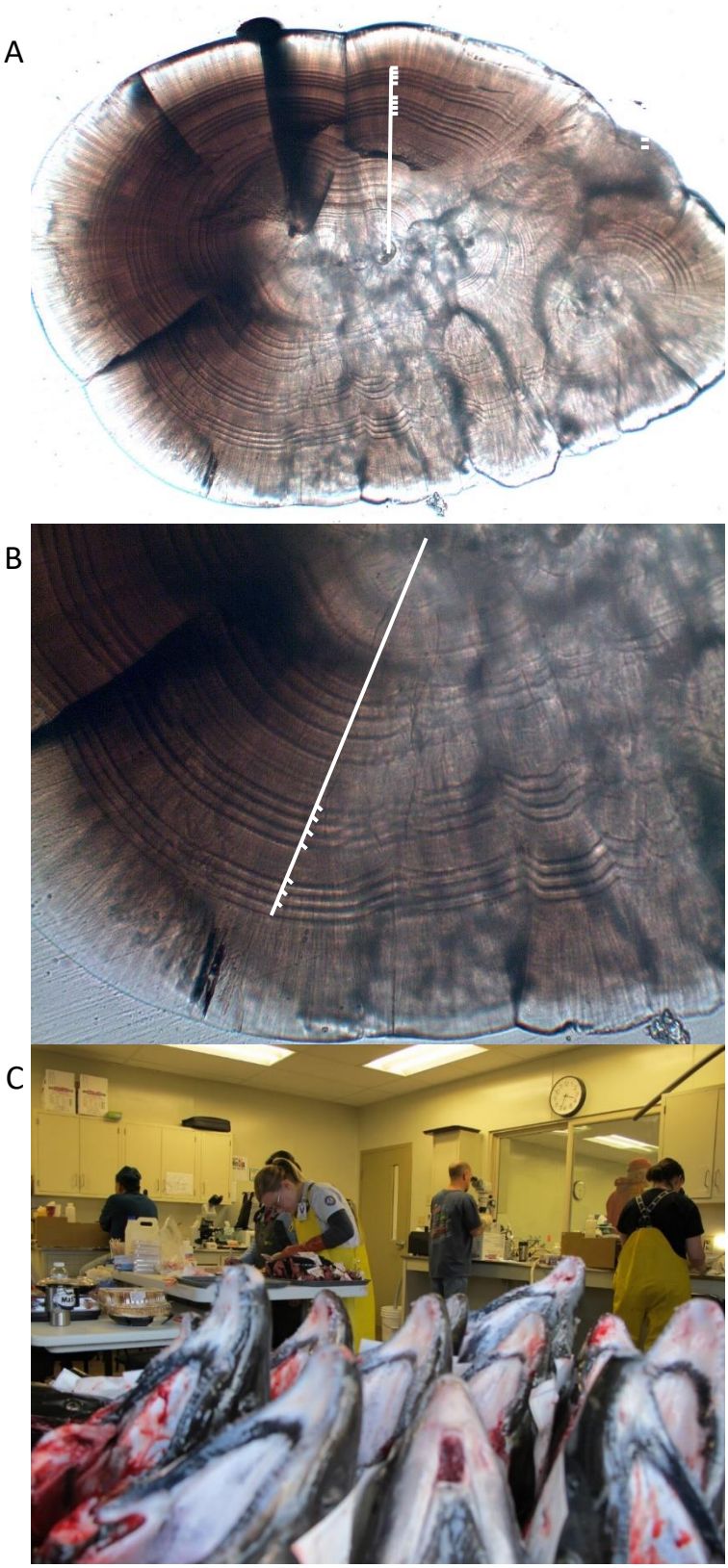

Figure 4. Priest Rapids Hatchery otolith marking and reading program: A) Otolith from juvenile fall Chinook Salmon magnified 100x showing marking applied by manipulating water

temperature (magnification 100x); B) Same otolith shown in A magnified 200x; C) WDFW personnel conducting real-time otolith reading to screen for hatchery origin of brood fish during hatchery spawning events. Otolith images in A and B courtesy of Wade Smith, Washington Department of Fish and Wildlife, Fish Aging Lab.

Standard spawning protocol at Priest Rapids Hatchery consists of combining the eggs from two females with milt from one male into a single 20 L bucket, combining the contents of two buckets, and moving the batch of fertilized eggs to the incubation room. Modifications to this protocol were made during real-time otolith reading in 2018. Every natural-origin male identified by otolith reading (e.g., 2014-2017) was used to fertilize eggs from four females. Hatchery-origin males identified by otolith reading were only used to fertilize females, if production goals could not be met with available natural-origin males. In this situation, one hatchery-origin male was using to fertilize two females. It is important to meet production goals in order to meet mitigation requirements for which the hatchery was originally built. Increasing the male to female ratio from 1:2 to 1:4 does reduce effective population size. However, modifications to standard Priest Rapids Hatchery spawning protocols sought to balance risks of domestication selection with risks of reducing effective population size.

Four pieces of information contributed to the final decision on altering hatchery spawning protocols: 1) Priest Rapids Hatchery is a large program (> 5,000 broodstock) with a large number of families produced; 2) the naturally spawning Hanford Reach population is large (median number of returning fish has been greater than 50,000 since 1991; Richards and Pearsons 2019); 3) the naturally spawning Hanford Reach population is typically composed of only a small proportion of hatchery-origin fish (average pHOS of 0.12 since 2012; Table 3); and 4) male Chinook Salmon often spawn with multiple females in the natural environment (Hankin et al. 2009; Schroder et al. 2010, 2012). Additionally, since HSRG recommendations focus on PNI as a primary driver of modifications to Priest Rapids Hatchery program management, the possibility of reducing effective population size by using a 1:4 rather than the standard 1:2 ratio of natural-origin males: females in hatchery spawning was viewed as an acceptable risk in order to increase pNOB and achieve the PNI goal.

Table 3. PNI estimates for Hanford Reach fall Chinook salmon supplementation programs during return years 2012-2018. PNI was calculated from multiple population gene flow model (Busack 2016).

Return Year	pNOB	pHOS	PNI
2012	0.12	0.14	0.60
2013	0.13	0.28	0.46
2014	0.21	0.10	0.78
2015	0.18	0.10	0.76
2016	0.16	0.12	0.70
2017	0.25	0.08	0.84
2018	0.39	0.07	0.89
Mean	**0.21**	**0.12**	**0.72**

In 2018, the real-time otolith-reading program was eliminated from Priest Rapids Hatchery spawning operations due to the large number of natural-origin fish obtained from the King of the Reach tournament. While most individual ABC males (58%; N = 554) were paired with four females during spawning operations, many individuals (42%; N = 401) could only be paired with one female due to lower availability of females on some spawning dates as the season progressed. Although not included in real-time otolith reading, otolith samples were collected from a subsample of females and males that were part of the broodstock during all years to determine the proportion of natural-origin broodstock and their contribution to the final determination of pNOB at the hatchery.

Effect of reform efforts on Proportionate Natural Influence (PNI): Prior to implementation of hatchery reform measures, the Priest Rapids Hatchery program relied on the hatchery trap, with little effort to target natural-origin fish for broodstock. Given the low number of natural-origin fish returning to the hatchery trap, resulting PNI values were well below the HSRG recommendation. In recent years (2014-2018) the cumulative impact of targeted selection of natural-origin broodstock has resulted in PNIs ranging from 0.70 to 0.89, which exceed the HSRG goal of 0.67 intended to reduce domestication selection (Table 3). Reform efforts have varied in their effectiveness in raising PNI values. The high proportion of hatchery-origin fish in the hatchery trap and inability to identify hatchery-origin fish without an external mark, greatly limits efforts to select fish at the trap to increase hatchery pNOB. However, the availability of alternate broodstock sources at Priest Rapids Dam and from King of the Reach tournament angling, as well as the capacity to alter spawning protocols using real-time otolith reading, have led to substantial PNI increases.

While the Hanford Reach population has spawners from both Priest Rapids and Ringold Springs hatcheries, Ringold Springs fish are progeny of the Priest Rapids Hatchery program. Hanford Reach PNI, estimates, derived from the model for multiple hatchery programs (Busack,

2016), presently exceed the HSRG goal of 0.67 (Table 3) with appreciable increases in pNOB, as hatchery protocols have been adapted. The Priest Rapids Hatchery program continues to evolve with guidance from agencies, tribes, and the HSRG. The problem-solving approach and creative use of resources at Priest Rapids Hatchery to achieve a paradigm shift in operations illustrates how such cooperation can address hatchery reform challenges.

Furthermore, expanding decisional partnerships can result in new challenges as well as solve existing challenges in cases beyond hatchery reform, such as in harvest reform and habitat restoration. Adding diverse interests, representatives, and personalities to decision making can reduce management options when differing objectives collide. For example, the compromise about marking and tagging at the hatchery reduced the options for achieving the overall goal. The compromise about marking and tagging at Priest Rapids Hatchery was a good example of how new decisional partnerships can result in reduced options to achieve goals. These new decisional partnerships add benefit to the program by providing broad support for an action.

New operational partnerships can help solve existing problems, as well as address new challenges created by new decisional partners. Partnerships with multiple organizations can help solve problems by bringing in new creative people. This occurred when WDFW personnel were mobilized to read otoliths in real time, and the Coastal Conservation Association called upon their recreational angler base to increase broodstock collection efforts at the King of the Reach tournament. In existing management or science programs, particularly those where goals have changed, expanding partnerships in decision making may also increase the need for developing partnerships in implementation and innovation. In short, the benefit of achieving broad support for a management action created by increased participation in decision-making can often result in new challenges that can inspire innovative implementation through expanding operational partnerships.

Acknowledgments

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Distribution of Hatchery- and Natural-origin Adult Chinook Salmon Carcasses in the Hanford Reach and the Influence of Carcass Drift

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Abstract

Adult carcasses are frequently used in long-term monitoring to index the spawning distribution of hatchery- and natural-origin Salmon. We show that hatchery- and natural-origin Chinook Salmon carcasses were well distributed throughout the Hanford Reach of the Columbia River and that the proportion of hatchery-origin carcasses generally matched that of natural-origin. In addition, we found that the sex ratios of carcasses were different in different sections (14-21 km long) of the Hanford Reach, and the number of redds in a section were associated with higher proportions of females. This suggested that carcasses may drift between sections. We tagged approximately 1,000 aged 2-6 Chinook Salmon carcasses annually between 2012 and 2018 and recovered carcasses during annual carcass surveys approximate 1-30 days later to evaluate carcass drift. We found that carcasses could drift the full length of Hanford Reach (94 km), it was common for carcasses to drift over 40 km, and that males were more likely to be found in downstream sections than females. This suggested that female carcasses were likely to be a better index of spawning location than male carcasses. It was likely that the deep water, low structural complexity, and variable flows of the Columbia River were partly responsible for the large drift distances we observed. Despite large amounts of drift in the Hanford Reach, carcasses were useful for assessing spawner distribution at large spatial scales and decreased in reliability with decreasing spatial scale. Furthermore, it is important to understand the scale of resolution of carcass surveys relative to evaluating management objectives.

Introduction

Spawning location of hatchery- and natural-origin Salmon can be an important determinant of reproductive success (Williamson et al. 2010, Schroder et al. 2008; Ford et al. 2015). Salmon likely use a combination of homing and habitat selection to determine where to spawn (Keefer and Caudill 2014; Cram et al. 2012, 2017, Pearsons and O'Connor 2020). Artificial propagation has the potential to disrupt imprinting and result in suboptimal spawning locations (Keefer and Caudill 2014; Pearsons and O'Connor 2021). Furthermore, the location of release and acclimation sites can have strong influence on where fish spawn and if these sites are located in suboptimal spawning areas, then spawners will likely have reduced reproductive success (Hoffnagle et al. 2008; Dittman et al. 2011; Ford et al. 2015). In short, monitoring spawning locations of hatchery- and natural-origin salmon can help explain why differences in reproductive success occur if they exist.

The recovery location of adult carcasses of Chinook Salmon (*Oncorhynchus tshawytscha*) is a common way to index the spawning location of hatchery- and natural-origin fish (Hoffnagle et al. 2008, Murdoch et al. 2009a, Dittman et al. 2011). Typically, redd surveys are also conducted in conjunction with carcass surveys and redds indicate where fish spawn and data on carcasses found in proximity to the redds are used to estimate the demographic features of the spawning population and their origin (e.g. hatchery- or natural-origin) (Gallagher et al. 2007; Crawford et al. 2007). However, an important assumption of this method is that carcasses were found sufficiently close to where the fish spawn.

The location of female spring-run Chinook Salmon carcasses has been determined a relatively good proxy for spawning location with male salmon found at greater distance from redds. For example, in the Chiwawa River, drift distances for females and males were 150 m and 4,465 m from redds, respectively with no difference between hatchery- and natural-origin females (Murdoch et al. 2009a). This system is a relatively small river, with low flows during spawning, and relatively high habitat complexity that facilitate retention of carcasses (Hughes and Murdoch 2017). Carcass surveys are currently used to index and monitor the distribution of hatchery- and natural-origin fall-run Chinook Salmon in the Hanford Reach of the Columbia River (Richards and Pearsons 2019). The Hanford Reach is one of the last free flowing sections of the Columbia River and is large, deep, and has variable flows during 24-hour periods that could mobilize carcasses (Harnish et al. 2014, Langshaw et al. 2017). Carcasses in other rivers that are deep, have fluctuating flows, and low structural habitat complexity, such as the Columbia River, may produce different patterns of carcass drift (Zhou 2002). Thus, additional work is necessary to determine how carcass surveys can be used effectively in these large mainstem rivers where fall run Chinook Salmon spawn.

The objectives of this study were to: 1) characterize the distribution of male and female hatchery- and natural-origin spawners in the Hanford Reach, 2) characterize carcass drift in the Hanford Reach, and 3) evaluate the impact of carcass drift on interpreting spawning location.

Methods

Study Area: The Hanford Reach of the Columbia River is located in south central Washington with boundaries defined by Priest Rapids Dam and the city of Richland, WA (Figure 1). The

study area includes the entire Hanford Reach and an additional 4 km of impounded river immediately downstream. The estimated spawning escapement of fall run Chinook Salmon of the Hanford Reach is large; from 2012 to 2018 the spawning escapement ranged from 46,624 to 266,346 per year (Richards and Pearsons 2019). Fall run Chinook Salmon spawning occurs in the Hanford Reach between October and December with peak spawning activity occurring during November. These fish spawn in a variety of depths and velocities in large cobble substrate (Geist et al. 2000). The Hanford Reach is one of the only non-impounded portion of the Columbia River, upstream of Bonneville Dam, but upstream dams modify the flows substantially (Harnish et al. 2014, Langshaw et al. 2017). Upstream dams have modified flows that facilitate higher production of fall Chinook Salmon smolts through mechanisms such as reducing desiccation of redds and reducing flow fluctuations that could entrap and strand juveniles (Harnish et al. 2014, Langshaw et al. 2017). However, during the spawning season flows over 24 hours are highly variable with flows low during the day and high at night (59 - 180kcfs; https://waterdata.usgs.gov/wa/nwis/rt).

The Hanford Reach has been partitioned into five survey sections for describing the distributions of redds and post spawn carcasses. These sections are arranged around natural breaks in prominent spawning areas (Figure 1). Aerial redd counts for the Hanford Reach are a primary index of spawning abundance and distribution and from 2012 to 2018 redd counts ranged from 5,429 to 20,678 per year (Richards and Pearsons, 2019) with redds distributed throughout survey sections 1-4; the majority of redds were found in section 3 and no redds were observed in section 5 (Figure 2).

Characterization of Carcass Distribution during surveys of the Hanford Reach: Fall-run Chinook Salmon carcass surveys were conducted annually in the Hanford Reach as part of ongoing monitoring and evaluation protocols associated with the fall-run Chinook Salmon programs of Priest Rapids and Ringold Springs hatcheries (Richards and Pearsons 2019). Carcass surveys occurred from early November to mid-December with the goal of recovering all accessible carcasses in each section at least once per week during the survey period. Three survey crews sampled carcasses seven days per week and were active throughout the spawning season. Carcasses were collected while walking the shorelines and islands in the river or by gaffing carcasses from a boat. Sections containing large numbers of carcasses were frequently surveyed twice weekly. Crews do not search for carcasses downstream of Section 5 which was outside of the study area and an area of low or no suitable spawning habitat as it is part of the slow-moving McNary reservoir. All carcass recovered within each of the five survey sections were identified as males or females, scanned for coded-wire tags (CWT), examined for external tags or marks (operculum, floy-tags, adipose clip), and other data that contributed to the long-term data series monitoring natural- and hatchery-origin fish. Proportions of hatchery- and natural-origin fish were estimated by identification of coded wire tags, clipped adipose fins, and marked otoliths as described by Pearsons et al. (2020).

The frequencies of males versus females and hatchery-origin versus natural-origin in each section for the period of 2012 to 2018 were summarized and the proportions of carcasses found in each section determined. Linear regressions were performed to characterize the relationships between the paired observations of redd abundance determined by aerial survey and total carcasses recovered in each section, female carcasses recovered in each section, and male carcasses recovered. A two-factor analysis of variance was conducted to determine if the

proportions of hatchery- and natural-origin carcasses were distributed equally across all survey sections following an arcsine transformation of the square root of the percent values. Similarly, a two-factor analysis of variance of transformed percent values was also performed to determine if the distribution male and female carcasses was similar across all survey sections. In each case the threshold of significance was set at $P < 0.05$.

Characterization of Carcass Drift in the Hanford Reach: From 2012 – 2018, a portion of the carcasses gathered during carcass surveys were used to characterize drift of post-spawn carcass in the Hanford Reach. During this period, we tagged from 626 to 1,073 yearly at known locations. Three different tagging and release methods were used as observations of data gathered prompted adaptations to existing protocols. In all years, date, and the release and recovery sections were recorded.

Method 1:

During 2012 and 2013, we tagged and released 989 and 1,073 carcasses, respectively, distributed among all five survey sections. We placed roughly half in near shore areas and the other half in the thalweg of the river adjacent to these nearshore release sites. A numbered tag (Model 337P, Ketchum Manufacturing Company. Inc., East Lucerne, NY) was stapled to the inside surface of each operculum so that it protruded ~1 cm outside of the operculum. The date, tag number, fish sex, and release section were recorded for each fish prior to release. When these animals were found during normal annual carcass surveys, tag number and survey section were recorded for recovered tagged fish. The frequency of recaptures was summarized to illustrate the movement of carcasses within and among different survey sections.

Method 2

In 2014, we tagged 994 carcasses in situ in shallow water areas with numbered dart styled tags (Model FT1-94, Floy Tag and Manufacturing Inc, Seattle, WA) in survey sections 1-4; the tag applicator was attached to a ~3 m long 2.5 cm diameter aluminum pole. Of these fish, 976 had two tags applied to evaluate tag loss. The number of carcasses tagged by section ranged from 107 in Section 2 to 485 in Section 1. The date, tag number, release section, and GPS location were recorded (Model eTrex 20, Garmin International, Olathe, Kansas) at time of tagging and the same data were also recorded for the tagged fish that were recovered. The distance (km) that a recovered carcass drifted was estimated as the most direct river route between the release and recovery GPS points using Google Earth. The frequency of recaptures and the distance traveled (km) between release and recapture was summarized to illustrate the movement of carcasses within and among different survey sections. The drift distance data were skewed by outliers and following rank transformation a one-way ANOVA was performed to determine differences in drift distances among the four upper sections followed by a Tukey's HSD procedure to identify specific differences among individual means

Method 3

During 2015-2018, we tagged and released from 626 to 997 tagged carcasses per year. A numbered tag (Ketchum Mfg. Co. Inc., Model 337P#) was stapled to the inside surface of each operculum so that it protruded ~ 1 cm outside of the operculum and be visible externally. Tagged fish were then transported and released from a boat over known active redd locations in survey sections 1-4. Date, tag number, fish sex, survey section, and GPS location were recorded for each fish. After release into the river, the carcasses sunk to the bottom of the river quickly (<

5 seconds). The date, tag number, fish sex, survey section, and GPS location were also recorded for tagged fish recovered. The distance (km) that a recovered carcass drifted was estimated as the most direct river route between release and recovery GPS points using Google Earth. Each year, the drift measurements for recaptures was summarized by section. The mean of the annual statistics for release number, carcasses recovered, and distance traveled were summarized. Male and female drift differences were also summarized by section but the recapture frequency was small and the data for each section was pooled for all years to determine any difference attributed to fish sex. Values were rank transformed and a two-way ANOVA performed on the data from all years followed by a Tukey's HSD procedure to identify specific differences among individual means

Results

Characterization of Carcass Distribution in Hanford Reach: Chinook Salmon carcasses were found throughout the Hanford Reach, but were uneven in their distribution. Linear regressions revealed significant positive relationships between the paired observations of redds and total carcasses recovered for each section ($P = 0.023$) and for redds and female carcasses ($P = 0.012$) although the strength of these relationships was weak for both regressions ($r^2 < 0.20$; Figure 3). No relationship between redds and male carcasses was detected ($P = 0.316$). Hatchery- and natural-origin carcasses varied across all five survey sections. Both hatchery- and natural-origin carcasses were found predominantly in sections 1, 3, and 4 (76% of all carcasses; Figure 4). The main effect of origin (hatchery vs natural) was not significant (df=1, F = 0.008, $P = 0.978$). The main effect of release section (df = 4, F 38.439, $P = 0.000$) and the interaction between origin and survey section (df = 4, F = 3.115, $P = 0.021$) were both significant by ANOVA. Higher proportions of hatchery-origin fish in survey section 1 combined with higher proportions of natural-origin carcasses in sections 3-5 appear to drive this interaction (Figure 4).

The majority of females were found in sections 3 and 4 (71%; Figure 5). While large numbers of males were also found in sections 3 and 4, section 5 also contributed large numbers to the fish collected during surveys (Figure 5). Analysis of variance revealed that the main effect of fish sex was not significant (df = 4, F = 1.849, $P = 0.179$) while the main effect of survey section (df = 4, F = 76.105, $P < 0.001$) and the interaction between fish sex and survey section (df = 4, F = 42.495, $P < 0.001$) were both highly significant. This interaction appears driven by different spatial patterns for carcass recovery with the highest proportion of males recovered in section 5; an area where low numbers of females were recovered (Figure 5).

Carcass Drift Studies

Method 1

Overall, the recovery of tagged carcasses released was 14% during 2012 and 10% during 2013 (Table 1a). No apparent differences were observed between the patterns for males and females (Table 1b and 1c). The percentage of carcasses recovered in the thalweg were lower than nearshore releases in both years of the study, 6% and 8% of the thalweg releases versus 21% and 12% for nearshore releases. In both years, the majority of carcasses recovered from fish released nearshore were found in the same section that they were released, regardless of

release location. In contrast, for sections 1-3 the majority of fish released in the thalweg were recovered in survey sections different than they were released in and the majority of fish released in sections 4 and 5 were recovered in the same section they were released in. The highest recovery rates were observed for carcasses released in nearshore areas of section 5 (37%) while the lowest observed were carcasses released in the thalweg of section 2 (3.2%). Low recapture rates were also reported for section 4 in both thalweg (5.7%) and nearshore areas (5.1%).

Method 2

A total of 289 carcasses were recovered representing 29% of the total tagged (Table 2). A total of 18 carcasses that had been double tagged were recovered after having lost one of the original tags representing 6% of the double tagged group. The percent of release recoveries for these carcasses ranged from 17% of fish released in Section 3 to 37% for fish released Section 4. The highest number of tagged carcasses were recovered in their corresponding release section; 90-94% of the carcasses were found in the section that they had been tagged. The distance (km) in which carcasses traveled between tag and recovery locations was highly variable, ranging between 0 – 87,098 m. The average distance traveled between release and recapture ranged from 2,407 to 3,642 m in the four survey sections (Table 2) and the overall mean distance traveled was 3,072 m. The travel distance data were skewed by outliers and following rank transformation ANOVA revealed differences among sections ($P < 0.0001$). The travel distance of carcasses recaptured from section 1 (Median = 16 m) was significantly smaller than that observed for all other sections (47 – 62 m).

Method 3

Studies during 2015 through 2018 released from 626 to 997 tagged carcasses annually distributed over spawning locations in sections 1-4 (Table 3). The average rate of recovery for section 1-4 ranged from 4% to 6 %. Over the course of the study, the distance (km) in which carcasses traveled between release and recovery locations ranged between 0 – 80 km. The mean over the four years for the average distance traveled for carcasses released in sections 1-3 ranged from 27.8 to 31.8 km while only 8.6 km for section 4. Analysis of rank-transformed drift differences for males and females revealed that the main effect of fish sex was not significant ($df = 1$, $F = 3.078$, $P < 0.081$) while the main effect of release section ($df = 3$, $F = 23.454$, $P < 0.001$) and the interaction between fish sex and release section ($df = 4$, $F = 3.555$, $P < 0.016$) were significant. The significant interaction appears to be the result of an inconsistent pattern of drift distances for male and female fish released across all four survey sections. In Section 1 females were observed to travel significantly longer distances than males ($P = 0.041$) while no differences between males and females observed in the remaining sections (Table 4).

Table 1a. Locations and numbers of tagged fall-run Chinook carcasses released and recovered during studies in the Hanford Reach of the Columbia River during 2012-2013.

Year	Release Section	Released	Recoveries by Section 1	2	3	4	5	Total	Percent Recovered
2012 Thalweg	1	131	2	0	6	2	0	10	7.6
	2	14		0	0	0	0	0	0.0
	3	129			3	7	0	10	7.8
	4	162				6	1	7	4.3
	5	64					3	3	4.7
	Total	500	2	0	9	15	4	30	6.0
2012 Nearshore	1	128	20	0	7	4	0	31	24.2
	2	14		2	0	0	0	2	14.3
	3	124			27	2	0	29	23.4
	4	158				10	2	12	7.6
	5	65					30	30	46.2
	Total	489	20	2	34	16	32	104	21.3
2013 Thalweg	1	97	2	1	3	1	0	7	7.2
	2	112		6	0	1	0	7	6.3
	3	148			8	1	2	11	7.4
	4	112				8	0	8	7.1
	5	50					6	6	12.0
	Total	519	2	7	11	11	8	39	7.5
2013 Nearshore	1	107	11	1	1	2	0	15	14.0
	2	126		6	2	2	1	11	8.7
	3	152			22	2	0	24	15.8
	4	119				2	1	3	2.5
	5	50					14	14	28.0
	Total	554	11	7	25	8	16	67	12.1

Table 1b. Locations and numbers of tagged confirmed female fall-run Chinook carcasses released and recovered during studies in the Hanford Reach of the Columbia River, Years 2012-2013

	Release		Recoveries by Section						Percent
Year	Section	Released	1	2	3	4	5	Total	Recovered
2012 Thalweg	1	76	2	0	4	1	0	7	9.2
	2	5		0	0	0	0	0	0.0
	3	57			0	2	0	2	3.5
	4	91				4	0	4	4.4
	5	2					0	0	0.0
	Total	231	2	0	4	7	0	13	5.5
2012 Nearshore	1	75	11	0	0	4	0	15	20.0
	2	11		2	0	0	0	2	18.2
	3	52			15	0	0	15	28.9
	4	93				6	1	7	7.5
	5	7					7	7	100.0
	Total	238	11	2	15	10	8	46	19.3
2013 Thalweg	1	25	0	0	0	1	0	1	4.0
	2	16		0	0	0	0	0	0.0
	3	52			5	0	0	5	9.6
	4	40				3	0	3	7.5
	5	4					1	1	25.0
	Total	137	0	0	5	4	1	10	7.3
2013 Nearshore	1	30	2	0	0	1	0	3	10.0
	2	22		2	1	1	0	4	18.2
	3	55			4	2	0	6	10.9
	4	43				1	0	1	2.3
	5	6					1	1	16.7
	Total	156	2	2	5	5	1	15	9.6

Table 1c. Locations and numbers of tagged confirmed males fall-run Chinook carcasses released and recovered during studies in the Hanford Reach of the Columbia River, Years 2012-2013

Year	Release Section	Released	Recoveries by Section 1	2	3	4	5	Total	Percent Recovered
2012 Thalweg	1	55	0	0	2	1	0	3	5.5
	2	9		0	0	0	0	0	0.0
	3	72			3	5	0	8	11.1
	4	71				2	1	3	4.2
	5	62					3	3	4.8
	Total	269	0	0	5	8	4	17	6.3
2012 Nearshore	1	53	9	0	7	0	0	16	30.2
	2	3		0	0	0	0	0	0.0
	3	72			12	2	0	14	19.4
	4	65				4	1	5	7.7
	5	58					23	23	39.7
	Total	251	9	0	19	6	24	58	23.1
2013 Thalweg	1	72	2	1	3	0	0	6	8.3
	2	96		6	1	0	0	7	7.3
	3	96			3	1	2	6	6.2
	4	72				5	0	5	6.9
	5	46					5	5	10.9
	Total	382	2	7	7	6	7	29	7.6
2013 Nearshore	1	77	9	1	1	1	0	12	15.6
	2	104		4	1	1	1	7	6.7
	3	97			18	0	0	18	18.6
	4	76				1	1	2	2.6
	5	44					13	13	29.6
	Total	398	9	5	20	3	15	52	13.1

Table 2. Distances (km) traveled for fall-run Chinook carcasses tagged in situ in different survey sections and recovered during the 2014 evaluation of carcass drift in the Hanford Reach of the Columbia River.

	Survey Section			
	1	2	3	4
Number of carcasses released	486	107	225	176
Number of carcasses recovered	152 (31%)	34 (32%)	39 (17%)	64 (36%)
Drift distance (Mean ± SD)	3.64 ± 14.21	2.09 ± 10.19	2.81 ± 7.80	2.41 ± 7.84
Drift distance (Median, Range)	0.02, 0-87.10	0.00, 0-59.14	0.00, 0-33.94	0.00, 0-40.47

Table 3. The mean number of carcasses released, mean number of carcasses recovered, and distances traveled (km) for fall-run Chinook carcasses tagged and released over spawning locations in different survey sections and recovered during the 2015-2018 evaluations of carcass drift in the Hanford Reach of the Columbia River.

	Survey Section			
	1	2	3	4
Carcasses released	252 ± 31	97 ± 47	273 ± 75	275 ± 90
Carcasses recovered	15 ± 6 (6%)	4 ± 2 (4%)	15 ± 4 (5%)	10 ± 5 (4%)
Drift Distance (Mean ± SD)	31.8 ± 4.5	29.7 ± 13.4	27.8 ± 3.4	8.6 ± 0.6

Table 4. The mean drift distances (Mean km ± SD (N)) for male and female carcasses recovered for fall-run Chinook carcasses tagged and released in different survey sections and recovered during the 2015-2018 evaluations of carcass drift in the Hanford Reach of the Columbia River. The asterisk indicates a significant difference between males and females for that section.

	Survey Section			
	1	2	3	4
Males	25 ± 19 (30)	24 ± 21 (9)	29 ± 13 (35)	10 ± 7 (24)
Females	39 ± 21 (29)*	31 ± 20 (8)	25 ± 11 (25)	7 ± 4 (15)

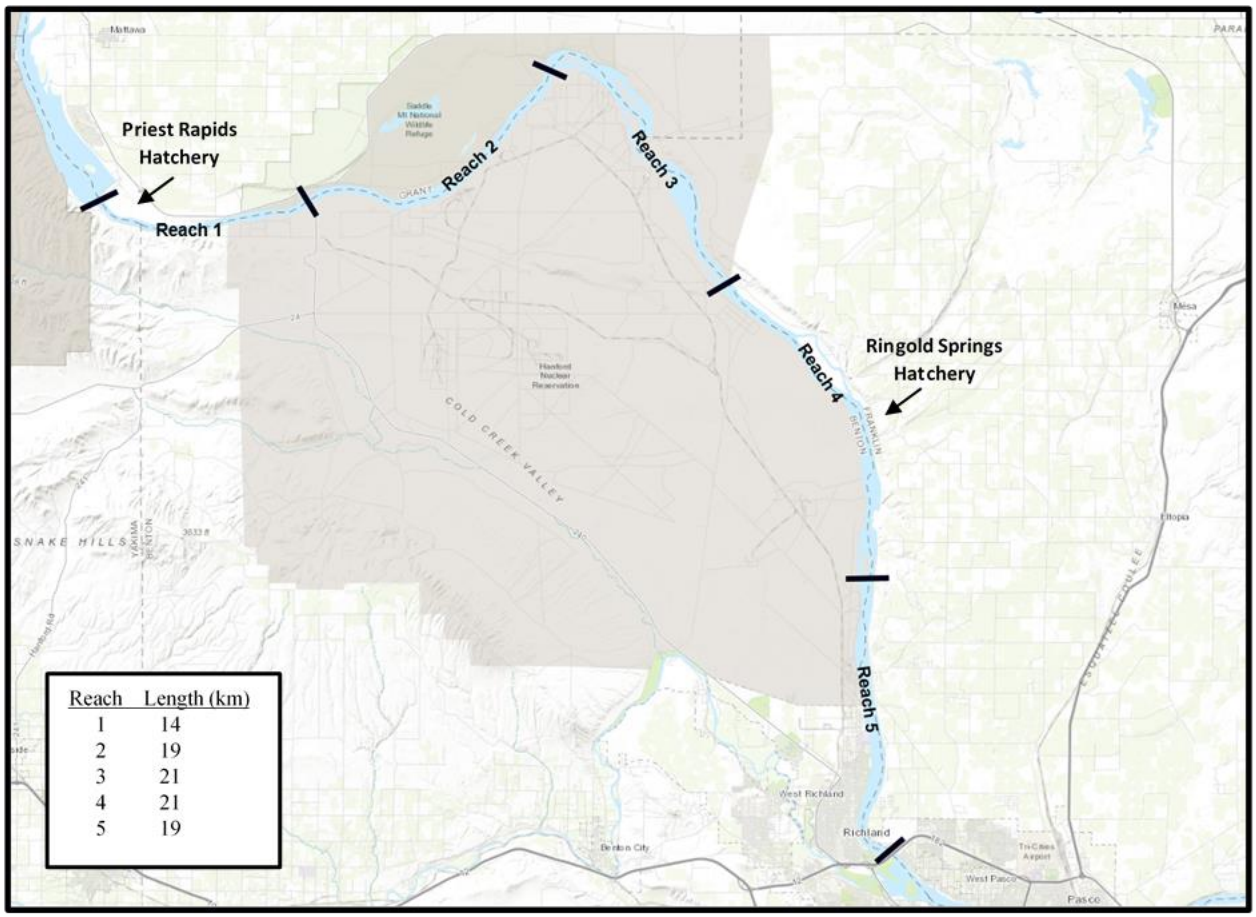

Figure 1. Location of the Hanford Reach portion of the Columbia River in Washington. Bars represent breaks in the Hanford Reach that define the five survey sections.

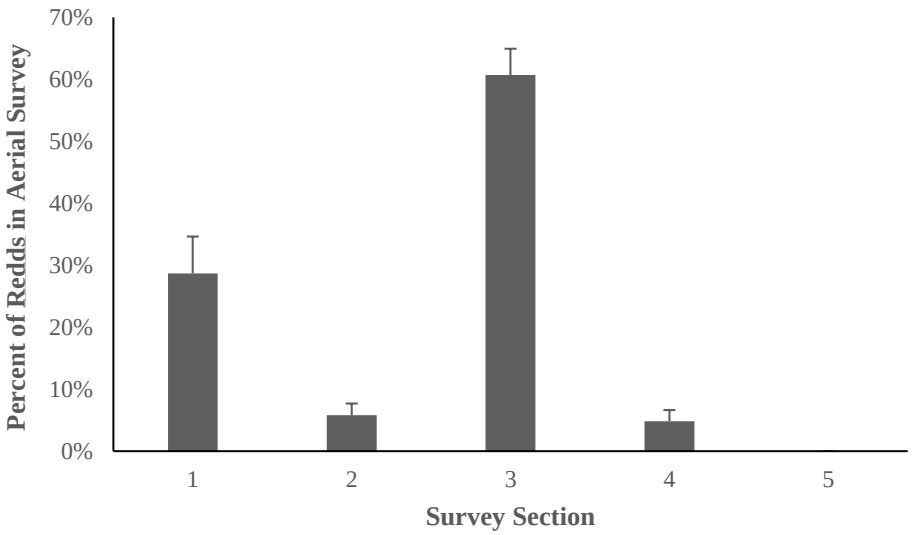

Figure 2. The mean percentage of redds found in each survey section of the Hanford Reach as determined by aerial surveys performed from 2012 to 2018. Bars above each mean represent one standard deviation.

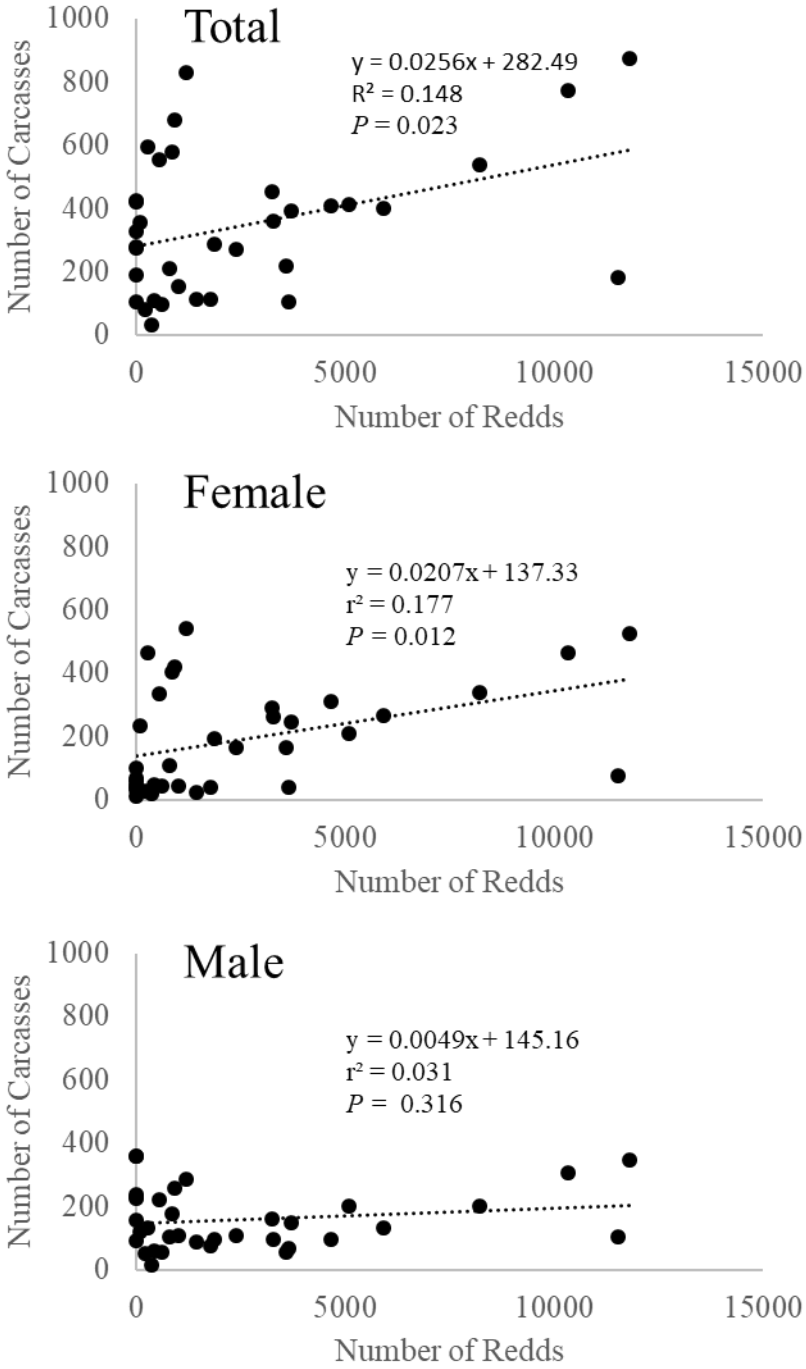

Figure 3. Linear regression of paired data illustrating the relationship between the number of redds surveyed from each section of the Hanford Reach and the number of carcasses recovered in the same section.

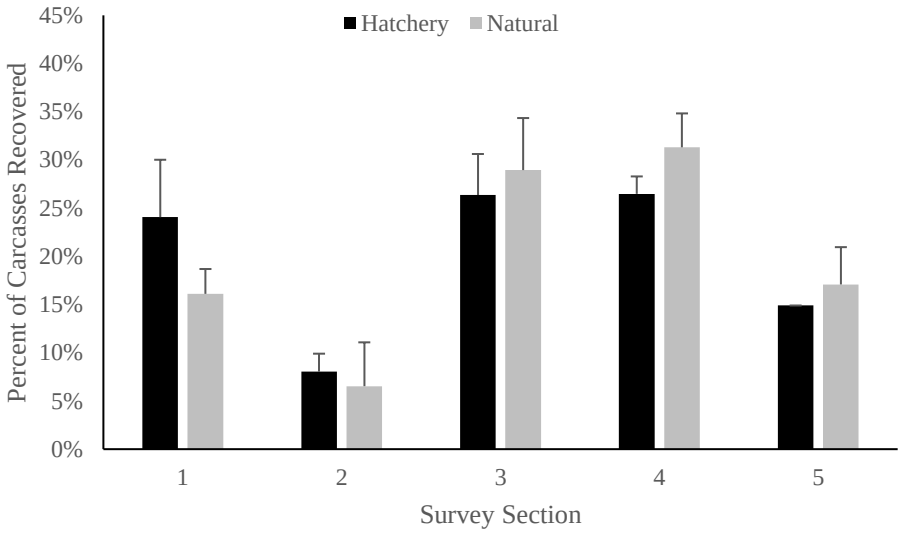

Figure 4. The mean percentage of hatchery- and natural-origin fall-run Chinook Salmon carcasses recovered in each section of the Hanford Reach during carcass surveys conducted from 2012-2018. Bars above each mean represent one standard deviation.

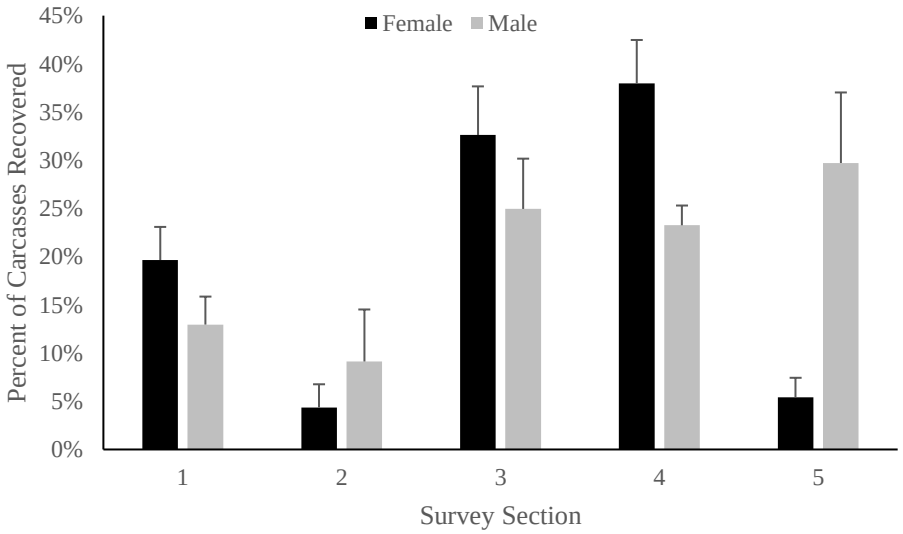

Figure 5. The mean percentage of male and female fall-run Chinook Salmon carcasses recovered in each section of the Hanford Reach during carcass surveys conducted from 2012 to 2018. Bars above each mean represent one standard deviation.

Discussion

The spawning locations of hatchery- and natural-origin Chinook Salmon as indexed by carcasses were quite similar in the Hanford Reach which suggests that spawn location is unlikely to contribute to differences in reproductive success, if they exist. However, the scale of our evaluation and the distance of carcass drift that we observed precludes us from making conclusions at small spatial scales. Fish that spawn in the most upstream sections of the river may have different reproductive success than those that spawn in downstream sections because the flow fluctuations are most pronounced below Priest Rapids Dam and fluctuations are attenuated downstream. These flow fluctuations may improve egg-to-fry survival unless redds are dewatered which is very rare (Harnish et al. 2014; Langshaw et al. 2017). Furthermore, egg-to-fry survival in the Hanford Reach is exceptionally high (McMichael et al. 2002; Harnish et al. 2014; Langshaw et al. 2017) and fish that spawn in the various sections of the Hanford Reach likely have good survival.

Our findings are consistent with management objectives and should not be surprising because Salmon were released at the upper (PRH) and lower (RSH) ends of the spawning distribution and recent work indicates that homing of hatchery-origin fall Chinook Salmon are very high (Pearsons and O'Connor 2021). Salmon that were released from PRH were incubated, reared, and acclimated using local water sources and were not transported, two factors that contribute to high rates of homing (Dittman et al. 2015, Pearsons and O'Connor 2021). However, the fish released from RSH were spawned at PRH, reared at Bonneville Hatchery and then transported to RSH prior to release. These fish might be more likely to stray than those released from PRH.

Carcass Drift

The downstream movement of salmon carcasses was much larger than what has previously been reported for spring Chinook Salmon (Murdoch et al. 2009a). It is likely that the deep water, low structural complexity, and managed flows of the Columbia River were partly responsible for the large drift distances we observed. In contrast, the Chiwawa River, where the Murdoch et al. (2009a) study was conducted, was much shallower, more structurally complex, and the flows were less variable during carcass collections. The variation in drift distances between rivers suggests caution about application of our findings to other rivers with different depths, structural complexities, and flow fluctuations or in using models derived from other systems that don't account for variation in environmental conditions.

Similar to the work in the Chiwawa River, females in this study were found in higher frequency in areas of high redd location and likely to be a better index of spawning location than male carcasses. This characteristic of females is likely because of the different behaviors that Chinook Salmon exhibit when mating and after spawning. Female Salmon will often create one redd (Murdoch et al. 2009b) whereas males will often spawn with many females and move between many redds (Ford et al. 2015, Schroder et al. 2010). Furthermore, after spawning females will guard redds and stay as close to their redds as possible until death (Schroder et al. 2008). In contrast, males generally do not guard redds after spawning and are often found swimming far from redds when near death (Schroder et al. 2010). However, our experimental data characterizing drift distances does not correspond with carcass survey data; male and female travel distances being more similar to one another than suggested by carcass survey data

The length of carcass drift influences the level of precision and potentially the usefulness of results at different spatial scales. At large spatial scales such as the Hanford Reach, carcass location is a good index of spawning location because carcasses are unlikely to drift out of the Hanford Reach and into other spawning areas. At medium spatial scales such as the river section (10s of kms), carcasses found in the most upstream sections are good examples of where they spawned. However, downstream sections are increasingly likely to have carcasses from fish that spawned in upstream locations as well as fish that spawned in those sections. In some cases, carcass location at a small scale (100s of m) is likely a good estimate of where the fish spawned, particularly if female. However, carcasses at this spatial scale are the least reliable. In short, the reliability of carcass location as an index of spawning location decreases with decreasing spatial scale. The inter-annual variation in redd locations of spring Chinook Salmon in the Yakima River also increases with decreasing spatial scale and interannual spawning distribution was markedly consistent at 2 km scales and longer (Cram et al. 2017).

The three different methods that we used to investigate carcass drift were inadequate to accurately evaluate carcass recovery bias. The high incidence of male carcasses detected in sections 4 and 5 is evidence that males travel away from redd locations prior to death. This finding was not replicated in any of the three methods we evaluated; males and females carcasses behaved similarly. The three methods we evaluated contributed to different strengths and weaknesses about the behavior of carcasses, but none of them could adequately mimic the different prespawn behavior of males and females that can contribute to differences in indexing spawn location. Each of these methods reflect the difficulty in developing a cost-effective approach to designing experiments in assessing post spawning drift characteristics for fall run Chinook Salmon in large river systems.

For studies or monitoring that rely upon Salmon carcasses to index spawn distribution, we recommend that carcass drift be evaluated where deep water, changing flows, low structural complexity, or post-spawn movement behavior could be large. In addition, it is important to determine what scale of spawning distribution is necessary to evaluate study or monitoring objectives. Carcass recoveries in rivers with long drift rates may still be sufficient to address important study or monitoring questions related to spawn location if the spatial scale of interest is comparatively large. Female carcasses may be a better index of spawning location than total carcasses and this has been found to be true in smaller rivers too (Murdoch et al. 2009a). Finally, the use of inexpensive techniques for evaluating carcass recovery bias, such as the ones used in this study, are unlikely to represent the complexities that contribute to bias such as post spawning behavior.

Acknowledgments

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A Comparison of Run and Spawn Timing of Hatchery- and Natural-Origin Fall Chinook Salmon

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Abstract

Hatcheries have the potential to alter run and spawn time of adult Chinook Salmon which has the potential to affect natural production goals. We sought to evaluate whether adult run and spawn timing differed in hatchery- and natural-origin fall Chinook Salmon that spawn in the Hanford Reach of the Columbia River. Run timing was evaluated using PIT tag detections of adults ascending Bonneville Dam between 2010 and 2018. Spawn time was evaluated by comparing the proportion of hatchery- and natural-origin carcasses that were collected at different times after spawning between 2012 and 2018. Run times were similar between hatchery- and natural-origin fish; no significant differences were detected between natural- and hatchery-origin adults arriving at Bonneville Dam at 10^{th} percentile (df = 8, t = 1.5, P = 0.1618), 50^{th} percentile (df = 8, t = 0.7, P = 0.5334) or 90^{th} percentile (df = 8, t = -2.1, P = 0.0668) of the day of year. In contrast, there were significant differences detected between natural- and hatchery-origin fish for the recovery timing of female carcasses at the 10^{th} (df = 7, t = 4.8, P = 0.0031), 50^{th} (df = 7, t = 01.9, P = 0.0090) and 90^{th} percentile (df = 7, t = 2.5, P = 0.0465) with natural-origin fish recovery day of year being later at all percentiles than their hatchery-origin counterpart. However, the time differences were typically 2-4 days. There was no evidence of a trend in female carcass recovery time between 2005 and 2018 (r^2 <0.1, P >0.05). The similarity of run and spawn timing of hatchery- and natural-origin salmon suggests that these factors are unlikely to contribute to large differences in natural production if they exist.

Introduction

Hatcheries have the potential to alter run and spawn time of adult Chinook Salmon which has the potential to affect natural production goals. This might occur by non-random selection of broodstock of early or late run fish or by non-random spawning of fish at unnaturally early or late times. In addition, production of unnaturally large smolts can change the age-at-adult return which may influence run time. Differences in the run and spawn time of hatchery- and natural-origin fish may result in differences in survival and ultimately reduce reproductive output. Disparities in run timing may expose fishes to different assemblages of predators and harvesters. For example, earlier run fish may be exposed to higher harvest pressures than later run fish. Furthermore, if run timing influences the time of spawning, then difference in run timing can change spawn timing.

Spawn timing can influence progeny survival through a variety of mechanisms. For example, early spawning fish may be more susceptible to redd superimposition, particularly during years when the abundance of spawners is large relative to the available spawning habitat. In addition, the eggs or larvae of early or late spawning fish may be more susceptible to scour, desiccation, or sedimentation than eggs or larvae of optimally timed spawners. Finally, emergence of progeny of early or late spawning fish may occur at suboptimal times for juvenile fish growth. For example, early emerging fish may not have access to much food and late emerging fish may be at a competitively inferior size to compete for food with larger fish that emerged earlier.

We sought to evaluate whether adult run and spawn times differed in hatchery- and natural-origin fall Chinook Salmon that spawn in the Hanford Reach of the Columbia River during return years 2010 - 2018. We also evaluated female carcass recovery time between 2005 and 2018 to evaluate whether spawn time has changed during this period. This population of Chinook Salmon is of interest because it is large, harvested at very high exploitation rates, and has received hatchery augmentation for multiple decades.

Methods

Study area

The Hanford Reach is one of the last non-impounded reaches of the Columbia River and the location of the largest and most productive natural spawning fall Chinook Salmon population in the United States (Harnish et al. 2014, Langshaw et al. 2015, Harnish 2017, Langshaw et al. 2017). The Hanford Reach extends 82 km upriver from the city of Richland to the base of Priest Rapids Dam. The spawn timing of fall Chinook Salmon in the Hanford Reach occurs from late October through mid-December. The offspring produced emerge from the substrate in the spring and rear there until outmigration during the summer months. Located at the base of Priest Rapids Dam, Priest Rapids Hatchery (rkm 635) currently releases ~ 7.3 million subyearling fall Chinook Salmon smolts annually into the Hanford Reach as part the mitigation requirements of Grant County Public Utility District's (GCPUD) and United States Army Corps of Engineer's (USACE) for hydropower impacts on salmon populations in the Columbia River. A second fall Chinook Salmon program at Ringold Spring Hatchery (RSH) is located at rkm 567 near the middle portion of the Hanford Reach and has a target release of 3.5 million subyearling smolts.

Since 2009, broodstock collected at PRH have been the source of the juvenile production at RSH.

Only a portion of the smolts annually released from PRH are adipose clipped or possess a CWT; however, since the 2007 brood year, all fish released from PRH have a thermal mark applied to fish during incubation. Beginning with brood year 2007, all of juveniles released annually from RSH were to be adipose clipped. Annual quality control sampling by RSH staff suggests that about 1% of the smolts are either poorly or not clipped. In addition, the RSH production for brood years 2010 through 2016 were thermally otolith marked during early incubation at PRH. Otolith samples were examined by the WDFW Otolith Lab to help assign origin.

Estimates based on recovery of coded-wire tags from the Hanford Reach fall Chinook Salmon spawning escapement suggest that between 2005 and 2018, hatchery-origin adults from PRH and RSH comprised 8.1% (SD = 4.5%) of spawning escapement (Richards and Pearsons 2019). Strays from other hatchery programs are also recovered albeit at rates less than 1% annually.

Both natural- and hatchery-origin populations are large contributors to commercial and non-commercial harvest (McMichael et al. 2019) and subject to ongoing monitoring and evaluation activities (Richards and Pearsons 2019). To estimate survival and migration timing of smolts released from PRH, approximately 3,000 fish were tagged with passive integrated transponders (PIT) annually for brood years 1995 through 2010. The number of PIT tags was increased to approximately 43,000 fish for brood years 2011 to 2018. Presumed natural-origin smolts for brood years 1993 to 2018 were also tagged ranging from 2,955 – 22,634 annually (median 5,042,) during 2002 and 2006 no fish were tagged. These smolts were collected with seines and PIT tagged by the Columbia River Intertribal Fisheries Commission and provide an estimate of survival and run-timing of the natural-origin component of the Hanford Reach fall Chinook Salmon population (Fryer 2020, Dehart 2019). Adults returning to the Hanford Reach or PRH to spawn, first pass through the adult fishways at Bonneville Dam which are equipped with antennas that detect PIT tags and provide information on run timing of adult fish. Since the mid-1980s, staff with the Washington State Department of Fish and Wild (WDFW) annually perform surveys in the Hanford Reach to recover fall Chinook Salmon carcass to recover coded-wire tags and collect demographic data. Methods, level of effort, and reporting associated with the carcass surveys have evolved over time. The time series used for our analysis includes data from 2005 to 2018.

Migration Timing

The PTAGIS database, the repository of PIT tag information throughout the Columbia Basin, was searched for PRH (hatchery-origin) and Hanford Reach (natural-origin) adult salmon returns between 2010 and 2018 and the date of detection by year (DOY) at Bonneville Dam recorded as the number of days since January 1. The 10th, 50th, and 90th percentiles of the DOY were determined for natural- and hatchery-origin fish for each return year. Passage timing by return year was chosen over brood year to account for any interannual variation in fish passage conditions related to river environment or hydroelectric operations. All ages were pooled due to the limited number of observations for both natural- and hatchery-origin fish. Paired t-tests were used to detect differences between natural- and hatchery-origin DOY at each of the percentiles. The threshold of significance was set at $P < 0.05$.

Spawning Timing

Carcass surveys of fall Chinook Salmon were conducted annually for return years 2005 - 2018 by Washington Department of Fish and Wildlife in the Hanford Reach from early November to mid-December as part of monitoring the Hanford Reach population and for monitoring and evaluation of PRH and RSH programs beginning in 2010 (Richards and Pearsons 2019). Carcasses were collected while walking the shorelines and islands of the river or by gaffing submerged carcasses from boats. Up to four teams, consisting of two or three staff, survey different sections of the Hanford Reach seven days per week throughout the entire field season. Staff systematically subsampled a portion of the recovered carcasses for demographic data that contributes to the long-term monitoring of natural- and hatchery-origin salmon found in the Hanford Reach. The demographic sample ranged from about 500 to 2,500 fish per year. Subsample rates were based on the estimated escapement to the Hanford Reach which ranged from 23,273 to 266,327 fish. Rates remained constant during a specific year but ranged from 1:2 to 1:10 (sampled carcasses:recovered carcasses) among years.

The demographic data gathered during the surveys of individual carcasses included fish sex, fork length (cm), and the presence or absence of a coded-wire tag (CWT) or adipose clip. Fish sex was determined by either external morphological characteristics or by inspection of the gonads. Fish age was obtained from the scale samples examined by the WDFW Scale Ageing Lab. CWT were extracted, and codes read to determine origin.

Beginning in 2012, carcasses for all age classes were assigned hatchery-origin if they had an adipose clip, a CWT of hatchery-origin, or a thermal mark. Carcasses not possessing any form of these hatchery marks were classified as natural-origin. Two analyses were performed to characterize spawn timing. First, the DOY for the 10%, 50%, and 90% percentiles for all female carcasses recovered in the demographic sample as a surrogate for spawn timing were determined for years 2005 -2018. All ages of fish were pooled due to the limited number of recoveries of hatchery-origin females found on the Hanford Reach. Linear regression analysis was used to identify any change in spawn time (DOY) over the length of these observations. The threshold of significance was set at $P < 0.05$. Second, the DOY for natural- and hatchery-origin female carcasses in the demographic sample were recorded for return years 2012 – 2018. The 10th, 50th, and 90th percentiles of the DOY for females recovered were determined for natural- and hatchery-origin fish for each return year. Paired t-tests of each percentile grouping were performed to detect differences in DOY for carcass recovery of females between natural- and hatchery-origin fish paired by return year.

Results

Migration Timing

The PIT tag observations at Bonneville Dam revealed that both hatchery- and natural-origin adults typically began arriving to Bonneville mid-August. The mean DOY for the 10th percentile of natural- and hatchery-origin fish was 240 (SD = 4) and 243 (SD = 5), respectively (Figure 1). The mean DOY for the 50th percentile of natural- and hatchery-origin was 255 (SD = 2) and 256 (SD = 4), respectively. The mean DOY for the 90th percentile of natural- and hatchery-origin was 276 (SD = 7) and 270 (SD = 6), respectively. No significant differences

were detected between natural- and hatchery-origin fish arriving at Bonneville Dam at 10th percentile (df = 8, t = 1.5, *P* = 0.1618), 50th percentile (df = 8, t = 0.7, *P* = 0.5334) or 90th percentile (df = 8, t = -2.1, *P* = 0.0668) of DOY.

Spawn Timing

The number of female carcasses recovered annually in the demographic sample ranged from 354 – 1,493 (Median = 870) during 2005 - 2018. The mean DOY for recovery of the 10th percentile was 317 (SD = 2). The mean 50th percentile DOY was 328 (SD = 3). The mean 90th percentile DOY was 339 (SD = 3). For this same period, the simple linear regression for each percentile grouping across time revealed no evidence of a pattern of change attributed to time (r^2 <0.1, *P* >0.05) (Figure 2).

The mean DOY for recovery of the 10th percentile for natural- and hatchery-origin female carcasses was 317 (SD = 3) and 313 (SD = 3), respectively (Figure 3). The mean 50th percentile DOY for natural- and hatchery-origin female carcasses was 328 (SD = 3) and 325 (SD = 3), respectively. The mean 90th percentile DOY for natural- and hatchery-origin female carcasses was 340 (SD = 4) and 338 (SD = 3), respectively. There were significant differences detected between natural-and hatchery-origin fish for the recovery timing of female carcasses at the 10th (df = 7, t = 4.8, *P* = 0.0031), 50th (df = 7, t = 01.9, *P* = 0.0090) and 90th percentile (df = 7, t = 2.5, *P* = 0.0465) with natural-origin fish recovery DOY being later at all percentiles than their hatchery origin counterpart.

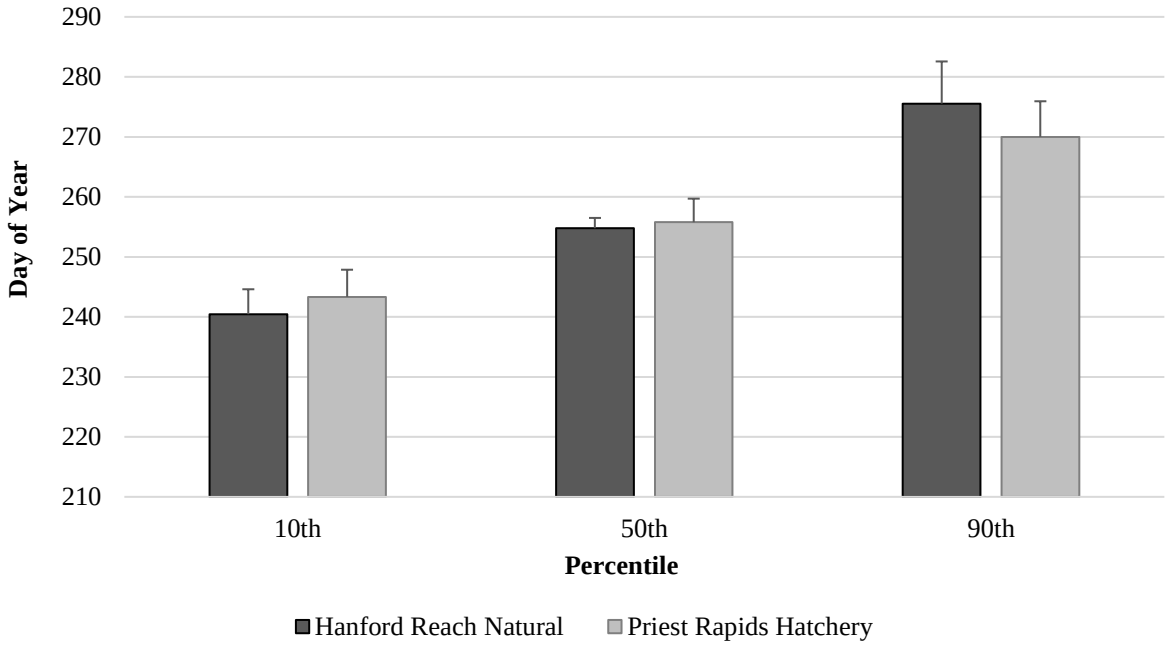

Figure 1. Mean day of year (January 1 = DOY 1) for the 10th, 50th, and 90th percentile for arrival timing of PIT tagged adult Priest Rapids Hatchery origin and Hanford Reach origin fall Chinook Salmon at Bonneville Dam, Return Years 2010 – 2018. Error bars indicate one standard deviation. A paired t-test performed for each percentile group failed to detect a significant difference between the mean arrival timing between origins of fish (*P* > 0.05).

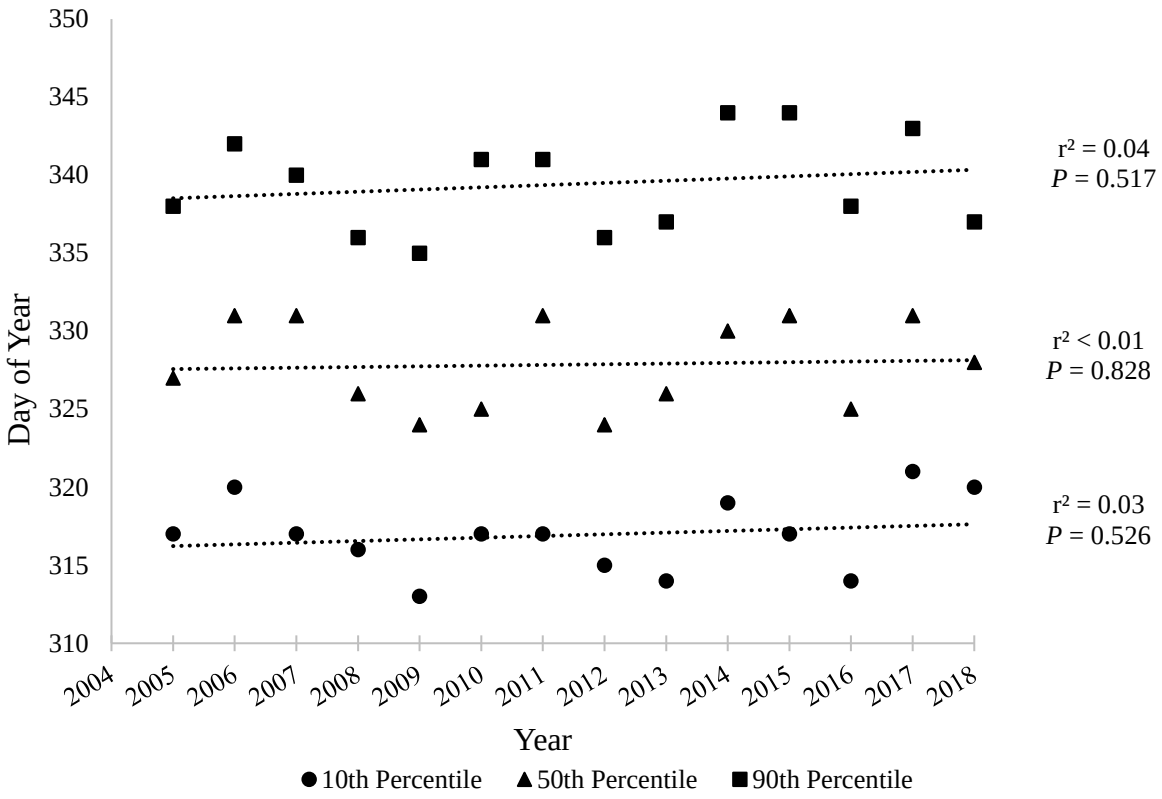

Figure 2. Linear regression results characterizing the relationship between year and the Day of Year for the 10th, 50th and 90th percentile of post spawn female fall Chinook Salmon carcasses recovered in the Hanford Reach, Returns Years 2005 – 2018.

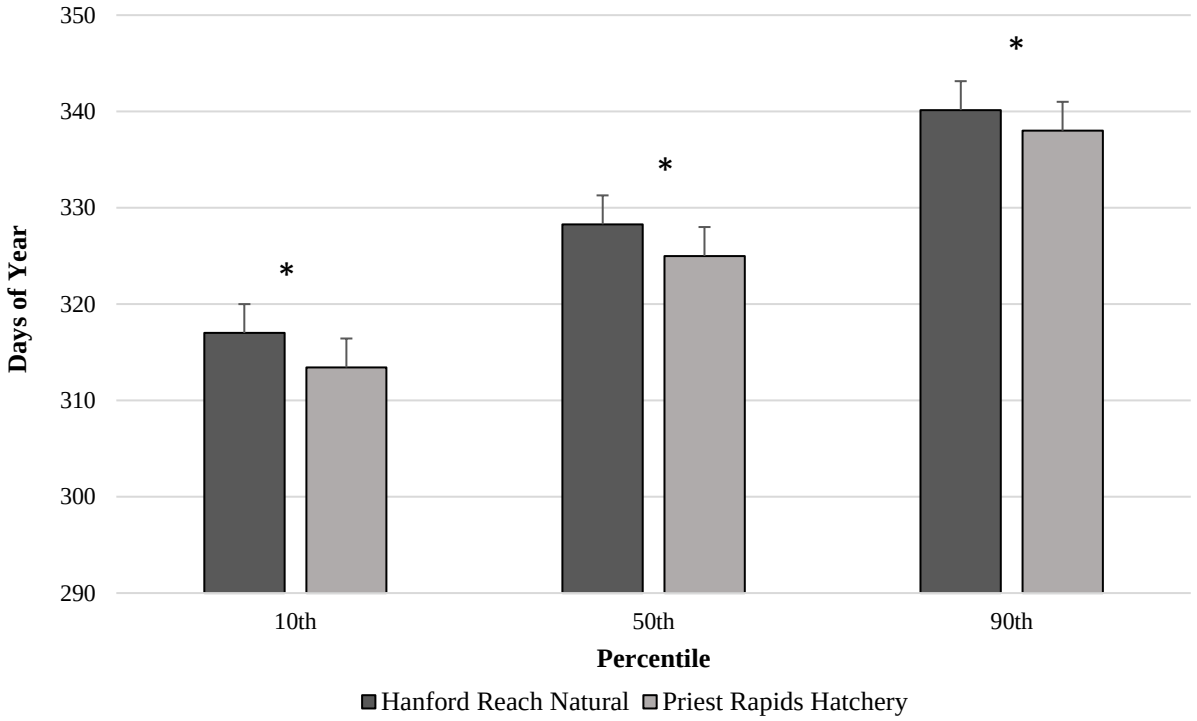

Figure 3. Mean day of year (January 1 = DOY 1) for the 10th, 50th, and 90th percentile of female carcasses recovered of in the Hanford Reach of natural-origin and Priest Rapids Hatchery-origin fall Chinook Salmon; Return Years 2012 – 2018. Error bars indicate one standard deviation. An asterisk denotes results of a significant difference between the paired bars for a given percentile (P <0.05).

Discussion

The run time of natural- and hatchery-origin adults was similar which was consistent with a general program objective to pattern hatchery-origin metrics after natural-origin templates. In addition, time related mortality such as harvest or predation might be similar among origins if all other variables that might affect harvest were the same (e.g., size, age, sex). This may be desirable if the objective of the hatchery is primarily to increase natural production (i.e., conservation hatchery), but may not be desirable if the primary objective of the hatchery is to increase harvest – such as the Priest Rapids Hatchery program. Differences in run timing among origins could be exploited by harvesters if harvest rate objectives differed among origins. In short, there are benefits to natural production that are assumed by matching hatchery-origin to natural-origin adult run timing, but this may come at a cost to increase harvest rate on hatchery-origin fish.

Spawn timing of hatchery-origin females was 2-4 days earlier than natural-origin fish, but it is unclear how much this difference influenced productivity. Redd superimposition by natural-origin fish could occur in years where spawning capacity is exceeded and might reduce productivity for earlier spawning hatchery-origin females, however this appears to be rare except

when abundance is very high (Langshaw et al. 2017). It's possible that the progeny of hatchery-origin females may emerge earlier than natural-origin females which may give them a competitive advantage in acquiring food and growing faster. In short, hypotheses are available to explain differences in productivity associated with spawn timing if differences in productivity exist, however they are mainly speculative. It does not appear that the hatchery has had negative impacts on abundance and productivity of fish that spawn in the Hanford Reach (see chapter in this report). Furthermore, reduced reproductive success of hatchery-origin fish from mechanisms such as redd superimposition can be viewed as another means to reduce domestication selection of the naturally produced population.

Although we detected earlier spawn time of hatchery- than natural-origin fish, we did not detect a trend towards earlier spawn timing of the overall population between 2005-2018. This could be because of the relatively low proportion of hatchery-origin fish in the spawning population, which is typically less than 15%, that could result in a small influence on the population spawn time relative to our ability to detect changes. Alternatively, the reproductive success of earlier spawned fish may have been lower and not contributed as much to altering the spawn time of subsequent spawners. The length of time that we had available to detect trends (2005-2018) may have also been too short to detect changes.

Acknowledgments

We thank the many partners that have made the Priest Rapids Hatchery program such a success. This includes Grant County Public Utility District project manager, Eric Lauver; Priest Rapids Hatchery management staff, Mike Lewis, Brian Lyon, and Glen Pearson; WDFW science division staff, Shawnaly Meehan and Dennis Werlau; and WDFW otolith readers led by Jeff Grimm and Lance Campbell. We also thank the Priest Rapids Coordinating Committee's Hatchery Subcommittee. Grant County Public Utility District funded this work.

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Stray Rates of Natural-Origin Chinook Salmon and Steelhead in the Upper Columbia Watershed

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Abstract

Despite the importance of straying in understanding the ecology of salmon and steelhead, most of what is known about salmon and steelhead straying comes from tagged hatchery fish. We provide donor estimates of natural-origin spring, summer, and fall Chinook Salmon *Oncorhynchus tshawytscha* and steelhead *Oncorhynchus mykiss* straying at three spatial scales in the upper Columbia watershed using Passive Integrated Transponder (PIT) tags. A total of 823,770 natural-origin spring, summer, and fall Chinook Salmon and summer steelhead were PIT-tagged as juveniles in the Wenatchee, Entiat, Methow, and Okanogan River subbasins and tributaries and the upper Columbia River between 2002 and 2017. Anadromous adults with PIT tags were detected at a variety of antenna arrays in the Columbia River Basin between 2004 and 2018 (n=2,611). Mean donor stray rates of each population were less than 1% at the basin scale (range 0.0%-0.7%), less than 10% at the subbasin scale (range 0.0%-9.8%) and less than 15% at the tributary scale (range 0.0%-14.3%). Many of the populations (11 of 28) that were evaluated across all spatial scales did not have any strays detected, and the mean of means of all species stray rates at all spatial scales was generally less than 5% (range 0.2%-4.0%). Chinook Salmon and steelhead strayed at similar rates when originating from the same subbasins and tributaries. Most straying occurred in an upstream direction at the subbasin (84%) and tributary scales (94%). Variation in stray rates was most consistently associated with spatial scale and location and was less than 15% for all species at all spatial scales.

Introduction

Straying by salmon and steelhead is an important mechanism for colonizing new habitats (Quinn 2005; Keefer and Caudill 2014; Westley et al. 2015). However, it can also reduce the spawning population of donor populations and disrupt local adaptation of recipient populations if it occurs at high rates (Ford 2002; Mobrand et al. 2005; Brenner et al. 2012). Most of what is known about salmon and steelhead straying comes from studies of tagged hatchery fish (Dittman et al. 2010; Westley et al. 2013; Keefer and Caudill 2014). Access to large numbers of fish in controlled environments and high tag rates provide great opportunities to learn about straying (Dittman et al. 2010; Westley et al. 2013; Bond et al. 2017). Although estimates of hatchery-origin fish straying are informative, they may be very different from estimates of natural-origin salmon and steelhead (Keefer and Caudill 2014; Dittman et al. 2015).

Surprisingly few estimates of natural-origin Chinook Salmon *Oncorhynchus tshawytscha* and steelhead *Oncorhynchus mykiss* straying have been published despite the importance to understanding the metapopulation dynamics of these fish and how these estimates might inform expectations about stray rates of hatchery-origin salmon and steelhead (Quinn 2005; Keefer and Caudill 2014; Fullerton et al. 2016). Dispersal rate was found to be very important in metapopulation structure of modelled Chinook Salmon populations in the Snake River Basin, however they acknowledged that they had few empirical data to estimate dispersal rates among populations (Fullerton et al. 2016). Because of the difficulty of capturing, tagging and recapturing sufficient numbers of wild juveniles there are a lack of studies on stray rates of natural-origin fish. This is particularly true for species with low survival rates following tagging because more fish have to be collected to generate reasonable estimates. Shapovalov and Taft (1954) performed one of the earliest studies of stray rates of natural-origin fish involving more than one species. They studied stray rates of tagged Coho Salmon and steelhead in two coastal California creeks that were less than 8 km apart. Other creeks were not evaluated for strays beyond the two nearby creeks; thus, their stray rates should be considered minimums. The minimum stray rate of Coho Salmon was 14.9% for Coho Salmon originating from Waddell Creek and 26.8% from Coho Salmon originating from Scott Creek. The minimum stray rate for steelhead was 1.9% for steelhead originating from Waddell Creek and 2.9% from steelhead originating from Scott Creek. It is likely that environmental conditions influenced access to home tributaries and influenced stray rates, particularly for Coho Salmon.

More recently, Ford et al. (2015a) estimated stray rates of natural-origin spring Chinook Salmon in the upper Wenatchee watershed of the Columbia River in Washington using genetic techniques. Stray rates were 4.1% for fish originating from the Chiwawa River, 17.5% for fish originating from the Little Wenatchee River, 9.0% for fish originating from Nason Creek, 1.3% for fish originating from the White River, and 100% for fish originating from the upper Wenatchee River (Ford et al. 2015a). Variation in spring Chinook Salmon stray rates were related to origin (e.g., hatchery and natural) and tributary location. They also suggested that the difference in stray rates between origins could be a genetic or environmental effect. Finally, a maximum recipient population stray rate of natural-origin fish into the Columbia River was less than 0.1% using genetic methods (Hess et al. 2014).

Data from the studies described above indicated that stray rates of natural-origin fish at various scales ranged between 0% and 100% but all but one estimate was below 30%. Additional estimates of natural-origin stray rates would contribute to understanding the

magnitude of straying and the distribution of stray rates among species, populations, and environments. Knowing the magnitude of straying is important to understanding meta-population dynamics, interpreting genetic data, informing scale of management units, and placing stray rates of hatchery origin fish into context (Keefer and Caudill 2014; Fullerton et al. 2016; Bett et al. 2017). Furthermore, discovering patterns related to natural-origin fish stray rates may contribute to identifying mechanisms associated with the variation in stray rates and also where fish may stray to. For example, adult salmon and steelhead have been shown to undershoot (Bond et al. 2017) and overshoot their natal area (Weigel et al. 2013; Richins and Skalski 2018) when they migrate home, in part because of access to cold water refugia.

In this paper, we provide estimates of donor natural-origin spring, summer, and fall Chinook Salmon and steelhead straying in the upper Columbia Watershed using PIT tags. The term of this type of straying is donor straying (Keefer and Caudill 2014). The upper Columbia watershed has one of the largest network of PIT tag antenna arrays in the United States which provides great opportunities to look at stray rates at a variety of scales. Three spatial scales of straying were evaluated: the upper Columbia basin, subbasins of the upper Columbia basin, and tributaries of upper Columbia subbasins (Figure 1; also see definition in Methods). These scales were selected because they were important homing targets for management, recovery, and understanding of population dynamics. We also looked for patterns in the data to identify whether there is a tendency for natural-origin spawners to stray in an upstream or downstream direction. We hypothesized that: 1) stray rates would increase as spatial scale decreased, 2) stray rates of steelhead would be higher than Chinook Salmon, and 3) stray rates would be similar in an upstream and downstream direction. We also hypothesized that stray rates would be towards the lower end of the range of stray rates that have been reported for natural origin Salmon and steelhead (0-100%).

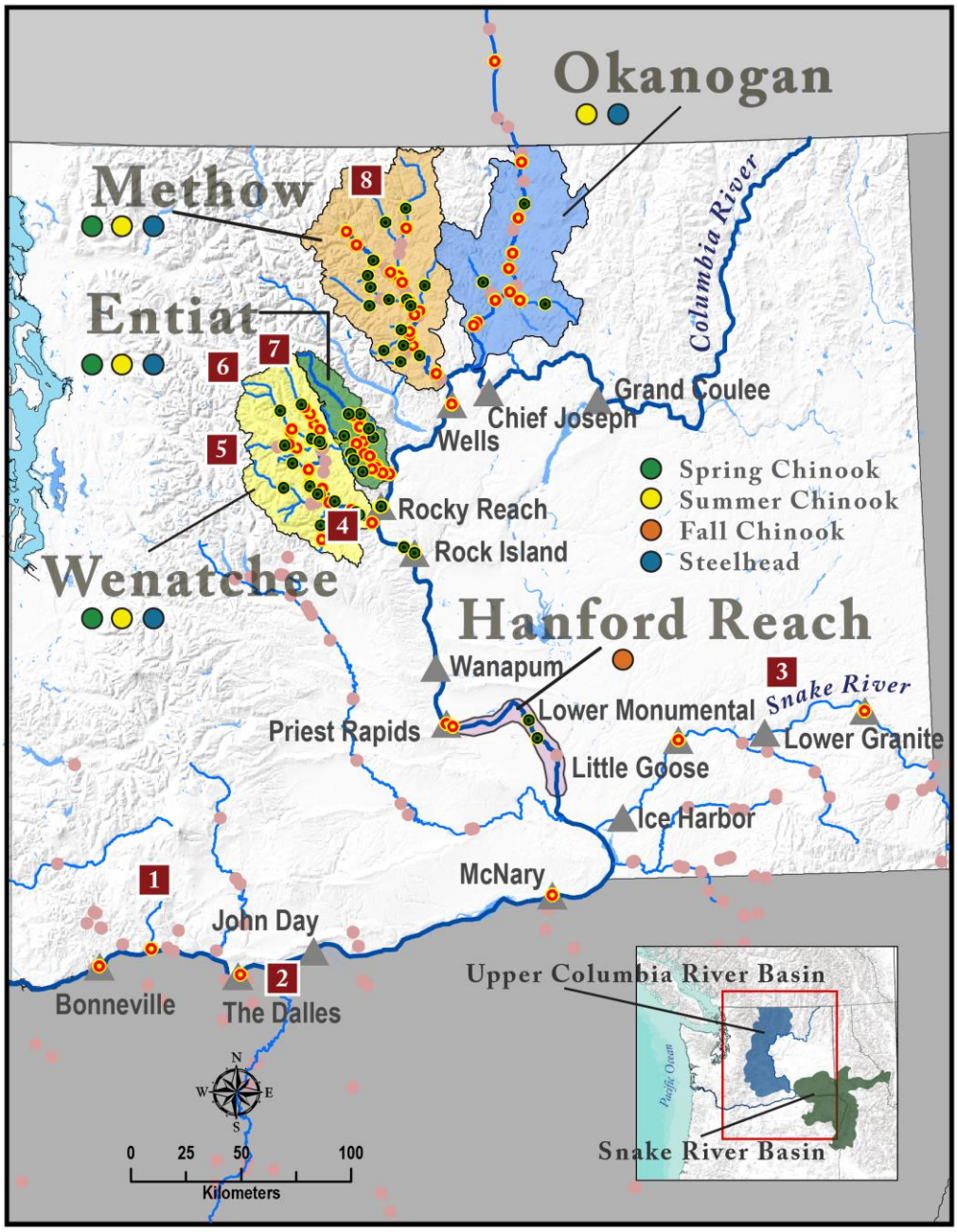

FIGURE 1. Release locations (green bullseye) and final PIT tag detection locations (yellow bullseye) of Chinook Salmon and steelhead originating from the upper Columbia River Basin. Other PIT tag detection sites are displayed as shaded dots for reference. Hydropower dams are denoted with triangles. The subbasins are the Okanogan, Methow, Entiat, and Wenatchee rivers and the Hanford Reach of the Columbia River. Collectively, these named subbasins represent the Upper Columbia Basin. Numbered tributaries indicate locations of straying individuals at the basin and tributary scales. The tributaries are (1) Little White Salmon River, (2) Deschutes River, (3) Snake River, (4) Peshastin Creek, (5) Nason Creek, (6) Little Wenatchee River, (7) White River, (8) Lost River.

Methods

Study Area

This study was conducted in the Columbia River watershed, USA, and most of the work was conducted in the upper Columbia Basin above the confluence with the Snake River (Figure 1). Three races of Chinook Salmon and one race of steelhead inhabit this area and are the focus of this study. Races are defined by the timing that they enter freshwater. Sockeye and Coho salmon also inhabit the upper Columbia, but there were insufficient numbers of natural-origin fish that were PIT tagged to include them in the analysis. Fall Chinook Salmon spawn in one of the few free flowing reaches of the Columbia River downstream of Priest Rapids Dam, are one of the largest Chinook Salmon populations in the United States, and contribute large numbers of fish to harvest in the Pacific Ocean and Columbia River, making this population economically very important (Harnish et al. 2014; Langshaw et al., 2017; Pearsons et al. in press). Summer Chinook Salmon spawn primarily in the mainstems of four subbasins of the upper Columbia River (e.g., Wenatchee, Entiat, Methow, and Okanogan) and support considerable fisheries in the Pacific Ocean and Columbia River. The naturally produced juveniles of summer and fall run Chinook Salmon migrate to the sea as sub-yearlings. Spring Chinook Salmon spawn in tributaries to mainstem subbasins and in upper portions of mainstem subbasins (Williamson et al. 2010; Murdoch et al. 2010; Ford et al. 2015a). The naturally produced juveniles of spring Chinook Salmon migrate to the sea as yearlings. They are listed under the Endangered Species Act as endangered (McClure et al. 2008). Summer steelhead spawn throughout subbasins and are listed as threatened (Ford et al. 2016). Naturally produced juvenile steelhead migrate to the sea at ages 1-7, but most migrate at ages 2 and 3 (Peven et al. 1994). All races of Chinook Salmon and steelhead have a long history of interactions with hatchery programs and hatchery- and natural-origin fish overlap in much of their spawning distributions (e.g., Williamson et al 2010; Pearsons et al. 2012; Ford et al. 2015a; Ford et al. 2016; Johnson et al. 2018).

Tagging and detection

Natural origin spring, summer, and fall Chinook Salmon and summer steelhead were PIT-tagged as juveniles in the upper Columbia River basin between 2002 and 2017. Chinook Salmon races and steelhead were only found, and later released, in portions of the upper Columbia River basin in which they historically spawn (See Methods: Study Area). Fish were collected with a variety of methods and for various purposes unrelated to straying. Fish were collected with rotary screw traps in subbasins and their tributaries, electrofishing in tributaries, fish bypasses at dams, and seining in the Columbia River (Johnson et al. 2007; Hillman et al. 2018). Fish were at least 50 mm FL when tagged (range 50 to 267 mm FL) but less than 4% of fish were less than 60 mm FL to minimize potential effects of tag burden (Brown et al. 2010), and were released at the location of tagging or in the near vicinity. Fish were anesthetized and identified as natural-origin based upon absence of hatchery specific marks (e.g., adipose fin clip) and tags ((e.g., Coded Wire Tag (CWT)), the timing of collections (e.g., before hatchery fish are released), and the condition of fish (e.g., size, fin condition). Except for fall Chinook Salmon produced at Priest Rapids Hatchery, almost all of the hatchery-origin fish were tagged and/or marked. Tagging of natural origin fall Chinook Salmon in the Hanford Reach generally occurred prior to the release of hatchery origin fall Chinook Salmon in the Hanford Reach, and were also selected based upon size differences between hatchery and natural origin fish. PIT tags were 12

mm long, 2.1 mm diameter, and cylindrically shaped and were injected into the coelomic cavity of juveniles with syringes. In most cases, fish were allowed to recover before they were released. Short-term tag retention was generally high (e.g., >99%) and mortality was low (e.g., <2%) (Caisman 2018).

Anadromous adults with PIT tags were detected at a variety of antenna arrays in the Columbia River Basin between 2004 and 2018 (Figure 1). Antennas were able to read PIT tags in fish as they swam close enough to the antenna. Arrays were located in the fish ladders of many dams as well as the mouths of subbasins and their tributaries. Subbasin and tributary arrays were typically anchored to the bottom of rivers or streams. The efficiency of adult detections in most mainstem Columbia River dams was near 100% (Pearsons et al. 2016). The efficiencies of subbasin and tributary arrays were less certain but likely varied with flow and fish migration behavior. Efficiencies were likely to be lower at high flows and when fish migrate high in the water column. Recent work suggest that efficiencies of subbasin and tributary arrays exceed 90% for steelhead (methods described by Connolly et al. 2008) and that stray estimates using CWT, that do not rely upon arrays, were similar to estimates using PIT tags for hatchery spring and fall Chinook Salmon (Grant County Public Utility District, unpublished data). Data from fish that passed arrays were uploaded to a centralized database.

Analysis

The PIT Tag Information System (PTAGIS) maintained by the Pacific States Marine Fisheries Commission (PSMFC) was queried for adult salmon and steelhead returns to the Upper Columbia Basin. Individuals with known locations of tagging and release as juveniles were included in the analysis. Release quantities and detection records were used to create datasets for analysis. All detection records for natural-origin spring, summer, and fall Chinook Salmon and summer steelhead that were PIT-tagged as juveniles and originated from the Wenatchee, Entiat, Methow, and Okanogan River subbasins and the upper Columbia River were included in the analysis (Figure 1). Fish with last detections at hatcheries were excluded because these fish did not have an opportunity to self-correct and therefore inclusion of these detections would overestimate straying, however we only detected two fish with last detections at a hatchery so this rule was rarely implemented. Occurrence of straying was evaluated at three spatial scales; fish that originated from and returned to: (1) the upper Columbia River Basin (e.g., basin scale; all rivers and creeks above the confluence with the Snake River); (2) a subbasin within the Upper Columbia (e.g., subbasin scale; Wenatchee, Entiat, Methow, or Okanogan River subbasins and their tributaries; and the mainstem of the Columbia River); and (3) a tributary of a subbasin (e.g., tributary scale; Chiwawa River or Nason Creek, which are tributaries to the Wenatchee River).

A combination of time gaps and behavior, as determined by detection history, were used to exclude or include fish in the analyses. The time gap between release and final detection was used to generate a list of potential fish to include in the analysis. Chinook with at least 1.0 year and steelhead with at least 3 months between release and final detection were further evaluated to determine if the behavior of tagged individuals was consistent with that of anadromous salmonids. In this way, we attempted to eliminate fish that precociously matured and completed their life in freshwater (Pearsons et al. 2009). Detections of PIT tagged individuals in fish ladders at mainstem Columbia River dams were used to assess adult migration behavior. Fish detected at consecutive mainstem Columbia River dam fish ladders (i.e., Bonneville, McNary,

and Priest Rapids dams) were further evaluated to determine the occurrence of straying at the basin, subbasin, and tributary scales (Figure 1).

Fish that displayed behavior consistent with returning adults were further evaluated to determine final detection locations within the upper Columbia River. The occurrence of straying was determined using both brood year and return year for Chinook Salmon and return year only for steelhead. Brood year of spring Chinook was determined by tagging date within the calendar year. Fish tagged between January 1 and June 30 were classified as yearlings with brood year two years prior to tagging year. Fish tagged between July 1 and December 30 were classified as subyearlings with brood year one year prior to tagging year. This method aligned with trends observed in length of fish at tagging (Hillman et al. 2018). Fall Chinook were all collected and tagged in the upper Columbia River as subyearlings. Steelhead brood year was unknown because the age at migration was variable (e.g., 1 to 7 years) and length was not a good indicator of migration age because age-classes overlapped substantially (Peven et al. 1994). There were minor differences between stray estimates using brood year and return year (return year stray rates were minimally higher than brood year stray rates), however we present only return year results to allow comparison among all races of Chinook and between Chinook and steelhead.

We assumed that the last PIT detection in the database was the most likely spawning location. However, tagged individuals with final detections at mainstem Columbia River fish ladders were excluded from stray assignment at the subbasin and tributary scale, because it is unlikely that these fish spawned in the Columbia River. Fish with final detections within the subbasin where they were released, as determined by the river kilometer (RKM) of the subbasin, were assigned as homing to that subbasin. Fish with final detections in another subbasin in the upper Columbia River were assigned as straying to that subbasin. At the tributary scale, fish that originated from and had a final detection within a tributary were assigned as homing to that tributary. Fish with a final detection in another tributary of the same or different subbasin of origin were assigned as tributary strays. Only steelhead with final detections that corresponded with the spring spawning period (March through June) were included to exclude wandering behaviors from spawning behaviors.

Stray occurrence was calculated by summing the quantity of fish that strayed. The overall proportion of strays was calculated by dividing the stray total by the return total. Finally, the average stray occurrence was calculated by averaging the yearly stray occurrence when the quantity of returning fish was five or greater. Years with fewer than five returning fish were excluded from the calculation. We did not evaluate mechanisms of straying using mathematical models because of the low number of strays detected and because the main focus of this work was to document the magnitude of straying.

Results

Stray rate

A total of 823,770 PIT tags were injected into natural-origin fish and later evaluated to determine stray rates of natural-origin salmon and steelhead in the upper Columbia Watershed (Table 1). Despite a massive PIT tagging effort, the low survival rates between tagging of juveniles and returning adults resulted in low sample sizes for some years, species, and locations.

A total of 2,611 adults returned to the Columbia Basin and met our analytical criteria and were included in this analysis.

Table 1. Quantities (Qty) of PIT-tagged natural-origin Chinook Salmon and steelhead that homed to and strayed from the upper Columbia River basin, 2002-2018. Spring Chinook (SPC), summer Chinook (SUC), and steelhead (STH) that homed were detected at Priest Rapids or Rock Island dam fishways and locations upstream. Fall Chinook (FAC) that originated from the Hanford Reach of the Columbia River and were last detected at McNary or Priest Rapids dam fishways were assigned as home. Individuals assigned as strays were last detected outside the upper Columbia River. When more than one stray location is listed, the quantity of individuals is displayed in parentheses.

Species/race	Qty PIT Released	Qty Home	Qty Stray	Stray rate	Stray Location
SPC	352,109	1,000	0	0.0%	
SUC	100,273	98	0	0.0%	
FAC	140,114	286	2	0.7%	(1) Deschutes River, (1) Little White Salmon River
STH	231,274	1,223	2	0.2%	Snake River
Total	823,770	2,607	4		
Mean				0.2%	

The mean stray rates of spring, summer, and fall Chinook Salmon and steelhead originating in the upper Columbia Basin were below 15% at all spatial scales. Stray rates were lowest at the basin scale and highest at the tributary scale. Mean stray rates of each population were less than 1% at the basin scale (range 0.0%-0.7%, Table 1), less than 10% at the subbasin scale (range 0.0%-9.8%, Table 2), and less than 15% at the tributary scale (range 0.0%-14.3%, Table 3). Many of the populations that were evaluated across all spatial scales did not have any strays detected (11 of 28) and the mean of means of all species stray rates at all spatial scales was generally less than 5% (range 0.2%-4.0%). Summer and fall Chinook Salmon were never detected straying into tributaries. Stray rates of Chinook Salmon and steelhead were similar when compared from the same subbasins and tributaries (Figure 2).

Table 2. Release, homing, and straying quantities (Qty) of PIT-tagged natural-origin spring Chinook (SPC), summer Chinook (SUC), fall Chinook (FAC), and steelhead (STH), originating from the upper Columbia River and its subbasins from 2002-2018. The mean stray rate excludes years with < 5 homing adults. When more than one stray location is listed, the quantity of individuals is displayed in parentheses.

Species/race	Qty PIT released	Qty Home	Qty Stray[1]	Mean Stray Rate	Stray Location
Columbia River					
FAC[2]	140,114	286	2	0.7%	(1) Deschutes, (1) Little White Salmon
Wenatchee					
SPC	230,770	497	4	1.2%	(2) Entiat, (2) Methow
SUC	476	0	0	0.0%	
STH	58,960	241	2	0.5%	Entiat
Entiat					
SPC	72,759	250	5	2.0%	(1) Wenatchee, (2) Entiat, (2) Methow
SUC	86,401	51	6	9.8%	(1) Wenatchee, (4) Methow, (1) Okanogan
STH	80,570	241	12	3.7%	Methow
Methow					
SPC	48,580	67	3	5.2%	(1) Wenatchee, (2) Okanogan
SUC	6,676	2	0	0.0%	
STH	73,773	175	9	5.3%	(2) Snake, (7) Okanogan
Okanogan					
SUC	6,720	6	0	0.0%	
STH	17,971	20	0	0.0%	
Total	823,770	1,836	43		
Mean				2.8%	

[1]Strays were last detected outside the subbasins from which they originated.
[2]Fall Chinook were released into the Hanford Reach of the Columbia River and not into the Wenatchee, Entiat, Methow, or Okanogan rivers.

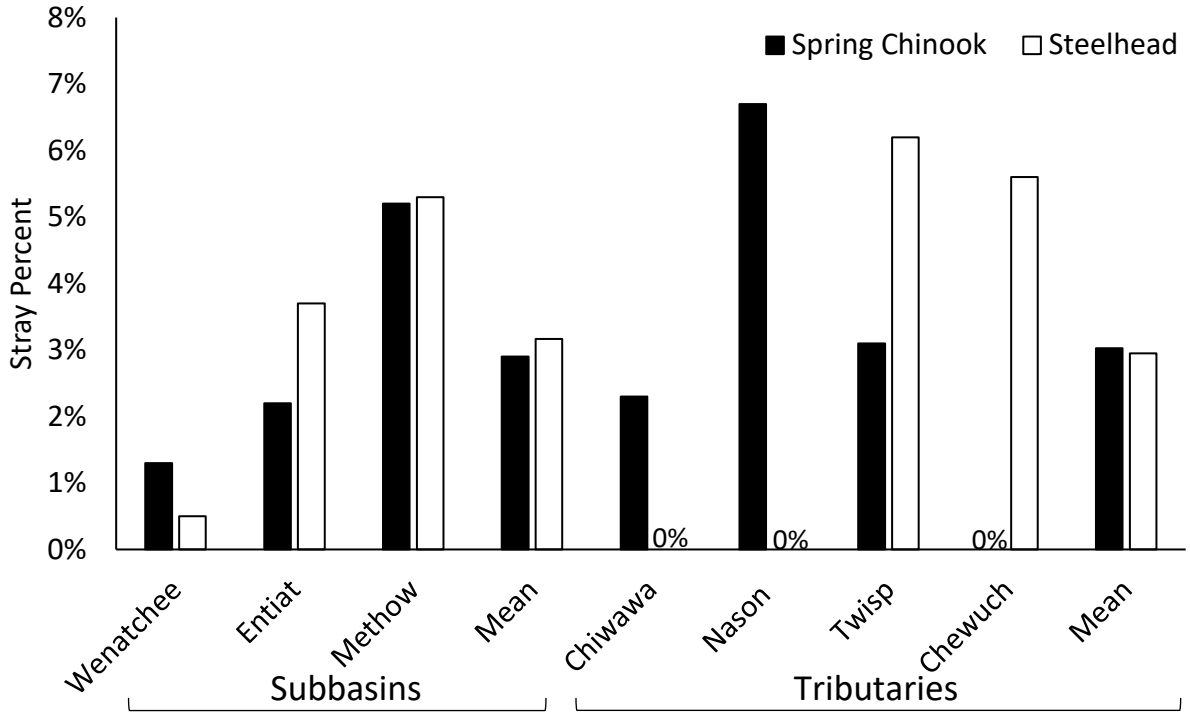

Figure 2. The percent of PIT-tagged natural-origin spring Chinook Salmon and steelhead that strayed away from their subbasins and tributaries of origin.

Stray direction

The small number of fish that strayed at the subbasin and tributary scales generally strayed upstream of their capture location. It was not possible for fish to stray upstream of the basin scale because there is no basin above the upper Columbia for fish to stray into. At the basin scale, only 4 fish strayed (2 steelhead and 2 fall Chinook), and all of them strayed into locations downstream of the upper Columbia River (Table 1). Two steelhead strayed into the Snake River and two Fall Chinook Salmon were detected in subbasins well downstream of Priest Rapids Dam (Deschutes River and the Little White Salmon River). Fall Chinook Salmon originating in the Hanford Reach below Priest Rapids dam were not detected in upper Columbia River subbasins.

At the subbasin scale, spring, summer, and fall Chinook Salmon and steelhead strays were generally detected in subbasins upstream of the home subbasin, however, there were instances of straying to a downstream subbasin within the upper Columbia (e.g., a spring Chinook Salmon that originated from the Entiat River but returned to the Wenatchee River). Of the 43 salmon and steelhead that strayed, 84% (36) were last detected in a subbasin upstream of home (Tables 2). One hundred percent (4 of 4) of spring Chinook Salmon from the Wenatchee subbasin, 80% from the Entiat subbasin (4 of 5), and 67% (2 of 3) from the Methow subbasin strayed upstream Eighty-three percent (5 of 6) of summer Chinook Salmon from the Entiat River strayed upstream. One hundred percent (2 of 2) of steelhead from the Wenatchee subbasin,

100% (12 of 12) from the Entiat subbasin, and 78% (7 of 9) from the Methow subbasin strayed upstream. One hundred percent (2 of 2) of fall Chinook strayed downstream. At the tributary scale, 94% of spring Chinook Salmon and Steelhead strayed upstream. Only 9 spring Chinook Salmon strayed and 8 of them strayed to an upstream tributary (89%) while 100% (9 of 9) steelhead strayed upstream (Table 3). Despite the tendency for Salmon and steelhead to stray upstream, the stray rates of fish originating from locations upstream (e.g., Methow subbasin) appeared higher than those originating from downstream locations (e.g., Wenatchee subbasin; Figure 2).

Table 3. Quantities (Qty) of PIT-tagged natural-origin spring Chinook Salmon (SPC) and steelhead (STH) originating from upper Columbia River subbasins (Wenatchee = W, Entiat = E, Methow = M, Okanogan = O) with homing and straying totals at the tributary scale 2002-2018. The mean stray rate excludes populations with < 5 homing adults. When more than one stray location is listed, the quantity of individuals is displayed in parentheses.

Species/race	Tributary	Qty PIT Released	Qty Home	Qty Stray	Stray Rate	Stray Location
SPC	Chiwawa [W]	167,953	216	5	2.3%	(2) Little Wenatchee [W], (1) Nason Cr [W], (1) Peshastin Cr [W], (1) White River [W]
SPC	Nason [W]	26,656	42	3	6.7%	(1) Little Wenatchee [W], (1) White River [W], (1) Twisp River [M]
SPC	White [W]	3,275	2	0	0.0%	
SPC	Twisp [M]	23,391	31	1	3.1%	Lost River [M]
SPC	Chewuch [M]	11,425	16	0	0.0%	
STH	Nason [W]	15,808	21	0	0.0%	
STH	Chiwawa [W]	15,065	25	0	0.0%	
STH	Mad [E]	9,538	16	1	5.9%	Libby Creek [M]
STH	Chewuch [M]	9,672	17	1	5.6%	Salmon Creek [O]
STH	Beaver/Gold/ Libby [M]	14,284	18	3	14.3%	Twisp River [M]
STH	Twisp [M]	28,075	61	4	6.2%	(1) Loup Loup Creek [O], (1) Bonaparte Cr [O], (1) Tunk Cr [O], (1) Hancock Springs [M]
STH	Omak [O]	10,462	13	0	0.0%	
Total		335,604	478	18		
Mean					4.0%	

Discussion

Our results indicated that mean stray rates of natural-origin Chinook Salmon and steelhead were below 15% at all three spatial scales and were at the low end of estimates that were previously published for natural-origin steelhead and spring Chinook Salmon (Shapovalov and Taft 1954; Ford et al. 2015a). Stray rates of natural-origin PIT tagged spring Chinook Salmon in the upper Wenatchee Basin were about 56-74% of those reported using genetic techniques in the same tributaries (Ford et al. 2015a). For instance, stray rates for spring Chinook Salmon originating from the Chiwawa River were 2.3% using PIT tags and 4.1% using genetic techniques. Furthermore, stray rates for spring Chinook Salmon originating from Nason Creek were 6.7% using PIT tags and 9.0% using genetic techniques. These differences may be within sample size and measurement error or be due to differences in the years included in the different studies. Alternatively, it is possible that the efficiency of the PIT antenna arrays was less than 100% and our methodology underestimated straying. However, recent work suggests that efficiencies of subbasin and tributary arrays exceed 90% for steelhead and that stray estimates using CWT, that do not rely upon arrays, were similar to estimates using PIT tags for hatchery-origin spring Chinook Salmon (Grant County Public Utility District, unpublished data). There is also a possibility of overestimating strays using the method of last PIT tag detections. This could occur if fish temporarily stray or wander (e.g. Bond et al. 2017; Richins and Skalski 2018) and then are not detected at a different antenna. Preliminary information from comparisons of hatchery-origin summer Chinook Salmon stray rates derived from CWT and PIT tags suggested PIT tag estimates were correlated with, but higher than CWT estimates (Grant County Public Utility District, unpublished data). This suggests that natural-origin stray rates of summer Chinook Salmon at the subbasin and tributary scales may be overestimates.

Unfortunately, we could not make comparisons to spring Chinook Salmon spawning populations with high stray rates reported by Ford et al. (2015a) (100% for fish originating from the upper Wenatchee River and 17.5% for fish originating from the Little Wenatchee River) because we didn't have sufficient PIT tags from those locations. However, PIT tag estimates for spring Chinook Salmon in five upper Columbia tributaries were substantially lower than these high stray rates (e.g., <7%). Estimating stray rates of small populations will likely be a challenge in the future, particularly using methods such as we described in this work. Another alternative method to estimate straying is to evaluate otolith chemistry in cases where water chemistry is sufficiently different (Brenner et al. 2012; Budnik et al. 2018; Watson et al., 2018). Differences in water chemistry signatures have been found in tributaries of the upper Wenatchee and there was ability to discriminate juvenile spring Chinook Salmon that resided in tributaries prior to migration as yearlings using chemical differences in fin rays (Linley et al. 2016). Thus, it may be possible to evaluate straying using fin rays or otoliths, but different emigration times of juveniles from tributaries may decrease discrimination of adults (Linley et al. 2016) and decrease the utility of stray estimates using this method.

The stray rates of natural-origin fish that we report may be higher than what occurred prior to habitat degradation and the large inputs of hatchery-origin fish (see descriptions in Williamson et al. 2010; Ford et al. 2015a; Johnson et al. 2018). Ford et al. (2015a) found that natural born offspring of spring Chinook Salmon with hatchery-origin parentage had higher stray rates than those from natural-origin parents. None of the natural born fish from natural-origin spring Chinook Salmon were detected as strays in that study. The natural-origin juveniles from our study were likely produced from a variety of matings of both hatchery and natural-origin

parents which may have increased the stray rate when compared to systems without hatchery-origin spawners. In addition, it has been speculated that degraded spawning habitat has contributed to increased stray rates (Ford et al. 2015a, Cram et al. 2012) and there has been habitat degradation in the upper Columbia Basin such as passage impediments, warming water temperature, and stream channelization. Furthermore, management actions that disrupt sequential imprinting or homing, such as barging or routing of water through irrigation canals and tributaries, can also increase straying (Keefer and Caudill 2014; Bond et al. 2017).

Stray rates were different depending upon the spatial scale of evaluation. Mean stray rates of each population were less than 1% at the basin scale, less than 10% at the subbasin scale, and less than 15% at the tributary scale. These findings highlight the importance of spatial scale in evaluations and the necessity of defining spatial scales when making comparisons and communicating results (Keefer and Caudill 2014). We could not generate a good estimate of stray rates at the Columbia River Basin scale because of insufficient PIT detection in other Basins. However, estimates of natural-origin strays into the Columbia River suggests that straying between large river Basins may be low (Hess et al. 2014) such as we found at the largest spatial scale we examined in this study. Many studies have evaluated straying of hatchery-origin fish at the subbasin and larger scales (Westley et al. 2013, 2015, Bond et al. 2017). Ford et al. (2015a) presented stray rate information at a finer spatial scale (e.g., within tributaries) than this study using genetic methods; something we could not do with the PIT tag methods that were used in this study.

Other studies may detect different patterns of stray rates depending upon the dendricity and spatial positioning of spawning habitats. It is also possible that the magnitude of natural-origin fish straying could differ depending upon differences in hatchery-origin fish abundance and spawning success, habitat degradation, barging, and water withdrawals. Hatchery-origin fall Chinook Salmon that were collected in the Snake River and barged downstream strayed at higher rates than those that were not barged (Bond et al. 2017). Similarly, the likelihood of straying increased during years of warmer river temperatures. If natural origin fish encounter these conditions, then it is likely that they would stray at higher rates than what we presented for the upper Columbia basin.

Our results do not support the reputation that steelhead have for high straying propensity (Richins and Skalski 2018, Budnik et al. 2018). The mean stray rates at all scales were relatively low and Chinook Salmon strayed at similar rates as steelhead at the scales that we examined. Furthermore, in another study Coho Salmon had dramatically higher rates of straying than steelhead in two coastal California streams (Shapovalov and Taft 1954). Perhaps steelhead have received their reputation for straying based upon their wandering behavior before spawning and because most of what is known about steelhead straying comes largely from hatchery-origin fish (Richins and Skalski 2018, Budnik et al. 2018). However, Westley et al. (2013) reported that hatchery Chinook Salmon strayed more than hatchery steelhead. The differences in straying that occurs among species may differ between regions depending upon the myriad of factors that influence straying, such as imprinting, hatchery influence, barriers to migration, water temperature, irrigation routing, and spawning habitat conditions (Keefer and Caudill 2014; Cram et al. 2012), and the relative frequency of those factors in the different regions. For instance, steelhead may stray more than Chinook Salmon in some regions but not in others.

Directionality

Most of the spring and summer Chinook Salmon and steelhead strays strayed in an upstream direction. This is interesting because the opportunities for straying in a downstream direction were much higher than for straying in an upstream direction. The further upstream a fish migrates the fewer opportunities it has to stray in an upstream direction. Salmon and steelhead pass many subbasins and tributaries as they migrate up the Columbia River and yet they tend to stray upstream of their natal rearing area. This may be a result of sequential imprinting errors (Dittman et al. 2015) or an adaptation to colonize new upstream habitats such as when glaciers retreat, volcanic eruptions cease, flood waters recede, or migration barriers are removed (Leider 1989; Pearsons et al. 1992; Weigel et al. 2013). For some species that migrate when water temperatures are relatively warm, such as steelhead and fall Chinook, fish may overshoot (Richins and Skalski 2018) or undershoot (Bond et al. 2017) natal areas in search of cold water refugia. As such, there are likely multiple factors that influence the direction of straying and the stray direction may be different in other locations outside the upper Columbia basin.

Management implications

The low stray rates that we observed in this study are consistent with the development of genetic differentiation among populations at various spatial scales in the upper Columbia Basin (McClure et al. 2008). However, even low stray rates can result in significant interbreeding with non-target populations and result in increased homogenization of spawning populations (Bett et al. 2017). This is particularly true: (1) when the donor populations are large, (2) when donor straying is frequent, and (3) when the recipient population is small (Bett et al. 2017). Furthermore, hatchery programs can disrupt patterns of natural-origin stray rates and decrease genetic differentiation (Ford et al. 2015a, b; Ford et al. 2016). This study focused on donor stray rates, but estimates of recipient population stray rate are more relevant when evaluating potential genetic effects on natural spawning populations and yet estimates of recipient population stray rate are relatively rare (Keefer and Caudill 2014). Until recipient population stray rates are available at multiple spatial scales, managers can use donor population stray rates to help inform management actions.

Estimates of natural-origin fish stray rates, such as those in this study, could be used to inform management targets for hatchery programs. However, the variation in donor population stray rates that have been observed for natural-origin salmonids has been highly variable ranging from 0-100% and can vary between species, geographic location, environmental condition, and spatial scale (Shapovalov and Taft 1954; Ford et al. 2015a). Some authors have suggested that universal management targets for donor strays are not appropriate (Quinn 2005; Brenner et al. 2012; Keefer and Caudill 2014). In contrast, recipient population stray compositions have been recommended based upon genetic and ecological risk toleration and have ranged between 2%-10% (Ford 2002; Mobrand et al. 2005; Brenner et al. 2012; Paquet et al. 2011; Hillman et al. 2018). It is likely that more information is necessary before donor population stray rate targets can be set and that site specific information will be needed to inform management targets. In addition, the objectives of a hatchery program will influence what donor stray rate targets are appropriate. For example, in cases of large-scale reintroduction, such as above Chief Joseph and Grand Coulee dams (Johnson et al. 2018), high stray rates may be desirable in order to colonize large areas. Furthermore, managers should consider whether estimates of donor stray rate targets of natural-origin fish are realistic to achieve for hatchery-origin fish that are cultured under dramatically different conditions. It remains to be seen whether natural- and hatchery-origin fish

stray rates differ at a variety of spatial scales and in different regions, however Ford et al. (2015a) indicated that stray rates of hatchery-origin spring Chinook Salmon were higher than natural-origin spring Chinook Salmon in the Chiwawa River.

The tendency for natural-origin fish to stray in upstream directions can be used to predict what groups of fish are likely to populate newly created habitats within subbasins and tributaries and also be candidates for reintroduction. Newly created habitats include removal of passage impediments such as culverts and also include locations exposed to floods, droughts, volcanic eruptions, and other disturbances (Pearsons et al. 1992, Leider 1989; Weigel et al. 2013). Selecting candidate populations for reintroduction, such as above Chief Joseph and Grand Coulee dams, might also be informed based upon what populations would likely colonize the area naturally. Natural-origin fish that stray might have some traits that make them particularly suitable for colonizing new habitats, although we are not aware of data that supports this idea.

Conclusion

We demonstrated that PIT tags can be an effective means to estimate the magnitude of natural-origin salmon and steelhead straying and can also be used to evaluate factors associated with straying. Unfortunately, massive efforts for PIT tagging and deployment of antenna arrays are necessary to generate estimates. One weakness of using PIT tags to estimate straying is there is no confirmation that a fish spawned within the area that it was last detected. We found that stray rates of natural-origin spring, summer, and fall Chinook Salmon and steelhead at three spatial scales were less than 15% and there was variation in stray rates between spatial scales. Furthermore, most of the fish that strayed into non-natal subbasins and tributaries strayed in an upstream direction. There continues to be a lack of studies that have evaluated stray rates of natural-origin fish, and further work would contribute to our understanding of the magnitude of straying by different populations in a variety of different habitats.

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Comparisons of Donor Stray Percentages Between Hatchery- and Natural-Origin Chinook Salmon and Steelhead in the Upper Columbia Watershed

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Abstract

Artificial propagation of salmon *Oncorhynchus* spp. and steelhead *O. mykiss* is a common strategy that is used to achieve conservation and harvest goals. However, unintended effects of artificial propagation, such as high donor stray percentages, can reduce the number of adults that return to target areas and also contribute spawners to different populations where they are not desired. Until recently, it was difficult to assess if hatchery-origin fish stray rates were atypical because few estimates of stray rates of natural-origin fish were available. We used last PIT-tag detections to estimate and compare donor stray percentages of hatchery-origin and natural-origin Chinook Salmon *O. tshawytscha* and steelhead in the upper Columbia River watershed between 2002-2018. Donor stray percentages of hatchery-origin spring, summer, and fall Chinook Salmon and steelhead were <0.3% at the upper-Columbia basin scale and generally not higher than natural-origin donor stray percentages at larger spatial scales but were higher (up to 62%) at smaller spatial scales. Returning hatchery-origin Chinook Salmon and steelhead generally strayed in an upstream direction and the proportions of fish that strayed upstream were not significantly higher than natural-origin fish. Juvenile spring Chinook Salmon that were moved 14 to 389 river kilometers from centralized hatcheries to tributaries for overwintering or final acclimation, strayed at a much higher rate than those that completed their incubation, rearing, and acclimation at a single location. In contrast, steelhead that were moved for acclimation, including direct releases from trucks, did not stray at higher rates than those that completed their incubation, rearing, and acclimation at a single location. Other adaptive management actions that were implemented to reduce straying produced mixed results. A variety of approaches can be considered to reduce undesirable production of strays, but most of them involve difficult trade-offs.

Introduction

Hatcheries are frequently used to increase harvest and conserve natural populations of salmon and steelhead but the large-scale production of salmon and steelhead in hatcheries poses a variety of unintended ecological and genetic risks to natural-origin populations (Busack and Currens 1995; Pearsons 2008; Pearsons et al. 2012) and straying is among the most significant concerns (Ford 2002; Mobrand et al. 2005; Paquet et al. 2011). Unusually high incidence of strays from hatchery programs are undesirable for a number of reasons. First, stray fish do not come back to the intended target area and therefore are not available for location specific harvest or conservation purposes (Keefer and Caudill 2014; Sturrock et al. 2019). Second, hatchery-origin strays that spawn with other recipient populations, may reduce genetic diversity among natural-origin populations (Quinn 2005; Mobrand et al. 2005; Brenner et al. 2012). Straying can be estimated as either the percentage of a source spawning population that strays (i.e., donor stray percentage) or the percentage of a recipient spawning population that is composed of non-natal spawners (i.e., recipient stray percentage) (Keefer and Caudill 2014). Stray fish that spawn with non-target populations can pose risks to both donor and recipient populations. The spatial scale of straying is also an important consideration (Keefer and Caudill 2014; Pearsons and O'Connor 2020) because long-distance straying is likely to pose more undesirable risks to harvest and conservation objectives than short-distance straying.

Salmon and steelhead are hypothesized to home by sequentially imprinting as juveniles and then following imprinted cues in reverse when returning as adults (Hasler and Scholz 1983; Dittman et al. 2010; 2015). Other factors such as habitat quality, pheromones of conspecifics, and geographic complexity can influence homing, particularly at finer scales (Cram et al. 2012; Keefer and Caudill 2014; Bett et al. 2017). Much uncertainty remains about how hatchery practices influence homing and straying, but some hatchery practices are generally thought to increase straying compared to naturally produced fish (Keefer and Caudill 2014) and achieving acceptably high homing is one of the greatest challenges for fish culturists (Westley et al. 2013; 2015; Ford et al. 2015a).

A variety of fish-husbandry methods are currently used to reduce straying of hatchery-origin fish and to return fish to target areas. For example, acclimation sites are used to imprint juvenile fish on surface water in specific areas prior to release in the hopes that they will return to the target area around the acclimation site (Dittman et al. 2010; Clarke et al. 2012; Keefer and Caudill 2014). The length of time that fish are acclimated can vary from a few weeks in the spring to over six months spanning the winter for yearling smolt programs (Dittman et al. 2010; Clarke et al. 2012; Ford et al. 2015a). Also, fish are generally released when they are undergoing smoltification, the time that fish have a very strong spike in the hormone thyroxine, which is thought to be associated with chemical imprinting (Scholz 1980; Hasler and Scholz 1983; Westley et al. 2013). Embryonic imprinting, where fish are exposed to natal water at the alevin to fry life stages, has been proposed for hatchery programs that incubate eggs and embryos at locations far from release locations (Dittman et al. 2015). Although embryonic imprinting has not been evaluated in cases where fish are transported prior to release, it does occur in locations where all life-stages are raised and released at the same location, however the water is often local ground water instead of surface water in order to reduce disease risk.

Most of what is known about salmon and steelhead straying is derived from studies of hatchery-origin fish (Westley et al. 2013, 2015; Keefer and Caudill 2014). It has been difficult to determine whether hatchery-origin fish stray rates are unusually high or low when compared

to natural-origin fish because natural-origin fish stray rate estimates were not available from the same area where hatchery-origin fish are released, and because observed natural-origin stray rates have been highly variable, ranging between 0 and 100% (Shapovalov and Taft 1954; Ford et al. 2015a; Keefer and Caudill 2014). Recently, estimates of natural-origin stray rates have been developed using genetic (Ford et al. 2015a) and passive integrated transponder tag (PIT tag) (Pearsons and O'Connor, 2020) methods. Mean donor stray percentages for natural-origin Chinook Salmon and steelhead in the Upper Columbia watershed were less than 1% at the upper Columbia basin scale, less than 10% at the subbasin scale, and less than 15% at the tributary scale (Pearsons and O'Connor, 2020). Most of the populations that were evaluated across all spatial scales did not have any strays detected. Chinook Salmon strayed at higher rates than steelhead. Straying mostly occurred in an upstream direction at both the subbasin and tributary scales. The directionality of straying is important because it provides information about which recipient populations are likely to be affected by strays as well as what new habitats may be colonized by strays.

In this paper, we used similar methods to estimate donor stray percentages of hatchery-origin salmon and steelhead in the upper Columbia watershed as we did to estimate donor stray percentages of natural-origin salmon and steelhead in the same area (Pearsons and O'Connor 2020), and made comparisons between natural-origin and hatchery-origin donor stray percentages. We focused our efforts on 'permanent strays' as opposed to adult wandering prior to spawning (Keefer and Caudill 2014) and also focused on 'management strays' which was defined as adults that did not return to spawn near the juvenile release location. We formed hypotheses that were informed by what we observed in natural-origin adults in the upper Columbia watershed as well as previously published information about straying by hatchery-origin adults (Pearsons and O'Connor 2020; Keefer and Caudill 2014). We hypothesized that: 1) donor stray percentages of hatchery-origin fish would increase with decreasing spatial scale similar to the pattern we observed for natural-origin fish (Pearsons and O'Connor 2020), 2) donor stray percentages of hatchery-origin fish would be higher than donor stray percentages of natural-origin fish, particularly at smaller spatial scales such as was suggested by other published studies (Keefer and Caudill 2014), 3) hatchery-origin fish stray direction would depend upon release location such as would be supported by the sequential imprinting hypothesis (Keefer and Caudill 2014), and 4) donor stray percentages would decline after management actions intended to reduce straying were implemented. We also evaluated the quality of PIT-tag-based stray estimates by comparing them to estimates generated using coded-wire tags (CWT).

Methods

Study Area

This study was conducted in the Columbia River, USA and most of the work was conducted in the upper Columbia watershed upstream of the confluence with the Snake River and downstream of Chief Joseph Dam, with fish from hatchery programs in the Wenatchee, Entiat, Methow, and Okanogan River subbasins and the upper Columbia River (Figure 1). The upper Columbia River watershed has an abundance of hatchery facilities as a result of mitigation for the construction and operation of hydropower dams (Figure 1). These hatcheries produce fall, summer, or spring Chinook Salmon, Coho Salmon *O. kisutch*, Sockeye Salmon *O. nerka*,

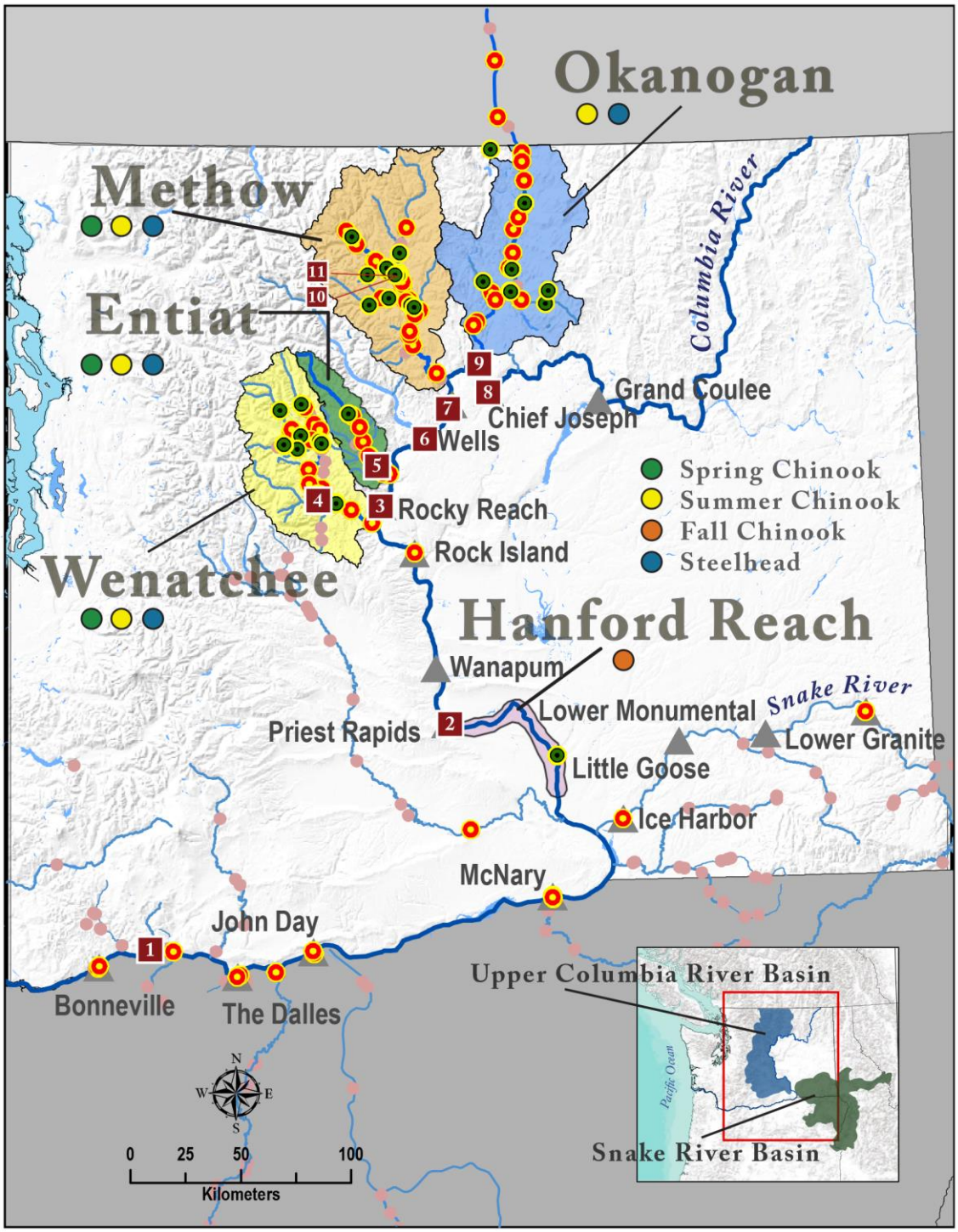

Figure 1. Release locations (green bullseye) and final detection locations (orange bullseye) of spring, summer, and fall Chinook Salmon and steelhead from the upper Columbia River Basin. Other points along rivers indicate PIT tag detection arrays. Numbered boxes represent locations of subject hatcheries including: (1) Little White Salmon, (2) Priest Rapids, (3) Eastbank, (4) Leavenworth, (5) Entiat, (6) Chelan, (7) Wells, (8) Chief Joseph, (9) Cassimer Bar, (10) Methow, and (11) Winthrop.

and steelhead for harvest, conservation, or a combination of both; but Chinook Salmon and steelhead are the only species considered here (Table 1). There were insufficient numbers of natural-origin Sockeye and Coho salmon that were PIT tagged to include these species in this comparative analysis. Some of the hatchery programs incubate, rear, and release fish from a single hatchery location, whereas other programs transport parr or smolts to acclimation sites for subsequent release (Table 1). The study area and biological background was previously described by Pearsons and O'Connor (2020) and is also briefly described below.

Fall Chinook Salmon spawn in the Hanford Reach, one of the few free-flowing reaches of the Columbia River downstream of Priest Rapids Dam, comprising one of the largest Chinook Salmon populations in the United States, and contribute large numbers of fish to harvest in the Pacific Ocean and Columbia River, making this population economically very important (Harnish et al. 2014; Langshaw et al. 2017; Pearsons et al. 2020). Summer Chinook Salmon spawn primarily in the mainstems of four subbasins of the upper Columbia River (e.g., Wenatchee, Entiat, Methow, and Okanogan) and support considerable fisheries in the Pacific Ocean and Columbia River. The naturally produced juveniles of summer and fall run Chinook Salmon generally migrate to the sea as sub-yearlings. Spring Chinook Salmon spawn in tributaries to mainstem subbasins and in upper portions of mainstem subbasins (Williamson et al. 2010; Murdoch et al. 2010; Ford et al. 2015a). Upper Columbia River spring Chinook Salmon are listed under the Endangered Species Act (ESA) as endangered (McClure et al. 2008). The naturally produced juveniles of spring Chinook Salmon migrate to the sea as yearlings. Summer steelhead spawn throughout upper Columbia subbasins and are ESA listed as threatened (Ford et al. 2016). Naturally produced juvenile steelhead migrate to the sea at ages 1-7, but most migrate at ages 1, 2 and 3 (Peven et al. 1994). All life history types of Chinook Salmon and steelhead have a long history of interactions with hatchery programs and hatchery- and natural-origin fish overlap in much of their spawning distributions (e.g., Williamson et al 2010; Pearsons et al. 2012; Ford et al. 2015a; Ford et al. 2016; Johnson et al. 2018).

Analytical Framework and Definitions

We used information from PIT tags and PIT-tag detection arrays deployed throughout the region for various purposes to evaluate donor stray percentages of hatchery-origin salmon and steelhead. The analytical methods and years used for these analyses were similar to those described for estimation of natural-origin donor stray percentages in the same geographic area of Pearsons and O'Connor (2020). We assumed that the last PIT detection in the database was the most likely spawning location. However, tagged individuals with final detections at mainstem Columbia River fish ladders were excluded from stray assignment at the subbasin and tributary scale, because it is unlikely that these fish spawned in the Columbia River, except fall Chinook Salmon in the Hanford Reach of the Columbia River. Fish with final detections within the subbasin where they were released, were assigned as homing to that subbasin. Fish with final detections in another subbasin in the upper Columbia River were assigned as straying to that subbasin. At the tributary scale, fish that originated from and had a final detection within a tributary were assigned as homing to that tributary. Fish with a final detection in another tributary of the same or different subbasin of origin were assigned as tributary strays. Only steelhead with final detections that corresponded with the spring spawning period (March through June) were included to exclude wandering behaviors from spawning behaviors.

Wandering behaviors included temporary residency in a subbasin or tributary during migration or overwinter periods. Final detections that aligned with spawning periods were assumed to be

Table 1. Locations of hatchery activities and PIT tag quantities (Qty) for hatchery programs in the upper Columbia Basin. All fish were released as yearlings except for fall Chinook Salmon and some summer Chinook Salmon which were released as subyearlings into the Okanogan and Columbia rivers. PIT-tagged juvenile summer Chinook Salmon reared at Wells Hatchery and released into the Methow and Okanogan rivers in 2010 for survival studies were included in basin-scale analyses but not for subbasin stray results.

Incubation and Rearing	Final Acclimation	Release	Years of release	Quantities (Qty) of PIT-tagged juvenile Chinook Salmon and steelhead
Spring Chinook Salmon				
Eastbank	Nason	Nason Creek	2015-2017	35,243
Eastbank	Chiwawa	Chiwawa River	2007-2017	99,940
Little White Salmon	White River and Lake Wenatchee	White River, Lake Wenatchee, Wenatchee River	2008-2015	277,729
Leavenworth	Leavenworth	Icicle Creek	2000-2017	995,661
Methow	Twisp	Twisp River	2004, 2012-2017	40,503
Summer Chinook Salmon				
Eastbank	Dryden	Wenatchee River	2007-2017	126,765
Eastbank	Carlton	Methow River	2007-2017	34,740
Eastbank	Similkameen	Similkameen River	2011, 2013	10,125
Entiat	Entiat	Entiat River	2010-2017	89,710
Wells	Wells	Columbia River	2000-2017	152,400
Wells	Wells	Methow River	2010	30,343
Wells	Wells	Okanogan River	2000, 2010	11,030
Chief Joseph	Omak	Similkameen and Okanogan rivers	2015-2017	24,718
Chief Joseph	Chief Joseph	Columbia River	2015-2017	29,971
Fall Chinook Salmon				
Priest Rapids	Priest Rapids	Columbia River	2000-2017	357,808
Steelhead trout				

Eastbank and Chelan	Turtle Rock	Chiwawa River, Nason Creek, Wenatchee River	2005, 2009-2011	235,451
Eastbank and Chelan	Chiwawa	Chiwawa River, Nason Creek, Wenatchee River	2003, 2005, 2009, 2011, 2012-2017	118,507
Eastbank and Chelan	Turtle Rock (Columbia River) and Chiwawa	Various throughout Wenatchee River subbasin	2003-2005, 2007-2017	314,077
Eastbank and Chelan	Blackbird Island	Wenatchee River	2010-2016	20,769
Eastbank	Nason (Rolfing)	Wenatchee River	2010	20,211
Wells	Wells	Columbia River	2000, 2003, 2012-2017	161,954
Wells	Twisp	Twisp River	2003-2005, 2010-2017	198,334
Wells	Methow Hatchery	Methow River	2003-2005, 2010-2017	275,839
Wells	Chewuch	Chewuch River	2003-2005, 2010-2011	123,312
Winthrop	Winthrop	Methow River	2003-2005, 2008-2017	380,202
Winthrop	Winthrop	Chewuch River	2010, 2012	996
Cassimer Bar	Cassimer Bar	Omak Creek	2005, 2007-2011	88,332
Cassimer Bar	Cassimer Bar	Stapaloop Creek	2004, 2006	23,334
Wells	Saint Mary's	Omak Creek	2003-2005, 2012-2017	90,249
Wells	Wells	Salmon Creek	2012, 2017	11,310
Wells	Wells	Similkameen River	2003-2005, 2012, 2017	93,613
Total				4,379,563

spawning fish. The donor stray percentages of natural-origin fish presented previously were used for comparisons to hatchery-origin fish (Pearsons and O'Connor 2020).

We defined donor straying as a fish that did not return to the location of release, which was the management intent of acclimation or location of release. Furthermore, we were interested in permanent rather than temporary straying, which is why we use last PIT detections in our evaluation. However, adults that returned to a hatchery or adjacent location where

juveniles had earlier rearing experience such as during embryonic development may have homed correctly, but were not consistent with the management objective. We did not include fish that were detected at hatcheries in this evaluation because they did not have the opportunity to escape once they entered a facility, facilities were not always equipped with a PIT detector, and fish were not always scanned for PIT tags at hatcheries.

A representative sample of fish were PIT tagged (typically 5,000-10,000 annually) at central hatcheries or acclimation sites between 2000 and 2017 and allowed to recover prior to release (Table 1). The timing of tagging varied depending upon the size of fish and the objective of the tagging. In general, fish were tagged in the fall or spring prior to release. Fish were PIT tagged when they were at least 60 mm FL and were anesthetized prior to tagging. The PIT tags were Biomark ™ model, 12 mm long, 2.1 mm diameter, and cylindrically shaped and were injected into the coelomic cavity of juveniles with syringes. Short-term tag retention was generally high (e.g., >99%) and mortality was low (e.g., <2%) (Hillman et al. 2019).

Two major hatchery management modifications to fish acclimation occurred during this study to reduce straying. We compared the donor stray percentages of fish before and during the modification to determine whether the modification reduced straying. The expectation was that the donor stray percentages would decrease substantially after the management action was implemented. First, we evaluated whether a new overwinter acclimation facility decreased summer Chinook Salmon donor stray percentages when compared to spring acclimation at the same site. It was hypothesized that longer periods of acclimation may improve imprinting and homing. Summer Chinook Salmon were raised at Eastbank Hatchery on the Columbia River and then transferred to the Carlton acclimation site in the Methow River subbasin in the spring for final acclimation and release in 2010 and 2011. A new overwinter acclimation facility was subsequently built on the same property with the first release in 2014. The fish released in 2014 were spring acclimated, but from 2015 through 2017 fish were overwinter acclimated. We compared donor stray percentages of summer Chinook Salmon that were spring acclimated (2010, 2011, 2014) and overwinter acclimated (2015-2017). Second, a change in hatchery and acclimation facilities for steelhead from a) Turtle Rock Hatchery on the Columbia River and using trucks to plant steelhead throughout the Wenatchee River subbasin (release years 2006-2008) to b) Eastbank hatchery and an overwinter acclimation facility and release on the Chiwawa River in the Wenatchee River subbasin (release years 2014, 2016, 2017). This change increased exposure to water from the Wenatchee River subbasin, where fish were targeted to return.

Analysis

The PIT Tag Information System (PTAGIS) maintained by the Pacific States Marine Fisheries Commission (PSMFC) was queried for hatchery-origin adult salmon and steelhead returns to the Upper Columbia Basin. Individuals with known locations of tagging and release as juveniles were included in the analysis. Release quantities and detection records were used to create datasets for analysis. All detection records for hatchery-origin spring, summer, and fall Chinook and summer steelhead that were PIT-tagged as juveniles and originated from the Wenatchee, Entiat, Methow, and Okanogan river subbasins and the upper Columbia River were included in the analysis (Figure 1). Occurrence of straying was evaluated at three spatial scales that include fish originating (released) from and returning to: (1) the upper Columbia River basin (e.g., above the confluence with the Snake and Yakima rivers); (2) a subbasin within the Upper Columbia (e.g., Wenatchee, Entiat, Methow, or Okanogan River subbasins or the Hanford

Reach of the Columbia River); and (3) a tributary of a subbasin (e.g., Chiwawa River, Nason Creek). These scales generally conform to management units of the Evolutionarily Significant Unit (Basin), the major spawning population (subbasin), and the spawning aggregate (tributary) (McClure et al. 2008). Summer Chinook Salmon reared at Wells Hatchery and released in the Methow and Okanogan rivers for survival studies in 2010 were included for upper Columbia River basin analyses but excluded from subbasin stray results because they were not acclimated consistent with the approved hatchery programs. Methods for assigning homing and straying are described in Pearsons and O'Connor (2020), but brief descriptions are provided below.

Donor stray percentage was calculated by summing the annual quantity of adults that strayed and dividing the annual stray total by the annual return total of the strayed and homed adults of the donor population. The average stray percentage was calculated by averaging the yearly stray percentages when the quantity of returning fish was five or greater. Years with fewer than five returning fish were excluded from the calculation because of potential extreme annual effects of low sample size.

We compared donor stray percentages using two different methods to evaluate the quality and consistency of the estimates made using PIT tags on return year and to reduce the number of metrics that were evaluated in this study. First, we compared return-year and brood-year donor stray percentages estimated using PIT tags. Brood-year donor stray percentages included all return years from a single brood and may reduce the influence of interannual environmental conditions on straying of adults when they migrate home. Second, we compared return-year donor stray percentages estimated using PIT with brood-year donor stray percentages estimated with CWT for Chinook Salmon only. Donor stray percentages derived from CWT were compiled from technical reports or generated from a United States Fish and Wildlife Service CWT database for upper Columbia River basin hatcheries (data accessed August 2019). Due to limited PIT tag samples for some programs, all spatial scales for CWT stray estimates were combined in order to make comparisons with PIT tag estimates. Only CWT stray estimates with temporal and spatial overlap for the PIT-based estimates were included. A correlation analysis was implemented to evaluate similarities among return- and brood-year estimates of donor stray percentages, and between PIT and CWT estimates of donor stray percentages.

Comparisons between donor stray percentages of hatchery- and natural-origin fish were made using the counts of PIT-tagged fish that homed and those that strayed at each spatial scale with all years pooled in a non-parametric contingency test (Fisher's Exact Test, Agresti 2002). Comparisons of the stray direction of hatchery- and natural-origin fish were made using Fisher's Exact contingency tests of the pooled counts of PIT-tagged fish that strayed downstream or upstream at each spatial scale. Donor stray percentages of fish that were moved to remote acclimation sites in the spring or fall were compared in a contingency test to those that were incubated, reared, acclimated and released from a single facility by pooling the years of each treatment for each facility. A one-tailed Fisher's Exact test p-value was used to test significance at an alpha of 0.05. A one-tailed test was used because we were interested in detecting whether hatchery-origin stray rates were higher than natural-origin stray rates.

Results

There were 5,652,887 PIT tags injected into hatchery-origin juvenile fish and later evaluated to determine donor stray percentages of hatchery-origin salmon and steelhead in the

upper Columbia Basin. These included tags from specific hatchery programs (4,379,563; Table 1) and tags that were part of studies or tagged at collection sites in the natural environment where origin was known based upon fin clips, tags, and geographic location (1,273,374). From those releases, 27,261 PIT tagged adult salmon and steelhead returned to the upper Columbia River Basin. Homing and straying totals for basin, subbasin, and tributary scales are presented in Table 2.

Table 2. Homing and straying of adult hatchery-origin PIT-tagged upper Columbia Watershed Chinook Salmon and steelhead 2000-2018. The range represents annual donor stray percentage.

Scale	Location	Total N Home	Total N Stray	Range
	Spring Chinook Salmon			
Basin	Upper Columbia River	5,378	3	0.06%
Subbasin	Wenatchee River	1,138	20	0-4.6%
Tributary	Nason Creek	93	3	0-7.3%
Tributary	Chiwawa River	241	104	8.3-55.6%
Tributary	White River	66	108	49.1-79.5%
Subbasin	Methow River	926	23	0-8.8%
Subbasin	Okanogan River	32	2	0-12.5%
	Summer Chinook Salmon			
Basin	Upper Columbia River	9,149	4	0.04%
Subbasin	Wenatchee River	190	57	6.1-35.0%
Subbasin	Entiat River	334	25	0-19.0%
Subbasin	Methow River	204	7	0-23.1%
Subbasin	Okanogan River	131	0	0%
	Fall Chinook Salmon			
Basin/Subbasin	Upper Columbia River/Hanford Reach	1,776	3	0.17%
	Steelhead trout			

Basin	Upper Columbia River	11,178	3	0.03%
Subbasin	Wenatchee River	978	131	0-31.4%
Tributary	Nason Creek	103	74	21.7-61.1%
Tributary	Chiwawa River	46	34	28.6-54.5%
Subbasin	Methow River	173	25	0-25.0%
Tributary	Twisp River	38	5	7.1-16.7%
Tributary	Chewuch River	6	7	0-28.6%
Subbasin	Okanogan River	466	7	0-15.8%
Tributary	Omak Creek	335	16	0-21.3%
Tributary	Salmon Creek	2	1	–

PIT-tag-based donor stray percentages by return year and brood year were highly correlated and were similar in magnitude for spring and summer Chinook Salmon and steelhead (Figure 2). In addition, the stray estimates generated from PIT tags and CWT were highly correlated and similar in magnitude for spring Chinook Salmon and highly correlated but different in magnitude for summer Chinook Salmon (Figure 2). Donor stray percentages of summer Chinook Salmon were about three times higher when estimated with PIT tags (<22% using PIT tags and <8% using CWT). Only one fall Chinook hatchery (Priest Rapids Hatchery) in the upper Columbia River was available to estimate straying and the CWT estimate (3.3%) was about 10 times higher than the PIT tag estimate (0.2%). Stray estimates using CWT were not available for steelhead so they could not be compared to PIT estimates. In summary, both methods were highly correlated and produced similar results for spring Chinook Salmon, return year and brood year estimates for steelhead were highly correlated, PIT estimates were higher than CWT estimates for summer Chinook Salmon, and lower for fall Chinook Salmon. Other than the results we describe above, we present only return year results using PIT tags to allow comparison among all life history types of Chinook Salmon and between Chinook Salmon and steelhead using the same metric and to facilitate clarity and efficiency of the presentation. The implications of using return year estimates on our findings are presented in the discussion section.

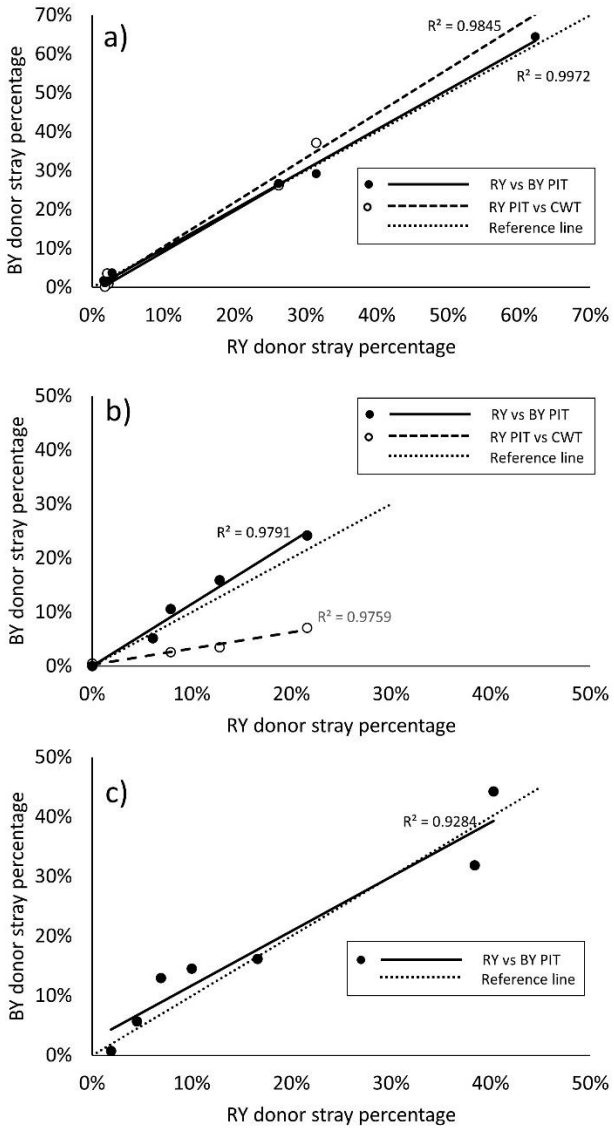

Figure 2. PIT-tag-based return-year (RY, spawn year) stray estimates versus brood-year (BY) stray estimates using either PIT tags or BY coded wire tags (CWT) for upper Columbia watershed a) spring Chinook Salmon, b) summer Chinook Salmon, and c) steelhead.

Spatial scale and taxa

Donor stray percentages of hatchery-origin fall, summer, and spring Chinook Salmon and steelhead were generally not higher than natural-origin donor stray percentages at larger spatial scales but were higher at smaller spatial scales. Donor stray percentages of hatchery-origin fall Chinook Salmon (P=0.98), summer Chinook Salmon (P=0.96), spring Chinook Salmon (P=0.60), and steelhead (P=0.99) were not significantly higher than natural-origin donor stray percentages at the basin scale and were <0.3% (Figure 3).

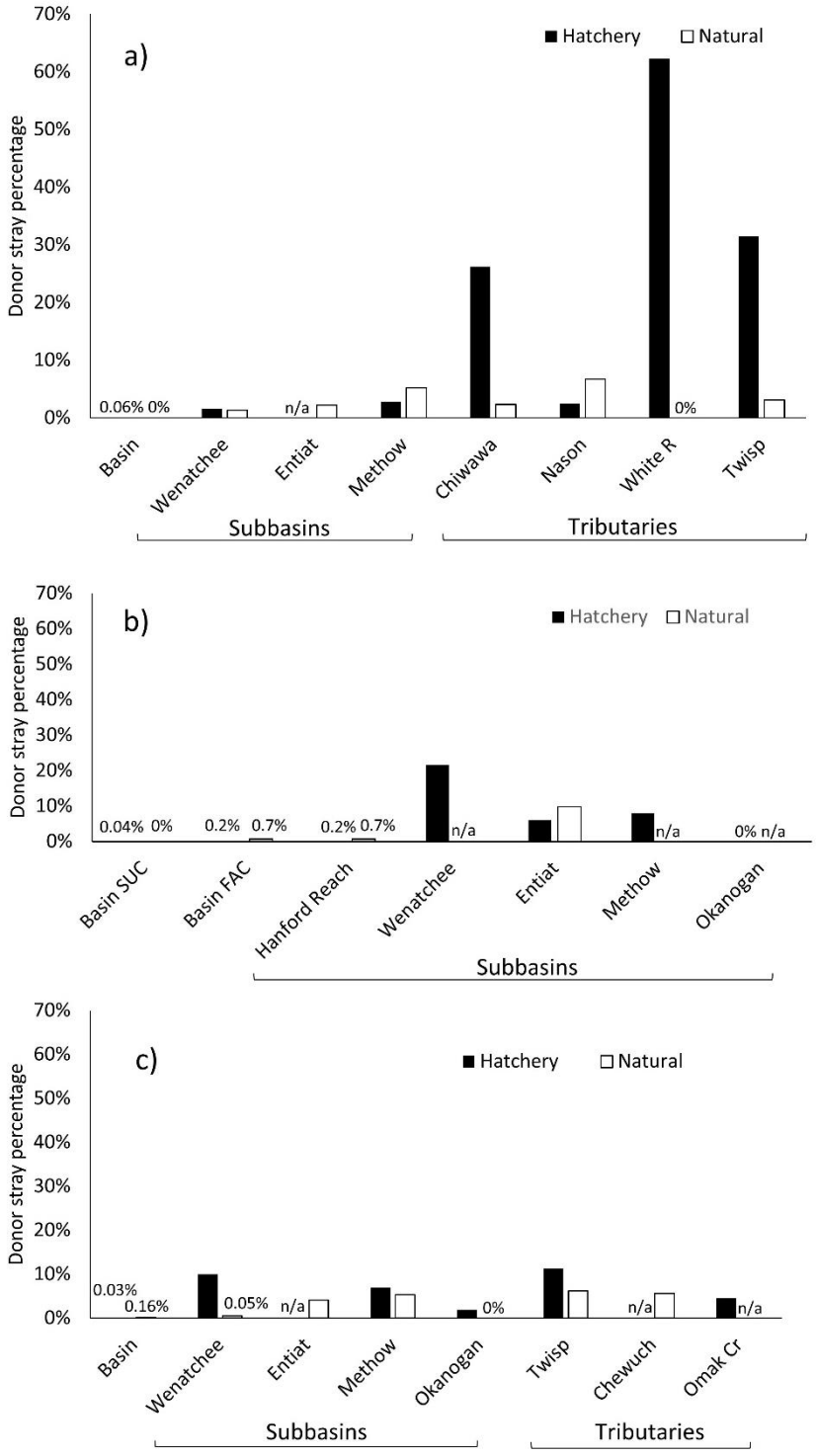

Figure 3. Donor stray percentages of hatchery- and natural-origin a) spring Chinook Salmon, b) summer Chinook Salmon (SUC) and fall Chinook Salmon, (FAC) and c) steelhead at basin, subbasin, and tributary scales.

Hatchery-origin spring Chinook Salmon donor stray percentages were <3%, hatchery-origin donor stray percentages of summer Chinook Salmon were <22%, hatchery-origin donor stray percentages of fall Chinook Salmon from the Hanford Reach was <1%, and hatchery-origin donor stray percentages of steelhead was <11% at the subbasin scale (Figure 3). At the subbasin scale, donor stray percentages of hatchery-origin fall Chinook Salmon (P=0.77), summer Chinook Salmon (P=0.45), and spring Chinook Salmon (P=0.16), were not significantly higher than natural-origin donor stray percentages, but donor stray percentages of hatchery-origin steelhead were significantly higher than natural-origin donor stray percentages (P<0.0001) (Figure 3). Results for spring, summer, and fall Chinook Salmon were consistent across individual subbasins (P>0.05), but donor stray percentages of hatchery-origin steelhead in the Okanogan subbasin were not significantly higher than natural-origin donor stray percentages (P=0.75) despite the other subbasins being different (P<0.05).

At the tributary scale, donor stray percentages of hatchery-origin spring Chinook Salmon (P<0.001), were significantly higher than natural-origin donor stray percentages (Figure 3). There was some variation in differences within each of the taxa and in some tributaries. For example, donor stray percentages of hatchery-origin spring Chinook Salmon in Nason Creek and the White River were not significantly higher than natural-origin donor stray percentages in those tributaries (P>0.05, n=2 natural-origin spring Chinook Salmon at White River). Donor stray percentages of hatchery-origin steelhead in the Twisp River were not significantly higher than natural-origin donor stray percentages (P=0.25). Hatchery-origin spring Chinook Salmon donor stray percentages were as high as 62% and 3 of 4 tributary hatchery-origin donor stray percentages were numerically higher than natural-origin donor stray percentages from the same tributary (Figure 3).

Stray direction

Hatchery-origin Chinook Salmon and steelhead generally strayed in an upstream direction (i.e., overshot the target destination such as a target tributary or subbasin as opposed to a location within a tributary or subbasin) and the proportions of hatchery fish that strayed upstream was not significantly different than natural-origin fish (P>0.05; Figure 4). In general, of those fish that strayed over 80% of hatchery-origin Chinook Salmon and steelhead strayed in an upstream direction and some hatchery populations only strayed in an upstream direction (Figure 4). The few exceptions to this pattern were cases with limited opportunities to stray in an upstream direction, such as fish released in the Okanogan subbasin.

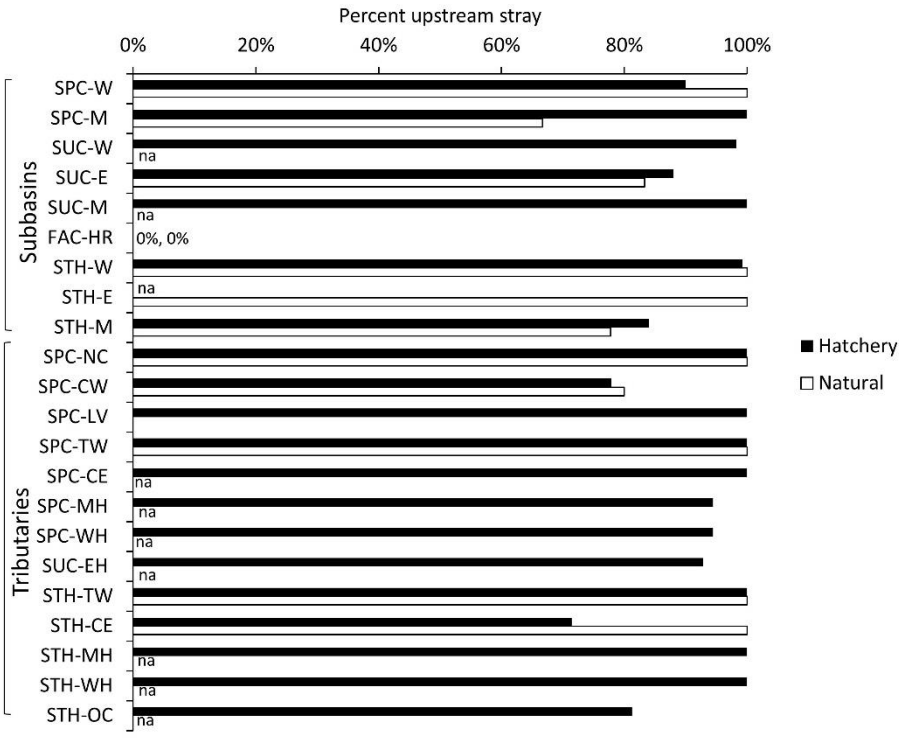

Figure 4. Direction of hatchery- and natural-origin straying. Abbreviations: SPC spring Chinook Salmon, SUC summer Chinook Salmon, FAC fall Chinook Salmon, STH steelhead. W Wenatchee River, M Methow River, E Entiat River, HR Hanford Reach, NC Nason Creek, CW Chiwawa River, LV Leavenworth Nation Fish Hatchery, TW Twisp River, CE Chewuch River, MH Methow Hatchery, WH Winthrop National Fish Hatchery, EH Entiat National Fish Hatchery, OC Omak Creek.

Movement for remote acclimation

Only spring Chinook Salmon and steelhead met the criteria for comparing donor stray percentages of fish that were moved between facilities for acclimation and those that were not. Spring Chinook Salmon that were moved to other tributaries for acclimation strayed at much higher percentages than those that completed their incubation, rearing, and acclimation at a single location ($P<0.0001$; Figure 5). In contrast, steelhead that were moved for acclimation did not stray at higher percentages than those that completed their incubation, rearing, and acclimation at a single location ($P=0.69$; Figure 5).

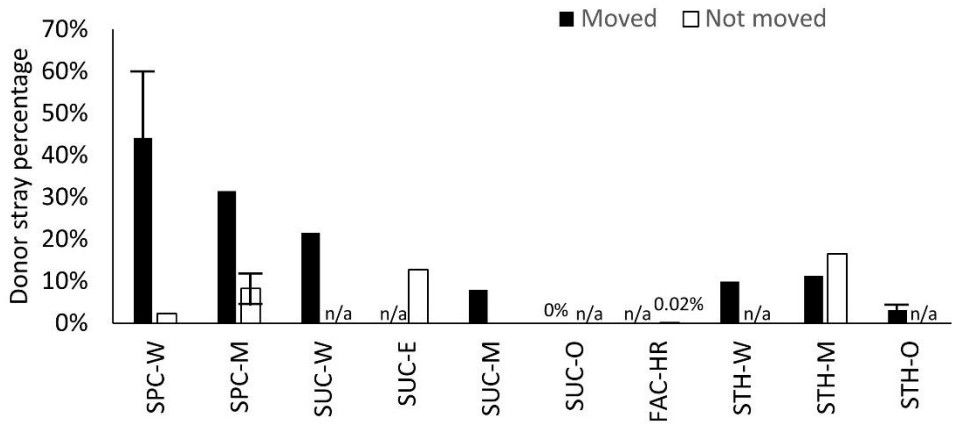

Figure 5. Mean donor stray percentages of hatchery-origin fish that were moved as juveniles among facilities prior to release (moved) or those that were incubated, reared, acclimated and released from a single facility (not moved). Error bars represent the range of values when more than one value was available. Abbreviations: SPC spring Chinook Salmon, SUC summer Chinook Salmon, FAC fall Chinook Salmon, STH steelhead. W Wenatchee River, M Methow River, E Entiat River, O Okanogan River, HR Hanford Reach.

Management changes

The management actions that were implemented to reduce straying produced mixed results. Donor stray percentages were not significantly different for summer Chinook Salmon released into the Methow subbasin in the years when they were both overwinter and spring acclimated (2015-2017) than when they were just spring acclimated (2010, 2011, 2014), $P=0.19$; (Figure 6). Overwinter acclimation of steelhead in the Wenatchee subbasin did result in lower donor stray percentages at the subbasin scale ($P<0.0001$, Figure 6).

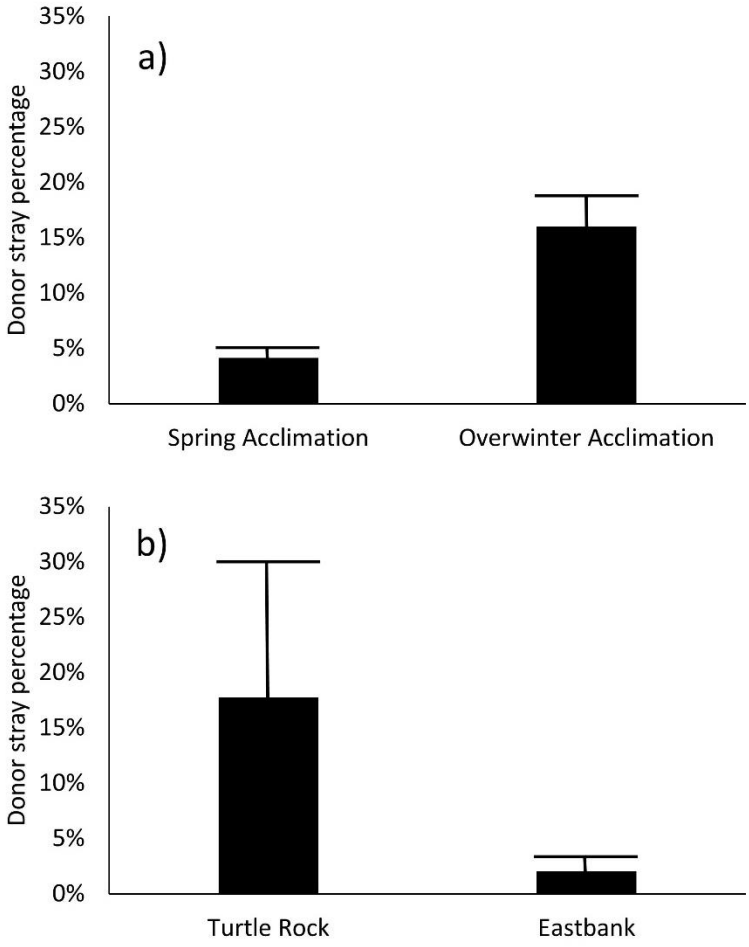

Figure 6. Mean donor stray percentages in periods of differing management regimes for a) summer Chinook Salmon released from the Carlton Acclimation Facility on the Methow River, and b) steelhead released into the Wenatchee River after being raised at either Turtle Rock or Eastbank Hatchery. Bars represent the mean of annual estimates and error bars are ranges.

Discussion

Spatial scale (size of the target) and risk

Hatchery-origin fish were able to return to the largest target (basin) with high accuracy and were as accurate as natural-origin fish. As the target size became smaller and more numerous, such as subbasins and tributaries, the accuracy decreased for both returning hatchery- and natural-origin fish, but more so for hatchery-origin fish (Figure 7). There are many factors that may contribute to increasing homing accuracy with increasing spatial scale. The most obvious factor is that it is easier to find a big target than a small one and that there are more opportunities to miss targets at the tributary level because there are more tributaries than basins or subbasins. Another factor that likely contributed to the basin accuracy was that most juvenile

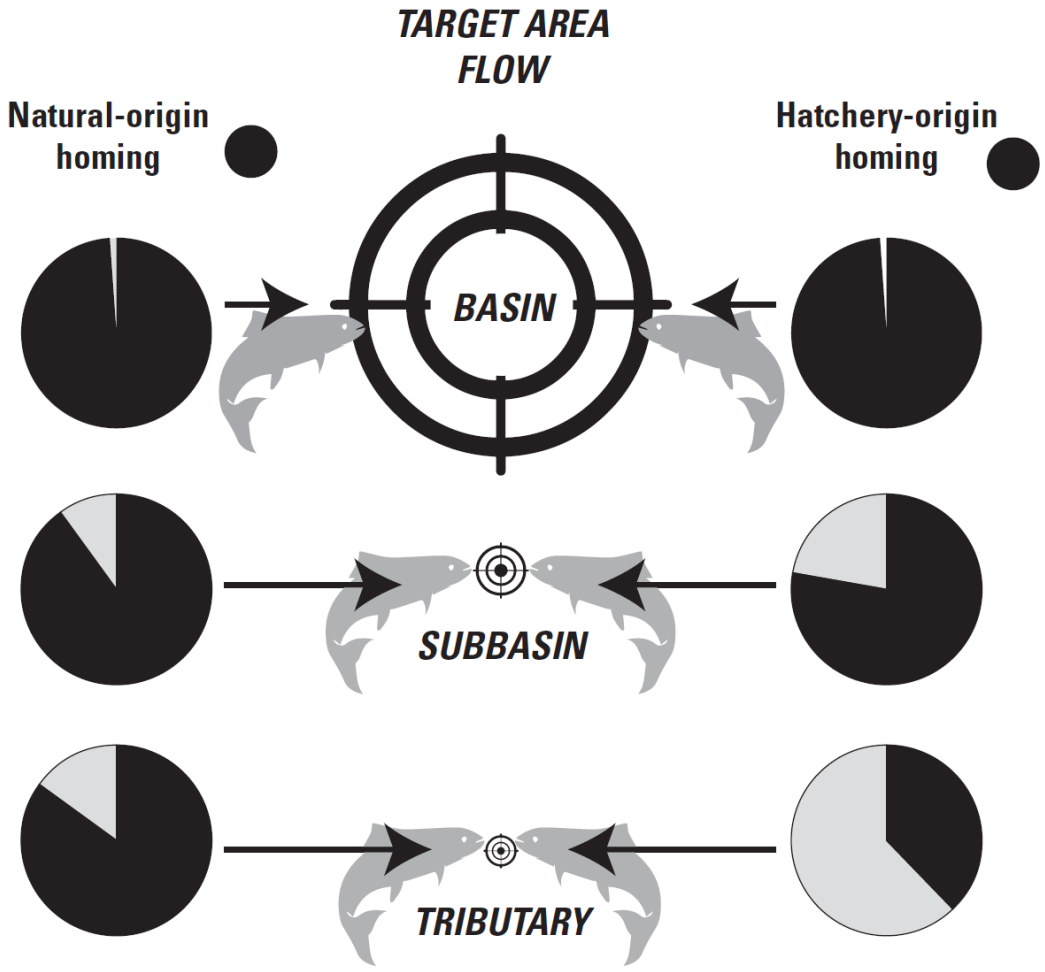

Figure 7. Comparisons of homing rates (minimums in black) and straying (maximums in grey) between hatchery- and natural-origin Salmon and steelhead at three spatial scales in the upper Columbia subregion. The size of the targets was scaled to the fall discharges of the upper Columbia River (basin), the mean of the Wenatchee, Entiat, Methow, and Okanogan subbasins (subbasin), and the mean of tributaries to subbasins (tributary).

fish were not moved outside of the basin: all of the PIT tagged fish that were released into the upper Columbia basin were spawned, incubated, reared and released into the upper Columbia basin except for White River spring Chinook Salmon. As such, with one exception, the fish were exclusively imprinted on upper Columbia basin water and oriented on upper Columbia basin geography. In contrast, many of the fish released into subbasins and tributaries were moved between two hatchery facilities prior to release which likely contributed to reduced homing by hatchery-origin fish (discussed below).

The demographic and genetic risks of hatchery-origin salmon and steelhead straying varied dramatically with spatial scale but risks to harvest were universally low. At the upper

Columbia basin scale over 99.7% of returning hatchery-origin fish homed to the basin of origin and the donor stray percentages were similar to natural-origin fish. In contrast, returning hatchery-origin fish donor stray percentages were as high as 62% at the tributary scale and the donor stray percentages were higher than natural-origin fish in many, but not all, tributaries. Straying posed little risk to harvest objectives at the spatial scales considered because fisheries occurred downstream of areas where fish stray, such as in the ocean, Columbia River, and subbasins; and not in tributaries (Hillman et al. 2019; Pearsons et al. 2020).

For conservation hatchery programs, straying had the potential to result in demographic risks at the tributary scale for spring Chinook Salmon and at tributary and subbasin scales for steelhead (excluding tributaries of the Wenatchee River) because strays did not contribute to target spawning populations in all cases and therefore may not contribute to population recovery of these ESA listed species. However, these strays might have also contributed to the demographics of other nearby non-target spawning aggregates or populations. For example, spring Chinook Salmon released in the Chiwawa River contributed substantial numbers of strays to the adjacent Nason Creek spawning aggregate and these fish contributed to natural production (Williamson et al. 2010; Ford et al. 2015a). In other cases, the scale of population management can influence whether a fish is characterized as a stray or not and management zones can influence the magnitude of demographic or genetic risks. In short, a portion of the hatchery-origin returns had the potential to contribute to target spawning aggregates while others strayed nearby and potentially contributed to the larger population at the subbasin and basin scale. Total numbers of fish produced naturally from hatchery-origin fish that homed or strayed away from target spawning locations in tributaries or subbasins may produce the same numbers of offspring in the basin as if they all spawned in target locations. However, among other things, this assumes that density-dependent mortality is equal among spawning and rearing locations and that the genetic characteristics of hatchery-origin fish does not influence the reproductive success in non-target areas. Both of these assumptions are unlikely to be true (Williamson et al. 2010; Ford et al. 2015a; Ford et al. 2016).

Finally, genetic risks to nearby spawning aggregates occur when strays potentially disrupt local adaptation (McClure et al. 2008; Keefer and Caudill 2014). These genetic risks are most likely to occur within spawning aggregates of a subbasin for spring Chinook Salmon, and for some spawning aggregates and major population groups for steelhead. The degree of risk is likely influenced by the amount of reproductive success that is influenced by genetic differentiation. Fish that stray into populations that are genetically similar to one another pose lower risk than those that are very different. In general, adjacent populations are genetically more similar than those that are geographically separated by longer distances (Hillman et al. 2019), so adjacent populations are also less likely to dramatically influence local adaptation. The genetic risks of straying are better evaluated by estimating recipient population stray percentage than donor stray percentage because recipient population stray percentage also incorporates the size of the recipient population relative to the abundance of strays (Keefer and Caudill 2014; Bett et al. 2017). For example, high donor population stray percentages may pose low genetic risks to large recipient populations but high genetic risks to small recipient populations.

The patterns and magnitudes of hatchery-origin fish straying that we present in this study were within the range of those presented by others that work in the Columbia Basin and elsewhere. For example, Ford et al. (2015a) found that donor stray rates of hatchery-origin spring Chinook Salmon in the Chiwawa River using CWT were higher than those estimated for natural-origin fish using genetic methods and that approximately 5% strayed to other subbasins.

Westley et al. (2013) assessed donor straying at the subbasin scale in the Columbia River Watershed and observed a wide range of stray rates of hatchery-origin Chinook Salmon and steelhead from 0.11%-54.9%. Donor stray rates of fish at the subbasin scale in the upper Columbia Basin (1.6-21.6%) were within the range of other parts of the Columbia Basin (Westley et al. 2013). Donor stray rates of returning hatchery-origin Chinook Salmon released as yearlings in the Yakima Basin were very low at the Yakima Basin and subbasin scale and relatively high at the tributary scale (Dittman et al. 2010; Fast et al. 2015). Over 55% of returning hatchery-origin spring Chinook Salmon were recovered over 25 km from their acclimation release site and donor stray rates of fish released from the Jack Creek Acclimation site were approximately 76% (Dittman et al. 2010; Cram et al. 2012). Finally, donor stray rates of returning hatchery-origin fall Chinook Salmon in California's Central Valley ranged between 0% and 89% (Sturrock et al. 2019).

The lack of differences that we found in at least one of our comparisons was likely the result of low sample size and associated low statistical power (Ham and Pearsons 2000). We did not detect a difference in donor stray percentages of hatchery- and natural-origin spring Chinook Salmon in the White River even though the estimated donor stray percentages were 62% and 0%, respectively, and was the highest donor stray percentage of hatchery-origin fish that we evaluated. The sample size of the natural-origin population was only two fish, which was lower than the standard we used for hatchery-origin fish ($n>4$), and was the reason why the statistical test did not result in a statistically significant result. The donor stray percentages of natural-origin spring Chinook Salmon in other tributaries of the upper Columbia with higher sample sizes has been below 7% (Pearsons and O'Connor 2020) and it is likely that even with a larger sample size, these rates also apply to natural-origin spring Chinook Salmon in the White River. Thus, it is likely that hatchery-origin donor stray percentages in the White River were substantially higher than natural-origin donor stray percentages and we simply couldn't detect it because of the low sample size that was used to estimate natural-origin donor stray percentages. It is possible that lack of detectable differences occurred for other comparisons in our evaluation, but visual examinations of the graphs (Figures) do not indicate dramatic omissions in detectable differences such as occurred in the White River.

Factors influencing straying

There are multiple factors that may influence hatchery-origin spring Chinook Salmon and steelhead to stray at higher percentages than natural-origin fish in tributaries. In addition to the transportation of fish from incubation and rearing sites to release and/or acclimation sites described below, the hatchery rearing environment may also be a factor that affects homing success (Ford et al. 2015a). In a review of straying, Keefer and Caudill (2014) reported that hatchery-origin fish were widely believed to have reduced imprinting compared to natural-origin fish, in part because of reduced stimuli in the hatchery environment and lower olfactory activity and reduced brain development compared to natural-origin fish. In addition, Westley et al. (2013) found that the hatchery practice of rearing ocean-type Chinook Salmon as yearlings rather than the subyearlings (the natural age at migration) was associated with increased straying. The hatchery management approach of extended rearing is used in the upper Columbia for summer Chinook Salmon and results in a possible trade-off between increased post-release survival and increased straying (see Unwin and Quinn 1993). Without addressing the trade-offs of survival inside and outside hatcheries, rearing conditions in hatcheries that may be responsible for

reduced imprinting at finer scales of resolution, and straying, it may not be possible to achieve management objectives of homing.

Responses of hatchery- and natural-origin fish to factors outside of the hatcheries may also explain the variation in straying we observed. For example, barrier weirs for collecting broodstock near acclimation sites may increase straying and also result in a higher propensity for hatchery-origin fish to be displaced than natural-origin fish (Bugert 1998; Clarke et al. 2012) because they are often located closer to hatchery acclimation sites than natural spawning sites farther upstream which may result in less drive to negotiate a barrier if they are near their homing target site (Hoffnagle et al. 2008). In addition, thermal attractants, or thermal or physical barriers may increase wandering behavior and ultimately straying (Leider 1989; Bond et al. 2017; Richins and Skalski 2018), but it is unclear how this would influence hatchery-origin fish differently than natural-origin fish, unless run and spawn timing differed between origins (Hoffnagle et al. 2008). Finally, poor habitat quality in areas near acclimation sites may increase straying outside of a tributary by hatchery-origin fish returning to the area around the acclimation facility (Cram et al. 2012; Fast et al. 2015; Ford et al. 2015a). In short, using best practices for imprinting hatchery-origin fish may not result in achieving management objectives because factors outside of the hatchery can influence straying too. Therefore, management actions inside and outside hatcheries should be considered in order to increase the potential of meeting management objectives for homing. Alternatively, managers could shape objectives for homing in accordance with the physical constraints of the river systems and facility infrastructure, and the biological characteristics of the supplemented species.

Stray direction

Contrary to our hypothesis that the direction (upstream vs. downstream) of donor stray percentages would vary depending upon hatchery locations, hatchery-origin fish generally strayed in an upstream direction similar to natural-origin fish (Pearsons and O'Connor, 2020). There may be fitness advantages to stray in an upstream direction if there is a higher probability of colonizing new habitats that are more productive than target or downstream habitats (Pearsons and O'Connor, 2020). In contrast, Dittman et al. (2010) found that hatchery-origin spring Chinook Salmon in the Yakima Basin spawned upstream of their acclimation site when the acclimation site was low in the system and downstream of their acclimation sites when they were located high in the system. This result may have been confounded by limited spawning habitat upstream of acclimation sites because of the presence of a dam and reservoir or because of an increase in stream gradient. In addition, differences between studies may be the result of differences in the spatial scales that were assessed. In our work we did not evaluate straying direction within a specific spatial scale such as a subbasin such as was done by Dittman et al. (2010), but rather between tributary and subbasin junctures. Similar to our findings, straying between spawning aggregations in the Yakima Basin was in an upstream direction. Knowing the direction of straying can be used to assess risks to nearby populations and to plan appropriate management actions to reduce impacts and achieve acceptable escapement goals. For example, genetic risks to upstream populations would be assessed to be higher than to downstream populations if suitable spawning areas were available upstream. One approach to reduce straying is to locate hatcheries or to release fish far upstream of where populations of concern exist and where upstream straying could be contained. It is also possible that locating releases far upstream in a tributary might reduce wandering behavior to other tributaries that could occur in

the absence of embryonic imprinting. This strategy is not without risk because the farther upstream fish are released the greater migration distance and lower migration survival as well as the potential for increased ecological risks (Pearsons and Hopley 1999; McMichael et al. 1999; Pearsons et al. 2012).

Moved vs. non-moved

Donor stray percentages of hatchery-origin spring Chinook Salmon that were transported for acclimation and/or release (but not mainstem Columbia River truck or barge transport) had greater deviations from donor stray percentages of natural-origin fish than those that were not transported. This observation is consistent with the sequential imprinting hypothesis (Scholz 1980; Hasler and Scholz 1983; Dittman et al. 2015) and also with evaluations of downstream transportation during spring outmigration (Bond et al. 2017; Sturrock et al. 2019). It appears that fish were able to find their way back to the subbasin of release, but then fish strayed possibly because they were searching for the location of their birth and that location was far from the release location. It is not clear whether the transportation of spring Chinook Salmon results in straying because of imprinting on another water source at an earlier life stage or because of disruption of the appropriate geographic cues or some other factor. If imprinting on another water source is the primary factor contributing to straying, then transportation of water to a centralized hatchery facility or exposure to unique odors could be used to imprint fish, particularly if it can be done when fish are embryos (Dittman et al. 2015). If disruption of appropriate geographic cues caused by transportation is the primary factor contributing to straying, then it is not clear what could be done to reduce donor straying if fish must be transported. High straying of hatchery-origin spring Chinook Salmon at the tributary scale also occurred in a Yakima Basin tributary, North Fork Teanaway River, even though the tributary was located within the same subbasin as the central hatchery facility and fish were moved during the spring for acclimation in the North Fork Teanaway River (Dittman et al. 2010; Cram et al. 2012); a scenario very similar to spring Chinook Salmon management within the Methow subbasin. It is unclear why steelhead did not exhibit the same patterns of differences associated with movement between hatchery facilities that spring Chinook Salmon did.

The highest donor stray percentage that we observed occurred in the White River Captive Broodstock spring Chinook Salmon program. The fish that were released for this program were founded from local broodstock and incubated, hatched, and reared to yearlings at the Little White Salmon National Fish Hatchery located on the Little White Salmon River, a tributary that enters the Columbia River hundreds of kilometers downstream of the upper Columbia Basin (Ford et al. 2015b). During the spring, spring Chinook Salmon yearling parr were trucked to the White River or Lake Wenatchee for at least six weeks of acclimation (Figure 1). Most fish were acclimated in streamside tanks or in net pens in the lake and released in those locations or trucked and released in the Wenatchee River below Lake Wenatchee to avoid low migration survival in the lake. The convoluted sequence of transportation and acclimation these fish experienced likely contributed to the highest donor stray percentages we observed.

The management action with the highest potential to reduce donor stray percentages is to reduce or eliminate the transportation of fish after the eyed-egg stage. However, this action is problematic for a variety of reasons. First, there is often not enough water to complete incubation, rearing, and acclimation at many remote sites such as in smaller tributaries. Some sites that do not have enough water to provide single-pass water through rearing vessels may

have enough water to consider high amounts (e.g., >95%) of water recirculation, but this might pose other fish-culture risks such as disease and poor fish quality. However, these risks have not been manifested for summer Chinook Salmon reared with 60% reuse water at Eastbank Hatchery or Wenatchee steelhead reared with reuse water at Chiwawa Acclimation Facility (Chelan Public Utility District, unpublished data). Second, the cost of building and operating new infrastructure for existing programs may be prohibitive and there is potential that additional infrastructure within spawning and rearing areas could reduce habitat quality for salmon and steelhead. New hatchery programs should consider ways to minimize fish transportation if donor stray percentages between tributaries are an important consideration for program success.

Responses to management actions

The management actions that were implemented to reduce straying had mixed results, suggesting that there is much to learn about the factors governing straying (Keefer and Caudill 2014). Management actions at the Carlton overwinter acclimation facility for summer Chinook Salmon assumed that additional imprinting occurred during the winter. The lack of detectable stray differences in this program suggests that imprinting may not be important during the winter for these yearling Chinook Salmon. In addition, donor stray rates of returning Chinook Salmon released as yearlings were not different in a study involving two- and four- month acclimation prior to release in early March into the Umatilla River, Oregon (Clarke et al. 2012), suggesting further that acclimation during the winter period may not be a strong factor influencing straying of returning Chinook Salmon released as yearlings.

One of the main reasons for acclimating fish during both the winter and into spring is to reduce straying (Clarke et al. 2012). However, our results indicate that homing at the tributary and larger scales was not improved by providing overwinter acclimation of Chinook Salmon at satellite sites. It was hypothesized that longer periods of acclimation may improve imprinting, however, the length of time may be less important than specific periods when salmon are known to imprint such as during embryonic development and smoltification (Scholz 1980; Dittman et al. 2015). Overwinter acclimation can provide other benefits to fish besides the potential for improved homing by exposing them to more natural water temperatures that modulates fish growth (Clarke et al. 2012; Larsen et al 2013). However, overwinter acclimation may also result in undesirable impacts to fish. For example, acclimation at remote sites is typically more challenging than at centralized locations because of higher exposure to pathogens downstream of decaying carcasses, higher turbidity, and debris and icing risks to intakes that compromise access to water and these factors may result in high on-site juvenile mortality. It is unclear whether the high financial costs and additional ecological and demographic risks associated with overwinter acclimation is sufficient to outweigh the benefits of overwinter acclimation if the acclimation does not reduce straying enough to meet management objectives. Assessments of the risks and benefits of overwinter acclimation are likely to be idiosyncratic for each hatchery program, resulting in the need to evaluate them on a case-by-case basis. For example, spring Chinook Salmon that were reared at the same central hatchery facility and then acclimated at three different satellite sites in the Yakima River had significantly different homing patterns relative to their acclimation site (Dittman et al. 2010); a phenomenon that was also observed in our study.

In contrast to the Chinook Salmon example, the management action to reduce steelhead straying appeared to be successful in the Wenatchee subbasin. Multiple factors may have contributed to improved homing of steelhead in the Wenatchee River including longer term

acclimation and changing water sources during rearing. In addition, summer steelhead overwinter as adults so multiple cues over a longer time may benefit steelhead homing more than Chinook Salmon. The variability in success of management actions prompt us to recommend that the mechanisms of straying be better understood before making large investments in costly management actions.

Tag methods and influence on conclusions

Our data suggests that donor stray percentages estimated by run year or brood year could be used interchangeably for all species but that the type of tag used resulted in varying differences of estimates depending upon the species. For example, donor stray percentages estimated using PIT and CWT were similar for spring Chinook Salmon, PIT estimates were three times higher than CWT for summer Chinook Salmon, and ten times lower than CWT for fall Chinook Salmon (although estimates using each method were <5% for fall Chinook Salmon). These differences could result from the logistics of tag detection for each tag type. PIT tag detections at in-stream arrays were easier to reconcile with physically recovered CWT tags at the tributary scale where spring Chinook Salmon spawn, less so at the subbasin scale because the larger flows where summer Chinook Salmon primarily spawn could make it more difficult to both detect PIT tags and recover CWT, and most difficult at the basin scale (mainstem Columbia River) where fall Chinook Salmon spawn because PIT tags are nearly always detected at mainstem dams while CWT recovery is more challenging. The physical placement of PIT detection arrays throughout the upper Columbia Watershed allowed us to assess whether the locations of the last detection were in the vicinity of expected spawning locations and limit which fish were included at each spatial scale. We used consistent methods in this study by only using PIT tags so the comparisons between hatchery- and natural-origin fish should not be influenced by our methods. However, the magnitude of stray estimates could be influenced by the methodology associated with the different type of tag that we used. In general, the magnitude of spring Chinook Salmon estimates are likely accurate, summer Chinook Salmon are likely overestimates, and fall Chinook Salmon are likely underestimates.

Applications

All hatchery programs are unique and therefore the findings we describe for the Upper Columbia Basin may differ in other locations. Indeed, substantial variation in donor stray percentages between hatcheries occurred within the Upper Columbia Basin. Furthermore, the hatchery programs in the Upper Columbia are well funded and managed with a high degree of oversight and hatchery programs that deviate from the practices used in the Upper Columbia may generate different results.

This work focused on donor population strays, but recipient population stray evaluations should also be considered. Recipient population stray rates are influenced by factors such as the size of the hatchery program, the size of the recipient population, and the donor stray rate (Bett et al. 2017). Large hatchery programs that are adjacent to small natural populations must have very low donor population stray rates in order to meet recipient population stray rates of 5 or 10%. In some cases, difficult trade-offs will be necessary to achieve potentially competing stray, survival, and program size objectives. In some cases, fish culture techniques such as raising summer Chinook Salmon to yearlings, moving fish to remote acclimation sites, and maintaining large

program sizes will need to be evaluated relative to the amount of straying that occurs. In still other cases, the only way to comply with mandated recipient population stray rates will likely be to reduce hatchery program size or change release locations.

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Stray Compositions of Hatchery-Origin Chinook Salmon *Oncorhynchus tshawytscha* and Steelhead *O. mykiss* in Recipient Natural Populations of the Upper Columbia Watershed

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Abstract

One of the biggest concerns of operating hatchery Salmon and steelhead programs is high straying of returning adults into non-target populations and the possible homogenization of genetic diversity among populations caused by spawning of stray fish. The composition of hatchery-origin stray Chinook Salmon *Oncorhynchus tshawytscha* and steelhead *O. mykiss* relative to the natural spawning populations, termed recipient population stray rate, was evaluated in the Upper Columbia Basin. Chinook Salmon carcasses were collected from 1999-2018 in spawning areas shortly after spawning and carcasses were examined to determine origin. Adipose fin clips and coded-wire-tags were used to distinguish non-target hatchery, target hatchery, and natural-origin fish; coded-wire-tags were read in the lab to determine the origin of hatchery-origin fish. Steelhead strays and spawning escapement were evaluated using passive-integrated transponder (PIT) tags between 2013-2018. The recipient population stray rates ranged between 0.02-87.35% and increased with decreasing spatial scale. Recipient stray rates of all taxa at the basin scale were <3%, and summer Chinook and fall Chinook salmon were <0.5%. Stray rates in subbasins for all taxa ranged between 0.07-33.04%; spring and summer Chinook Salmon exceeded 5% in some 10 year periods in the Entiat and Methow subbasins, but stray rates for all Chinook Salmon were <5% in the Wenatchee, Okanogan, and Hanford Reach for all periods. All steelhead stray rates exceeded 5% except for those in the Wenatchee subbasin. Stray rates of spring Chinook Salmon in tributaries (the only taxa that met the tributary criteria) ranged between 0.61%-87.35% and only the Chiwawa, Icicle, and Twisp rivers were consistently below 10%; the Chiwawa River was consistently below 5%. In cases where recipient stray management targets were exceeded, some were the result of single hatchery contributions, but others were the result of cumulative contributions from multiple hatcheries. Options to achieve recipient stray management targets include reducing donor stray rates, reducing hatchery program size, removing hatchery-origin adults prior to spawning in the natural environment, and increasing the natural-origin population. It is likely that balancing trade-offs among hatchery program size and recipient population stray rate will be necessary in order to achieve management targets in some locations.

Introduction

Hatcheries are frequently used to increase abundance of Chinook Salmon *Oncorhynchus tshawytscha* and steelhead *O. mykiss* for harvest and conservation, but because of the large numbers of fish produced and the manner in which they are produced, unintended consequences can occur that pose genetic risks to natural populations that are not the target of the production (Keefer and Caudill 2014; Bett et al. 2017; Pearsons and O'Connor 2021). Hatchery-origin Chinook Salmon stray at higher rates than natural-origin fish at some spatial scales, and they are often more abundant than natural-origin fish on the spawning grounds (Keefer and Caudill 2014; Pearsons and O'Connor 2021). In addition, migration and spawning habitats have been altered by humans, which can increase the magnitude of straying (Cram et al. 2012; Ford et al. 2015; Bett et al. 2017). These factors can result in large numbers of stray fish spawning with fish that were not the intended target of hatchery augmentation. Furthermore, many naturally spawning populations of salmon and steelhead have declined from historic levels and therefore hatchery-origin strays can make up large proportions of the spawning population even when the stray rate is low (Bett et al. 2017; Sturrock et al. 2019).

One of the main concerns with straying of hatchery-origin Chinook Salmon and steelhead is the reduction of local adaptation that occurs through inter-breeding of hatchery- and natural-origin fish in the natural environment (Keefer and Caudill 2014; Bett et al. 2017). This could occur through mechanisms such as outbreeding depression and domestication (Busack and Currens 1995). Local adaptation can be reduced if sufficient numbers of hatchery-origin fish stray into non-target populations and if they reproduce successfully. This can further result in a reduction in genetic diversity between populations, which can increase extinction risk. Alternatively, straying can result in demographic or genetic rescue in cases of high disturbance or low population size (Bett et al. 2017; Pearsons and O'Connor 2020).

The best stray metric to assess the risk of straying to genetic diversity is referred to as recipient population stray rate (Keefer and Caudill 2014). Recipient population stray rate is quantified as the proportion of the total spawning population that is composed of non-target hatchery-origin strays (Bett et al. 2017). It is distinguished from supplementation programs that intentionally produce fish to contribute to the natural production of a target population (Mobrand et al. 2005; Paquet et al. 2011; Fast et al. 2015). Recipient population stray rates are underrepresented in the literature compared to donor rates, the stray rates of contributing hatcheries, despite the higher management importance of recipient stray rates (Keefer and Caudill 2014; Bett et al. 2017). In addition, relatively few studies have evaluated recipient population straying from multiple hatcheries, species, and spatial scales (Bett and Hinch 2015).

Fisheries managers set recipient stray rate targets for hatchery programs in efforts to maintain local adaptation and trigger management actions to control excessively high stray rates. These targets were informed by genetic modelling of how much gene flow could occur without losing important genetic diversity of recipient populations (Craig Busack, NOAA Fisheries, personal communication). Targets generally range between 2 and 10%, and can vary depending upon management objectives and risks to local adaptation (Ford 2002; Mobrand et al. 2005; Paquet et al. 2011; Brenner et al. 2012; Hillman et al. 2018). Strays from distant locations are generally regarded as higher risk than those from adjacent locations because they are hypothesized to be less adapted to local conditions than nearby populations (Fraser et al. 2011). For example, the recipient stray management targets for the upper Columbia Basin are: 1)

hatchery-origin strays make up less than 5% of the spawning escapement within non-target recipient populations, and 2) hatchery-origin strays from a spawning aggregate within a population make up less than 10% of the non-target spawning aggregate within the same population (Hillman et al. 2019).

Recent work has estimated donor population stray rates for both natural- and hatchery-origin Salmon and steelhead in the upper Columbia Basin (Pearsons and O'Connor 2020, Pearsons and O'Connor 2021). This work demonstrated that stray rates of hatchery- and natural-origin fish increased with decreasing spatial scale but the disparity was more pronounced by hatchery-origin fish, particularly at the tributary scale. Furthermore, the magnitude of hatchery-origin fish straying posed risks to the genetic diversity of the populations and warranted estimation of recipient population straying. This paper fills that gap for the upper Columbia subregion. More specifically we: 1) assess the magnitude and composition of recipient population stray rates of spring, summer, and fall Chinook Salmon and summer steelhead spawning populations at three spatial scales, 2) assess (i.e., basin, subbasin and tributary) factors that influence recipient population stray rates, and 3) discuss trade-offs of achieving recipient stray management targets.

Methods

Study Area

This study was conducted in the Columbia River, USA, and most of the work was conducted in the upper Columbia Basin upstream of the confluence with the Snake River and downstream of Chief Joseph Dam, with fish from hatchery programs in the Wenatchee, Entiat, Methow, and Okanogan subbasins and the upper Columbia River (Figure 1). The upper Columbia River Basin has an abundance of hatchery facilities as a result of mitigation for the construction and operation of hydropower dams (Figure 1). These hatcheries produce fall, summer, or spring Chinook Salmon, Coho Salmon *O. kisutch*, Sockeye Salmon *O. nerka*, and steelhead for harvest, conservation, or a combination of both; but Chinook Salmon and steelhead are the only species considered for this assessment. Some of the hatchery programs incubate, rear, and release fish from a single hatchery location, whereas other programs transport parr or smolts to acclimation sites for subsequent release. The study area and biological background was previously described by Pearsons and O'Connor (2020, 2021) and is also briefly described below.

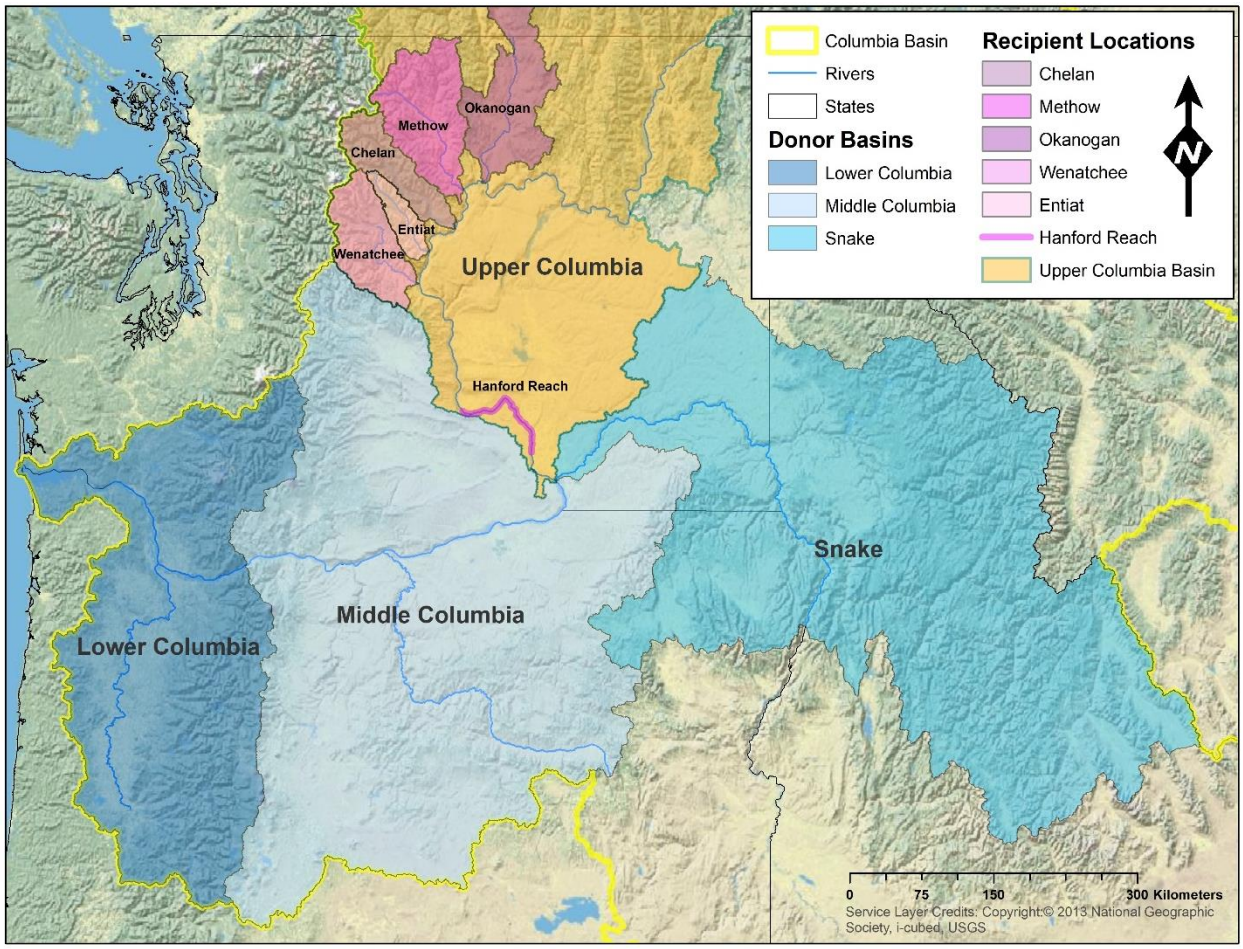


Figure 1. Map of the study area of the upper Columbia Basin and areas outside of the upper Columbia Basin that contributed strays to recipient populations within the upper Columbia Basin.

Fall Chinook Salmon spawn in the Hanford Reach, the only free-flowing reach of the Columbia River between Grand Coulee and Bonneville dams These spawners comprise one of the largest Chinook Salmon populations in the United States, and contribute large numbers of fish to harvest in the Pacific Ocean and Columbia River, making this population economically very important (Harnish et al. 2014; Langshaw et al. 2017; Pearsons et al. 2020). Summer Chinook Salmon spawn primarily in the mainstems of four subbasins of the upper Columbia River (e.g., Wenatchee, Entiat, Methow, and Okanogan) and support considerable fisheries in the Pacific Ocean and Columbia River. The naturally produced juveniles of summer and fall run Chinook Salmon generally migrate to the sea as sub-yearlings. Spring Chinook Salmon spawn in tributaries to mainstem subbasins and in upper portions of mainstem subbasins (Williamson et al. 2010; Murdoch et al. 2010; Ford et al. 2015a). Upper Columbia River spring Chinook Salmon are listed under the Endangered Species Act (ESA) as endangered (McClure et al. 2008). The naturally produced juveniles of spring Chinook Salmon migrate to the sea as yearlings. Summer steelhead spawn throughout upper Columbia subbasins and are ESA listed as threatened (Ford et al. 2016). Naturally produced juvenile steelhead from the upper Columbia migrate to

the sea at ages 1-7 years, but most migrate at ages 1- 3 (Peven et al. 1994). All races of Chinook Salmon and steelhead in the upper Columbia have a long history of interactions with hatchery programs and hatchery- and natural-origin fish overlap in much of their spawning distributions (e.g., Williamson et al 2010; Pearsons et al. 2012; Ford et al. 2015a; Ford et al. 2016; Johnson et al. 2018).

Hatchery description and tagging

Hatchery-origin fish were produced in a variety of hatcheries throughout the Upper Columbia River Basin; see Pearsons and O'Connor, (2021) for information about hatchery programs and release and recovery locations. Most hatchery-origin Chinook Salmon were marked and tagged to facilitate identification to identify their hatchery of origin when recovered as carcasses on the spawning grounds. Fish were tagged with coded-wire tags (CWTs) as juveniles. Tags were generally placed in the snout and each CWT was specific to a hatchery. In a few instances, CWTs or blank wire tags were placed in the caudal peduncle near the adipose fin. Fish were tagged months before release and then released during the spring as subyearlings or yearlings. Steelhead were tagged with PIT tags to identify the hatchery of origin because of the inability to collect carcasses on the spawning grounds (Pearsons and O'Connor 2021). Fish migrated to the ocean and then returned to spawn 1 to 5 years later.

Spawning escapement and composition

A variety of field methods were used to estimate the two derived metrics needed for calculating recipient population stray rate; spawning escapement, and origin composition of spawners. Spawning escapement of spring and summer Chinook Salmon was estimated by multiplying the number of redds by the number of fish per redd (Hillman et al. 2019). The number of fish per redd was estimated at dams or hatcheries by dividing the total abundance by the number of males (Murdoch et al. 2010) and assuming one female per redd (Murdoch et al. 2008). Spawning escapement of fall Chinook Salmon was estimated by counting the number of fall Chinook at McNary Dam and subtracting the number of fish counted at Ice Harbor dam as well as harvest and hatchery returns (Basin estimate; Richards and Pearsons 2019). The escapement of fish to the Hanford Reach of the Columbia River also involved subtracting counts of fall Chinook from the Yakima subbasin and Priest Rapids Dam. Spawning escapement of steelhead was estimated by a mark-recapture method (Hillman et al. 2019).

About 15% of returning adult steelhead passing Priest Rapids Dam were PIT tagged and subsequently detected or "recaptured" at upstream antennas located in subbasins and tributaries throughout the upper Columbia Basin. A mathematical model was used to estimate escapement to subbasins based upon the number of steelhead PIT tagged at Priest Rapids Dam and the detection of fish at PIT tag antenna arrays within each subbasin (Hillman et al. 2019). We subtracted the number of steelhead harvested, collected for broodstock, or removed for other management purposes in each subbasin from the modelled subbasin escapement to estimate spawning escapement for each subbasin. Spawning escapement estimates for all tributaries could not be generated using available data and procedures.

The composition of spawners on the spawning grounds was estimated using CWTs (Chinook Salmon) and PIT tags (steelhead). Coded-wire tags were collected from Chinook Salmon carcasses. The CWTs were expanded based upon hatchery-specific marking rate (e.g., proportion of the hatchery production that was tagged) and the sampling rate. Hatchery-origin

fish that were not part of the target spawning population were classified as strays. The abundance of the natural-origin population was estimated by subtracting the number of target and non-target hatchery-origin fish by the total escapement.

Field Methods

Spawning-ground surveys were conducted annually throughout the upper Columbia Basin to estimate the number of Chinook Salmon redds and the composition of spawners (Murdoch et al. 2009 a, b; 2010; Hillman et al. 2019; Richards and Pearsons 2019; Snow et al. 2019). Surveys were conducted by foot, raft, and motorized boat throughout the entire spawning distribution and season. In general, spring run Chinook Salmon surveys were conducted by foot, summer Chinook Salmon by raft, and fall Chinook Salmon by motorized boat. Carcass surveys were conducted weekly and carcasses were measured, sexed, evaluated for marks and tags, scales removed for age determination, and presence of the adipose fin was noted. Heads were removed from adipose fin clipped fish and CWTs were extracted and decoded in a laboratory or office to determine hatchery release information. Females were cut open to determine the proportion of eggs retained by the females. The sampling goal for carcasses was approximately 20% of the spawning population.

Spring Chinook Salmon redd and carcass surveys were conducted during August through September in all of the spawning areas of the Wenatchee, Entiat, and Methow subbasins (Figure 1). Summer Chinook redd and carcass surveys were conducted from September through November throughout the entire spawning distributions of the Wenatchee, Entiat, Methow, Chelan and Okanogan rivers. Fall Chinook Salmon carcass surveys were conducted from October through the beginning of December in the Hanford Reach of the Columbia River.

Analysis

The recipient population stray rate for each spawning population was estimated by dividing the annual number of strays by the total annual spawning escapement regardless of fish origin (Bett et al. 2017). This was done for each non-target hatchery program that contributed strays to the recipient population. All non-target hatchery contributions were then summed annually to derive a total recipient population stray rate. Donor strays originated from a large number of hatcheries, so some were grouped with others based on similar regions of the Columbia River basin to facilitate a clear presentation of results. Stray rates were assessed at the tributary, subbasin, and basin levels for spring Chinook Salmon and at the subbasin and basin levels for summer Chinook, fall Chinook, and steelhead. Mean stray rates of Chinook Salmon were calculated for 1999-2018, 2009-2018, and 2014-2018. Mean stray rates of steelhead were 2013-2018 and 2014-2018 because reliable PIT tag analyses were not available prior to 2013. These periods were selected to correspond to modifications and maturity of hatchery programs so that temporal changes could be assessed. In addition, all periods were inclusive of latter years to reveal the potential of long-term influence. Mean stray rates for each period were compared to the management targets of 5% and 10%. The causes of variation in recipient stray rates for each run type were evaluated by examining the number of hatcheries contributing strays, recipient population size, proximity to non-target hatcheries, and spatial scale.

Results

The recipient population stray rates for all time periods ranged between 0.02-87.35% and increased with decreasing spatial scale (Tables 1-3). Recipient stray rates of all taxa at the basin scale were <3% and summer Chinook and fall Chinook salmon were <0.5% (Table 1). Recipient stray rates in subbasins ranged between 0.07-33.04% and spring and summer Chinook Salmon exceeded 5% in some periods in the Entiat and Methow subbasins, but stray rates for all Chinook were <5% in the Wenatchee, Okanogan, and Hanford Reach for all periods (Table 2). All steelhead recipient stray rates exceeded 5% for all periods except for those in the Wenatchee subbasin (Table 2). Recipient stray rates of spring Chinook Salmon in tributaries (the only taxa that met the tributary criteria) ranged between 0.61%-87.35% and only the Icicle, Chiwawa, and Twisp rivers were consistently below 10%, and only the Chiwawa River was consistently below 5% (Table 3).

Table 1. Mean percent strays of non-target spring Chinook Salmon, summer Chinook Salmon, fall Chinook Salmon and steelhead hatchery-origin recruits to the Upper Columbia River basin for the periods 1999-2018, 2009-2018, and 2014-2018. Steelhead includes the time period from 2013-2018 and 2014-2018. The percent natural and hatchery-origin fish is a mean calculated over multiple years for each time period.

				Target		Non-target strays	
	Upper Columbia Basin	Natural-origin recruits		Hatchery-origin recruits		Hatchery-origin recruits	
Spawn year	escapement	Number	Percent	Number	Percent	Number	Percent
			Spring Chinook				
Mean (1999-2018)	3,929	1,915	45.07	1,959	53.55	54	1.38
Mean (2009-2018)	3,735	1,440	40.92	2,236	57.79	59	1.29
Mean (2014-2018)	2,473	1,081	45.92	1,367	53.25	25	0.83
			Summer Chinook				
Mean (1999-2018)	20,240	15,292	75.66	4,944	24.32	4	0.02
Mean (2009-2018)	20,353	15,698	77.35	4,647	22.62	8	0.03
Mean (2014-2018)	19,594	16,569	84.21	3,020	15.77	5	0.02
			Fall Chinook				
Mean (1999-2018)	131,807	122,587	83.49	8,643	6.58	578	0.47
Mean (2009-2018)	172,991	161,663	94.01	10,644	5.62	685	0.37
Mean (2014-2018)	192,989	181,155	93.20	11,100	6.39	734	0.41
			Steelhead				
Mean (2013-2018)	4,043	2,024	48.82	1,906	48.48	113	2.70
Mean (2014-2018)	4,009	2,073	50.14	1,840	47.57	96	2.30

Table 2. Mean percent strays of non-target spring Chinook Salmon, summer Chinook Salmon, fall Chinook Salmon and steelhead hatchery-origin recruits to the Hanford Reach of the Columbia River, Wenatchee, Entiat, Methow, Chelan and Okanogan river subbasins of the Upper Columbia River basin for the periods 1999-2018, 2009-2018, and 2014-2018. Steelhead includes the time period from 2013-2018 and 2014-2018. The percent natural and hatchery-origin fish is a mean calculated over multiple years for each time period.

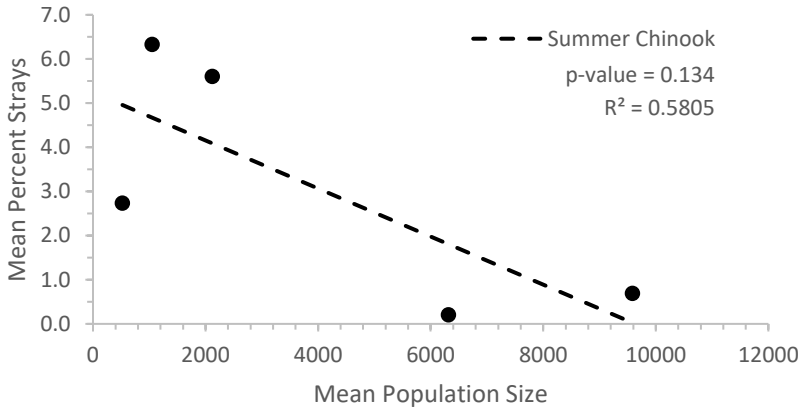
				Target		Non-target strays	
	Subbasin	Natural-origin recruits		Hatchery-origin		Hatchery-origin	
Spawn year	escapement	Number	Percent	Number	Percent	Number	Percent
Wenatchee Spring Chinook Salmon							
Mean (1999-2018)	1,740	644	37.83	1,084	61.53	12	0.65
Mean (2009-2018)	1,876	747	39.28	1,123	60.45	6	0.28
Mean (2014-2018)	1,198	441	38.35	756	61.58	1	0.07
Entiat Spring Chinook Salmon							
Mean (1999-2018)	292	228	79.44	14	4.91	50	15.65
Mean (2009-2018)	320	244	80.75	8	2.09	68	17.16
Mean (2014-2018)	260	239	92.62	0	0.00	21	7.38
Methow Spring Chinook Salmon							
Mean (1999-2018)	1,897	1,047	43.28	798	52.71	52	4.01
Mean (2009-2018)	1,539	452	35.31	1,017	59.34	70	5.35
Mean (2014-2018)	1,015	405	46.23	570	47.13	40	6.63
Wenatchee Summer Chinook Salmon							
Mean (1999-2018)	8,695	7,427	84.92	1,234	14.69	34	0.40
Mean (2009-2018)	7,597	6,501	86.28	1,078	13.47	18	0.25
Mean (2014-2018)	6,315	5,804	91.02	500	8.77	10	0.20
Entiat Summer Chinook Salmon							
Mean (1999-2018)	391	330	83.91	19	3.64	43	12.45
Mean (2009-2018)	447	367	78.49	37	7.28	43	14.24
Mean (2014-2018)	524	439	83.33	72	13.94	12	2.73
Chelan Summer Chinook Salmon							
Mean (1999-2018)	796	420	53.49	160	13.47	216	33.04
Mean (2009-2018)	1,128	637	58.67	319	26.94	172	14.39
Mean (2014-2018)	1,053	624	58.26	365	35.40	64	6.33
Methow Summer Chinook Salmon							
Mean (1999-2018)	2,430	1,625	67.89	462	19.25	343	12.87
Mean (2009-2018)	2,429	1,636	67.77	558	23.00	235	9.23
Mean (2014-2018)	2,119	1,612	74.36	374	20.04	132	5.60
Okanogan Summer Chinook Salmon							
Mean (1999-2018)	7,929	5,479	69.42	2,260	28.15	190	2.43
Mean (2009-2018)	8,752	6,529	74.55	2,112	24.11	111	1.34
Mean (2014-2018)	9,585	8,050	85.58	1,457	13.73	77	0.69
Hanford Reach Fall Chinook Salmon							
Mean (1999-2018)	85,180	76,806	90.47	7,820	8.83	554	0.70
Mean (2009-2018)	111,820	101,049	91.23	10,129	8.25	643	0.53
Mean (2014-2018)	137,369	126,614	91.76	10,098	7.76	657	0.48
Wenatchee Steelhead							
Mean (2013-2018)	1,323	770	59.54	541	38.10	13	2.36
Mean (2014-2018)	1,176	736	62.31	425	34.86	15	2.83
Entiat Steelhead							
Mean (2013-2018)	395	333	80.30	0	0.00	63	19.70
Mean (2014-2018)	400	350	83.21	0	0.00	50	16.79

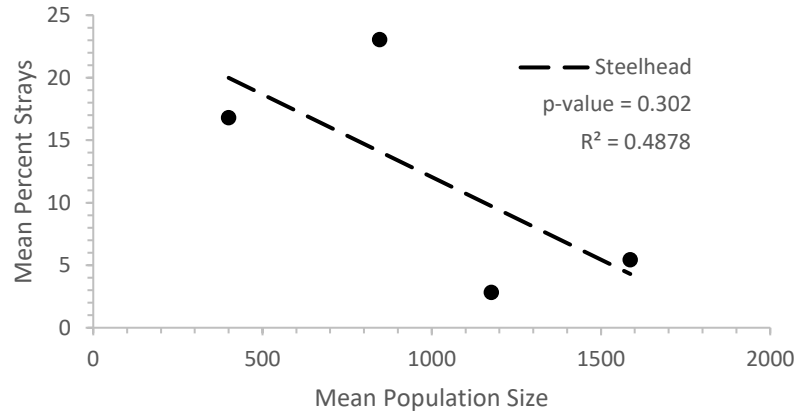
			Methow Steelhead				
Mean (2013-2018)	1,574	674	42.89	778	49.42	123	7.69
Mean (2014-2018)	1,587	713	45.15	784	49.40	90	5.45
			Okanogan Steelhead				
Mean (2013-2018)	752	248	32.69	328	43.25	175	24.06
Mean (2014-2018)	846	274	30.66	378	46.29	194	23.04

Table 3. Mean percent strays of non-target spring Chinook Salmon hatchery-origin recruits to tributaries of the Wenatchee, Entiat, and Methow river subbasins of the Upper Columbia River basin for the periods 1999-2018, 2009-2018, and 2014-2018. The percent natural and hatchery-origin fish is a mean calculated over multiple years for each time period.

				Target		Non-target strays	
		Natural-origin recruits		Hatchery-origin recruits		Hatchery-origin recruits	
Spawn year	Escapement	Number	Percent	Number	Percent	Number	Percent
			Chiwawa River Spring Chinook Salmon				
Mean (1999-2018)	922	347	40.51	560	57.25	16	2.24
Mean (2009-2018)	1,087	418	37.72	663	61.66	6	0.61
Mean (2014-2018)	708	248	36.32	456	63.03	3	0.65
			Nason Creek Spring Chinook Salmon				
Mean (1999-2018)	371	160	46.85	7	4.35	204	48.80
Mean (2009-2018)	358	145	40.42	13	8.70	200	50.88
Mean (2014-2018)	166	62	40.75	26	17.40	78	41.85
			White River Spring Chinook Salmon				
Mean (1999-2018)	82	59	76.98	2	1.97	21	21.05
Mean (2009-2018)	90	68	75.70	4	3.94	18	20.37
Mean (2014-2018)	64	50	74.80	7	7.88	7	17.32
			Little Wenatchee River Spring Chinook Salmon				
Mean (1999-2018)	65	40	67.61	0	0.00	25	32.40
Mean (2009-2018)	68	44	67.66	0	0.00	24	32.34
Mean (2014-2018)	35	26	73.33	0	0.00	9	26.67
			Upper Wenatchee River Spring Chinook Salmon				
Mean (1999-2018)	99	18	24.56	0	0.00	81	75.77
Mean (2009-2018)	55	11	16.10	0	0.00	45	84.57
Mean (2014-2018)	46	9	13.99	0	0.00	38	87.35
			Icicle Creek Spring Chinook Salmon				
Mean (1999-2018)	155	20	14.38	119	76.46	15	9.16
Mean (2009-2018)	202	37	14.14	143	77.21	23	8.65
Mean (2014-2018)	172	13	5.22	153	92.82	6	1.95
			Peshastin Creek Spring Chinook Salmon				
Mean (1999-2018)	46	29	67.47	0	0.00	17	32.53
Mean (2009-2018)	16	15	72.92	0	0.00	2	27.08
Mean (2014-2018)	6	6	75.00	0	0.00	1	25.00
			Entiat River Spring Chinook Salmon				
Mean (1999-2018)	292	229	79.69	14	4.91	50	15.40
Mean (2009-2018)	320	244	80.75	8	2.09	68	17.16
Mean (2014-2018)	260	239	92.62	0	0.00	21	7.38
			Methow River Spring Chinook Salmon				
Mean (1999-2018)	1,219	652	40.51	387	39.96	180	19.53
Mean (2009-2018)	982	209	28.89	563	50.74	210	20.38
Mean (2014-2018)	655	201	40.32	375	46.55	78	13.13
			Chewuch River Spring Chinook Salmon				
Mean (1999-2018)	479	298	54.65	116	28.41	65	16.95
Mean (2009-2018)	394	160	44.92	143	33.62	91	21.46
Mean (2014-2018)	231	128	56.49	53	22.14	50	21.37
			Twisp River Spring Chinook Salmon				
Mean (1999-2018)	199	132	59.52	56	34.35	11	6.13
Mean (2009-2018)	163	83	50.89	63	39.26	17	9.86
Mean (2014-2018)	130	75	57.49	46	34.74	9	7.77

Recipient stray rates for each taxa were negatively associated with the abundance of spawners (Figure 2). That is, stray rates increased as total spawner abundance decreased. For example, large populations such as summer Chinook Salmon in the Okanogan and Wenatchee and fall Chinook Salmon in the Hanford Reach had stray rates <5%. The Chiwawa River was the only spring Chinook population with stray rates <5% and is the largest of the spring Chinook spawning aggregates (Table 3). The two largest steelhead populations were the only steelhead populations with stray rates <10% (Table 2). In contrast, small populations such as Entiat spring and Summer Chinook, and upper Wenatchee River, Little Wenatchee River, and White River spring Chinook Salmon had high stray rates (Tables 2-3). The highest stray rate was for spring Chinook in the upper Wenatchee River, in which almost all the spawners were stray hatchery fish (Table 3).


Summer Chinook
p-value = 0.134
R² = 0.5805
Mean Percent Strays
Mean Population Size
0.0
1.0
2.0
3.0
4.0
5.0
6.0
7.0
0
2000
4000
6000
8000
10000
12000


Steelhead
p-value = 0.302
R² = 0.4878
Mean Percent Strays
Mean Population Size
0
5
10
15
20
25
0
500
1000
1500
2000

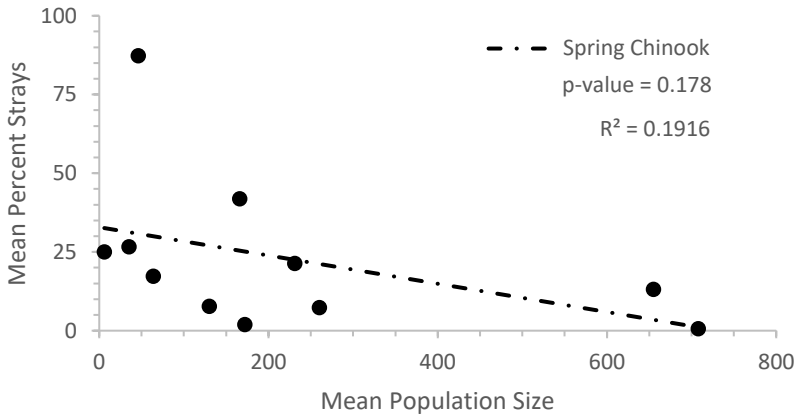

Spring Chinook
p-value = 0.178
R² = 0.1916
Mean Percent Strays
Mean Population Size
0
25
50
75
100
0
200
400
600
800

Figure 2. The relationship between recipient population size and mean stray rate for summer Chinook Salmon, steelhead, and spring Chinook Salmon.

Proximity to non-target hatcheries or the location of a non-target hatchery relative to the migration sequence of an adult returning to a target location seemed also to influence recipient stray rates. For example, although the spring Chinook spawning aggregate in Nason Creek had a fairly large population size, it had high recipient stray rates from the nearby Chiwawa Acclimation Facility. Similarly, the Chewuch River confluence with the Methow River is between and within one kilometer of two hatcheries that release spring Chinook to the Methow River, one of which also releases spring Chinook to the Chewuch River, and stray rates of spring Chinook Salmon to the Methow and Chewuch rivers were high even though population sizes were among the highest evaluated (Table 3).

The contribution of strays from multiple hatcheries increased the cumulative stray rate in many populations, but in some instances a single hatchery was the primary contributor to stray rate (Figures 3-8). In some cases, an individual hatchery would not result in exceedance of recipient stray targets, but because multiple hatcheries contributed strays, a target was exceeded. At the Basin scale between 2014-2018, all of the strays originated from the Snake River Basin and Middle Columbia River subbasins (Figure 3). At the subbasin scale between 2014-2018, no single spring, summer, or fall Chinook Salmon hatchery contributed >5% of the stray rate, but when the contributions of all hatcheries were combined the total stray rate exceeded 5% (e.g., Entiat and Methow spring Chinook Salmon, and Chelan and Methow summer Chinook Salmon), it was the result of multiple hatchery contributions (Figure 4-5). In contrast, steelhead recipient stray rates in the Entiat and Okanogan had multiple hatcheries exceeding contributions of 5% stray rate (Figure 6).

Only spring Chinook Salmon met the criteria for evaluating recipient strays at the tributary scale. All of the recipient strays in spawning aggregates of the Wenatchee subbasin originated from within the Wenatchee subbasin. Almost every spawning aggregate in tributaries of the Wenatchee subbasin exceeded 10% because of strays from the Chiwawa River (Figure 7). In Entiat and Methow river spawning aggregates, no single hatchery exceeded the 5% or 10% target criteria, but when all hatcheries were combined, the targets were exceeded (Figure 8).

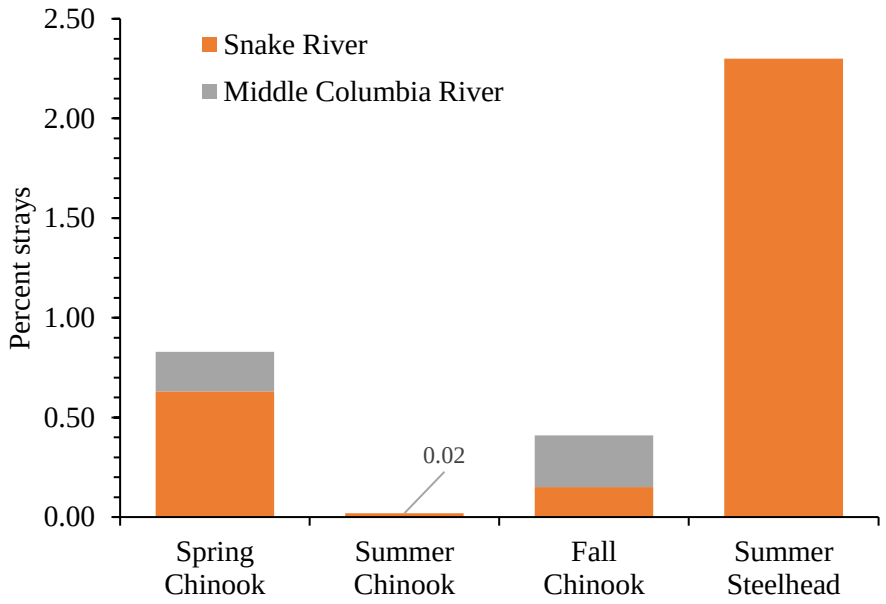


Figure 3. Mean percent hatchery stray Chinook Salmon and steelhead observed in the Upper Columbia River Basin from other regions of the Columbia River Basin from 2014 to 2018.

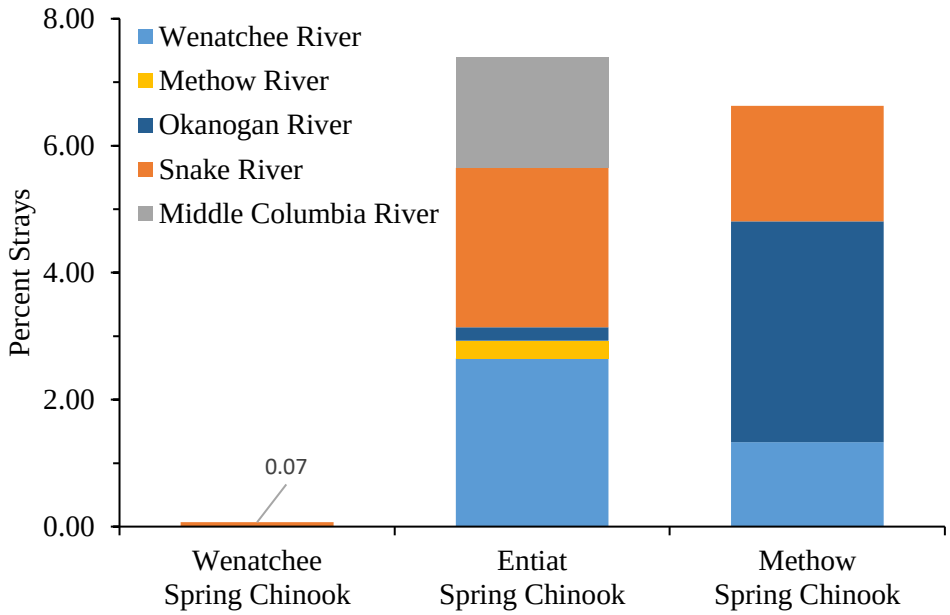


Figure 4. Mean percent hatchery stray spring Chinook Salmon observed in the Upper Columbia River subbasins from other regions of the Columbia River Basin from 2014 to 2018. The management target is <5%.

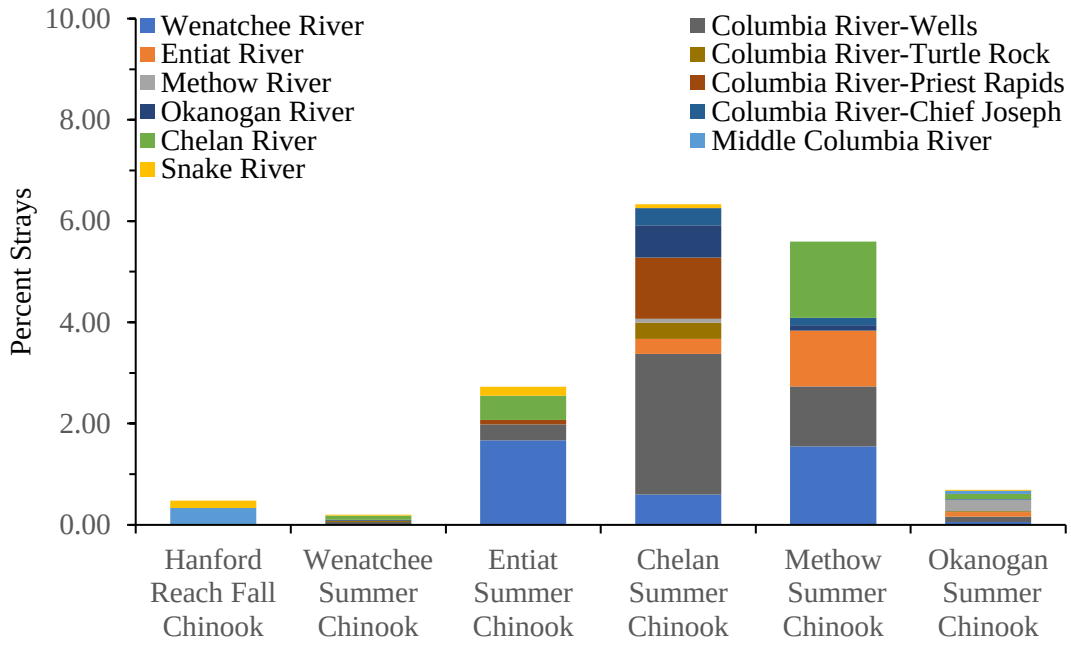


Figure 5. Mean percent hatchery stray summer and fall Chinook Salmon observed in subbasins of the Upper Columbia River basin from 2014 to 2018. The management target is <5%.

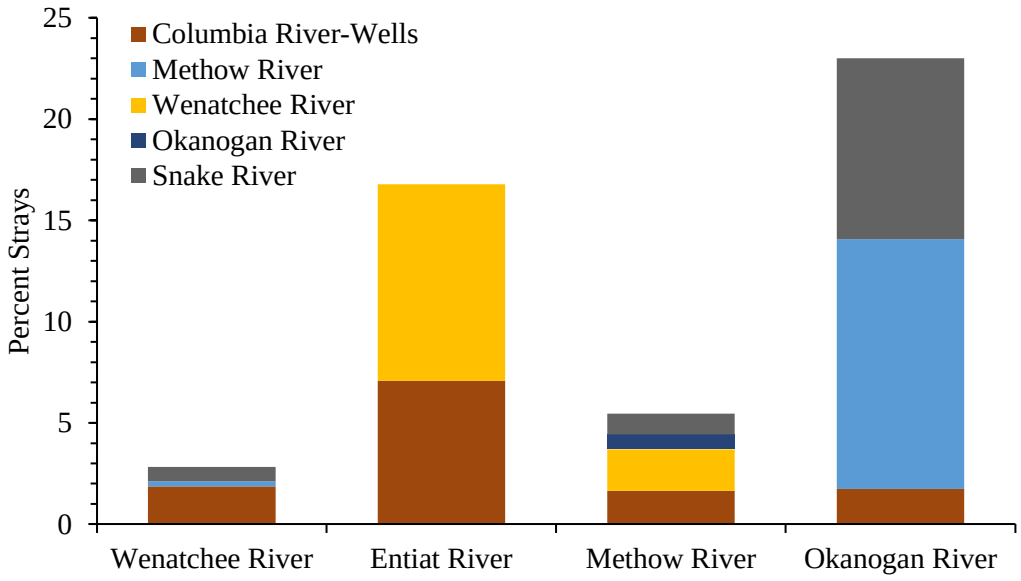


Figure 6. Mean percent hatchery stray steelhead observed in subbasins of the Upper Columbia River basin from 2014 to 2018. The management target is <5%.

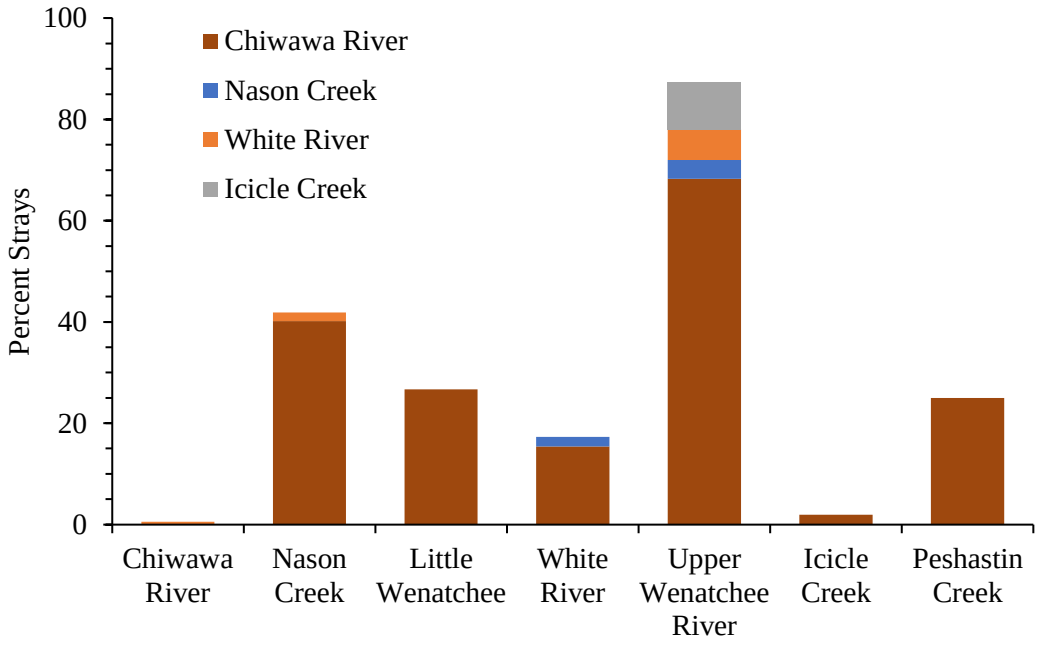


Figure 7. Mean percent hatchery stray spring Chinook Salmon observed in tributaries of the Wenatchee subbasin from 2014 to 2018. The management target is <10%.

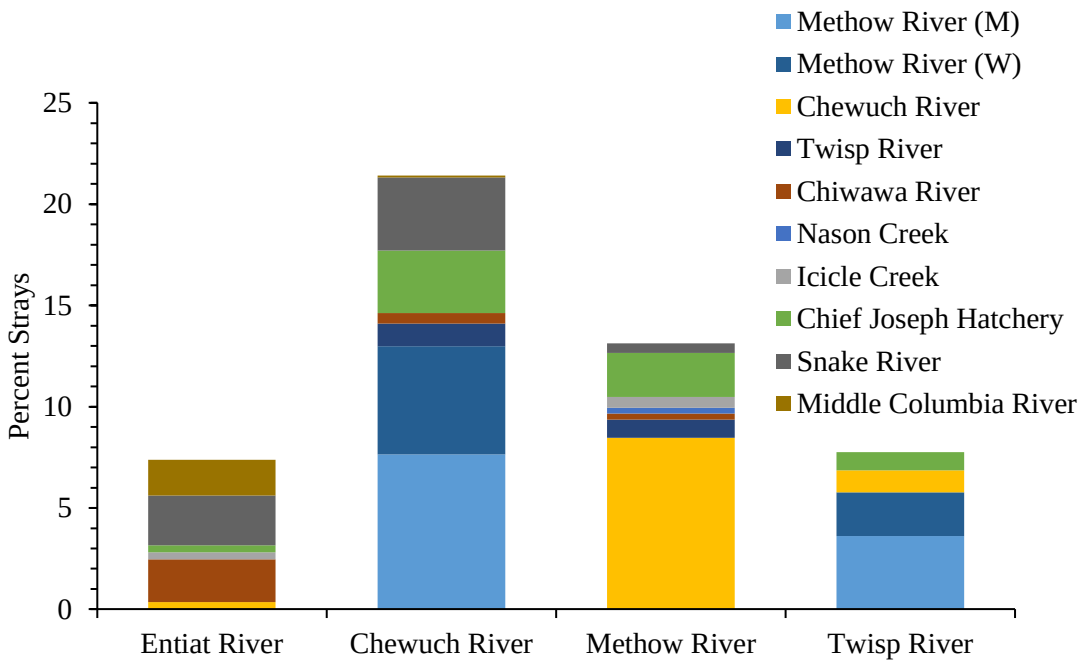


Figure 8. Mean percent hatchery stray spring Chinook Salmon observed in the Entiat River and Methow River and tributaries (Chewuch and Twisp rivers) from 2014 to 2018. The management target is <10% except for the Entiat River which is <5%.

Spatial variation in mean recipient stray rates was substantially higher than temporal variation in mean recipient stray rates although annual variation in both could be quite high for some taxa and locations. Spatial variation ranged from 0.02-87.35%, a 4,368-fold difference, across all taxa and maximum temporal variation ranged from 0.07-0.65 within a taxa a 9.29-fold difference (Wenatchee spring Chinook Salmon; Table 2). Recipient stray rates were relatively stable for most populations particularly at large spatial scales and when changes occurred most of them decreased between 1999 and 2018 (Tables 1-3). There were some notable decreases in recipient stray rates between 1999 and 2018 (e.g., Entiat and Chelan Summer Chinook, Icicle Creek spring Chinook) and these were likely the result of reductions in hatchery program size, tributary acclimation, other program modifications, and possibly reductions in donor stray rates (Tables 2-3).

Discussion

It is clear that recipient population stray rates exceeded management targets (e.g., >5-10%) in: 1) many upper Columbia Basin populations of spring Chinook Salmon and steelhead and 2) some summer Chinook Salmon at subbasin and tributary scales, but fall Chinook was lower than management targets. In some cases, this exceedance is the result of many different

hatcheries contributing spawners to a non-target population, while in others it is the result of a single hatchery. Most management targets are structured around the stray contribution of single hatcheries (e.g., Hillman et al. 2018), but cumulative influences of all hatcheries are more biologically relevant because they represent the total spawning population. The complexity of managing strays from multiple hatcheries, some of which are in different states and operated by different organizations with different objectives, is a difficult socio-political challenge. For example, should strays from harvest augmentation hatcheries be considered similarly as those produced to aid in species recovery or should greater leeway be given to hatcheries used to recover species? Should stray rates be managed based upon donor stray rates (e.g., % of a hatchery population that strays) or the total number of strays contributed to a recipient population?

Recipient population straying has the potential to reduce between-population genetic diversity at the levels that we observed in this study (e.g., >5-10%). However, this assumes that stray fish contribute towards natural production. Relative reproductive success studies indicate that hatchery-origin fish generally produce fewer offspring than natural-origin counter parts (Williamson et al 2010. Ford et al. 2016). Genetic risks of straying are increased if strays successfully spawn and nullified if they do not spawn. This can be evaluated by examining whether female strays void their eggs, an index of spawning success. Stray fish that retain their eggs and die, pose low genetic risks to recipient populations. Upper Columbia Chinook Salmon have very high rates of egg voidance often exceeding 95%, suggesting that they successfully spawned in the areas where carcasses were collected (Murdoch et al. 2009; Richards and Pearsons 2019). An early evaluation of the hatchery effects on genetic diversity in the upper Columbia Basin did not reveal decreases in genetic diversity (Hillman et al. 2019). A more current genetic evaluation that incorporates the time periods of this study is currently in progress.

Recipient population stray rates can be managed in three primary ways (Bett et al. 2017). The first is to manage donor population stray rate through improved fish-culture approaches. This might include techniques to improve imprinting such as raising fish on natal target waters to the greatest extent practicable during the time of imprinting (Dittman et al. 2015, Pearsons and O'Connor 2021). However, even low donor-stray rates can result in high recipient population stray rates if the hatchery program is large and the recipient population is small. Furthermore, donor population stray rates can be influenced by factors other than fish culture such as migration and spawning habitat quality (Cram et al. 2012; Bond et al. 2017; Pearsons and O'Connor 2021), so improvements in fish culture alone may not result in desired management outcomes. The second approach is to manage the number of adults that could potentially stray by reducing hatchery program size, removal at weirs, and removals through harvest. The adult removal approach may not be effective if the intent is to supplement a population because available control measures are often downstream of the target population and it is unclear which fish should be removed and which fish should be allowed to spawn. This may be the case for most listed species. The third approach is to increase natural escapement because escapement is an important factor influencing stray rates. Most large populations in this study met targets and small populations typically did not. Escapements are influenced by many factors beyond the specific hatchery; for example, harvest and natural production as influenced by factors such as ocean conditions, and habitat conditions. In short, multiple factors influence recipient population stray rates, and changes in hatchery practices alone may not achieve dual objectives of increasing abundance and keeping recipient stray rates below target levels.

Trade-offs will have to be made in some cases where hatchery improvements such as improvements in imprinting are limited or unfeasible. For example, acclimation sites are used to cause fish to return to particular locations; however fish that are transported from a downstream hatchery and acclimated at remote sites may stray at higher rates (Pearsons and O'Connor 2021) than those that are not transported. In addition, transportation is likely necessary to get fish to return to the target location for supplementation programs. The value of returning fish to a target location will have to be weighed against the cost of straying. In some cases, the supplementation value will be lower than the cost of straying necessitating a reduction in hatchery-program size to achieve management optima.

Some straying of hatchery-origin fish may occur between spawning aggregates but because the tributaries were part of the same genetic management zone, they were not considered a genetic concern. For example, straying of spring Chinook Salmon occurred between the Methow and Chewuch River, but because they were part of the same genetic management zone, the genetic strays were acceptable to managers from a genetic perspective. However, there was concern that these strays did not return to the target location and therefore were a demographic shortfall to the target population.

In some cases, high recipient stray rates may be keeping a population from extinction. For example, the Nason Creek and White River spring Chinook Salmon spawning aggregates regularly experience recipient stray rates of 30-50%. The upper Wenatchee River is likely a sink population because it has regularly comprised over 85% strays and none of the progeny of naturally produced fish that spawned there returned to spawn there (Ford et al. 2015). It is possible that some genetic diversity may have been lost from this high gene flow; however, it is also possible that these contributions have maintained some level of genetic differentiation as opposed to losing the population altogether because of unsustainably low survival rates.

In summary, recipient population stray rates of Salmon and steelhead varied dramatically in the upper Columbia Basin and some exceeded management targets at subbasin and tributary scales. In some cases, this was the result of many different hatcheries contributing spawners to a non-target population while in others it was the result of a single hatchery. Targets for recipient-stray rates were never exceeded in large recipient populations but were often exceeded in small recipient populations. This was likely one of the reasons why recipient population stray rates increased with decreasing spatial scale because the smaller the scale the lower the population size. Difficult management trade-offs between increasing abundance and minimizing recipient stray rates to within acceptable limits are likely. Some solutions to minimize recipient stray rates will likely involve a combination of changes to hatchery, harvest, and habitat management.

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Examining the Genetic Structure of Upper Columbia Summer/Fall Chinook Salmon and Evaluating the Effects of the Supplementation Program

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Abstract

We examined baseline (1982-1994) and contemporary (2017-2018) summer and fall Chinook Salmon (*Oncorhynchus tshawytscha*) from the Upper Columbia River Watershed to determine if hatchery supplementation programs have had any impacts on the genetic diversity and structure of these populations. Baseline collections included both hatchery- and natural- origin samples where available. Contemporary collections exclusively consisted of samples collected at broodstock collection facilities; their origin (hatchery or natural) was only sometimes known. Summer Chinook Salmon populations with paired baseline and contemporary samples included the Methow River, the Wenatchee River, and the Okanogan River. Populations with only contemporary samples included Chelan Falls, Entiat National Fish Hatchery, and Wells Fish Hatchery. Fall Chinook Salmon were represented by collections from the Hanford Reach spawning grounds and Priest Rapids Hatchery. Measures of genetic diversity (allelic richness, heterozygosity, linkage disequilibrium, and effective number of breeders) showed little differentiation among baseline and contemporary populations for either summer or fall Chinook, suggesting that hatchery programs have not led to a decrease in genetic diversity. There was a general pattern where F_{ST} was higher among baseline than contemporary collections suggesting that genetic drift and homogenization among stocks has occurred over time. Despite these patterns, pairwise comparisons of F_{ST} were generally statistically non-significant both for baseline and contemporary collections. Similar to previous evaluations, there appears to be little evidence for neutral genetic divergence between contemporary hatchery programs in the upper Columbia watershed and baseline samples collected in the late 1980s and early 1990s. The large population sizes of summer and fall Chinook Salmon relative to the hatchery program sizes in the upper Columbia basin, low recipient population stray rates in natural populations, and the management strategies that were implemented to reduce genetic risk all likely contribute to the lack of neutral genetic change. This evaluation did face two limitations: first, we were not able to evaluate potential differentiation among contemporary hatchery and natural origin individuals due to lack of data on individual origin; second, we were not able to evaluate potential shifts in adaptive genetic diversity using genetic techniques and it is possible for adaptive genetic diversity (i.e., run-timing, age at maturity) to change in response to selection (i.e., domestication) while neutral genetic diversity remains the same. While adaptive genetic variation was not directly monitored, phenotypic metrics measured as part of other portions of the monitoring plan can serve as a proxy for adaptive genetic variation.

Introduction

One of the main concerns associated with using artificial propagation to supplement natural populations and to increase harvest is the reduction in long-term fitness associated with interbreeding and loss of local adaptation in naturally spawning populations (Ford 2002, Mobrand et al. 2005, Paquet et al. 2011). Interbreeding can result in changes to the genetics of progeny and result in changes to the productivity of populations. Interbreeding can be intentional and substantial such as when the objective of the hatchery program is to increase natural production (Williamson et al. 2010, Ford et al. 2015a). Interbreeding can also be an unintentional byproduct of operating a hatchery program when hatchery-origin fish stray to non-target spawning populations (Keefer and Caudill 2014, Ford et al. 2015b, see Pearsons and O'Connor and Pearsons and Miller chapters in this report). Despite the long-term risks of interbreeding between hatchery- and natural-origin fishes, we are not aware of standardized methods for long-term monitoring of the effects of hatcheries on naturally spawning populations.

The long-term fitness of natural populations is related to their genetic diversity. However, hatchery programs select a subset of individuals whose probability of passing on genetic material to the next generation is increased by reducing mortality associated with freshwater rearing and development. This subset is often a relatively small number of individuals that then produce a large number of adult offspring and thus these programs can change allele frequencies and reduce effective population size (Ryman and Laikre 1991). Therefore, it is important to monitor the genetic status of the natural populations to determine if there are signs of changes in genetic distance among populations, changes in allele frequencies, linkage disequilibrium, and to estimate effective population size.

Background

Construction of the Grand Coulee Dam in 1939 eliminated upstream migration of anadromous salmon past the dam. To mitigate the effects of this habitat loss, the Grand Coulee Fish Maintenance Project (GCFMP) was initiated. This project aimed to maintain fish runs by improving salmon habitat and establishing hatchery operations (Fish and Hanavan 1948). From 1939 to 1943, all adult fish passing Rock Island Dam were collected and either spawned artificially at U.S. Fish and Wildlife Service (USFWS) hatcheries on the Wenatchee or Methow rivers, or transported and allowed to spawn naturally in fenced reaches of the Wenatchee or Entiat rivers. “Early-run” fish, presumably spring run, were separated from “late-run fish”, presumably summer and fall run, however no effort was made to separate summer or fall components of the run (Waknitz et al. 1995). There are relatively few 6-year old adult Chinook Salmon in the Columbia River (<1%), and the Rock Island Dam collection program lasted five years. As a result, nearly all contemporary late-run Chinook Salmon above Rock Island Dam are progeny of mixed Chinook Salmon stocks and mixed summer and fall run-timings collected during this program (Waknitz et al. 1995).

The Chinook Salmon population below Rock Island Dam did not experience the same machinations associated with the GCFMP. The primary spawning and rearing area of the Chinook Salmon spawning below Rock Island Dam is the Hanford Reach of the Columbia River which spans ~51 miles from the Priest Rapids dam (constructed in 1956) to the town of

Richland, WA. Early operations of the dam resulted in large variations in discharge, which lead to dewatering sections with redds, and stranding of Chinook Salmon individuals (Langshaw et al. 2018). Ultimately, the Hanford Reach Fall Chinook Protection Program Agreement (HRFCPPA) was implemented to mitigate and further protect Hanford fall Chinook. Fall Chinook Salmon that spawn in the upper Columbia River Basin are considered to be one of the few remaining "robust" stocks in the basin (Langshaw et al. 2018). The Hanford Reach of the upper Columbia River supports the largest spawning population of fall Chinook Salmon in the Pacific Northwest (Huntington et al. 1996, Dauble and Watson 1997, Harnish et al. 2012, Langshaw et al. 2018)).

The Public Utility Districts (PUDs) of Chelan, Douglas, and Grant counties agreed to implement hatchery programs to mitigate for unavoidable mortality caused by construction and operation of hydroelectric projects on the Columbia River. Initial hatchery program sizes were negotiated with fisheries managers and later refined using estimates of mortality caused by hydropower projects and survival of hatchery fish. Committees consisting of a representative from the USFWS, National Marine Fisheries Service (NMFS), Washington State Department of Fish and Wildlife (WDFW), Yakama Nation (YN), Confederated Tribes of the Colville Reservation (CCT), and each PUD were formed to oversee the implementation of PUD hatchery programs. These hatchery committees were tasked with developing long-term plans for monitoring the hatchery programs and with adaptive management of the programs as new information became available.

Hanford fall Chinook at Priest Rapids Hatchery

Natural-origin fall Chinook Salmon produced in the Hanford Reach emerge from the substrate in the spring and rear there until outmigration in the summer. Egg-to-fry survival and egg-to-pre smolt survival of natural production within the Hanford Reach have been estimated to be ~71% and 40.2-63.4%, respectively (Harnish et al. 2012, Oldenburg et al. 2012, Harnish 2017).

The Priest Rapids Hatchery (PRH) was constructed at the top end of the Hanford Reach to mitigate for losses associated with the inundation of the portions of the Columbia River caused by the construction of Priest Rapids (1959) and Wanapum dams (1963). The PRH has evolved from a spawning channel initially constructed downstream from Priest Rapids Dam in 1963 to a state-of-the-art hatchery facility completed in 2014. While operating as a spawning channel from 1963 through 1971, summer/fall Chinook Salmon adults trapped in the east ladder of Priest Rapids Dam were used as broodstock. This practice was generally ineffective at producing juveniles because of a variety of factors leading to mortality of both adult broodstock and in eggs deposited in redds. Artificial propagation of fall Chinook Salmon at the site began in 1972 with the collection and spawning of broodstock derived from adults returning to the spawning channel. In 1978, use of the spawning channel was terminated and all fish released from PRH were derived from artificial production at that facility (Chapman et al. 1994). A major rebuild of the facility was completed in 2014 including a renovated trapping facility, new adult holding ponds, new adult sorting capabilities, a new incubation building, 30 new raceways, and five renovated acclimation ponds.

The annual release of fall Chinook Salmon smolts from PRH has ranged considerably since the initial release of roughly 150,625 smolts from the 1977 brood year to over roughly 10.30 million from the 1982 brood year. From 1977 to 2013 the release goal of the PRH program was 5 million subyearling smolts and additional production was produced for USACE. In 2013, the target number of fish to release at PRH was revised to 7,299,504 (5,599,504 combined with the ongoing USACE's John Day mitigation of 1,700,000 smolts). In addition to production released by PRH, the United States Army Corps of Engineers (USACE) also released subyearling fall Chinook Salmon from Ringold Springs Hatchery (RSH) into the lower end of the Hanford Reach beginning in 1994. The smolts released by RSH were derived from adult salmon returning to Bonneville Hatchery prior to 2009 and PRH during years afterwards to collect eggs sufficient to release 3.5 million subyearling smolts. Thus, a total annual release goal of 10,799,504 hatchery reared subyearling smolts was planned for the Hanford Reach from 2014 to present.

The age at maturity for naturally produced fish in the Hanford Reach varies between age-1 mini-jack and age-6 adults: albeit recoveries of age-1 and 6 fish are generally rare. The abundance of mini-jacks maturing as age-1 males is currently not known. Age-2 male fall Chinook Salmon (jacks) return to the Hanford Reach after spending roughly one year in the ocean. The majority of the natural-origin adults return after spending three to four years in the ocean (age-4 and 5). A small portion, typically less than 2%, will spend up to five years in the ocean and return as age-6. Adults return to the mouth of the Columbia River between August and October and spawn in large cobble substrate between October and December (Langshaw et al. 2018, Richards and Pearsons 2019).

Wenatchee Summer Chinook

The goal of summer Chinook Salmon supplementation in the Wenatchee Subbasin is to use artificial production to replace Chinook Salmon lost because of mortality at Priest Rapids, Wanapum, and Rock Island dams, while not reducing the natural production or long-term fitness of the extant summer Chinook Salmon population in the basin. The Rock Island Fish Hatchery Complex began operation in 1989 under funding from Chelan PUD and subsequently Grant PUD began cost-sharing the program in 2012. The Complex operated originally through the Rock Island Settlement Agreement, but since 2004 has operated under the Rock Island Anadromous Fish Agreement and Habitat Conservation Plan (HCP) as well as the Priest Rapids Project Salmon and Steelhead Settlement Agreement.

Adult summer Chinook Salmon are collected for broodstock from the Wenatchee River run-at-large at the right- and left-bank traps at Dryden Dam, and at Tumwater Dam if weekly quotas cannot be achieved at Dryden Dam. Before 2012, the goal was to collect up to 492 natural-origin adults for the Wenatchee program for an annual release of 864,000 yearling smolts. In 2011, the Hatchery Committees reevaluated the amount of hatchery compensation needed to achieve no net impact (NNI). Based on that evaluation, the smolt-production goal of the program was reduced. The current goal (beginning with brood year 2012) was to collect up to 274 adult natural-origin adults for an annual release of 500,001 yearling smolts. The 500,001 smolts were the combined Grant PUD and Chelan PUD smolt production target, with Chelan PUD's obligation at 318,000 and Grant PUD's obligation at 182,001. Broodstock collection

occurred from about 1 July through 15 September with trapping occurring up to 24 hours per day, seven days a week at Dryden Dam and up to 16 hours per day, three days per week at Tumwater Dam. If natural-origin broodstock collection fell short of expectation, hatchery-origin adults were collected to meet the collection quota.

Adult summer Chinook Salmon are spawned at Eastbank Fish Hatchery, where the majority of juveniles are reared in raceways, and a portion in circular tanks. Juveniles are transferred from the hatchery to Dryden Acclimation Pond on the Wenatchee River, in March of each release year, and they are released from the pond volitionally beginning mid-April and pushed out by the end of April.

Before 2012, the production goal for the Wenatchee summer Chinook salmon supplementation program was to release 864,000 yearling smolts into the Wenatchee River at ten fish per pound. Beginning with the 2012 brood, the revised production goal is to release 500,001 yearling smolts into the Wenatchee River at 18 fish per pound. Targets for fork length and weight are 163 mm (CV = 9.0) and 45.4 g, respectively. Over 95% of these fish are marked with CWTs. In addition, since 2009, about 20,000 juveniles were PIT tagged annually.

Entiat National Fish Hatchery Summer Chinook

Entiat National Fish Hatchery (NFH) operates a segregated harvest program that currently produces summer Chinook Salmon for commercial, sport, and tribal harvest while attempting to minimize adverse impacts to the environment. The United States Fish and Wildlife Service (USFWS) operates the facility with funds provided by the Bureau of Reclamation (BOR). Summer Chinook Salmon from this program are not intended to spawn naturally, supplement, or support any summer Chinook Salmon populations. The release target of 400,000 yearling adipose-clipped summer Chinook Salmon was established after discussion with the relevant co-managers and is described in the U.S. v. Oregon Columbia River Management Agreement.

Entiat NFH is a mitigation hatchery originally established by the Grand Coulee Fish Maintenance Project (1937) and began operations in 1942 as partial mitigation for the loss of anadromous fish production due to the construction and operation of Grand Coulee Dam. Since 1942, Entiat NFH has released a variety of species from multiple stocks however spring and summer Chinook Salmon (Oncorhynchus tshawytscha) have been the primary stocks reared to meet mitigation requirements. The hatchery began rearing spring Chinook Salmon that originated from mixed upriver stocks intercepted at Rock Island Dam in 1942 and 1944. No spring Chinook Salmon were reared from 1945 to 1974. In 1974, spring Chinook Salmon production resumed and egg sources included: Cowlitz River (1974), Carson NFH (1975–1982), Little White Salmon NFH (1976, 1978, 1979, 1981), Leavenworth NFH (1979–1981, 1994), and Winthrop NFH (1988). Returning adults that voluntarily entered the hatchery were the primary broodstock in 1980 and from 1982 to 2006. The spring Chinook Salmon rearing program was terminated in 2006 to reduce the impact of Entiat NFH-origin spring Chinook Salmon on ESA-listed natural-origin spring Chinook Salmon in the Entiat River. The last on-station release of spring Chinook Salmon to the Entiat River occurred in 2007 and the last adults returned in 2010.

In the fall of 2009, the hatchery began a new program propagating summer Chinook Salmon with broodstock captured at Wells Fish Hatchery. Wells Fish Hatchery (Wells stock) was selected as the broodstock because they are genetically part of the upper Columbia River summer Chinook Salmon stock (Kassler et al. 2011). Additionally, a genetic evaluation of the existing natural-origin stock in the Entiat River determined the population to not be genetically distinct from the Wells stock or the upper Columbia River summer Chinook Salmon population (Smith et al. 2011). Entiat NFH reared and released juvenile summer Chinook Salmon into the Entiat River from 1941–1964, and in 1976 (Mullan 1987). Summer Chinook Salmon egg sources have included: mixed upriver stocks intercepted at Rock Island Dam (1939–1943), Methow River (1944), Carson NFH (1944), Entiat River (1946–1965), Spring Creek NFH (1964), and Wells Hatchery (1974, 2009–2013). Adult summer Chinook Salmon returning to Entiat NFH have been the primary brood source since 2014 (Fraser et al. 2020).

Chelan Falls Hatchery Summer Chinook

The Chelan Falls summer Chinook program is a segregated harvest program. Adult returns spawn in the lower Chelan River; however, there is no escapement goal for natural spawning. Chelan Falls summer Chinook are available for harvest in ocean and Columbia River commercial, tribal, and recreational fisheries. The Chelan Falls summer Chinook program (formerly the Turtle Rock program) included the production of 200,000 fish for No Net Impact (NNI) compensation for passage mortalities associated with Rocky Reach Dam and a 400,000 subyearling/yearling program for compensation for lost spawning habitat as a result of the construction of Rocky Reach Dam. In 2011, as part of the periodic recalculation of NNI for Rocky Reach Dam (inundation), the previous 200,000 NNI program was reduced to 176,000 fish. This reduced the combined Chelan Falls summer Chinook production from 600,000 to 576,000 beginning with the 2012 brood.

The original program consisted of both subyearling (normal and accelerated groups) and yearling releases. Subyearlings were transferred to Turtle Rock Acclimation Facility for acclimation in May. These fish were released in June after about 30 days of acclimation on Columbia River water. The production goal of this program was to release 1,620,000 subyearling summer Chinook (810,000 normal and 810,000 accelerated subyearlings) into the Columbia River. In 2010, the subyearling program was converted to a 400,000-yearling program. The production goal of the yearling program was to release 200,000 summer Chinook smolts into the Columbia River from the Turtle Rock Acclimation Facility. Beginning with the 2006 brood year, yearling summer Chinook were acclimated at both Turtle Rock Acclimation Facility and the Chelan River net pens. With the conversion of the subyearling program to a yearling program and the reduction of the NNI component to 176,000, the current goal is to release 576,000 yearling summer Chinook smolts (176,000 from the NNI program plus 400,000 from the converted subyearling program). Beginning in 2012, the 576,000 yearlings are acclimated overwinter at the Chelan Falls Acclimation Facility on Chelan River water. In 2012, the Turtle Rock program officially became the Chelan Falls summer Chinook program and all fish were overwinter-acclimated at the Chelan Falls Acclimation Facility.

Before 2012, broodstock were collected at the Wells Dam volunteer trap (WDVT). Summer Chinook were spawned at Wells Fish Hatchery and fertilized eggs were then transferred

to Eastbank Fish Hatchery for hatching and rearing. In 2012, adults were collected at the WDVT and then transferred to Eastbank Fish Hatchery for spawning, hatching, and rearing. Beginning in 2013, broodstock collection was initiated at the Eastbank Fish Hatchery Outfall. With returns to the Outfall diminishing, a pilot broodstock collection program was initiated in 2016 at the outlet structure of the water conveyance canal for the Chelan Tailrace Pump Station (Chelan Falls Canal Trap) and continued through 2018. Concurrently, while collection of broodstock from the Chelan Falls Canal Trap was evaluated, the Entiat National Fish Hatchery and WDVT were used as backup broodstock collection sites. Beginning in 2019, a weir was installed in the habitat channel adjacent to the conveyance canal as another pilot location for broodstock collection. The WDVT was used once again as a backup to this pilot effort. The Chelan Falls summer Chinook program collects hatchery-origin broodstock; approximately 390 adults are necessary for the program. Over 90% of yearling summer Chinook have been marked with CWTs and 85 to 100% were ad-clipped. In addition, juvenile summer Chinook were PIT tagged within each of the circular and standard raceways.

Wells Fish Hatchery Summer Chinook

The goal of the summer Chinook artificial propagation program at Wells Hatchery is to mitigate for the loss of summer Chinook salmon adults and associated fishing opportunity (harvest) that would have been available in the region in the absence of the construction of the Wells Hydroelectric Project (Wells Project). Wells Hatchery began operation in 1967 and is located on the Columbia River west bank of the Wells Dam tailrace. This facility was constructed and is funded by Douglas PUD to mitigate for loss of summer Chinook salmon spawning habitat inundated by Wells Dam. Originally built as a spawning channel, it was reprogrammed to serve as an extended rearing facility in 1977. Since brood year 1993, the program has included two components: 1) a yearling program that releases 320,000 smolts (at 10 fish per pound) annually, and 2) a subyearling program that releases 484,000 fish (at 50 fish per pound) annually, directly to the Columbia River in mid-April (yearlings) and late-May (subyearlings).

The Wells Hatchery summer Chinook program is a segregated harvest program, although up to 10% of the broodstock may be composed of natural-origin fish. Adult returns are not intended to spawn naturally; therefore, there is no escapement goal for natural spawning areas. However, the goal for the stray rate of Wells Hatchery summer Chinook to natural spawning areas is to comprise less than 5% of the naturally spawning population. Thus, management of adult returns is necessary to meet program objectives. Wells Hatchery summer Chinook are available for harvest in ocean and Columbia River commercial, tribal, and recreational fisheries. Also, other summer Chinook hatchery programs, including Turtle Rock, Chelan Falls, Entiat, and Yakima, have relied on returns from the Wells Hatchery program. Returns to the Wells Hatchery in excess of broodstock needs for this program or other programs, are collected and surplussed by WDFW to authorized recipients, primarily tribes.

The Wells Hatchery summer Chinook program collects hatchery-origin broodstock with up to 10% natural-origin broodstock at the Wells Hatchery volunteer channel. Approximately 602 adults are necessary for the two program components, with 230 adults needed for the yearling program, and 372 adults for the subyearling program. Broodstock collection has

historically began on July 1, and continued as late as August 31, but typically most broodstock are collected in July. The spawning facilities at Wells Hatchery are integrated into the broodstock-holding facilities, allowing the sorting of broodstock for sexual maturity followed immediately by spawning. Fertilization, incubation, and rearing also occur at the Wells Hatchery, with final rearing in very large ponds.

For each brood year included in this analysis, 100 percent of the summer Chinook produced were adipose clipped and marked with CWTs (multi-year mean CWT mark-retention rate of 97.6% for subyearlings and 95.8% for yearlings), and 6,000 of the subyearlings were PIT tagged. Beginning in brood year 2018, 5,000 of the yearlings were also PIT tagged. Most (63%) Wells Hatchery subyearlings return as age-4 adults, and most (51%) yearlings as age-5 adults.

Methow Summer Chinook

The original goal of summer Chinook Salmon supplementation in the Methow Basin was in part to use artificial production to replace Chinook Salmon lost because of mortality at Wells, Rocky Reach, and Rock Island dams, while not reducing the natural production or long-term fitness of summer Chinook Salmon in the basin. The Rock Island Fish Hatchery Complex began operation in 1989 under funding from Chelan PUD. The Complex operated originally through the Rock Island Settlement Agreement, but from 2004 to 2012 operated under the Rock Island and Rocky Reach HCPs. Beginning with broodstock collection in 2012, Grant PUD took over funding and operation of the summer Chinook Salmon supplementation program in the Methow River basin. Grant PUD constructed a new overwinter acclimation facility adjacent to the Carlton Acclimation Pond and the first release of fish from this facility was in 2014. The first fish that were overwinter acclimated in the facility were released in 2015. The new facility includes eight, 30-foot diameter dual-drain circular tanks.

Presently, adult summer Chinook Salmon are collected for broodstock from the run-at-large at the east-ladder trapping facility at Wells Dam. Before 2012, the goal was to collect up to 222 natural-origin adults for the Methow program. In 2011, the Hatchery Committees reevaluated that amount of hatchery compensation needed to achieve NNI. Based on that evaluation, the goal of the program was revised. The current goal (beginning with brood year 2012) is to collect up to 102 natural-origin adults for the Methow program. Broodstock collection occurs from about 1 July through 15 September with trapping occurring no more than 16 hours per day, three days a week. If natural-origin broodstock collection falls short of expectation, hatchery-origin adults can be collected to make up the difference.

Adult summer Chinook Salmon were spawned and progeny reared at Eastbank Fish Hatchery. Before the initiation of overwinter acclimation with juveniles from the 2013 brood year, juveniles were transferred from the hatchery to Carlton Acclimation Pond in March. Beginning with brood year 2013, juveniles have been transferred to the Carlton Acclimation Facility in October or November and released from the new facility the following spring in mid-April to early May.

Before 2012, the production goal for the Methow summer Chinook Salmon supplementation program was to release 400,000 yearling smolts into the Methow River at 10

fish per pound. Beginning with the 2012 brood, the revised goal is to release 200,000 yearling smolts at 13-17 fish per pound. Targets for fork length and weight are 163 mm (CV = 9.0) and 45.4 g, respectively. Over 90% of these fish were marked with CWTs. In addition, since 2009, 5,000 juveniles have been PIT tagged annually.

Okanogan Summer Chinook

The Chief Joseph Hatchery (CJH) program was designed to increase the abundance, productivity, distribution, and diversity of naturally spawning populations of summer/fall Chinook salmon (Oncorhynchus tshawytscha) in the Okanogan River and in the Columbia River above Wells Dam. Program operations began in 2013 and consists of integrated and segregated summer/fall Chinook programs that release up to 2 million smolts to meet conservation and harvest objectives to partially fulfill Federal and Public Utility District mitigation obligations for Columbia River Dam impacts to anadromous salmonids. The integrated summer/fall Chinook program expanded on, and now incorporates the previous Chelan PUD and WDFW Similkameen Pond program. The previous Similkameen program was in operation from 1989 to 2012 and released up to 576,000 smolts that originated from a natural origin brood collected at Wells Dam. Since 2010, the Colville Tribes have been collecting brood at the confluence of the Okanogan and Columbia using a purse seine, as a means of avoiding the previous Methow and Okanogan composite brood collection at Wells Dam. The integrated summer/fall Chinook program uses a high proportion of Okanogan natural-origin broodstock while management actions (e.g., selective harvest and weir removals) maintain a low proportion of hatchery-origin spawners to achieve population objectives for conservation (i.e. PNI > 0.67; pHOS < 0.30) that ensure that the natural environment has the majority of influence on local adaptation. The smolt release targets at full program for the integrated program are 800,000 yearling smolts from the Omak and Similkameen acclimation ponds and 300,000 subyearlings from the Omak acclimation pond. The integrated program is 100% adipose fin clipped and coded-wire tagged with 10,000 PIT tags. The segregated summer/fall Chinook program is intended for harvest and uses primarily first generation returns from the integrated program to minimize multi-generation hatchery affects. The segregated program smolt release goals are 500,000 yearlings and 400,000 subyearlings from the Chief Joseph Hatchery on the Columbia River (upstream of the confluence with the Okanogan River). The segregated program is 100% adipose fin clipped and includes 200,000 coded-wire tags and 10,000 PIT tags.

Objectives

In response to the need for evaluation of the supplementation program, both a monitoring and evaluation plan (Murdoch and Peven 2005) and the associated analytical framework (Hays et al. 2006) were developed for the Habitat Conservation Plans Hatchery Committee through the joint effort of the fishery co-managers (CCT, NMFS, USFWS, WDFW, and YN) and Chelan County, Douglas County, and Grant County PUDs. This plan was updated in 2019 (Hillman et al. 2020) and includes twelve objectives to be applied to various species assessing the impacts of hatchery operations mitigating the operation of Rock Island and Rocky Reach Dams. This report pertains to Upper Columbia summer and fall Chinook Salmon and the Chinook Salmon supplementation program as addressed by Objective 7, evaluating population genetics to determine if genetic diversity, population structure, and effective population size have changed

in Upper Columbia summer and fall Chinook Salmon as a result of the conservation and safety-net hatchery programs and assess genetic changes of hatchery-origin returns.

To address Objective 7, the WDFW Molecular Genetics Lab (MGL) obtained baseline and contemporary tissue or genotype collections and samples, surveyed genetic variation with SNP markers using our standard laboratory protocols, and calculated the relevant genetic metrics and statistics. Genotypes from baseline and contemporary hatchery and natural origin collections were analyzed to evaluate differences between baseline and contemporary and between hatchery and natural origin collections. In most cases, baseline sample collections consisted of the oldest samples available from each population and contemporary sample collections were from spawn years 2017 and 2018.

Methods

Sample collections

Baseline sample collections consisted of the oldest samples found for each population. Baseline collections had all been used in previous monitoring and evaluation projects (Blankenship et al. 2007, Small et al. 2007, Kassler et al. 2011), except for Hanford fall Chinook Salmon. Baseline for the Hanford fall Chinook Salmon came from scales from 1982 and 1988 that were found in the WDFW scale lab archive. Although some salmon were externally marked in the 1980s, marks were typically made for research purposes and could have been either hatchery- or natural- origin. Origin of Hanford fall Chinook Salmon samples was inferred from sample location. Natural-origin fish were thought to enter the Priest Rapids hatchery trap at low levels, therefore the hatchery-origin baseline was drawn from among those fish that swam into the trap because they were likely of hatchery-origin. Hatchery-origin fish were thought to make up a small proportion of the fish on the spawning grounds, and when they did, it was likely they were mainly found near the upstream hatchery or dam areas. Thus, Hanford fall Chinook Salmon samples taken from carcasses found near Locke Island and White Bluffs spawning grounds were considered natural-origin.

Contemporary Chinook Salmon samples consisted of broodstock spawned in 2017 and 2018 from each of the upper Columbia Chinook Salmon programs. All other genotypes from contemporary Chinook Salmon collections were genotyped by CRITFC and were obtained from the FishGen.net online data repository. Contemporary samples for Hanford fall Chinook, and Wenatchee and Methow summer Chinook Salmon were mixed hatchery and natural origin, and data on individual origin were not available. However, broodstocks targeted certain origins and these targets were usually met. It is likely that the summer Chinook Salmon samples were of natural-origin and the fall Chinook Salmon samples were a mix of hatchery and natural-origin fish.

Genetic sample processing

Briefly, at WDFW Molecular Genetics Laboratory, genomic DNA was extracted using silica membrane column extraction kits following manufacturers protocols. We used an amplicon sequencing procedure, Genotyping in Thousands (GTseq, Campbell et al. 2015), to

assay 332 Chinook SNPs (Appendix A). GTseq amplifies pools of targeted SNPs in a highly multiplexed PCR reaction, attaching sequence adapters that assign amplicons to an individual sample and primer. After we sequenced the pooled library, we used a series of custom Perl scripts (*c.f.*, Campbell et al. 2015) to separate the sequences by sample identifiers. A Perl script in the bioinformatics pipeline assigned genotypes based on allele ratios by counting allele-specific amplicons at each locus. The MGL-specific GTseq protocol is described in more detail in Appendix B.

Data processing

All data processing and analysis were completed using a series of custom R markdown scripts (G.M. - WDFW; R Core Team 2019). All genotype data, baseline and contemporary, were evaluated for missing data and species ID. Species ID was determined using diagnostic markers and homozygosity (non-target species typically have very high homozygosity). Samples with more than 30% missing genotypes were removed as were samples identified as non-target species.

Only neutral loci were used in further analysis. SNP marker designations, neutral or adaptive, were established by testing in multiple laboratories, including CRITFC and WDFW laboratories, during development of the SNP panel or by designation as adaptive by CRITFC for markers CRITFC ascertained (Jeff Stephenson – CRITFC, pers. comm.). Neutral loci were evaluated for missing data, deviations from Hardy-Weinberg expectations (HWE), and diversity. Loci 1) with more than 30% missing data across the entire dataset, 2) that were invariant across the entire dataset, or 3) with deviations from HWE in most collections were excluded from further analysis.

Data analysis

The monitoring and evaluation plan calls for evaluation of four general questions: 1) are contemporary allele frequencies different from baseline allele frequencies (Q7.1.1 and Q7.1.2); 2) is linkage disequilibrium (LD) in contemporary collections different from baseline LD (Q7.2.1 and Q7.2.2); does genetic distance among subpopulations change over time (Q7.3.1); and 4) does the ratio of effective population size (N_e) to census population size (N) change over time (Q7.4.1)? All analyses were conducted using R markdown scripts using many different R packages (R Core Team 2019). R scripts are available upon request.

Question 1, Allele frequency – To visualize structure among collections associated with allele frequencies, we performed Principal Component Analysis (PCA) on allele frequencies of collections and graphed the first two axes and separately calculated and graphed average allelic richness among all loci within a collection. We statistically evaluated allele frequency similarity by performing pairwise AMOVA analyses, comparing heterozygosity of baseline and contemporary samples, and by evaluating changes in allelic richness. Comparisons of observed and expected heterozygosity were evaluated with a two-sided permutation test where individuals were permuted to obtain the reference distribution.

Question 2, Linkage Disequilibrium – Linkage Disequilibrium (LD) is the correlation of alleles among loci within an individual. Loci may be in LD because they are physically linked (near one another on a chromosome and as such are inherited together) or they may be statistically linked (e.g., alleles are correlated because of relatedness among individuals within a population). No minimum or maximum allowable LD target exists. Because increased LD indicates a reduction in diversity, advice is generally to avoid increasing LD. Hatchery activities may increase the amount of LD present, in particular due to relatedness among individuals. We evaluated LD two ways. First, we calculated allelic correlation coefficients for all pairwise locus comparisons within collection using PLINK (Purcell 2007, Purcell et al. 2007). Second, we performed a probability test of LD for all pairwise locus comparisons within collection using GENEPOP with default parameters (Rousset 2008). Comparisons of baseline and contemporary collections were made by counting the number of statistically significant ($\alpha = 0.05$) pairwise tests before and after correction for multiple tests. At $\alpha = 0.05$, ~5% of all pairwise tests should have a P value < 0.05, before correction for multiple tests. Collections with frequencies of P values < 5% greater than 5% were inferred to have high levels of LD (Waples 2015). Differences among collections in the frequency of significant pairwise tests of LD within collection were tested using Mann-Whitney rank tests. Correction for multiple testing achieved a table-wide $\alpha = 0.05$ for each collection via false discovery rate (Verhoeven et al. 2005).

Question 3, Genetic Distance – To estimate genetic distance among collections we calculated pairwise F_{ST} and 95% confidence intervals with the R package *hierfstat* using default parameters (Goudet 2005). No minimum viable genetic distance has been identified. Instead, the goal is to avoid reducing genetic distances among populations. Increased genetic distance between a hatchery and natural collection of the same population is an indication that the hatchery broodstock were not a representative sample of the population.

Question 4, Effective Population Size – The effective population size (N_e) of a population is an important metric for populations that roughly indicates the amount of within-population genetic variation that exists because genetic variation generally increases with the effective number of spawners. There is disagreement among experts on minimum viable N_e values, and as such the recommendation is generally to avoid reductions in N_e. Effective population size (N_e) for each collection separately was estimated using the LDNE algorithms employed by the software NE ESTIMATOR (Do et al. 2014). Using this method with the available tissue collections, LDNE is estimating N_b, the effective number of breeders, rather than N_e; N_b is a better metric for monitoring (Luikart et al. 2021). Because hatchery programs are integrated programs, hatchery and natural fish belong to the same population. Thus, we also estimated N_b with the contemporary hatchery and natural components combined for each of the two years of samples. Loci with very low minor allele frequencies (MAF; in particular, loci where only one copy of the minor allele exists) cause an upward bias in N_b estimates using LDNE (Waples and Do 2008). Inclusion or exclusion of such loci is accomplished by setting a MAF critical value. Because of variable sample sizes and missing data, problem loci have different MAFs. To choose a critical value, for several collections we evaluated the MAF and counted the number of loci that would be dropped at various critical values. Setting the critical value at 0.02 eliminated all or nearly all problem loci, whereas significantly higher numbers of loci that had higher MAFs were dropped when the critical value was set at 0.05. Thus, we report results based on the critical value of 0.02. We report the jack-knife 95% confidence interval (CI) for each collection. Statistical

significance of comparisons was evaluated by overlapping CIs. All previous generations impact N_b estimates to some degree and N_b estimates may be biased due to overlapping generations (Waples et al. 2014). To calculate unbiased N_b/N ratios, we estimated the impacts of multiple generations of influence and corrected bias due to overlapping generations (Waples et al. 2014, c.f. Waters et al. 2015) using escapement estimates for as many spawn years prior to the spawn years of our collections as were available in the WDFW SCoRE database (https://fortress.wa.gov/dfw/score/score/). We assumed a 5-year generation time for natural origin adults and a 4-year generation time for hatchery-produced adults.

Results

Sample collections

From 518 baseline samples from 1982 - 1994, 471 remained after data filtering. Baseline samples were identified as both hatchery- and natural-origin. Genotypes from 17,514 contemporary hatchery- and natural-origin summer and fall Chinook Salmon from 2017 and 2018 were available. To maintain consistent population sizes in baseline and contemporary samples, between 50 and 100 samples were randomly sampled from each population, resulting in 1,106 contemporary samples analyzed. All contemporary samples came from fish that had been used as broodstock for summer and fall Chinook Salmon hatchery programs.

Table 1. Samples of adult summer and fall Chinook Salmon used for genetic monitoring and evaluation.

Analysis Unit	Year	Collection Code	Origin	Run Timing	Collection Category	Year	Population	N available	N used	N fixed Loci	AvgRich	Het_obs	Het_exp	Avg F_{IS}	% HWE $p < 0.05$	% Pair LD $p < 0.05$	N_b [1]	95% CI Jackknife on samples		N [2]	N_b/N
ChelanFalls-Hatchery-Summer-2017	2017	OtsPBT17GHSu	Hatchery	Summer	contemporary	2017	Chelan Falls	333	100	9	1.26	0.26	0.26	0.0064	0	1514	201.7	144.4	317.3	NA	NA
ChelanFalls-Hatchery-Summer-2018	2018	OtsPBT18FESuFa	Hatchery	Summer	contemporary	2018	Chelan Falls	380	100	9	1.27	0.27	0.27	0.0063	0	1403	389.8	228.9	1090.9	NA	NA
Entiat_NFH-Hatchery-Summer-2017	2017	OtsPBT17-EntiatNFH	Hatchery	Summer	contemporary	2017	Entiat NFH	273	100	14	1.26	0.27	0.26	-0.0223	1	1516	229.9	162.2	375.6	NA	NA
Entiat_NFH-Hatchery-Summer-2018	2018	OtsPBT18-EntiatNFH	Hatchery	Summer	contemporary	2018	Entiat NFH	269	100	14	1.26	0.27	0.26	-0.028	0	1923	93.3	69.2	134.3	NA	NA
Hanford_Reach-Hatchery-1982	1982	82AAB	Hatchery	Fall	baseline	1982	Hanford_Reach	49	46	21	1.26	0.29	0.26	-0.111	0	1016	303.4	111.7	Infinite	30969	0.01
Hanford_Reach-Hatchery-1988	1988	88AAC	Hatchery	Fall	baseline	1988	Hanford_Reach	42	39	24	1.26	0.29	0.26	-0.1119	0	918	403.1	107.8	Infinite	84,299	0.00
Hanford_Reach-Natural-1982	1982	82AAA	Natural	Fall	baseline	1982	Hanford_Reach	77	57	20	1.26	0.27	0.26	-0.0139	0	1120	539.2	129.3	Infinite	30969	0.02
Hanford_Reach-Natural-1988	1988	88AAB	Natural	Fall	baseline	1988	Hanford_Reach	65	53	17	1.26	0.28	0.26	-0.0599	0	1038	1167.1	194.5	Infinite	84,299	0.01
Priest_Rapids_Fish_Hatchery-Hatchery-Fall-2017	2017	OtsPBT17-PRHFa	Unknown	Fall	contemporary	2017	Hanford Reach	6441	58	14	1.27	0.27	0.27	0.0197	1	1121	16246	795.3	Infinite	174,841	0.09
Priest_Rapids_Fish_Hatchery-Hatchery-Fall-2018	2018	OtsPBT18-PRHFa	Unknown	Fall	contemporary	2018	Hanford Reach	6418	58	11	1.27	0.27	0.27	0.0129	1	1252	619.6	335.3	3380.9	183,759	0.00
Methow_River-baseline-1994	1994	94EJ	Mixed	Summer	baseline	1994	Methow_River	60	58	19	1.26	0.25	0.25	0.0292	0	1090	331.7	175.4	1935.1	1,421	0.23
Methow_River-Natural-1993	1993	93EC	Natural	Summer	baseline	1993	Methow_River	29	29	23	1.26	0.26	0.26	0.0163	0	856	220.5	95.6	Infinite	495	0.45
Methow-Summer-contemporary-2017	2017	OtsPBT17GMSu	Unknown	Summer	contemporary	2017	Methow	109	50	8	1.26	0.26	0.26	0.0051	0	1082	4197	450.2	Infinite	3,582	1.17
Methow-Summer-contemporary-2018	2018	OtsPBT18FDSuFa	Unknown	Summer	contemporary	2018	Methow	131	50	16	1.26	0.26	0.26	0.0148	0	1090	17663.8	767.1	Infinite	1,625	10.87
Okanogan-natural-baseline-1992	1992	92FM	Natural	Summer	baseline	1992	Similkameen_River	48	46	18	1.26	0.27	0.26	-0.0225	0	1053	451.7	129.6	Infinite	1,392	0.32
Okanogan-natural-baseline-1993	1993	93ED	Natural	Summer	baseline	1993	Similkameen_River	49	46	16	1.27	0.27	0.27	0.0158	0	1092	339.5	141.9	Infinite	1,719	0.20
Okanogan-summer-contemporary-2017	2017	OtsPBT17-CJHInt-SuFa	Hatchery	Summer	contemporary	2017	Chief Joseph	682	50	13	1.26	0.26	0.26	0.0268	1	1052	557.2	268.5	Infinite	5,267	0.11
Okanogan-summer-contemporary-2018	2018	OtsPBT18-CJHInt-SuFa	Hatchery	Summer	contemporary	2018	Chief Joseph	737	50	14	1.27	0.27	0.27	0.013	0	1142	725.1	241.7	Infinite	10,407	0.07
Wells_Fish_Hatchery-Hatchery-Summer-2017	2017	OtsWellsSuPBT17	Hatchery	Summer	contemporary	2017	Wells Fish Hatchery	534	50	17	1.27	0.27	0.27	0.0087	0	1137	292.5	126.1	Infinite	NA	NA
Wells_Fish_Hatchery-Hatchery-Summer-2018	2018	OtsWellsSuPBT18	Hatchery	Summer	contemporary	2018	Wells Fish Hatchery	752	50	17	1.26	0.27	0.26	0.0021	0	1192	331.8	167.6	3428.3	NA	NA
Wenatchee_River-Natural-1993	1993	93DE	Natural	Summer	baseline	1993	Wenatchee_River	99	97	6	1.26	0.26	0.26	0.0297	4	1260	720	279.7	Infinite	14,331	0.05
Wenatchee-contemporary-Summer-2017	2017	OtsPBT17GLSu	Unknown	Summer	contemporary	2017	Wenatchee	248	100	8	1.26	0.26	0.26	0.0081	1	1235	1531.9	726.9	Infinite	9,210	0.17
Wenatchee-contemporary-Summer-2018	2018	OtsPBT18GLSu	Unknown	Summer	contemporary	2018	Wenatchee	207	100	11	1.26	0.26	0.26	0.0141	0	1250	1918.6	802.1	Infinite	10,673	0.18

[1] – N_b estimated using LDNE

[2] – escapement estimates for natural origin fish, broodstock counts for hatchery origin fish

Evaluation of loci

In total, genotypes from 381 loci were compiled, this includes the 332 SNP loci amplified by the WDFW and an additional 49 SNPs that were included in some of the previously genotyped datasets. Of 381 SNP loci compiled, 82 were identified as adaptive markers and were removed from further analysis as was the sex ID SNP. Of 298 neutral loci, 255 were used in the final analysis. Removed loci included invariant loci (n=2), loci with too much missing data (n=35), and loci with excess deviations from Hardy-Weinberg equilibrium (n=4) and that were excessively negative F_{IS} (n=2).

Data analysis

Allele frequencies – Question 7.1.1 and 7.1.2
Upper Columbia Summer Chinook Salmon collections

The PCA based on allele frequencies showed three outlier samples (Figure 1). Two of these samples had high heterozygosity relative to other samples in the dataset, suggesting potential contamination. The third outlier sample exhibited no unusual characteristics in terms of missing data or heterozygosity. Minor allele frequencies (MAF) of SNP loci ranged from 0.00 to 0.50 in Upper Columbia summer Chinook Salmon hatchery and natural adult collections. Average MAF of natural baseline and contemporary hatchery collections were similar (~0.190). Allelic richness of baseline natural and contemporary hatchery collections was also similar (~1.26). AMOVA based on allele frequencies showed a single significant difference between baseline natural-origin collections and contemporary hatchery collections within a population (Methow baseline 1994 vs Methow contemporary 2018). Observed heterozygosity ranged from 0.26 to 0.27 in contemporary HOR adult collections and from 0.25 to 0.27 in NOR baseline collections. No significant difference in average expected heterozygosity was detected among baseline and contemporary collections.

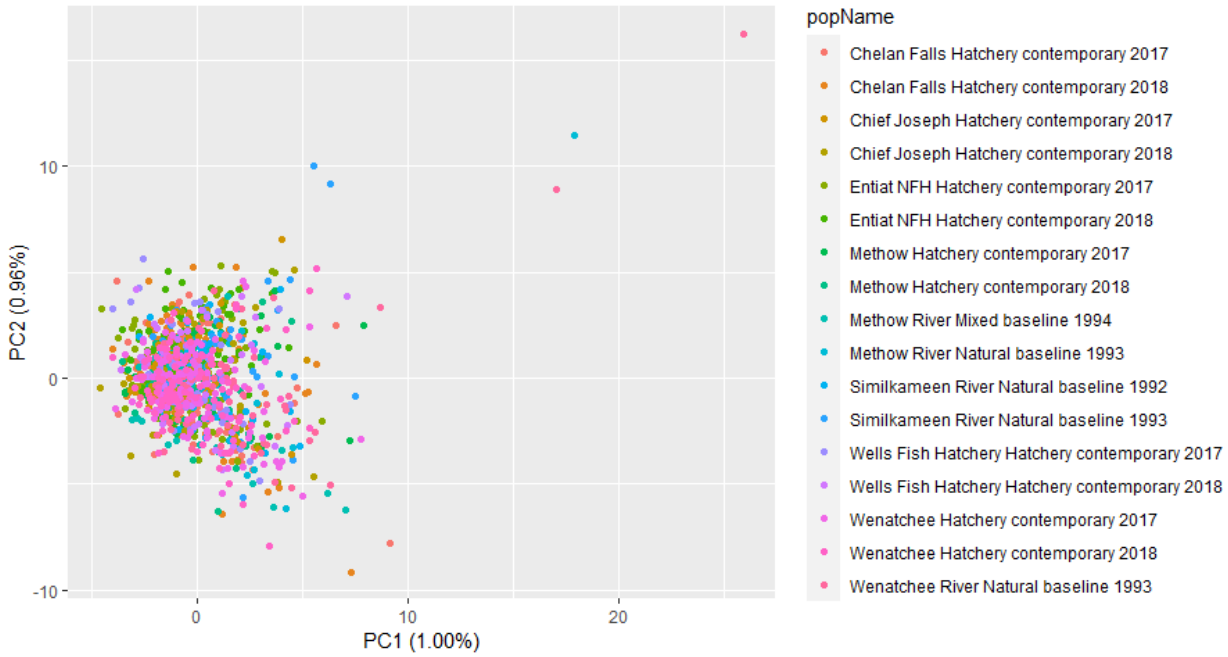
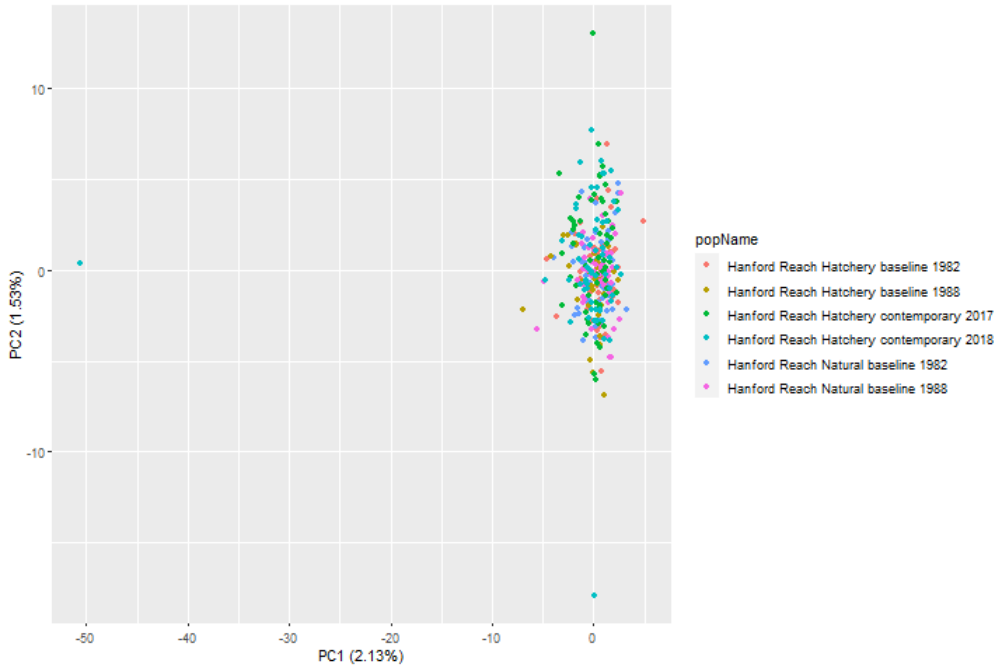


Figure 1. Graph of the first two axes of Principal Components Analysis (PCA) of Upper Columbia summer Chinook Salmon allele frequencies. There is no apparent structure in any of the collections. These graphs identify three outliers on Axis 1; two of these outliers have very high heterozygosity suggesting contamination.

Hanford fall Chinook Salmon collections

The PCA based on allele frequencies showed some structure, along axis two, which appeared to be driven by at least two outliers (Figure 2A). These individuals belonged to the 2018 Contemporary OtsPBT18-PRHFa-0451, and OtsPBT18-PRHFa-2601. In order to determine the origin of these outliers, we completed an assignment test of all individuals against a broad Chinook Salmon baseline. Analysis revealed individual OtsPBT18-PRHFa-0451 to assign with the lower Columbia fall collection (99% assignment probability). The other individual did not assign to a population outside of the Upper Columbia, and thus remained in the analysis. Once the Lower Columbia fall individual was removed, the scatter plot moved to the center of the plot, and no obvious structure was observed (Figure 2B). Minor allele frequencies (MAF) of SNP loci ranged from 0.00 to 0.50 in Hanford fall Chinook Salmon hatchery and natural adult baseline and contemporary collections. Average MAF of baseline and contemporary collections were similar (~0.17). Allelic richness of contemporary hatchery collections and baseline hatchery and natural populations were also similar (average N_A ~ 1.27). AMOVA based on allele frequencies showed the 1982 baseline collections (natural and hatchery) were significantly different from the 2017 contemporary hatchery collections. The other collections did not show significant differences. Observed heterozygosity ranged from 0.10 – 0.27 in the baseline natural/hatchery collections 0.13 – 0.33 and in the contemporary collections. Significant differences in average expected heterozygosity were detected among baseline (hatchery and natural) and contemporary collections.

(A)



(B)

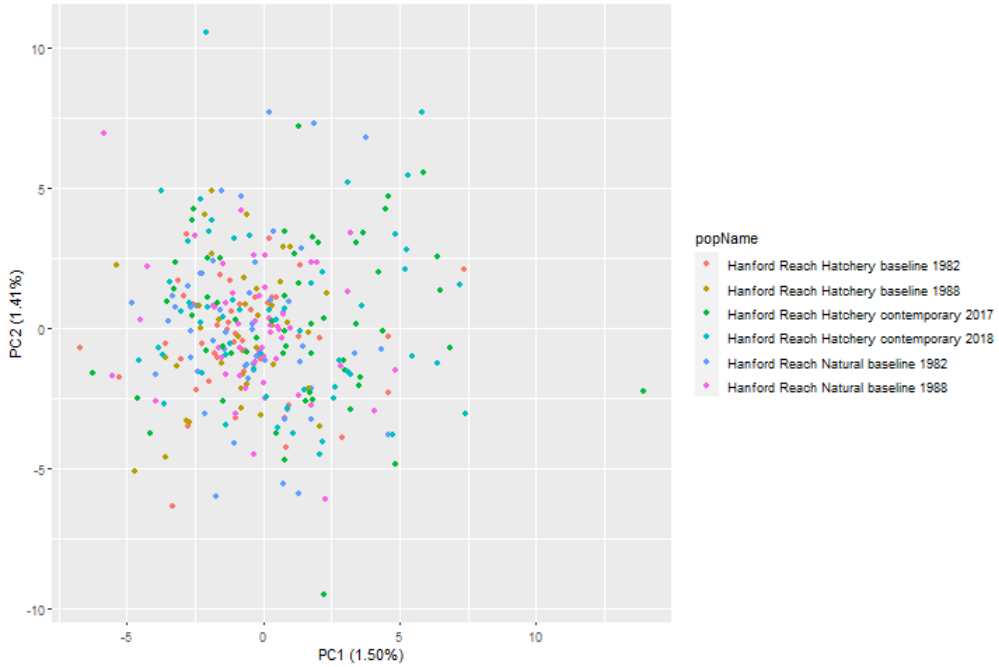


Figure 2. Graph of the first two axes of Principal Components Analysis (PCA) of Hanford fall Chinook Salmon allele frequencies (A) with all individuals included, and (B) outlier removed. There is no apparent structure across baseline and contemporary collections.

Linkage Disequilibrium – Question 7.2.1 and 7.2.2
Upper Columbia Summer collections

Weaker linkage disequilibrium existed within hatchery contemporary collections than within baseline natural collections (natural collections average $r^2 = 0.017$, hatchery collections average $r^2 = 0.026$). The Wenatchee, Chelan Falls, and Entiat summer Chinook also had lower r^2 on average than other summer Chinook populations (0.012 vs 0.024). Surprisingly, there tended to be a negative relationship between r^2 and the number of significant pairwise tests of LD, with populations with higher r^2 having fewer locus pairs in significant LD. Mann-Whitney tests of the distribution of *P* values showed that all pairwise comparisons of those distributions were statistically significant.

Hanford fall Chinook collections

Stronger linkage disequilibrium existed in baseline hatchery collections (1982 $r^2 = 0.027$; 1988 $r^2 = 0.032$) than in the baseline natural collections (1982 $r^2 = 0.021$; 1988 $r^2 = 0.021$). Contemporary hatchery collections exhibited similar levels of linkage disequilibrium to the baseline natural collections (2017 $r^2 = 0.18$; 2018 $r^2 = 0.019$). The collections with any significant pairwise tests of LD (one locus pair per each collection, for the same locus pair) were in the contemporary hatchery collections, and in the 1988 natural baseline collection. Mann-Whitney tests of the distribution of *P* values showed that all pairwise comparisons of the baseline and contemporary distributions were statistically significant, except for the comparison of the contemporary collections.

Genetic Distance – Question 7.3.1
Upper Columbia Summer collections

For summer Chinook Salmon, contemporary HOR adults were generally not significantly genetically different from baseline NOR adults as estimated by F_{ST} (Figure 3, Figure 4); however, there was a general trend where F_{ST} was elevated in baseline vs contemporary collections. In addition, F_{ST} among contemporary collections was generally lower than among baseline collections, suggesting homogenization among stocks.

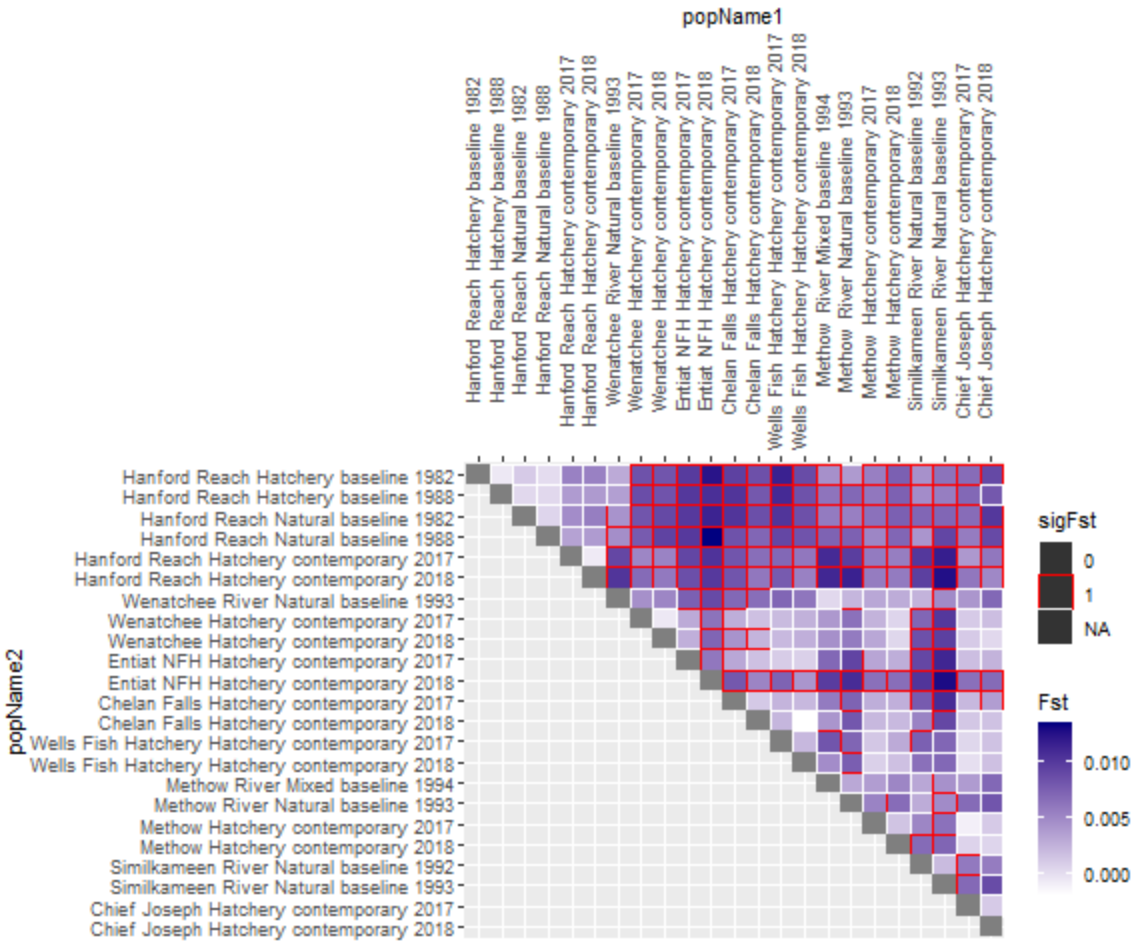


Figure 3. Plot of pairwise F_{ST} among summer and fall Chinook Salmon populations. 95% confidence intervals were estimated. Those F_{ST} estimates whose 95% confidence intervals lower bound was larger than zero were deemed significantly different from zero and are shown with red outline (1 = significant), F_{ST} estimates not different than zero have a white outline (0 = not significant).

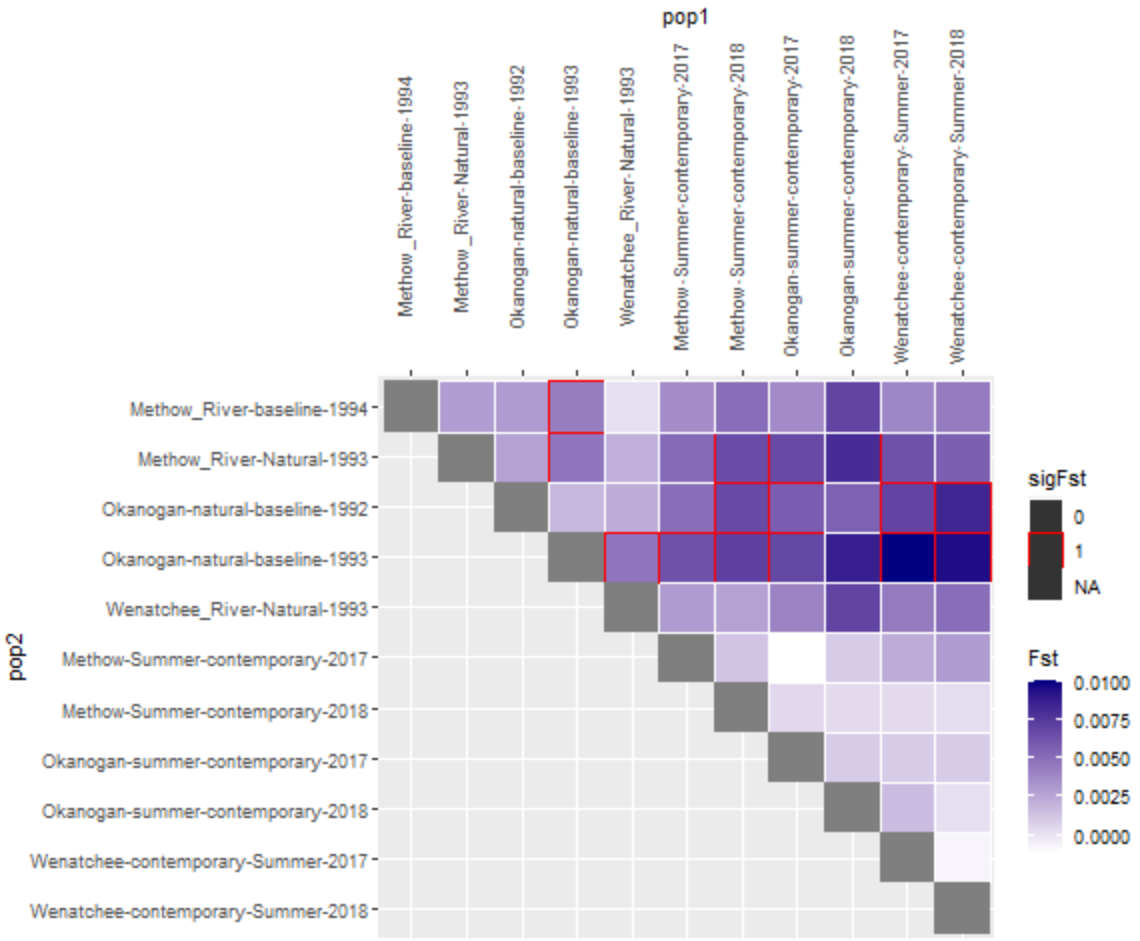


Figure 4. Heatmap of pairwise F_{ST} among baseline and contemporary summer Chinook Salmon populations. 95% confidence intervals were estimated. Those F_{ST} estimates whose 95% confidence intervals lower bound was larger than zero were deemed significantly different from zero and are shown with red outline (1 = significant), F_{ST} estimates not different than zero have a white outline (0 = not significant).

Hanford fall Chinook collections

Baseline collections were not significantly different from one another nor were they significantly different from almost all contemporary collections (Figure 5). The lone exception was the comparison of 1982 hatchery baseline to 2017 contemporary, which had a small F_{ST} (F_{ST} = 0.006) but was statistically significant. All pairwise values indicated little differentiation between all collections.

Figure 5. Heatmap of pairwise F_{ST} among baseline and contemporary Hanford fall Chinook Salmon collections. 95% confidence intervals were estimated. Those F_{ST} estimates whose 95% confidence intervals lower bound was larger than zero were deemed significantly different from zero and are shown with red outline (1 = significant), F_{ST} estimates not different than zero have a white outline (0 = not significant).

Effective Population Size (N_e) – Question 7.4.1
Upper Columbia Summer collections

There was no clear pattern in baseline vs contemporary N_b or N_b/N ratios (Figure 6). Estimates of N were not available for several baseline populations, preventing estimation of N_b/N ratios.

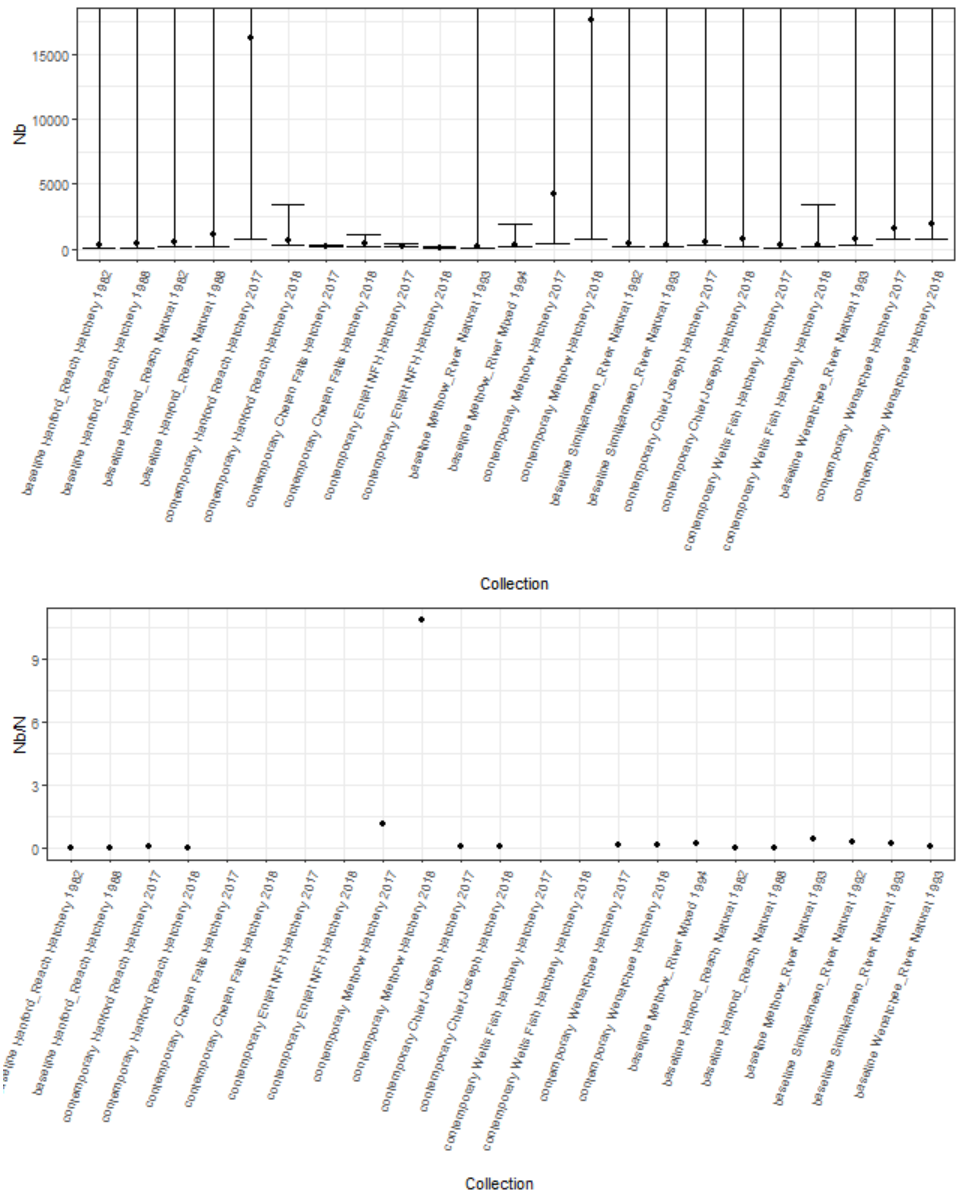


Figure 6. Estimated effective number of breeders (N_b; top) and ratio of N_b to abundance (N_b/N; bottom) for Upper Columbia Summer/Fall Chinook Salmon baseline and contemporary collections. No clear pattern in baseline N_b or N_b/N ratios compared to contemporary was evident (right).

Error bars extending past the graph boundary were infinite indicating not enough linkage disequilibrium existed to estimate the upper bound, i.e., N_b was large. The N_b was estimated using LDNE (Do et al. 2014). Abundance was escapement estimates of hatchery and natural origin fish as found in the WDFW SCoRE database. Since N_b estimates refer to parental generations, abundance from one generation prior was used assuming 5-year generation for natural origin and 4-year generation for hatchery origin.

Hanford fall Chinook collections

Estimates of N_b for baseline collections were slightly lower than those of contemporary collections, but confidence intervals overlapped greatly. The contemporary 2017 collection had a high estimate in relation to the other collections (N_b = 16,246), however, the confidence intervals

overlapped those of other collections (Figure 6). Baseline hatchery and natural collections, and the contemporary 2018 collection had low estimates of N_b, which were significantly different from the contemporary 2017 collection. There appeared to be no differences in all baseline and contemporary collection N_b/N ratios (Figure 6), except for the 2017 contemporary collection.

Discussion

To evaluate genetic impacts of hatchery programs on Upper Columbia summer/fall Chinook Salmon populations, we compared genetic data from baseline and contemporary natural and hatchery collections and evaluated genetic metrics. For summer Chinook Salmon, contemporary hatchery collections and baseline natural collections were similar for the genetic metrics measured (allelic richness, allele frequencies, levels of linkage disequilibrium, and N_b). This suggests that there has not been a significant loss of neutral genetic diversity in contemporary collections relative to baseline collections. For populations with both baseline and contemporary collections, patterns of pairwise F_{ST} showed slightly higher differentiation among baseline collections than among contemporary collections, and highest F_{ST} when comparing baseline vs contemporary. It is possible that contemporary populations have become homogenized, and that contemporary populations have differentiated from baseline populations, likely due to genetic drift; however, most of the F_{ST} comparisons were very low (< 0.01) and non-significant.

In general Hanford fall Chinook Salmon contemporary and baseline collections displayed similar levels for the genetic metrics measured (allele frequencies, allelic richness, F_{ST}, and N_b). Baseline hatchery collections (1982 and 1988) showed slightly higher levels of linkage disequilibrium than the other collections. This pattern is likely due to a relatively low number broodstock used in these years, at least in comparison to natural collections, and to the use of a high proportion of hatchery-origin broodstock which tends to increase LD as a result of higher relatedness. The patterns observed in the Hanford fall Chinook Salmon suggest little population differentiation between baseline and contemporary collections, which is most likely due to the large number of broodstock used. The low level of differentiation among contemporary and baseline collections for summer and fall Chinook Salmon is consistent with a previous evaluation that compared samples collected ~2006-2009 with the same baseline individuals, but using different genetic markers (Kassler et al. 2011).

The maintenance of genetic diversity in contemporary summer/fall Chinook Salmon hatchery programs is in contrast to Upper Columbia steelhead which show a reduction in genetic diversity relative to baseline natural populations. This difference is likely due to the larger census size and larger number of broodstock collected for summer and fall Chinook Salmon hatchery programs relative to steelhead. The larger broodstock numbers would help to prevent the loss of alleles due to genetic drift and promote genetic diversity. All of the natural populations of summer Chinook Salmon (Wenatchee, Methow, and Okanogan) and fall Chinook Salmon (Hanford Reach) are large and genetic changes from mechanisms such as genetic drift are less likely in large populations. In addition, large natural populations are less likely to be influenced by hatchery-origin strays because strays would make up a smaller percent of the total spawning population (Pearsons and Miller, see chapter in this report).

Mann-Whitney tests showed significant differences among all pairwise collections in the amount of linkage disequilibrium, which was not informative. This was likely a power issue. With 255 SNP loci we have a lot of power to detect small differences between collections that are not likely to be biologically significant. In the future, different methods of evaluating LD may need to be developed to obtain meaningful results.

Hatcheries can alter among-population genetic structure, and though the monitoring plan did not specifically call for evaluating among-population structure, we were able to evaluate it. In the upper Columbia, hatchery broodstock for the Grand Coulee Fish Maintenance Project beginning in 1939 were once collected in traps at mainstem Columbia River dams, spawned, and were spread throughout all populations we examined, promoting genetic homogenization. Our F_{ST} results suggest that very little genetic structure currently exists among the Upper Columbia summer or fall Chinook Salmon populations (Figures 3, 4, 5). While the magnitude of F_{ST} was greater in the baseline collections relative to contemporary samples, the values were still very low and consistent with genetic homogenization prior to the collection of baseline samples. Pearsons and O'Connor (2020) measured donor stray rates (rate of fish originating in a population that stray to a different location) of natural origin Chinook Salmon in the UCR ESU. Donor stray rates among basins was very low; most movement was within basin and from downstream to upstream locations. Straying only impacts among population diversity if strays successfully interbreed with the recipient population (effective strays). For hatchery-origin fish, recipient stray rates among basins were very low for populations of Upper Columbia River summer and fall Chinook Salmon (Pearsons and Miller, see chapter in this report). Since 1999, mean recipient stray rates from non-target hatcheries were <0.5% for Wenatchee summer Chinook Salmon, <13% for Methow summer Chinook Salmon, <2.5% for the Okanogan, and < 0.71% for the Hanford Reach. With the exception of the Methow summer Chinook Salmon, all of the recipient populations stray rates were lower than the widely used target of 5% that is used to reduce the risk of loss of between population genetic diversity (Mobrand et al. 2005, Paquet et al. 2011, Hillman et al. 2020). Recipient stray rates of populations that may have been created by human actions had higher stray rates: 14% for the Entiat River and 33% for the Chelan River. Recipient stray rates are currently unknown for natural-origin fish. Effective stray rates are currently unknown but likely lower than estimated recipient stray rates due to local adaptation reducing stray fish reproductive success, which may also drive divergence. Here, however, we used putatively neutral markers, so any divergence observed is likely due to random changes in allele frequencies, i.e., genetic drift.

The monitoring plan and the current implementation of the monitoring plan have limitations, but we are not aware of any other large-scale monitoring of hatchery genetic effects on natural populations that has been developed or implemented. The monitoring plan has been extensively reviewed by science and genetic experts (e.g., ISAB and genetic expert panel) and has been adapted based on evaluation of reviews. One of the challenges associated with long-term genetic monitoring is changes in genetic techniques. Over the years, upper Columbia hatchery evaluations have utilized allozyme, microsatellite, and SNP markers making direct comparisons of results problematic. Adding larger sample sizes to the M&E program may be appropriate when final analyses or specific issues need resolution, but interim evaluations may not need such level of precision, particularly if new and more powerful techniques are available

for future monitoring work. The monitoring plan also lacks monitoring of adaptive genetic diversity. The SNP markers associated with adaptive traits have been discovered and developed for run-timing (Prince et al. 2017, Narum et al. 2018, Thompson et al. 2020) and male age at maturity (McKinney et al. 2020, McKinney et al. 2021) and could be used to evaluate the impacts of hatchery propagation on allele frequencies at these markers. Surprisingly, instead of having polygenic associations with important traits, some of these adaptive traits are associated with single gene regions with only a few variant alleles (Ford et al. 2020). Under this simpler system, variability can be rapidly lost from a population. Monitoring of allele frequencies of these few available marker-trait associations may be important for those traits but also would serve as model data for other undiscovered marker-trait associations that may have a similar genetic architecture. The full PUD monitoring and evaluation plan includes many additional metrics that help evaluate adaptive traits (see other chapters in this report), including straying, productivity, age at maturity, size at age, run and spawn time, spawn distribution, and PNI. Evaluating genetic and other metrics together would provide the most comprehensive means of evaluating the hatchery programs, but it is unclear how additional metrics would influence adaptive management decisions.

This monitoring evaluation was the second timestep of the monitoring plan following initial baseline sampling (e.g., a total of 3 collection times representing multiple broodyears) and represented a large effort in genotyping and analysis to characterize patterns of genetic variation in hatchery and natural origin samples from different time points. However, this evaluation should be considered within the larger context of the long-term monitoring and evaluation plan. Future assessments will occur at 10 year intervals and will result in an increase in sample size and the broodyears included (e.g., evaluations in 2031, 2041, 2051). Definitive conclusions may not be possible during each 10 year timestep, but cumulative assessments should provide useful information to adaptively manage the hatchery programs. As mentioned above, one of the biggest challenges in this timestep and future timesteps is how to compare data and findings from evaluations that use different genetic and analytical techniques. We were able to compare only a subset of data and findings from the last genetic evaluation and we also reran the baseline samples using the most current techniques so that we could make direct comparisons to baseline samples. Future work would benefit by developing technical approaches that would facilitate more direct comparisons across 10 year timesteps. Another potential improvement would be to evaluate the sample sizes, cohorts, and number of timesteps necessary to detect specified genetic changes of interest to managers. The sample sizes and cohorts used in this evaluation were chosen by attempting to balance standard genetic sample sizes, inclusion of the most recent cohorts to provide maximum contrast, and cost. Power analyses could be conducted to refine sample sizes and cohorts necessary to detect changes at a reasonable cost. The power to detect declines in N_b is in part determined by the number of cohorts analyzed (Luikart et al. 2021). Improvements in the power to detect changes in N_b could be achieved by including future 10-year timesteps. Luikart et al. (2021) found that the power to detect a declining trend in N_b nearly doubled when the number of consecutive cohorts analyzed went from five to ten. Up to a point, power also increased when the number of samples and loci used increased. However, changing loci in different timesteps will make it more difficult to compare data across the duration of the monitoring program. While N_b estimates were high in this study, early detection of any future negative trends in N_b would allow for changes to be made to hatchery programs preventing further decline. This might be particularly important if census sizes, which are

monitored annually, decrease substantially. Finally, some of the contemporary collections used in this evaluation (Hanford Reach, Wenatchee, Methow) likely contained both natural- and hatchery-origin individuals; however, data on individual origin was not available, limiting our ability to evaluate whether contemporary natural- and hatchery-origin individuals show different genetic trends, as was clearly seen in upper Columbia steelhead. Obtaining data on individual origin should be considered for the next round of monitoring.

Summary – In agreement with previous analyses, the baseline and contemporary Upper Columbia River summer and fall Chinook Salmon collections showed similar levels of neutral genetic diversity suggesting that hatcheries have not led to a reduction in this genetic diversity within this time frame. These findings are consistent with observed recipient population stray rates and with current management strategies that are intended to minimize genetic risks. However, it is possible that differences in some variables were not detected because of low statistical power. Other assessments of phenotypic variables such as run and spawn timing and age-at-maturity were also evaluated in other chapters of this report. In addition, contemporary collections were composed of either hatchery-origin or a mix of hatchery- and natural-origin individuals, and in the latter case data on origin was not available for individual fish, preventing comparison of genetic patterns in natural- vs hatchery-origin fish in contemporary samples. The lack of genetic differentiation among contemporary and baseline samples is likely explained by a combination of the large population sizes of summer and fall Chinook Salmon relative to the hatchery program sizes in the upper Columbia basin, low recipient population stray rates in natural populations, and the management strategies that were implemented to reduce genetic risk.

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Appendix A. List of adaptive and neutral diploid single nucleotide polymorphic (SNP) loci used in this study. Primer and probe sequences for unpublished loci available by request.

Locus Name	Purpose	Allele 1	Allele 2	Reference
Ots_101770-82	Neutral	G	T	(Janowitz-Koch et al. 2019)
Ots_104048-194	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_105897-124	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_111312-435	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_98409-850	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_98683-796	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_aldb-177M	Neutral	T	A	(Janowitz-Koch et al. 2019)
Ots_Chin30up-211	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_crRAD12711-37	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_crRAD26541-47	Neutral	G	A	(Janowitz-Koch et al. 2019)
Ots_crRAD28677-65	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_crRAD292-21	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_crRAD30341-48	Neutral	T	A	(Janowitz-Koch et al. 2019)
Ots_crRAD33054-62	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_crRAD3758-51	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_crRAD38095-29	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_crRAD38746-36	Neutral	T	A	(Janowitz-Koch et al. 2019)
Ots_crRAD42058-48	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_crRAD48459-74	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_crRAD5061-27	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_crRAD57537-24	Neutral	A	C	(Janowitz-Koch et al. 2019)
Ots_FGF6A	Neutral	G	T	(Janowitz-Koch et al. 2019)
Ots_hsc71-5'-453	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_LEI-292	Neutral	G	A	(Janowitz-Koch et al. 2019)
Ots_MHC1	Neutral	G	A	(Janowitz-Koch et al. 2019)
Ots_SERPC1-209	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_Tnsf	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_u07-17.373	Neutral	A	Deletion	(Janowitz-Koch et al. 2019)
Ots_u07-19.260	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_u1004-117	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_u1006-171	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_USMG5-67	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_zP3b-215	Neutral	G	T	(Janowitz-Koch et al. 2019)
Ots_110495-380	Neutral	G	C	(Janowitz-Koch et al. 2019)
Ots_ARNT	Neutral	G	T	(Janowitz-Koch et al. 2019)
Ots_crRAD18289-33	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_crRAD55400-59	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_crRAD57376-68	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_100884-287	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_101119-381	Neutral	T	C	(Janowitz-Koch et al. 2019)

Locus Name	Purpose	Allele 1	Allele 2	Reference
Ots_101554-407	Neutral	C	G	(Janowitz-Koch et al. 2019)
Ots_101704-143	Neutral	T	G	(Janowitz-Koch et al. 2019)
Ots_102213-210	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_102414-395	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_102457-132	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_102801-308	Neutral	C	A	(Janowitz-Koch et al. 2019)
Ots_102867-609	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_103041-52	Neutral	G	A	(Janowitz-Koch et al. 2019)
Ots_103122-180	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_104063-132	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_104415-88	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_105105-613	Neutral	C	G	(Janowitz-Koch et al. 2019)
Ots_105132-200	Neutral	G	T	(Janowitz-Koch et al. 2019)
Ots_105385-421	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_105401-325	Neutral	G	T	(Janowitz-Koch et al. 2019)
Ots_105407-117	Neutral	T	A	(Janowitz-Koch et al. 2019)
Ots_106313-729	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_106419b-618	Neutral	G	T	(Janowitz-Koch et al. 2019)
Ots_106499-70	Neutral	C	G	(Janowitz-Koch et al. 2019)
Ots_106747-239	Neutral	C	A	(Janowitz-Koch et al. 2019)
Ots_107074-284	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_107285-93	Neutral	T	A	(Janowitz-Koch et al. 2019)
Ots_107607-315	Neutral	A	C	(Janowitz-Koch et al. 2019)
Ots_107806-821	Neutral	T	A	(Janowitz-Koch et al. 2019)
Ots_108007-208	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_108390-329	Neutral	G	C	(Janowitz-Koch et al. 2019)
Ots_108735-302	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_108820-336	Neutral	G	A	(Janowitz-Koch et al. 2019)
Ots_109525-816	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_109693-392	Neutral	T	G	(Janowitz-Koch et al. 2019)
Ots_110064-383	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_110201-363	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_110381-164	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_110551-64	Neutral	C	A	(Janowitz-Koch et al. 2019)
Ots_110689-218	Neutral	T	G	(Janowitz-Koch et al. 2019)
Ots_111084b-619	Neutral	C	A	(Janowitz-Koch et al. 2019)
Ots_111681-657	Neutral	G	T	(Janowitz-Koch et al. 2019)
Ots_112208-722	Neutral	C	A	(Janowitz-Koch et al. 2019)
Ots_112301-43	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_112419-131	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_112820-284	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_112876-371	Neutral	C	A	(Janowitz-Koch et al. 2019)

Locus Name	Purpose	Allele 1	Allele 2	Reference
Ots_113242-216	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_113457-40R	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_115987-325	Neutral	T	G	(Janowitz-Koch et al. 2019)
Ots_117242-136	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_117259-271	Neutral	T	G	(Janowitz-Koch et al. 2019)
Ots_117370-471	Neutral	G	T	(Janowitz-Koch et al. 2019)
Ots_117432-409	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_118175-479	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_118205-61	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_118938-325	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_120950-417	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_122414-56	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_123048-521	Neutral	A	C	(Janowitz-Koch et al. 2019)
Ots_123921-111	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_124774-477	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_126619-400	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_127236-62	Neutral	T	A	(Janowitz-Koch et al. 2019)
Ots_127760-569	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_128302-57	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_128693-461	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_128757-61R	Neutral	A	Deletion	(Janowitz-Koch et al. 2019)
Ots_129144-472	Neutral	C	A	(Janowitz-Koch et al. 2019)
Ots_129170-683	Neutral	C	A	(Janowitz-Koch et al. 2019)
Ots_129458-451	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_129870-55	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_130720-99	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_131460-584	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_131802-393	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_131906-141	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_94857-232R	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_94903-99R	Neutral	G	T	(Janowitz-Koch et al. 2019)
Ots_95442b-204	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_96222-525	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_96500-180	Neutral	G	T	(Janowitz-Koch et al. 2019)
Ots_96899-357R	Neutral	T	A	(Janowitz-Koch et al. 2019)
Ots_97077-179R	Neutral	G	T	(Janowitz-Koch et al. 2019)
Ots_97660-56	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_99550-204	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_afmid-196	Neutral	G	C	(Janowitz-Koch et al. 2019)
Ots_AldB1-122	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_AldoB4-183	Neutral	T	A	(Janowitz-Koch et al. 2019)
Ots_arp-436	Neutral	A	T	(Janowitz-Koch et al. 2019)

Locus Name	Purpose	Allele 1	Allele 2	Reference
Ots_AsnRS-60	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_aspat-196	Neutral	G	C	(Janowitz-Koch et al. 2019)
Ots_BMP2-SNP1	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_brp16-64	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_Cath_D141	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_CCR7	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_CD59-2	Neutral	G	A	(Janowitz-Koch et al. 2019)
Ots_CD63	Neutral	A	C	(Janowitz-Koch et al. 2019)
Ots_cgo24-22	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_CirpA	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_cox1-241	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_CRB211	Neutral	A	C	(Janowitz-Koch et al. 2019)
Ots_crRAD10447-25	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_crRAD11620-55	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_crRAD12037-39	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_crRAD13725-51	Neutral	C	A	(Janowitz-Koch et al. 2019)
Ots_crRAD16540-50	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_crRAD17527-58	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_crRAD18492-65	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_crRAD18937-60	Neutral	G	A	(Janowitz-Koch et al. 2019)
Ots_crRAD20262-46	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_crRAD20376-66	Neutral	G	A	(Janowitz-Koch et al. 2019)
Ots_crRAD20887-70	Neutral	G	A	(Janowitz-Koch et al. 2019)
Ots_crRAD21115-24	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_crRAD22960-32	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_crRAD23631-48	Neutral	G	A	(Janowitz-Koch et al. 2019)
Ots_crRAD24807-74	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_crRAD25367-50	Neutral	T	G	(Janowitz-Koch et al. 2019)
Ots_crRAD255-59	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_crRAD26081-28	Neutral	T	G	(Janowitz-Koch et al. 2019)
Ots_crRAD26165-69	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_crRAD27164-55	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_crRAD27515-69	Neutral	T	A	(Janowitz-Koch et al. 2019)
Ots_crRAD2806-42	Neutral	C	A	(Janowitz-Koch et al. 2019)
Ots_crRAD33491-71	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_crRAD34397-33	Neutral	C	G	(Janowitz-Koch et al. 2019)
Ots_crRAD35313-66	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_crRAD36072-29	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_crRAD36152-44	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_crRAD44588-67	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_crRAD46081-56	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_crRAD46751-42	Neutral	C	T	(Janowitz-Koch et al. 2019)

Locus Name	Purpose	Allele 1	Allele 2	Reference
Ots_crRAD47297-55	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_crRAD55475-26	Neutral	T	G	(Janowitz-Koch et al. 2019)
Ots_crRAD57520-66	Neutral	T	G	(Janowitz-Koch et al. 2019)
Ots_crRAD57687-34	Neutral	T	G	(Janowitz-Koch et al. 2019)
Ots_crRAD60614-46	Neutral	G	T	(Janowitz-Koch et al. 2019)
Ots_crRAD60620-51	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_crRAD61523-71	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_crRAD66330-60	Neutral	G	T	(Janowitz-Koch et al. 2019)
Ots_crRAD69327-53	Neutral	G	T	(Janowitz-Koch et al. 2019)
Ots_crRAD73823-60	Neutral	T	A	(Janowitz-Koch et al. 2019)
Ots_crRAD74766-28	Neutral	G	A	(Janowitz-Koch et al. 2019)
Ots_crRAD75581-70	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_crRAD76512-28	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_crRAD78968-46	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_crRAD92420-25	Neutral	G	T	(Janowitz-Koch et al. 2019)
Ots_crRAD9615-69	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_DDX5-171	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_E2-275	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_EndoRB1-486	Neutral	G	A	(Janowitz-Koch et al. 2019)
Ots_EP-529	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_Est1363	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_Est740	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_ETIF1A	Neutral	A	C	(Janowitz-Koch et al. 2019)
Ots_FARSLA-220	Neutral	G	A	(Janowitz-Koch et al. 2019)
Ots_FGF6B_1	Neutral	A	C	(Janowitz-Koch et al. 2019)
Ots_GCSH	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_GDH-81x	Neutral	C	Deletion	(Janowitz-Koch et al. 2019)
Ots_GH2	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_GnRH-271	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_GPDH-338	Neutral	G	A	(Janowitz-Koch et al. 2019)
Ots_GPH-318	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_GST-207	Neutral	G	A	(Janowitz-Koch et al. 2019)
Ots_GST-375	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_GTH2B-550	Neutral	C	G	(Janowitz-Koch et al. 2019)
Ots_HFABP-34	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_HMGB1-73	Neutral	G	T	(Janowitz-Koch et al. 2019)
Ots_hnRNPL-533	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_hsc71-3'-488	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_hsp27b-150	Neutral	G	A	(Janowitz-Koch et al. 2019)
Ots_Hsp90a	Neutral	G	C	(Janowitz-Koch et al. 2019)
Ots_HSP90B-100	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_IGF-I.1-76	Neutral	A	T	(Janowitz-Koch et al. 2019)

Locus Name	Purpose	Allele 1	Allele 2	Reference
Ots_Ikaros-250	Neutral	G	A	(Janowitz-Koch et al. 2019)
Ots_IL11	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_IL8R_C8	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_IsoT	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_LWSop-638	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_mapK-3'-309	Neutral	T	G	(Janowitz-Koch et al. 2019)
Ots_mapKpr-151	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_MetA	Neutral	T	A	(Janowitz-Koch et al. 2019)
Ots_MHC2	Neutral	T	G	(Janowitz-Koch et al. 2019)
Ots_mybp-85	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_Myc-366	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_myo1a-384	Neutral	A	C	(Janowitz-Koch et al. 2019)
Ots_myoD-364	Neutral	T	G	(Janowitz-Koch et al. 2019)
Ots_NAML12-SNP1	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_nelfd-163	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_NFYB-147	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_nkef-192	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_NOD1	Neutral	C	G	(Janowitz-Koch et al. 2019)
Ots_nramp-321	Neutral	G	A	(Janowitz-Koch et al. 2019)
Ots_ntl-255	Neutral	T	A	(Janowitz-Koch et al. 2019)
Ots_Ostm1	Neutral	C	G	(Janowitz-Koch et al. 2019)
Ots_OTALDBINT1-SNP1	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_OTDESMIN19-SNP1	Neutral	C	A	(Janowitz-Koch et al. 2019)
Ots_Ots311-101x	Neutral	A	Deletion	(Janowitz-Koch et al. 2019)
Ots_OTSMTA-SNP1	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_OTSTF1-SNP1	Neutral	G	T	(Janowitz-Koch et al. 2019)
Ots_P450-288	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_P450	Neutral	T	A	(Janowitz-Koch et al. 2019)
Ots_P53	Neutral	G	A	(Janowitz-Koch et al. 2019)
Ots_parp3-286	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_PEMT	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_PGK-54	Neutral	T	A	(Janowitz-Koch et al. 2019)
Ots_pigh-105	Neutral	A	Deletion	(Janowitz-Koch et al. 2019)
Ots_pop5-96	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_ppie-245	Neutral	C	A	(Janowitz-Koch et al. 2019)
Ots_Prl2	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_RAD4543-52	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_RAG3	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_RAS1	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_redd1-187	Neutral	A	G	(Janowitz-Koch et al. 2019)

Locus Name	Purpose	Allele 1	Allele 2	Reference
Ots_RFC2-558	Neutral	A	Deletion	(Janowitz-Koch et al. 2019)
Ots_S7-1	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_SClkF2R2-135	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_sept9-78	Neutral	G	A	(Janowitz-Koch et al. 2019)
Ots_SL	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_slc7a2-71	Neutral	G	T	(Janowitz-Koch et al. 2019)
Ots_stk6-516	Neutral	C	A	(Janowitz-Koch et al. 2019)
Ots_SWS1op-182	Neutral	T	A	(Janowitz-Koch et al. 2019)
Ots_TAPBP	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_TCTA-58	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_TGFB	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_Thio	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_TLR3	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_TNF	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_tpx2-125	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_trnau1ap-86	Neutral	G	T	(Janowitz-Koch et al. 2019)
Ots_txnip-321	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_u07-07.161	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_u07-17.135	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_u07-18.378	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_u07-20.332	Neutral	A	C	(Janowitz-Koch et al. 2019)
Ots_u07-25.325	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_u07-49.290	Neutral	G	A	(Janowitz-Koch et al. 2019)
Ots_u07-53.133	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_u07-57.120	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_u07-64.221	Neutral	G	C	(Janowitz-Koch et al. 2019)
Ots_u1002-75	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_u1007-124	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_u1008-108	Neutral	T	A	(Janowitz-Koch et al. 2019)
Ots_u202-161	Neutral	T	A	(Janowitz-Koch et al. 2019)
Ots_u211-85	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_U212-158	Neutral	G	A	(Janowitz-Koch et al. 2019)
Ots_U2305-63	Neutral	T	Deletion	(Janowitz-Koch et al. 2019)
Ots_U2362-227	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_U2362-330	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_U2446-123	Neutral	C	A	(Janowitz-Koch et al. 2019)
Ots_U2567-104	Neutral	G	A	(Janowitz-Koch et al. 2019)
Ots_u4-92	Neutral	T	C	(Janowitz-Koch et al. 2019)
Ots_U5049-250	Neutral	G	T	(Janowitz-Koch et al. 2019)
Ots_U5121-34	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_u6-75	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_unk1104-38	Neutral	C	T	(Janowitz-Koch et al. 2019)

Locus Name	Purpose	Allele 1	Allele 2	Reference
Ots_unk1832-39	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_unk3513-49	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_unk526	Neutral	A	G	(Janowitz-Koch et al. 2019)
Ots_unk7936-50	Neutral	C	G	(Janowitz-Koch et al. 2019)
Ots_unk9480-51	Neutral	G	C	(Janowitz-Koch et al. 2019)
Ots_vatf-251	Neutral	G	Deletion	(Janowitz-Koch et al. 2019)
Ots_zn593-346	Neutral	A	T	(Janowitz-Koch et al. 2019)
Ots_ZR-575	Neutral	G	A	(Janowitz-Koch et al. 2019)
Ots28_11073102	Adaptive	T	A	(Narum et al. 2018)
Ots28_11202863	Adaptive	C	A	(Narum et al. 2018)
Ots28_11186543	Adaptive	A	T	(Narum et al. 2018)
Ots28_11033282	Adaptive	G	A	(Narum et al. 2018)
Ots28_11202400	Adaptive	C	T	(Narum et al. 2018)
Ots28_11062192	Adaptive	C	G	(Narum et al. 2018)
Ots28_11025336	Adaptive	A	C	(Narum et al. 2018)
Ots28_11095755	Adaptive	A	T	(Narum et al. 2018)
Ots28_11077576	Adaptive	A	G	(Narum et al. 2018)
Ots28_11202190	Adaptive	T	C	(Narum et al. 2018)
Ots28_11077172	Adaptive	G	A	(Narum et al. 2018)
Ots28_11160599	Adaptive	G	T	(Narum et al. 2018)
Ots28_11205993	Adaptive	C	T	(Narum et al. 2018)
Ots28_11075712	Adaptive	C	T	(Narum et al. 2018)
Ots28_11072994	Adaptive	C	T	(Narum et al. 2018)
Ots28_11164637	Adaptive	C	A	(Narum et al. 2018)
Ots28_11201129	Adaptive	T	G	(Narum et al. 2018)
Ots28_11073668	Adaptive	T	A	(Narum et al. 2018)
Ots28_11023212	Adaptive	A	G	(Narum et al. 2018)
Ots28_11206740	Adaptive	T	C	(Narum et al. 2018)
Ots28_11143508	Adaptive	G	A	(Narum et al. 2018)
Ots28_11070757	Adaptive	A	G	(Narum et al. 2018)
Ots28_11071377	Adaptive	T	C	(Narum et al. 2018)
Ots28_11077016	Adaptive	C	T	(Narum et al. 2018)
Ots28_11207428	Adaptive	T	G	(Narum et al. 2018)
Ots28_11210919	Adaptive	C	T	(Narum et al. 2018)
Ots28_11205423	Adaptive	A	G	(Narum et al. 2018)
Ots28_11075348	Adaptive	G	A	(Narum et al. 2018)
Ots37124-12267397	Adaptive	C	T	SWFSC – Clemento unpubl.
Ots37124-12272852	Adaptive	C	T	SWFSC – Clemento unpubl.
Ots37124-12277401	Adaptive	T	A	SWFSC – Clemento unpubl.
Ots37124-12281207	Adaptive	A	T	SWFSC – Clemento unpubl.
Ots37124-12310649	Adaptive	A	T	SWFSC – Clemento unpubl.
Ots19_46172427	Adaptive	G	A	(Narum et al. 2018)

Locus Name	Purpose	Allele 1	Allele 2	Reference
Ots19_46172133	Adaptive	C	T	(Narum et al. 2018)
Ots17_22360456	Adaptive	T	G	(Narum et al. 2018)
Ots14_5453033	Adaptive	G	A	(Narum et al. 2018)
Ots4_42378741	Adaptive	C	T	(Narum et al. 2018)
Ots5_70908626	Adaptive	T	C	(Narum et al. 2018)
Ots11_32418659	Adaptive	A	T	(Narum et al. 2018)
Ots18_3550047	Adaptive	A	G	(Narum et al. 2018)
Ots3_57055518	Adaptive	T	C	(Narum et al. 2018)
Ots4_41638710	Adaptive	G	A	(Narum et al. 2018)
Ots29_18791740	Adaptive	T	G	(Narum et al. 2018)
Ots9_16115048	Adaptive	G	A	(Narum et al. 2018)
Ots29_23344676	Adaptive	T	C	(Narum et al. 2018)
Ots4_40942276	Adaptive	G	A	(Narum et al. 2018)
Ots30_17330688	Adaptive	T	C	(Narum et al. 2018)
Ots22_32650802	Adaptive	G	A	(Narum et al. 2018)
Ots3_34894254	Adaptive	T	C	(Narum et al. 2018)
Ots30_17330452	Adaptive	G	C	(Narum et al. 2018)
Ots7_50997124	Adaptive	G	T	(Narum et al. 2018)
Ots18_3426299	Adaptive	T	A	(Narum et al. 2018)
Ots6_10904949	Adaptive	C	T	(Narum et al. 2018)
Ots18_29943476	Adaptive	A	G	(Narum et al. 2018)
Ots4_64978818	Adaptive	C	A	(Narum et al. 2018)
Ots10_21244146	Adaptive	A	C	(Narum et al. 2018)
Ots17_885364	Adaptive	C	A	(Narum et al. 2018)
Ots2_38264269	Adaptive	A	C	(Narum et al. 2018)
Ots33_19359879	Adaptive	T	C	(Narum et al. 2018)
Ots6_33505144	Adaptive	T	A	(Narum et al. 2018)
Ots5_44795073	Adaptive	C	T	(Narum et al. 2018)
Ots18_32088284	Adaptive	T	C	(Narum et al. 2018)
Ots15_18157381	Adaptive	C	T	(Narum et al. 2018)
Ots12_23066874	Adaptive	A	G	(Narum et al. 2018)
Ots2_42405643	Adaptive	G	T	(Narum et al. 2018)
Ots7_51409415	Adaptive	T	C	(Narum et al. 2018)
Ots1_72858599	Adaptive	A	G	(Narum et al. 2018)
Ots7_53291035	Adaptive	G	A	(Narum et al. 2018)
Ots7_53631522	Adaptive	A	G	(Narum et al. 2018)
Ots18_30099101	Adaptive	C	T	(Narum et al. 2018)
Ots11_11925999	Adaptive	G	T	(Narum et al. 2018)
Ots18_3541813	Adaptive	T	C	(Narum et al. 2018)
Ots9_28975221	Adaptive	A	T	(Narum et al. 2018)
Ots_CHI06048618_5222	Adaptive	T	G	Chen unpublished
Ots_CHI06105101_18523	Adaptive	A	G	Chen unpublished

Locus Name	Purpose	Allele 1	Allele 2	Reference
Ots_CHI06105101_16717	Adaptive	C	T	Chen unpublished
Ots_CHI06035945_4547	Adaptive	C	T	Chen unpublished
Ots_CHI06027687_143477	Adaptive	G	A	Chen unpublished
Ots18_3417174	Adaptive	A	C	(Narum et al. 2018)
Ots11_32468959	Adaptive	G	C	(Narum et al. 2018)
Ots7_54212944	Adaptive	T	A	(Narum et al. 2018)
Ots_SEXY3-1	Sex ID	X	Y	(Janowitz-Koch et al. 2019)

Janowitz-Koch, I., Rabe, C., Kinzer, R., Nelson, D., Hess, M.A., and Narum, S.R. 2019. Long-term evaluation of fitness and demographic effects of a Chinook Salmon supplementation program. Evol. Appl. 12: 456-469. doi:10.1111/eva.12725.

Narum, S.R., Genova, A.D., Micheletti, S.J., and Maass, A. 2018. Genomic variation underlying complex life-history traits revealed by genome sequencing in Chinook salmon. Proc. R. Soc. B 285(1883): 20180935. doi:10.1098/rspb.2018.0935.

Appendix B. WDFW GTseq genotyping protocol details

The genotyping was done using a cost-effective method based on custom amplicon sequencing called Genotyping in Thousands (GTseq) (Campbell et al. 2015). GTseq is an efficient genotyping method that amplifies pools of targeted SNPs and then indexes individual samples. The pools are sequenced, de-multiplexed, and genotyped by generating a ratio of allele counts for each individual. The entire process can be broken down into four segments; extraction, library preparation, sequencing, and genotyping.

Genomic DNA was extracted for all samples by digesting a small piece of fin tissue with a Macherey-Nagel 96 column NucleoSpin kit, following the manufacturers recommendations (Macherey-Nagel GmbH & Co. KG, Duren, Germany). The DNA was then concentrated 2.5 times before proceeding to library preparation. Next, the multiplexed pool of targeted loci was amplified. The multiplex PCR consisted of 2uL of cleaned DNA extract, 3.5uL of Qiagen Multiplex PCR Plus mix (Qiagen, 10672201), and 1.5uL pooled primer mix (IDT, Appendix A, final volume = 7uL; final primer concentrations at each locus = 54nM). Thermal cycling conditions were as follows: 95°C-15 min; 5 cycles [95°C – 30 s, 5% ramp down to 57°C – 30 s, 72°C – 2 min]; 10 cycles [95°C – 30 s, 65°C – 30 s, 72°C – 30 s]; 4°C hold. Following the multiplex PCR, the amplified samples were diluted 20-fold. 3uL of diluted multiplex PCR product was then used in the barcoding PCR. The barcoding PCR adds indexes that identify each sample by well and by plate. For the barcoding PCR, 1uL of 10uM well-specific i5 tagging primer (IDT) and 1uL of 10uM plate-specific i7 tagging primer were added to the 3uL of amplified sample. 5uL of Qiagen Multiplex PCR Plus mix (Qiagen, 10672201) was then added for a final reaction volume of 10uL. Thermal cycling conditions were: 95°C – 15 min; 10 cycles [98°C – 10 s, 65°C – 30 s, 72°C – 30 s]; 72°C – 5 min; 4°C hold. Following the barcode PCR, each plate of samples (library) was normalized using the SequalPrepTM Normalization Plate Kit (Applied Biosystems, A1051001) according to the manufacturer's instructions. Upon completion of normalization, 10uL of each sample per 96-well plate was pooled into a 1.5mL tube constituting a library. A purification step was then performed on each library with Agencourt AMPure® XP magnetic beads (Agencourt, A63881) according to the manufacturer's instructions for size selection with a 2:1 and 1.43:1 ratio of library to beads. The purified libraries were then eluted with 15uL of TE pH 8.0. In order to complete the final process of library preparation, each library was quantified and normalized. The libraries were quantified using a Qubit 3 Fluorometer (Invitrogen) and QubitTMdsDNA HS Assay Kit reagents (Invitrogen, Q32854) according to the manufacturer's instructions. Following the quantification, the concentration of each library was calculated using the molecular weight specific to the multiplex pool used (i.e. One.382). Then each library was normalized to 4nM and pooled with other libraries that were sequenced on the same sequencing run. Pooled libraries were then sequenced at a 2.5pM loading concentration on an Illumnia NextSeq 500 instrument of a single-end read flow cell using 111 cycles with dual-index reads of six cycles each. To genotype the samples, a bioinformatics pipeline was used. This pipeline is explained and available online at https://github.com/GTseq/GTseq-Pipeline (Campbell et al. 2015). Essentially, there are a series of custom perl scripts that ultimately count amplicon-specific sequences for each allele. Allele ratios are then used to generate genotypes.

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Comparison of Age at Maturity, Size-At-Age, and Sex Ratio Between Hatchery- and Natural-Origin Fall Chinook Salmon in the Hanford Reach of the Columbia River

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Abstract

We characterized differences in age-at-maturity, size-at-age, and sex ratio between hatchery- and natural-origin adult fall Chinook Salmon carcasses collected during surveys of the Hanford Reach of the Columbia River during brood years 2007-2013. A shift to younger adult fish was observed in hatchery-origin fish in both males and females. The majority of adult natural-origin males and females and from brood years were age 4; whereas, increases in age 3 fish were observed in both hatchery-origin males and females with the majority of hatchery-origin males returning as age 3. A significant difference ($P < 0.0001$) in the relative frequencies of males and females was observed between natural-and hatchery-origin carcasses recovered in the Hanford Reach for all brood years; the M:F ratios of hatchery-origin fish were lower than natural-origin males were 0.67 and 1.04, respectively. Hatchery-origin fish were slightly larger than natural-origin at age 3 but not significantly ($P = 0.1420$) and natural-origin fish were significantly ($P < 0.0001$) larger than hatchery-origin fish at ages 4 and 5 regardless of fish sex. The interaction between fish age and fish sex was also significant ($P < 0.0001$) and the post-hoc Tuckey tests for fish age and fish sex revealed that females were significantly ($P < 0.0001$) larger than males at age 3, while males were significantly ($P<0.0001$) larger than females at ages 4 and 5. A carcass recovery bias for larger, older, male fish likely contributes to these results, particularly sex ratio. However, patterns of differences between origins for age and size are accurate even after accounting for carcass recovery bias.

Introduction

Hatchery supplementation of Chinook Salmon populations can influence a variety of population characteristics that include age-at-maturity, size-at-age, and sex ratio (Knudsen et al. 2006; Ford et al. 2015). These features of the population can influence the desirability of fish harvested and alter the demographics and other biological characteristics of the supplemented natural production. Large fish are more desirable by harvesters and have higher capacity to produce offspring by producing more eggs or by competitive dominance (Knudsen et al. 2008; Schroder et al. 2008; 2010; 2012). Speculations on mechanisms for difference in hatchery- and natural-origin adults include enhanced growth rates in the hatchery environment compared to the natural environment (Larsen et al. 2013) and the production of larger smolts can result in higher proportions of micro- or mini-jacks (Harstad et al. 2014; Ford et al. 2015) and increased numbers of jacks returning from the ocean after one year. Hatchery produced adults are often smaller, may also have lower fecundity, or are less successful in competing for desirable spawning partners or habitat leading to lower reproductive success (Knudsen et al. 2006; 2008; Ford et al. 2015). Hatchery supplementation can also alter sex ratios through these mechanisms or are coupled with different selection pressures on segments of the population (Fast et al. 2015).

The purpose of this evaluation was to examine age-at-maturity, size-at-age and sex ratio of fall run Chinook Salmon in the Hanford Reach of the Columbia River and determine if hatchery- and natural-origin fish differ. This work extends upon our previous work by providing other metrics influencing reproductive success of hatchery- and natural- origin salmon in the Hanford Reach.

Methods

Study Area

The Hanford Reach is one of the last non-impounded reaches of the Columbia River and the location of the largest and most productive natural spawning fall Chinook Salmon population in the United States (Harnish et al. 2014, Langshaw et al. 2015, Harnish 2017, Langshaw et al. 2017). The Hanford Reach extends 82 km from the city of Richland to the base of Priest Rapids Dam. Natural-origin fall Chinook Salmon produced in the Hanford Reach emerge from the substrate in the spring and rear there until outmigration in the summer with adults returning to the Columbia River two to five years later. The Priest Rapids Hatchery (PRH) was constructed by Grant County Public Utility District (GCPUD) at the top end of the Hanford Reach to mitigate for losses associated with the inundation of the portions of the Columbia River caused by the construction of Priest Rapids (1959) and Wanapum dams (1963). The PRH has evolved from a spawning channel initially constructed downstream from Priest Rapids Dam in 1963 to a state-of-the-art hatchery facility completed in 2014. The annual release of fall Chinook salmon smolts from PRH has ranged considerably since the initial release of roughly 150,625 million smolts in 1978 to over 10 million in 1983. The PRH program release goal was then set at 5 million subyearling smolts until 2006. After which the release goal was set at 6.7 million to include production at PRH for the United States Army Corps of Engineers (USACE). Later, adjustments to the GCPUD mitigation increased the total release goal to 7.3 million smolts in 2014. In addition to production released by PRH, the USACE has funded the release of fall Chinook Salmon from Ringold Springs Hatchery (RSH) into the lower end of the Hanford Reach

beginning in 1994. The smolts released by RSH were derived from adult salmon returning to Bonneville Hatchery prior to 2009; since then PRH has collected eggs sufficient to release 3.5 million subyearling smolts. Thus, a total annual release goal of 10.8 million hatchery reared subyearling smolts have been scheduled for release to the Hanford Reach from 2014 to present.

Carcass sampling

Carcass surveys were conducted annually by Washington Department of Fish and Wildlife in the Hanford Reach from early November through mid-December as part of monitoring and evaluation of PRH and RSH programs. Carcasses were collected while walking the shorelines and islands of the river or by gaffing submerged carcasses from boats. Two to four survey teams consisting of two or three staff survey different sections of the Hanford Reach seven days per week throughout the entire field season. Staff systematically subsample the carcasses for demographic data contributing to the long-term monitoring of natural- and hatchery-origin fish. The demographic data gathered during the surveys of individual carcasses included fish sex, fork length (cm), and the presence or absence of CWT or adipose clip. Additionally, CWT are collected, and scale and otolith samples are collected for later analysis. Fish sex was determined by either external morphological characteristics or by inspection of the gonads. Fish age was obtained from the scale samples examined by the WDFW Scale Ageing Lab. CWT were extracted and codes read to determine origin. Not all fish released by PRH have adipose clips or CWT; however, since the 2007 brood year, all fish released by PRH have a thermal mark applied to fish during incubation. Otolith samples of fish not identified by adipose clip or CWT were examined by the WDFW Otolith Lab to assign origin. Thus, the origin of all fish carcasses could be determined by the presence of a hatchery mark or coded-wire tag.

Fish carcasses were assigned hatchery-origin if they had an adipose clip, a CWT of hatchery-origin, or a thermal mark. Carcasses not possessing any form of these hatchery marks were classified as natural-origin. At the end of each return year the numbers of hatchery- and natural-origin could be summarized by sex and age and estimates for the total numbers of fish in each category determined using an expansion based on an estimated sample rate. This demographic sample rate varied among years and was determined by dividing the number of adult carcasses collected by the total adult estimated escapement to the Hanford Reach (Richards and Pearsons 2019). The frequencies of male and female carcasses were summarized by age and origin and the numbers expanded for each brood year from 2007 to 2013.

Age composition analysis

A chi-square test was performed (McDonald 2014) for males and females separately comparing the frequency distributions of hatchery- and natural- origin fish recorded in the ages 3 to age 5. Age 6 fish were excluded from the analysis due to the relative low frequency that they were observed. A threshold for significance was set at $P < 0.05$. Due to the large numbers examined, a Cramer's V value was also calculated for each test to show the strength of the association between the two categorical fields (Cohen 1988). The percentages of hatchery- and natural-origin male and female fish returning at ages 3-5 were calculated. The means and 95% confidence intervals for the percent of the total brood year cohort returning as age three to five were calculated for both males and females and compared.

Sex ratio analysis

A chi-square analyses was performed to compare the frequencies of male and female fish of hatchery- and natural-origin fish in the carcass samples for each year. A threshold for significance was set at $P < 0.05$. A Phi statistic was also calculated to characterize the strength of the association of fish sex and fish origin. The M:F ratio was calculated for each year and the mean M:F ratio with 95% confidence interval was calculated and the values for hatchery- and natural-origin fish compared.

Size at age analysis

A three-way analysis of variance was used to compare fork lengths recorded for each carcass. The main effects of age, sex and origin and all interactions were included in the model. Following analysis of variance, a Tukey's HSD test was applied to illustrate specific significant differences among means. A threshold for significance was set at $P < 0.05$.

Results

Age Composition

Significant differences were found in the frequency distributions of male and female fish between natural- and hatchery-origin fish in all age groups for all brood years (Table 1 and Table 2; $P < 0.0001$). Additionally, the corresponding Cramer's V values were all greater than 0.50 (Table 1 and Table 2) indicating strong associations of this relationship across all age classes. The source of these differences appears to be a shift to younger adult fish in hatchery-origin fish for both males and females. The majority of adult natural-origin males and females and from brood years 2007 – 2013 were age 4; whereas, higher frequencies of age 3 fish were observed in both male and female hatchery-origin fish with the majority of hatchery-origin males returning as age 3 (Figure 1). For the brood years examined, an average of 26% hatchery-origin females and 57% of the hatchery-origin males returned as age 3 fish versus 6% natural-origin females and 36% of the natural-origin males returning at age 3; in both these cases the 95% confidence interval did not overlap (Figure 1).

Sex Ratio

A significant difference ($P < 0.0001$) in the relative frequencies of male and female fish were observed between natural-and hatchery-origin carcasses recovered in the Hanford Reach for all brood years. Additionally, the corresponding the Phi values were all greater than > 0.50 (Table 1 and Table 2) suggesting a strong association between the variables of fish sex and fish origin. For all seven brood years, the M:F ratio of hatchery-origin fish was lower than natural-origin males (Table 3). The mean M:F ratio for hatchery-origin fish was 0.67 and the ratio for natural-origin fish was 1.04 and in both these instances the 95% confidence intervals did not overlap (Figure 2).

Size at Age

The three-way analysis of variance revealed significant ($P < 0.001$) contributions of the main effects of fish sex, fish age, and fish origin on the fork length of salmon carcasses collected on the Hanford Reach (Table 4). However, the significant interaction between fish sex and fish age and between fish origin and fish age indicate inconsistencies in the relative difference in fork length between males and females across a range of ages and between hatchery- and natural-origin fish across a rang of ages. The post-hoc Tukey tests for fish origin across a range of fish

ages revealed that hatchery-origin fish fork lengths were slightly larger than natural-origin at age 3 but not significantly ($P = 0.1420$) (Table 4) while natural-origin fish were significantly ($P < 0.0001$) larger than hatchery-origin fish at ages 4 and 5 (Figure 3) regardless of fish sex. The interaction between fish age and fish sex was also significant ($P < 0.0001$) and the post-hoc Tukey tests for fish age and fish sex revealed that females were significantly ($P < 0.0001$) larger than males at age 3, while males were significantly ($P<0.0001$) larger than females at ages 4 and 5 (Figure 4).

Table 1. Age composition of hatchery- and natural-origin female fall Chinook Salmon escapement to the Hanford Reach of the Columbia River, Brood Years 2007 - 2013 A Chi-square test for independence and Cramer's V score was performed for each brood year to determine if the age frequencies by origin were dependent on one another.

Brood Year	Origin	Age 3	Age 4	Age 5	X^2	P	Cramer's V
2007	Hatchery	3,237	1,808	860	37,678.672	<0.0001	0.86
	Natural	2,235	31,427	10,967			
2008	Hatchery	499	1,844	488	11,560.119	<0.0001	0.77
	Natural	1,953	11,357	3,415			
2009	Hatchery	851	12,930	302	13,528.836	<0.0001	0.52
	Natural	1,169	27,731	6,132			
2010	Hatchery	10,230	10,958	3,262	119,724.389	<0.0001	0.86
	Natural	3,594	74,650	59,477			
2011	Hatchery	265	9,300	2,442	65,107.624	<0.0001	0.81
	Natural	463	67,158	19,760			
2012	Hatchery	4,452	5,874	1,662	44,104.369	<0.0001	0.76
	Natural	8,267	35,200	21,104			
2013	Hatchery	1,040	2,704	575	16,323.398	<0.0001	0.76
	Natural	1,319	20,411	1,879			

Table 2. Age composition of hatchery- and natural-origin male fall Chinook Salmon escapement to the Hanford Reach of the Columbia River, Brood Years 2007 - 2013 A Chi-square test for independence and Cramer's V score was performed for each brood year to determine if the age frequencies by origin were dependent on one another.

Brood Year	Origin	Age 3	Age 4	Age 5	X^2	*P*	Cramer's V
2007	Hatchery	3,521	511	365	30,329	<0.0001	0.84
	Natural	14,430	18,490	5,305			
2008	Hatchery	545	644	168	14,419	<0.0001	0.89
	Natural	5,993	8,922	2,108			
2009	Hatchery	2,146	5,390	155	32,120	<0.0001	0.77
	Natural	11,004	31,530	3,622			
2010	Hatchery	20,071	2,671	845	104,409	<0.0001	0.79
	Natural	52,387	65,816	25,555			
2011	Hatchery	1,393	3,463	493	56,767	<0.0001	0.89
	Natural	12,819	44,634	9,567			
2012	Hatchery	5,143	1,766	130	50,032	<0.0001	0.84
	Natural	34,724	22,101	6,381			
2013	Hatchery	1,717	719	38	22,045	<0.0001	0.87
	Natural	12,714	12,127	1,879			

Table 3. Sex ratio of hatchery- and natural-origin fall Chinook Salmon escapement to the Hanford Reach of the Columbia River, Brood Years 2007 - 2013 A Chi-square test for independence and Phi score was performed for each brood year to determine if the sex ratios by origin were dependent on one another.

Brood Year	Origin	Female	Male	Sex Ratio (M:F)	X^2	*P*	Phi
2007	Hatchery	5,905	4,397	0.74	63,616	<0.0001	0.83
	Natural	44,629	38,306	0.86			
2008	Hatchery	2,831	1,822	0.64	25,938	<0.0001	0.81
	Natural	16,781	17,799	1.06			
2009	Hatchery	14,083	7,952	0.56	45,803	<0.0001	0.66
	Natural	35,139	47,767	1.36			
2010	Hatchery	24,450	24,645	1.01	194,670	<0.0001	0.76
	Natural	139,178	145,204	1.04			
2011	Hatchery	12,007	6,028	0.50	124,873	<0.0001	0.84
	Natural	87,599	71,189	0.81			
2012	Hatchery	11,987	7,622	0.64	95,819	<0.0001	0.80
	Natural	64,877	67,080	1.03			
2013	Hatchery	4,320	2,650	0.61	38,220	<0.0001	0.81
	Natural	23,608	27,507	1.17			

Table 4. Three-way ANOVA of fork length for fall Chinook Salmon escapement to the Hanford Reach during return years 2010 – 2018. The ANOVA tested for effect of age, origin, and sex (ages 3 to 5 for male and females) and all possible interactions.

		Mean Square		
Factor	DF	Error	F value	*P*
Scale Age (SA)	2	292753	7372.768	< 0.0001
Sex (S)	1	23653	595.685	< 0.0001
Origin (O)	1	520	13.099	0.0003
SA x S	2	17996	453.225	< 0.0001
SA x O	2	818	20.593	< 0.0001
S x O	1	97	2.447	0.1178
SA x S x O	2	48	1.217	0.2962
Residuals	12605	40		

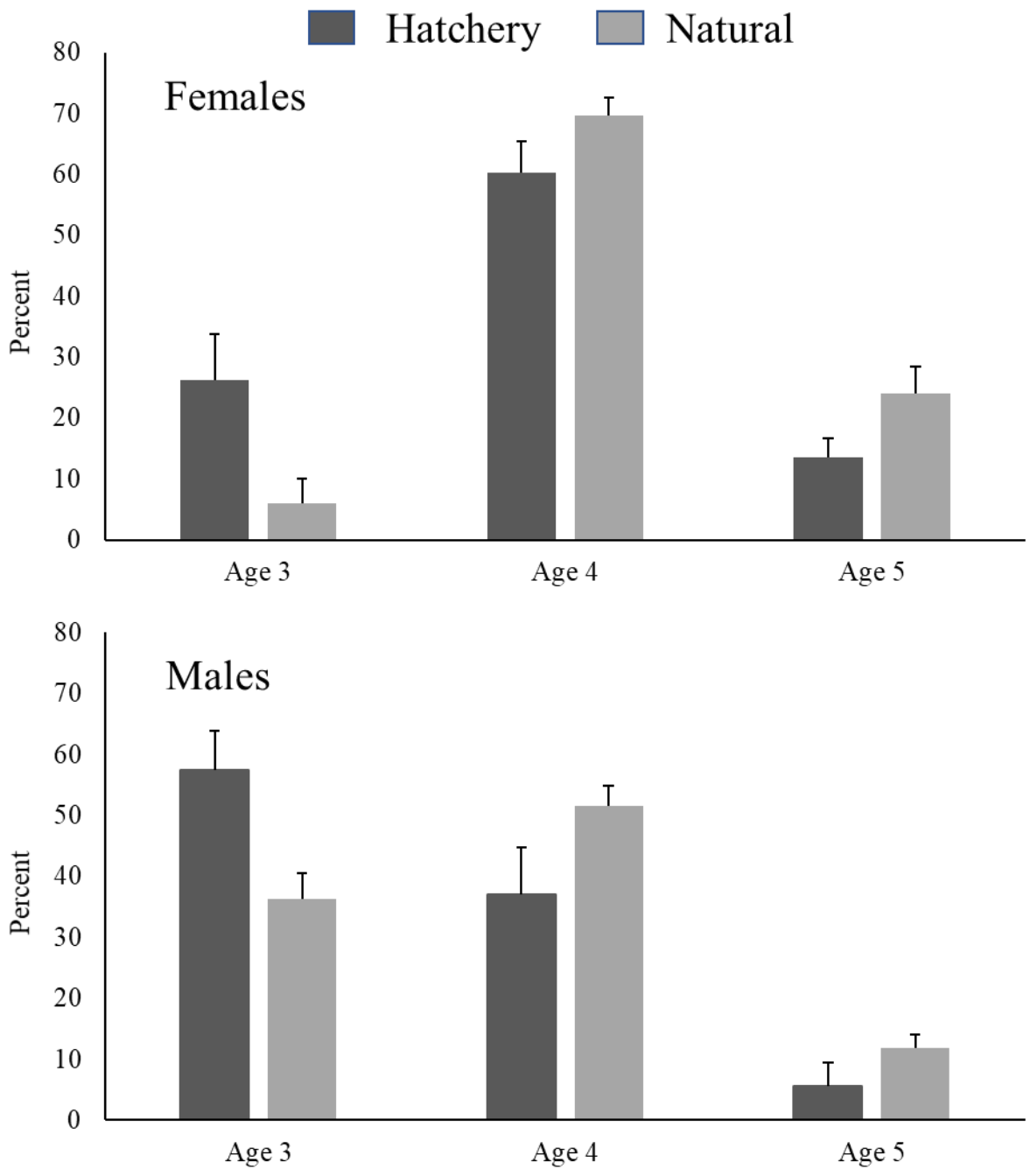

Figure 1. Mean percent composition of male and female fall Chinook Salmon carcasses of hatchery- and natural-origin over the ages of ages 3-5 that were recovered in the Hanford Reach for brood years 2007 – 2013. Vertical bars denote 95% confidence intervals.

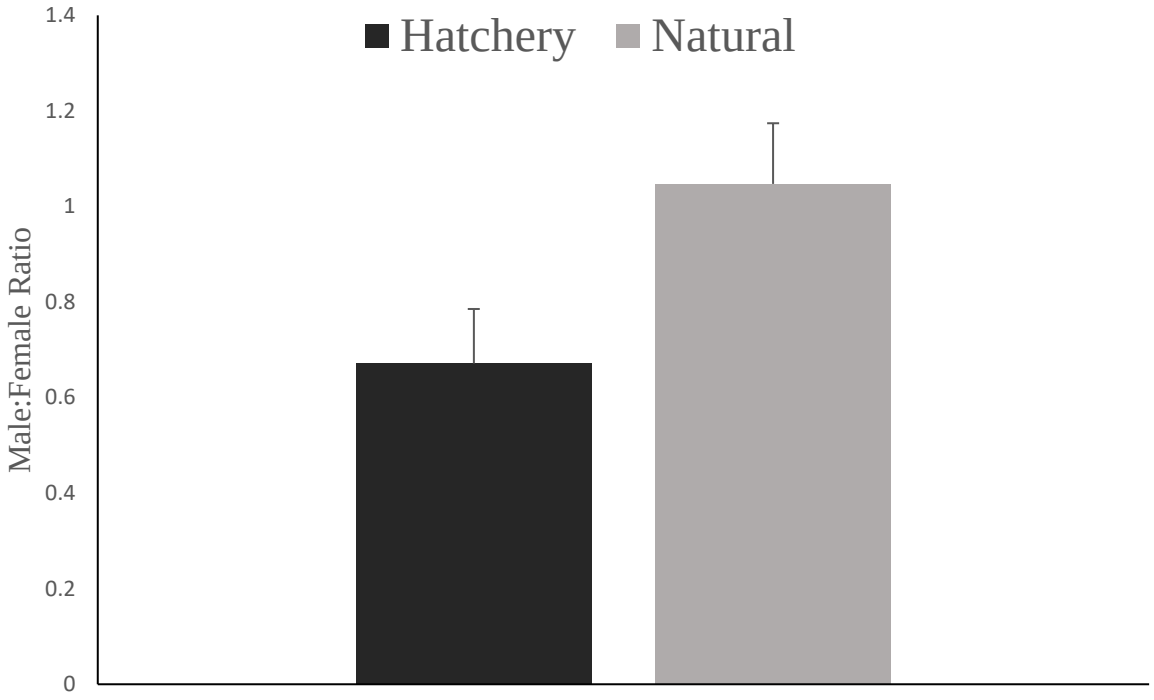

Figure 2. Mean Male:Female ratio of hatchery- and natural-origin fall Chinook Salmon carcasses recovered in the Hanford Reach for brood years 2007 – 2013. Vertical bars denote 95% confidence intervals.

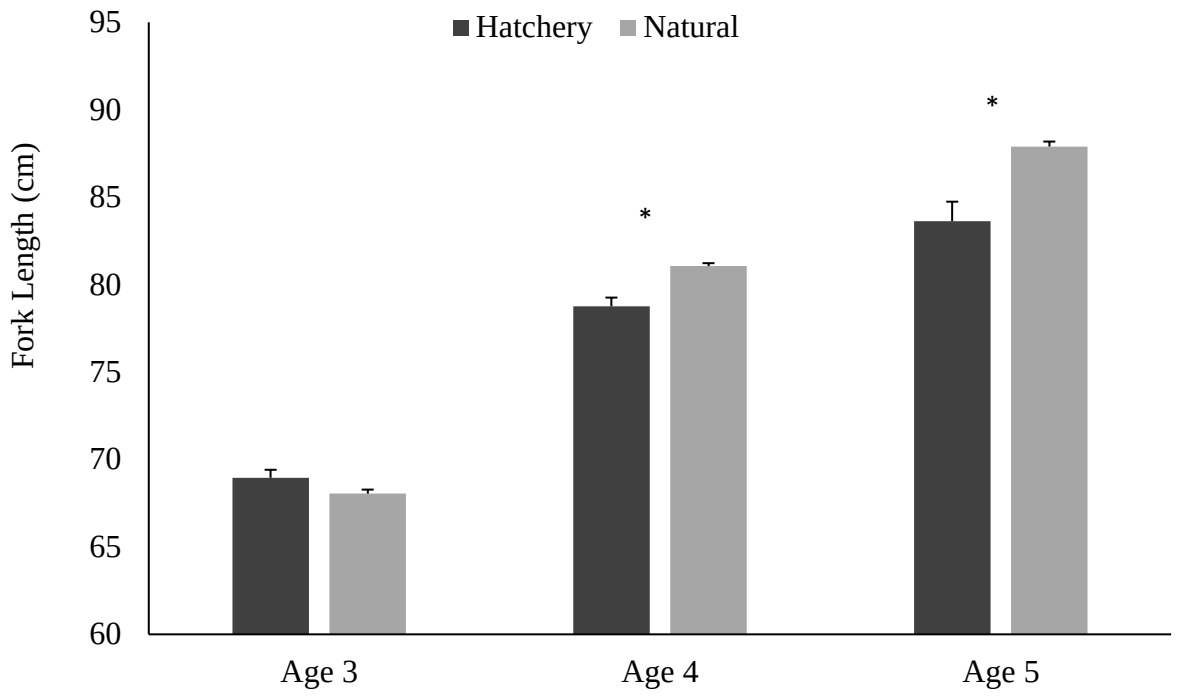

Figure 3. Mean fork lengths for hatchery- and natural-origin age 3 – 5 fall Chinook Salmon carcasses sampled during surveys of the Hanford Reach escapement for brood years 2007 – 2013. Vertical bars denote 95% confidence intervals. An asterisk denotes results of a significant difference Tukey test between the paired bars for a given age.

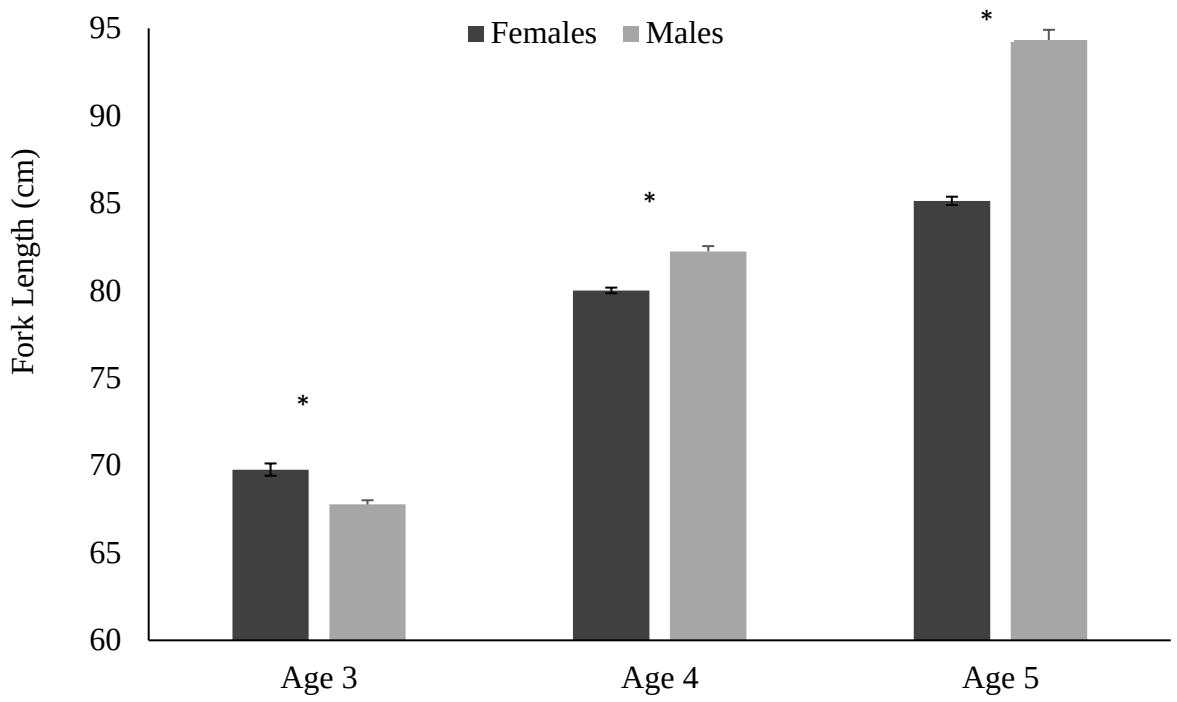

Figure 4. Mean fork lengths for male and female, age 3 – 5, fall Chinook Salmon sampled during surveys of the Hanford Reach escapement for brood years 2007 – 2013. Vertical bars denote 95% confidence intervals. An asterisk denotes a significant difference between the paired bars for a given age.

Discussion

Three clear differences were observed between hatchery- and natural-origin fish: 1) hatchery-origin fish return at younger age, 2) hatchery-origin fish were smaller as 4 and 5 year old fish, and 3) the sex ratio of hatchery-origin fish is skewed towards a higher proportion of females in the population. Intrinsic biological reasons for these observations include genetics and environmental characteristics of pre-emigration period. Age at sexual maturity is a heritable trait in salmonids (Appleby et al. 2003; Campton 2004; Ford et al. 2012) and there are concerns that hatchery supplementation could lead to a reduction in size of individuals in the supplemented population. Concern over an integration of less desirable traits into the natural population has prompted many reforms of hatcheries in Washington state and an increased effort surrounding natural-origin broodstock collection at PRH. The selection of higher proportions of natural-origin broodstock since 2010 (Pearsons et al. 2020) and the collection of broodstock throughout the natural run time are thought to minimize many of the deleterious outcomes of domestication and operational selection occurring in the hatchery.

The hatchery residence period is also thought to produce changes to life history trajectory that are prompted by the environment and not directly genomic in origin. During the hatchery residence, fish are frequently aggressively fed to reach release target sizes by specific dates and are often reared at temperatures that accelerate growth rates relative to their natural-origin

counterparts. Feeding and growth rates and the energetic status of fish at points in the juvenile stage all appear to contribute to the future life history trajectory outcomes (e.g. age at maturity). Food availability and high growth rates in the hatchery environment lead to shifts in maturity at younger ages with a loss of some life history diversity (Larsen et al. 2013; Beckman et al. 2017; Spangenberg et al. 2014).

Stark differences in the sex ratio of hatchery- and natural-origin fish were observed in the Hanford Reach with the proportion of males being smaller in hatchery-origin fish. In reference to this observation it should be noted that carcasses found on the Hanford Reach represent only a portion of the hatchery-origin fish that successfully return to the Hanford Reach. Traps at PRH and RSH also collect fish and may contribute to some of the observed differences in carcasses observed here.

It is likely that our results contain some bias because of the field methods that we used. Several studies have revealed that carcass recoveries represent a biased sample of the spawning population. Smaller and younger spring-run Chinook Salmon, which were generally males, were encountered less frequently than their actual abundance (Zhou 2002, Murdoch et al. 2010). In addition, carcasses collected in the Hanford Reach appear to be biased toward collecting larger, older, and more females than males. In particular, the recovery of age 2 jack males appear to be a strong source of carcass recovery bias. Thus, our observation of differences in sex ratios between hatchery- and natural-origin fish may be an artifact of not collecting jacks in proportion to their true abundances. However, it is likely that the patterns of age and size at maturity are correct, but the magnitude of differences may be biased. For example, Hanford Reach carcasses of hatchery-origin were larger, slightly older, and consisted of approximately 20% more females than PRH-origin adults collected at the PRH trap.

Recent work has demonstrated that here have been coast-wide reductions in the size of adult Chinook Salmon (Ohlberger 2018; 2020; Oke et al. 2020). This includes populations that are not supplemented with hatchery fish. Possible mechanisms for reduced size include competition for food in the ocean, selective harvest or predation of older individuals, and changes in ocean productivity associated with climate change (Ohlberger 2018; 2020; Oke et al. 2020). Hatchery-origin fish may indirectly contribute to some mechanisms of decreasing size through genetics, competition, and possibly through fisheries, but other factors also influence the size of Chinook Salmon.

Younger and smaller adult hatchery-origin fish are suboptimal because they are less desirable to harvesters and they have the potential to produce fewer offspring. Although hatchery- and natural-origin females produce similar number of eggs per length of fish, fish that mature at earlier ages or at a smaller size at age will produce fewer eggs (see fecundity chapter in this report). This concern is less important if natural production by hatchery-origin fish is not the primary objective for the hatchery, such as the case for Priest Rapids Hatchery.

In aggregate it appears that hatchery-origin fish that remain on the spawning grounds as adults in the Hanford Reach have some important characteristics that differ from natural-origin fish. The two hatchery programs have been in place for decades which provides some support for the argument of domestication selection but as increasing numbers of natural-origin broodstock are being introduced into these programs it would appear that environmental influences during the hatchery rearing phase must be increasingly viewed as a principle reason for these differences. While physiological models do exist that support growth rates in the hatchery as being a driver of younger (smaller) fish returning to the Hanford Reach, much of the data surrounding organismal differences in hatchery- and natural-origin Chinook Salmon is

derived from studies on spring and summer-run Chinook Salmon that are released as yearlings with a smaller number of reports on hatchery programs that release subyearlings changes (Harstad et al. 2014). Attempts to match natural-origin age and size at maturity by producing smaller, more natural sized juveniles in the hatchery may result in lower survival of hatchery-origin fish because of the survival advantages that larger fish have. This results in a difficult trade-off for managers to consider, producing smaller fish will likely result in older and larger adults at return, but there may be fewer of them.

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Egg Production and Deposition Between Hatchery- and Natural- Origin Fall Chinook Salmon in the Hanford Reach of the Columbia River

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Abstract

The reproductive potential of hatchery- and natural-origin fish is an important performance characteristic to compare when evaluating impact of supplementation hatchery programs and this was studied for fall Chinook Salmon that spawn in the Hanford Reach of the Columbia River. Hatchery- and natural-origin adults and carcasses were collected between 2004 and 2018 and reproductive traits were compared. Fecundity, individual egg weights, and total egg mass ranged from 1,356 – 6,385 eggs/female, 0.15 – 0.46 g/egg, and 255 – 2,205 g/female, respectively. All three reproductive characteristics increased significantly with fork length ($P < 0.0001$). Multiple linear regressions revealed significant differences between hatchery- and natural-origin fish for fecundity ($P = 0.0393$) and individual egg weight ($P = 0.0002$) although each result was confounded by a significant interaction between fork length and origin indicating heterogeneity of slope for these two populations. Multiple linear regression for total egg mass revealed no difference between hatchery- and natural-origin fish ($P = 0.3277$) and no interaction between origin and the fork length ($P = 0.2876$). At the extreme values of fork length, the relative outcomes for fecundity and individual egg mass for hatchery- and natural-origin fish change. Fecundities of the smallest natural-origin fish sampled were less than that observed among hatchery-origin fish while at the largest fork lengths the opposite was observed. For individual egg mass, greater values were observed among the smallest natural-origin fish than hatchery-origin fish while at the largest sizes the opposite was observed. No such inversion in the relative rank order was apparent for the total egg mass of hatchery- and natural-origin fish at the extremes of fork length. The mean fork length of hatchery-origin fish found on the Hanford Reach was significantly smaller than natural-origin females leading to hatchery-origin females with significantly lower fecundity, individual egg weight, and total egg mass weight than natural-origin females ($P<0.05$). The annual index of egg retention based on visual estimates of egg retention for years 2004 – 2018 ranged from 0.5 – 9.9% and with a mean of 2.1%. Over this same period there was not a significant change in the egg retention index over time ($df = 14$, $t = 0.559$ $P = 0.5855$). There was a significant difference in percentage of eggs retained with mean egg retention indices of 9% and 2% for hatchery- and natural-origin females, respectively ($X^2_{MH} = 370.76$, $df = 6$, $P = <0.0001$). Egg retention for hatchery-origin females were notably high during years 2013 and 2014. Recent changes to broodstock collection and adult management may decrease the disparity in allocation of reproductive investments between hatchery- and natural-origin females, however it is likely that younger maturation age of hatchery-origin fish will continue to result in differences in fecundity from natural-origin fish.

Introduction

The reproductive potential of hatchery- and natural-origin fish is an important performance characteristic to compare when evaluating impact of supplementation hatchery programs. Reproductive capacity of females in hatcheries is largely driven by fecundity which is influenced by both age and size at maturity (Knudsen et al. 2008; Ohlberger et al. 2018; 2020). The demographics of salmon populations frequently differ between hatchery- and natural-origin populations leading to differences in reproductive capacity (Knudsen et al. 2006; 2008) and lead to lower fecundity of hatchery-origin females. There are also occurrences of hatchery-origin fish being smaller than the same age cohort leading to lower reproductive capacity (Knudsen et al.

2006; 2008). Egg size of hatchery-origin females has been shown to be both larger and smaller than eggs of their natural-origin counterparts (Knudsen et al. 2008) and lead to variation in reproductive capacity.

Reproductive capacity of females in the natural environment can also be influenced by a larger suite of metrics that include pre-spawn mortality, egg retention, spawning location, and egg size (Schroder et al. 2008; Williamson et al. 2010). The capacity of individual animals to compete and choose desirable spawning habitat is an important characteristic and there are reported differences between some populations of hatchery- and natural-origin salmon (Dittman et al. 2011; Hughes and Murdoch 2017). Differences in pre-spawn mortality and egg retention in salmon populations is also reported (Bowerman et al. 2017; 2021). The purpose of this work was to evaluate if egg retention, fecundity (eggs/female), total egg mass, and individual egg weight differ between hatchery- and natural-origin fall Chinook Salmon in a hatchery supplemented population in the Hanford Reach of the Columbia River. The Hanford Reach population is ideal to study because of the long duration that the program has existed and efforts towards hatchery reform are documented and thus provide a substantive addition to the understanding of hatchery impacts on the reproductive characteristics of a supplemented salmon population.

Methods

Study Area

The Hanford Reach is one of the last non-impounded reaches of the Columbia River and extends ~90 km from the city of Richland to the base of Priest Rapids Dam (Figure 1). It is the location of the largest and most productive natural spawning fall Chinook Salmon *Oncorhynchus tshawytscha* population in the United States (Harnish et al. 2012, 2014, Langshaw et al. 2015, Harnish 2017, Langshaw et al. 2017). Since 2004 we have sampled female Chinook Salmon recovered within our systematic survey of carcasses that spawned naturally within the Hanford Reach for varying demographics and egg retention data to assess spawn success. Beginning in 2012, we were able to distinguish between hatchery- and natural-origin females by the presence of thermal otolith marks, a missing adipose fin, or the presence of a coded wire tag.

Within the Hanford Reach are two large fall Chinook Salmon production facilities. Priest Rapids Hatchery (river km 639) is located on the east bank of the Columbia River immediately downstream of Priest Rapids Dam and has been in operation since 1971. Production at Priest Rapids Hatchery (PRH) initially included the use of both an artificial spawning channel and an incubation facility. By 1982, the upper sections of the spawning channel were converted to rearing ponds and all the production originated from the incubation facility. Since 1982, annual releases have ranged from 4,548,307 to 10,296,700 smolts. The current operations target annual releases of 7.3 million sub yearling fall Chinook Salmon smolts as part of the Public Utility District No. 2 of Grant County, Washington (Grant PUD) mitigation of 5.6 million smolts for the construction and operation of Priest Rapids and Wanapum dams and 1.7 million smolts for the United States Army Corps of Engineers' (USACE) mitigation for the construction and operation of John Day Dam. Ringold Springs Hatchery (river km 567) is located downstream of PRH and has been annually operated as an acclimation and release site for sub yearling fall Chinook Salmon since 1993. The source of broodstock from 1993 – 2007 was from Bonneville Hatchery (river km 233) located in the lower Columbia River. Since 2008, broodstock has been sourced

from Priest Rapids Hatchery. Annual releases from Ringold Springs Hatchery have ranged from 69,902 to 4,217,491 smolts.

Egg characteristics of hatchery- and natural origin fish

Fall-run Chinook Salmon broodstock are collected for PRH during September to early December. Fecundity (number of eggs/female), individual egg weight (grams), and total egg mass per female (grams) were recorded for samples of fish collected at PRH from 2013 to 2018. The broodstock collected for PRH are derived from several nearby locations but predominantly gathered from the volunteer trap at PRH (Pearsons et al. 2020). The eggs from females obtained from these sources were collected between October and December during production spawning activities that provided eggs from both hatchery- and natural-origin fish. Fish selected for sampling represented a wide range of sizes (55 – 97 cm). The assignment of hatchery-origin was based on the presence of marks to the otoliths applied by temperature changes to hatchery production before release or the presence of a coded-wire tag or the absence of an adipose fin (Pearsons et al. 2020). Fish with none of these hatchery-origin marks or tags were assumed to be of natural-origin. Fork length (cm) was recorded from each fish that contributed eggs to fecundity assessments and over the course of these studies data from 389 hatchery-origin fish and 315 natural-origin fish were collected. Eggs were obtained from individual gravid females euthanized by a sharp blow to the head and eggs collected in a 19-L plastic bucket when a slice was made ventrally using a Wyoming knife to release the eggs. Females were excluded from the study if their ovaries contained eggs that were not entirely free to be released. The eggs were drained of coelomic fluid, and the total egg mass was weighed (0.1 g). A weight of 100 eggs was then recorded (0.1g) and divided by 100 to derive a mean individual egg weight from each female. A gravimetric estimate of fecundity (eggs/female) was then derived as the total egg mass / individual egg weight.

Data gathered over all years of the study were pooled and multiple linear regressions performed to model the relationships between the reproductive indices (fecundity, individual egg weight, and total egg mass) and the origin of female, the fork length and their interaction.

Model: Reproductive Index = Origin + Fork Length + Origin*Fork Length

The model was then used to predict outcomes and 95% confidence intervals surrounding the minimum and maximum fork lengths recorded and the inner quartile range (25^{th}, 50^{th}, and 75^{th} percentile values) of fork lengths. Finally, egg characteristics of females sampled at PRH were used to characterize reproductive potential of fish collected within the Hanford Reach and compare hatchery- and natural-origin fish. A predictive equation for hatchery- and natural-origin fish was derived from the linear regression of values for egg characteristics and fork length. For each year of the study, the mean fork length was determined for hatchery- and natural-origin females sampled within the Hanford Reach. These mean fork lengths were used to calculate estimates of fecundity, individual egg weight, and total egg weight by origin and then compared using a paired t-test. The threshold for a significant difference for each test was set at $P = 0.05$.

Egg retention in naturally spawning fish

From 2004-2018, fork length (cm) and egg retention based on visual observations were recorded from fish recovered during carcass surveys of the Hanford Reach of the Columbia River. The visual estimates of egg retention during 2004 to 2009 were categorized in bins of 0%,

50%, and 100%. In 2010, additional bins of 25% and 75% were included in the visual estimates. In addition, egg retention based on quantitative estimates that included individual egg counts or gravimetric counts were performed from 2015 to 2018. Both estimates were performed from 2015 to 2018 to evaluate any difference between the two methods. Quantitative estimates of egg retention were also categorized into one of five bins: 0% (range 0 – 12%), 25% (range 13 – 37%), 50% (range 38 – 62%), 75% (range 63 – 87%) and 100% (range 88 – >100%). The percentages of eggs retained based on quantitative measures were calculated by dividing the number of eggs retained by an estimated fecundity of the pre-spawn fish. The fecundity estimate used for pre-spawn fish was calculated from linear regressions describing the relationship between fork length and fecundity derived from hatchery- and natural broodstock data collected at PRH.

We calculated an index of egg retention for the female escapement to the Hanford Reach for each year to estimate the overall impact of egg retention on the naturally spawning population using the following equations.

Equation 1 for data gathered 2004-2009:

Index of Egg Retention = (1 – sum ((count of fish $_{0\%}$ x 0.0) + (count of fish$_{50\%}$ * 0.50) + (count of fish$_{100\%}$ * 1.0))) * / Total Females Sampled 100

Equation 2 for data gathered 2010-2018:

Index of Egg Retention = (1 – sum ((count of fish $_{0\%}$ x 0.0) + (count of fish 25% * 0.25) + (count of fish$_{50\%}$ * 0.50) + (count of fish$_{75\%}$ * 0.75) + (count of fish$_{100\%}$ * 1.0))) / Total Females Sampled

The egg retention indices from 2004 to 2018 were used to illustrate any trend in egg retention over time for naturally spawning fall Chinook Salmon in the Hanford Reach, regardless of origin. A linear regression was performed using the paired values of retention indices and return year to determine any significant change over time. Egg retention index values of hatchery- and natural- origin fish based on visual estimates from 2012 to 2018 were calculated to provide origin specific means of egg retention. We summarized the frequencies of hatchery- and natural-origin fish gathered from 2012-2018 in each egg retention bin and performed a Cochran-Mantel-Haenszel test to determine if the frequencies were independent of origin. We also performed a Cochran-Mantel-Haenszel test to determine if there was a difference in the index of egg retention based on visual and quantitative methods during 2015 - 2018. A Woolf Test was performed subsequent to significant Cochran-Mantel-Haenszel to determine the presence of a significant interaction with time. The threshold for a significant difference for all test was set at $P = 0.05$.

Results

Egg characteristics of hatchery- and natural-origin fish

Fecundity, individual egg weights, and total egg mass recorded over the course of the study ranged from 1,356 – 6,385 eggs/female, 0.15 – 0.46 g/egg, and 255 – 2,205 g/female, respectively. All three reproductive characteristics increased significantly with fork length ($P <$ 0.0001; Figures 2-4). Multiple linear regressions revealed significant differences between

hatchery- and natural-origin fish for fecundity (P = 0.0393) and individual egg weight (Table 1; P = 0.0002) although each result was confounded by a significant interaction between fork length and origin indicating heterogeneity of slope for these two populations. Multiple linear regression for total egg mass revealed no difference between hatchery- and natural-origin fish (Table 1; P = 0.3277) and no interaction between origin and the fork length (Table 1; P = 0.2876). The model predictions for fecundity, individual egg weight further clarify the significant interactions with the covariate of fork length by illustrating that at extreme values of fork length the relative outcomes for fecundity and individual egg mass for hatchery- and natural-origin fish change (Figure 5). Fecundities of the smallest natural-origin fish sampled were less than that observed among hatchery-origin fish while at the largest fork lengths the opposite was observed. For individual egg mass, larger values were observed among the smallest natural-origin fish than hatchery-origin fish while at the largest sizes the opposite was observed.

The mean fork length of hatchery-origin fish found on the Hanford Reach was significantly smaller than natural-origin females (Figure 6) leading to hatchery-origin females with significantly lower fecundity, individual egg weight, and total egg mass weight than natural-origin females (Figures 7, 8, 9).

Egg retention in naturally spawning fish

The annual index of egg retention based on visual estimates of egg retention for years 2004 – 2018 ranged from 0.05 – 9.9% (Table 2). Two methods for determining the egg retention index were used over the course of this time period providing means of 1.3% (2004-2009) and 2.7% (2010-2018). Over the entire period there was no significant change in the egg retention index over time (Figure 10; df = 14, t = 0.559 P = 0.5855). The distribution of frequencies of egg retention index values (2012-2018) in the assigned bins differed between hatchery- and natural-origin fish (Table 2; X^2_{MH} = 370.76, df = 6, P = <0.0001) with the Woolf test statistic revealing no interaction with frequencies and time (X^2 = 0.9604, df = 1, P = 0.3362). The significant difference in frequencies contributed to the apparent difference in the mean egg retention indices of 9% and 2% for hatchery- and natural-origin females, respectively (Table 3). Egg retention for hatchery-origin females were notably high during years 2013 and 2014 (Figure 11). The frequencies of egg retention index values for both egg count and visual scoring methods were similar (X^2_{MH} = 0.0094, df = 3, P = 1.000). The egg retention indices of the egg count and visual scoring method were highly correlated (r^2=0.97; Figure 12).

Table 1. Results of multiple linear regression for the model predicting fecundity, individual egg weight, and total egg mass as a function of the relationships with origin (hatchery and natural) and fork length and their interaction for female salmon sampled from 2013 to 2018 at Priest Rapid Hatchery.

Fecundity (eggs/female)

Source	Sum of Squares	d.f.	F	P
Origin (O)	1466730	1	4.265	0.0393
Fork Length (FL)	64458553	1	187.448	$2.2 * 10^{-16}$
O * FL	1502953	1	4.371	0.0369
Residuals				

Individual Egg Weight (g/egg).

Source	Sum of Squares	d.f.	F	P
Origin (O)	0.09773	1	13.623	0.0002
Fork Length (FL)	0.02637	1	300.145	$2.2 * 10^{-16}$
O*FL	0.02546	1	13.156	0.0003
Residuals				

Total Egg Mass (g/female).

Source	Sum of Squares	d.f.	F	P
Origin (O)	24515	1	0.096	0.3277
Fork Length (FL)	23388004	1	915.359	$2.2 * 10^{-16}$
O* FL	28940	1	1.133	0.2876
Residuals				

Table 2. Visual estimates of egg retention for female fall Chinook Salmon based on carcass surveys in the Hanford Reach of the Columbia River, Return Years 2004- 2018. Two methods for categorizing egg retention were used with three categories during 2004-2009 and five categories during 2010-2018.

Return Year	Females Sampled	Egg Retention Category 0%	25%	50%	75%	100%	Index of Egg Retention (%)
2004	1,070	1,046	--	20	--	4	1.3%
2005	1,225	1,213	--	6	--	6	0.7%
2006	324	316	--	7	--	1	1.4%
2007	435	424	--	8	--	3	1.6%
2008	550	544	--	6	--	0	0.5%
2009	471	458	--	5	--	8	2.2%
2010	1,124	1,103	12	1	0	8	1.0%
2011	1,223	1,157	48	5	1	12	2.2%
2012	742	719	14	4	1	4	1.4%
2013	666	520	88	20	16	22	9.9%
2014	1,586	1,275	286	3	1	21	6.0%
2015	1,401	1,368	21	8	4	0	0.9%
2016	952	924	12	11	3	2	1.3%
2017	1,074	1,055	14	3	2	0	0.6%
2018	684	675	4	1	1	3	0.8%
Mean (SD)							
2004-09	679(373)	667(370)	--	9 (6)	--	4 (3)	1.3% (0.6%)
2010-18 (SD)	902(323)	853(288) (348)	55 (90)	7 (6)	3 (5)	7 (7)	2.1% (2.5%)

Table 3. Frequencies of female fall Chinook Salmon egg visually scored in one of five egg retention categories for hatchery- and natural-origin carcasses collected in the Hanford Reach of the Columbia River during 2012- 2018.

Return Year	Origin	N	Egg Retention Category 0%	25%	50%	75%	100%	Index of egg retention
2012	Hatchery	38	31	5	1	0	1	7%
	Natural	684	669	9	3	1	2	1%
2013	Hatchery	174	108	32	9	10	15	20%
	Natural	183	158	18	5	1	1	5%
2014	Hatchery	115	66	40	0	1	8	16%
	Natural	1,035	866	162	0	0	7	5%
2015	Hatchery	149	128	12	4	4	1	6%
	Natural	1,256	1,233	11	4	3	5	1%
2016	Hatchery	138	126	5	4	1	2	4%
	Natural	857	841	7	7	2	0	1%
2017	Hatchery	109	99	6	2	2	0	4%
	Natural	1,071	1,060	9	2	0	0	0%
2018	Hatchery	46	43	1	0	0	2	5%
	Natural	712	700	8	1	1	2	1%
Mean (SD)	Hatchery	110 (51)	86 (39)	14 (15)	3 (3)	3 (1)	4 (5)	9% (6%)
	Natural	828 (350)	790 (341)	32 (57)	3 (2)	4 (1)	2 (3)	2% (2%)

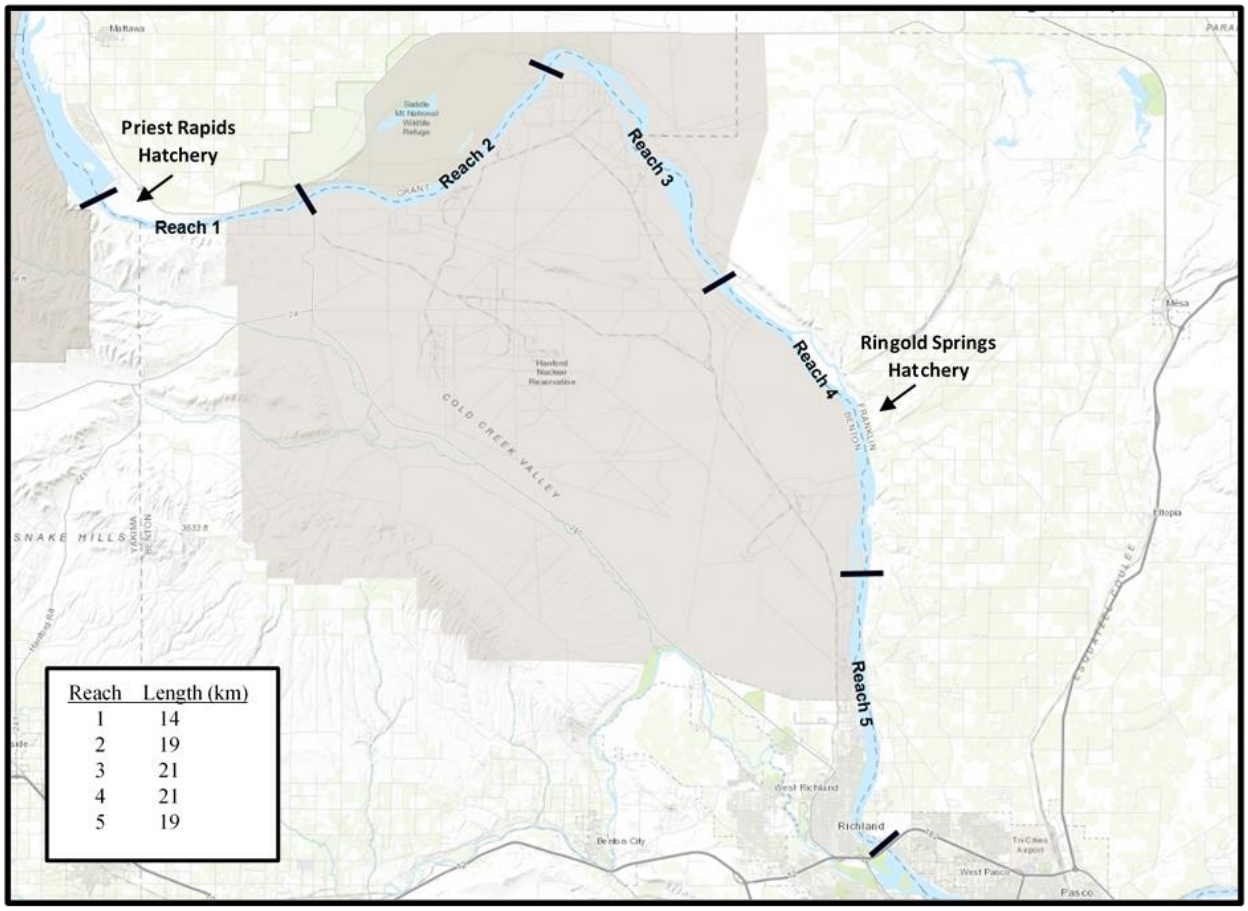

Figure 1. Location of the Hanford Reach portion of the Columbia River in Washington. Bars represent breaks in the Hanford Reach that define the five survey sections.

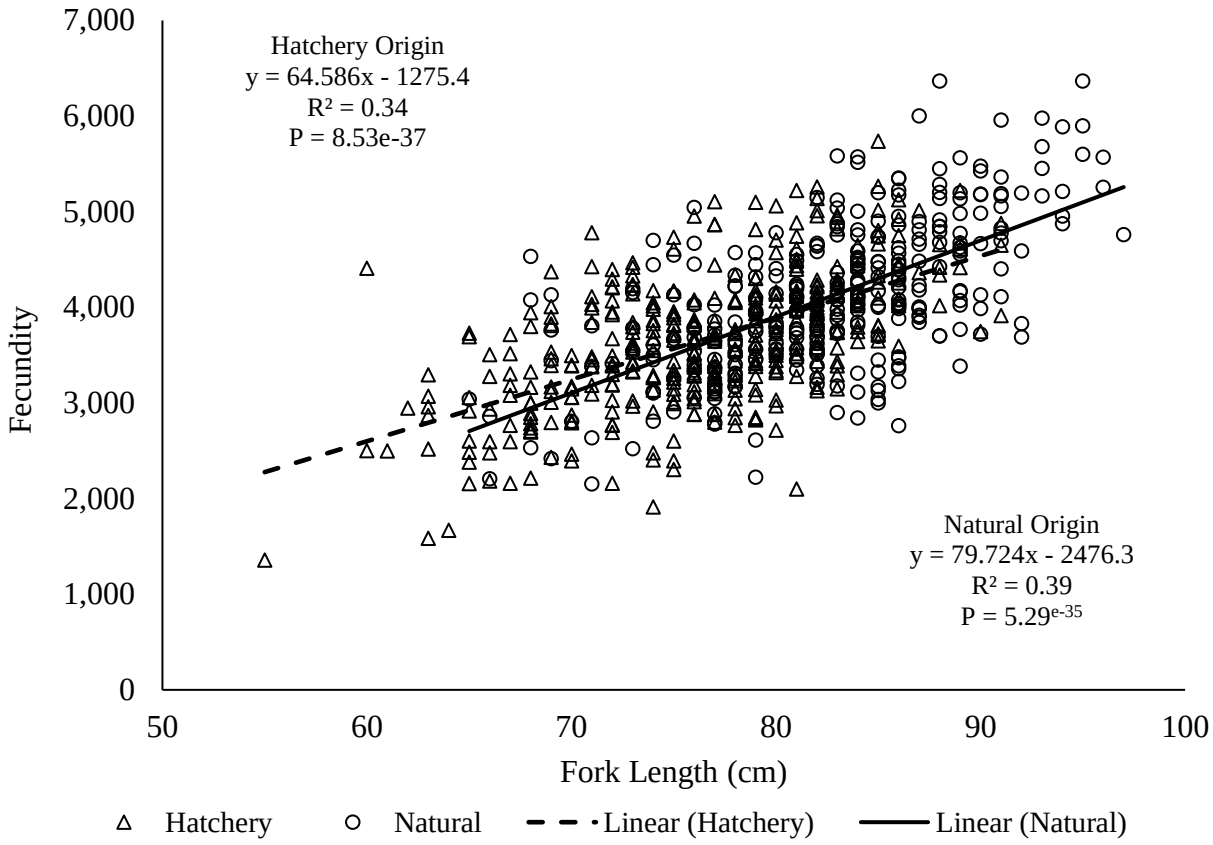

Figure 2. Relationship between fork length and fecundity for hatchery- and natural-origin fall Chinook Salmon sampled at Priest Rapids Hatchery during returns years 2013 – 2018.

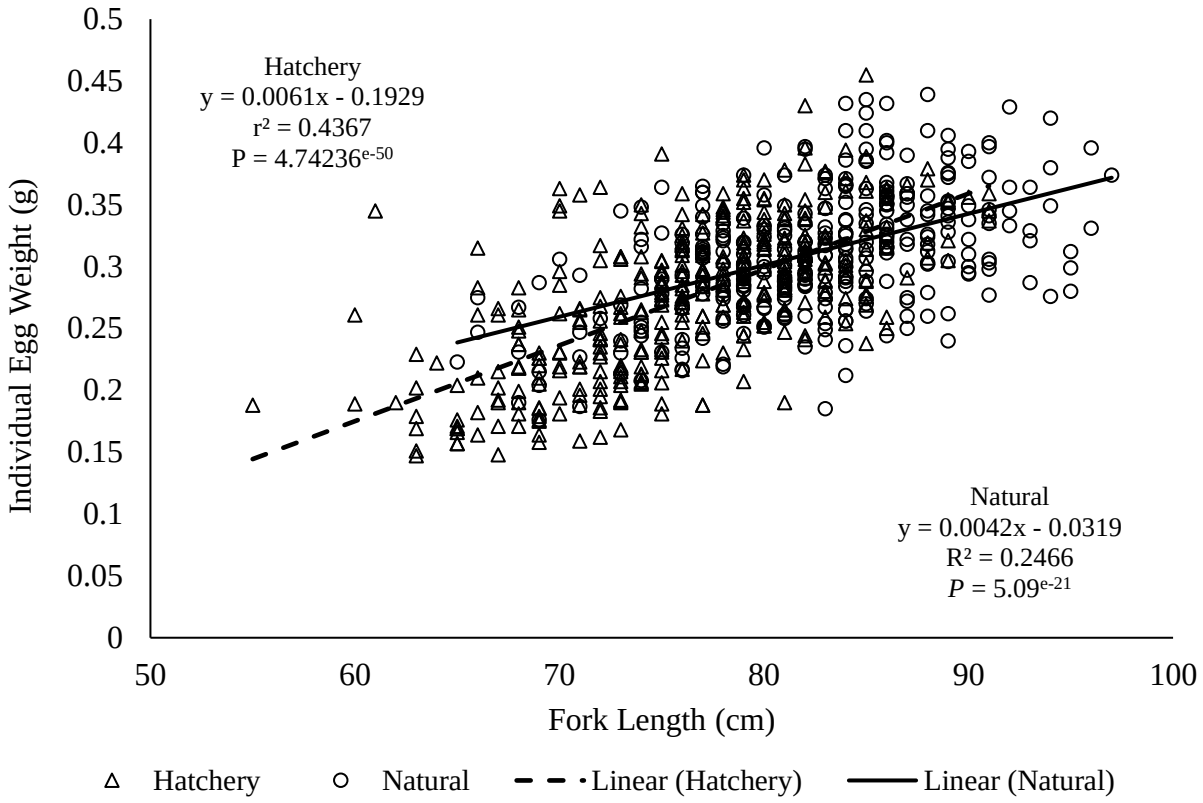

Figure 3. Relationship between fork length and individual egg weight for hatchery- and natural-origin fall Chinook Salmon sampled at Priest Rapids Hatchery during returns years 2013 – 2018.

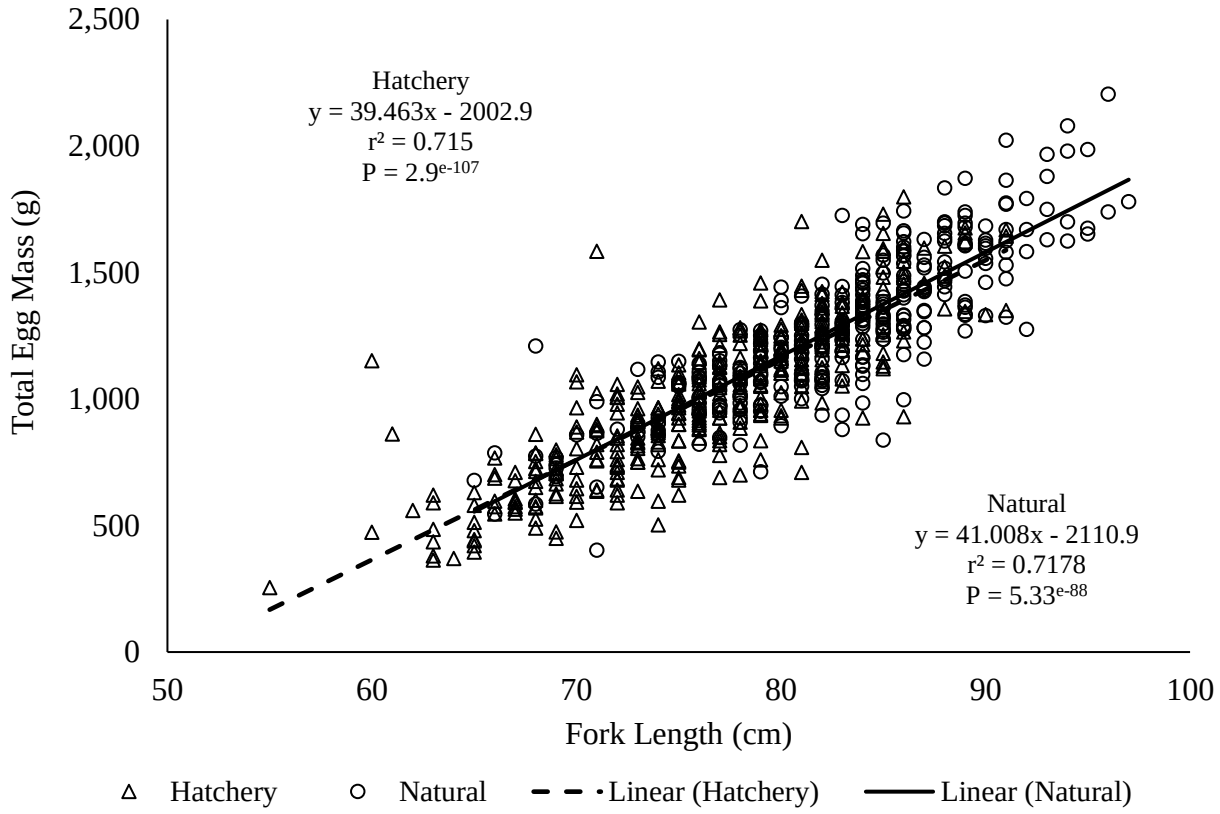

Figure 4. Relationship between fork length and total egg mass for hatchery- and natural-origin fall Chinook Salmon sampled at Priest Rapids Hatchery during returns years 2013 – 2018.

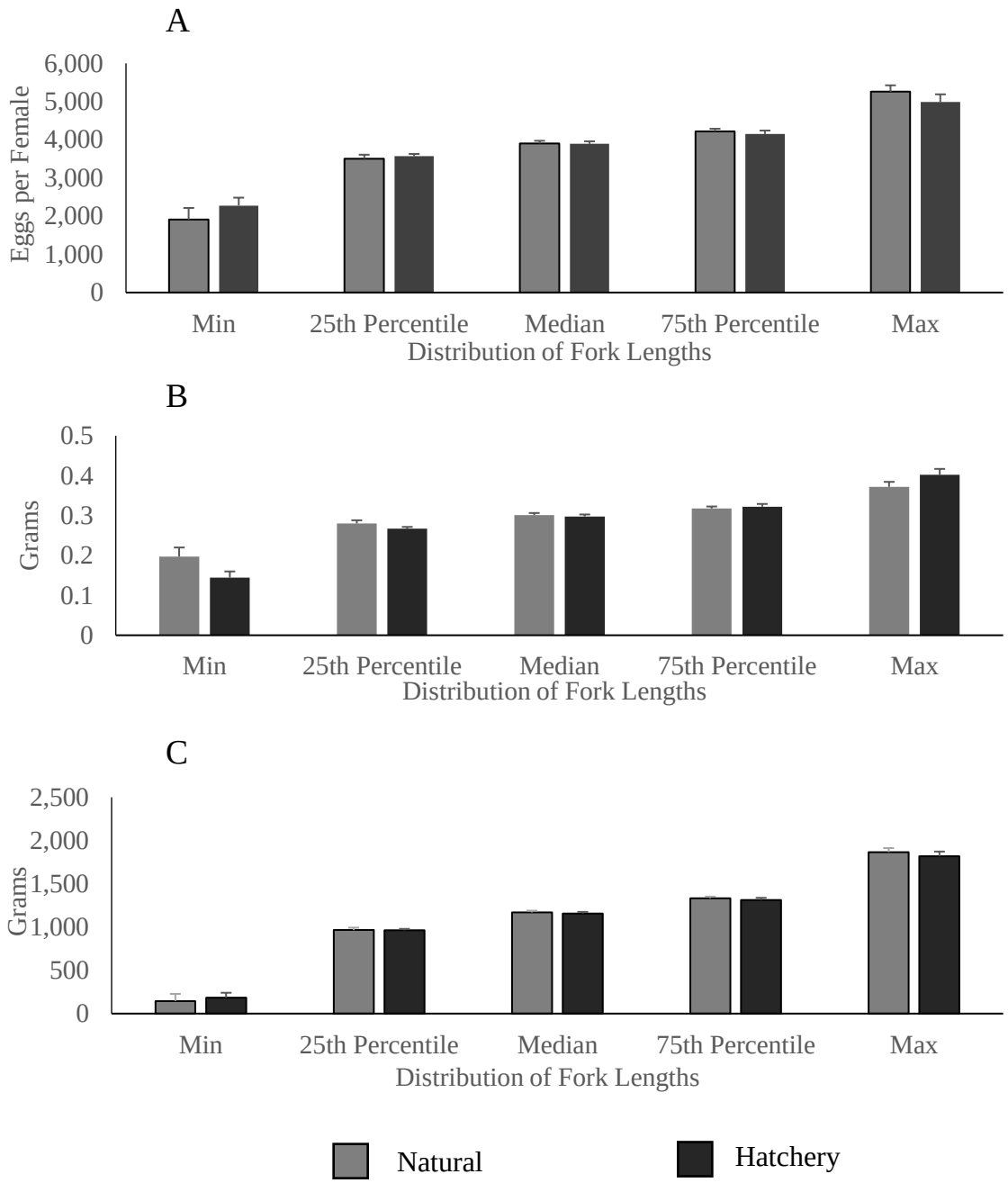

Figure 5. Model predictions from linear regressions and 95% confidence intervals for fecundity (A), individual egg weight (B), and total egg mass (C) for female salmon sampled at Priest Rapids Hatchery during spawning operations during 2013 – 2018.

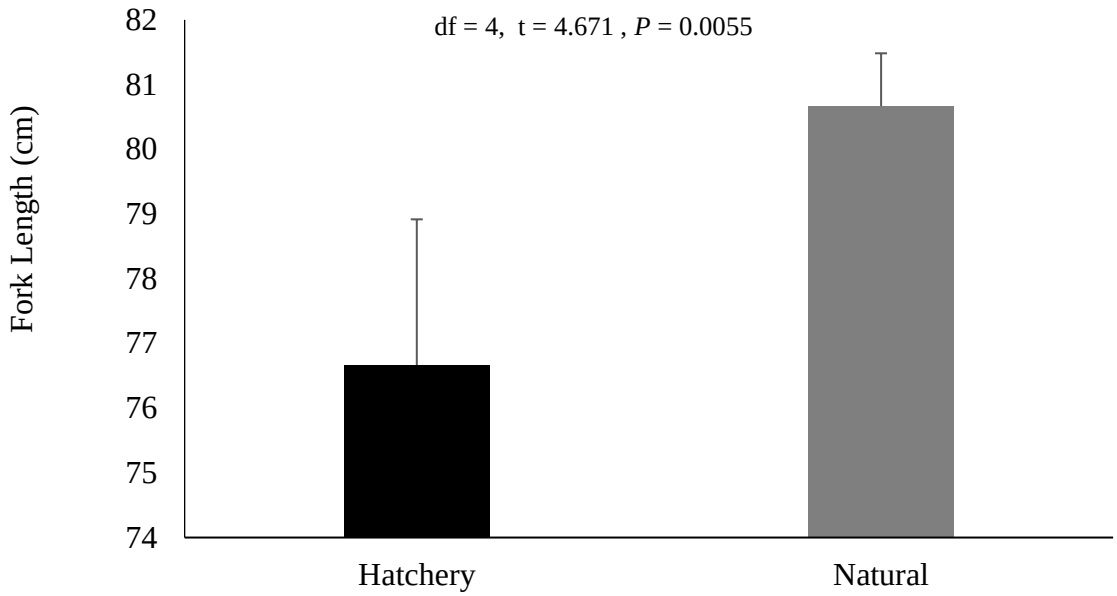

Figure 6. Mean of means fork length and standard deviation for hatchery- and natural-origin fall Chinook Salmon sampled in the Hanford Reach carcass survey during return years 2013 – 2018.

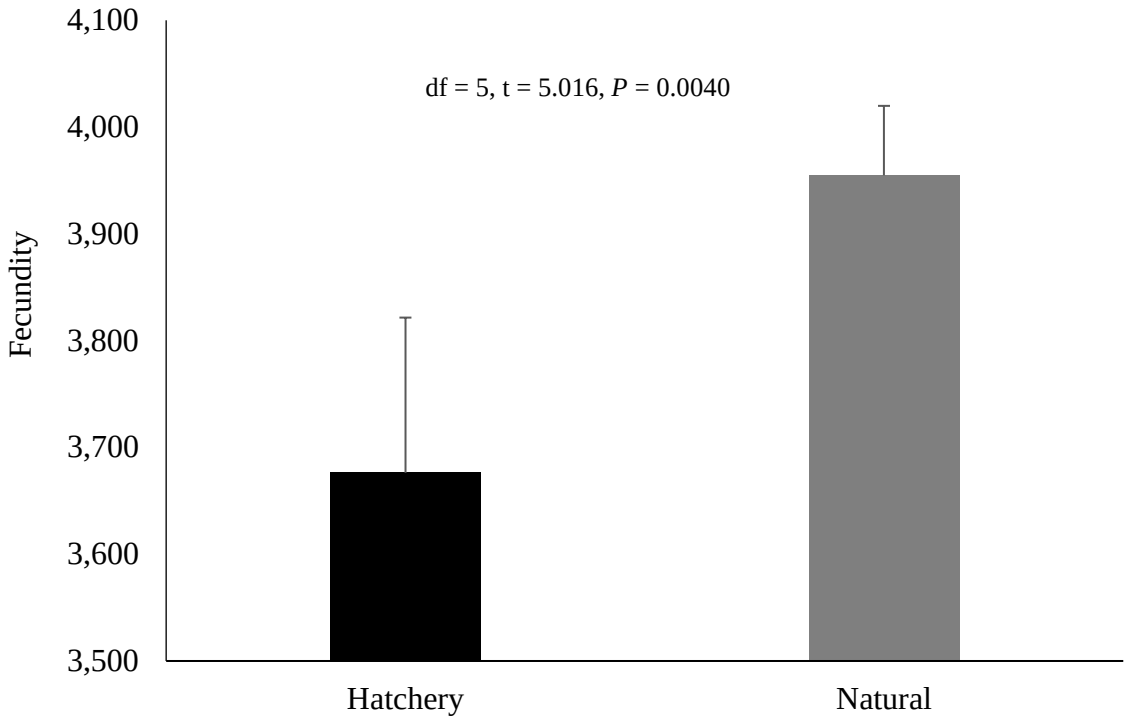

Figure 7. Mean of means fecundity and standard deviation estimated for hatchery- and natural-origin fall Chinook Salmon sampled in the Hanford Reach carcass survey during return years 2013 – 2018

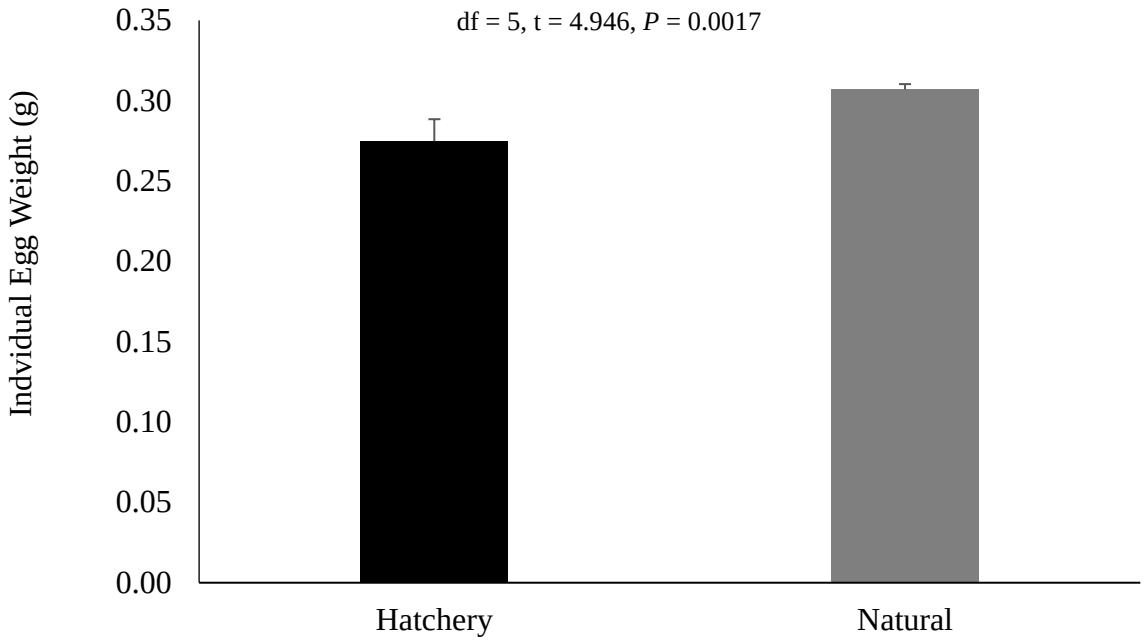

Figure 8. Estimated mean of means individual egg weight and standard deviation for hatchery- and natural-origin fall Chinook Salmon sampled in the Hanford Reach carcass survey during return years 2013 – 2018.

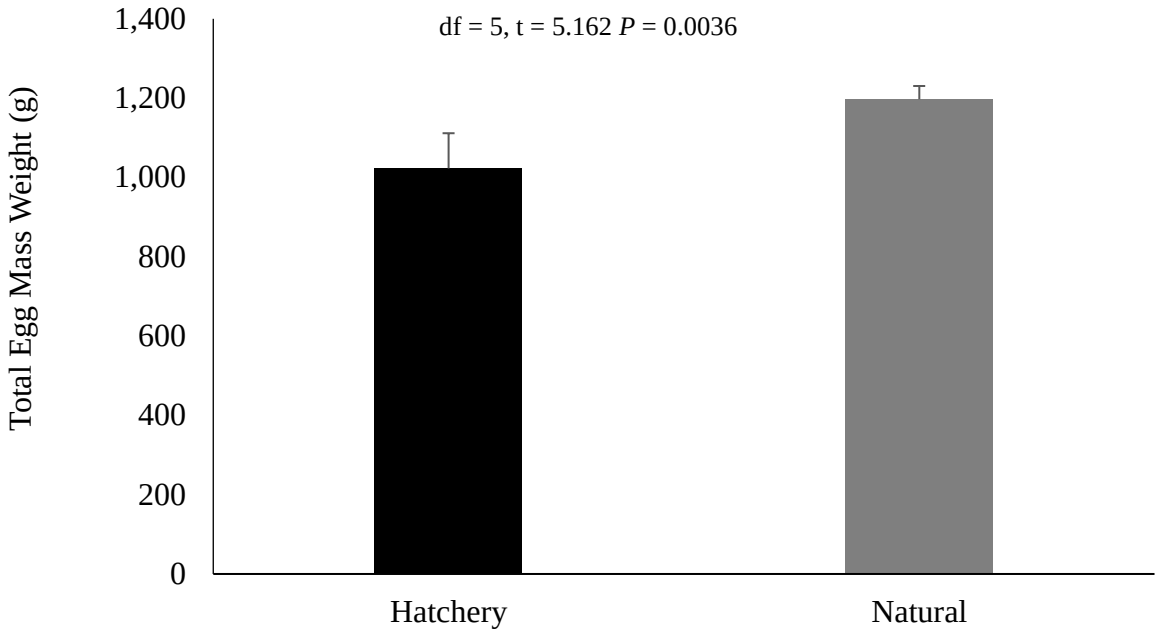

Figure 9. Estimated mean of means for total egg mass weight and standard deviation for hatchery- and natural-origin fall Chinook Salmon sampled in the Hanford Reach carcass survey during return years 2013 – 2018.

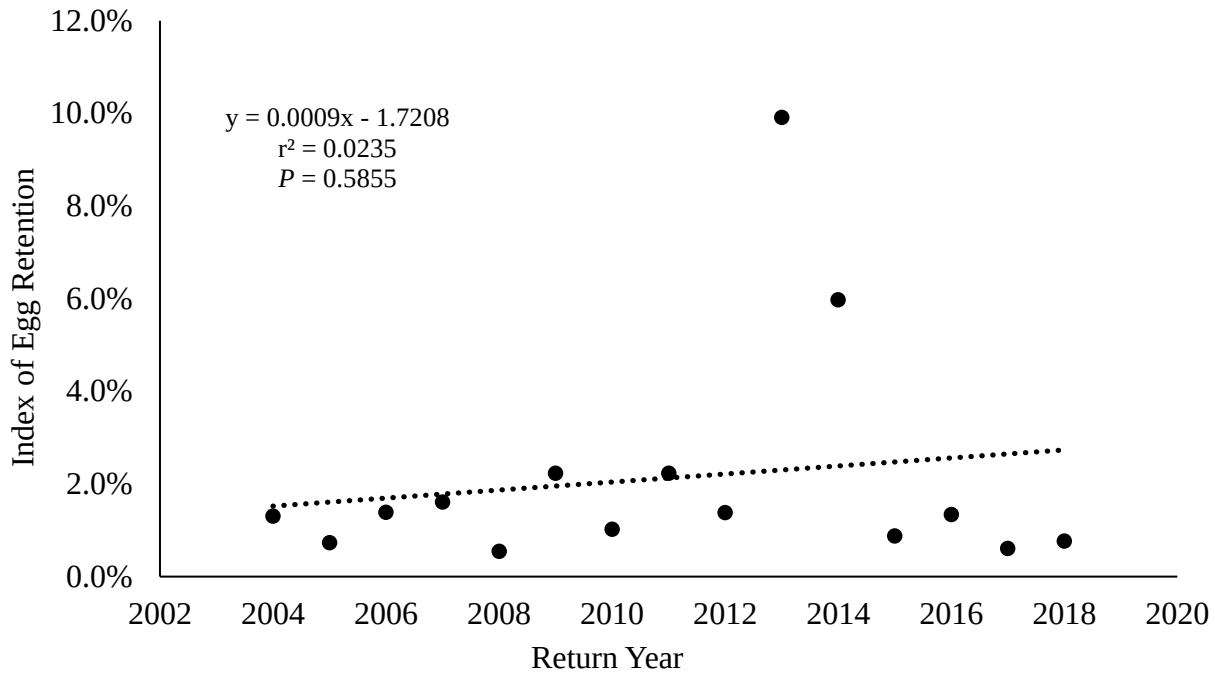

Figure 10. Linear regression results characterizing the relationship between the annual egg retention index value determined using visual estimates of egg retention over time from female fall Chinook Salmon carcasses collected during surveys of the Hanford Reach, 2004 – 2018.

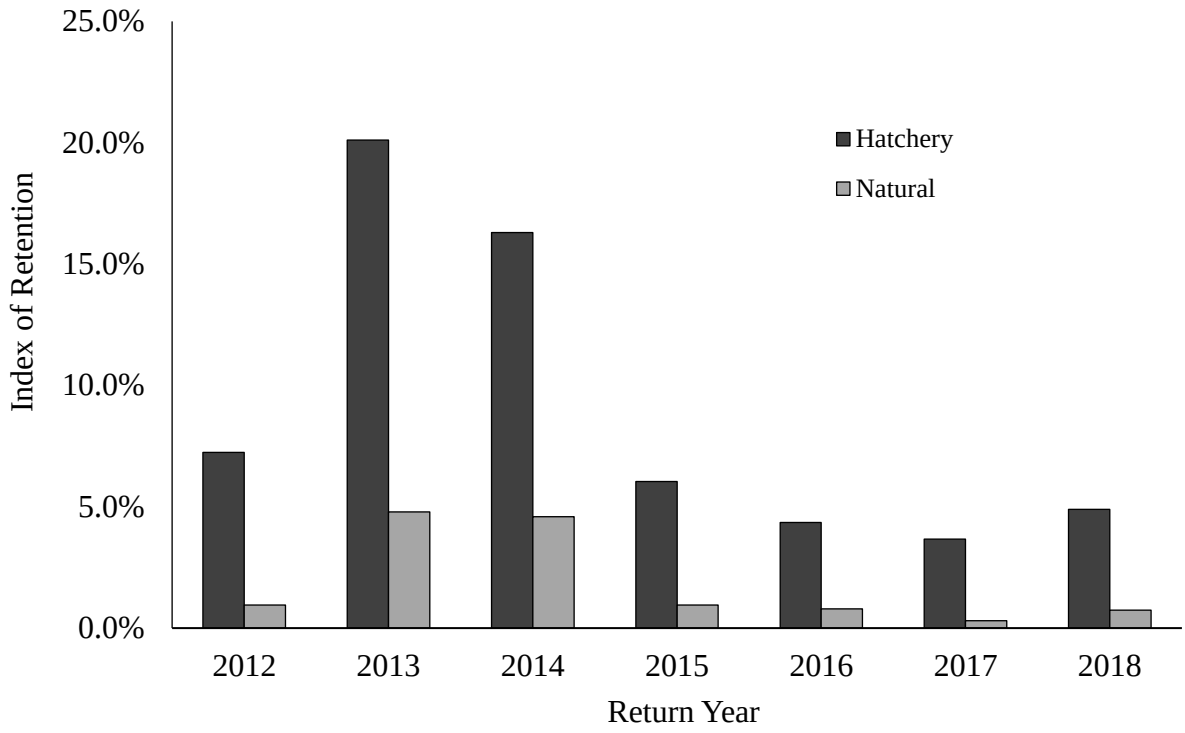

Figure 11. Index of egg retention for hatchery- and natural-origin Chinook Salmon based on visual estimates for carcasses sampled in the Hanford Reach, years 2012 – 2018.

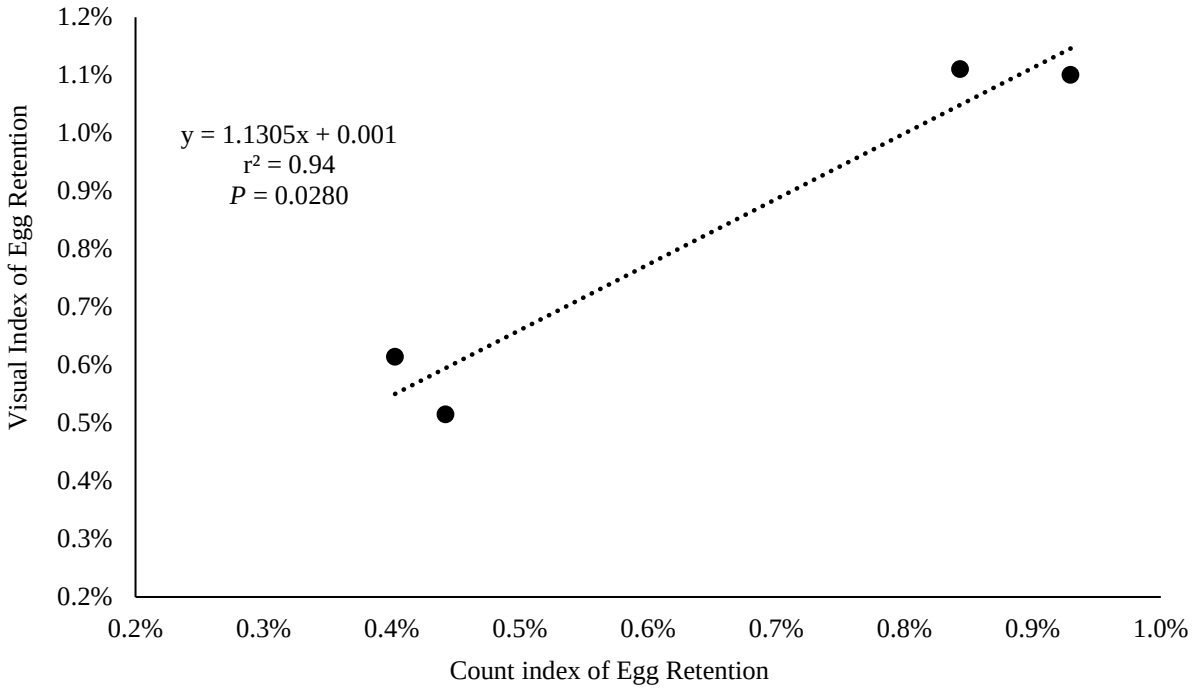

Figure 12. Linear regression results illustrating the relationship between egg retention index values determined using visual scoring and egg count methods for Chinook Salmon for carcasses collected during surveys of the Hanford Reach, years 2015 – 2018.

Discussion

The per capita reproductive potential (e.g., total egg mass) of female hatchery- and natural-origin fall Chinook Salmon in the Hanford Reach was similar when standardized by the length of fish. However, the hatchery-origin females were smaller than natural-origin females and therefore the per capita reproductive potential was lower for hatchery-origin females. Furthermore, hatchery-origin females retained higher percentages of their eggs than natural-origin females. Both of these findings indicate that per capita hatchery-origin females deposit fewer eggs into the gravels of the Hanford Reach than natural-origin females. However, females that are spawned in the hatchery may still produce female offspring that deposit more eggs into the gravels than natural-origin females that are produced in the Hanford Reach because of the higher survival of hatchery-origin fish than natural-origin fish (e.g., HRR>NRR) resulting in larger number of females per female spawned.

The lower per capita reproductive potential of hatchery-origin fish has implications for estimation of a common index of domestication selection. Each spawner in the estimation of proportionate natural influence (PNI) is treated as if the reproductive potential is equal (Paquet et al. 2011). However, we observed that the per capita reproductive potential was lower for hatchery-origin than natural-origin females which may suggest that we were underestimating PNI. Future estimates of PNI might warrant adjustment of hatchery-origin females so that gene flow among hatchery- and natural-origin components of the population and ultimately PNI are estimated better (Pearsons et al. 2020).

Even though total egg mass was the same when controlling for female length, it appeared that hatchery-origin females allocated reproductive investment (fecundity and egg size) differently than natural-origin females. The smallest hatchery-origin females produced more eggs/length and lighter egg mass/length than natural-origin females. The opposite relationship was observed for the largest hatchery-origin females. Production of more numerous and smaller eggs may be advantageous in hatchery environments where egg to fry survival is universally high among different egg sizes. Although this strategy may be effective in hatchery environments, it may not be beneficial to production in natural environments. It is assumed that natural-origin fish allocate their reproductive investment in ways that produced the most offspring, so it is likely that the smallest and largest hatchery-origin fish are likely allocating reproductive investments in ways that are not beneficial for optimal production in the Hanford Reach of the Columbia River. Recent changes to broodstock collection and adult management may decrease the disparity in reproductive investments between hatchery- and natural-origin females (Pearsons et al. 2020).

Acknowledgments

We thank the many partners that have made the Priest Rapids Hatchery program such a success. This includes Grant County Public Utility District project manager, Eric Lauver; Fisheries Scientist, Russell Langshaw, Priest Rapids Hatchery management staff, Mike Lewis, Brian Lyon, and Glen Pearson; WDFW science division staff, Shawnaly Meehan and Dennis Werlau; and WDFW otolith readers led by Jeff Grimm and Lance Campbell. We also thank the Priest Rapids Coordinating Committee's Hatchery Subcommittee. We also appreciate the contributions of Jeff Fryer who leads the CWT effort in the Hanford Reach. The funding for this work was provided by Grant County Public Utility District, the United States Army Corps of Engineers, and the Washington Department of Fish and Wildlife.

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Juvenile Release Numbers and Size Metrics at the Priest Rapids Hatchery

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Abstract

Objective 9 of the Grant County Public Utility District's (GPUD) hatchery monitoring and evaluation plan is to determine if hatchery fish were released at the programmed size and number at the Priest Rapids Hatchery (PRH). The subyearling fall Chinook Salmon released from the Priest Rapids Hatchery were produced as part of two mitigation programs: GPUDs mitigation and the Army Corp of Engineers mitigation. This report is focused on GPUDs mitigation. Prior to 2014, GPUDs mitigation was 5 million subyearling fall Chinook Salmon smolts with a target size of 50 fish per pound. Beginning in 2014, GPUDs mitigation was increased to 5,599,504 with a target weight of 50 fish per pound and a target coefficient of variation in length of <10 mm. Releases from 2014-2018 were within 10% of the release number target and ranged from 5,374,566 to 6,129,355. The mean annual weight of fish was between 49-52 fish per pound and the coefficient of variation was <10 mm for all years (annual range = 6.1-8.4 mm). The range in annual condition factor (K) was 1.2-1.3. In summary, GPUD met its fall Chinook Salmon hatchery mitigation target every year between 2014-2018.

Introduction

Objective 9 of the Grant County Public Utility District's (GPUD) hatchery monitoring and evaluation plan is to determine if hatchery fish were released at the programmed size and number at the Priest Rapids Hatchery (PRH). The subyearling fall Chinook Salmon released from the Priest Rapids Hatchery were produced as part of two mitigation programs: GPUDs mitigation and the Army Corp of Engineers mitigation. This report is focused on GPUDs mitigation. Prior to 2014, GPUDs mitigation was 5 million subyearling fall Chinook Salmon smolts with a target size of 50 fish per pound. Beginning in 2014, GPUDs mitigation was increased to 5,599,504 with a target weight of 50 fish per pound and a target coefficient of variation in length of <10 mm. Mitigation credit is generally assumed when release numbers are within 10% of the release number target.

Methods

From early March to late-June roughly 1,200,000 to 1,600,000 juvenile fall Chinook Salmon produced at PRH were reared and acclimated in each of five concrete channel ponds. These rectangular ponds measure ~81 x 11 meters and 1.2 meters deep. Total static water capacity is ~942,951 cubic liters. These ponds were connected to the PRH discharge channel by a 1.5 km long concrete channel. The PRH discharge channel flows into the Columbia River below Priest Rapids Dam. Release timing for each pond has varied but since 2017, two ponds have been released in late May and the others by mid to late June. These staggered releases were part of an evaluation to evaluate the effects of release time on survival.

Abundance of fall Chinook produced was estimated by weight, counts, and mortality between the time of sampling and fish release from PRH. Non adipose clipped or coded wire tagged juveniles were gravimetrically inventoried into each pond whereas adipose clipped or coded wire tagged juveniles were counted into each pond. During rearing, the mortalities were collected and counted from each pond. The number of smolts released from each pond was calculated by subtracting the total number of mortalities from the numbers inventoried into the pond. The total number of smolts annually released included the numbers released from each of the five ponds.

The data associated with fish size and condition at release from PRH prior to release year 2014 were obtained from the fish culture staff. On the day of release, this staff used large dip nets to capture fish from each of the five rearing ponds. The mean fish weight was obtained by weighing groups of roughly 300 fish sampled from each pond to the nearest gram and then dividing the group weight by the total number of fish weighed. The fork length of each fish from the group weight was measured to the nearest millimeter to calculate mean length, coefficient of variation and the condition factor (K). The results were pooled to provide mean estimates for the facility. The size and condition data for the 2014 through 2018 release years were collected by PRH monitoring and evaluation staff the day prior to or day of release for each pond. Samples of fish were captured with a cast net from multiple sections within each rearing pond. Each fish collected was individually weighed to the nearest 0.1 gram and measured for fork length to the nearest millimeter to calculate mean length, coefficient of variation and the condition factor (K). The results were pooled to provide mean estimates for the entire facility production.

Results

Releases from 2014-2018 were within 10% of the release number target and ranged from 5,374,566 to 6,129,355 (Table 1). The mean annual weight of fish was between 49-52 fish per pound and the coefficient of variation was <10 mm for all years (annual range = 6.1-8.4 mm). The range in annual condition factor (K) was 1.2-1.3. In summary, GPUD met its fall Chinook Salmon hatchery mitigation target every year between 2014-2018.

Table 1. Numbers, fish per pound (FPP), coefficient of variation in length (CV) and condition factor (K) for fall Chinook Salmon smolts released from Priest Rapids Hatchery, Return Years 1992 - 2018. Targets values for Release 1992 - 2013 = 5,000,000, Release 2014 - 2018 = 5,599,504; Targets values for FPP = 50, CV = <10.0 mm.

Release Year		Total Release	GPUD Release	FPP	CV	K
1992		7,000,100	5,000,000	55	8.7	1.0
1993		7,134,159	5,000,000	54	8.6	1.1
1994		6,705,836	5,000,000	49	6.9	1.1
1995		6,702,000	5,000,000	47	6.7	1.1
1996		6,700,000	5,000,000	45	6.6	1.1
1997		6,644,100	5,000,000	52	11.0	1.0
1998		6,737,600	5,000,000	45	8.9	0.9
1999		6,504,800	5,000,000	48	6.5	1.1
2000		6,856,000	5,000,000	51	6.6	1.1
2001		6,862,550	5,000,000	45	6.3	1.1
2002		6,779,035	5,000,000	45	6.9	1.1
2003		6,777,605	5,000,000	48	6.9	1.1
2004		6,814,560	5,000,000	48	6.8	1.1
2005		6,599,838	5,000,000	48	5.9	1.1
2006		6,876,290	5,000,000	45	6.3	1.1
2007		6,743,101	5,000,000	46	7.0	1.1
2008		4,548,307	4,548,307	45	8.3	1.0
2009		6,788,314	5,070,192	49	6.7	1.1
2010		6,776,651	5,057,211	49	7.3	1.1
2011		6,798,390	5,073,435	47	9.1	1.2
2012		7,056,948	5,266,389	49	7.1	1.1
2013		6,822,861	5,091,696	47	7.6	1.1
2014		7,267,248	5,574,779	50	8.4	1.2
2015		7,039,544	5,400,105	52	6.6	1.2
2016		7,242,054	5,555,452	49	6.1	1.2
2017		7,006,252	5,374,566	49	6.1	1.3
2018		7,990,190	6,129,355	50	6.6	1.2
2009 - 2018	Mean of Means	7,078,845	5,359,318	49	7.2	1.2
	SD	368,162	336,088	1	1.0	0.1
1992 - 2018	Mean of Means	6,806,457	5,116,351	48	7.3	1.1
	SD	534,188	287,308	3	1.2	0.1

Discussion

The PRH has a long history of meeting the target number and size of subyearling fall Chinook Salmon smolts in fulfillment of Grant PUDs hatchery fall Chinook Salmon mitigation. These fish provide substantial harvest in ocean and freshwater fisheries (see harvest chapter in this report) and may also contribute to natural production in the Hanford Reach. In addition, the hatchery program has been adapted to correspond to hatchery reform principles. Fish culture activities by the Washington Department of Fish and Wildlife has been instrumental to the success of this program.

Acknowledgments

We thank the many partners that have made the Priest Rapids Hatchery program such a success. This includes Grant County Public Utility District project manager, Eric Lauver, Hatchery Habitat Supervisor, Deanne Pavlik-Kunkel; Priest Rapids Hatchery management staff, Mike Lewis, Brian Lyon, Glen Pearson and Renee Shaw; WDFW science division staff, Shawnaly Meehan and Dennis Werlau, and WDFW District 4 Fish and Wildlife Biologist, Paul Hoffarth. We also thank the Priest Rapids Coordinating Committee's Hatchery Subcommittee.

Harvest of Chinook Salmon and Steelhead Originating from Upper Columbia River Hatchery Programs

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Abstract

The objective of this evaluation was to determine if a diversity of upper Columbia Basin Chinook Salmon and steelhead hatchery programs contributed to harvest. More specifically, we were interested in evaluating whether harvest rates were consistent with management objectives and where fish were harvested. Harvest rates were lowest on endangered spring Chinook Salmon with annual brood year means of 5-6% for Methow, Chewuch, and Twisp spawning aggregates (annual range 0 to 59%) and 26% for the Chiwawa spawning aggregate (annual range 0 to 95%). The percent of the population harvested was not correlated with spawning escapement ($P>0.05$) and the total number of fish harvested was correlated with spawning escapement ($P<0.05$) in the Chiwawa and Twisp rivers but not in the Methow or Chewuch rivers. Most harvest of spring Chinook Salmon occurred in freshwater. Harvest rates were much higher for the more abundant summer and fall Chinook Salmon programs with annual brood year averages around 53-75% and annual ranges of 14 to 91%. Percent harvest increased with increasing spawning escapement for summer Chinook in the Methow ($P=0.01$) and Okanogan ($P=0.0002$) rivers but not for summer Chinook in the Wenatchee River ($P=0.49$), Chelan Falls/Turtle Rock program ($P=0.43$), and Hanford Reach fall Chinook ($P=0.28$). The total number fish harvested was not correlated with spawning escapement ($P>0.05$) for the Wenatchee River, Wells subyearling, Methow River, or Okanogan River programs, but significant correlations were detected ($P<0.05$) for the Chelan Falls/Turtle Rock yearling and Wells yearling programs and for fall Chinook Salmon from Priest Rapids Hatchery. Most of the harvest of summer Chinook Salmon occurred in the ocean and harvest of fall Chinook Salmon occurred evenly between freshwater and the ocean. Harvest rates averaged 16% (range 0-54%) for threatened hatchery-origin steelhead and less than 5% (range 0 to 4%) for natural-origin steelhead. The percent of steelhead harvested increased with increasing escapement in the Okanogan River ($P=0.006$) but was not significantly correlated in the Methow ($P=0.29$) and Wenatchee rivers ($P=0.85$). Total harvest of hatchery steelhead was not significantly correlated with spawning escapement in the Methow or Wenatchee rivers ($P>0.05$) but was correlated in the Okanogan River ($P=0.006$). Every hatchery program that was evaluated contributed to harvest and sometimes substantially. The magnitude of harvest generally corresponded to the status of the population: the lowest harvest occurred on the most imperiled stocks and the highest harvest occurred on the healthiest stocks. However, harvest sometimes hindered meeting broodstock collection goals and harvest management of endangered or threatened species could impede conservation objectives and might be improved by tailoring harvest to abundance, weak stocks, and weak broodyears.

Introduction

One of the main functions of salmon and steelhead hatcheries is to increase the opportunity for harvest. However, there are a diversity of harvest objectives associated with different types of hatcheries. In some cases, the sole objective of hatcheries is to produce maximal harvest. These hatcheries are often segregated from naturally spawning populations and the goal of harvesters is to harvest all the fish produced by the hatchery except for those needed for the next brood cycle (Mobrand et al. 2005; Paquet et al. 2011). In other cases, the main objective of a hatchery is to aid in the recovery of depressed populations and harvest is

incidental to natural production objectives. These hatcheries are often referred to as conservation or integrated, and harvest is intentionally negligible so that returns from these programs can contribute to natural production. Finally, other hatcheries fall on a continuum between the two extremes described above, sharing both harvest and conservation objectives within the same hatchery. Harvest from such programs is largely determined by what the population can sustain into the future as well as constraining impacts to non-target populations within acceptable levels.

Harvest rates and allocations are set within complicated processes and agreements among fisheries co-managers. Harvest rates can be determined based upon maximum sustainable yield (MSY), allowable take of ESA listed species or weak stocks, desired escapement objectives, need for removal of hatchery-origin fish for conservation purposes, and a variety of other approaches (Maier 2020). In some cases, fisheries managers focus on selectively harvesting hatchery-origin fish so that the natural-origin fish escape to the spawning grounds. One of the main assumptions of science-based harvest management is that harvestable surplus increases with increasing population sizes particularly when carrying capacity is exceeded.

Harvest of upper Columbia River Chinook Salmon and steelhead occurs across three primary fisheries: ocean commercial (treaty and non-treaty, reported together), Columbia River commercial (treaty and non-treaty, reported separately), and recreational fishing. The timing of each fishery is set to target stocks intended for harvest. For example, ocean commercial fisheries typically begin in early summer to avoid harvest of Upper Columbia spring Chinook Salmon, which primarily enter the river from March through June, and instead focus on summer and fall Chinook Salmon stocks. In the upper river, conservation fisheries for recreational anglers are timed to remove hatchery-origin adults to prevent them from reaching spawning areas when that outcome is desired. Some fisheries are mark-selective, meaning that only hatchery-origin fish with a visible external mark (i.e. a clipped adipose fin) may be retained. The goal of mark-selective fisheries is to allow unmarked fish to be released to continue migration and reach spawning areas. Non-selective fisheries allow harvest of all stocks but are timed to reduce impacts to non-target and/or natural-origin fish.

Most, but not all, hatchery programs mark or tag some portion of annual releases. This practice necessitates an expansion calculation to estimate overall harvest from monitoring data collected from each fishery. In addition to visible external marks, other common methods include coded-wire tags (CWT) implanted in the snout of juvenile fish allowing identification of fish origin and brood year, and passive integrated transponder tags (PIT) implanted in the body cavity of juvenile fish or dorsal musculature of adults that provide a unique identification code. Coded-wire tags must be recovered from dead fish to be read, while PIT-tags can be read by transponders located in mainstem Columbia River dams and throughout the Columbia River watershed as fish move throughout the system (Pearsons and O'Connor 2020). Both CWT and PIT-tag records are aggregated in regional databases for the purpose of analysis.

Harvesting fish can produce undesirable unintended consequences. For example, overharvest is one factor that has contributed to species or population declines. It can also result in changes to population demographics resulting in reduced population productivity and difficulty in evaluating hatchery effects on natural populations. For example, non-random harvesting of the hatchery- and natural-origin components of the population can skew sex ratios, decrease age at maturity, or influence run and spawn timing, resulting in changes in these metrics through time. In addition, selective harvest of hatchery-origin fish can result in differences in these metrics within a year. The size of Chinook Salmon has decreased during the past decades and one possible mechanism for this reduced size is harvest (Ohlberger et al. 2018, 2020).

The upper Columbia River Public Utility Districts' (Grant, Chelan, and Douglas PUDs) hatchery programs are guided by harvest monitoring indicators described in the Monitoring and Evaluation Plan for PUD Hatchery Programs (Hillman et al. 2019). The plan states that "Harvest will be applied to different types of programs in an effort to achieve the management objectives of those programs. Programs designed to augment harvest should routinely contribute to harvest at a rate that greatly reduces the incidence of straying to natural spawning grounds, but also allows the program to be sustained. Safety-net programs may be harvested as part of an adult management strategy to minimize excessive escapement of hatchery-origin fish to spawning grounds. Similarly, conservation programs may undergo harvest to manage returning adults, but the emphasis for these programs should be to achieve escapement goals. In all cases, harvest effort should not have the unintended consequence of removing excessive numbers of conservation or natural-origin fish. In years when the expected returns of hatchery adults are above the level required to meet program goals (i.e., supplementation of spawning populations and/or brood stock requirements), surplus fish may be available for harvest." The plan broadly captures the differences in harvest goals of each hatchery program and sets forth monitoring questions to "determine if appropriate harvest rates have been applied to conservation, safety-net, and segregated harvest programs to meet the Habitat Conservation Plan (HCP)/Salmon and Steelhead Settlement Agreement (SSSA) goal of providing harvest opportunities while also contributing to population management and minimizing risk to natural populations".

The objective of this analysis was to determine whether a diversity of upper Columbia Basin salmon and steelhead hatchery programs contributed to harvest. More specifically our objective was to determine whether harvest levels were consistent with management objectives of the hatchery programs. To evaluate these goals we report spawning escapement, number of fish harvested, percent of brood year harvested, and the proportion harvested in various fisheries for each hatchery program.

Methods

Spawning escapement, number of fish harvested, percent of brood year harvested, and fishery proportion data were aggregated from Grant, Chelan, and Douglas PUD hatchery monitoring and evaluation reports (Richards and Pearsons 2019; Hillman et al. 2020; Snow et al. 2020). The quantities of harvested Chinook Salmon and percent of brood year harvested represent the totals from the hatchery program and exclude natural-origin stocks. Creel survey data for natural-origin steelhead were included in our analyses. We compared among conservation and safety-net hatchery programs for spring Chinook Salmon and steelhead as well as harvest-augmentation programs for summer and fall Chinook Salmon. We also compared percent of brood year harvested with spawning escapement abundance to assess trends when there was a range of spawning escapement. For all Chinook Salmon comparisons, the spawning escapement data were reported for return years (spawn year) and harvest data were reported for brood years. Both spawning escapement and harvest data for steelhead were reported as the span of return migration year and spawn year (i.e. 2002-2003). The plots of spawning escapement versus percent of brood year harvested and total number harvested show a line of best fit, equation of the fit, the R^2 value, and F-test results. Other plots used actual values from the annual reports and means of fishery proportions for the included brood years.

As described in the PUD hatchery monitoring and evaluation reports, the Regional Mark Information System (RMIS) database was used to estimate harvest of coded-wire tagged hatchery stocks using an expanded sample rate during the data collection event and the tag-code-specific mark rate for the population. Percent of brood year harvested for Chinook Salmon represents the sum of all harvest in fisheries divided by sum of all harvest in fisheries plus spawning escapement and broodstock collection. Local creel sampling was used to estimate steelhead harvest.

Table 1. Types of harvest that occurred for spring Chinook Salmon (SPC), summer Chinook Salmon (SUC), fall Chinook Salmon (FAC), and steelhead (STH) in the upper Columbia River Public Utility District's conservation and harvest-augmentation hatchery programs. Salmon harvest results were reported for brood years (BY) and steelhead results were reported for return years (RY).

Species / race	Program	Program Type	Years	Ocean Commercial	Columbia River Tribal	Columbia River Commercial	Recreational
SPC	Chiwawa	Conservation	BY 1989-2012	x	x	x	x
SPC	Methow	Conservation	BY 1993-2012	x	x	x	x
SPC	Twisp	Conservation	BY 1992-2012	no data	x	x	x
SPC	Chewuch	Conservation	BY 1992-2012	x	x	x	x
SUC	Wenatchee	Harvest-augmentation	BY 1989-2012	x	x	x	x
SUC	Chelan Falls/ Turtle Rock	Harvest-augmentation	BY 1995-2012	x	x	x	x
SUC	Wells Hatchery subyearling	Harvest-augmentation	BY 1993-2012	x	x	x	x
SUC	Wells Hatchery yearling	Harvest-augmentation	BY 1993-2012	x	x	x	x
SUC	Methow	Harvest-augmentation	BY 1989-2012	x	x	x	x
SUC	Okanogan	Harvest-augmentation	BY 1989-2012	x	x	x	x
FAC	Priest Rapids Hatchery	Harvest-augmentation	BY 1997-2012	x	x	x	x
STH	Wenatchee	Conservation	RY 2007-2019		x		x
STH	Methow	Conservation	RY 2002-2019		x		x
STH	Okanogan	Conservation / safety net	RY 2003-2019		x		x

Results

Hatchery Spring Chinook Salmon

Annual spawning escapement of upper Columbia River hatchery-origin Spring Chinook Salmon to the Methow, Twisp, and Chewuch rivers was typically fewer than 1,000 individuals and average harvest was less than 10% of brood year production (Figure 1). Chiwawa River spawning escapement was generally 1,000-2,000 individuals and harvest averaged 25.6% of brood year production between 2003-2012. The percent of brood year harvested was as high as 95% for the Chiwawa and 60% for some brood years in the Methow, and these high harvest rates occurred when spawning escapement was relatively low. The percent of harvest was not significantly correlated with spawning escapement ($P>0.05$; Figure 2). The total number of fish harvested was correlated with spawning escapement ($P<0.05$) in the Chiwawa and Twisp rivers but not in the Methow or Chewuch rivers. The bulk of harvest occurred in tribal ($\bar{x}$ = 47%) and sport ($\bar{x}$ = 31%) fisheries (Figure 3). Commercial fisheries in the ocean ($\bar{x}$ = 9%) and lower Columbia River ($\bar{x}$ = 13%) accounted for the remaining harvest.

Spawning escapement for Chiwawa River spring Chinook Salmon was low enough in the late 1980's and throughout the 1990's that the broodstock collection goal of 379 individuals was rarely met. Beginning in brood year 2000, spawning escapement improved, and broodstock collection goals were met in most years. Broodstock collection was revised down to 74 individuals beginning in 2009 and spawning escapement has been well above that number since then. Ocean and non-treaty Columbia River commercial harvest was low for these fish; however, tribal harvest exceeded 100 individuals in 7 of 24 years and recreational harvest exceeded 100 individuals in 14 out of 24 years.

The spawning escapement for the aggregated Methow River Basin spring Chinook Salmon programs, which includes production in the Twisp and Chewuch rivers, followed a pattern similar to the Chiwawa River program. The broodstock collection goal of 104 individuals was rarely met in the 1990s but since brood year 2000 the goal has generally been met. While ocean and non-treaty Columbia River harvest was low, there were two years when tribal and recreational harvest of Methow River hatchery-origin Spring Chinook salmon both exceeded 100 individuals.

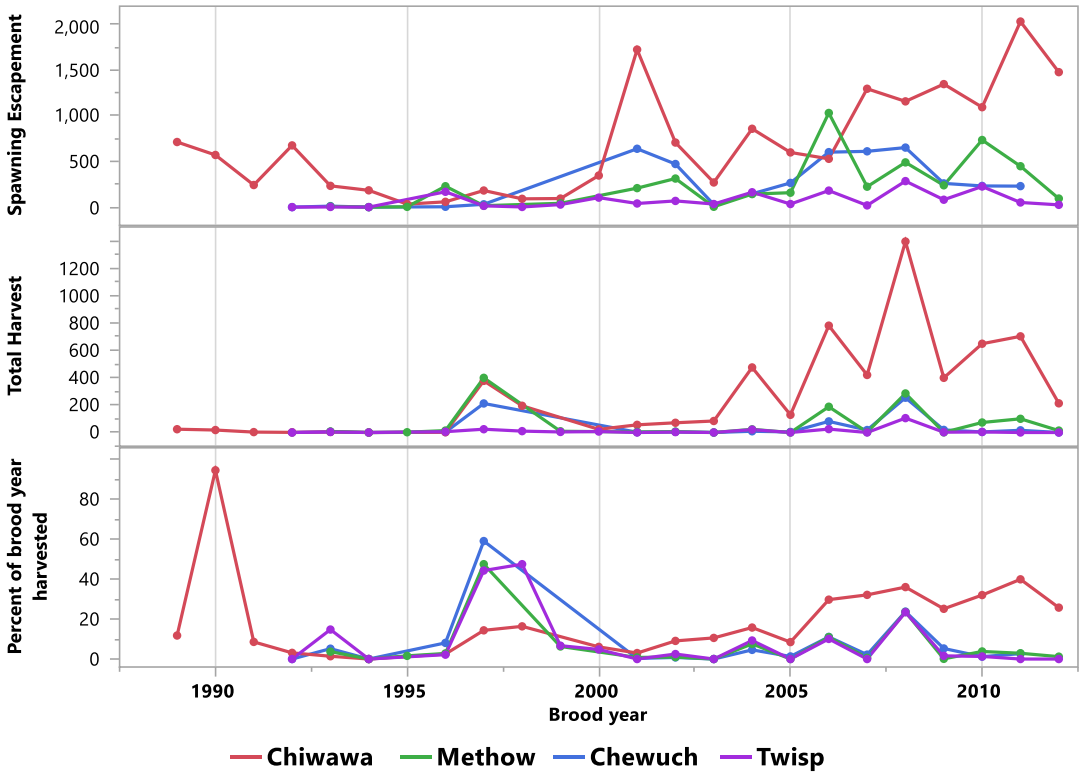
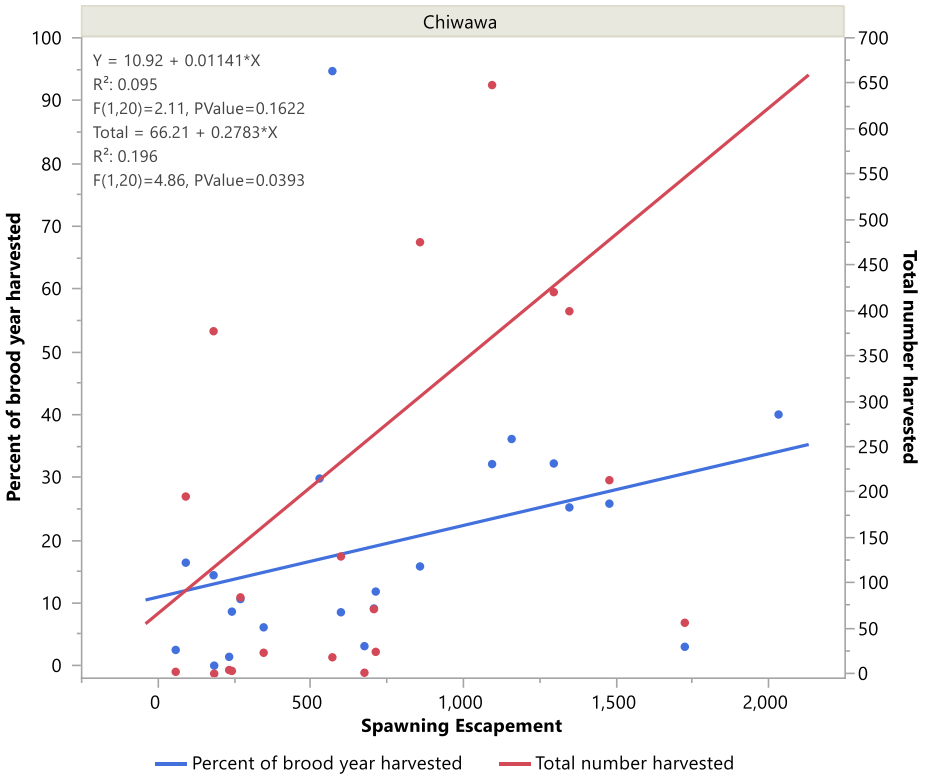
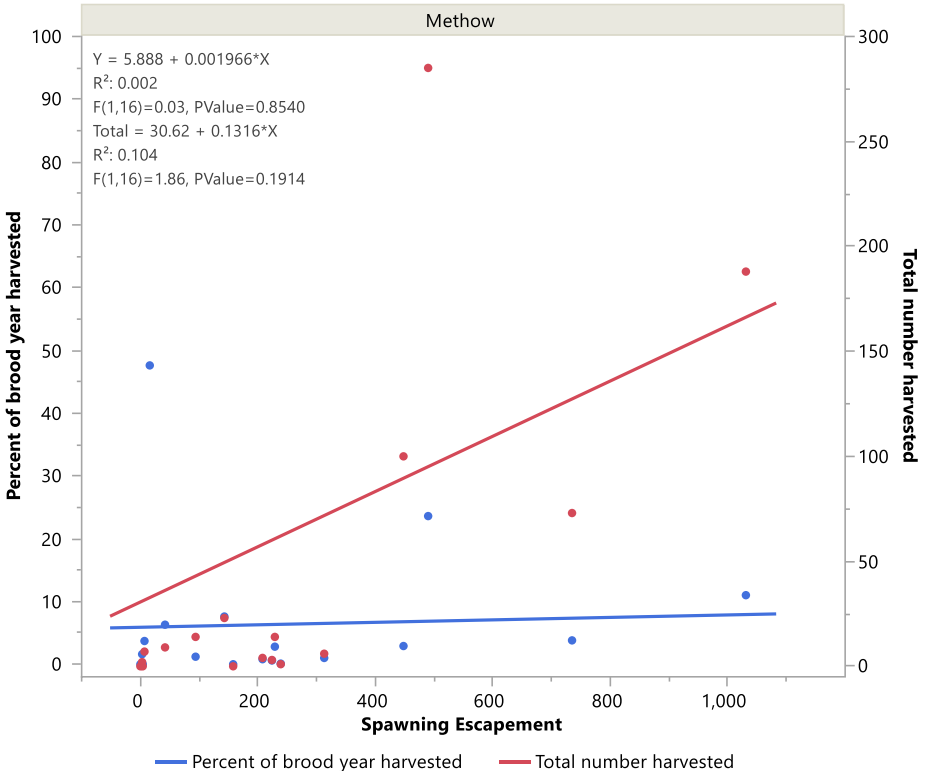


Figure 1. Spawning escapement, total harvest, and percent of brood year harvested for hatchery spring Chinook Salmon from the Chiwawa ($\bar{x}$ = 25.6%), Methow ($\bar{x}$ = 5.1%), Chewuch ($\bar{x}$ = 5.8%), and Twisp ($\bar{x}$ = 4.6%) rivers (averages represent percent of brood year harvested over brood years 2004-2012).


Chiwawa
Y = 10.92 + 0.01141*X
R²: 0.095
F(1,20)=2.11, PValue=0.1622
Total = 66.21 + 0.2783*X
R²: 0.196
F(1,20)=4.86, PValue=0.0393
Percent of brood year harvested
Total number harvested
Spawning Escapement
Percent of brood year harvested
Total number harvested


Methow
Y = 5.888 + 0.001966*X
R²: 0.002
F(1,16)=0.03, PValue=0.8540
Total = 30.62 + 0.1316*X
R²: 0.104
F(1,16)=1.86, PValue=0.1914
Percent of brood year harvested
Total number harvested
Spawning Escapement
Percent of brood year harvested
Total number harvested

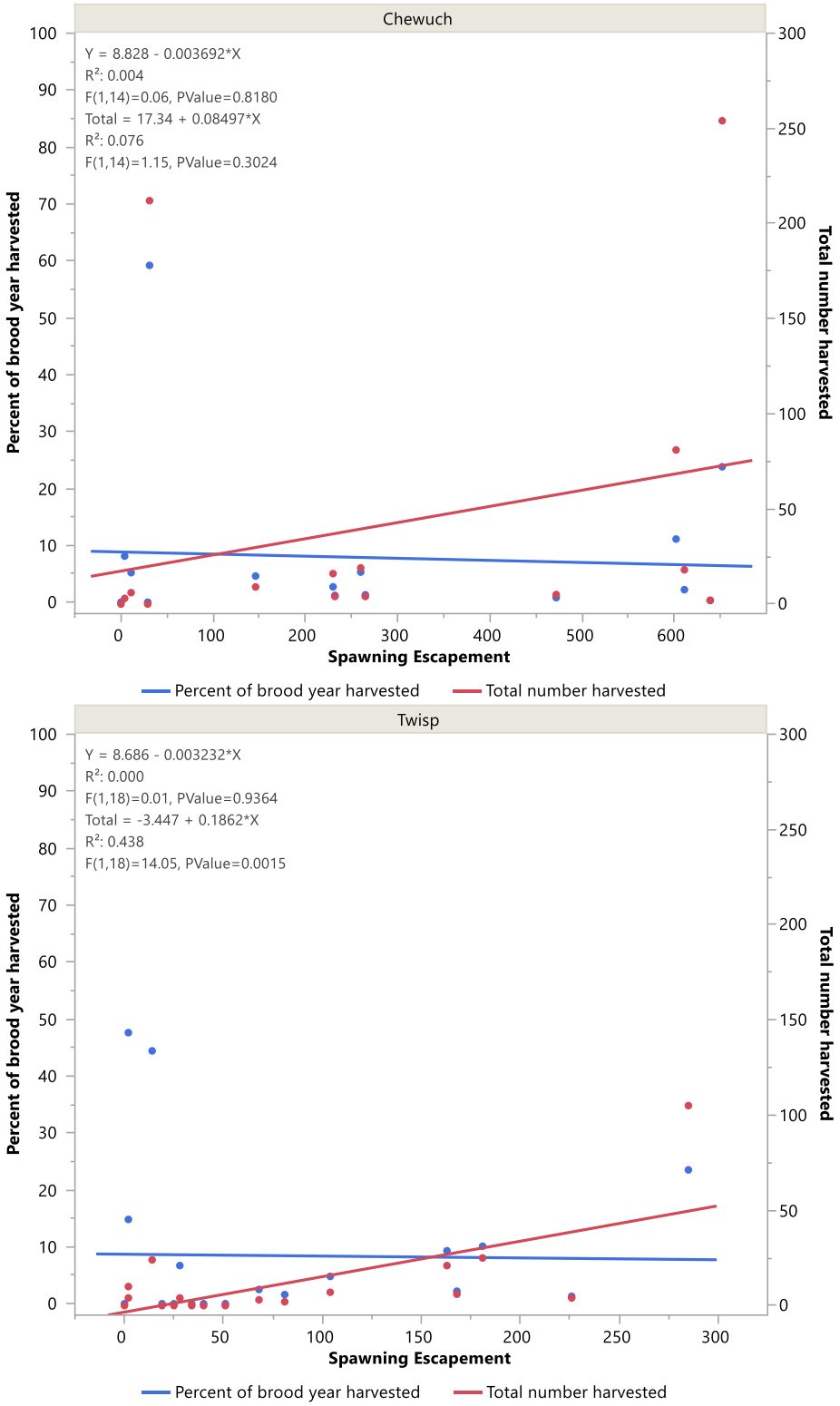


Figure 2. Spawning escapement versus percent of brood year harvested and total number of hatchery fish harvested for spring Chinook Salmon from the Chiwawa, Methow, Chewuch, and Twisp rivers.

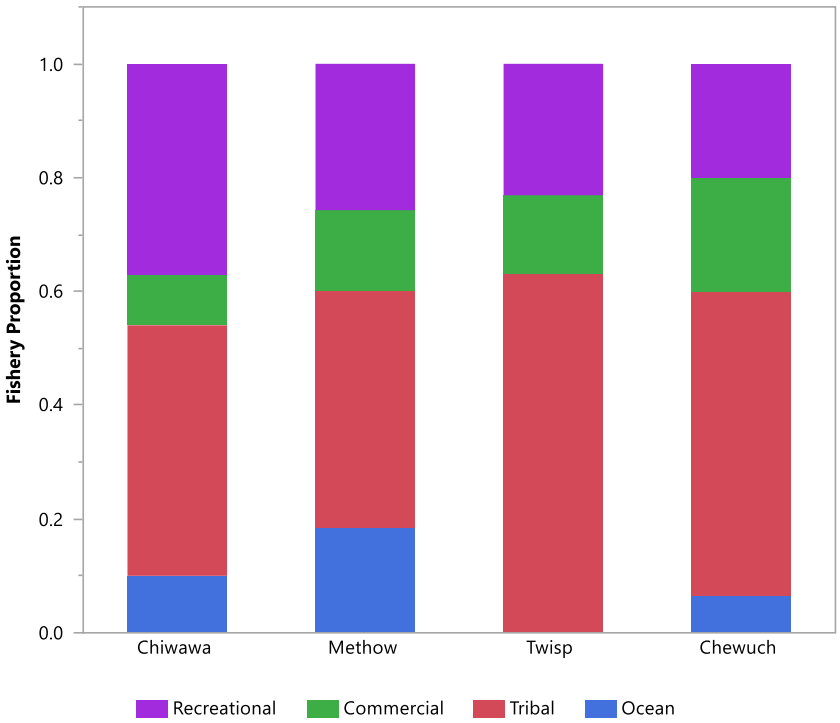


Figure 3. Fishery proportions (mean values) for spring Chinook Salmon harvested from the Chiwawa, Methow, Twisp, and Chewuch rivers.

Hatchery Summer and Fall Chinook Salmon

Annual spawning escapement of Upper Columbia River hatchery summer and fall Chinook Salmon to the Hanford Reach of the Columbia River, Wenatchee, Chelan, Methow, and Okanogan rivers was highly variable among programs and ranged from fewer than 100 individuals for releases directly into the Columbia River from Wells Hatchery to over 90,000 individuals in a single year for Priest Rapids Hatchery fall Chinook Salmon released into the Hanford Reach (summer Chinook Salmon Figure 4, fall Chinook Salmon Figure 5). The average escapement for most programs was fewer than 10,000 individuals. The annual brood year harvest of summer Chinook Salmon ranged from 25.4 – 80.2% in the Wenatchee, 17.6-75.6% in the Methow, 14.0-89.4% in the Okanogan, 42.9-91.4% for subyearlings from Wells Hatchery, 24.5-89.5% for yearlings from Wells Hatchery, 50.2-84.3% for yearlings from Chelan Falls Hatchery, and 33.8-72.5% for fall Chinook Salmon from Priest Rapids Hatchery. The percent of brood year harvested increased with increasing spawning escapement for summer Chinook Salmon in the Methow ($P=0.01$) and Okanogan ($P=0.0002$) rivers but not for summer Chinook Salmon in the Wenatchee River ($P=0.49$) and Hanford Reach fall Chinook ($P=0.28$) (Figure 6). The total number of fish harvested was not correlated with spawning escapement ($P>0.05$) for the Wenatchee River, Wells subyearling, Methow River, or Okanogan River programs, but significant correlations were detected ($P<0.05$) for the Chelan Falls/Turtle Rock yearling and Wells yearling programs and for fall Chinook Salmon from Priest Rapids Hatchery. Harvest of Wells Hatchery summer Chinook Salmon was generally high, averaging 67% but uniformly small escapement numbers precluded our ability to assess trends in harvest. Ocean commercial

fisheries accounted for an average of 61% of observed harvest for all populations (Figure 7). Tribal ($\bar{x}$ = 21%), recreational ($\bar{x}$ = 14%), and lower Columbia commercial fishing ($\bar{x}$ = 4%) accounted for the remaining harvest.

The upper Columbia River hatchery augmentation programs for summer and fall Chinook Salmon have sustained harvest rates often exceeding 50% of brood year production since the late 1990s. The Methow, Chelan Falls/Turtle Rock, and Wells programs are segregated hatchery programs and returning adults are not intended for spawning in the natural environment. As such, spawning escapement was fewer than 5,000 individuals. Spawning escapement was fewer than 10,000 in the Wenatchee and Okanogan rivers. From 1989-1999, the broodstock collection goal for Wenatchee River summer Chinook Salmon (n=492 individuals) was met only once. From 2000-2011, collection was met or within 10% of the goal in all but two years as escapement improved. The broodstock collection goal was revised down to 262 individuals in 2012 and the goal has been met each year since. The percent of brood year harvested was at least 60% twice during the period of 1989-1999 when escapement was low. The broodstock collection goals for the Methow/Okanogan (n=222), Wells age-0 (n=284) and age-1 (n=178) programs were met in all years. Broodstock collection for the Chelan Falls/Turtle Rock summer Chinook Salmon program ranged from 318-591 fish from brood year 2013 to brood year 2019 but no specific collection goal is specified. The broodstock collection goals for fall Chinook Salmon at Priest Rapids Hatchery have varied since 1991 but the goal was met each year except for an unusually low return year in 2007.

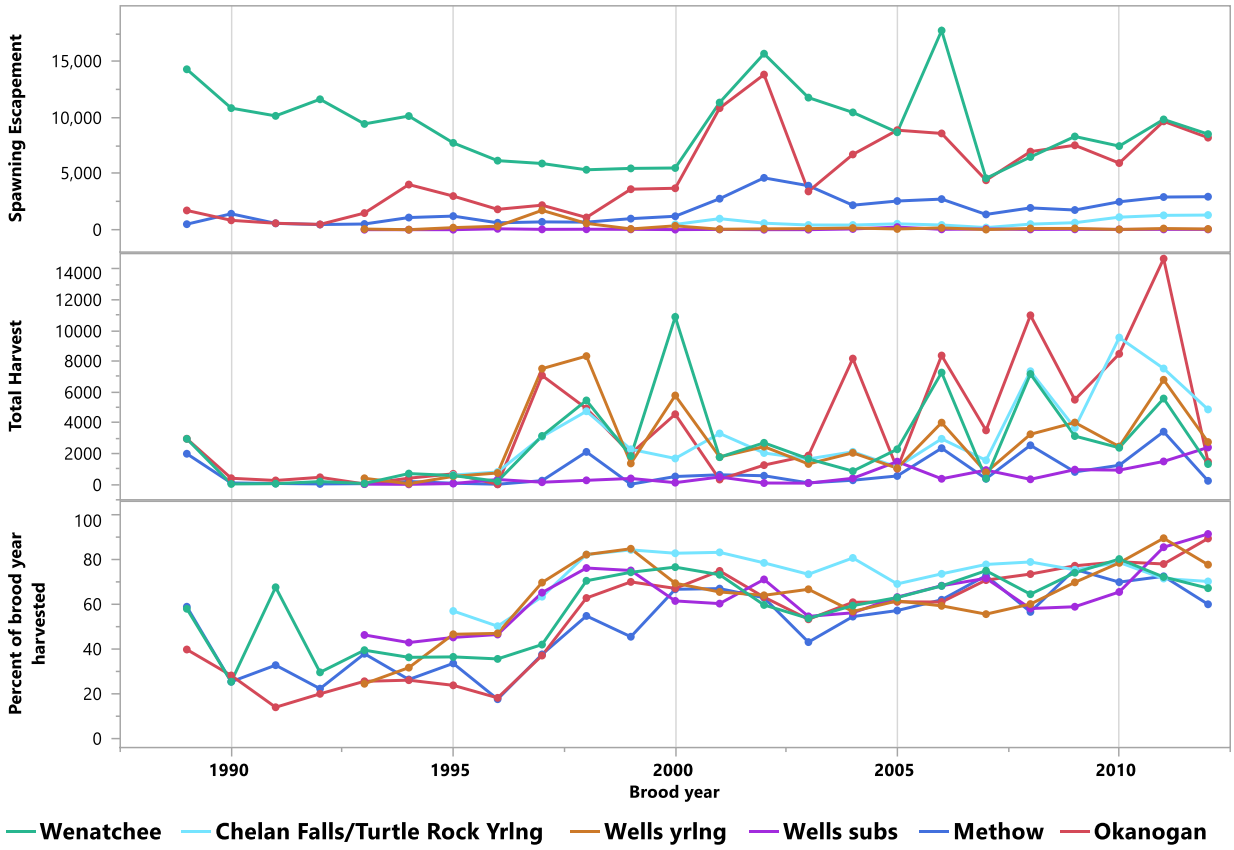


Figure 4. Spawning escapement, total harvest, and percent of brood year harvested for hatchery-origin summer Chinook Salmon from the Wenatchee River ($\bar{x}$ = 67.8%), Chelan Falls/Turtle Rock yearling program ($\bar{x}$ = 74.6%), Wells Hatchery yearling program ($\bar{x}$ = 67.6%), Wells Hatchery subyearling program ($\bar{x}$ = 67.3%), Methow River ($\bar{x}$ = 62.4%), and Okanogan River ($\bar{x}$ = 70.4%) programs (averages represent percent of brood year harvested over brood years 2004-2012).

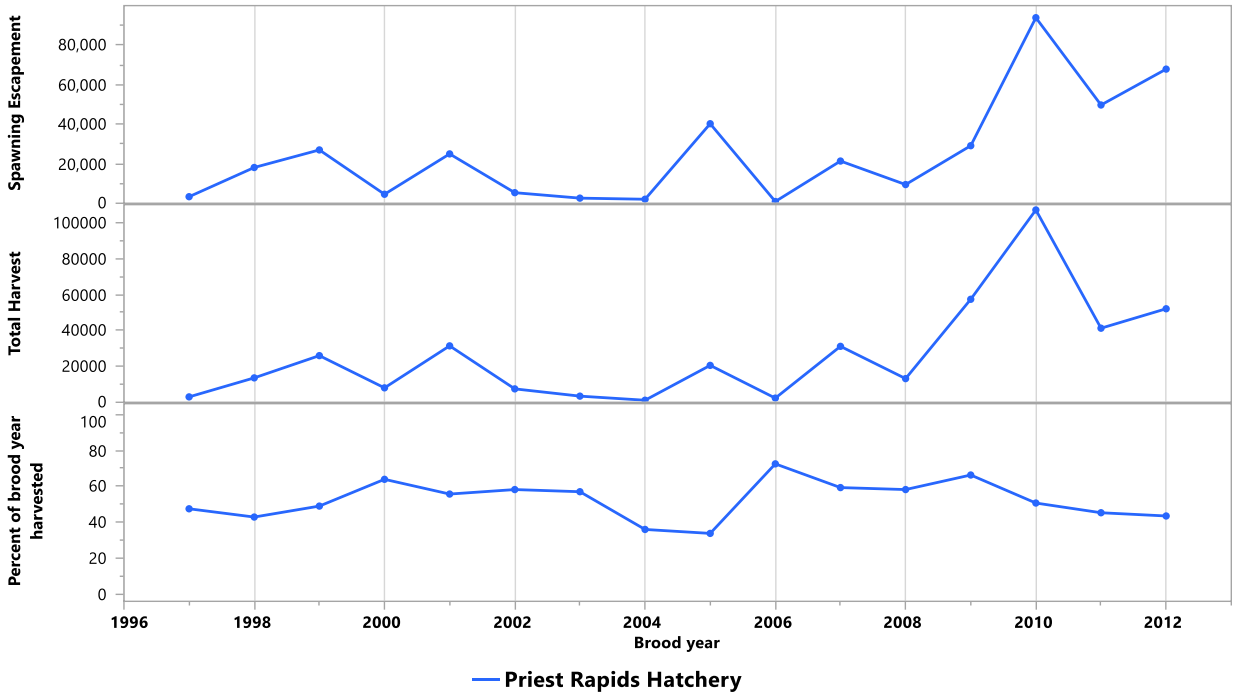
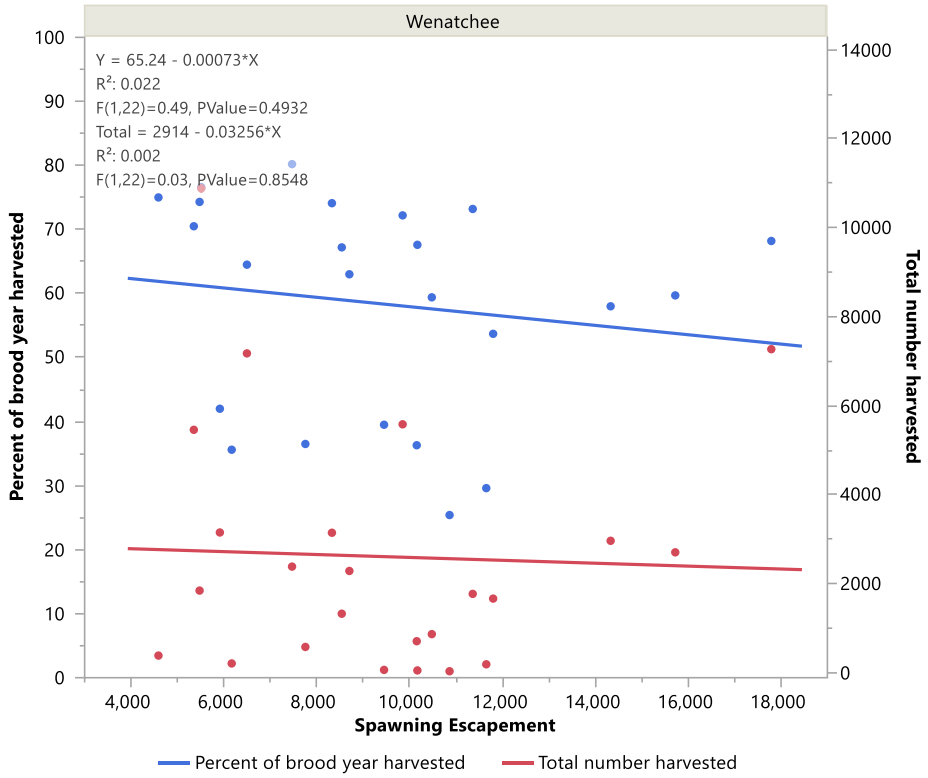
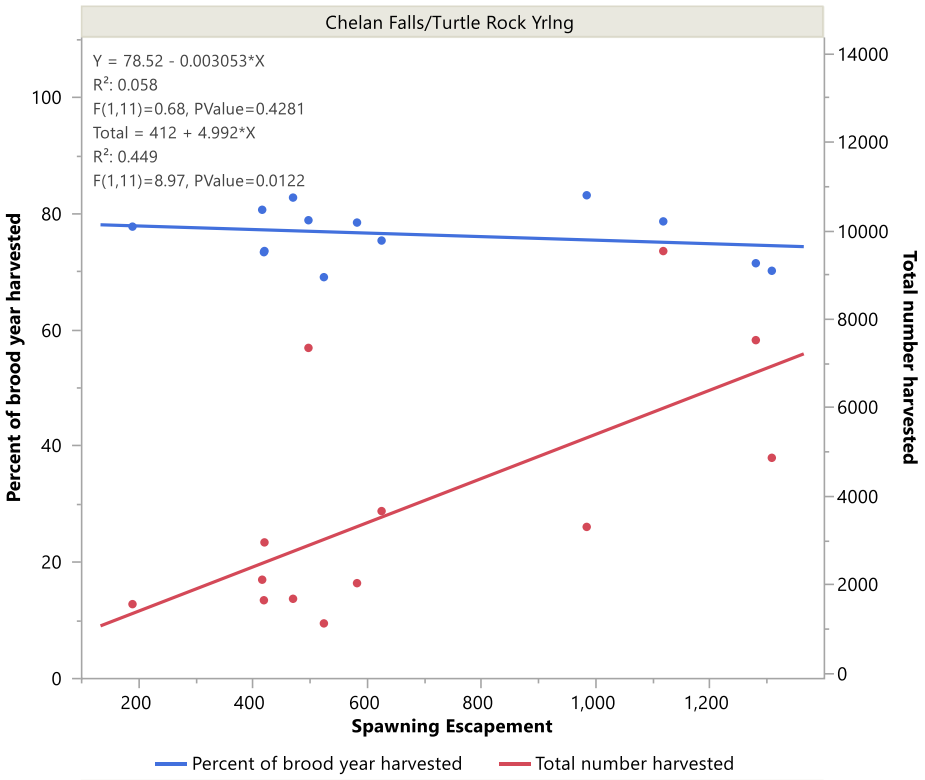
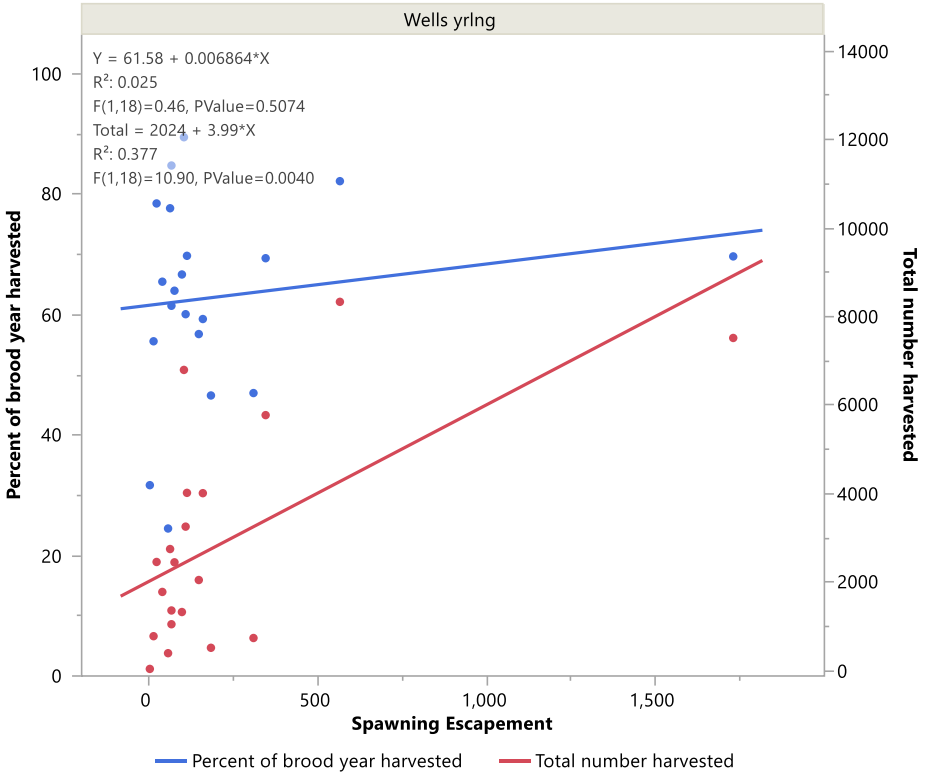
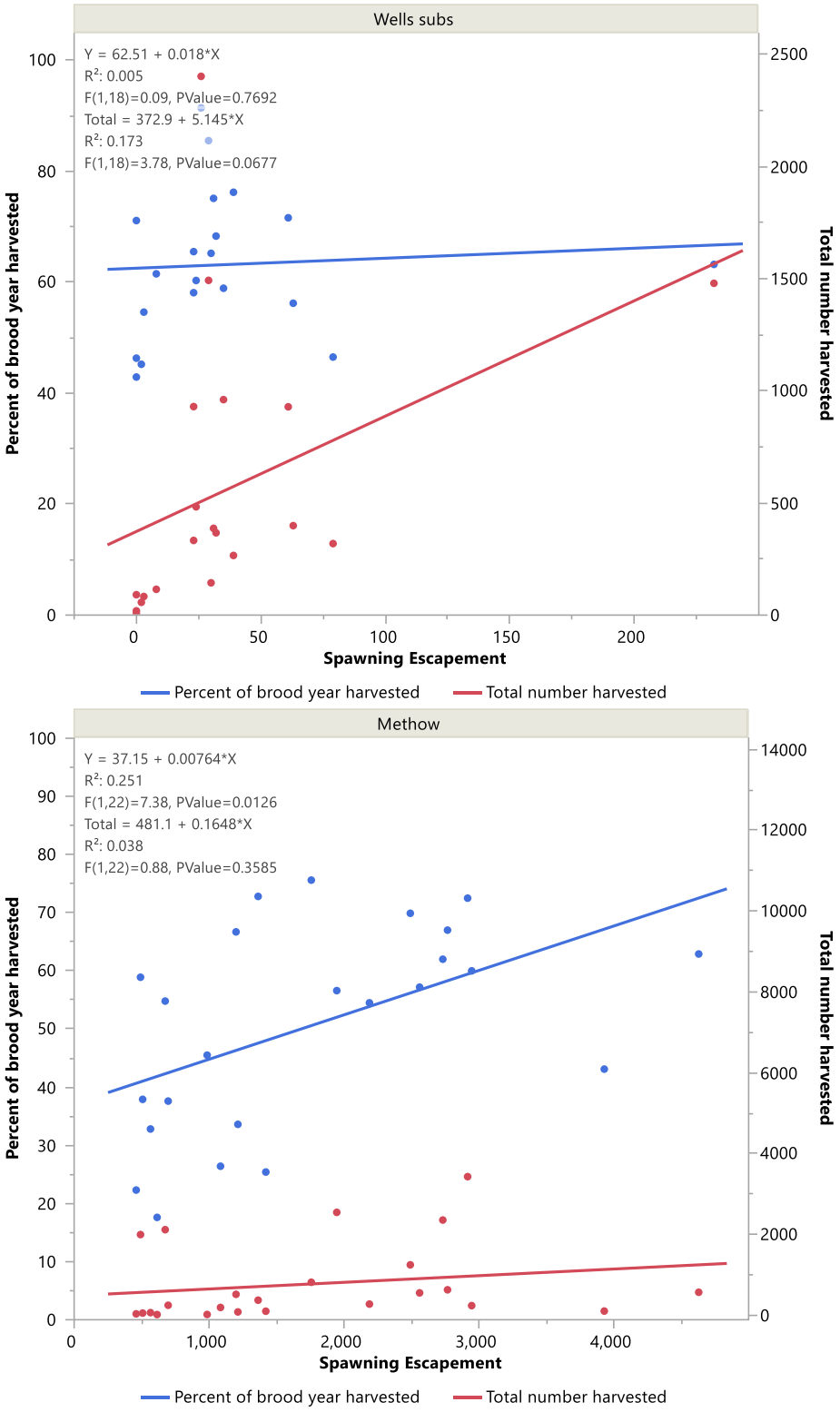


Figure 5. Spawning escapement, total harvest, and percent of brood year harvested for hatchery fall Chinook Salmon from Priest Rapids Hatchery ($\bar{x}$ = 52.5%) program (average represent percent of brood year harvested over brood years 2004-2012).




Chelan Falls/Turtle Rock Yrlng
Y = 78.52 - 0.003053*X
R²: 0.058
F(1,11)=0.68, PValue=0.4281
Total = 412 + 4.992*X
R²: 0.449
F(1,11)=8.97, PValue=0.0122
Percent of brood year harvested
Total number harvested
Spawning Escapement
Percent of brood year harvested
Total number harvested


Wells yrlng
Y = 61.58 + 0.006864*X
R²: 0.025
F(1,18)=0.46, PValue=0.5074
Total = 2024 + 3.99*X
R²: 0.377
F(1,18)=10.90, PValue=0.0040
Percent of brood year harvested
Total number harvested
Spawning Escapement
Percent of brood year harvested
Total number harvested


Wells subs
Y = 62.51 + 0.018*X
R²: 0.005
F(1,18)=0.09, PValue=0.7692
Total = 372.9 + 5.145*X
R²: 0.173
F(1,18)=3.78, PValue=0.0677
Percent of brood year harvested
Total number harvested
Spawning Escapement
Percent of brood year harvested
Total number harvested
Methow
Y = 37.15 + 0.00764*X
R²: 0.251
F(1,22)=7.38, PValue=0.0126
Total = 481.1 + 0.1648*X
R²: 0.038
F(1,22)=0.88, PValue=0.3585
Percent of brood year harvested
Total number harvested
Spawning Escapement
Percent of brood year harvested
Total number harvested

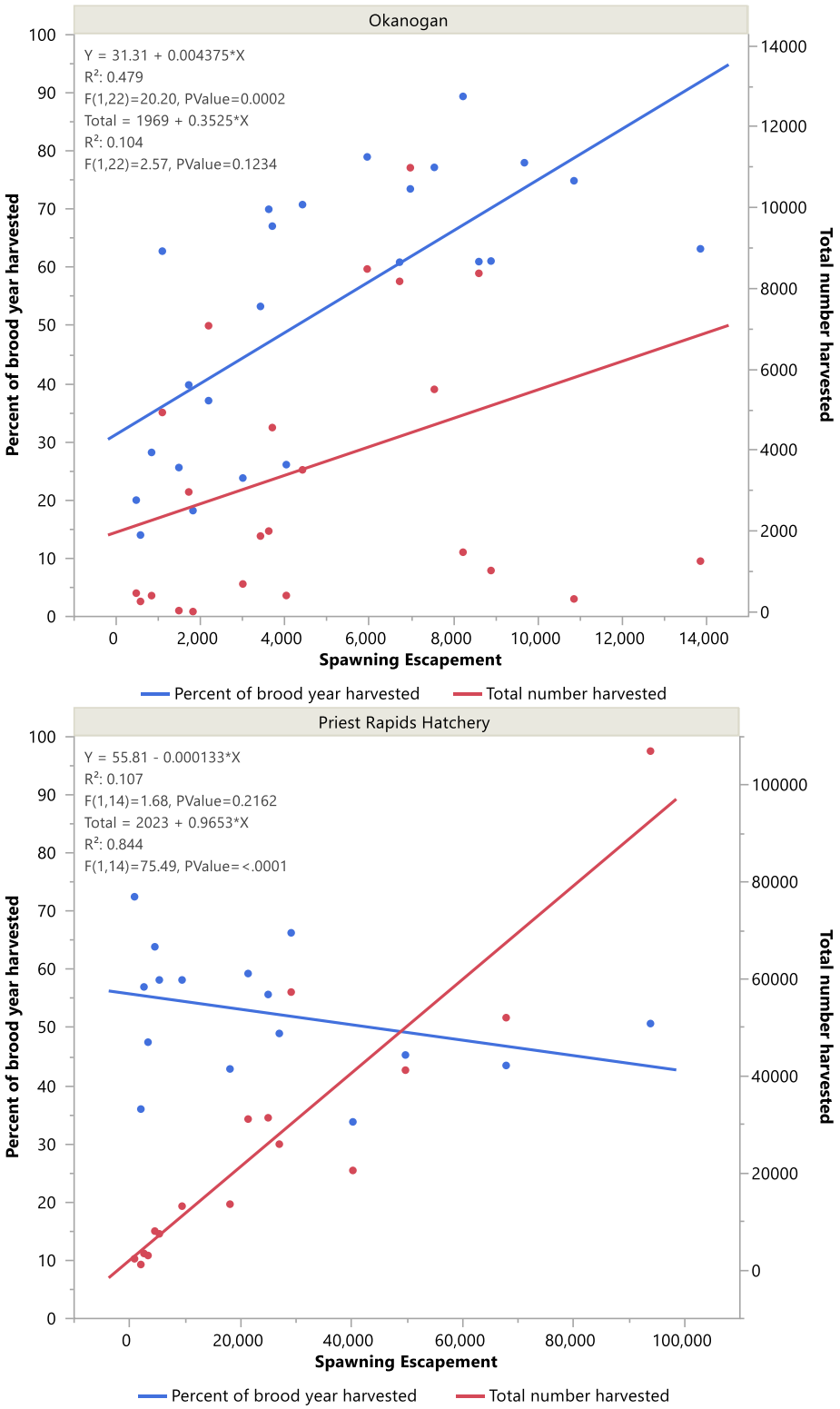


Figure 6. Spawning escapement versus percent of brood year harvested and number harvested for hatchery-origin summer Chinook Salmon from the Wenatchee River, Chelan Falls/Turtle Rock yearling program, Wells Hatchery yearling program, Wells Hatchery subyearling program, Methow River, Okanogan River, and fall Chinook Salmon from Priest Rapids Hatchery.

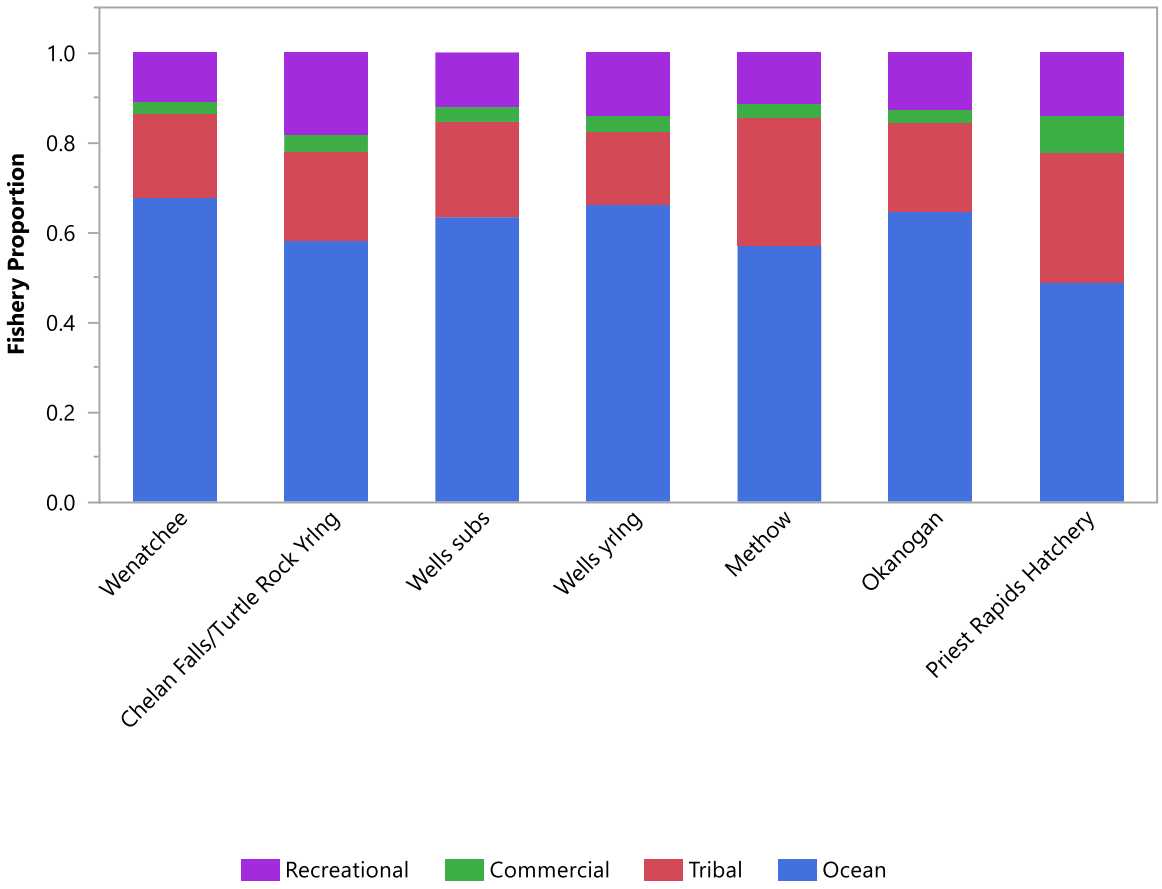


Figure 7. Fishery proportions (mean values) for summer Chinook Salmon harvested from the Wenatchee River, Chelan Falls/Turtle Rock yearling program, Wells Hatchery subyearling program, Wells Hatchery yearling program, Methow River, Okanogan River, and fall Chinook Salmon from Priest Rapids Hatchery.

Steelhead

Escapement and harvest of hatchery steelhead was greatest in the Methow River, followed by the Okanogan and Wenatchee rivers (Figure 8). Escapement and percent harvest of hatchery steelhead peaked from 2010-2012 with 6,000-11,000 individuals escaped to the Okanogan and Methow rivers respectively, and harvest rates of 40-50%. Harvest ranged from 5.3-53.9% in the Methow, 4.5-47.4% in the Okanogan, and from 8.0-12.5% in the Wenatchee River. Origin-based escapement estimates for steelhead returning to the Wenatchee River were not available prior to the 2011-2012 return year, but since then, hatchery-origin escapement was consistently below the Methow and Okanogan rivers, with a peak of around 2,000 individuals. Percent harvest increased with increasing escapement in the Okanogan ($P=0.006$) river but was not significantly correlated with escapement in the Methow ($P=0.29$) and Wenatchee rivers ($P=0.85$) (Figure 9). Total harvest of hatchery steelhead was not significantly correlated with spawning escapement in the Methow or Wenatchee rivers ($P>0.05$) but was correlated in the Okanogan River ($P=0.006$).

Escapement of natural-origin steelhead was greatest in the Methow and Wenatchee rivers, with peaks of greater than 1,200 individuals in the Methow River during the 2009-2010 and 2015-2016 return years and peaks of similar magnitude in the Wenatchee River during the 2011-2012, 2012-2013, and 2015-2016 return years (Figure 10). Origin-based escapement estimates were not available for the Wenatchee River prior to the 2011-2012 return year. Escapement to the Okanogan River was typically 200-400 individuals and was consistently lower than the Wenatchee and Methow rivers. Reported harvest of natural-origin steelhead was less than 6% of escapement. Harvest was greatest in the Methow and Okanogan rivers (up to 5% of escapement in return year 2011-2012), and lower in the Wenatchee (range 1-2% of escapement). Harvest increased with increasing escapement in the Methow (P=0.004) and Okanogan (P=0.09) but did not in the Wenatchee (P=0.89) (Figure 11). Total harvest of natural-origin steelhead was correlated with spawning escapement in the Methow and Okanogan rivers (P<0.05) but not in the Wenatchee River (P=0.44).

Spawning escapement for hatchery-origin Wenatchee River steelhead has exceeded the broodstock collection goal of 140 individuals since return year 2011-2012, when origin-based escapement data were available. Escapement of hatchery-origin steelhead to the Methow and Okanogan was more than the 170 individuals required for the Douglas PUD safety-net program for all years examined. Escapement of natural-origin steelhead to the Methow River was well above the 28 individuals required for the Twisp River conservation program. Escapement was sufficient to allow harvest of steelhead in the Wenatchee River in 8 of the last 12 return years. Harvest in the Methow and Okanogan rivers occurred in 13 of the last 17 return years.

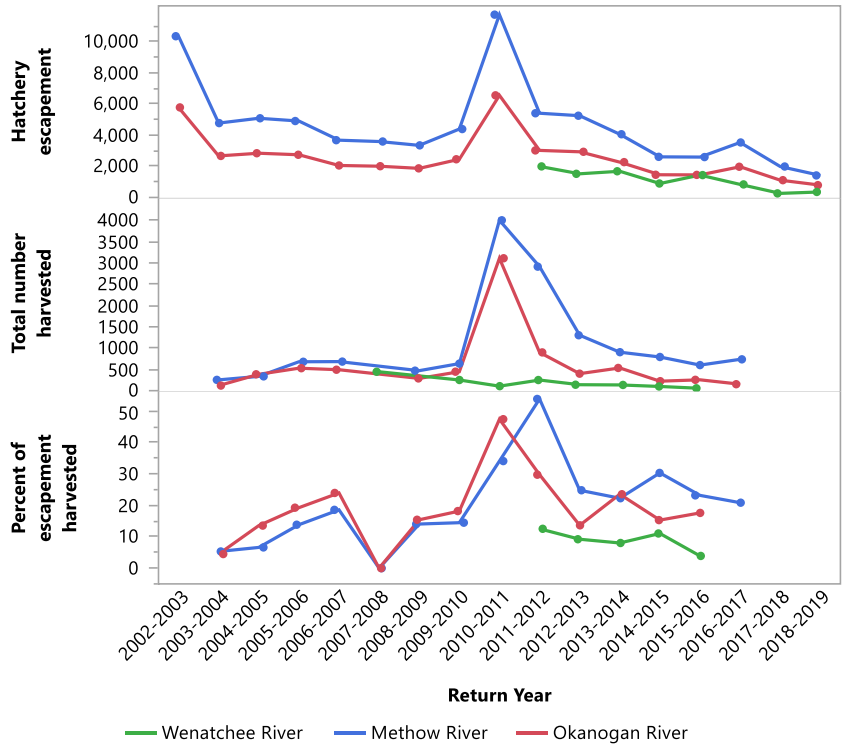
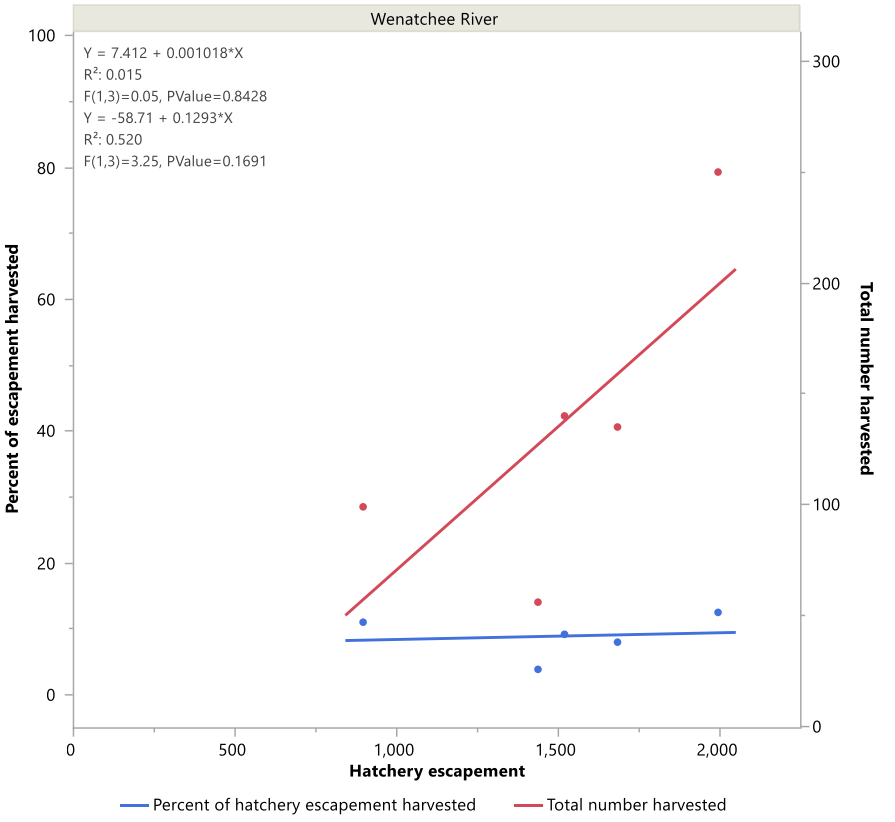
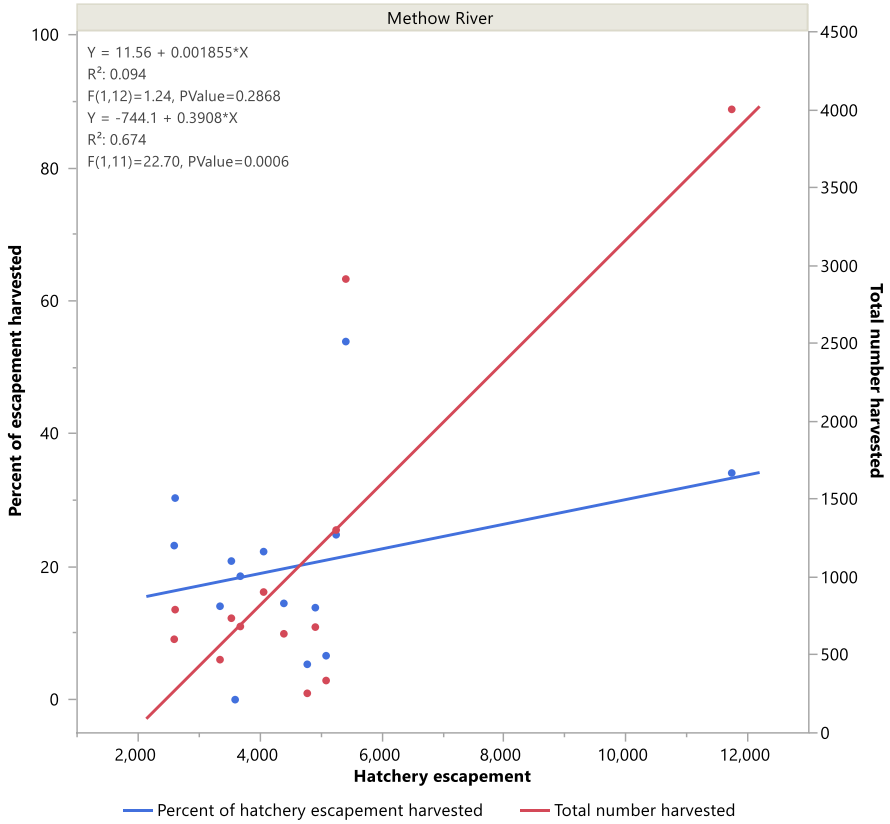


Figure 8. Escapement, total number harvested, and percent harvest of hatchery-origin steelhead escapement to the Wenatchee ($\bar{x}$ = 8.7%), Methow ($\bar{x}$ = 20.2%), Okanogan ($\bar{x}$ = 18.6%) rivers (averages represent return years 2003-2017 for the Methow and Okanogan rivers and 2011-2016 for the Wenatchee River).


Wenatchee River
Y = 7.412 + 0.001018*X
R²: 0.015
F(1,3)=0.05, PValue=0.8428
Y = -58.71 + 0.1293*X
R²: 0.520
F(1,3)=3.25, PValue=0.1691
Percent of escapement harvested
Total number harvested
Hatchery escapement
Percent of hatchery escapement harvested
Total number harvested


Methow River
Y = 11.56 + 0.001855*X
R²: 0.094
F(1,12)=1.24, PValue=0.2868
Y = -744.1 + 0.3908*X
R²: 0.674
F(1,11)=22.70, PValue=0.0006
Percent of escapement harvested
Total number harvested
Hatchery escapement
Percent of hatchery escapement harvested
Total number harvested

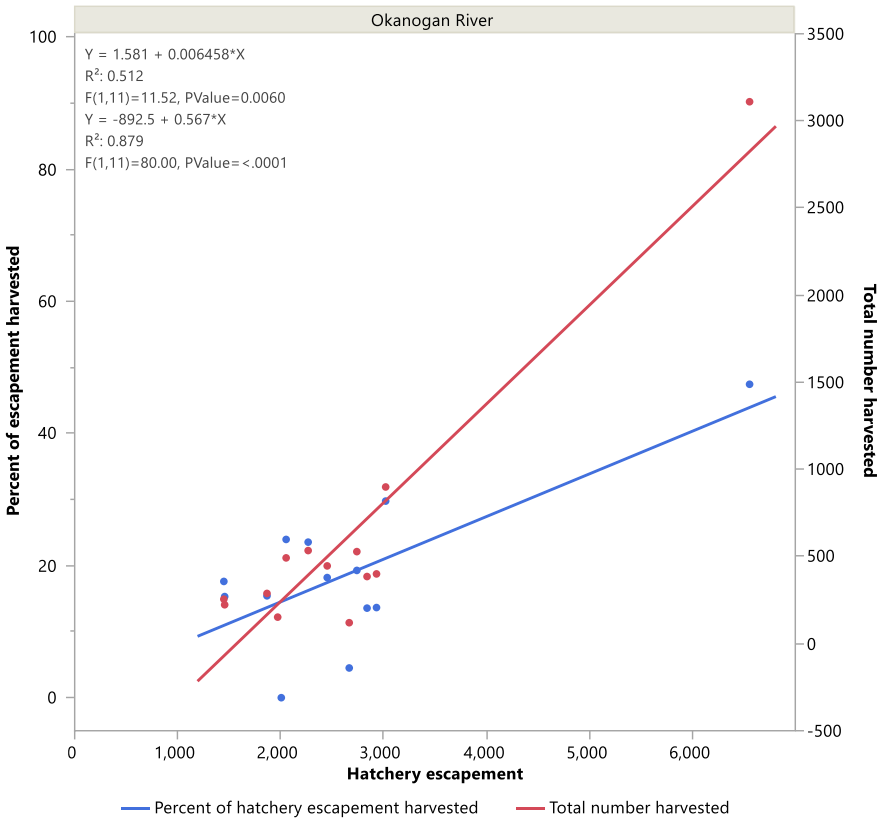


Figure 9. Escapement versus percent of escapement harvested and number harvested of hatchery-origin steelhead from the Wenatchee, Methow, and Okanogan rivers.

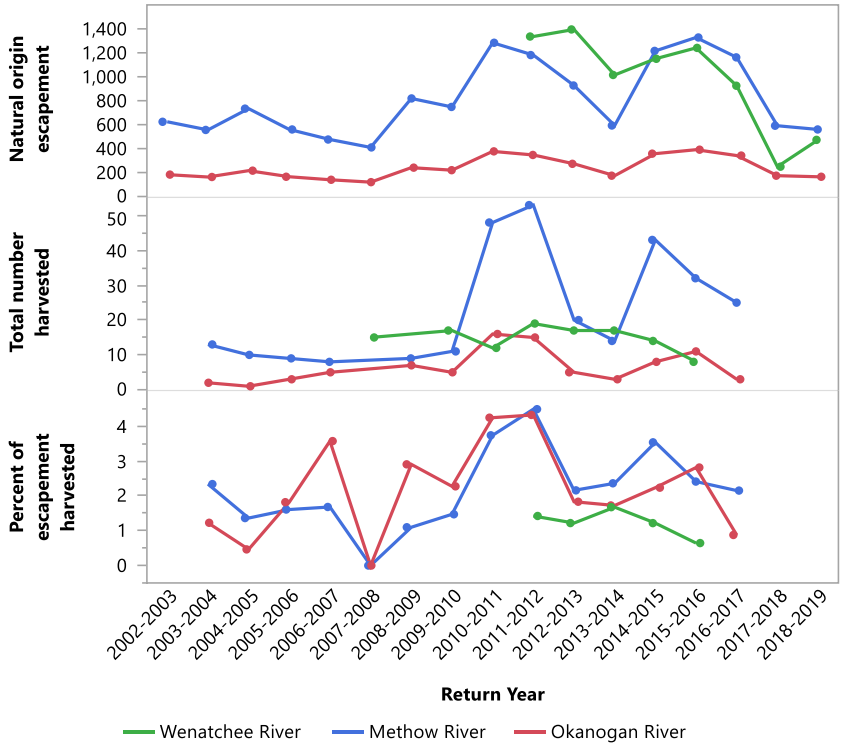
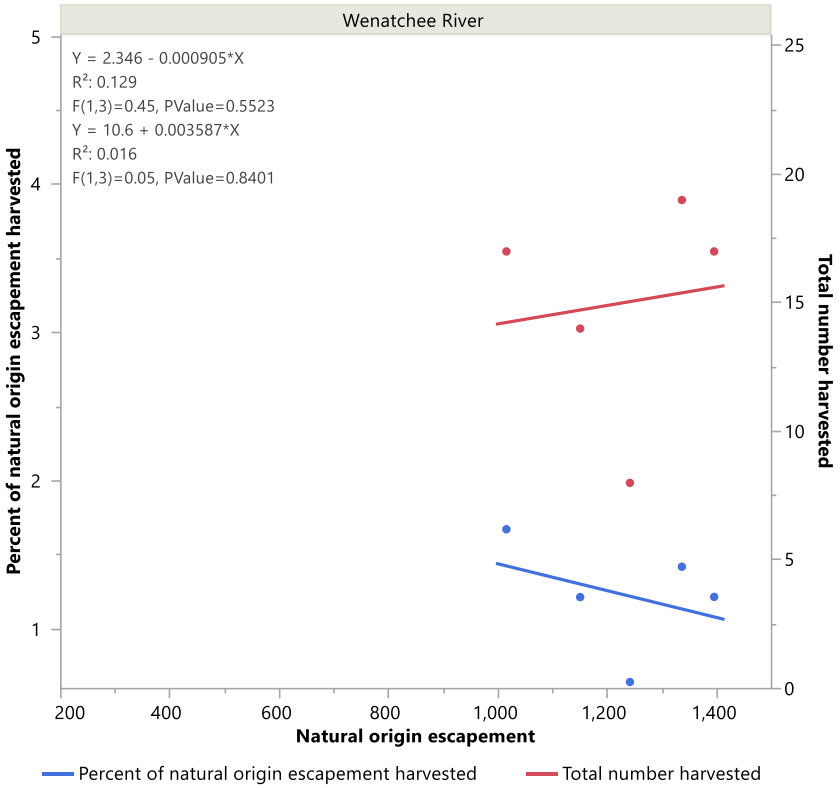
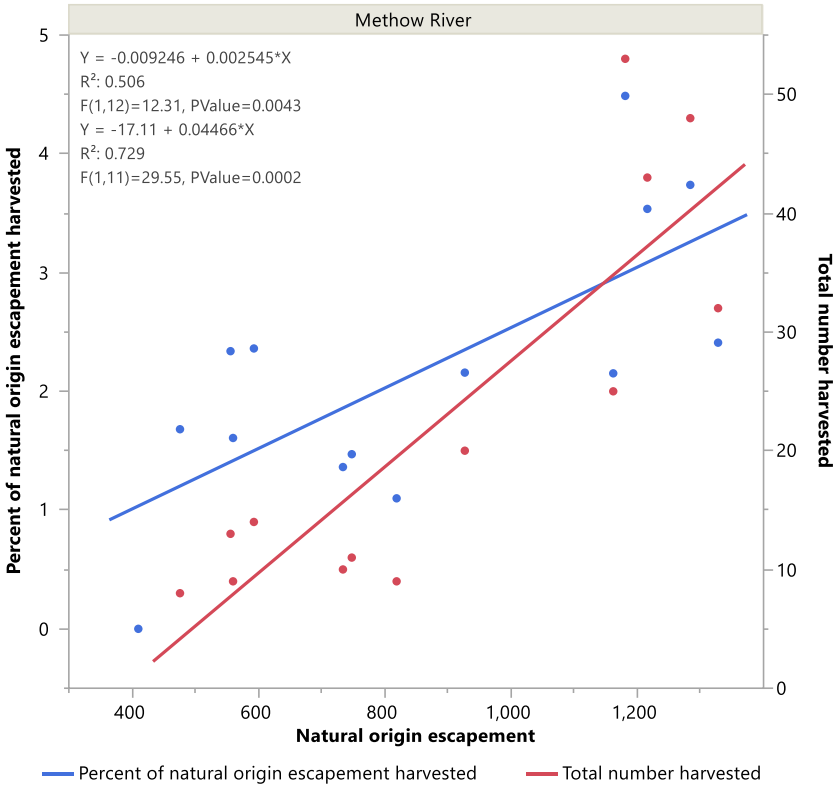


Figure 10. Escapement, total number harvested, and percent of escapement harvested of natural-origin steelhead for the Wenatchee ($\bar{x}$ = 1.36%), Methow ($\bar{x}$ = 2.17%), and Okanogan ($\bar{x}$ = 2.16%), rivers (averages represent returns years 2003-2017 for the Methow and Okanogan rivers and 2011-2016 for the Wenatchee River).


Wenatchee River
Y = 2.346 - 0.000905*X
R²: 0.129
F(1,3)=0.45, PValue=0.5523
Y = 10.6 + 0.003587*X
R²: 0.016
F(1,3)=0.05, PValue=0.8401
Percent of natural origin escapement harvested
Total number harvested
Natural origin escapement
Percent of natural origin escapement harvested
Total number harvested


Methow River
Y = -0.009246 + 0.002545*X
R²: 0.506
F(1,12)=12.31, PValue=0.0043
Y = -17.11 + 0.04466*X
R²: 0.729
F(1,11)=29.55, PValue=0.0002
Percent of natural origin escapement harvested
Total number harvested
Natural origin escapement
Percent of natural origin escapement harvested
Total number harvested

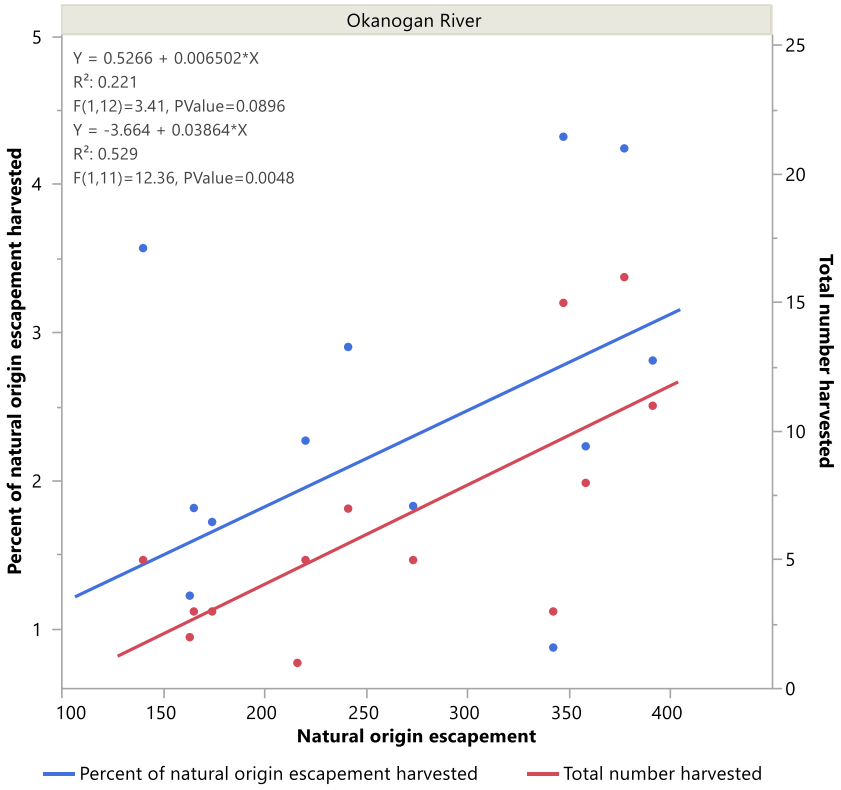


Figure 11. Escapement versus percent of escapement harvested and total number harvested of natural-origin steelhead from the Wenatchee, Methow, and Okanogan rivers.

Discussion

The Chinook Salmon and steelhead hatchery programs of the upper Columbia River contributed to treaty and non-treaty commercial fisheries in the ocean and Columbia River as well as recreational fishing. For the programs examined here, harvest rates for upper Columbia River hatchery Chinook Salmon and steelhead were generally in line with the goals of each program. Conservation and safety-net programs for spring Chinook Salmon and steelhead sustained lower multi-year average rates of harvest (5-26% for spring Chinook Salmon, 5-54% for steelhead) than augmentation programs for summer and fall Chinook Salmon (53-75%). Every hatchery program that was evaluated contributed to harvest and sometimes substantially. The magnitude of harvest generally corresponded to the status of the population: the lowest harvest occurred on the most imperiled stocks and the highest harvest occurred on the healthiest stocks. However, harvest sometimes hindered meeting broodstock collection goals, particularly during earlier years of the programs, and harvest management of endangered or threatened species could impede achieving conservation objectives.

Spawning escapement of listed species would have been higher if harvest was lower than what occurred. However, it is difficult to evaluate how harvest of hatchery-origin fish influenced population recovery without considering the factors that can influence natural production such as spawner abundance, domestication selection, and recipient stray proportions. In some years, the number of natural-origin recruits was limited by the number of spawners and any harvest likely

reduced the number of natural-recruits. In other years, the proportion of hatchery origin spawners (pHOS) was higher than management objectives and targeted harvest may have benefitted natural production by reducing the effects of domestication selection (e.g., steelhead in the Methow River). However, even in cases where fisheries targeted harvest augmentation programs, fisheries were not efficient enough to remove the desired number of hatchery-origin fish particularly in years of very large abundance or when weak stock fisheries limited the allowable harvest under the Endangered Species Act. Finally, higher harvest of hatchery-origin fish may have aided managers achieve targeted recipient population stray percentages (see recipient stray chapter in this report). However, most fisheries occur in areas downstream of what would be desirable locations to manage stray rates. Uncertainty remains about the effects of harvest on individual brood years and resulting viability of endangered or threatened populations of Chinook Salmon and steelhead. Mixed and weak stock fisheries in the ocean and mainstem Columbia River pose challenges to achieving conservation goals in the upper Columbia Watershed.

Abundance of all races of Chinook Salmon were limited by several factors including smolt-to-adult return survival (SAR), which has collapsed in recent years to around 1% along the entire Pacific coast (Welch 2020). Steelhead are also likely affected by this trend. While hatcheries can compensate for some of the effects of poor survival, opportunities for harvest, conservation, and recovery will be limited if SARs remain low.

Spring Chinook Salmon

The harvest rates of spawning aggregates within the Upper Columbia River were variable which suggests that some spawning aggregates may be affected by harvest more than others. Among the spring Chinook Salmon hatchery conservation programs examined here, the Chiwawa River program had the highest percent of brood year harvested and the highest spawning escapement. Spawning escapement was sufficient to reach broodstock collection goals in most years since the population began to recover from the low numbers of the 1990's. Since the early 2000's there has been more harvest on the Chiwawa program than the Methow Basin spring Chinook Salmon conservation programs. The difference was greatest in 2009-2012 when harvest for the Methow programs, including the Twisp and Chewuch rivers, ranged between 5-22% (and were trending together) while harvest of the Chiwawa program ranged from 10-40% over the last 10 brood years and as high as 95% in years previous. During this same period the spawning escapement for the Methow Basin programs remained consistently low (around 1,000 individuals) while escapement in the Chiwawa was generally greater, reaching a peak of almost 2,500 individuals in 2011. The combined tribal and recreational fisheries regularly harvest more than 100 adult Spring Chinook Salmon (up to 40% of escapement) from the Chiwawa program, but rarely harvest greater than 100 individuals (up to 25% of escapement) from the combined Methow River spring Chinook programs. This difference in exploitation rate may result from differences in return timing (Sorel et al. 2020), or other potential behavioral differences between Methow and Chiwawa program fish. More Chiwawa program fish may overlap with summer Chinook Salmon fisheries in the Upper Columbia if they tend to arrive later than Methow fish. Further investigation of differences between harvest of spring Chinook Salmon returning to the Wenatchee versus the Methow river basins may be useful for fisheries managers and provide insight into appropriate rates of exploitation. Furthermore, mixed stock fisheries pose challenges

to providing sustainable harvest rates for weak stocks or spawning aggregates within an Evolutionary Significant Unit (ESU).

The poor returns of upper Columbia River spring Chinook in the 1990's were apparent in the escapement numbers for the Chiwawa, Methow, Twisp, and Chewuch programs. Escapement improved by brood year 2000 and broodstock collection goals for the Chiwawa were reduced in 2009. Broodstock collection goals for the Methow Basin were reduced in 2012 following hatchery production recalculation. Since reduced broodstock collection goals were adopted, upper Columbia spring Chinook Salmon hatchery programs have typically met broodstock collection goals. Despite attempts by fishery managers to structure seasons to reduce harvest of Upper Columbia spring Chinook Salmon, harvest rates have averaged 12% (range 9.3-13.8%) since 2008 (Maier 2020).

Summer and fall Chinook Salmon

By design, all hatchery summer and fall Chinook Salmon programs in the upper Columbia have sustained relatively high rates of harvest compared with spring Chinook Salmon. While all anadromous salmonids in the upper Columbia declined significantly in the 1990's, the recovery of summer and fall Chinook Salmon since 2000 has led to robust fisheries, particularly in the ocean. Summer and fall Chinook Salmon in the Upper Columbia support some of the highest harvest rates in the Columbia River Basin and yet the populations continue to be relatively healthy. Upper Columbia River summer and fall Chinook Salmon tend to move north to forage after leaving the Columbia River estuary and are harvested in the Gulf of Alaska, the southeast Alaska coast, and off the coast of British Columbia including around Vancouver Island (Weitkamp 2010).

Steelhead

In contrast with upper Columbia River Chinook Salmon, steelhead harvest is uncommon in the ocean. Because steelhead are harvested primarily in recreational fisheries in the spawning tributaries, impacts on natural-origin stocks are closely monitored and the fisheries are closed upon reaching a predetermined impact limit (e.g. 5% of escapement, determined by local creel sampling). This also means that steelhead are not reliably available for harvest because the fisheries open only when a surplus of hatchery-origin fish are available. Escapement of hatchery-origin steelhead in the upper Columbia River has been trending down since return year 2011 and as such, recreational fisheries have been uncommon in recent years, last occurring in return years 2015-2016 for the Wenatchee and return years 2016-2017 for the Methow. Even with decreasing escapement, broodstock collection goals have generally been met for all hatchery programs.

Summary

In summary, PUD hatchery programs in the upper Columbia Basin have consistently provided opportunities for harvest in a variety of ocean and freshwater locations. Fall and summer Chinook Salmon were harvested at high levels and the populations continue to thrive. In contrast, relatively low but uneven harvest rates occurred on ESA listed spring Chinook Salmon and steelhead and the populations struggle to persist. Differences in population status among salmon and steelhead pose challenges to manage mixed stock fisheries in ways that

protect weak stocks, achieve harvest goals, and achieve other conservation objectives such as straying and pHOS management.

Acknowledgments

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Evaluation of Fall Chinook Salmon Carcass Recovery Bias in the Columbia River

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Abstract

A common way to inventory the characteristics of a Chinook Salmon (*Oncorhynchus tshawytscha*) spawning population is to collect their carcasses after spawning. However, this method can produce biased results. Two approaches to characterize bias in carcass samples when examining population demographics were evaluated with fall-run Chinook Salmon from the Hanford Reach of the Columbia River. A mark recapture approach and a comparison of hatchery-origin carcasses collected in river versus those recruited to a hatchery trap. In each instance the post-orbital hypural lengths and sex ratios were compared to determine differences in the characteristics of each sample. In the mark recapture study, the recaptured carcasses had similar lengths and sex ratios as the original marked group. In the evaluation of carcass and trap populations, the hatchery-origin carcasses found in the river contained lower proportions of smaller fish sampled and a lower relative frequency of male fish than were collected at the hatchery trap. Taken together the results illustrate that younger male salmon may be under-represented in carcass samples; a phenomenon commonly reported. This feature of carcass sampling contributes to a weakness in the design of mark recapture study as the original marked fish may be weighted towards larger animals that were subsequently recaptured at similar sizes and sex ratios. Furthermore, carcass recovery bias should be considered when interpreting data collected from salmon carcasses.

Introduction

A common way to inventory the characteristics of a Chinook Salmon (*Oncorhynchus tshawytscha*) spawning population is to collect their carcasses after spawning (Crawford et al. 2007, Hoffnagle et al. 2008, Murdoch et al. 2010). Pacific salmon die after spawning and provide an opportunity to collect data about the spawners (Crawford et al. 2007, Cram et al. 2012, 2017). Carcasses can be used to generate information such as spawner sex ratio, origin (e.g., hatchery or natural), age at maturity, size at maturity, spawner distribution, and egg retention. A common assumption is that the carcasses recovered are a representative sample of the spawning population. However, several studies have revealed that carcass recoveries represent a biased sample of the spawning population. Smaller and younger spring-run Chinook Salmon, which were generally males, were encountered less frequently than their actual abundance (Zhou 2002, Murdoch et al. 2010). In the Salmon River in Oregon, carcass surveys for fall-run Chinook Salmon underestimated the proportions of small fish and males while overestimating those of large fish and females (Zhou 2002). The location of female spring Chinook Salmon carcasses has been shown to be a better proxy for spawning location in the Chiwawa River than males that were found further away from redds (Murdoch et al. 2009).

It is likely that the impact of carcass recovery bias in characterizing spawning location vary among basins. Spawning populations are found in streams and rivers of different sizes, flows, and habitat complexity and discrete populations may have different spawning behavior and ages at maturity. Observations by Murdoch et al. (2009, 2010) were from spring-run Chinook Salmon in the relatively small Chiwawa River basin (4 m^3/s) and those of Zhou (2002) were from fall-run Chinook Salmon in the larger Salmon River basin (17.7 m^3/s). However, findings from these studies may not apply to larger river systems with high, variable flows containing areas of deep water such those that characterize the Hanford Reach portion of the Columbia River (Harnish et al. 2014; Langshaw et al. 2017). The Hanford Reach hosts the largest Chinook Salmon population in the contiguous United States and is one of the few remaining non-impounded reaches of the Columbia River accessible to spawning (Harnish et al. 2014, Langshaw et al. 2017). The median flow during the spawning season is routinely above 2,608 m^3/s and vary substantially during a 24-hour period (Langshaw et al. 2017). In spite of the differences in physical characteristics between the Hanford Reach and basins where sampling bias has been better characterized, fall-run Chinook Salmon carcass recoveries are still used to evaluate the status of the population and monitor the effects of hatchery programs on the naturally spawning population with no accounting for sample bias (Richards and Pearsons 2019). Presumably these differences alter the size and nature of bias and may result in erroneous interpretations about this population. This paper will characterize bias in carcass recovery attributed to fish sex, fish age, and fish size in the Hanford Reach.

Methods

Study Area

Our study included the entire Hanford Reach section of the Columbia River that extends from Priest Rapids Dam (Rkm 639) downstream to the City of Richland, WA (Rkm 549) and 4 km of river adjacent to the downstream end. The Hanford Reach has been organized (Richards and Pearsons 2019) into five survey sections around natural breaks in prominent spawning areas (Figure 1). These sections range from 14 km to 21 km in length. Annual surveys were performed by WDFW personnel in the Hanford Reach from early November to mid-December to collect post-spawning salmon carcasses. Survey crews active throughout this period were scheduled for seven days per week and each survey section is sampled at least once per week during the survey period. Sections containing large numbers of carcasses may be surveyed as often as twice weekly to ensure collection of all available carcasses. Carcasses were collected while walking the shorelines and islands of the river or by gaffing available carcasses from boats within each survey section. All carcasses recovered were scanned for coded-wire tags (CWT) and examined for external tags or marks (operculum tags, floy-tags, adipose clip). Other data and samples contributing to the long-term monitoring of natural- and hatchery-origin fish included fish sex and fish length (cm), and scales and otolith samples from a sub sample of carcasses were also collected at a sample rate that varied in each year of the study (Richards and Pearsons 2019).

We used two methods to define the impact of carcass recovery bias. First, we compared attributes of tagged carcasses released in the Hanford Reach to the tagged carcasses that we recovered to determine any differences observed between the released and recovered carcasses. Second, we summarized Priest Rapids Hatchery (PRH) origin coded-wire tag (CWT) recoveries from PRH and CWT recoveries from carcasses collected in the Hanford Reach to characterize any differences in fish size, size at age, and sex composition between these two populations.

Method 1 - Mark and Recapture

From 2011-2013 and 2015–2018, a portion of the carcasses gathered during carcass surveys were tagged, released (N = 493 – 987 per year) in the thalweg or directly over redds. Ultimately some of these were recaptured and sex and length data collected to characterize differences between the released and recovered animals. There were different tagging and release strategies (i.e., near-shore, thalweg, and over redd locations) over the course of these trials but the release of animals in the thalweg or directly over areas with redds occurred across all years of observations. A numbered plastic tag (model 337P#, ~8 cm x 6 cm, Ketchum Mfg. Co. Inc., Lake Luzerne, NY) was stapled to the underside of the operculum of each carcass so that it protruded ~1 cm from the operculum to be visible externally. Carcasses from nearshore releases were excluded from our statistical analyses as these included areas of slow flow that limited any distribution of carcasses following release and were atypical of spawning areas in the Hanford Reach. In all years, date, fish sex, fork length (FL), and survey sections were recorded. Post-orbital to hypural length (POHL) was either measured directly or derived from a prediction equation generated from a linear regression describing the relationship between FL and POHL (data not shown) and POHL measurements used in subsequent analysis. An effort was made to release equal number of males and females in each release group. However, large numbers of age-3 males during 2013 resulted in a skewed male:female ratio (2.6:1) of carcasses released. Carcasses were recovered during our normal monitoring of carcasses in November and

December (Richards and Pearsons 2019). The tag number, recovery section and date were recorded upon recovery of tagged carcasses.

The distributions of POHL measurements of carcasses released were compared to those recaptured and differences determined using a two-sample Kolmogorov-Smirnov test (Zar 1996). These comparisons of POHL distributions were done for each year and pooled for all years to generate a larger population size for recaptured animals after determining no significant differences for any individual year. The frequencies of male and female carcasses released and recovered were compared and differences in the sex ratio were determine using a chi square test with a Yates correction for each year of data. Finally, a paired t-test was used to determine if there was a difference in the percentage of males in the released versus recaptured carcasses. For all statistical analyses examining the frequencies of males in the populations, all male age classes including jacks were summed. In each of these instances the threshold for significant differences was set at $P < 0.05$.

Method 2- Comparison of PRH and Hanford Reach Collections

Before release as juveniles, CWT were applied to a proportion of fish at PRH. For release cohorts contributing to this analysis 0.2-1.7 million CWT were applied annually representing 3-25% of the total fish released. All fish arriving at PRH as adults and all carcasses collected in the Hanford Reach were scanned for the presence of CWT and these codes recorded (Pearsons et al. 2020). This effort provided a larger sample size of known PRH origin fish recovered than the mark recapture method previously described. For the period from 2011 to 2018 we recovered fish with CWT at PRH and in the Hanford Reach and recorded the CWT code, the post orbital-hypural length, and fish sex for each of these fish. The distributions of POHL measurements of PRH origin fish recovered at PRH and the Hanford Reach were compared and a difference determined using a two-sample Kolmogorov-Smirnov test. The frequencies of male and female fish recovered from each location were summarized and a chi square test with a Yates correction was used to determine any difference in sex ratio between fish gathered at PRH and the Hanford Reach for each year. Finally, the percentages of male fish were determined for fish collected in each location and any difference between location was determined using a paired t test. In each of these instances the threshold for significance was set as $P = 0.05$.

Results

Method 1 - Mark and Recapture

Overall, annual recoveries of tagged carcasses ranged from 4.3% to 17.2% of the marked population (Table 2). The median POHL measurements for released and recovered carcasses was 64 and 65 cm, respectively. The aggregated distributions of POHL across all years were similar between the length distributions of the release group and recovery group ($D = 0.472$, $D_{crit} = 0.08$, $P > 0.05$; Figure 2). Similar frequencies of male and female carcasses were present in both the released and recovered populations ($P = 0.214$ - 0.963; Table 2). The percentage of male carcasses released ranged from 40.2 to 73.6%; overall years, the average percentage of males in the release group was 53.2% (SD = 10.1) was similar (df=6, t= -1.456, P=0.196) to that in the recovered group, 56.2% (SD= 12.2; Figure 3).

Method 2 – CWT information at PRH and Hanford Reach

From 2011 to 2018 data derived from CWT included 41,302 fish recovered at PRH and 1,255 fish collected in the Hanford Reach (Table 2). The distribution of POHL measurements differed between fish collected at the PRH trap and carcasses collected in the Hanford Reach ($D = 0.1017$, $D_{crit} = 0.0390$, $P < 0.05$; Figure 2). The median POHL measurements for the PRH sample and the Hanford Reach sample released were 58 and 59 cm, respectively, but smaller fish were more frequently collected in the PRH sample (Figure 2). A significant difference in the sex ratio was observed between fish samples collected at PRH and carcasses collected in the Hanford Reach in seven of the eight years of the study (2012-2018; Table 4). The mean percentage of male carcasses in the PRH group was 65.2% (SD = 14.4) and was significantly larger ($df=7$, $t= 9.2$, $P < 0.001$) than carcasses collected in the Hanford Reach, 44.8% (SD= 17.7; Figure 3).

Table 1. The numbers of fish tagged and numbers recovered during studies conducted to characterize bias in size distributions and sex composition in fall-run Chinooks Salmon from the Hanford Reach**.**

Year	Number of Fish Tagged	Number of Fish Recovered	Percent Recovered
2011	493	61	12.4
2012	500	34	6.8
2013	521	45	8.6
2015	997	38	3.8
2016	987	46	4.7
2017	981	42	4.3
2018	626	51	8.1

Table 2. Number of released and recovered tagged male and female adult fall Chinook salmon placed in either the thalweg or over redd location in the Hanford Reach during the carcass drift study. A two-way Yates' Chi-square test was performed for each return year to determine if the sex ratios were dependent of one another.

Year	Source	Females	Males	% Males	X^2	P
2011	Released	295	198	40.2	0.526	0.468
	Recovered	40	21	34.4		
2012	Released	231	269	53.8	0.014	0.907
	Recovered	13	17	56.7		
2013	Released	137	382	73.6	0.011	0.918
	Recovered	10	29	74.4		
2015	Released	476	521	52.3	0.437	0.509
	Recovered	16	23	59.0		
2016	Released	473	514	52.1	0.355	0.551
	Recovered	19	26	57.8		
2017	Released	482	499	50.9	1.547	0.214
	Recovered	16	26	61.9		
2018	Released	317	309	49.4	0.002	0.963
	Recovered	26	25	49.0		

Table 3. Number of Priest Rapids hatchery-origin male and female adult fall Chinook salmon recovered at Priest Rapids Hatchery and in the Hanford Reach fall Chinook salmon carcass survey. A two-way Chi-square test with a Yates correction was performed for each return year to determine if the sex ratios were dependent of one another.

Return Year	Survey	Females	Males	% Males	X^2	*P*
2011	Priest Rapids Hatchery	241	834	77.6	3.1	0.080
	Hanford Reach Carcass	8	11	57.9		
2012	Priest Rapids Hatchery	525	3,412	86.7	5.4	0.020
	Hanford Reach Carcass	13	38	74.5		
2013	Priest Rapids Hatchery	1,744	5,572	76.2	80.7	0.000
	Hanford Reach Carcass	222	315	58.7		
2014	Priest Rapids Hatchery	6,406	7,229	53.0	52.4	0.000
	Hanford Reach Carcass	129	43	25.0		
2015	Priest Rapids Hatchery	4,462	6,006	57.4	53.2	0.000
	Hanford Reach Carcass	144	68	32.1		
2016	Priest Rapids Hatchery	2,107	2,403	53.3	5.7	0.017
	Hanford Reach Carcass	63	44	41.1		
2017	Priest Rapids Hatchery	1,398	1,225	46.7	12.0	0.001
	Hanford Reach Carcass	55	19	25.7		
2018	Priest Rapids Hatchery	591	1,426	70.7	6.8	0.009
	Hanford Reach Carcass	13	10	43.5		

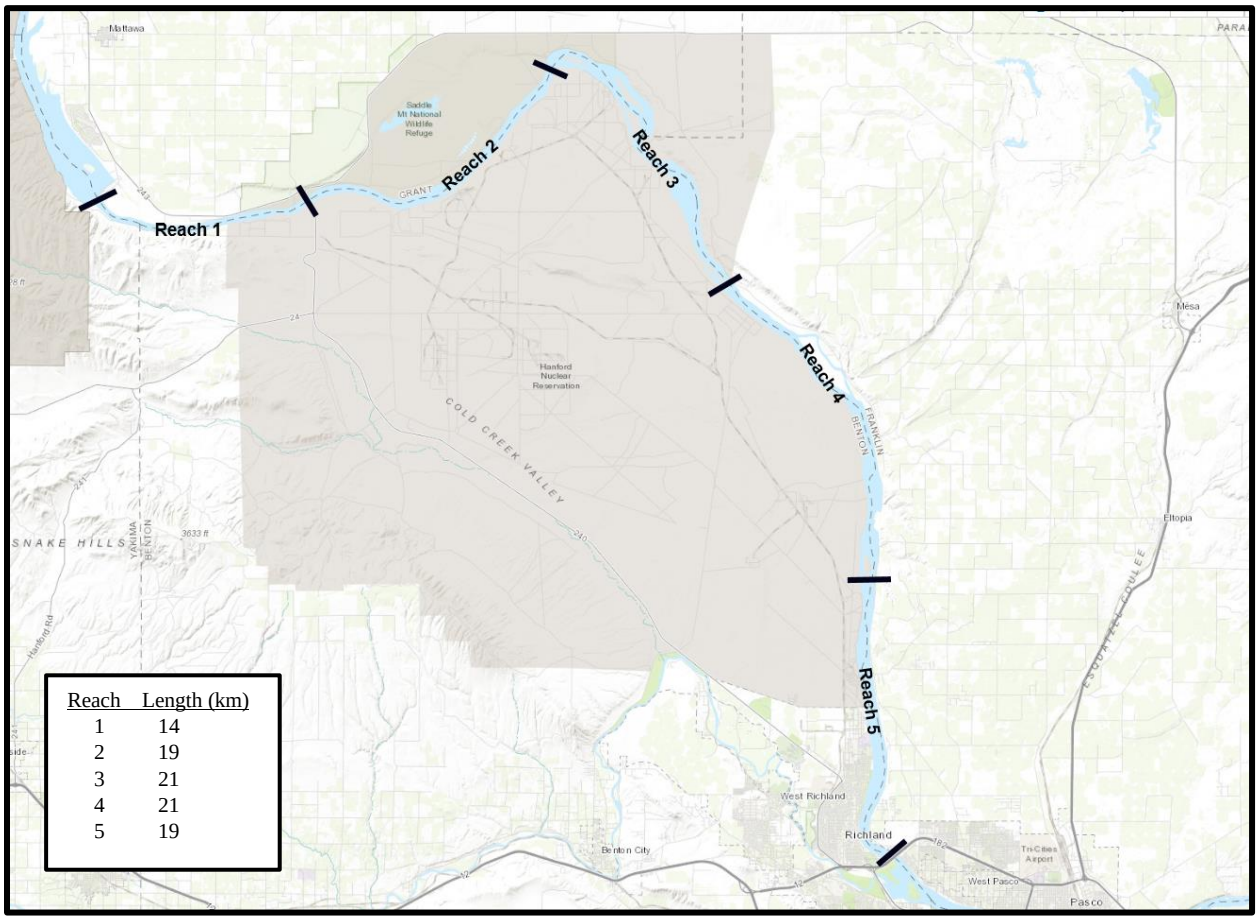

Figure 1. Location of the Hanford Reach portion of the Columbia River in Washington. Bars represent breaks in the Hanford Reach that define the five survey sections.

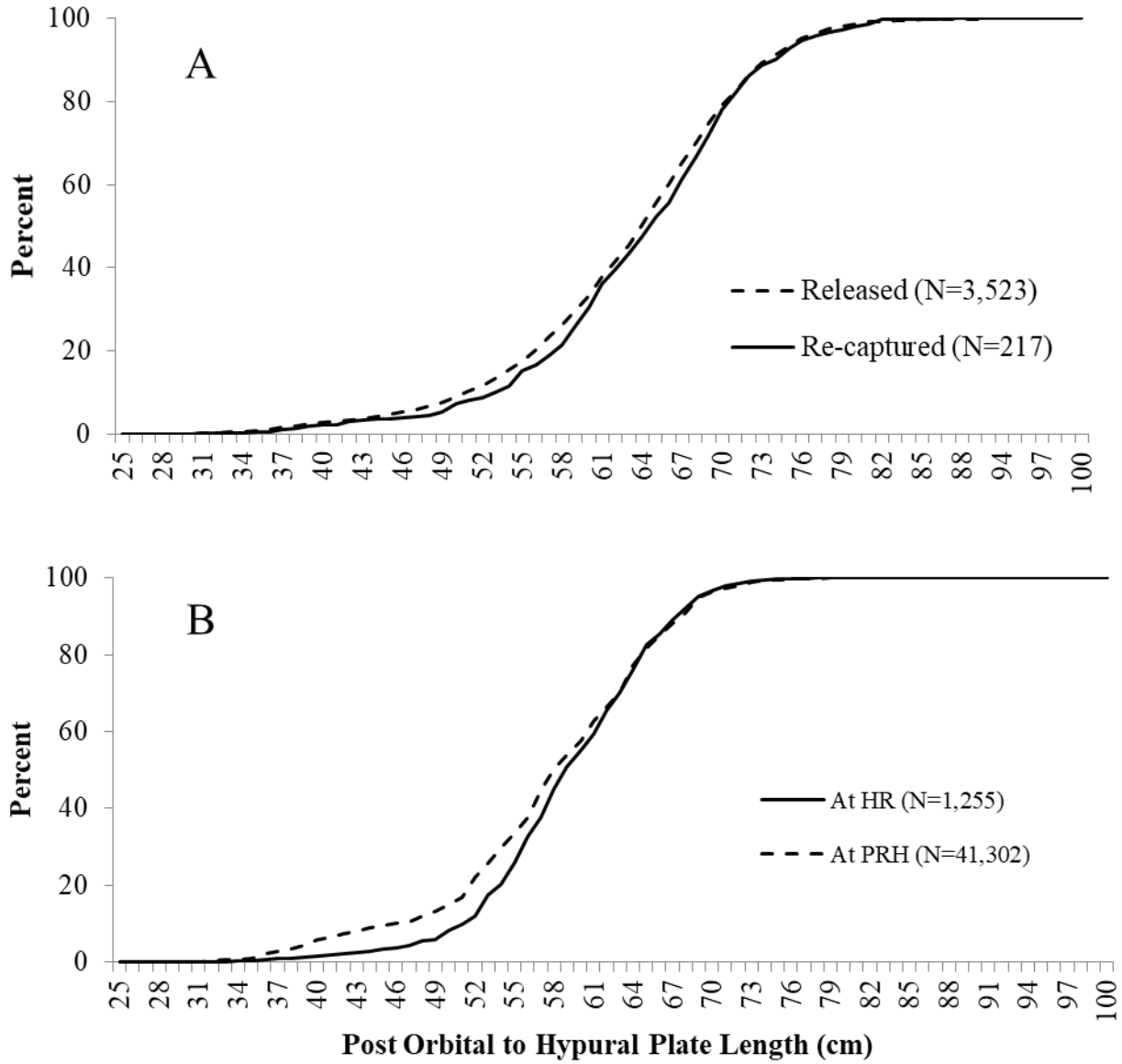

Figure 2. Comparison of the POHL distributions of A) carcasses released and recaptured in experiments conducted 2011-2013 and 2015-2018 have similar POHL distributions and B) fish recovered at the PRH volunteer trap and in the Hanford Reach (2011-2018) are different.

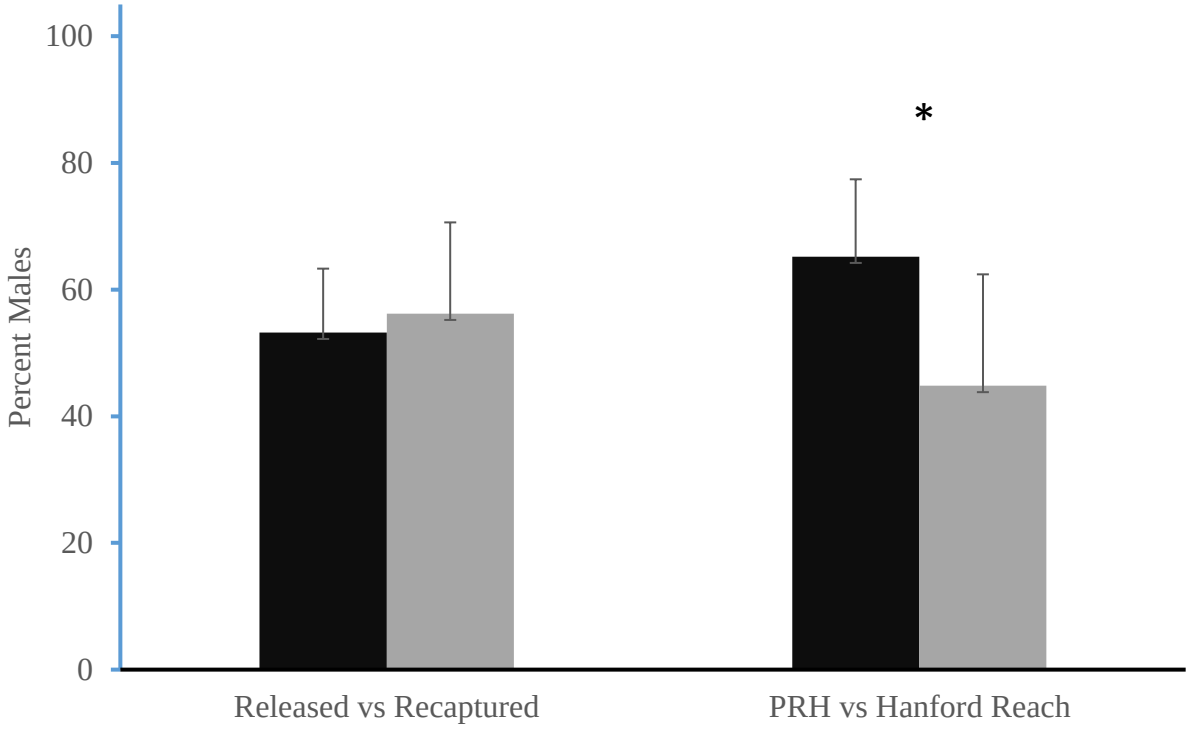

Figure 3. The average percentage of males released (dark bar) and recaptured (gray bar) in the Hanford Reach and fish collected at the PRH trap (dark bar) and the Hanford Reach (grey bar). Error bars indicate the standard deviation. A paired two sample for means t-test was performed for determine if the percentage of males in each sample were significantly different. An asterisk indicates a significant difference between means.

Discussion

When examined superficially, the two evaluations characterizing bias in carcass sampling provide different conclusions; however, when examined holistically there are areas of support that provide a greater understanding of bias in carcass sampling in the Hanford Reach. The mark recapture approach provided no evidence for bias as no differences in size distributions or the sex ratios between the marked and recaptured population were observed. The comparison of hatchery-origin animals collected from the Priest Rapids Hatchery Trap to carcasses sampled in the Hanford Reach did reveal differences with greater numbers of smaller fish and higher proportions of male fish observed in the sample collected at the trap than in the carcasses sampled in the Hanford Reach. These differences between the two methods may be explained by a weakness in the mark recapture approach taken here. The original marked population were carcasses sampled during routine carcass surveys. If, as others have reported (Zhou 2002, Murdoch et al. 2010), that a bias leading to reduced numbers of smaller male salmon in carcass

samples is present, it is not entirely surprising that the marked and recaptured population have similar size and sex ratios. However, this finding could have also been an artifact of the small number of small males that were used in this study. Ideally, a systematic approach that included larger numbers of smaller salmon should have been included in the marked population. The examination of hatchery-origin fish from trap indicates that the trap is more effective at recruiting the smaller males that are likely missed during carcass sampling. Finally, the evaluation of fish containing CWT represent much larger sample size which contributes to the power of the analysis and the capacity to detect significant differences. It is likely that the trap is the most accurate estimate of hatchery-origin fish that spawn in the Hanford Reach and trap estimates might be useful in providing a correction to carcass recovery data.

The reason for the observed bias in the CWT evaluation appears to be related to differences in the behavior of fish prior to death or differences in sex ratio related size and age (e.g., bias in female collections and females are older and bigger than males). Previous mechanisms attributed to bias such as scavenging on smaller dead fish does not seem to explain the magnitude of bias that we observed. It is possible that smaller fish degrade faster or are simply unable to be seen as well as larger carcasses, however this mechanism was not supported by the mark and recovery method. Alternatively, males, and particularly jack males may be more likely to be recovered far downstream of spawning locations because of their wandering behavior after they spawn (Murdoch 2010). Finally, some of the males may have drifted into areas that we could not recover them. We recommend caution about exclusive use of release and recovery of dead carcasses as a means to correct for carcass recovery bias.

It is clear that carcass recovery bias may differ in different environments and with use of different evaluation methods. However, we generated similar conclusions using the CWT method as those generated for spring and fall Chinook Salmon in dramatically smaller streams, different flow conditions, and using different methods (Zhou 2002, Murdoch et al. 2010); namely that carcass recoveries are biased against collecting smaller male fish. We recommend that evaluation of carcass recovery bias be a standard practice in studies and monitoring programs that rely upon data from carcass recoveries. However, it is important that evaluations of carcass recovery bias use methods that can accurately evaluate bias. In some cases, correction factors will need to be applied to carcass recovery data in order to derive accurate estimates and conclusions.

Acknowledgments

We thank the many partners that have made the Priest Rapids Hatchery program such a success. This includes Grant County Public Utility District project manager, Eric Lauver; Priest Rapids Hatchery management staff, Mike Lewis, Brian Lyon, and Glen Pearson; WDFW science division staff, Shawnaly Meehan and Dennis Werlau; and WDFW otolith readers led by Jeff Grimm and Lance Campbell. We also thank the Priest Rapids Coordinating Committee's Hatchery Subcommittee. Grant County Public Utility District funded this work.

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Examination of Sources of Error in Estimating Abundance of Adult Chinook Salmon Derived from Expansion of Juvenile Mark and Tag Rates

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Abstract

Marks and tags such as adipose fin clips (Ad-Clip) and coded-wire-tags (CWT) are applied at most salmon and steelhead hatcheries in the Pacific Northwest to identify origin and characterize abundance, survival, and other important population parameters. Error and/or bias associated with these estimates are infrequently evaluated. We compared estimates of adult abundance returning to the Priest Rapids Hatchery (PRH) between 2012 and 2018 using juvenile expansions of tagging rates for Ad-Clip and CWTs to estimates generated from a subsample of fish with a 100% mark rate (thermally marked otoliths). The average estimates derived from the otolith mark (90±12%), the CWT (80±13%), the adipose clipped and CWT (77±11%), and Ad-Clip (86±12) were highly variable but not significant over the time period of the study. We also evaluated possible systematic sources of these errors that may have occurred either before release or as adults were returning: 1) we compared proportions of tagged animals in pre-release sampling efforts to values reported from hatchery inventory, 2) we evaluated our methods of detection of CWT, and 3) we examined error rates attributed to aging scales. Each of these sources of error may contribute to underestimation, but none of the data gathered provide an explanation for the magnitude of underestimation derived from the partially tagged population in earlier years (e.g., 2012-2013). However, the size of underestimation has been diminished over the course of the study suggesting that quality control steps are providing better estimates.

Introduction

The evaluation and adaptive management of hatchery supplementation programs requires some method of differentiation of fish of hatchery- and natural-origin. Coded-wire-tags (CWT) inserted into the flesh of salmon are the most common tag used to identify salmon and steelhead produced by hatcheries, by specific hatchery, or by specific hatchery production group (Vander Haegen et al. 2002; 2005). Common metrics derived from CWTs include: harvest, distribution, the proportion of hatchery-origin spawners, stray rates, and survival (Weitkamp 2010; Cram et al. 2012; Westley et al. 2013, 2015). In addition, demographic comparisons that include size at maturity, size at age, and fecundity between hatchery and natural-origin fish are also routinely performed using data derived from the presence and absence of CWT (Vander Haegen et al. 2005). Washington Department of Fish and Wildlife and its partners use these data to determine if hatchery programs are meeting hatchery reform benchmarks originally defined by the Hatchery Scientific Review Group (HSRG; Mobrand et al. 2005, Paquet et al. 2011). Screening procedures for CWT typically involves: 1) defining the sample of fish to screen for CWT (e.g., standardized sample rate, all fish), 2) scanning the fish for a CWT with a specialized metal detector, 3) removing the tissue containing the tag, and 4) extracting the tag and recording the code to determine origin and associated tagging details. Population abundance estimates are based upon mark fraction expansions of the CWT to total fish and it is routinely assumed that tagged fish are representative of the population providing estimates unaffected by systematic bias or error. However, both bias and random error can contribute to the veracity of these estimates.

Tag loss, relative survival of tagged groups, and straying have all been considered as sources of bias when interpreting CWT data (Blankenship 1990; Blankenship and Thompson 2003). Blankenship (1990) reported a short-term tag loss ranging from 1.1 – 5.3% in Chinook Salmon *O. tshawytscha* and Coho Salmon *O. kisutch*. Rates of CWT loss in the Yakima River for spring Chinook Salmon were reported as 3.4% before fish were released and an additional 6.7% of the fish after they were released but loss rate was not appreciably different among different age cohorts as they returned to the hatchery (Knudsen et al. 2009). Placement of the tag into nervous tissue was reported to diminish homing capacity of other *Oncorhynchus spp*. (Habicht et al. 1998; Thedinga et al. 2011). It is also thought that CWT procedures can enhance the rate of transmission of certain fish pathogens (Elliott and Pascho 2001). In aggregate, these factors would reduce the numbers of CWT relative to an unmarked population and lead to a bias in estimates of abundance for the population under study. However, these findings may be site specific as survival, growth, and homing were reported to be similar for CWT tagged and untagged spring Chinook Salmon (*Oncorhynchus tchawytscha*) at three different Columbia basin hatcheries (Vander Haegen et al. 2005).

Errors in detection of tags and marks might contribute to random error or bias and methodology when screening has been observed to contribute to error. Tests using the handheld Blue Wand CWT detector (Northwest Marine Technology, Shaw Island, WA) illustrate that the technique when using this tool can lead to underreporting of CWT; by inserting the wand into the mouth, rather than waving the wand over the snout, the detection rate of CWT improved by 8% (89% versus 99%; Vander Haegen et al. 2002). Additionally, the detection rates using hand-held devices were variable among five hatcheries ranging from 71.0% to 99.4% (Vander Haegen et al. 2002) and instances of missed CWT were thought to increase as fish size increased. Different types of equipment have been used; while older reports used the Blue Wand, more recent

detectors include the T Wand or large tunnel detection units (Northwest Marine Technology, Shaw Island, WA) are in use without a thorough understanding of error rates.

Priest Rapids Hatchery (PRH), a Grant County Public Utility District funded facility operated by Washington Department of Fish and Wildlife offers a unique opportunity to evaluate the impact of bias/error on abundance estimates for adult salmon returns. It is a very large hatchery responsible for producing large numbers of fall-run Chinook Salmon, has multiple marking and tagging schemes, uses multiple detector types, and has a long history of monitoring. Due to the importance of metrics derived from CWT in monitoring and evaluation and associated management decisions, we aimed to: 1) characterize the magnitude of error existing at Priest Rapids Hatchery, and 2) evaluate potential mechanisms causing error.

Methods

Study Area

PRH is located near the base of Priest Rapids Dam on the east bank of the Columbia River upstream of Richland, WA. PRH has produced and released over 4.5 million sub-yearling Chinook Salmon smolts annually since 2007 that contributed to a variety of fisheries from Alaska to the Columbia River (Weitkamp 2010, Richards and Pearsons 2018). Broodstock collection has used a variety of different techniques with a recent emphasis to incorporate larger proportions of natural-origin fish (Pearsons et al. 2020). Fish were spawned from October to December and the fertilized eggs were incubated in vertical incubation trays. The fry were transferred to outdoor raceways when they are ready to receive artificial feeds. The parr were ultimately transferred from raceways to one of five large ponds at ~2 – 6 g per fish where they were grown until release as sub-yearlings into the Hanford Reach of the Columbia River during May and June at a fork length of ~ 95 mm (Richards and Pearsons 2018). Adult fish that escaped fisheries and did not stray returned to the trap located on the hatchery discharge channel from September to December at ages of 2 to 6.

Tagging and Marking of Juveniles

Salmon released from PRH do not universally receive external marks and a variety of tags and marks have been applied to portions of the annual production of fall Chinook Salmon at PRH since the inception of the program. Considerations in these decisions have included inter-organizational values, monitoring and evaluation needs, feasibility, and cost. A portion of the hatchery production were tagged with CWT, a second group received both a CWT and an adipose clip (Ad-CWT), and a third group received only Ad-Clip (Table 1). Fish were routinely tagged or marked with Ad-Clip, CWT, or Ad-CWT when they reached a fork length of ~55-95 mm (Apr-June). During marking/tagging fish were netted from the outdoor raceways and after marking placed into the final rearing pond. The process of marking fish receiving only an Ad-Clip was routinely initiated first and was frequently completed prior to initiating marking CWT and Ad-CWT groups. Regardless of the mark or tag they received, the fish were counted as they were handled and following marking, they were placed into final rearing ponds and distribute themselves among the remaining population until they were released one to six weeks later.

A juvenile tag rate was determined as the proportion of marked fish in the total number of fish released. The number of unmarked fish was determined by first measuring the total weight

of a sample of known number of fish to determine the number of fish/kg, recording the total weight of fish loaded into the pond, and then converting that weight into number of fish (Piper et al. 1982). The number of marked fish was recorded as they were added to the general population in the rearing pond. The relative numbers of PRH fish with Ad-Clip, CWT and Ad-CWT have become more consistent since the 2011 brood year (Table 1). Beginning with the 2007 brood year 100% of the annual hatchery production at PRH have had a thermal mark applied to their otoliths by varying water temperature during incubation (Volk et al. 1999) and as these fish returned a systematic sample of otoliths was gathered (Pearsons et al. 2020).

Estimation of PRH-origin fish returning to the hatchery using four methods

Comparisons of methods for generating population estimates using data of two general formats were performed: 1) interrogation of PRH production for a mark applied to a portion of the population (CWT, Ad-Clip, Ad-CWT) versus, 2) screening a systematic sample of otoliths from a population of fish with a presumed 100% mark rate. All adult fall Chinook Salmon recovered at PRH were screened for the presence of CWT and the presence of an adipose fin and the data recorded while a smaller systematic sample of otoliths were used. Each of these marks and tags provided an alternative method of estimating PRH- and natural-origin fish abundance.

Two types of handheld CWT detectors were used during these studies, the Blue Wand and the T Wand (Northwest Marine Technology, Shaw Island, WA). In 2012 only the Blue Wand was used to screen fish for CWT. In 2013 and 2014, the Blue Wand and the T Wand were used. In 2014, the use of a tunnel detector (Model R9500, Northwest Marine Technology, Shaw Island, WA) was initiated. Since 2014, the T Wand and the tunnel detector were used almost exclusively for routine monitoring and evaluation. The CWT from all fish returning to PRH were recovered and the code information recorded. After retrieving code information, the total number of PRH-origin fish returning to the hatchery trap were derived by expanding the counts by the juvenile tag rate for each age cohort and then summing the numbers of all age cohorts. Estimates derived from Ad-Clip fish were determined similarly except that non-PRH-orign with an Ad-Clip (strays) were estimated and subtracted. The number of stray fish were identified by tags and marks and expanding these numbers appropriately using data collected from the Regional Mark Information System (www.rmpc.org, Pacific States Marine Fisheries Commission). A third group, fish possessing an Ad-CWT, was also identified, and expanded by juvenile mark/tag rate to estimate PRH-origin fish returning to the hatchery. The otolith mark rate used for the identification of PRH-origin fish assumed a 100% mark rate in the systematic sample of otoliths collected and expansion of these numbers by sample rate. Between 2012 and 2018 the number of these fish sampled ranged from 1,833 to 3,245 fish per year. Otoliths submitted for screening for PRH marks represented a subsample from these initial collections. Both scales and otoliths are collected during otolith sampling and fish age is determined for these individuals from annuli patterns on the scales. The scale ages associated with the decoded otoliths are used to create a demographic profile of the entire return to PRH. An initial random listing of otolith sample numbers was used to sub-sample otoliths from the sample pool. This original subsample contained fish with other tags or marks that provided information surrounding origin (18-51% of the sub-sample). When these samples were identified they were replaced with fish with no identifiable mark or tag. Since origin of some hatchery fish could be inferred from other marks and tags, this step of adding samples to the otolith analysis pool allowed for selection of additional fish that represented age and sex combinations that were underrepresented in the initial random sample. As a result, while the initial list of otoliths ranged

in size from 640 to 1,315 fish a total of 1,488 to 2,325 fish in the systematic sample could be identified by a combination of otoliths and other marks and tags. The final selection of otolith samples was submitted to the WDFW fish aging laboratory and screened for the PRH mark. The proportions of PRH-origin fish derived from all marks/tags identifying PRH-origin (otolith, CWT, and Ad-Clip) in this sample were then applied to each age and sex category in order to yield an estimate of the number of PRH-origin fish returning to the volunteer trap. Estimates of the numbers of PRH-origin fish returning to the hatchery trap were derived by the four methods and the percentage of PRH-origin fish calculated. A mean and standard deviation of these percentages were calculated and a simple linear regression performed to characterize any trend in the coefficient of variation over time. A threshold of significance was established at $P < 0.05$. Pearson correlation coefficients were determined and used to determine the strength of the relationships for estimates of the percentage of PRH-origin among all methods.

Errors Attributed to Scale Aging and Detection Equipment

Erroneous scale readings assigning age to a fish identified for otolith sample analysis would influence estimates of the numbers of fish assigned to each age cohort. From 2012 to 2018 we summarized the proportions of age cohorts (age 2-5) derived from CWT and ages derived from scales. Low numbers of age 6 fish, 1-3 per year, in this sample prompted their removal from these comparisons. The percentage of fish scales returning an incorrect age was determined for each year and the mean error across the range of the study determined. Similarly, the percentage of scales incorrectly assigned younger and older were determined for each year of the study and the mean across the range of the study determined. In each case the trend in error rate as fish aged was determined using linear regression.

Fish have been screened for the presence of CWT using a variety of tools and when CWT was detected the presence was verified by removal and reading of tag code. General comparisons of screening tools for the rate of CWT missed were conducted from 2013 to 2018. In 2013, we selected 1,063 adult salmon that had been determined to have no CWT using the T Wand were re-scanned with the Blue Wand. If a CWT was detected using a Blue Wand the fish was scanned again with a T Wand. If the T Wand still did not detect a CWT the snout was removed from the fish and presence/absence of CWT was confirmed by passing it through a V-detector (Northwest Marine Technology, Shaw Island, WA). Only 0.4% of fish with CWT detected by blue wands were determined to have been missed by the T Wand. Between 2014 and 2018, 14,283 (1,679 – 5,943 per year) fish were scanned first with a tunnel detector. Samples of fish (~25-75 fish/day) that did not have a CWT detected by the tunnel detector were rescanned with Blue Wand or T Wand. The proportion of CWT missed by the tunnel detector was ~1-2 %. In 2017, replicate trials were performed on male salmon where the same groups of fish were scanned for CWT using a Blue Wand, T Wand, and tunnel detector. For each tool the counts of fish with and without CWT were recorded; a total of 119 fish with an average fork length of 60 cm were used. A similar test was performed using female salmon on two dates. A chi square test of independence was performed to determine if the outcomes recorded for males during the 2017 simultaneous evaluation of the three detection methods differed. This test was performed on each replicate individually and then on the aggregate data set.

Comparison of Hatchery Inventory to Pre-Release Sampling

Juvenile mark rates reported by hatchery personnel were based on hatchery inventory of the number of unmarked fish that were added to each of the five ponds with the number of

marked fish added to each pond provided by the marking and tagging operators. Beginning with fish releases in 2013 (Brood Year 2012), data from samples of fish collected before release and screened for the presence of CWT were compared to hatchery reports. Fish were collected using cast nets from at least 10 casts from different portions of the pond. A minimum of 991 and a maximum of 2,228 fish were collected from each of the ponds. Fish were screened for CWT using a V detector and returned to their respective ponds following data collection. An aggregate facility tag rate from the pre-release sample was determined using pond averages from the pre-release sample weighted by the total number of fish in each pond. A paired t-test was performed to determine any significant difference between pre-release sample data and hatchery inventory data and the threshold of significance set at $P = 0.05$.

Otolith sample validation

During return years 2017 and 2018 subsamples of otoliths of known origin were submitted to the Washington Department of Fish and Wildlife aging lab for screening for otolith marks. The group's origins included 311 PRH-origin fish and 65 fish originating from Ringold Springs Hatchery that had been tagged with CWT and received otolith marks at the hatchery before their release and a group of 62 fish presumed to have no mark as they contained CWT derived from sites with no history of thermal marks. Samples submitted included otoliths from fish ranging in age from 2 to 6 years old. Small numbers of six-year old fish were recovered and they were excluded from subsequent statistical analysis because of low sample size. The actual number of fish in each category were categorized by return year and age of fish and these frequencies were compared to the observed number as determined by the WDFW aging lab. A Wilcoxon Sign Rank test with continuity correction was performed to determine differences between the actual number of otolith marked fish and the observed frequencies with the threshold of significance set at $P < 0.05$.

Results

Estimation of PRH-origin fish returning to the hatchery using four methods

All methods of estimation indicated that the majority of fish returning to the PRH in each of the years were of PRH-origin (Table 2). Overall, the means for percent PRH-origin fish derived from the otolith marked sample were 90±12%, CWT 80±13%, Ad-CWT 77±11%, and Ad-Clip 86±12% (Table 2). The first two years of the study had the highest variation among the four % PRH-origin estimates and a significant linear relationship revealed a reduction of variation among methods was observed over the duration of the study (Table 2; Figure 1). Pearson correlation coefficients indicated very strong relationships between estimates derived by otoliths and Ad-Clip (0.905) and between estimates derived by CWT and Ad-CWT (0.983). The weakest relationships were estimates derived from otolith versus Ad-CWT (0.539). Correlation coefficients for the remaining contrasts fell between 0.670 and 0.770 (Table 3).

Errors Attributed to Scale Aging and Detection Equipment

The percentage of fish assigned the incorrect age from scales increased as fish aged from 1.2% at age 2 to 11.5% at age 5 (Figure 2a). Fish were incorrectly assigned ages of both older and younger than their real age with error rates increasing as fish aged in both instances (Figure 2 b-c). In simultaneous testing of all three tools in male fish, the Blue Wands reported 1.5%

fewer CWT than the T wands (Range = 0-3.5%; Table 4). However, chi square tests of independence revealed no significant difference attributed to the type of tool used. Female salmon in the two replicates yielded 100% correspondence among all three screening tools for both replicates.

Comparison of Hatchery Inventory to Pre-Release Sampling

Over seven years of evaluations the mean juvenile tag rate for the hatchery inventory method and from pre-release sampling were 16.7% versus 18.1%, respectively (Figure 3). No significant differences were detected between these paired data.

Otolith sample validation

The errors associated with incorrectly assigning origin to fish on the basis of otolith marks were universally in the direction of assigning fish that were known to originate from a thermally marked population to an unmarked designation (Table 5). For PRH-origin fish, this error ranged from 0% to 12.5% of under reporting of PRH-origin samples categorized by return year and fish age and over the two years of study a 3.7% error across all age classes (Table 5). For PRH fish, two to five years in age, this consistent pattern of under reporting led to a significant difference between Expected and Observed otolith marks (N=6; $P = 0.033$).

Table 1. Numbers of fish released by the Priest Rapids Hatchery fall Chinook Salmon program and the numbers of fish receiving adipose clips and coded wired tags and adipose clips+coded wire tags. Since brood year 2007 a thermal mark has been applied to 100% of the population.

Brood Year	Return Years	Total Released	Number Ad-CWT	Number CWT Only	Number Ad-Clip Only
2007	09-13	4,548,307	202,568	0	813
2008	10-14	6,788,314	218,082	0	1,719,388
2009	11-15	6,776,651	619,568	1,026,561	1,717,188
2010	12-16	6,798,390	602,580	1,108,990	1,702,961
2011	13-17	7,056,948	595,608	598,031	2,768,643
2012	14-18	6,822,861	603,930	601,009	2,712,228

Table 2. Percentages of PRH-origin fish returning to the hatchery trap using four methods.

Return Year	Total Return	Method				
		Otolith	CWT	Ad-Clip	Ad-CWT	Mean (SD)
2012	28,038	94.9	69.4	88.5	67	80.0 (13.9)
2013	41,831	98.2	74.5	88	68.8	82.4 (13.3)
2014	77,779	93.3	83.1	87.3	79	85.7 (6.1)
2015	63,978	93.2	91.8	88.2	87	90.1 (2.9)
2016	28,785	94.4	90.8	87.5	86.8	89.9 (3.5)
2017	17,013	93.2	90.6	99.1	87.1	92.5 (5.1)
2018	20,465	62.9	58	61.2	61.1	60.8 (2.0)
Mean (SD)		90.0 (12.1)	79.7 (12.9)	85.7 (11.6)	76.7 (11.0)	

Table 3. Pearson's correlation coefficients characterizing relationships between estimates of the percentage of PRH-origin determined by four different methods.

	Otolith	CWT	Ad-Clip	Ad-CWT
Otolith	---	---	---	---
CWT	0.670	---	---	---
Ad-Clip	0.906	0.770	---	---
Ad-CWT	0.539	0.984	0.687	---

Table 4. Results of three replicate tests performed on male salmon in 2017 comparing three different detector types used to scan fish for the presence of CWT. Data include the number of fish with and without CWT when scanned by different tools and the results of chi square test for independence. In each case and in the aggregated data the level of significance was > 0.05 and provide no evidence that the results are dependent on the tool used.

	Blue Wand	T Wand	R Detector	χ (p)
Trial 1				
CWT	74	78	78	
No-CWT	298	294	294	0.18 (0.92)
Trial 2				
CWT	13	13	13	
No-CWT	65	65	65	0 (1)
Trial 3				
CWT	9	10	11	
No-CWT	48	47	46	0.24 (0.89)
Aggregate				
CWT	96	101	102	
No-CWT	411	406	405	0.26 (0.88)

Table 5. Frequencies of expected and observed thermal marks in otoliths from adult fall-run Chinook Salmon from sources known to have otolith marks (PRH, RSH) and those with no thermal marks applied to their otoliths.

		PRH		RSH		Unmarked	
Year	Age	Expected	Observed	Expected	Observed	Expected	Observed
2017	2	8	7	1	0	0	2
	3	49	48	0	0	5	6
	4	120	117	51	48	13	19
	5	35	32	11	11	17	20
	6	1	1	0	0	0	0
2018	2	3	3	0	0	0	0
	3	42	40	1	1	6	8
	4	25	24	0	0	17	18
	5	9	9	0	0	4	4
	6	2	2	1	1	0	0

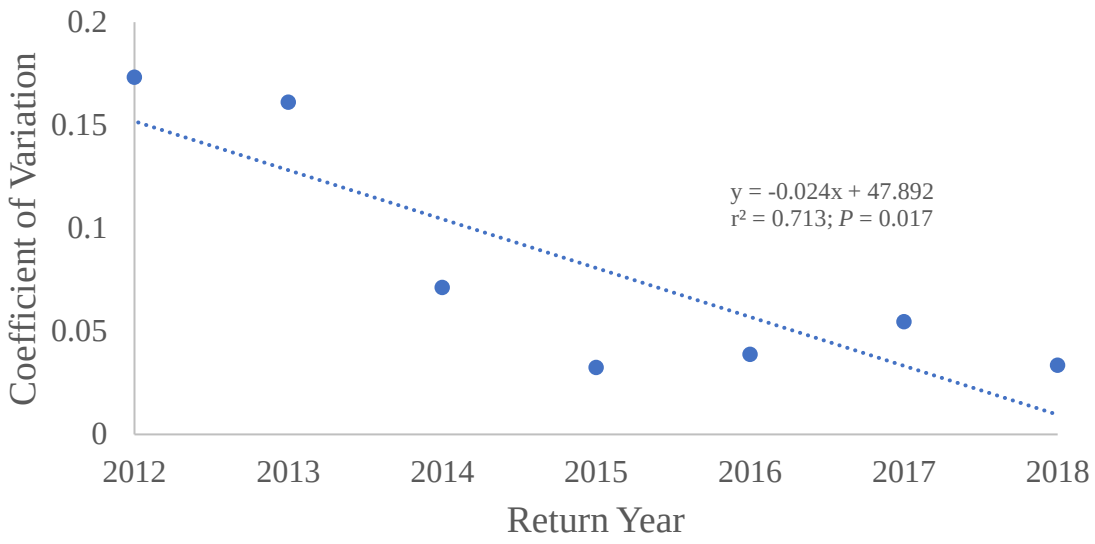

Figure 1. A linear regression of the coefficients of variation for estimates of percent PRH-origin determined using four different marking and tagging methods annually.

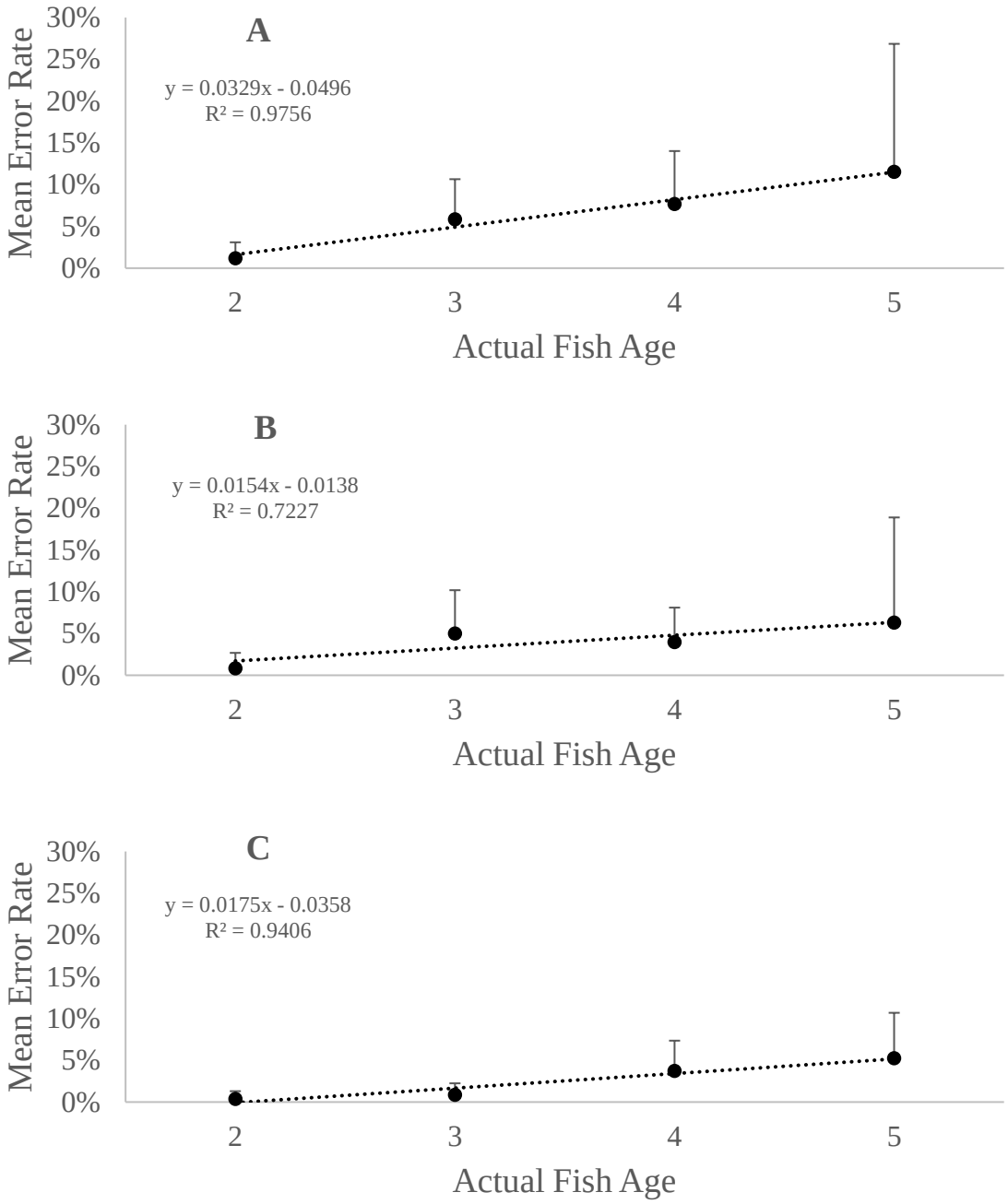

Figure 2. Error rates in assigning age from scales of adult fall-run Chinook Salmon; (A) total errors, (B) incorrectly designated as older than actual, (C) incorrectly designated as younger than actual. Bars extending above each mean represent one standard deviation.

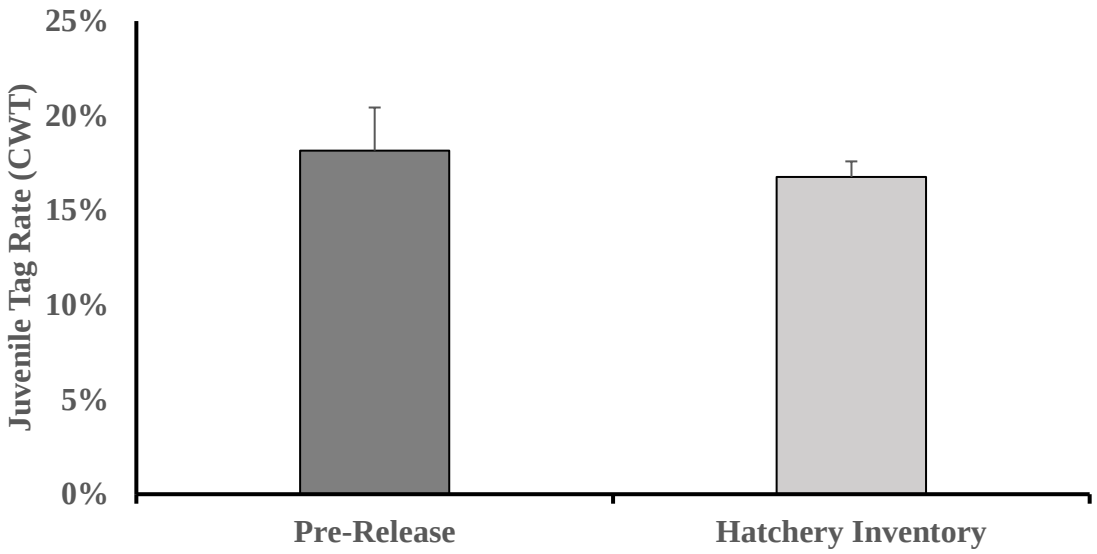

Figure 3. The mean juvenile tag rates for coded wire tags (CWT) applied to progeny of brood year 2012 to 2018 PRH fall run Chinook Salmon determined using data gathered during pre-release sampling or by hatchery inventory methods.

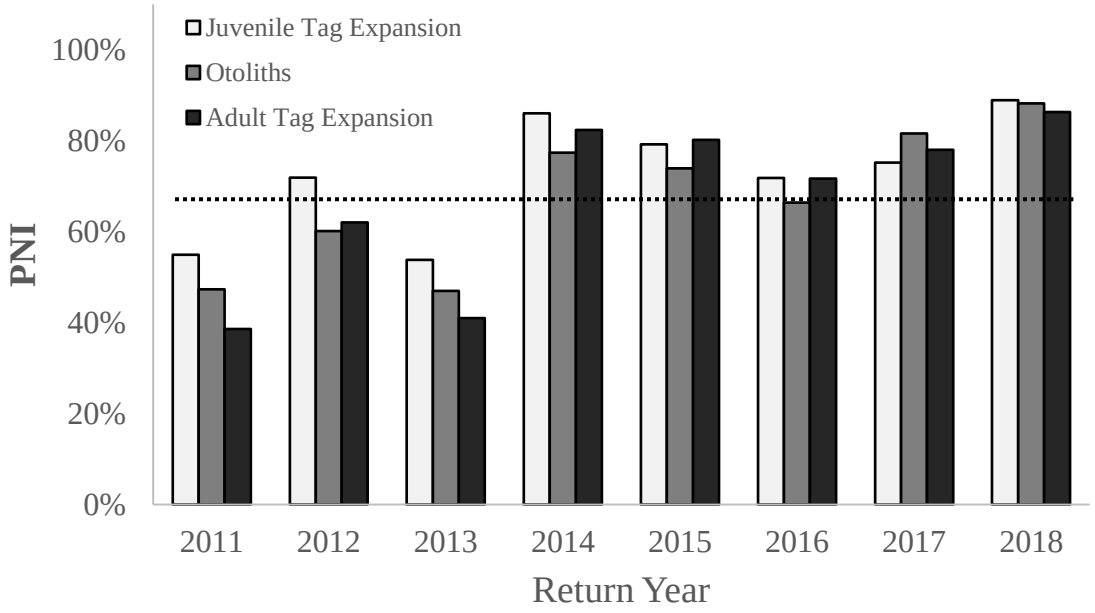

Figure 4. Estimates of Proportional of Natural Influence derived from three methods of determining adult abundance returning to the Hanford Reach: Juvenile Tag Rate Expansion, Otolith Samples, and Adult Tag Recovery Expansion. The dotted line indicates hatchery reform targets for the supplementation program.

Discussion

Overall, the four methods used to derive the percentage of PRH-origin fish returning to the hatchery trap varied considerably within each year of the study. However, we observed a trend towards consensus of all four methods over time coincident with increased emphasis on monitoring and the increase in mark and tag rates for the population. Values derived from otolith marks were, in nearly all cases, higher than other estimates of abundance even though otolith estimates were known to underestimate the % of PRH-origin fish.

Deviations of other marking strategies from otolith derived estimates may indicate CWT loss, tagging induced delayed mortality, or inefficient tag detection as likely mechanisms. However, our evaluations of different CWT detectors did not detect appreciable differences that could account for the > 20% difference observed between estimates derived from otoliths and CWT during 2012 and 2013. Similarly, juvenile tag rates derived from hatchery inventory and from pre-release sampling did not differ, suggesting that estimation errors in tag rates could not explain differences observed in 2012 and 2013. Partial adipose clips may also contribute to errors and result in underestimates of hatchery-origin fish. Perhaps additive errors from multiple sources occur in some years which contribute to high error rates that were observed in some years.

Our confidence in estimates derived from the subsample of otoliths with a 100% mark rate is enhanced by general agreement we see among all abundance estimates in the final years of these study. In addition, Ad-Clip estimates appear to strongly correlate with those derived from otoliths over the course of this study. The close association between estimates derived from Ad-Clip and otoliths may be the result of larger numbers of Ad-Clip animals and that the mark is less likely to be lost or misidentified as the fish mature to adult. The detection efficiency for CWT that we present for PRH was substantially higher than what has been presented for other hatcheries (Vander Haegen et al. 2002). For example, detection efficiency was 71.0% for Soos Creek Hatchery (Vander Haegen et al. 2002).

We did not find strong evidence for large magnitudes of tag loss or differential survival on CWT fish, particularly in the latter years of the study. For example, estimates of adult PRH-origin fish were only 6% different when juvenile CWT or Ad-Clip expansion rates were used. If large losses of CWT occurred, then estimates of PRH-origin fish would be lower for estimates of CWT than Ad-Clip. Furthermore, abundance estimates derived from Ad-Clip adults with and without CWT were similar suggesting that CWT fish did not lose tags and that there was not differential loss of fish with CWT. Rates of CWT loss in the Yakima River for spring Chinook Salmon were reported as 6.7% between the time of release and when they returned to the hatchery (Knudsen et al. 2009). Interestingly, there is a 6% difference in the grand mean of abundance estimates between CWT and Ad-Clip estimates the differences appear weighted heavily towards the early years of the study and are generally more in agreement after the numbers of CWT released were increased and the monitoring was improved.

Errors in the ages of fish could also contribute to abundance errors particularly in years with older age fish at return. During brood years with young ages at return, the error rates of ages are likely to be lower than during years when age at adult return is older. This variation in error rate might explain some of the differences in error variation that were observed in this study.

A potential source of systematic bias contributing to estimates was the underreporting of otolith marked fish. Overall, the two years of data reported represented an error rate of 3.7% of fish that would be reported as non-hatchery origin. This would lead to an increase in reporting of natural-origin fish on the spawning grounds and an increase in the percentage of natural-origin broodfish in the spawning population at the hatchery. Additional data are being collected and if the pattern continues to be consistent, it may allow for a correction factor to be applied.

Management Implications Method

Our data suggest that underestimation of Ad-Clip and CWT may be relatively low if the fish that are marked or tagged occur in ample numbers and the monitoring is robust. However, in years where these conditions cannot be met or verified, then other methods are needed to correct historical data sets. This is true of many hatcheries that have been in existence for decades and have only been recently implementing measures of hatchery reform. For example, mark rates were lower and perhaps not representative of the entire production at PRH in early years of operation and sampling of marks and tags has only been conducted recently at PRH to estimate representation of different portions of the hatchery population (Pearsons et al. 2020). There is value in developing long term data sets into monitoring and evaluation programs to understand the efficacy of the hatchery program and a strong desire to develop unbiased estimates of abundance when expansion of juvenile tag rates are questionable. Prior to 2012,

estimates were based upon CWT recoveries and suggested that less than 70% of fish returning to the hatchery trap were of PRH-origin (Richards and Pearsons 2020) and the first two years of this study illustrate results that suggest that underestimates of abundance estimates for PRH-origin fish was a continuing problem when using these data to determine hatchery reform benchmarks that include the proportion of natural influence (Pearsons et al. 2020) meant to minimize domestication selection attributed to the hatchery environment. Underestimates of PRH-origin fish based upon interpretations of mark or tag frequency could lead to an erroneous interpretation of the impact of the PRH program. The correlation between Ad-Clip and otolith derived estimates suggests that expansion of Ad-Clip mark rate would be preferable to CWT mark rates over a longer time series, but CWT expansions have been used recently.

Different techniques using CWT have been used to develop estimates for hatchery reform parameters. A technique that uses the CWT proportions of adults has been used informally to determine abundance of natural-and hatchery-origin populations on the Hanford Reach for several years (Paul Hoffarth, WDFW, personal communication). Total returns for each age cohort to PRH are estimated using the return numbers and age data gathered from the demographic sample. The number of fish with PRH CWT are summarized for each age cohort and an expanded number for fish straying into PRH is estimated using reported expansion rates for CWT (www.rmpc.org, Pacific States Marine Fisheries Commission) and removed to yield the number of PRH-origin fish. An expansion rate for adult fish with PRH CWT can then be determined for each age class as the Total PRH Return/Number of PRH CWT recovered. The PRH CWT recovered during carcass surveys is then expanded using the sample rate and the adult based expansion rate. As an exercise we have derived data on the PRH program proportion of natural influence using alternate approaches and the adult expansion rate approach appears to mitigate some of the differences attributed to CWT bias in the early portions of this study (Figure 4). This type of estimate for the number of PRH-origin fish based on the adult-to-adult expansion holds promise in developing long term data sets that characterize trends surrounding the impact of a hatchery program on the supplemented population.

Lessons learned

The accuracy of estimates derived from CWT or other tags and marks is a function of the practices employed in marking, tagging, and inventory. These practices include tagging appropriate proportions of the population and distributing fish to each rearing vessel to produce representative mark rates. Additional time, effort, and handling of fish at PRH have led to improvements in the consistency of values produced by all methods employed. Developing methods to monitor and evaluate tag bias is an important step for ensuring the collection of high quality data that can be used to make management decisions. We recommend that monitoring and evaluation programs incorporate methods of characterizing bias in tagging and marking as a routine practice. In so doing, the quality of data and the decisions that rely upon them will be improved or at least be more defensible.

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