Comprehensive Evaluation of Middle Columbia River Public Utility District's Spring Chinook Salmon Hatchery Programs

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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 Grant, Chelan, and Douglas County PUD's spring Chinook Salmon hatchery programs through 2018. Other covered species (e.g., fall 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., T. W. Hillman, P. J. Graf, C. C. Willard, T. H. Kahler, and G. Mackey. The effects of hatchery supplementation on the abundance and productivity of adult spring Chinook Salmon in the upper Columbia Basin.

Managers frequently select hatchery supplementation as a tool to increase natural production of spring Chinook Salmon (*Oncorhynchus tshawytscha*), particularly when populations have severely declined or face extinction. We evaluated four continuous, adaptively managed supplementation programs, and one intermittent and unintentional supplementation occurrence between 1992-2018 at two spatial scales in the Upper Columbia Watershed where spring Chinook Salmon are endangered. Comparisons between supplemented streams and reference (un-supplemented) streams were made using a Before-After-Control-Impact (BACI) design to evaluate whether supplementation changed abundance of total spawners, natural-origin adult recruits, natural-origin spawners, adult productivity, and density-adjusted adult productivity. Adults collected and spawned in hatcheries produced considerably more adult recruits per spawner than those that spawned in the natural environment except for the captive broodstock program in the White River, which produced fewer. However, abundance of total spawners, natural-origin spawners, natural-origin adult recruits, productivity, and density-adjusted productivity in supplemented streams decreased more or increased less during supplementation compared to reference streams, although few were statistically significant. The size of BACI contrasts that could be detected using statistical power analysis was variable among references streams; however, minimum detectable differences stabilized 10-20 years after supplementation, which was within the timeframe of this evaluation. Based on our analyses, spring Chinook Salmon supplementation has not measurably improved abundance or productivity of natural-origin spring Chinook Salmon in the Upper Columbia Basin relative to un-supplemented, reference populations located outside the Upper Columbia Basin.

2) Buchanan, R. A., R. L. Townsend, and G. Mackey. Investigations into association between proportion of hatchery spawners and juvenile productivity for spring Chinook, summer Chinook, and summer steelhead in the Wenatchee and Methow river basins.

Conservation hatchery programs implemented in the Wenatchee and Methow river basins are intended to increase the abundance of the target populations. The strategy of the hatchery programs is to return hatchery adults that increase the spawning population, resulting in an increase in the number of offspring that will maintain and recover naturally reproducing populations. However, there is a concern that the hatchery programs may lower the juvenile productivity in supplemented watersheds. The populations are managed under the concept of Proportionate Natural Influence (PNI), a framework that uses genetic modeling to estimate risk of hatchery introgression in natural populations and prescribes management benchmarks intended to allow hatchery programs to operate within an acceptable risk level to the natural population. One of the metrics in the PNI framework is the proportion of hatchery origin spawners (pHOS). Our investigation of whether higher pHOS may result in lowered juvenile productivity was largely inconclusive. For most populations studied, no evidence of an effect of pHOS was observed. For the single population that demonstrated a possible negative effect of pHOS on juvenile productivity (Twisp River Summer Steelhead), the evidence was weak: when density dependence was accounted for, the perceived negative association between pHOS and juveniles per redd was no longer observed. Additionally, the significant result was observed only when a possible outlier in emigrant counts was omitted, which may not be justified depending on the cause of the unusual emigrant count for that brood year. Thus, even when some evidence of a negative effect of pHOS was found, the evidence was particularly weak. For all three stock-recruitment models considered, there was often high uncertainty in model parameter estimates even when the models could be fit to the data. This was indicated by wide confidence intervals that often included maximum smolt or emigrant values far beyond the range of observed data, and by the high correlation in model parameter estimates. High correlation lowers the ability to distinguish between different model fits and increases uncertainty in the results; it arises from lack of contrast in the data or violation of modeling assumptions. Given all the complicating factors identified here, only the most extreme effect of pHOS on juvenile productivity could have been detected. Thus, we caution against concluding that such an effect is truly absent. We conducted a power analysis based on the Chiwawa spring Chinook data—the most robust dataset in this study. Simulated power analyses revealed that studies shorter than 70 years will have low power to detect an effect on recruitment for all but the strongest effect sizes of pHOS. Future data-collection efforts could be substantially improved by increasing the contrast in pHOS levels and including suitable in-basin unsupplemented references. More specifically, a planned experiment using deliberately chosen pHOS levels could be implemented in order to achieve the necessary contrast and remove confounding analyses with temporal and age-structured processes. Appropriate power analyses must be performed on the study design prior to commencing work to ensure that a result may be obtained within an acceptable time frame.

3) Mackey, G., T. N. Pearsons, and T. W. Hillman. The effect of hatchery programs on Proportionate Natural Influence (PNI) in the upper Columbia Basin.

Hatchery programs and natural populations in the Wenatchee and Methow subbasins were managed under the Proportionate Natural Influence (PNI) strategy, whereby gene flow between the hatchery and natural populations was manipulated to achieve greater overall genetic influence from the natural population as opposed to the hatchery population. The target PNI value was 0.67. Steelhead programs in the Wenatchee and Methow had PNI averages or medians below 0.67. The new management regime for steelhead in the Methow was not initiated until 2017. Therefore, data in this report do not reflect the future management of the steelhead in the Methow subbasin for gene flow. Spring Chinook Salmon PNI in the Wenatchee Subbasin was below 0.67 for all populations under the contemporary management strategy but exceeded 0.50 in all cases. Methow subbasin spring Chinook PNI was 0.29, and has not increased appreciably in the two years of adult returns following reduction in program sizes in 2013. Wenatchee and Methow summer Chinook both had PNI means that exceeded 0.67. Both of these programs appear successful in meeting PNI objectives with the Wenatchee PNI an impressive 0.87. The results of this analysis indicate that the Spring Chinook and steelhead programs require adjustment to meet the PNI targets. In some cases, the PNI values may improve as new management strategies mature. The Methow steelhead and particularly Methow spring Chinook may require substantial management changes in order to achieve the gene-flow objectives. In general, PNI targets were not met for small populations (spring Chinook Salmon and steelhead) but were for large populations (summer Chinook Salmon).

4) Graf, P. J., C C. Willard, T. W. Hillman, T. N. Pearsons, T. H. Kahler, and G. Mackey. Adult migration timing, spawn timing, and spawning distribution of spring Chinook Salmon and summer Chinook Salmon in the Wenatchee and Methow basins.

The migration timing, spawn timing, and spatial spawning distribution of hatchery- and natural-origin salmon in the natural environment can be important metrics in the evaluation of integrated hatchery programs. The timing of migration and spawning of hatchery- and natural-origin spring Chinook Salmon were generally similar in the Wenatchee and Methow sub-basins. Although the difference in arrival timing was small and not statistically significant, the visual observation and PIT-tag data at Tumwater and Wells dams suggests a tendency for hatchery-origin spring Chinook Salmon to arrive later than natural-origin fish. Differences in migration timing between spring Chinook Salmon populations in the Wenatchee versus Methow sub-basins were observed and may result in differences in survival at the adult life-stage. With summer Chinook Salmon, hatchery-origin fish in the Wenatchee sub-basin consistently passed Dryden Dam later than their natural-origin counterparts whereas the migration timing for Methow and Okanogan sub-basin hatchery-origin fish was a near match with natural-origin fish at Wells Dam. Summer Chinook Salmon spawn timing in both Wenatchee and Methow hatchery-origin fish was later than natural-origin fish, with Methow-origin fish having a larger average difference. For spatial distribution of spawning spring Chinook Salmon, differences between hatchery- and natural-origin spawner distribution across the historical survey reaches were observed in all programs except the White River program. In general, hatchery-origin females spawned lower in the watershed. However, the proportion of hatchery-origin fish was high (i.e., greater than 50%) in the majority of survey reaches (33 out of 51), particularly in those reaches that were the primary spawning areas by natural-origin fish. The proportion of hatchery-origin spring Chinook Salmon exceeded 30% in 48 of the 51 survey reaches. The distributions of spawning Wenatchee and Methow hatchery-origin summer Chinook Salmon also differed from the spawner distributions of the natural-origin populations, with hatchery-origin females more often spawning lower in the watershed. This difference in spawning distribution was consistent with management objectives. The proportion of hatchery-origin summer Chinook Salmon was greater than 30% in 6 of the 17 survey reaches.

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) Small, M. P., Todd R. Seamons, S. Brown, A. Louden, G. McKinney, T. N. Pearsons, and T. H. Kahler. Evaluating genetic metrics of adult natural- and hatchery-origin Spring Chinook Salmon in the Upper Columbia Basin.

In 1999, the upper Columbia River spring Chinook Salmon evolutionarily significant unit (ESU), was listed as endangered under the Endangered Species Act (ESA). Hatchery programs already underway were used to supplement wild populations in the Wenatchee and Methow rivers for conservation and fishery benefits. Hatchery-origin spring Chinook Salmon that spawn with conspecifics in the natural environment may decrease short- and long-term fitness of natural populations through genetic mechanisms such as domestication selection and loss of within- and among-population genetic variation. Using genetic data from baseline and contemporary collections of hatchery- and natural-origin samples we evaluated the impact of hatchery propagation on within and among population genetic diversity of upper Columbia River spring Chinook Salmon, as required by a monitoring and evaluation plan. The DNA from the earliest available tissue collections, in some locations prior to the onset of local hatchery programs (1989-1993), constituted the baselines and were compared to DNA from tissues collected from contemporary samples (2017, 2018). Analysis indicated genetic changes among spawning aggregates over time. Among the Wenatchee collections the baseline Chiwawa, Nason and White collections were different from each other while the contemporary collections for these populations, along with the Little Wenatchee, were indistinguishable from each other. This is in contrast to Blankenship et al. (2007) who found that the contemporary (in 2006) and baseline collections were undifferentiated. A similar pattern was observed among the Methow collections, where the baseline Twisp, Chewuch and Methow collections were different from each other while the contemporary Chewuch and Methow natural collections were indistinguishable from each other and barely distinguishable from the contemporary Twisp natural collection. Similar to Small et al. (2007) there were differences between baseline and contemporary (in 2006) samples in both the Wenatchee and Methow rivers. It is likely that the management decisions to create composite spawning aggregates, straying hatchery-origin fish, and genetic drift from low effective numbers of breeders contributed to the patterns we observed.

9) Graf, P. J., T. W. Hillman, T. H. Kahler, C. C. Willard, and T. N. Pearsons. The effects of hatchery supplementation on size and age at maturity and fecundity of spring and summer Chinook Salmon in the upper Columbia Basin.

A common objective of conservation hatchery programs is to produce fish with phenotypic traits similar to individuals from the natural population. We evaluated the size and age at maturity, and fecundity of five spring Chinook Salmon and three summer Chinook Salmon hatchery programs.

Comparisons to natural-origin fish from the targeted populations over multiple generations and during two periods of hatchery production releases (high and low number of smolts) were made for applicable programs. Generally, the hatchery-populations were composed of more, younger fish and fewer older fish, but the predominate age at maturity was similar between hatchery- and natural-origin populations. The size at maturity of returning adults was significantly affected by age and sex, and in some cases origin and period. However, when matched by age and sex, the differences in size at maturity by origin and period that were statistically significant were minor and likely of little biological relevance. For all populations, the fecundity metrics were significantly affected by fish size and weight, but fecundity differed between origins in only two populations. For all metrics, the high/low program release numbers did not substantially affect these phenotypic traits. Future analyses of these metrics should consider changes over time and consider trends between hatchery-origin and natural-origin fish. Declines in age and size at maturity are a range-wide concern for Pacific salmonids and therefore a temporal analysis of the dataset generated for the monitoring of these hatchery programs would benefit the region.

10) Mackey, G., and T. W. Hillman. Numbers and sizes of fish released from hatcheries in the upper Columbia Basin.

Chelan, Douglas, and Grant PUDs produce salmon and steelhead for mitigation under various agreements including the Rock Island Habitat Conservation Plan (HCP), the Rocky Reach HCP, the Wells HCP, and the Priest Rapids Settlement Agreement and associated Biological Opinion. The various hatchery programs are monitored for the number of fish released, as well as metrics for fish size at release and condition. The programs include Summer Chinook Salmon, Spring Chinook Salmon, and summer steelhead produced and released at a variety of facilitates in the Wenatchee River Subbasin, Methow River Subbasin, and Columbia River. Programs generally met or exceeded the release-number targets. Specific programs did not meet the release-number targets in all years, but all programs met or exceeded targets in the majority of years, with the exception of the White River spring Chinook Salmon captive broodstock program. This program was in development for all of its history and tested numerous fish culture and release strategies. Therefore, the program was not able to meet targets that remained consistent across years. Most programs met or were close to meeting the CV target on average. Meeting the CV targets for steelhead programs was more difficult than for the Chinook Salmon programs. Meeting fish-per-pound (fpp) targets was more difficult in Spring Chinook Salmon and conservation steelhead programs, potentially because these programs use natural-origin broodstock. Spring Chinook Salmon exhibited near-isometric growth. Steelhead exhibited negative allometric growth, as did Wells and Methow summer Chinook Salmon. However, Wenatchee and Chelan Falls summer Chinook Salmon exhibited isometric or positive allometric growth. Condition factors across all programs were very close to or exceeded 1. Trade-offs between post-release survival and age at maturation influence hatchery rearing strategies. Large Chinook Salmon generally survive better than small fish, but they also are more prone to mature at younger ages. Hatchery programs that use natural-origin fish for broodstock may experience higher levels of precocial maturation than those that use hatchery-origin fish for broodstock. In addition, larger fish also pose ecological risks to other fish through mechanisms such as competition or predation. In general, the length targets, and some of the metrics that used a single value (e.g., length and weight) associated with a range of fpp targets, were not useful. Adaptation of targets may occur to achieve a better suite of benefits among the many trade-offs involved in growing fish to a target size or weight.

11) 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.

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.

Introduction

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, Chelan, and Douglas PUD's spring Chinook Salmon hatchery programs through 2018. Other covered species (e.g., summer Chinook, fall 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 (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, also known 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 that 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
2	Determine if the proportion of hatchery fish on the spawning grounds affects the freshwater productivity of supplemented stocks.	2
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.	3
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.	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
9	Determine if hatchery fish were released at the programmed size and number.	10
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.	11

One of the topics identified for the hatchery program review has already been published in a peer-review journal, the highest standard of the profession. The citation of the publication is 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

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.

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 to this report. 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

Thanks are due to 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 Region. Finally, we thank the HCP Hatchery Committees and the PRCC Hatchery Subcommittee for their input and review of the hatchery and M&E programs.

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The Effects of Hatchery Supplementation on the Abundance and Productivity of Adult Spring Chinook Salmon in the Upper Columbia Basin

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Abstract

Managers frequently select hatchery supplementation as a tool to increase natural production of spring Chinook Salmon (*Oncorhynchus tshawytscha*), particularly when populations have severely declined or face extinction. We evaluated four continuous, adaptively managed supplementation programs, and one intermittent and unintentional supplementation occurrence between 1992-2018 at two spatial scales in the Upper Columbia Watershed where spring Chinook Salmon are endangered. Comparisons between supplemented streams and reference (un-supplemented) streams were made using a Before-After-Control-Impact (BACI) design to evaluate whether supplementation changed abundance of total spawners, natural-origin adult recruits, natural-origin spawners, adult productivity, and density-adjusted adult productivity. Adults collected and spawned in hatcheries produced considerably more adult recruits per spawner than those that spawned in the natural environment except for the captive broodstock program in the White River, which produced fewer. However, abundance of total spawners, natural-origin spawners, natural-origin adult recruits, productivity, and density-adjusted productivity in supplemented streams decreased more or increased less during supplementation compared to reference streams, although few were statistically significant. The size of BACI contrasts that could be detected using statistical power analysis was variable among references streams; however, minimum detectable differences stabilized 10-20 years after supplementation, which was within the timeframe of this evaluation. Based on our analyses, spring Chinook Salmon supplementation has not measurably improved abundance or productivity of natural-origin spring Chinook Salmon in the Upper Columbia Basin relative to un-supplemented, reference populations located outside the Upper Columbia Basin.

Introduction

Hatchery supplementation is a tool frequently used to increase natural production of spring Chinook Salmon (*Oncorhynchus tshawytscha*), particularly when populations have severely declined or face extinction (Cuenco et al. 1993; Pearsons 2002; Mobrand et al. 2005). Supplementation using smolts (migratory juveniles) is often chosen because it has the potential, in a relatively short period of time, to provide increased numbers of adult returns that spawn in nature. It has been demonstrated repeatedly that well-run hatchery programs can increase the number of Chinook Salmon spawners (Fast et al. 2015; Scheuerell et al. 2015; Venditti et al. 2018). However, far fewer studies have conclusively demonstrated that supplementation increases the number of naturally produced (hereafter natural-origin) adults (Scheuerell et al. 2015; Venditti et al. 2018). Such studies are difficult and expensive to conduct, requiring analysis of data collected over protracted timescales (Ham and Pearsons 2000; Fast et al. 2015; Venditti et al. 2018). In contrast, some studies have indicated reduced productivity of supplemented populations (Buhle et al. 2009; Williamson et al. 2010; Chilcote et al. 2011); although, some of these studies included programs using practices now considered sub-optimal, such as use of non-local broodstock (Mobrand et al. 2005; Paquet et al. 2011). Thus, although widely applied as a management action, many uncertainties remain about the utility of supplementation to achieve management objectives; therefore, it remains appropriate to consider it an experimental tool until more evaluations are available (ISAB 2003; Fraser 2008).

At least three important assumptions support using supplementation to increase natural production: 1) the per capita adult return rate for fish used as hatchery broodstock will be higher than those that spawn in rivers, 2) hatchery adults can produce enough adult offspring in the natural environment to warrant the removal of their parents from the spawning grounds for use as hatchery broodstock, and 3) there is unused capacity in the target environment to support additional spawners and offspring (Cuenco et al. 1993, Pearsons 2002, Paquet et al. 2011). Violation of any of these assumptions can result in failure to meet management objectives and costs to the natural population that outweigh any benefits. Unfortunately, it is uncommon to rigorously estimate the carrying capacity of the environment before starting a supplementation program, and it is often assumed that there is surplus capacity because of low population densities (Walters et al. 2013, ISAB 2015).

The increased sophistication of genetic techniques has allowed simultaneous evaluations of relative reproductive success of hatchery and natural-origin spawners in the natural environment (Ford et al. 2012; Hess et al. 2012; Janowitz-Koch 2019). For example, hatchery-origin spring Chinook Salmon produced fewer offspring than their natural-origin counterparts in the Wenatchee Sub-basin, largely because of differences in spawning location within the Chiwawa River (Williamson et al. 2010; Hughes and Murdoch 2017). In addition, eggs deposited by natural-origin Yakima River spring Chinook Salmon in an artificial stream had a 5.6% higher survival rate than hatchery-origin females (Schroder et al. 2008). In contrast, hatchery-origin males in the same artificial stream produced similar numbers of offspring as natural-origin males (Schroder et al. 2010). Although studies of relative reproductive success are important ways to understand the mechanisms of population productivity, they generally do not directly assess whether supplementation increases natural-origin adults (Christie et al. 2014). More direct methods of assessing the effects of supplementation on population abundance and productivity can be used to address this uncertainty.

By comparing un-supplemented (reference) stocks to supplemented stocks, we evaluated the effects of four different spring Chinook Salmon supplementation programs and one intermittent and unintended supplementation program on the total number of adult spawners (includes both hatchery and natural-origin spawners), the number of natural-origin spawners, and the productivity of endangered spring Chinook Salmon in the upper Columbia Basin (area between Rock Island Dam and Chief Joseph Dam). Our evaluation was conducted at two scales: 1) tributary (Chiwawa, Nason, White, Twisp, Methow-Chewuch) and 2) subbasin (Wenatchee and Methow). Evaluations at different spatial scales allows for comparisons among programs, inclusion of unintentional supplementation at the subbasin scale (e.g., Nason Creek), as well as averaging of all programs at the largest spatial scale. The range of programs included two-generation captive broodstock; full life-cycle single hatchery location; central hatchery location coupled with overwinter acclimation; central hatchery location coupled with spring acclimation; and a short-term captive broodstock program coupled with a recent intentional supplementation program with unintentional supplementation because of straying from a large hatchery program. These programs were implemented to mitigate for unavoidable losses of juvenile emigrants at hydroelectric projects on the Columbia River operated by three Public Utility Districts.

We compared adult-to-adult productivities of fish that spawned in the hatchery and in the river to determine if per capita hatchery production exceeded that in the river. In addition, we used Before-After-Control-Impact Paired (BACIP) and multiple BACIP (MBACI(P)) evaluations, with multiple replicates before and after supplementation, to determine whether supplementation increased abundance and productivity in supplemented streams relative to reference streams (Stewart-Oaten and Bence 2001; Pearsons and Temple 2010; Chevalier et al. 2019). BACIP and MBACI(P) designs and analyses are among the most useful ways to evaluate the effects of long-term field treatments such as supplementation (Pearsons 2012), and recent improvements in analytical metrics have improved the utility of data interpretation from these evaluations (Chevalier et al. 2019).

Methods

Background

Spring Chinook Salmon that spawn in the upper Columbia River Basin have persisted despite a variety of challenges in their history. The numbers of spring Chinook Salmon were already dramatically low in the early 1900s. Aside from the typical patterns of overharvest and of habitat alteration from beaver removal, dams, channelization, and deforestation that contributed to declines of spring Chinook Salmon throughout the Columbia River Basin (Lichatowich 2001), upper Columbia spring Chinook Salmon were also uniquely managed because of the construction of Grand Coulee Dam. Perhaps most important, all of the upper Columbia spring Chinook Salmon were collected at Rock Island Dam on the Columbia River between 1939 and 1943 and transported and released into Nason Creek, a tributary to the Wenatchee River, to spawn as part of the Grand Coulee Fish Maintenance Program (Fish and Hanavan 1948). Transported spring Chinook Salmon adults were contained in Nason Creek by weirs with the objective that they would spawn there. In addition, hatchery programs were initiated following the transplanting of adult spring Chinook Salmon into Nason Creek. Furthermore, Grand Coulee Dam, and later Chief Joseph Dam, became the upstream limits of spring Chinook Salmon distribution because fish passage was not provided at these dams. The combined activities of transplantation, early artificial propagation, and habitat blockage did not result in thriving spring Chinook Salmon populations as evidenced by the low abundance of natural-origin spring Chinook Salmon in the upper Columbia Basin in recent times (McClure et al. 2008).

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 United States Fish and Wildlife Service, National Marine Fisheries Service, Washington State Department of Fish and Wildlife, Yakama Nation, Colville Confederated Tribes, and each Public Utility District 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.

Spring Chinook Salmon in the upper Columbia form an ESU that was listed as Endangered in 1999 when abundance was extremely low (McClure et al. 2008). The ESU consists of three populations that correspond to the Wenatchee, Entiat, and Methow subbasins. The Wenatchee population consists of five major spawning aggregates (Chiwawa, Nason, White, Little Wenatchee, and upper Wenatchee River), the Entiat population consists of one major spawning aggregate, and the Methow population consists of three major spawning aggregates

(Twisp, Methow, and Chewuch) (Figure 1). A recovery plan identifies criteria for abundance, productivity, spatial structure, and diversity that are necessary for upper Columbia spring Chinook Salmon ESU to be delisted (McClure et al. 2008).

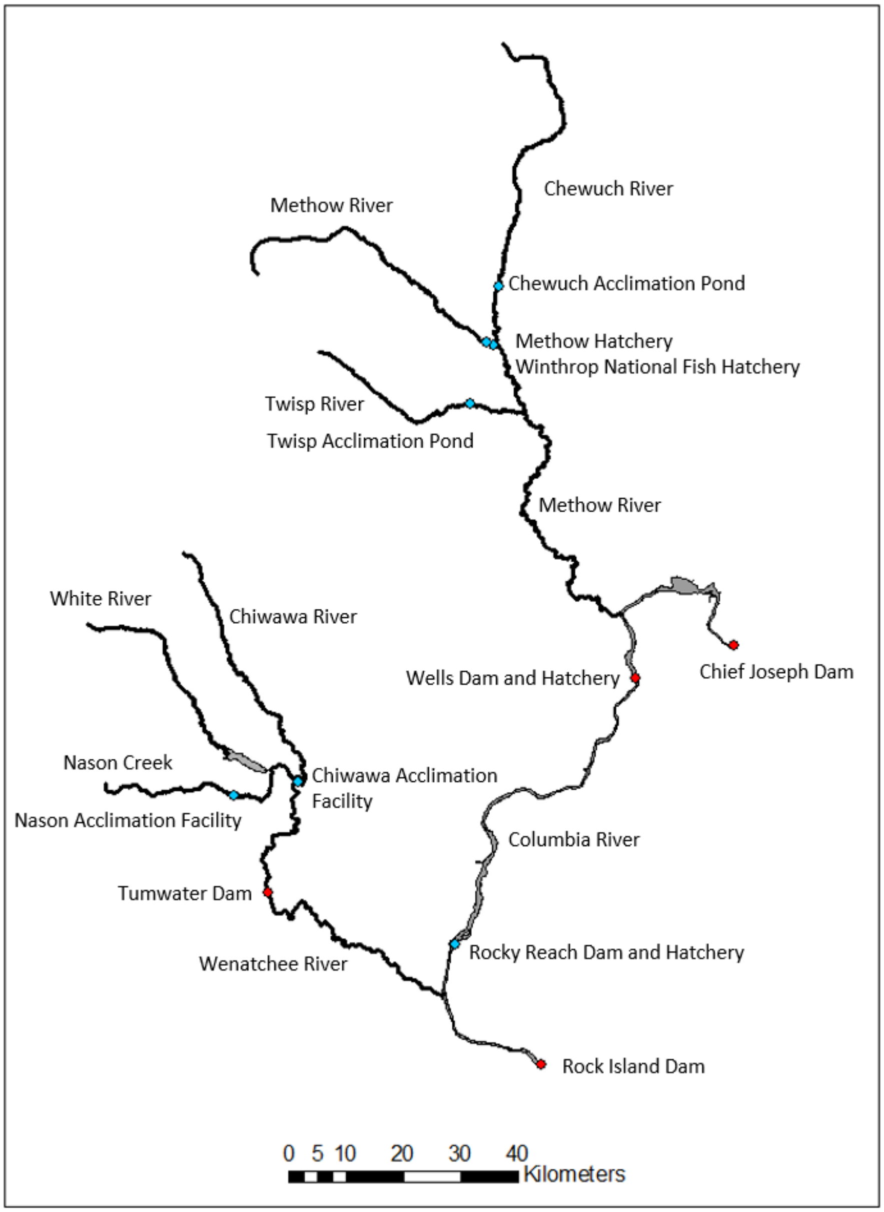


Figure 1. Locations of spring Chinook Salmon hatchery facilities and spawning areas.

The PUDs' hatchery programs in the upper Columbia Basin were operated using a variety of methods that are considered best management practices. For example, broodstock were collected in places or identified using genetic methods to achieve the desired target fish; factorial mating strategies were implemented to maximize effective population size; juveniles were reared at low densities; pathogen management was implemented using best practices; and juveniles were acclimated in places where they were targeted to return as adults. Each hatchery program also had several idiosyncrasies that allow for a diversity of evaluations. For example, hatchery programs were started in different years; captive broodstock was implemented in a few programs; fish were acclimated for different lengths of time (e.g., spring vs. overwinter acclimation); fish were reared in different vessel types (e.g., raceways, circular tanks, large ponds); and fish were released in different ways (e.g., volitional vs. forced release). Some important commonalities of the hatchery programs include a primary purpose of increasing natural production while minimizing long-term reduction in productivity, generally releasing smolts at the yearling stage, and adaptive management of the programs by the hatchery committees. Brief descriptions of each of the five hatchery programs are provided below and other background can be found in Pearsons et al. (2012), and Linley et al. (2016).

Chiwawa River Program

An integrated spring Chinook Salmon hatchery program was initiated for the Chiwawa River spawning aggregate in 1989. The Chiwawa River is approximately 60 km long, drains an area of 47,397 hectares and enters the Wenatchee River at river km (RKM) 77.9. The Chiwawa River was host to the largest spawning aggregate of spring Chinook Salmon in the Wenatchee sub-basin. The hatchery program has contributed a high percentage of hatchery-origin spawners that have spawned in the Chiwawa River, Nason Creek, White River, upper Wenatchee River, and the Little Wenatchee River since 2001 (Hillman et al. 2020; Pearsons and Miller 2021). Adults were collected at a weir on the Chiwawa River and/or at Tumwater Dam for broodstock. Broodstock were held and spawned at Eastbank Hatchery on the Columbia River, located 9 KM upstream of the confluence with the Wenatchee River. Fish were reared at Eastbank Hatchery on well water until they were transferred in late September or early October to the Chiwawa Acclimation Facility, located on the lower Chiwawa River, where they were reared and acclimated until the following spring. During the spring, the yearling smolts were allowed to exit the pond volitionally for a week (Johnson et al. 2015) and any fish that remained were forced out of the facility by late May.

The production goal for the Chiwawa spring Chinook Salmon supplementation program for brood years 1989 to 2009 was to release 672,000 yearling smolts into the Chiwawa River at 12 fish per pound (fpp). Brood years 2010-2011, and 2012 were transition years to a reduced program of 298,000 smolts and 205,000 smolts, respectively. Beginning with the 2013 brood, the revised production goal was to release 144,026 smolts as part of a conservation program at 18 (fpp). Targets for fork length and weight were 155 mm (CV = 9.0) and 37.8 g, respectively. Over 90% of these fish were marked with coded wire tags (CWTs). In addition, since 2006, a proportion of the juvenile spring Chinook Salmon smolts have been passive integrated transponder (PIT) tagged annually before release.

Nason Creek Program

Nason Creek is the second largest spawning aggregate in the Wenatchee subbasin, but is much smaller than the Chiwawa River spawning aggregate. Nason Creek is approximately 37 km long, drains an area of 26,547 hectares and enters the Wenatchee River below Lake Wenatchee at RKM 86.3. It enters the Wenatchee River approximately 8.4 km above the mouth of the Chiwawa River. A captive brood hatchery program was initiated by collecting eyed-eggs and alevins between 1999 and 2000 because of the precariously low abundance of adults (Hillman et al. 2020). In 2003, 36 adult captive broodstock were released into Nason Creek for natural spawning. In 2004 and 2005, 8,986 and 4,244 yearling smolts, respectively, were acclimated and released into Nason Creek. The captive broodstock program was discontinued after adult abundance increased.

A smolt supplementation program was initiated with adult collections in 2013 and the first yearling smolts were released from this program in 2015. Natural-origin adults were collected in Nason Creek for broodstock in 2013 and 2014. Since 2015, broodstock have been collected at Tumwater Dam, but most of these fish have been genetically assigned to the Chiwawa spawning aggregate, so very few Nason-origin broodstock have been used in the current supplementation program. The first adult females from the Nason Creek hatchery program returned to Nason Creek in 2017. Fish were spawned and reared at Eastbank Hatchery, similar to the Chiwawa River hatchery program. In the fall prior to release, fish were transferred to 30-foot-diameter, dual-drain circular tanks at the Nason Creek Acclimation Facility. Fish were released as yearlings in the spring when fish migration readiness, flows, and temperatures were acceptable.

In addition to the two hatchery programs in Nason Creek, a substantial number of strays from the Chiwawa River supplementation program have spawned in Nason Creek and strays have comprised over 50% of the spawners in some years (Pearsons and Miller 2021). In summary, the natural-origin offspring produced in Nason Creek are likely the result of natural-origin spawners and hatchery-origin spawners from the target hatchery programs in Nason Creek and strays from the Chiwawa hatchery program (Williamson et al. 2010).

White River Program

The White River spring Chinook Salmon captive brood program was initiated in 1997 as a risk aversion measure to prevent the extinction of, to conserve, and to aid in the recovery of the naturally spawning salmon population in the White River (Ford et al. 2015). The White River is approximately 51 km long, drains an area of 38,850 hectares, and flows directly into Lake Wenatchee. The first-generation (F1) component of the White River captive brood program was from eggs and fry collected in the White River (brood-years 1997-2009) and reared in a hatchery until spawning. The number of eggs or fry that were used for the first-generation component of the program (10,353 from 122 redds) represented at least 122 families although it was less than what would be produced from three average-sized females (average estimated fecundity/female is 4,669). The resulting progeny (F2) were then reared in a hatchery until final acclimation and released in the upper Wenatchee watershed. The first large number of juveniles was released in 2008, the last release occurred in 2015, and adults had the potential to return from juvenile releases until 2018.

The F1 and F2 rearing programs were initially located at the AquaSeed Corporation facility in Rochester, Washington. The resource managers decided to move the program to another facility because the quality of the F2 fish produced at AquaSeed was poor (e.g., poor fin quality). Transition of the programs to the Little White Salmon National Fish Hatchery (LWSNFH) near Cook, Washington began in May 2006 and was completed in February 2009.

To limit adverse domestication effects from the captive brood program, plans were to transition after two generations toa supplementation program based on broodstock captured as returning adults. Initial broodstock collections were well below program goals and disease issues limited production and release of F2 juveniles. The number of broodstock collected for the program increased dramatically in 2002 and became sufficient to meet F2 production goals. Because initial production was limited, it was decided to continue broodstock collections until 2010. As a result of this extension, broodstock collection approached or met program goals for eight consecutive years (2002-2009).

A variety of acclimation and release scenarios were conducted since 1997. Acclimation scenarios have involved naturalized features such as in-channel enclosures, stream-side tanks supplied with pass-through surface water, and net pens in Lake Wenatchee near the mouth of the White River. Release scenarios have included on-site releases from tanks, in-channel enclosures, and net pens in Lake Wenatchee. Net pens containing acclimated fish were towed to the mouth of the lake for releases during 2010, as well. Tank and net-pen acclimated fish have been loaded into transport trucks and released into the Wenatchee River (2011-2015), and direct releases of sub-yearlings and yearlings have also been conducted from a transport truck into Lake Wenatchee and the White River with no acclimation. A total of 944,591 juveniles were released between 2004 and 2015.

Methow-Chewuch Program

The Methow River is approximately 143 km long, drains an area of approximately 489,508 hectares, and enters the Columbia River at RKM 843. The Chewuch River is the largest tributary to the Methow River entering at RKM 80 at the town of Winthrop. It is approximately 80 km long and drains an area of 137,528 hectares. The hatchery program intended to supplement the Methow and Chewuch rivers and was initiated with broodstock collection in 1992. The first smolts were released in 1994, and the first hatchery fish returned in 1995. The Methow Hatchery is on the right bank of the Methow River at RKM 82, and approximately 2 km upstream from the mouth of the Chewuch River. Broodstock were collected at Fulton Dam at RKM 1.8 on the Chewuch River; Foghorn Dam at RKM 82.5 on the Methow River; Wells Dam at RKM 830 on the Columbia River, 13 km downstream from the mouth of the Methow River; or at the Methow Hatchery outfall. Broodstock were assigned to the Methow-Chewuch or Twisp spawning aggregates using genetic methods. Adult brood fish were spawned, incubated, and reared at the Methow Hatchery. Final acclimation in the spring occurred primarily at the Methow Hatchery or at an acclimation pond on the Chewuch River at RKM 13.3. However, in some years, a portion of the fish from the Methow Hatchery have been spring-acclimated and released by the Yakama Nation from remote ponds on small tributaries to the Methow River upstream from the Methow Hatchery, including one on Wolf Creek (RKM 88; broods 2002, 2008, and 2009), Mid-Valley Pond (RKM 90; broods 2010, 2011, and 2012), and Goat Wall Pond (RKM 117; broods 2015-2017).

Prior to brood year 2001, resource managers attempted to maintain genetic distinction between Chewuch and Methow production, releasing progeny of presumed Chewuch-origin adults (based on capture location or CWT) only to the Chewuch River, and likewise releasing progeny of presumed Methow-origin adults only to the Methow. However, beginning with brood year 2001, resource managers composited production of Methow and Chewuch stocks into the single Methow-Chewuch stock due to chronic difficulties collecting sufficient broodstock to maintain a distinct Chewuch program. The loss of trapping facilities at Fulton Dam in 2005 ended directed broodstock collection efforts in the Chewuch River. With the historic challenges obtaining natural-origin broodstock, the proportion of natural-origin fish used in the broodstock (pNOB) has varied under pressure from fisheries managers to maintain production targets.

The production goal for the Methow-Chewuch program for brood-years 1992 through 1997 was variable depending upon brood availability, with the nominal target of 500,000 yearling smolts. Releases ranged from 16,000 to 495,000 (mean, 223,000) yearling smolts, due to inconsistent broodstock-trapping efficiency at Fulton Dam on the Chewuch River and Foghorn Dam on the Methow River, and collection efforts at these locations were supplemented with collection at the Methow Hatchery outfall and Wells Dam beginning in 1996. Average pNOB during this period was 45% and ranged from zero to 79%.

For brood years 1998 through 2011, the nominal production goal was 366,000 yearling smolts. However, with consistent shortfalls in brood collection in the Twisp River, resource managers compensated for resultant shortfalls in Twisp smolt production by increasing production in the Methow-Chewuch program commensurate with the Twisp shortfall in each brood year. Smolt production for the Methow-Chewuch program averaged 357,000 (range, 196,000-498,000) yearling smolts for brood years 1998-2011. Average pNOB during this period was 19% and ranged from zero to 58%. Since brood year 2012, the production goal of 193,000 yearling smolts has been consistently achieved, and pNOB has averaged 71% (range 30% to 99%).

All spring Chinook Salmon produced for the Methow-Chewuch program were marked with CWTs, and prior to brood year 2000, were also adipose-fin clipped. For brood years 1992-2017, annual CWT mark rate ranged from 88-100 percent. A portion of the releases were also PIT tagged prior to release in 2003, 2004, and every year since 2010.

Twisp River Program

The Twisp River is a major tributary to the Methow River entering at RKM 66. It is approximately 62 km long and drains an area of about 63,714 hectares. The hatchery program intended to supplement the Twisp River spawning aggregate, was initiated with broodstock collection in 1992, and was implemented in a similar manner as the Methow-Chewuch program. Broodstock were collected at a trap in the Twisp River or at Wells Dam with subsequent genetic identification to the Twisp River. Adult brood fish were spawned, incubated, and reared at the Methow Hatchery. Final acclimation in the spring occurred at an acclimation pond on the Twisp River at RKM 11.5.

The nominal production goal for the Twisp River program for brood-years 1992 through 1997 was 250,000 yearling smolts (average pNOB of 65%; range zero to 100%). For brood years 1998 through 2011, the nominal production goal was 183,000 yearling smolts (average pNOB of 34%; range zero to 75%). Since brood year 2012, the production goal has been 30,000 yearling smolts (average pNOB of 74%; range 41% to 100%).

To maintain genetic distinction between the Twisp River spawning aggregate and the Methow-Chewuch composite aggregate, resource managers limited broodstock for the Twisp River program to either natural- or hatchery-origin fish from the Twisp River. Difficulty in obtaining Twisp-origin brood resulted in consistent brood limitation for the Twisp River program. Thus, annual smolt production averaged approximately 52,000 (range zero to 116,000) over the life of the program, with consistent production of approximately 30,000 smolts beginning with brood year 2012. All spring Chinook Salmon produced for the Twisp program were marked with CWTs, and prior to brood year 2000, were also adipose-fin clipped. For brood years 1992-2017, annual CWT mark rate ranged from 94-100 percent. A portion of the releases were also PIT tagged prior to release in 2003, 2004, and every year since 2010.

In 1996 and 1997, resource managers implemented a captive brood program for the Twisp spawning aggregate by vacuuming a small number of eggs from redds from naturally spawning fish in the Twisp River. Subsequent brood years through 2002 reserved 45 eggs from each crossing of Twisp broodstock for the captive brood program (goal of 30 families). Incubation and initial rearing occurred at Methow Hatchery for the 1996 and 1997 broods, but progeny from subsequent brood years were reared at the AquaSeed Corporation facility in Rochester, Washington. The captive brood program contributed little to total annual smolt production for the Twisp River program, and captive production ended with the release of F2 smolts that were progeny of F1 adults from eggs collected from adults returning to the Twisp River in 2002.

Data Collection and Derived Metrics

Spring Chinook Salmon spawning ground surveys have been conducted since at least 1981 within the Wenatchee and Methow subbasins to determine the abundance, distribution, and origin of spring Chinook Salmon spawners. Field methods were consistent with those described in Gallagher et al. (2007) and Murdoch et al. (2010). Surveyors walked or floated the entire distribution of spring Chinook Salmon spawning habitat and identified and counted new redds weekly throughout the spawning season. Redds were flagged and locations recorded on a Global-Positioning-System device to avoid recounting in subsequent surveys. Chinook Salmon carcasses were also counted and examined to determine sex, origin (e.g., hatchery or natural origin; nearly all hatchery-origin fish were marked with a tag such as a CWT and/or adipose fin clipped prior to release), size, distribution, and other biological characteristics. In addition, scales collected from carcasses were used to determine fish age and origin.

We expanded spawning ground data into derived estimates of total adult abundance (combined hatchery- and natural-origin adults), natural-origin spawners (NOS) abundance, natural-origin adult recruits (NOR) abundance, adult-to-adult productivity, and adjusted adult-to-adult productivity. The latter productivity was adjusted based on population carrying capacity (described below). We assumed that each female made one redd (Murdoch et al. 2009a), female carcass location was a good surrogate for spawning location by origin (Murdoch et al. 2009b), and that redd counts and carcass data could be used to estimate spawning escapement for hatchery- and natural-origin Chinook Salmon (Murdoch et al. 2010). Total adult spawning abundance was estimated by multiplying redd counts by the male:female sex ratio estimated at Tumwater Dam (for Wenatchee programs) or at Wells Dam (for Methow programs). Natural-origin adult recruits were estimated by summing all adults produced from a brood year including adult spawners, hatchery broodstock, and harvest. Natural-origin spawners were estimated by multiplying the proportion of natural-origin carcasses by the total adult spawning abundance. Productivity was calculated by dividing the natural-origin adult recruits by the total number of spawners for each cohort. A density-adjusted estimate of productivity was calculated by assigning the productivity value at carrying capacity to brood years that exceeded the minimum estimated spawner abundance necessary to generate the asymptotic number of adult recruits as modelled using the Smooth Hockey Stick stock-recruitment function (Froese 2008). We used natural logarithms to transform recruitment data to satisfy modeling assumptions.

Finally, we evaluated whether adult productivity estimates were higher in hatchery or natural environments. Natural replacement rates (NRRs; natural-origin productivity) were calculated as the ratio of natural-origin recruits (NOR) to the parent spawning population (spawning escapement). Natural-origin recruits were naturally produced fish that survived to contribute to harvest, to broodstock, and to spawning grounds. Hatchery replacement rates (HRRs) were the hatchery adult-to-adult returns and were calculated as the ratio of hatchery-origin recruits (HOR) to the parent broodstock collected. Both NOR and HOR included fish that spawned naturally, fish harvested, and fish used as broodstock in hatchery programs. A paired-sample T-test evaluated the hypothesis that there was no difference between mean HRR and NRR. In addition, annual HRRs were compared to HRRs targets established by the managers of the hatchery programs.

Selection of Reference Streams for BACIP and MBACI(P) Analyses

Reference streams and their associated fish populations are an important component of an effectiveness monitoring program because they provide the standard to which treatment conditions are compared (ISRP and ISAB 2005; Galbreath et al. 2008). Selecting appropriate reference streams and maintaining them over long periods of time is needed to assess the effectiveness of supplementation programs using BACIP and MBACI(P) analyses. Ideal reference streams possess biotic and abiotic characteristics similar to that of the supplemented streams. We developed a three-step process for identifying suitable reference streams for use in evaluating the effectiveness of hatchery supplementation programs. Each step served as a filter. That is, potential reference streams were evaluated based on specific criteria under each step. Streams that pass through each step were considered suitable references for specific supplemented streams. Based on the work of Galbreath et al. (2008), we began with a pool of 25 potential reference populations.

The first step in selecting suitable reference populations included comparing general attributes of both supplemented and reference populations. Attributes included 1) no or few hatchery-origin spawners in the reference stream (proportion of hatchery-origin spawners (pHOS) less than 10%), 2) similar life-history characteristics (similar run timing, age structure, and spawn timing), 3) similar out-of-basin effects (similar migration and ocean survivals), 4) similar trends in freshwater habitat, 5) harvest estimates available for adjusting escapements, and 6) a long time series of natural-origin abundance and productivity estimates. We supplemented information in Galbreath et al. (2008) with data from the Yakama Nation, Nez Perce Tribe, NOAA Fisheries Salmon Population Database, Coordinated Assessments Data Exchange Standard database, and recovery plans. Reference streams with high (>10%) pHOS, no harvest data, or short time series were excluded from further consideration.

Reference streams that were deemed similar to supplemented populations based on Step 1 attributes where then evaluated for similar trends and synchronicity during the pre-supplementation period. Abundance, NOS, NOR, and productivity data were transformed with natural logarithms and compared graphically to evaluate trends and synchronicity between reference and supplemented streams before supplementation. In addition to graphic analysis, we calculated the Pearson correlation coefficient, which is an index of the strength of the association between reference and supplemented streams, and compared trends using analysis of covariance. Although there is some redundancy in these methods, in concert they allowed us to evaluate trends, fluctuations, and synchronicity between reference and supplemented streams prior to supplementation, and they improved precision of final analyses. As a final exercise under Step 2, we conducted power analyses to determine minimum differences that could be detected when comparing reference streams to supplemented streams. Because our study used BACIP and MBACI(P) designs, which includes replication before and after supplementation in both the supplemented and reference streams, we calculated difference scores using natural-log transformed data (Stewart-Oaten et al. 1992; Smith et al. 1993). We calculated minimal detectable differences assuming the use of an independent two-sample t-test with a type-I error rate of 0.05, power of 0.80 (beta or type-II error rate of 0.20), and sample sizes (supplementation years) evaluated at five-year increments out to 100 years during supplementation. Our objective here was to find reference populations with the lowest minimal detectable differences.

During the final step in selecting suitable reference streams, we developed a method to quantify and rank potential reference streams. In order to reduce subjectivity, we developed a method of scoring and weighting selection criteria. For consistency, criteria were scored from 0 to 1, with 0 being the worst possible score and 1 being the best. We also weighted each criterion. For example, Step 1 attributes, especially proportion of hatchery-origin spawners, were assigned higher weights than statistical attributes (e.g., graphic analysis, correlation, and trends). We calculated a total score for each reference population by multiplying the estimated value, which ranged from 0 to 1, by its weight. The sum of the weighted values provided a total score that ranged from 0 to 100. Based on several simulations, we set the cut-off score at 80. That is, if the total score for a given reference stream exceeded 80, the population was included as a suitable reference. If the total score was equal to or less than 80, the stream was not considered a suitable reference.

Using the three-step process, we identified six reference streams for each of the supplemented streams: Naches River, American River, Marsh Creek, Secesh River, Bear Valley Creek, and Big Creek. There were no reference streams in the upper Columbia Region that satisfied the criteria mainly because most were supplemented and those that were not supplemented had a high proportion of hatchery-origin strays in the spawning population.

Data Analysis

We made comparisons between supplemented and reference streams using BACIP and MBACI(P) analyses (Stewart-Oaten and Bence 2001; Downes et al. 2002; Pearsons and Temple 2010; Chevalier et al. 2019). The objective of the comparison of supplemented to reference streams was to determine whether the addition of a hatchery supplementation treatment increased the total spawning abundance, NOS abundance, NOR abundance, and adult-to-adult productivity metrics described above. The after period for total spawning abundance was defined as the period after age-3 hatchery-origin adults returned from the first broodstock collections. The after period for NOS, NOR, and productivity metrics was defined as three years after the first age-4 hatchery-origin females spawned in the natural environment. For example, if the first broodstock for a program was collected in 1989, the after period would begin in 1992 for total spawning abundance and in 1996 for NOS, NOR, and productivity. Because supplementation programs began at different times, before and after periods differed among programs; the analyses includes adults returns up to 2018 (Table 1). For the Chiwawa, Methow-Chewuch, and Twisp programs, we did not evaluate the effects of reduced hatchery smolt production on population metrics because the period following smolt reduction was too short to evaluate adequately. Thus, in our analyses, the supplementation (after) period included years both before and after reduction in smolt production and was considered as a single adaptively managed program.

Table 1. Year of initiation of Spring Chinook Salmon supplementation programs, years before and during supplementation periods for different population metrics, and year of reduction in hatchery production; NOS = natural-origin spawners, NOR = natural-origin adult recruits, and Prod = adult-to-adult productivity. The analyses includes adult returns up to 2018.

Hatchery program	**First year of broodstock collection**	**Population metric**	**Before supplementation period**	**Beginning of supplementation period**	**Year programs were reduced**	**Supplementation period before reduction**	**Supplementation period after reduction**
Chiwawa	1989	Abundance	≤1991	1992	2012[1]	1992-2014	2015-present
		NOS, NOR, Prod	≤1995	1996		1996-2018	2019-present
Nason[2]	--	Abundance	≤2000	2001	--	--	--
		NOS, NOR, Prod	≤2004	2005		--	--
White	1997	Abundance	≤2007	2008	2015 (program ended)	2008-2017	2018-present
		NOS, NOR, Prod	≤2011	2012		2012-2022	2023-present
Twisp	1992	Abundance	≤1994	1995	2012	1995-2014	2015-present
		NOS, NOR, Prod	≤1998	1999		1999-2018	2019-present
Methow-Chewuch	1992	Abundance	≤1994	1995	2012	1995-2014	2015-present
		NOS, NOR, Prod	≤1998	1999		1999-2018	2019-present

[1] Chiwawa River hatchery smolt production was reduced continually over the period 2010-2013. We selected 2012 as the break point between periods.

[2] The first 4-year old adults from the current Nason Creek supplementation program returned in 2017.

As described above, Nason Creek has received large numbers of hatchery strays from the Chiwawa Program, experienced a short-term captive brood program, and is currently being supplemented under the Nason Creek Supplementation Program. Because of the short timeline during which these events have occurred, we were unable to examine individual treatment effects on spring Chinook Salmon abundance, NOS, NOR, and productivity in Nason Creek. As a result, we examined the cumulative effects of the captive brood program, supplementation program, and hatchery straying on Nason Creek spring Chinook Salmon. The treatment (after) period began in 2001 with the large number of hatchery strays spawning in Nason Creek. The after period for NOS, NOR, and productivity began in 2005 (Table 1).

In addition to evaluating each supplemented stream separately, we also evaluated the effects of supplementation programs on spring Chinook Salmon within the entire Wenatchee and Methow subbasins. For the Wenatchee subbasin, the Chiwawa program set the evaluation time periods because it was the largest and earliest supplementation program in the Wenatchee subbasin. In the Methow subbasin, the Methow-Chewuch and Twisp programs began at the same time and set the evaluation time periods for that subbasin.

To evaluate the effect of the supplementation programs, we calculated three BACI metrics: BACI Contrast (effect), Control Impact (CI)-contribution, and CI-divergence (Chevalier et al. 2019). The formulas to calculate the metrics were:

BACI Contrast = $(\mu_{TA} - \mu_{TB}) - (\mu_{CA} - \mu_{CB})$

CI-contribution = $|\mu_{TA} - \mu_{TB}| - |\mu_{CA} - \mu_{CB}|$

CI-divergence = $|\mu_{TA} - \mu_{CA}| - |\mu_{TB} - \mu_{CB}|$

where μ is the mean, T is treatment (supplemented), C is control (reference), A is after (period of supplementation), and B is before (period before supplementation). Evaluation of a combination of BACI metrics contributes to an understanding of why BACI contrast values differ (Chevalier et al. 2019).

In this evaluation, we interpret a significant ($P \leq 0.05$) BACI Contrast value as an indication that the dependent variable (e.g., NOS) has become significantly different in the supplemented stream relative to the reference stream between the before and after time periods. A significant positive value indicates that the dependent variable has increased more (or decreased less) in the supplemented stream than the reference stream, and a significant negative value indicates that the dependent variable decreased more (or increased less) in the supplemented stream than the reference stream (Chevalier et al. 2019). For BACIP evaluations, we tested differences between paired supplemented and reference streams using an Aspin-Welch unequal-variance test. This test evaluated the hypothesis that the mean difference before supplementation equals the mean difference during supplementation. This test was conducted separately for each pair of supplemented and reference streams. In addition, for MBACI(P) evaluations, we used a mixed-model analysis of variance (ANOVA) to compare each of the supplemented streams to the combined reference streams (Downes et al. 2002). Using ANOVA, we evaluated two sources of variation: 1) BACI contrast and 2) short-term effects of supplementation (here a significant interaction indicates there was a short-term change following supplementation, but the effect did not last). All analyses were conducted on natural-log-transformed data. In total, this work resulted in the calculation of 192 Aspin-Welch tests and 32 ANOVA tests. We did not adjust the value for significance ($P \leq 0.05$) based on the large number of tests conducted. Rather, we reported the actual P-value for each test.

Following the BACI Contrast evaluations, the relationship between supplemented and reference streams was further evaluated using a CI-contribution value and CI-divergence value (Chevalier et al. 2019). The CI-contribution value was used to identify which stream (supplemented or reference) is making the larger contribution to the change from the before to the after period. The sign (negative or positive) of the CI-contribution value indicates which stream has changed more between the before and after period. For example, a positive value indicates that the observed difference in the BACI Contrast was largely attributable to changes in the supplemented stream, whereas a negative value indicates that the difference was largely attributable to changes in the reference stream. The CI-divergence value was used to indicate the change in similarity or dissimilarity between the supplemented and reference streams from the before to the after period. A positive value indicates that the two streams were more different in the after period than the before (i.e., diverged), whereas a negative value indicates that the supplemented and reference streams were more similar in the after period than the before period (i.e., converged).

Power Analysis

Power analyses were conducted to determine the length of time that is needed to detect different effect sizes in BACI contrasts. This analysis calculates the minimum detectable difference between mean difference scores (Treatment-Control) before and after treatment and was a different analysis than the one that was done to evaluate the suitability of reference streams describe above. The variance estimates during the pretreatment period and post-treatment period were used to calculate minimum detectable differences. The null hypothesis to be tested was that the mean difference before treatment equals the mean difference after treatment. The alternative hypothesis is that the mean difference before treatment is different than the mean difference after treatment (two-tail test). This analysis assumes that mean difference scores will be compared using an independent t-test with an alpha of 0.05, beta of 0.20, and sample sizes (post-treatment years) of 5 to 100 by 5.

Many other analyses specified in the monitoring and evaluation plan (Hillman et al. 2019) were conducted but were not presented here because of the redundancy of test results and complexity of presentation. Additional statistical tests supported the conclusions in this study. In addition, we show results only for adjusted productivity because analyses of productivity and adjusted productivity resulted in the same conclusions and were redundant. We prioritized simplicity and statistical power in this report in order to distill the main findings of the analysis. The full suite of analyses is available upon request.

Results

Comparison of Hatchery- and Natural-Origin Replacement Rates

The mean HRR was higher than the mean NRR for three of the hatchery programs and lower in the captive broodstock program (Table 2). The mean HRR was 7.0, 1.6, and 2.9 times higher than the mean NRR in the Chiwawa, Twisp, and Methow-Chewuch, respectively. Statistically, however, there was little difference in mean HRR and NRR for the Twisp (Table 2). The mean HRR was 0.04 times lower than the mean NRR in the White River.

During most years, HRRs were greater than or equal to NRRs for all programs except the White River captive broodstock program (Table 2). At no time did the HRRs exceed or equal the NRRs for the White River program. The Chiwawa, Twisp, and Methow-Chewuch HRRs exceeded or equaled the HRR targets for those programs 40-55% of the time (Table 2). The White River HRRs never equaled or exceeded the HRR target for that program.

Table 2. Adult spring Chinook Salmon natural replacement rates (NRR) and hatchery replacement rates (HRR), statistical comparisons between mean NRR and HRR, and comparisons of annual HRR to NRR and HRR to target HRR for supplementation programs in the Upper Columbia Basin. The Nason Creek supplementation program, which began with collection of broodstock in 2013, is not shown because analysis of effects of the supplementation program on Nason Creek spring Chinook Salmon NRR and HRR do not begin until 2020.

Program/Stock	**Number of years of data**	**Mean NRR**	**Mean HRR**	**Paired-sample T-test**		**No. yrs HRR≥NRR**	**HRR target**	**No. yrs HRR≥Target**	**No. yrs HRR<Target in last 5 yrs**
				t-value	**P-value**				
Chiwawa	22	1.10	7.75	5.979	0.000	21	6.7	12	1
White	7	1.08	0.05	-2.712	0.035	0	6.7	0	5
Twisp	20	2.09	3.24	1.195	0.247	16	2.7	8	2
Methow-Chewuch	21	1.63	4.71	2.836	0.010	19	3.8	11	0

MBACI(P) and BACIP Analyses

We present results at both the program scale (e.g., Chiwawa River Program) and at the population (sub-basin) scale. We present results for each population metric except productivity. That metric was highly correlated with adjusted productivity and in all cases the sign of all BACI metrics were the same for both adjusted and unadjusted productivity (Appendix 1). In most cases, the P-values for the BACI contrasts were smaller for adjusted productivity than for unadjusted productivity; however, there were generally no large disparities between P-values for adjusted and unadjusted productivities. For each program, we first present results based on MBACI(P) analysis and then report results based on BACIP analysis.

Chiwawa River Program

MBACI(P) Analysis—For the Chiwawa supplementation program, all MBACI contrasts were negative; however, only NOS was significant (MBACI Contrast = -1.074; P = 0.009) (Table 3). Both NOS and NOR showed significant short-term supplementation effects. Total spawners and NOS changed more in the Chiwawa than in reference areas between the before and after periods, while the opposite occurred for NOR and adjusted productivity. Mean scores for total spawners, NOS, and NOR between the supplemented and reference areas converged over time. In contrast, mean scores for adjusted productivity between the supplemented and reference areas diverged over time.

BACIP Analysis—Mean total spring Chinook Salmon spawners within the Chiwawa River decreased from the before to after period, while mean total spawners within most reference areas decreased or increased slightly (Figure 2a). Likewise, mean NOS decreased from the before to after period in the Chiwawa River, while mean NOS increased slightly in all reference areas (Figure 2a). BACI contrasts for total spawners were all negative but only two of the six were significant. Similarly, BACI contrasts for NOS were all negative and four of the six contrasts were significant. Both mean NOR and adjusted productivity increased in the Chiwawa River and reference areas from the before to after period (Figure 2b). Although BACI contrasts for NOR and adjusted productivity were negative for all comparisons, none were significant for NOR and only two of the six were significant for adjusted productivity.

Nason Creek Program

MBACI(P) Analysis—For Nason Creek, all MBACI contrasts were negative but only NOS was significant (MBACI Contrast = -1.142; P = 0.018) (Table 3). There were no significant short-term supplementation effects on population metrics in Nason Creek. NOS and adjusted productivity changed more in Nason Creek than they did in reference areas between the before and after periods. In contrast, total spawners and NORs changed more in the reference areas than they did in Nason Creek. Mean scores for all population metrics between the supplemented and reference areas diverged over time. (Table 3).

BACIP Analysis—Mean total spring Chinook spawners increased from the before to the after period in Nason Creek and the reference areas (Figure 3a). None of the BACI contrasts were significant for total spawners. Mean NOS, on the other hand, decreased from the before to the after period in Nason Creek, while mean NOS increased or remained unchanged in the reference areas during the same period. All of the BACI contrasts for NOS were negative and significant. Mean NOR increased from the before to the after period in Nason Creek and the reference areas (Figure 3b). Five of the six BACI contrasts for NOR were negative and three of those were significant. In contrast, adjusted productivity declined in Nason Creek from the before to after period but increased in the reference areas. All six BACI contrasts for adjusted productivity were negative and significant.

White River Program

MBACI(P) Analysis—Because of the initiation time of the White River captive brood program, data are only available for total spring Chinook Salmon spawners and NOS. For this program, all MBACI contrast were negative but none were significant (Table 3). There were, however, significant short-term supplementation effects. Although both population metrics changed more in the reference areas than in Nason Creek, mean total spawner scores between the supplemented and reference areas converged over time, while mean NOS scores diverged over time.

BACIP Analysis—Mean total spring Chinook salmon spawners increased from the before to after period in the White River and reference areas (Figure 4). Four of the six BACI contrasts for total spawners were negative and two were significant. Mean NOS decreased from the before to after period in the White River; mean NOS changed little or increased in the reference areas (Figure 4). Five of the six BACI contrasts for NOS were negative and three were significant.

Wenatchee Sub-basin

MBACI(P) Analysis—At the scale of the Wenatchee Sub-basin, all MBACI contrasts were negative; however, only NORs and adjusted productivity were significant (Table 3). There were no significant short-term supplementation effects for any of the population metrics. Total spawners changed more in the Wenatchee Sub-basin than in reference areas between the before and after periods, while the opposite occurred for NOS, NOR, and adjusted productivity. Mean scores for total spawners and NOS between the supplemented and reference areas converged over time. In contrast, mean scores for NOR and adjusted productivity between the supplemented and reference areas diverged over time.

BACIP Analysis—At the population scale, mean total spring Chinook Salmon spawners decreased from the before to after period in the Wenatchee Sub-basin, while mean total spawners within reference areas decreased or increased slightly (Figure 5a). BACI contrasts for total spawners were all negative; however, only two were significant. In contrast, mean NOS increased from the before to after period in both the Wenatchee Sub-basin and reference areas. Although BACI contrasts were all negative for NOS, none were significant. Both mean NOR and adjusted productivity changed little in the Wenatchee Sub-basin from the before to after period, while both population metrics increased in reference areas during the same period (Figure 5b). BACI contrasts for both NOR and adjusted productivity were all negative; four of the six comparisons for NOR were significant and five of the six comparisons for adjusted productivity were significant.

Methow-Chewuch Program

MBACI(P) Analysis—For the Methow-Chewuch supplementation program, all MBACI contrasts were negative but only adjusted productivity was significant (MBACI Contrast = -0.559; P = 0.010) (Table 3). Both NOS and NOR showed significant short-term supplementation effects. Adjusted productivity changed more in the supplemented area than it did in reference areas between the before and after periods. The opposite occurred for total spawners, NOS, and NOR. Mean scores for total spawners and NOR between the supplemented and reference areas converged over time. In contrast, mean scores for NOS and adjusted productivity between the supplemented and reference areas diverged over time.

BACIP Analysis—Mean total spring Chinook salmon spawners within the Methow and Chewuch rivers decreased slightly from the before to after period, while mean total spawners within reference streams decreased or increased slightly over the same period (Figure 6a). All BACI contrasts for total spawners were negative but only two were significant. Mean NOS increased in both the supplemented and reference areas with three comparisons having negative BACI contrasts and three with positive BACI contrasts (Figure 6a). However, none of the NOS comparisons were significant. Both mean NOR and adjusted productivity decreased in the Methow and Chewuch rivers from the before to after period, while those same metrics in the reference areas generally stayed the same or increased slightly during the same period (Figure 6b). All BACI contrasts for NOR were negative with two of the six contrasts being significant. Likewise, all BACI contrasts for adjusted productivity were negative; however, all were significant.

Twisp River Program

MBACI(P) Analysis—For the Twisp River, all MBACI contrasts were negative and total spawners, NOR, and adjusted productivity were significant (Table 3). Both NOS and NOR showed significant short-term supplementation effects. Total abundance, NOR, and adjusted productivity changed more in the Twisp River than they did in reference areas between the before and after periods. In contrast, NOS changed more in the reference areas than in the Twisp River over time. Mean scores for all population metrics between the Twisp River and reference areas diverged over time.

BACIP Analysis—Mean total spring Chinook Salmon spawners decreased during the before to after period in the Twisp River, while those in reference streams changed little or increased slightly during the same period (Figure 7a). All BACI contrasts for total spawners were negative and five of the six contrasts were significant. On the other hand, mean NOS increased in both the Twisp River and reference areas between the before and after period (Figure 7a). Although all BACI contrasts for NOS were negative, none were significant. Both mean NOR and mean adjusted productivity decreased within the Twisp River from the before to after period, while those same metrics generally changed little or increased slightly in reference areas during the same period (Figure 7b). All BACI contrasts for both NOR and adjusted productivity were negative; five of the six NOR comparisons were significant and all six adjusted productivity comparisons were significant.

Methow Sub-basin

MBACI(P) Analysis—At the scale of the Methow Sub-basin, all MBACI contrasts were negative; however, only NOR and adjusted productivity were significant (Table 3). Both NOS and NOR showed significant short-term supplementation effects. Total spawners and adjusted productivity changed more in the Methow Sub-basin than they did in reference areas between the before and after periods, while the opposite occurred for NOS and NOR. Mean scores for total spawners and NOR between the Methow Sub-basin and reference areas converged over time. In contrast, mean scores for NOS and adjusted productivity between the Methow Sub-basin and reference areas diverged over time.

BACIP Analysis—At the population scale, mean total spring Chinook Salmon spawners decreased during the before to after period in the Methow Sub-basin, while those in reference streams changed little or increased slightly during the same period (Figure 8a). All BACI contrasts for total spawners were negative but only two of the six contrasts were significant. Unlike total spawners, mean NOS increased in the Methow Sub-basin and reference areas between the before and after period (Figure 8a). None of the BACI contrasts for NOS were significant. Both mean NOR and mean adjusted productivity decreased within the Methow Sub-basin from the before to after period, while those same metrics generally changed little or increased slightly in reference areas during the same period (Figure 8b). All BACI contrasts for both NOR and adjusted productivity were negative; four of the six NOR comparisons were significant and all six adjusted productivity comparisons were significant.

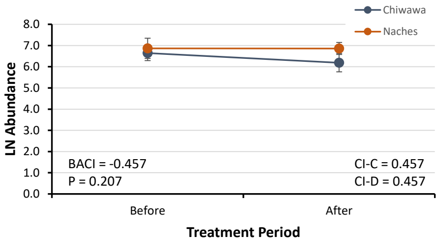
Power Analyses

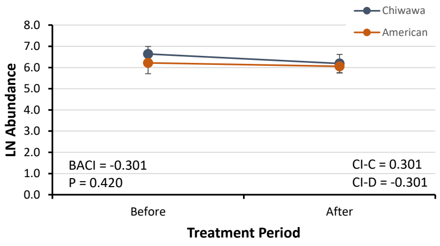
There was considerable annual variation in abundance and productivity in both supplemented and reference streams. This variation influenced the statistical power of our tests. The size of BACI contrasts that could be detected using statistical power analysis was variable among reference streams; however, minimum detectable differences stabilized about 10-20 years after initiation of supplementation, which was within or beyond the timeframe of this evaluation (Figure 9). The number of years where supplementation effects were evaluated included: abundance and NOS in the Wenatchee = 27 years (1992-2018); productivity and NOR in the Wenatchee = 17 years (BY 1996-2012); abundance and NOS in the Methow = 24 years (1995-2018); and productivity and NOR in the Methow = 14 years (BY 1999-2012).

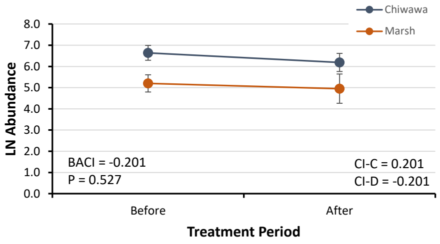
Table 3. Mixed-model analysis of variance results for MBACI(P) design. P-values and BACI metrics are shown for each population metric and supplemented stream. Sources of variation include BACI contrast (Treatment x Period interaction) and short-term effects (Treatment x Time(Period) interaction). Population metrics include total spawners, number of natural-origin spawners (NOS), number of natural-origin recruits (NOR), and adjusted productivity (productivity adjusted for carrying capacity).

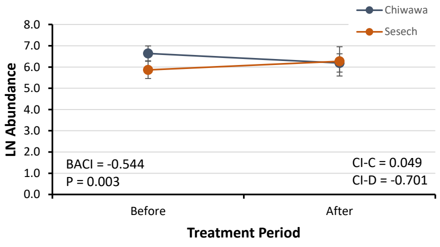
Supplemented stream	Population metric	Source of variation	P-value	BACI contrast	CI-contribution	CI-divergence
Chiwawa River	Total Spawners	Treatment x Period	0.152	-0.555	0.349	-0.555
		Treatment x Time(Period)	0.341			
	NOS	Treatment x Period	0.009	-1.074	0.104	-0.004
		Treatment x Time(Period)	0.006			
	NOR	Treatment x Period	0.075	-0.686	-0.686	-0.016
		Treatment x Time(Period)	0.023			
	Adj Productivity	Treatment x Period	0.097	-0.337	-0.337	0.337
		Treatment x Time(Period)	0.721			
Nason Creek	Total Spawners	Treatment x Period	0.585	-0.231	-0.231	0.231
		Treatment x Time(Period)	0.667			
	NOS	Treatment x Period	0.018	-1.142	0.255	1.142
		Treatment x Time(Period)	0.240			
	NOR	Treatment x Period	0.365	-0.627	-0.627	0.627
		Treatment x Time(Period)	0.304			
	Adj Productivity	Treatment x Period	0.081	-0.522	0.103	0.522
		Treatment x Time(Period)	0.419			
White River	Total Spawners	Treatment x Period	0.404	-0.415	-0.415	-7.891
		Treatment x Time(Period)	0.021			
	NOS	Treatment x Period	0.175	-0.643	-0.164	0.643
		Treatment x Time(Period)	0.005			
Wenatchee River sub-bain	Total Spawners	Treatment x Period	0.137	-0.580	0.375	-0.580
		Treatment x Time(Period)	0.915			
	NOS	Treatment x Period	0.318	-0.596	-0.596	-0.596
		Treatment x Time(Period)	0.992			
	NOR	Treatment x Period	0.017	-0.994	-0.994	0.994
		Treatment x Time(Period)	0.572			
	Adj Productivity	Treatment x Period	0.049	-0.412	-0.399	0.412
		Treatment x Time(Period)	0.731			
Methow-Chewuch rivers	Total Spawners	Treatment x Period	0.255	-0.370	-0.055	-0.370
		Treatment x Time(Period)	0.095			
	NOS	Treatment x Period	0.727	-0.151	-0.151	0.151
		Treatment x Time(Period)	0.004			
	NOR	Treatment x Period	0.055	-0.772	-0.305	-0.111
		Treatment x Time(Period)	0.004			
	Adj Productivity	Treatment x Period	0.010	-0.559	0.540	0.559
		Treatment x Time(Period)	0.514			
Twisp River	Total Spawners	Treatment x Period	0.020	-0.944	0.519	0.944
		Treatment x Time(Period)	0.451			
	NOS	Treatment x Period	0.174	-0.646	-0.646	0.646
		Treatment x Time(Period)	0.020			
	NOR	Treatment x Period	0.005	-1.362	0.286	1.362
		Treatment x Time(Period)	0.003			
	Adj Productivity	Treatment x Period	0.003	-0.733	0.714	0.419
		Treatment x Time(Period)	0.590			
Methow River sub-basin	Total Spawners	Treatment x Period	0.162	-0.466	0.041	-0.466
		Treatment x Time(Period)	0.198			
	NOS	Treatment x Period	0.573	-0.246	-0.246	0.246
		Treatment x Time(Period)	0.013			
	NOR	Treatment x Period	0.036	-0.864	-0.213	-0.720
		Treatment x Time(Period)	0.026			
	Adj Productivity	Treatment x Period	0.008	-0.585	0.566	0.312
		Treatment x Time(Period)	0.523			

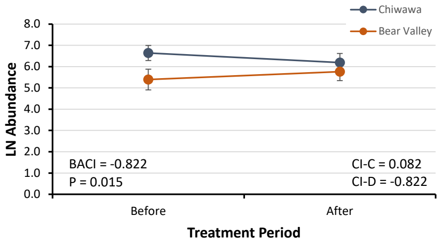
Total Spawners

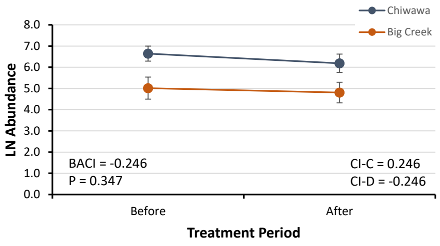




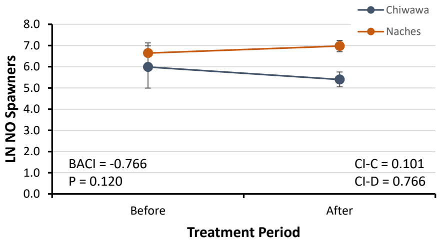


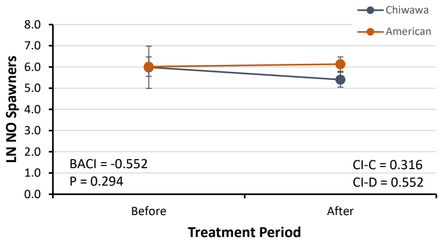


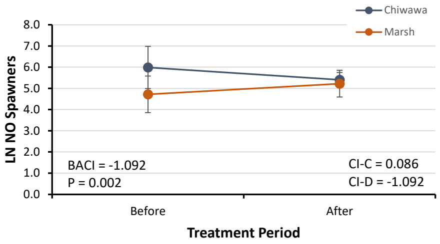


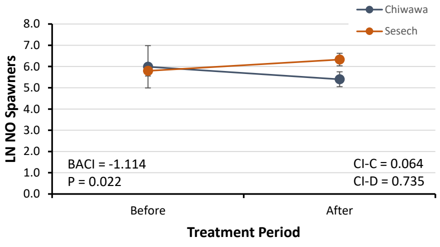


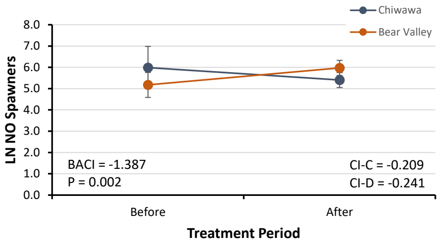
NOS











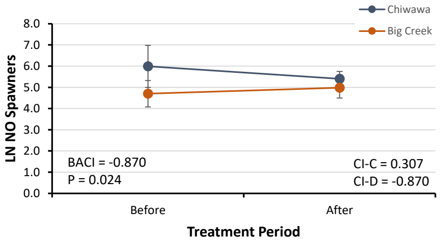
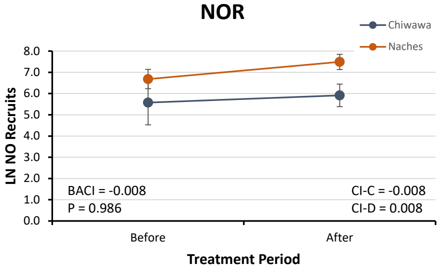
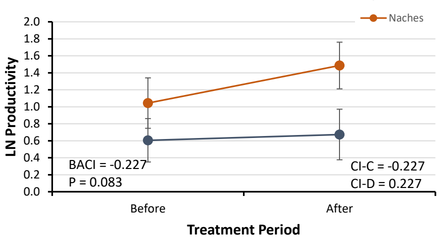


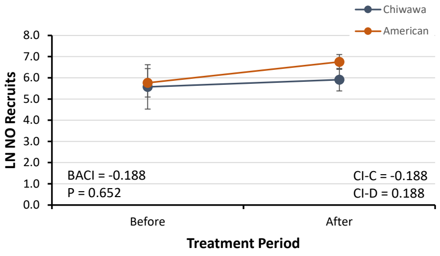
Figure 2a. Comparisons of mean total spawning abundance and natural-origin spawners (NOS) (with 95% CI) before and after hatchery supplementation of spring Chinook Salmon in the Chiwawa River and in reference streams. Graphs include BACI contrasts and their significance (P-values based on Aspin-Welch test), CI-contribution values, and CI-divergence values.

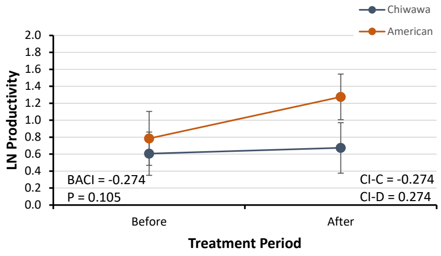
NOR

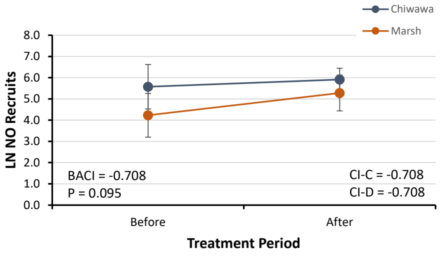
Adj Productivity

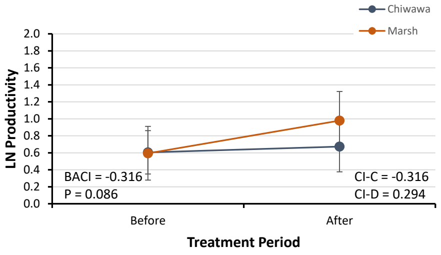


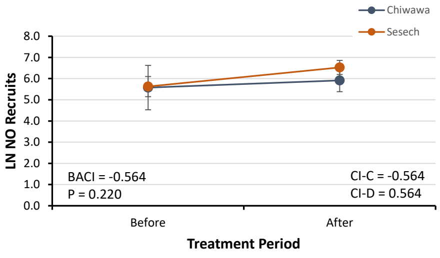


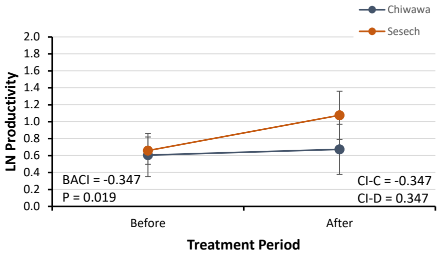


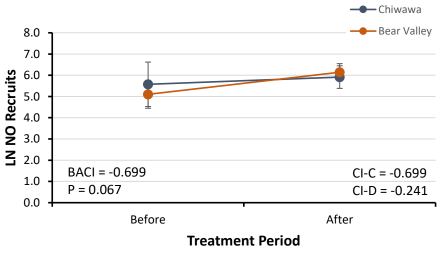


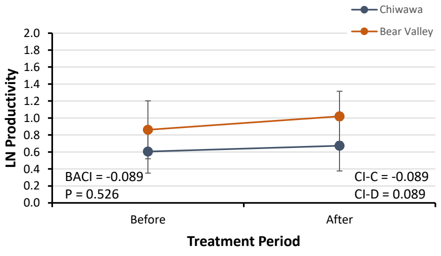


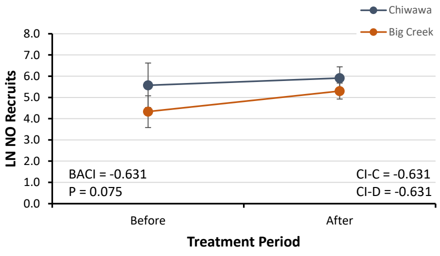












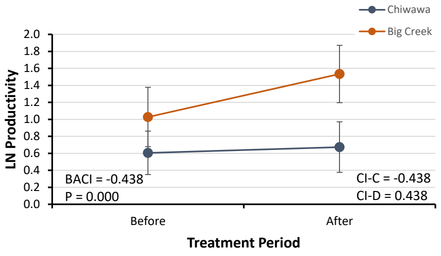
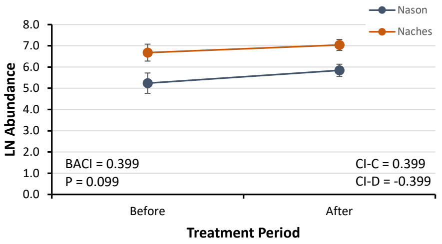
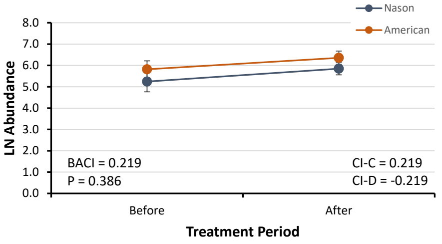
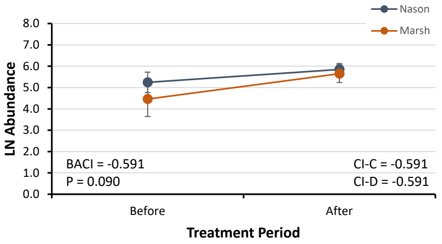


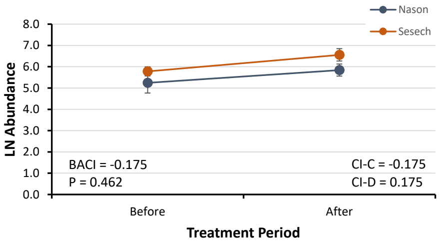
Figure 2b. Comparisons of mean natural-origin recruits (NOR) and adjusted productivity (with 95% CI) before and after hatchery supplementation of spring Chinook Salmon in the Chiwawa River and in reference streams. Graphs include BACI contrasts and their significance (P-values based on Aspin-Welch test), CI-contribution values, and CI-divergence values.

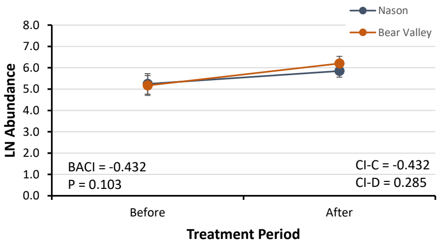
Total Spawners

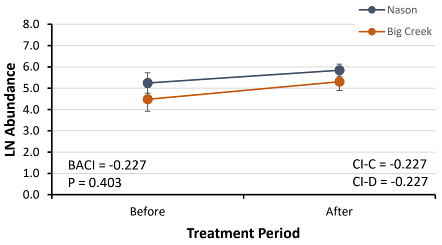




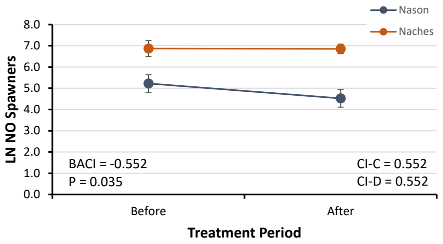


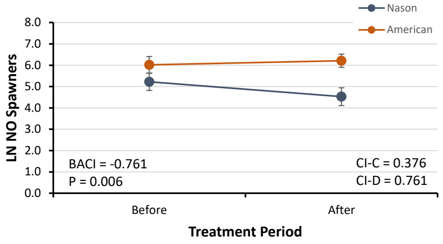


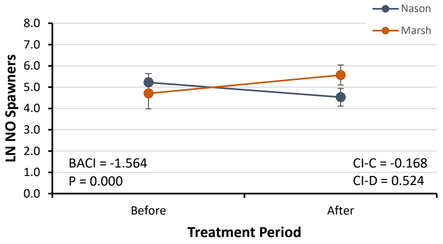


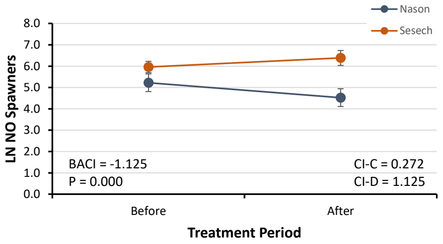


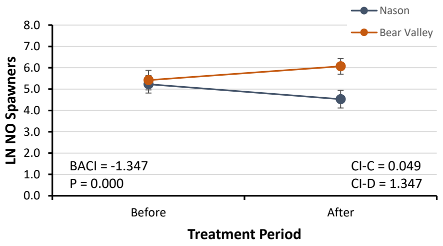
NOS











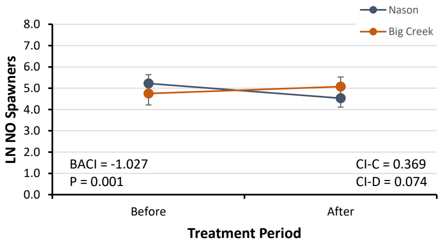
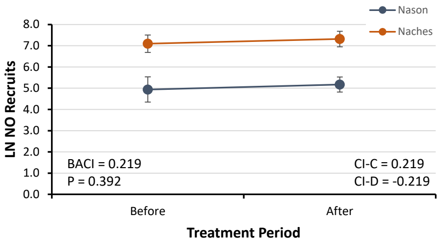
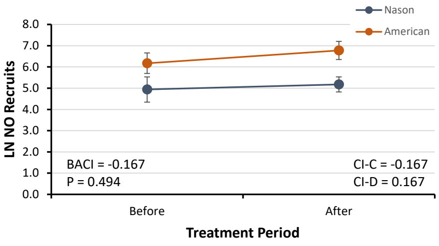
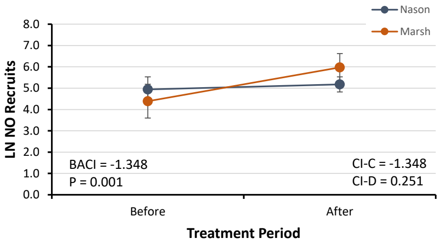


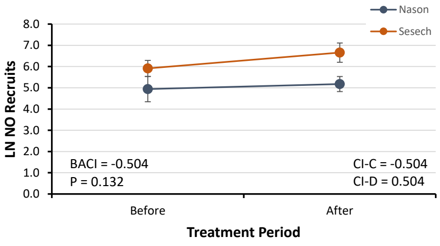
Figure 3a. Comparisons of mean total spawning abundance and natural-origin spawners (NOS) (with 95% CI) before and after hatchery supplementation of spring Chinook Salmon in Nason Creek and in reference streams. Graphs include BACI contrasts and their significance (P-values based on Aspin-Welch test), CI-contribution values, and CI-divergence values.

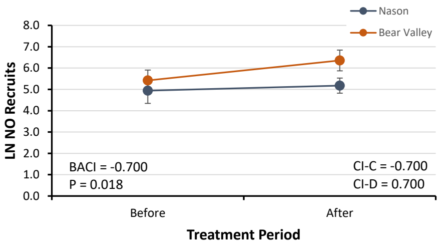
NOR

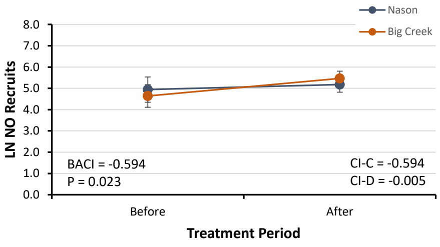




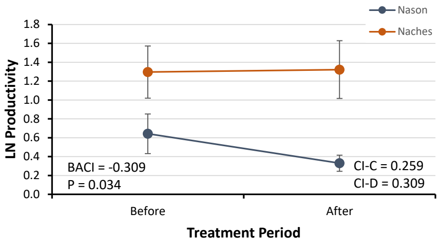


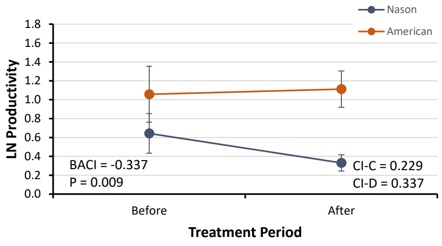


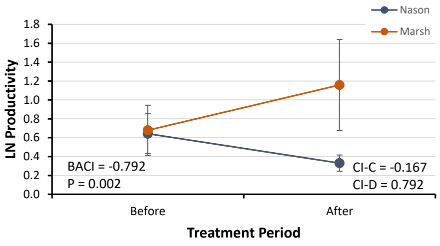


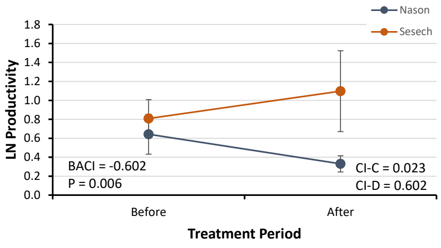


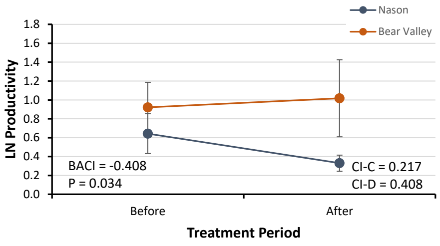
Adj Productivity











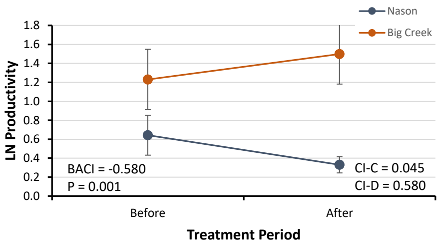
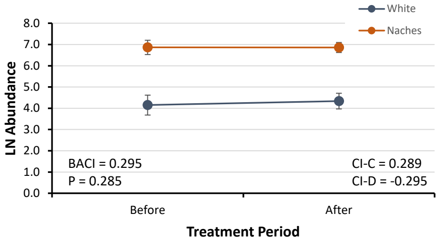
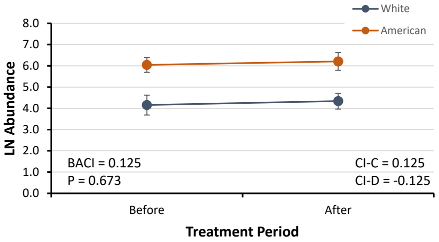
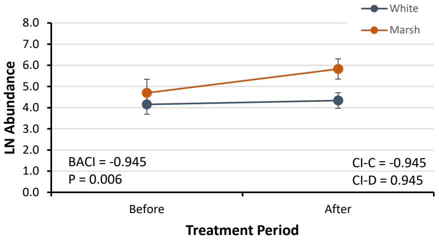


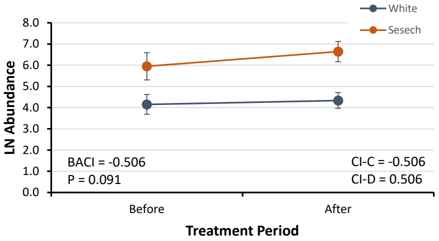
Figure 3b. Comparisons of mean natural-origin recruits (NOR) and adjusted productivity (with 95% CI) before and after hatchery supplementation of spring Chinook Salmon in Nason Creek and in reference streams. Graphs include BACI contrasts and their significance (P-values based on Aspin-Welch test), CI-contribution values, and CI-divergence values.

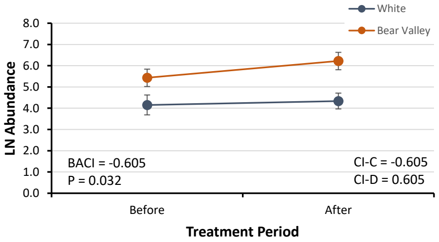
Total Spawners

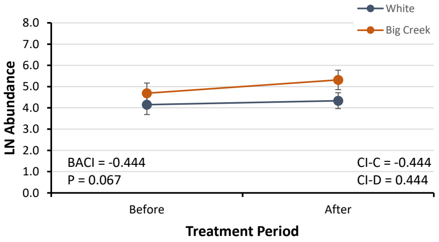




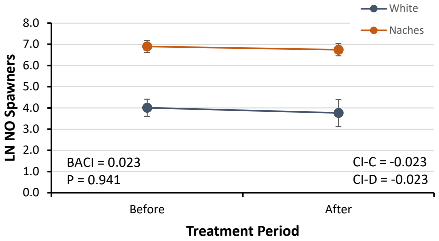


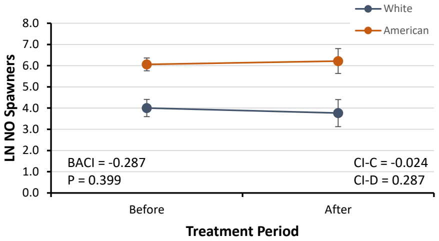


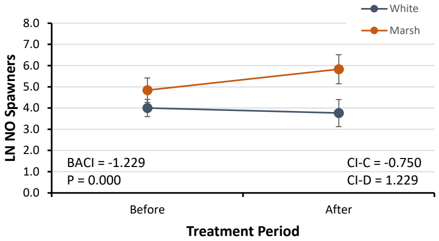


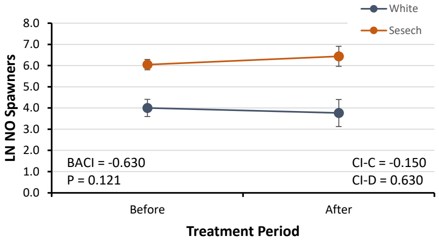


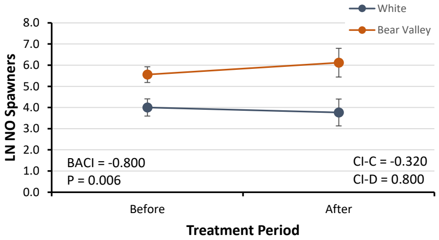
NOS











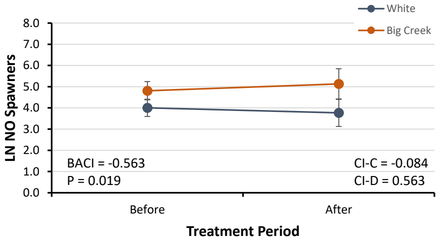
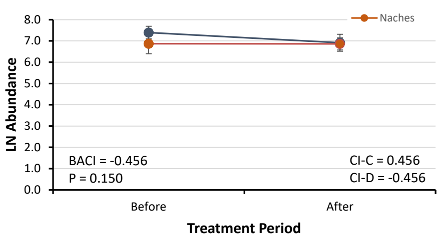
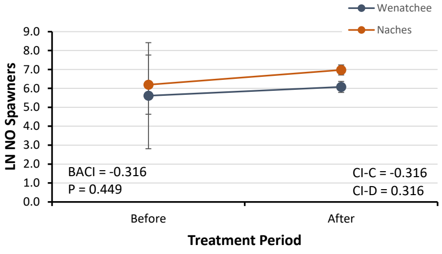


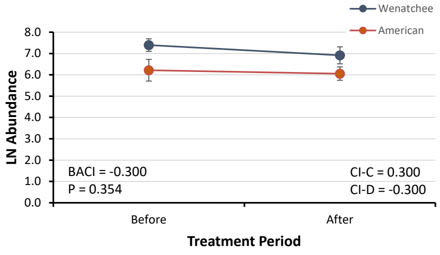
Figure 4. Comparisons of mean total spawning abundance and natural-origin spawners (NOS) (with 95% CI) before and after hatchery supplementation of spring Chinook Salmon in the White River and in reference streams. Graphs include BACI contrasts and their significance (P-values based on Aspin-Welch test), CI-contribution values, and CI-divergence values.

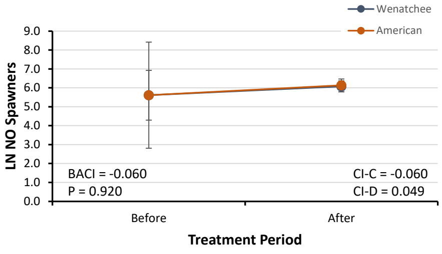
Total Spawners

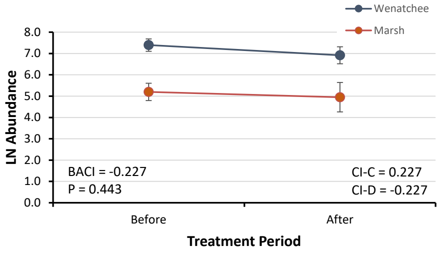
NOS

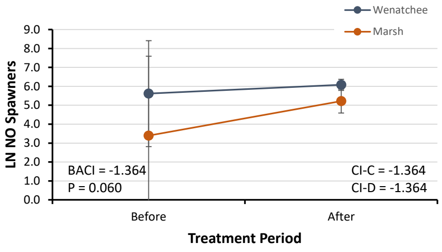


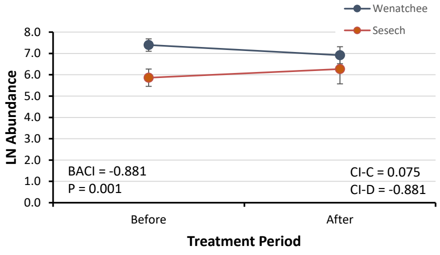


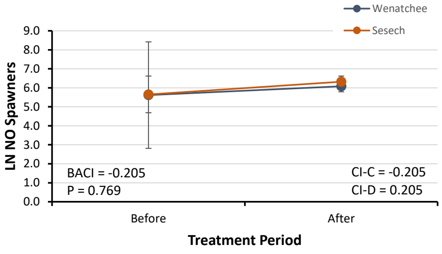


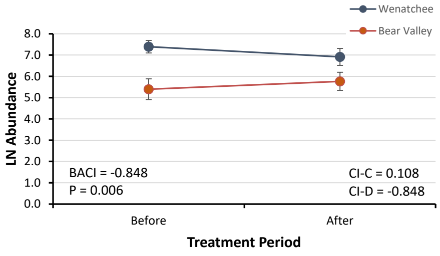


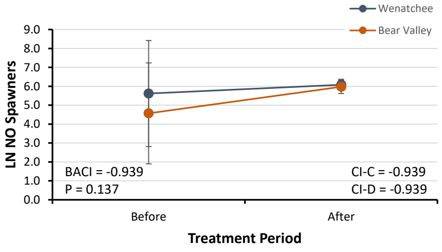


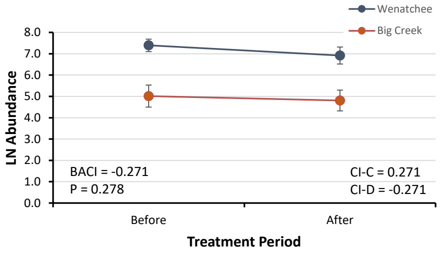












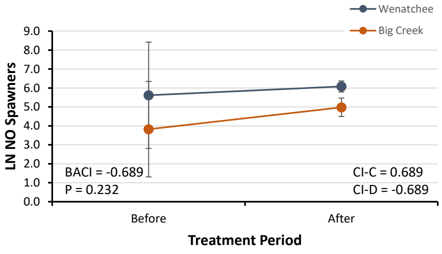
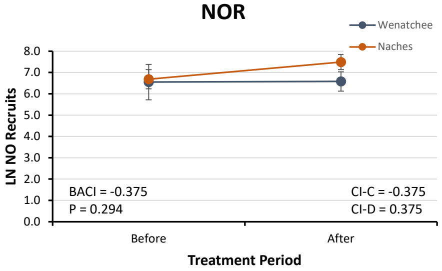
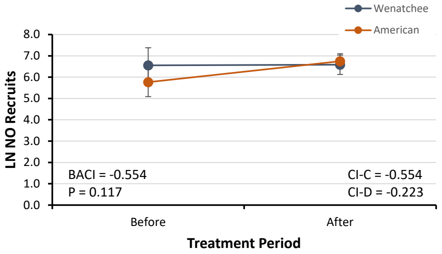
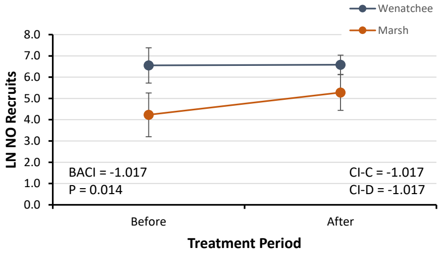


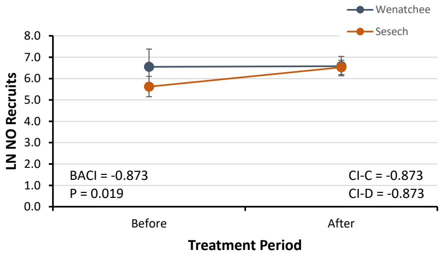
Figure 5a. Comparisons of mean total spawning abundance and natural-origin spawners (NOS) (with 95% CI) before and after hatchery supplementation of spring Chinook Salmon in the Wenatchee River sub-basin and in reference streams. Graphs include BACI contrasts and their significance (P-values based on Aspin-Welch test), CI-contribution values, and CI-divergence values.

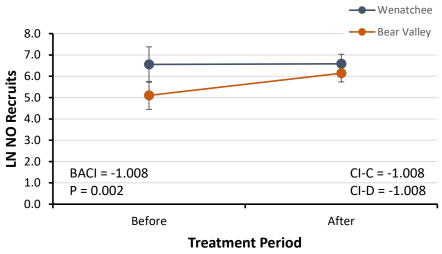
NOR

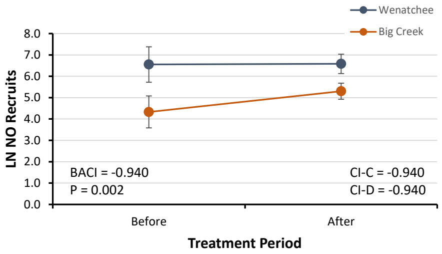




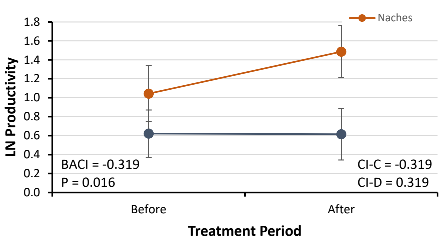


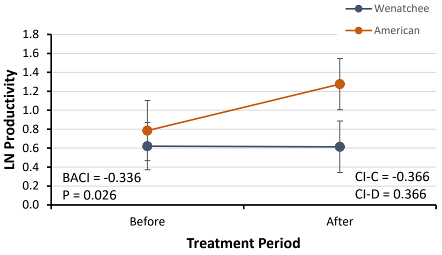


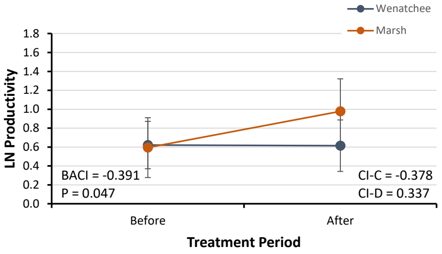


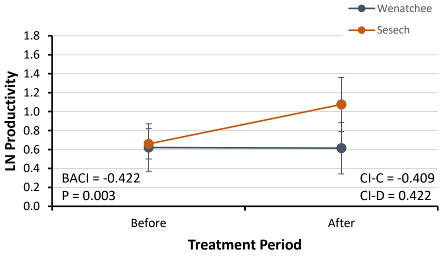


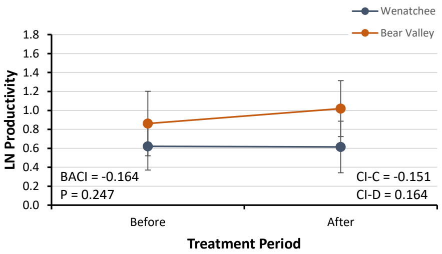
Adj Productivity











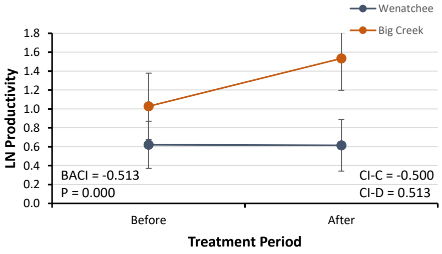
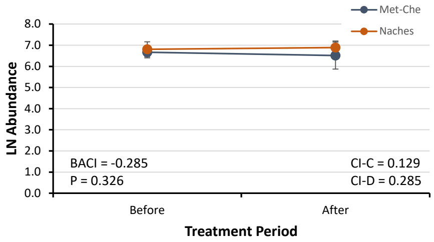
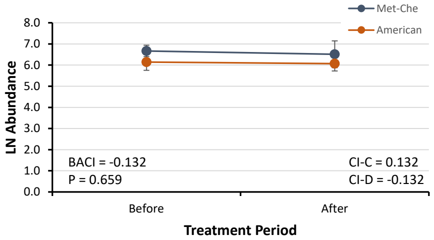
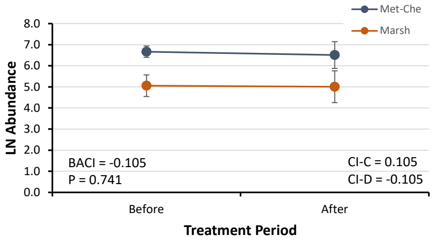


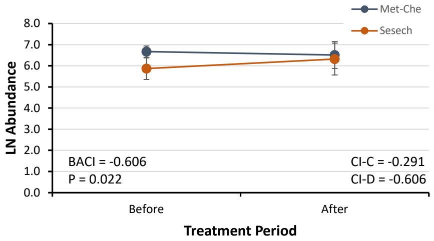
Figure 5b. Comparisons of mean natural-origin recruits (NOR) and adjusted productivity (with 95% CI) before and after hatchery supplementation of spring Chinook Salmon in the Wenatchee River sub-basin and in reference streams. Graphs include BACI contrasts and their significance (P-values based on Aspin-Welch test), CI-contribution values, and CI-divergence values.

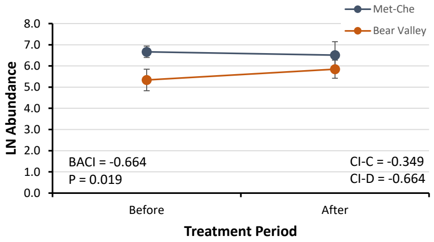
Total Spawners

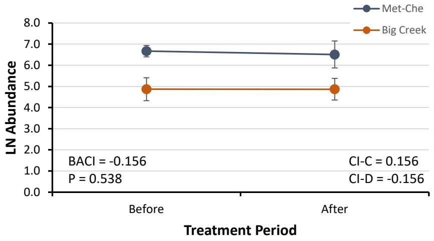




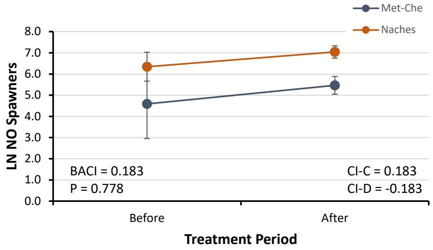


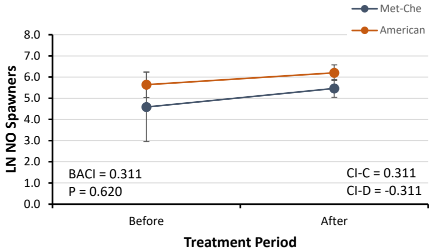


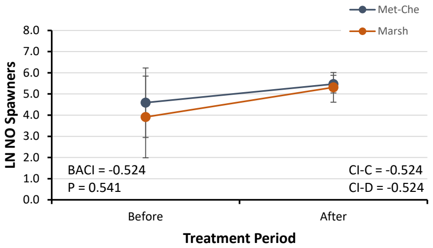


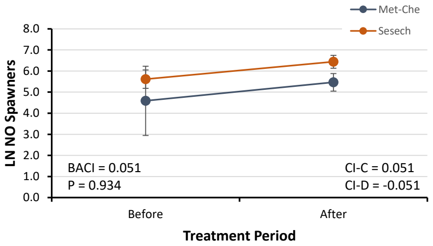


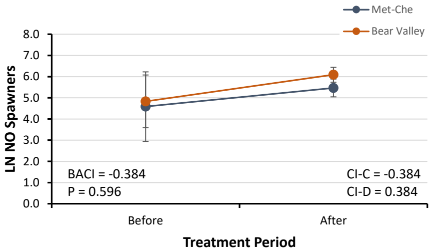
NOS











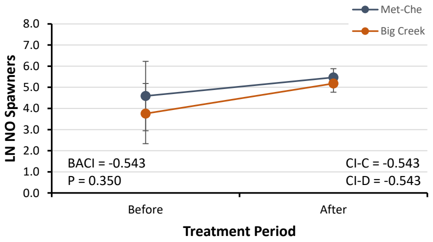
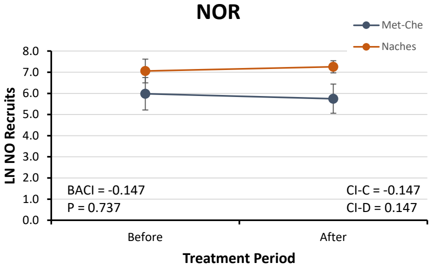
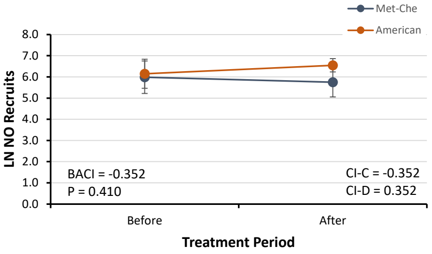
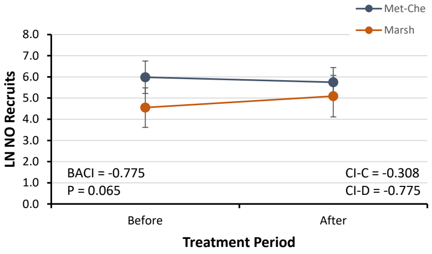


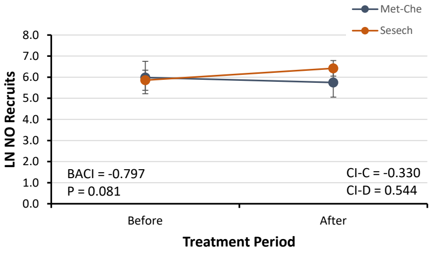
Figure 6a. Comparisons of mean total spawning abundance and natural-origin spawners (NOS) (with 95% CI) before and after hatchery supplementation of spring Chinook Salmon in the Methow-Chewuch rivers and in reference streams. Graphs include BACI contrasts and their significance (P-values based on Aspin-Welch test), CI-contribution values, and CI-divergence values.

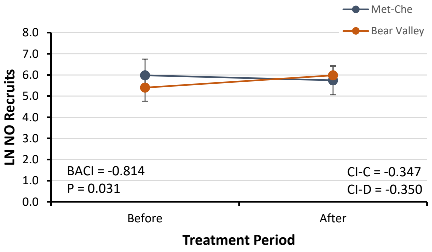
NOR

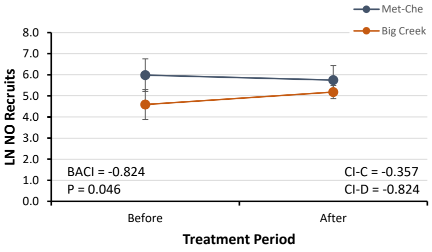




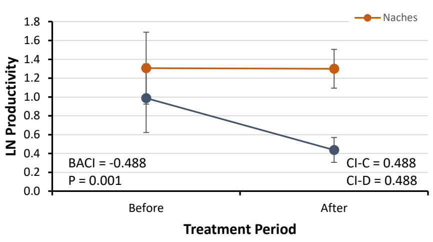


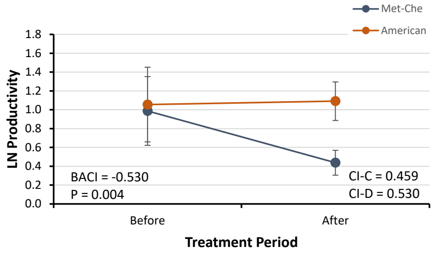


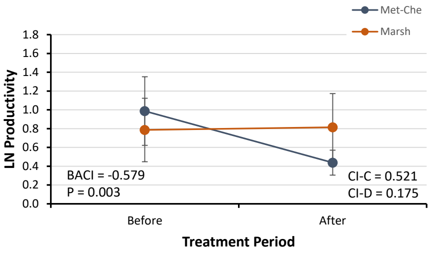


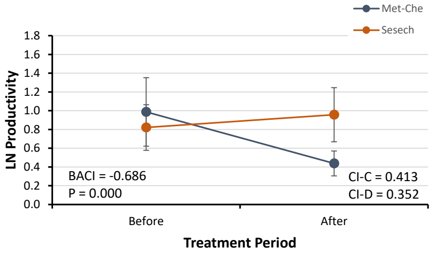


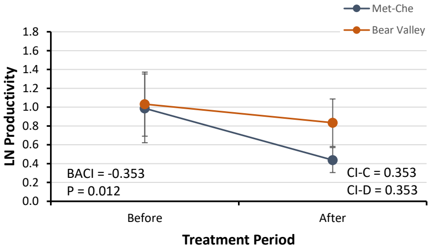
Adj Productivity











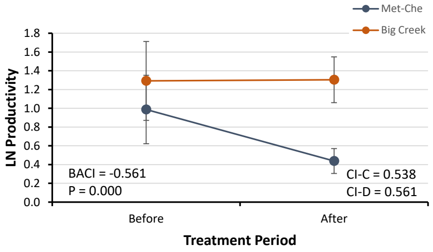
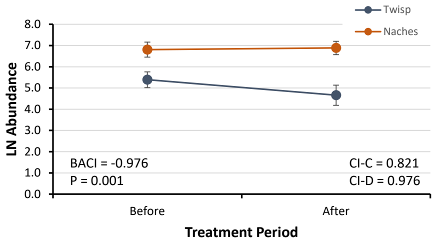
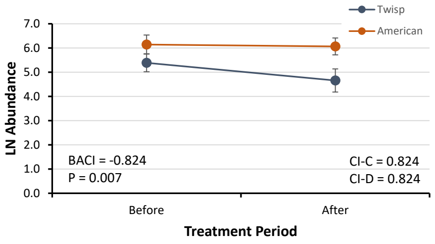
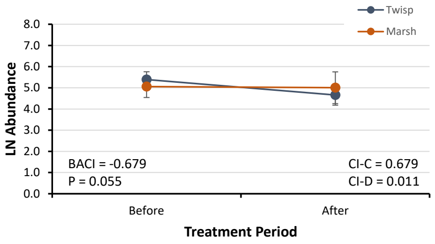


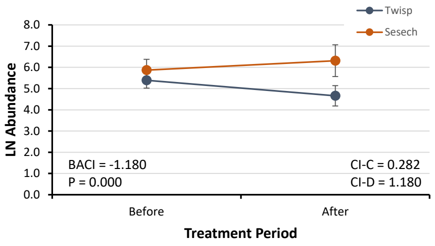
Figure 6b. Comparisons of mean natural-origin recruits (NOR) and adjusted productivity (with 95% CI) before and after hatchery supplementation of spring Chinook Salmon in the Methow-Chewuch rivers and in reference streams. Graphs include BACI contrasts and their significance (P-values based on Aspin-Welch test), CI-contribution values, and CI-divergence values.

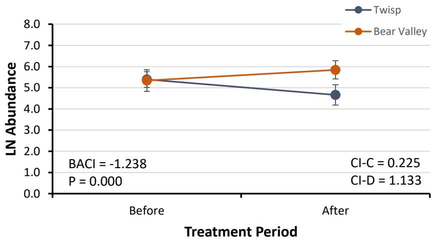
Total Spawners

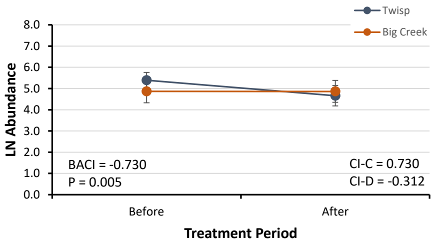




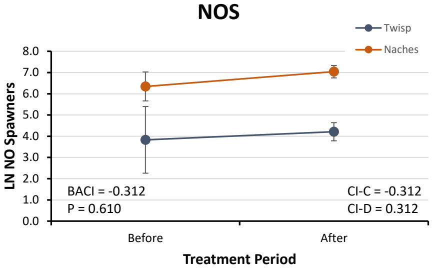


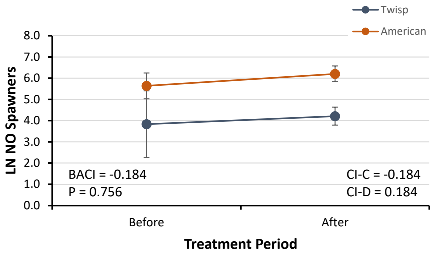


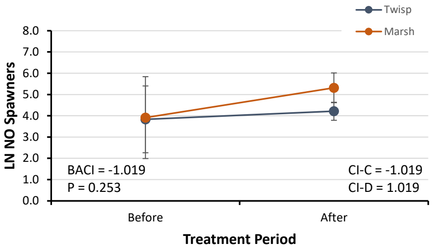


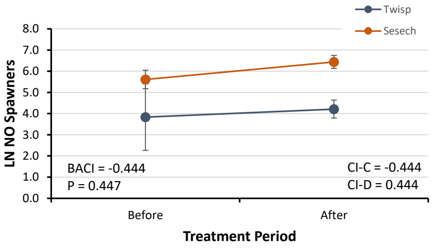


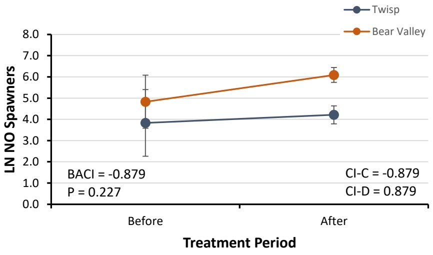
NOS











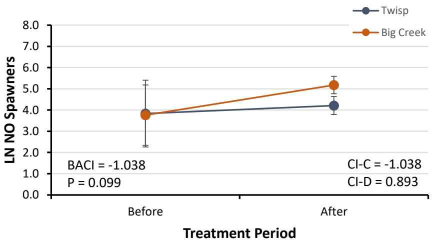
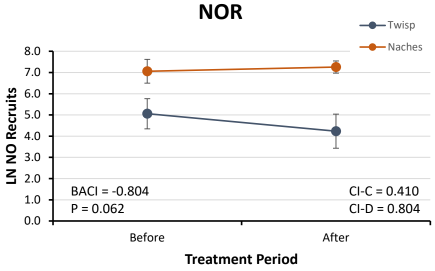
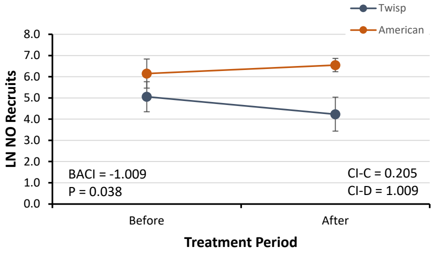
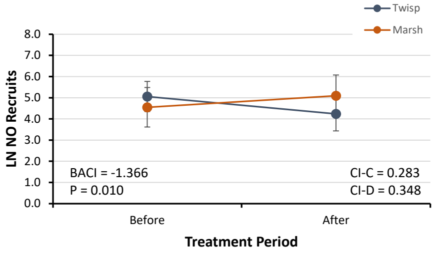


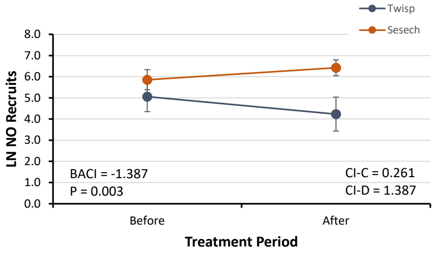
Figure 7a. Comparisons of mean total spawning abundance and natural-origin spawners (NOS) (with 95% CI) before and after hatchery supplementation of spring Chinook Salmon in the Twisp River and in reference streams. Graphs include BACI contrasts and their significance (P-values based on Aspin-Welch test), CI-contribution values, and CI-divergence values.

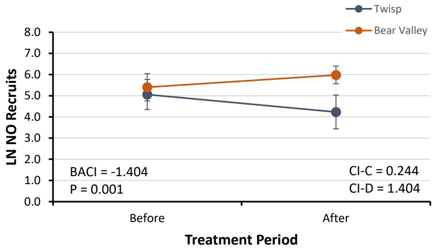
NOR

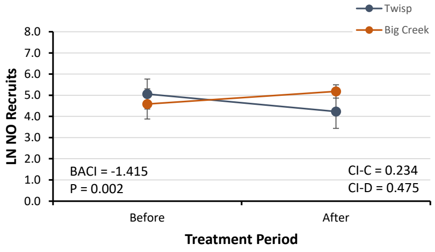




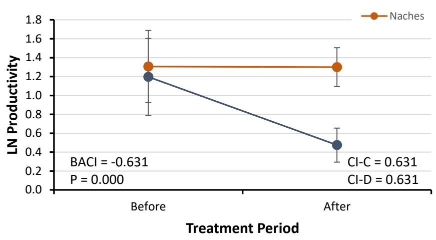


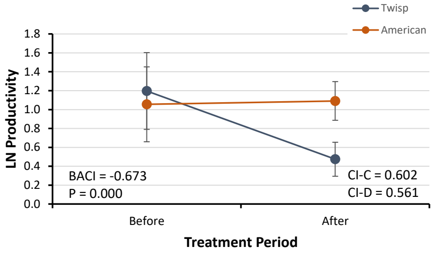


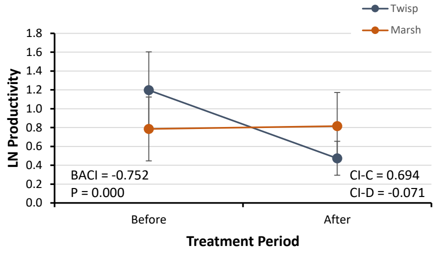


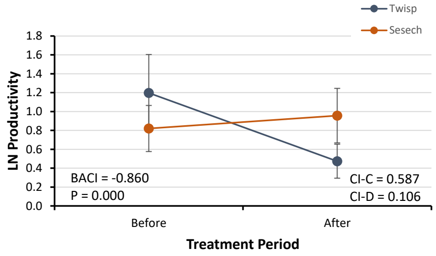


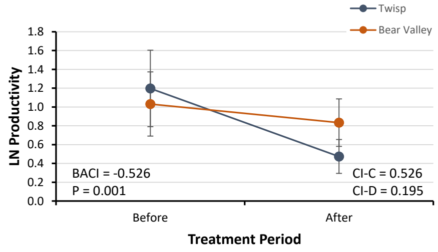
Adj Productivity











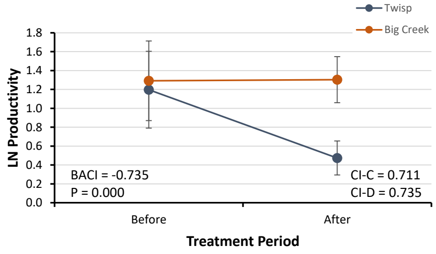
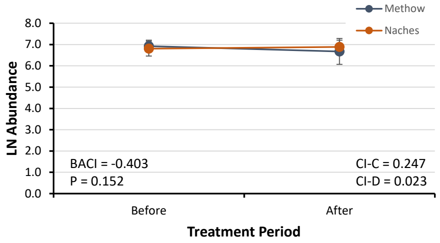
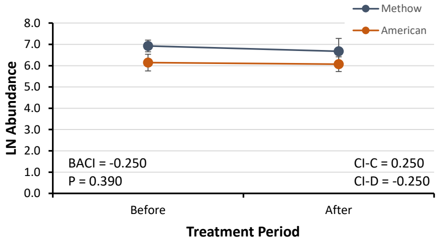
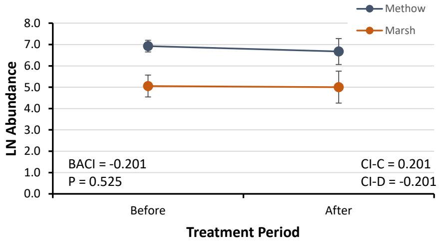


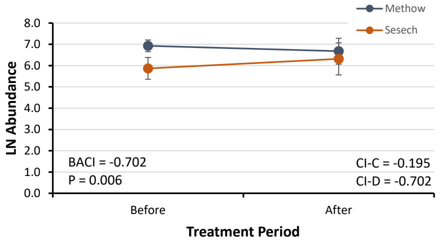
Figure 7b. Comparisons of mean natural-origin recruits (NOR) and adjusted productivity (with 95% CI) before and after hatchery supplementation of spring Chinook Salmon in the Twisp River and in reference streams. Graphs include BACI contrasts and their significance (P-values based on Aspin-Welch test), CI-contribution values, and CI-divergence values.

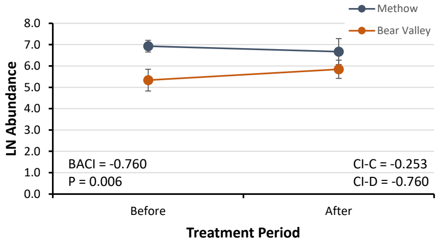
Total Spawners

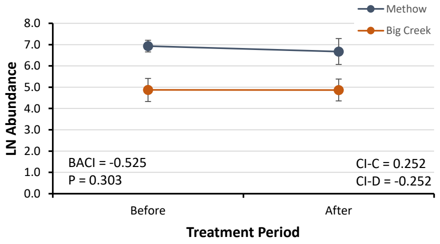




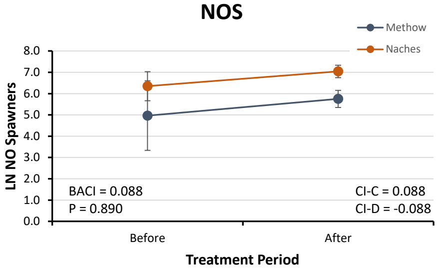


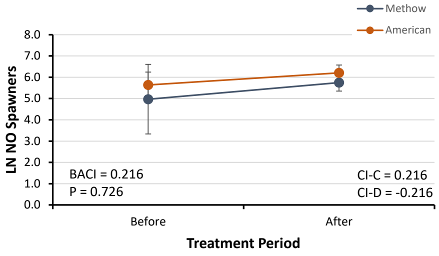


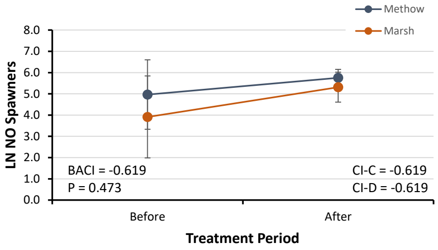


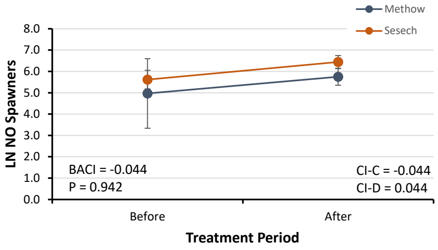


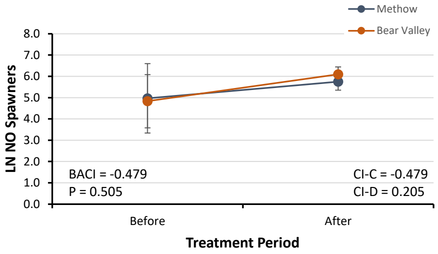
NOS











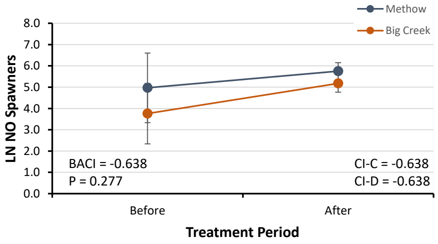
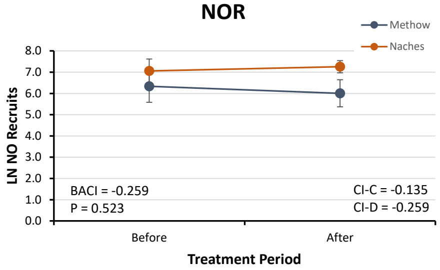
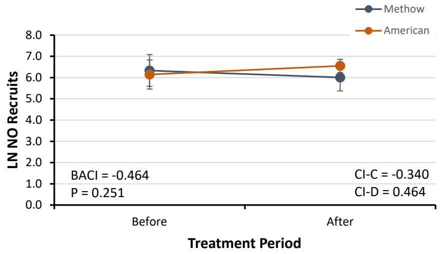
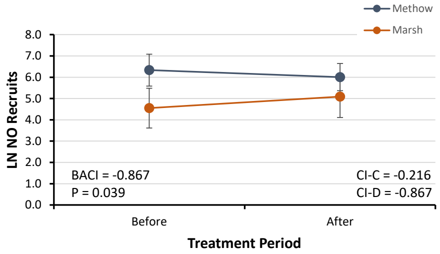


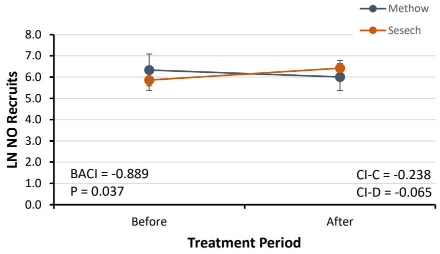
Figure 8a. Comparisons of mean total spawning abundance and natural-origin spawners (NOS) (with 95% CI) before and after hatchery supplementation of spring Chinook Salmon in the Methow River sub-basin and in reference streams. Graphs include BACI contrasts and their significance (P-values based on Aspin-Welch test), CI-contribution values, and CI-divergence values.

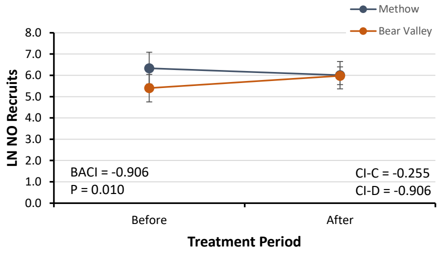
NOR

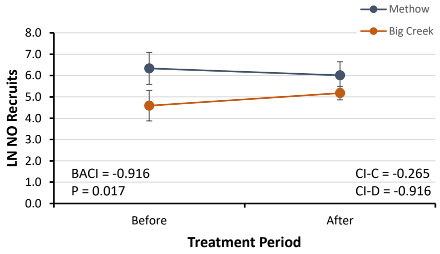




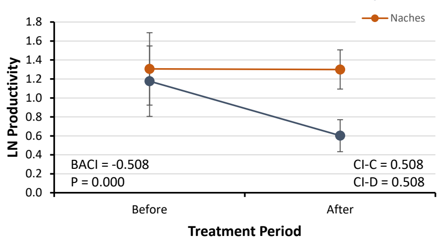


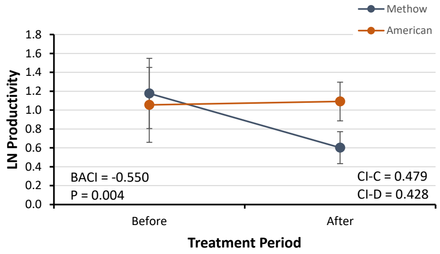


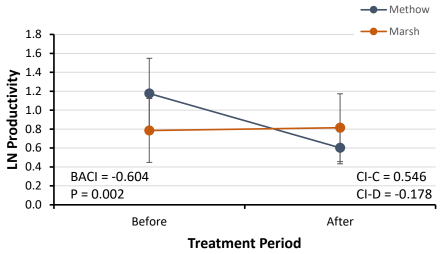


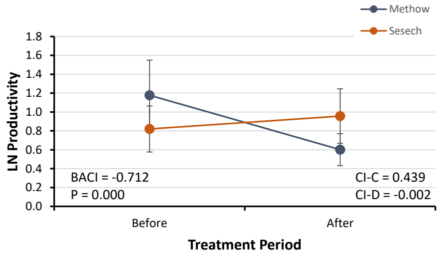


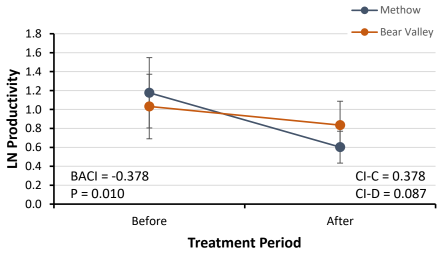
Adj Productivity











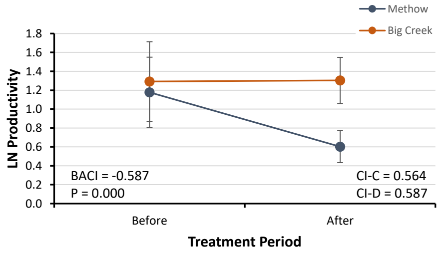


Figure 8b. Comparisons of mean natural-origin recruits (NOR) and adjusted productivity (with 95% CI) before and after hatchery supplementation of spring Chinook Salmon in the Methow River sub-basin and in reference streams. Graphs include BACI contrasts and their significance (P-values based on Aspin-Welch test), CI-contribution values, and CI-divergence values.

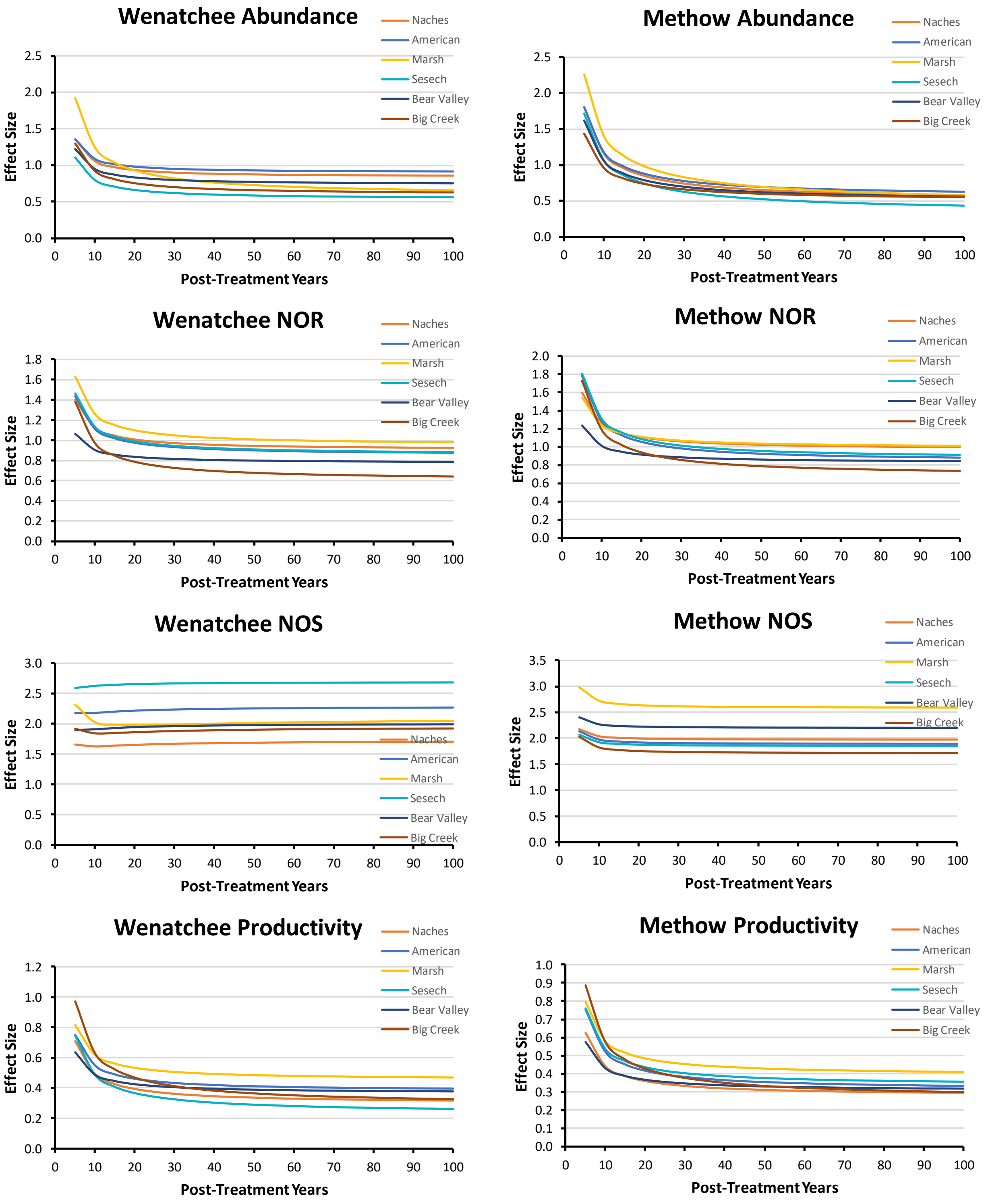


Figure 9. Power analysis of post-treatment years and effect size for abundance and productivity metrics in the Wenatchee and Methow subbasins (supplemented) compared to un-supplemented references.

Discussion

The spring Chinook Salmon supplementation programs in the Upper Columbia Basin generally produced adults at rates higher than the natural spawning population. Except for the captive broodstock program in the White River, HRRs were higher than NRRs in most years. However, when we compared supplemented populations to reference areas, our analyses indicate that supplementation has not significantly increased abundance and productivity of spring Chinook Salmon in the Upper Columbia Basin. Of the 26 MBACI contrasts evaluated, all had negative values and ten were significant. This appears to indicate that supplementation in some cases may have had a negative effect on spring Chinook Salmon populations in the Upper Columbia Basin. We caution making such a conclusion for reasons described below.

In order for supplementation to effectively increase abundance of natural-origin fish, the total combined abundance of natural-origin and hatchery-origin spawners must be greater than if supplementation had not occurred. Despite the implementation of a variety of state-of-the-art supplementation techniques (e.g., Mobrand et al. 2005, Paquet et al. 2011), total abundance of spawners at the basin scale decreased during supplementation relative to reference streams. This finding was contrary to findings of other Chinook Salmon supplementation evaluations (Buhle et al. 2009; Hess et al. 2012; Fast et al. 2015; Venditti et al. 2018) and was unexpected because adults taken to the hatchery produced more per capita adult recruits than adults that spawned in the river (see Table 2). In short, though the hatcheries were operating consistent with fish-culture targets, the hatchery programs did not achieve the desired management objectives of increasing abundance of natural-origin adults or total spawners in the natural environment.

The difference in findings between this evaluation and others might be explained by the suitability of the reference streams, differences in the calculation of abundance metrics, or by reduction in the productivity of fish spawning in the natural environment. Although we developed a rigorous method for selecting suitable reference streams, all of the available reference streams were outside of the Upper Columbia watershed and those populations may have responded differently to factors unrelated to supplementation during the periods of this evaluation. Habitat-restoration projects have occurred throughout the Columbia Basin and some may have been more effective in some regions and times than others. In addition, pinniped predation on adults may have differed among supplemented and reference populations (Sorel et al. 2020). However, the reference populations were selected based on a number of similarities of the populations before supplementation occurred and they were well correlated to the supplementation streams prior to supplementation. It is unlikely that all six of the reference populations would have changed to produce the results we observed during the period of supplementation. In addition, many of the supplementation programs started in different years, which strengthens our evaluation by reducing the effect of time-related influences outside of our treatment (Walters et al. 1988).

The effects of hatchery-origin fish on the spawning grounds may have reduced the productivity of the natural population such that the anticipated benefit of the higher number of hatchery-origin adults produced by the hatchery was nullified by the reduced number of fish produced in the natural environment. Indeed, overwhelming evidence indicated that the number of naturally produced adults and productivity in the supplemented populations was lower than that in the reference populations. It may be the case that natural-origin fish were replaced by hatchery-origin fish in the supplemented populations and this resulted in lowered production of natural-origin adults. In an earlier study in the Wenatchee subbasin, the relative reproductive success of hatchery-origin spawners was lower than that of natural-origin spawners, largely because of differences in spawning location within the Chiwawa River (Williamson et al. 2010; Hughes and Murdoch 2017). Furthermore, the supplementation programs were instituted in rivers that have already had a very long legacy of hatchery introductions and ongoing large-scale releases of spring Chinook Salmon. In the Wenatchee River, the Leavenworth National Fish Hatchery has released spring Chinook Salmon since 1942, with many years exceeding 1,000,000 fish. Similarly, the Winthrop National Fish Hatchery in the Methow River has operated since 1942 and released spring Chinook Salmon with many years exceeding 600,000 fish. The long-term operation of these facilities may have already affected the populations, reducing their ability to respond positively to conservation hatchery supplementation.

Reduction in the productivity of supplemented populations relative to reference streams may result from genetic, fish culture, and ecological factors. However, these factors are difficult to tease apart because they may occur simultaneously. Hatchery-origin fish tend to mature at a smaller size and therefore have fewer and smaller eggs, which can reduce productivity (Knudsen et al. 2008; Ohlberger et al. 2018, 2020). In addition, adult salmon have decreased in size, which leads to lower reproductive output (Ohlberger et al. 2018, 2020; Oke et al. 2020). Spawn location was a factor that was associated with lower productivity of hatchery-origin spawners than natural-origin spawners in the Wenatchee River subbasin and location of hatchery-origin spawners was likely the result of where the acclimation site was located in the Chiwawa River (Williamson et al. 2010; Hughes and Murdoch 2017). However, the spawning-location disparity was likely highest in the Chiwawa River and does not adequately explain our results in other locations. Straying of hatchery-origin spring Chinook Salmon from programs where they are moved for final acclimation is also higher at tributary scales than straying of natural-origin fish (Ford et al. 2015; Pearsons and O'Connor, 2020, 2021). Thus, more hatchery-origin fish spawn outside of their natal tributary than natural-origin fish. In addition, hatchery-origin fish may have lower productivity in the natural environment because of domestication selection effects on factors such as competition and predation (Fritts et al. 2007; Pearsons et al. 2007; Williamson et al. 2010).

Finally, differences in the carrying capacity among streams may influence comparisons of productivity between supplemented and reference streams. Populations in streams near carrying capacity will exhibit lower productivities than those in streams well below capacity (Walters 2013, ISAB 2015). Although possible, this mechanism did not appear to strongly influence our findings because productivity and density-adjusted productivity results were similar. In summary, it is likely that many mechanisms may contribute to the findings in our study.

Recently, it was observed that estimates of hatchery-origin and natural-origin abundance generated using carcass recoveries were biased (Murdoch, personal communication), in that estimates of hatchery-origin fish were underestimated, natural-origin fish were overestimated, but total abundance was likely accurate. This bias was likely associated with carcass recovery where smaller male fish (jacks) were found in lower proportions than their true abundance (Murdoch et al. 2010). We did not correct for this carcass recovery bias because correction factors were only available for supplemented streams in the Wenatchee subbasin. However, if the abundance of natural-origin fish was overestimated in supplemented streams, then our findings are conservative, and the true differences are likely larger than what we presented.

It is clear that including reference streams in the Upper Columbia watershed would have enhanced our ability to definitively evaluate the influence of supplementation. We cannot exclude the possibility that differences in responses occurred between the supplemented and reference streams before or during supplementation. Therefore, we may have only detected an Upper Columbia watershed effect unrelated to supplementation. Although this is possible, we think it is unlikely for the reasons described above, such as: many different reference streams evaluated from different geographic regions, treatment streams were well correlated with reference streams prior to supplementation, and, to our knowledge, no obvious changes occurred in our study area during our evaluation that would reduce population performance relative to that of reference streams.

The results that we presented were mostly the effects of the original hatchery production targets coupled with adaptive management of the programs. Beginning in 2014, the release numbers were greatly reduced for most long-term programs (e.g., Chiwawa, Methow-Chewuch) as a result of adjustments in hatchery production required by the Federal Energy Regulatory Commission licenses for the respective hydroelectric projects for which the hatchery programs mitigate. Because of the timing of these changes, we were unable to evaluate the totality of their affects at this time. Initial results indicate that the reduction in smolt production has resulted in increases in abundance and productivity. However, power analyses indicated that minimum detectable differences stabilized approximately 10-20 years after supplementation and therefore it is likely that statistical power to detect differences would not be fully realized in less than 10 years. In addition, specific modifications to program management (e.g., changes in program size every 10 years) would be difficult to detect because they rarely exceed 10 years. In contrast, evaluation of the full adaptively managed programs since inception provided statistical power as high as could be expected because the number of treatment years exceeded the time interval necessary to detect differences (e.g., 14-27 years).

While the findings in this study suggest that the hatchery programs have not been effective in increasing abundance of spawners, several aspects of the management of these hatchery program may be able to be adjusted to increase the likelihood of success and to make assessment of the programs more rigorous and defensible. First, the number of fish released in these programs is based on mortality estimates at the hydroelectric projects in addition to final adjustments on program sizes based on negotiation; smolt releases are intended to replace fish lost to mortality at the hydro-electric projects and is adjusted every 10 years. While the impetus for this approach is sensible as a mitigation approach, the distribution of fish among the programs could be established based on carrying capacity of the rivers, natal population status, identification of life stage(s) limiting population growth, and explicitly stated desired effect of the hatchery program. Second, reference streams could be established within the Wenatchee and Methow subbasins. These streams should have high quality habitat and should also not be the subject of hatchery releases of other species, such as summer steelhead, Coho Salmon, or summer Chinook Salmon. Third, the programs should be run under an adaptive management framework that *a priori* states uncertainties, hypothesis, goals, assessment approach, and actions to be taken dependent on possible outcomes. Implementation of these measures will greatly increase managers’ ability to understand the complex systems that support spring Chinook Salmon and make informed decisions over time as data reveal the population response to the management actions.

Acknowledgments

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Appendix 1. Summary of BACI metrics for different population metrics and hatchery programs in the Upper Columbia Basin.

Supplemented stream	Population metric	BACI metric	Reference stream						No. of neg CIs
			Naches	American	Marsh	Sesech	Bear V	Big C	
Chiwawa River	Abundance	BACI Contrast	-0.457	-0.301	-0.201	-0.855	-0.822	-0.246	6
		P-value	0.207	0.420	0.527	0.003	0.015	0.347	
		CI-contribution	0.457	0.301	0.201	0.049	0.082	0.246	0
		CI-divergence	0.457	-0.301	-0.201	-0.701	-0.822	-0.246	5
	NOR	BACI Contrast	-0.008	-0.188	-0.708	-0.564	-0.699	-0.631	6
		P-value	0.986	0.652	0.095	0.220	0.067	0.075	
		CI-contribution	-0.008	-0.188	-0.708	-0.564	-0.699	-0.631	6
		CI-divergence	0.008	0.188	-0.708	0.564	-0.241	-0.631	3
	NOS	BACI Contrast	-0.766	-0.552	-1.092	-1.114	-1.387	-0.870	6
		P-value	0.120	0.294	0.002	0.022	0.002	0.024	
		CI-contribution	0.101	0.316	0.086	0.064	-0.209	0.307	1
		CI-divergence	0.766	0.552	-1.092	0.735	-0.241	-0.870	3
	Productivity	BACI Contrast	-0.006	-0.227	-0.298	-0.220	-0.046	-0.373	6
		P-value	0.970	0.207	0.106	0.134	0.768	0.030	
		CI-contribution	-0.006	-0.227	-0.298	-0.220	-0.046	-0.373	6
		CI-divergence	0.006	0.227	0.279	0.220	0.046	0.373	0
	Adjusted Productivity	BACI Contrast	-0.227	-0.274	-0.316	-0.347	-0.089	-0.438	6
		P-value	0.083	0.105	0.086	0.019	0.526	0.000	
		CI-contribution	-0.227	-0.274	-0.316	-0.347	-0.089	-0.438	6
		CI-divergence	0.227	0.274	0.294	0.347	0.089	0.438	0
Nason Creek	Abundance	BACI Contrast	0.399	0.219	-0.591	-0.175	-0.432	-0.227	4
		P-value	0.099	0.386	0.090	0.462	0.103	0.403	
		CI-contribution	0.399	0.219	-0.591	-0.175	-0.432	-0.227	4
		CI-divergence	-0.399	-0.219	-0.591	0.175	0.285	-0.227	4
	NOR	BACI Contrast	0.219	-0.167	-1.348	-0.504	-0.700	-0.594	5
		P-value	0.392	0.494	0.001	0.132	0.018	0.023	
		CI-contribution	0.219	-0.167	-1.348	-0.504	-0.700	-0.594	5
		CI-divergence	-0.219	0.167	0.251	0.504	0.700	-0.005	2
	NOS	BACI Contrast	-0.552	-0.761	-1.564	-1.125	-1.347	-1.027	6
		P-value	0.035	0.006	0.000	0.000	0.000	0.001	
		CI-contribution	0.552	0.376	-0.168	0.272	0.049	0.369	1
		CI-divergence	0.552	0.761	0.524	1.125	1.347	0.074	0
	Productivity	BACI Contrast	-0.277	-0.354	-0.755	-0.472	-0.356	-0.424	6
		P-value	0.135	0.016	0.003	0.043	0.082	0.107	
		CI-contribution	0.277	0.213	-0.130	0.153	0.268	0.201	1
		CI-divergence	0.277	0.354	0.755	0.472	0.356	0.424	0
	Adjusted Productivity	BACI Contrast	-0.309	-0.337	-0.792	-0.602	-0.408	-0.580	6
		P-value	0.034	0.009	0.002	0.006	0.034	0.001	
		CI-contribution	0.258	0.229	-0.167	0.023	0.217	0.045	1
		CI-divergence	0.309	0.337	0.792	0.602	0.408	0.580	0
White River	Abundance	BACI Contrast	0.295	0.125	-0.945	-0.506	-0.605	-0.444	4
		P-value	0.285	0.673	0.006	0.091	0.032	0.067	
		CI-contribution	0.289	0.125	-0.945	-0.506	-0.605	-0.444	4
		CI-divergence	-0.295	-0.125	0.945	0.506	0.605	0.444	2
	NOS	BACI Contrast	0.023	-0.287	-1.229	-0.630	-0.800	-0.563	5
		P-value	0.941	0.399	0.000	0.121	0.006	0.019	
		CI-contribution	-0.023	-0.024	-0.750	-0.150	-0.320	-0.084	6
		CI-divergence	-0.023	0.287	1.229	0.630	0.800	0.563	1
Wenatchee River sub-basin	Abundance	BACI Contrast	-0.456	-0.300	-0.227	-0.881	-0.848	-0.271	6
		P-value	0.150	0.354	0.443	0.001	0.006	0.278	
		CI-contribution	0.456	0.300	0.227	0.075	0.108	0.271	0
		CI-divergence	-0.456	-0.300	-0.227	-0.881	-0.848	-0.271	6
	NOR	BACI Contrast	-0.375	-0.554	-1.017	-0.873	-1.008	-0.940	6
		P-value	0.294	0.117	0.014	0.019	0.002	0.002	
		CI-contribution	-0.375	-0.554	-1.017	-0.873	-1.008	-0.940	6
		CI-divergence	0.375	-0.223	-1.017	-0.873	-1.008	-0.940	5
	NOS	BACI Contrast	-0.316	-0.060	-1.364	-0.205	-0.939	-0.689	6
		P-value	0.499	0.920	0.060	0.769	0.137	0.232	
		CI-contribution	-0.316	-0.060	-1.364	-0.205	-0.939	-0.689	6
		CI-divergence	0.316	0.049	-1.364	0.205	-0.939	-0.689	3
	Productivity	BACI Contrast	-0.097	-0.319	-0.373	-0.295	-0.120	-0.447	6
		P-value	0.497	0.063	0.059	0.036	0.428	0.014	
		CI-contribution	-0.097	-0.319	-0.359	-0.281	-0.107	-0.433	6
		CI-divergence	0.097	0.319	0.326	0.295	0.120	0.447	0
	Adjusted Productivity	BACI Contrast	-0.319	-0.366	-0.391	-0.422	-0.164	-0.513	6
		P-value	0.016	0.026	0.047	0.003	0.247	0.000	
		CI-contribution	-0.319	-0.366	-0.378	-0.409	-0.151	-0.500	6
		CI-divergence	0.319	0.366	0.337	0.422	0.164	0.513	0
	Abundance	BACI Contrast	-0.285	-0.132	-0.105	-0.606	-0.664	-0.156	6

Supplemented stream	Population metric	BACI metric	Reference stream						No. of neg CIs
			Naches	American	Marsh	Sesech	Bear V	Big C	
Methow-Chewuch rivers		P-value	0.326	0.659	0.741	0.022	0.019	0.538	
		CI-contribution	0.129	0.132	0.105	-0.291	-0.349	0.156	2
		CI-divergence	0.285	-0.132	-0.105	-0.606	-0.664	-0.156	5
	NOR	BACI Contrast	-0.147	-0.352	-0.775	-0.797	-0.814	-0.824	6
		P-value	0.737	0.410	0.065	0.081	0.031	0.046	
		CI-contribution	-0.147	-0.352	-0.308	-0.330	-0.347	-0.357	6
		CI-divergence	0.147	0.352	-0.775	0.544	-0.350	-0.824	3
	NOS	BACI Contrast	0.183	0.311	-0.524	0.051	-0.384	-0.543	3
		P-value	0.778	0.620	0.541	0.934	0.596	0.350	
		CI-contribution	0.183	0.311	-0.524	0.051	-0.384	-0.543	3
		CI-divergence	-0.183	-0.311	-0.524	-0.051	0.384	-0.543	5
	Productivity	BACI Contrast	-0.311	-0.542	-0.663	-0.646	-0.396	-0.524	6
		P-value	0.036	0.003	0.001	0.001	0.007	0.006	
		CI-contribution	0.311	0.542	0.663	0.646	0.396	0.524	0
		CI-divergence	0.311	0.542	0.394	0.430	0.396	0.524	0
	Adjusted Productivity	BACI Contrast	-0.488	-0.530	-0.579	-0.686	-0.353	-0.561	6
		P-value	0.001	0.004	0.003	0.000	0.012	0.000	
		CI-contribution	0.488	0.459	0.521	0.413	0.353	0.538	0
		CI-divergence	0.488	0.530	0.175	0.352	0.353	0.561	0
Twisp River	Abundance	BACI Contrast	-0.976	-0.824	-0.679	-1.180	-1.238	-0.730	6
		P-value	0.001	0.007	0.055	0.000	0.000	0.005	
		CI-contribution	0.821	0.824	0.679	0.282	0.225	0.730	0
		CI-divergence	0.976	0.824	0.011	1.180	1.133	-0.312	1
	NOR	BACI Contrast	-0.804	-1.009	-1.366	-1.387	-1.404	-1.415	6
		P-value	0.062	0.038	0.010	0.003	0.001	0.002	
		CI-contribution	0.410	0.205	0.283	0.261	0.244	0.234	0
		CI-divergence	0.804	1.009	0.348	1.387	1.404	0.475	0
	NOS	BACI Contrast	-0.312	-0.184	-1.019	-0.444	-0.879	-1.038	6
		P-value	0.610	0.756	0.253	0.447	0.227	0.099	
		CI-contribution	-0.312	-0.184	-1.019	-0.444	-0.879	-1.038	6
		CI-divergence	0.312	0.184	1.019	0.444	0.879	0.893	0
	Productivity	BACI Contrast	-0.290	-0.520	-0.677	-0.660	-0.410	-0.538	6
		P-value	0.049	0.004	0.001	0.000	0.007	0.005	
		CI-contribution	0.290	0.520	0.677	0.660	0.410	0.538	0
		CI-divergence	0.290	0.479	0.046	0.082	0.214	0.361	0
	Adjusted Productivity	BACI Contrast	-0.631	-0.673	-0.752	-0.860	-0.526	-0.735	6
		P-value	0.000	0.000	0.000	0.000	0.001	0.000	
		CI-contribution	0.631	0.602	0.694	0.587	0.526	0.711	0
		CI-divergence	0.631	0.561	-0.071	0.106	0.195	0.735	1
Methow River sub-basin	Abundance	BACI Contrast	-0.403	-0.250	-0.201	-0.702	-0.760	-0.252	6
		P-value	0.152	0.390	0.525	0.006	0.006	0.303	
		CI-contribution	0.247	0.250	0.201	-0.195	-0.253	0.252	2
		CI-divergence	0.023	-0.250	-0.201	-0.702	-0.760	-0.252	5
	NOR	BACI Contrast	-0.259	-0.464	-0.867	-0.889	-0.906	-0.916	6
		P-value	0.523	0.251	0.039	0.037	0.010	0.017	
		CI-contribution	-0.135	-0.340	-0.216	-0.238	-0.255	-0.265	6
		CI-divergence	0.259	0.464	-0.867	-0.065	-0.906	-0.916	4
	NOS	BACI Contrast	0.088	0.216	-0.619	-0.044	-0.479	-0.638	4
		P-value	0.890	0.726	0.473	0.942	0.505	0.277	
		CI-contribution	0.088	0.216	-0.619	-0.044	-0.479	-0.638	4
		CI-divergence	-0.088	-0.216	-0.619	0.044	0.205	-0.638	4
	Productivity	BACI Contrast	-0.328	-0.558	-0.682	-0.664	-0.415	-0.543	6
		P-value	0.022	0.002	0.001	0.000	0.005	0.004	
		CI-contribution	0.328	0.558	0.682	0.664	0.415	0.543	0
		CI-divergence	0.328	0.558	0.322	0.358	0.415	0.543	0
	Adjusted Productivity	BACI Contrast	-0.508	-0.550	-0.604	-0.712	-0.378	-0.587	6
		P-value	0.000	0.004	0.002	0.000	0.010	0.000	
		CI-contribution	0.508	0.479	0.546	0.439	0.378	0.564	0
		CI-divergence	0.508	0.428	-0.178	-0.002	0.087	0.587	2

Investigations into Association between Proportion of Hatchery Spawners and Juvenile Productivity for Spring Chinook, Summer Chinook, and Summer Steelhead in the Wenatchee and Methow River Basins

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Abstract

Conservation hatchery programs implemented in the Wenatchee and Methow river basins are intended to increase the abundance of the target populations. The strategy of the hatchery programs is to return hatchery adults that increase the spawning population, resulting in an increase in the number of offspring that will maintain and recover naturally reproducing populations. However, there is a concern that the hatchery programs may lower the juvenile productivity in supplemented watersheds. The populations are managed under the concept of Proportionate Natural Influence (PNI), a framework that uses genetic modeling to estimate risk of hatchery introgression in natural populations and prescribes management benchmarks intended to allow hatchery programs to operate within an acceptable risk level to the natural population. One of the metrics in the PNI framework is the proportion of hatchery origin spawners (pHOS). Our investigation of whether higher pHOS may result in lowered juvenile productivity was largely inconclusive. For most populations studied, no evidence of an effect of pHOS was observed. For the single population that demonstrated a possible negative effect of pHOS on juvenile productivity (Twisp River Summer Steelhead), the evidence was weak: when density dependence was accounted for, the perceived negative association between pHOS and juveniles per redd was no longer observed. Additionally, the significant result was observed only when a possible outlier in emigrant counts was omitted, which may not be justified depending on the cause of the unusual emigrant count for that brood year. Thus, even when some evidence of a negative effect of pHOS was found, the evidence was particularly weak. For all three stock-recruitment models considered, there was often high uncertainty in model parameter estimates even when the models could be fit to the data. This was indicated by wide confidence intervals that often included maximum smolt or emigrant values far beyond the range of observed data, and by the high correlation in model parameter estimates. High correlation lowers the ability to distinguish between different model fits and increases uncertainty in the results; it arises from lack of contrast in the data or violation of modeling assumptions. Given all the complicating factors identified here, only the most extreme effect of pHOS on juvenile productivity could have been detected. Thus, we caution against concluding that such an effect is truly absent. We conducted a power analysis based on the Chiwawa spring Chinook data—the most robust dataset in this study. Simulated power analyses revealed that studies shorter than 70 years will have low power to detect an effect on recruitment for all but the strongest effect sizes of pHOS. Future data-collection efforts could be substantially improved by increasing the contrast in pHOS levels and including suitable in-basin unsupplemented references. More specifically, a planned experiment using deliberately chosen pHOS levels could be implemented in order to achieve the necessary contrast and remove confounding analyses with temporal and age-structured processes. Appropriate power analyses must be performed on the study design prior to commencing work to ensure that a result may be obtained within an acceptable time frame.

Introduction

Conservation hatchery programs implemented in the Wenatchee and Methow river basins are intended to increase the abundance of the target populations. The strategy of the hatchery programs is to return hatchery adults that increase the spawning population, resulting in an increase in the number of offspring that will maintain and recover naturally reproducing populations. The assumptions are that 1) increasing the number of spawners will increase the naturally reproducing population abundance in future generations, and 2) hatchery-origin spawners have similar fitness to natural-origin spawners and will not decrease the productivity of natural spawning fish. Assessment of the production of juvenile offspring prior to entering the ocean provides information on freshwater productivity and avoids ocean effects on the abundance and productivity of the population. However, there is a concern that the hatchery programs may lower the juvenile productivity in supplemented watersheds. The populations are managed under the concept of Proportionate Natural Influence (PNI; Hatchery Scientific Review Group, 2009), a framework that uses genetic modeling to estimate risk of hatchery introgression in natural populations and prescribes management benchmarks intended to allow hatchery programs to operate within an acceptable risk level to the natural population. PNI is composed of two metrics: Proportion of Hatchery Origin Spawners (pHOS; the proportion of hatchery fish in the naturally spawning population), and Proportion of Natural Origin Broodstock (pNOB; the proportion of natural-origin fish in a hatchery broodstock). Part of ongoing monitoring and evaluation (M&E) activities is to assess the relationship between pHOS and measures of juvenile productivity including the number of recruits to the smolt or emigrant populations and the average number of juveniles per redd. This report describes the statistical methods and results used to investigate these questions. In addition, we performed a power analysis to estimate the sample sizes required to detect an effect of pHOS on recruitment at varying pHOS effect strengths.

Methods

Section 3.1 of the monitoring and evaluation plan for the hatchery programs (Hillman et al. 2019) addresses freshwater juvenile productivity and presents two questions:

Question 1: Has the supplementation program changed the number of juveniles (smolts, parr, and/or emigrants) per redd within the supplemented population?

Question 2: Does the number of juveniles per redd decrease as the proportion of hatchery spawners increases?

The first question could not be assessed because it requires reference populations that are unavailable for the target populations. Furthermore, estimates of juvenile production are not available in a long enough time series to estimate the juvenile productivity before and after a hatchery program was implemented. However, the basic concepts of Question 1 are addressed in Questions 2, to the extent the available data allowed.

The second question was assessed in this report. The data and methods used to assess Question 2 are described below.

Data

All data were collected under the Monitoring and Evaluation Programs operated to assess the hatchery programs of Douglas County, Chelan County, and Grant County PUDs (Hillman et al. 2020; Snow et al. 2020). The abundance of spawners and redds was assessed by conducting spawning ground surveys. The number of redds was tabulated and for semelparous species, carcass recoveries were used to estimate the proportions of males and females by origin (hatchery and natural origin). Summer steelhead biological data for gender and origin were obtained at sampling points (Wells Dam and Twisp Weir). Abundance of semelparous spawners was estimated by expansion of redd counts based on the estimated portions of males to females, by origin, and assuming the number of redds created by a single female. Abundance of steelhead was estimated by adjusting dam and/or trap counts for proportions of fish estimated to return to the various tributaries in the Upper Columbia based on previous radio telemetry studies. Escapement estimates were adjusted to compensate for fall back and re-ascension at dams and to exclude fish removed from the spawning population through harvest and broodstock collection.

Juvenile abundance was estimated using rotary screw traps to sample migrating juveniles. Estimates were generated by conducting trap efficiency trials across a range of river flows, generating a regression model (flow versus trap efficiency), and using the model to predict the number of emigrants based on mean daily flow and daily captures. The daily estimates were summed for each year (season) to estimate the total abundance of emigrating juveniles per population. Juvenile steelhead were parsed into cohorts based on age determined through scales.

Spring chinook juveniles were yearlings assumed to be emigrating to the ocean. Age 0+ spring Chinook migrants were not included in the analysis because their life history and survival are not well understood and we preferred to focus on emigrating fish when possible. However, age 0+ spring Chinook that migrate for tributaries to main stem rivers may be an important component of the population (Copeland, et al. 2014). These age 0+ migrants would be assessed by the lower rotary screw trap population estimates as age 1 emigrants. Summer Chinook emigrants were subyearlings and assumed to be exhibiting an ocean-type life history. All age classes (excluding age 0) of steelhead from each cohort were included in the estimate of cohort emigrants because of the difficulty in knowing how to parse emigrating fish from those that are not leaving the freshwater system. Therefore, steelhead brood year cohorts include the entire range of observed age classes for each cohort. For the sake of simplicity, we refer to the steelhead juveniles caught in the screw traps as “emigrants.”

Douglas County PUD compiled the productivity data described above for the populations listed in Table 1. The size of the adult spawning stock, number of redds, and proportion of hatchery origin spawners (pHOS) were provided for each brood year, in addition to the number of smolts or emigrants. No data were available for Summer Steelhead from the Wenatchee River because juveniles have not been assigned to brood year cohorts in the available data (Josh Williams, WDFW, personal communication).

Table 1. Summary of spawner and recruitment data compiled by Douglas County PUD. The size of the adult spawning stock, number of redds, and proportion of hatchery origin spawners (pHOS) were provided for each brood year, in addition to the number of smolts or emigrants.

Species and Run	Population	Brood Years	Smolts	Emigrants[a]	Source	Comment
Spring Chinook	Chiwawa	1991–2017	X		Hillman et al. 2020	
Spring Chinook	Nason	2002–2017	X		Hillman et al. 2020	
Spring Chinook	White	2005–2017	X		Hillman et al. 2020	
Spring Chinook	Twisp	2003–2017	X		Snow et al. 2020	
Spring Chinook	Methow	2002–2017	X		Snow et al. 2020	
Summer Chinook	Wenatchee	1991–2018		X	Hillman et al. 2020	No emigrant data: 2010, 2011
Summer Chinook	Methow	2006–2018		X	Snow et al. 2020	No emigrant data: 2012
Summer Steelhead	Wenatchee				Hillman et al. 2020	No data
Summer Steelhead	Methow	2003–2015		X	Snow et al. 2020	
Summer Steelhead	Twisp	2003–2015		X	Snow et al. 2020	

a = Emigrant data were provided for Spring Chinook Salmon populations from the Chiwawa, Methow, and Twisp rivers but were not used in the analysis. On average, 52% of Chiwawa and 57% of Twisp spring Chinook emigrate from these rivers as age 0+ fish.

Statistical Methods

Spawner, redd count, and juvenile recruitment data were analyzed together with proportion of hatchery spawners to address Question 2, stated above (Hillman et al. 2019): does the number of juveniles per redd decrease as the proportion of hatchery spawners increases? The following statistical hypotheses were investigated:

$H0_{2.2.1.1}$: There is no association between the proportion of hatchery-origin spawners (pHOS) and the residuals from the smooth hockey stick stock-recruitment curve; $\rho = 0$.

$H0_{2.2.1.2}$: The slope between proportion of hatchery spawners and juveniles/redd is ≥ 0.

Three stock-recruitment models were used to account for density dependent mortality in assessment of the two hypotheses. The Smooth Hockey Stick model assumes that recruitment increases quickly at low levels of spawners and asymptotes to a maximum recruitment level as spawners increase:

$$R = R_\infty \left(1 - e^{-\left(\frac{\alpha}{R_\infty}\right)S}\right) \tag{1}$$

where R = recruits and S = spawners for a given brood year, R_∞ is the maximum number of recruits (population carrying capacity), and α is the slope at low levels of spawner abundance (Froese 2008).

The Beverton-Holt model also assumes asymptotic growth to a maximum:

$$R = \frac{\alpha S}{\beta + S} \tag{2}$$

where R = recruits and S = spawners for a given brood year, α is the asymptotic maximum number of recruits (population carrying capacity), and β is the predicted spawner abundance required to produce half the maximum recruits (Hilborn and Walters 1992).

The Ricker model assumes that recruitment increases at lower levels of spawners and declines at higher spawner abundance:

$$R = \alpha S e^{-\beta S} \tag{3}$$

where R = recruits and S = spawners for a given brood year, α is the increase in recruits per spawner at low levels of spawners and β is the intensity of the decrease in recruitment at high levels of spawner abundance (Ricker 1954). The maximum number of recruits is defined as $K = (\alpha/\beta)e^{-1}$.

Modeling assumptions were (based on Hillman et al. 2019):

1. Density-dependent mortality: The brood instantaneous mortality rate is proportional to the number of spawners for the brood year (Ricker 1954).

2. Lognormal errors: The variation in recruitment about the modeled recruitment for a given spawner abundance is lognormally distributed and acts multiplicatively (Quinn and Deriso 1999).

3. Negligible measurement error: Measurement error in spawning stock size and recruitment is small relative to the range of observed spawning stock sizes and variation in recruitment, respectively (Hilborn and Walters 1992).

4. Stationarity: The average stock-recruitment relationship is constant over time, with the possible exception of effects of changes in pHOS (Hilborn and Walters 1992).

The proportion of hatchery origin spawners may have the effect of lowering the maximum recruitment or recruits per spawner. The pHOS variable may be introduced into the Beverton-Holt model to reduce maximum recruitment when pHOS is high as follows:

$$R = \frac{\alpha e^{-\beta_2 P_{HOS}} S}{\beta + S} \tag{4}$$

or equivalently

$$ln(R/S) = ln(\alpha) - ln(\beta + S) - \beta_2 P_{HOS} \tag{5}$$

In Equations (4) and (5), the maximum number of recruits per brood year is α when pHOS is 0 and decreases asymptotically to $\alpha e^{-\beta_2}$ when pHOS is 1.

The pHOS variable may be introduced into the Ricker model in such a way as to lower the slope in the spawner-recruitment curve at low levels of spawner abundance as follows:

$$R = \alpha e^{-\beta_2 P_{HOS}} S e^{-\beta S} \tag{6}$$

or equivalently

$$ln(R/S) = ln(\alpha) - \beta_2 P_{HOS} - \beta S. \tag{7}$$

Alternatively, if higher levels of pHOS are expected to increase the intensity of the decrease in recruitment at high spawner levels, then pHOS may be incorporated as follows:

$$R = \alpha S e^{-(\beta+\beta_2 P_{HOS})S} \tag{8}$$

or equivalently

$$ln(R/S) = ln(\alpha) - (\beta + \beta_2 P_{HOS})S. \tag{9}$$

Both models in Equation (6) and Equation (8) result in lower maximum recruitment for higher pHOS if $\beta_2 > 0$.

Hypothesis H0$_{2.2.1.1}$ Effect of pHOS on Recruitment:

Hypothesis H0$_{2.2.1.1}$ was investigated by fitting a stock-recruitment model to the available data and regressing the residuals from the model against pHOS. The Smooth Hockey Stick model, Beverton-Holt model, and Ricker model were considered.

Modeling assumption 1 was assessed by investigating the linear relationship between the log of recruits per spawner with the number of spawners; a negative relationship was consistent with density-dependent mortality. Modeling assumption 2 was assessed via quantile-quantile plots and Shapiro-Wilk tests (Shapiro and Wilk 1965) performed on the residuals from the fitted stock-recruitment model on the log scale. Modeling assumption 4 was assessed by plotting model residuals versus brood year and examining for autocorrelation. The available data did not allow for assessment of assumption 3; violation of assumption 3 would result in lower ability to detect a relationship between spawner abundance and recruitment (Hilborn and Walters 1992).

The fits of the three stock-recruitment models in Equations (1), (2), and (3) to the data were ranked using AICc (Burnham and Anderson 2002). Models with ΔAICc$\leq$2 compared to the minimum observed AICc were used to assess the association between residuals and pHOS. The Smooth Hockey Stick model was included regardless of its AICc rank. Additionally, bias, uncertainty, and correlation in estimates of model parameters were estimated using bootstrapping with at least 1,000 bootstrap samples. Point estimates, 95% bootstrap confidence intervals, and bootstrap correlation coefficients between model parameters were reported for each model. In the event that bootstrapping failed, asymptotic (normal theory) confidence intervals and correlation coefficients were provided. Bias and correlation were considered in assessment of model fit.

For a given model, the residual for brood year i $(i = 1, \dots, n)$ was defined as

$$r_i = R_i - \hat{R}_i, \tag{10}$$

where R_i is the observed number of recruits for brood year i, and $\hat{R}_i$ is the predicted number of recruits from the model for brood year i. The association between the residuals r_i $(i = 1, \dots, n)$

and pHOS was investigated using the Pearson correlation coefficient and visual inspection of the fitted linear model

$$r_i = \beta_0 + \beta_1 pHOS_i + \epsilon_i, \tag{11}$$

for regression coefficients β_0 and β_1 and random error $\epsilon_i \sim N(0, \sigma_r^2)$. Hypothesis H02.2.1.1 was rejected if the Pearson correlation coefficient between r_i and pHOS was negative and significantly different from 0 (P<0.05). In this event, we concluded that there was evidence that hatchery fish may be reducing the productivity of the wild population.

An additional assessment of the effect of pHOS on juvenile productivity was performed by fitting the pHOS-enhanced stock-recruitment models in Equations (4), (6), and (8) and testing whether $\beta_2 = 0$ using likelihood ratio tests.

Hypothesis H0$_{2.2.1.2}$ Effect of pHOS on Juveniles per Redd:

Hypothesis H02.2.1.2 was investigated in two ways. First, the ratio of recruits per redd was modeled using pHOS in a linear model:

$$\frac{R_i}{S_i} = \beta_0 + \beta_1 pHOS_i + \epsilon_i, \tag{12}$$

where R_i is the observed number of recruits for brood year i, S_i is the observed number of redds for brood year i, β_0 and β_1 are regression coefficients, and $\epsilon_i \sim N(0, \sigma_r^2)$. The estimated regression coefficient $\hat{\beta}_1$ was tested against 0 using a one-sided t-test. If $\hat{\beta}_1$ was significantly <0 (P<0.05) (equivalently, significant negative Pearson correlation coefficient), we rejected hypothesis H02.2.1.2 and concluded there was evidence that hatchery fish may be reducing the productivity of the wild population. Modeling assumptions were that the error terms ϵ_i $(i = 1, \dots, n)$ are independent normal random variables with mean 0 and common variance (σ_r^2). The observed error terms from the fitted model in Equation (12) were examined for non-normality using quantile-quantile plots and Shapiro-Wilk tests (Shapiro and Wilk 1965). Heteroscedasticity was examined using plots of $\hat{\epsilon}_i$ against fitted values of R_i/S_i. In the event of heteroscedasticity and non-normal errors, R_i/S_i was log-transformed in Equation (12).

The approach described above assumes that there is no density dependence in recruits per redd, that is, that any density dependence observed in analysis of hypothesis H02.2.1.1 occurs during spawning rather than during incubation and rearing. This assumption was assessed by inspection of recruits per redd compared to redd counts: a negative association (i.e., negative Pearson correlation coefficient) was interpreted as evidence of density dependence after spawning. In this event, an additional assessment was implemented in which we modeled recruits per redd as a function of both redd counts and pHOS using the Beverton-Holt model in Equation (5) and the Ricker model in Equation (7), using redd counts in place of spawner counts. A negative association between pHOS and juveniles per redd was assessed by the 95% bootstrap confidence interval for β_2 using at least 1,000 bootstrap samples. In the event that bootstrapping failed, asymptotic (normal theory) confidence intervals and correlation coefficients were provided. If the 95% confidence interval was entirely >0, it was concluded that there was a negative association between pHOS and juveniles per redd, and that hatchery fish may result in lowered juvenile productivity of naturally spawning fish.

Power Analysis

The statistical power was computed to detect a reduction in mean juvenile recruitment with Type I error probability of $\alpha = 0.10$ when the actual reduction in mean recruitment associated with a change in the pHOS level was 5%. Power was computed at varying sample sizes, where sample size = number of years of observations, and both with and without measurement error in the number of spawners and pHOS. The stock-recruitment model was a Ricker model with parameters taken from the Chiwawa River spring Chinook Salmon population. The Chiwawa population was selected because it has the longest time series of stock and juvenile recruitment data of the populations available and the stock recruitment curves have fit the juvenile productivity from this population relatively well (Buchanan and Townsend 2021). Power was calculated for sampling sizes from N=5 to N=100 years for varying levels of pHOS effect size, β_P. (see Appendix B for details on the power analysis).

Results

Spring Chinook Salmon

Chiwawa River Spring Chinook salmon adult spawner, smolt recruitment, pHOS, and redd count data were available for the 1991–2017 brood years. Adult stock abundance (spawners) ranged from 33 in 1995 to 2,032 in 2011 and averaged 723, and smolt recruitment ranged from 3,830 in 1995 to 82,845 in 2002 and averaged 36,318. Redd counts averaged 328.2 (range = 13 to 1,078), and pHOS averaged 0.508 (range = 0.00 to 1.00).

Nason Creek Spring Chinook data were available for the 2002–2017 brood years. Spawner abundance ranged from 132 (2017) to 702 (2011) and averaged 398, and smolt recruitment ranged from 930 (2014) to 8,696 (2005) and averaged 4,774. Redd counts averaged 176.9 (range = 68 to 413), and pHOS averaged 0.599 (range = 0.20 to 0.86). The analysis was performed with and without the low smolt count of 930 from the 2014 brood year.

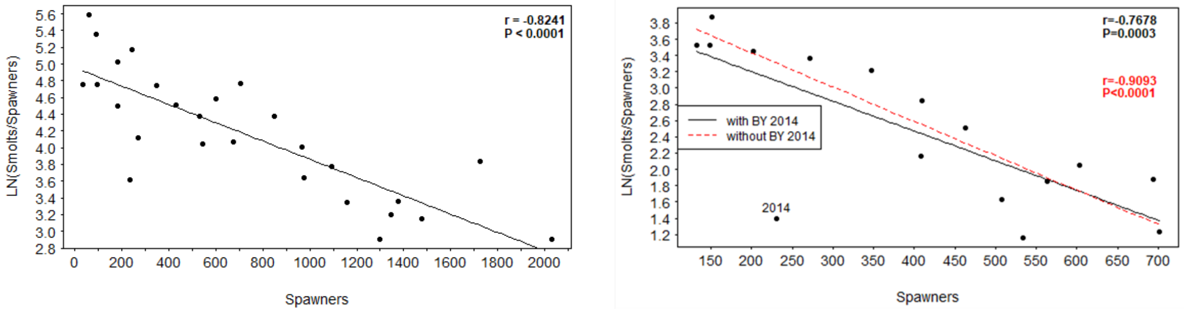
White River Spring Chinook data were available for the 2005–2017 brood years. Spawner abundance ranged from 31 (2017) to 173 (2009) and averaged 94, and smolt recruitment ranged from 580 (2014) to 11,170 (2016) and averaged 5,079. Redd counts averaged 44.1 (range = 16 to 86), and pHOS averaged 0.412 (range = 0.00 to 0.75). The analysis was performed with and without the low smolt count of 580 from the 2014 brood year.

Twisp River Spring Chinook data were available for the 2003–2017 brood years. Spawner abundance ranged from 43 (2003) to 341 (2004) and averaged 165, and smolt recruitment ranged from 900 (2003) to 16,415 (2006) and averaged 5,295. Redd counts averaged 79.3 (range = 18 to 145), and pHOS averaged 0.52 (range = 0.28 to 0.76).

Methow River Spring Chinook salmon data were available for the 2002–2017 brood years. Spawner abundance ranged from 417 (2017) to 2,692 (2011) and averaged 1,417, and smolt recruitment ranged from 5,163 (2007) to 51,325 (2010) and averaged 23,624. Redd counts averaged 705 (range = 210 to 1,366), and pHOS averaged 0.77 (range = 0.57 to 0.97).

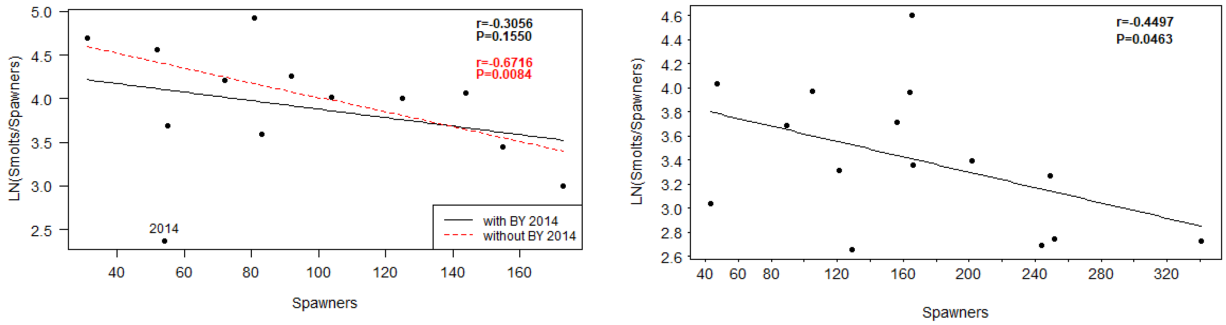
Hypothesis $H0_{2.2.1.1}$ *Effect of pHOS on Recruitment:*

Negative linear relationships between spawners and smolt recruitment indicated the presence of density dependence in mortality in one or more life stages between spawner data collection and smolt data collection in the Chiwawa, Nason, and Twisp populations. Weak negative linear relationships were observed between spawners and smolt recruitment in the White and Methow, but were non-significant, providing inconclusive evidence of density dependence in mortality between the spawning and smolt life stages. Without the 2014 brood year, density dependent mortality was detected in the White River population as well (Figure 1).



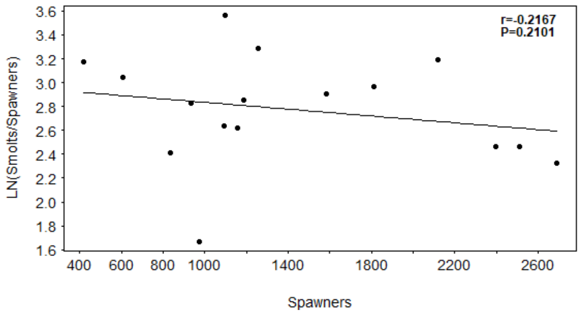
Chiwawa

Nason



White

Twisp



Methow

Figure 1. Smolts per spawner (log scale) versus spawner abundance for each population, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. Plots with and without the 2014 brood year (possible outlier) are shown for Nason and White.

The Smooth Hockey Stick, Beverton-Holt, and Ricker stock-recruitment models were attempted to be fit to the spawner and smolt data for each population. All three models were successfully fit to the data from the Chiwawa, White, Twisp, and Methow populations (Figure 2). Only the Ricker model could be fit to the Nason Creek data (Figure 3). For the Chiwawa, White, Twisp, and Methow populations, there was little difference in the model fits among the three models, demonstrated by the fitted recruitment curves, AICc, and correlation coefficients between the model parameters (Figure 2; Table 2). There was high uncertainty in the model fits for the White, Twisp, and Methow populations, as seen by the wide confidence intervals on parameter estimates (Table 2). For Nason Creek, the pattern of observed spawner and smolt data did not support the assumption of asymptotic growth in recruitment as spawner abundance increases that is required by the Smooth Hockey Stick and Beverton-Holt models, and neither of those models could be fit to the Nason Creek data. The Ricker model was fit to Nason Creek data with and without the 2014 brood year (Figure 3); when the 2014 brood year was included, the model assumption of lognormal errors was not supported.

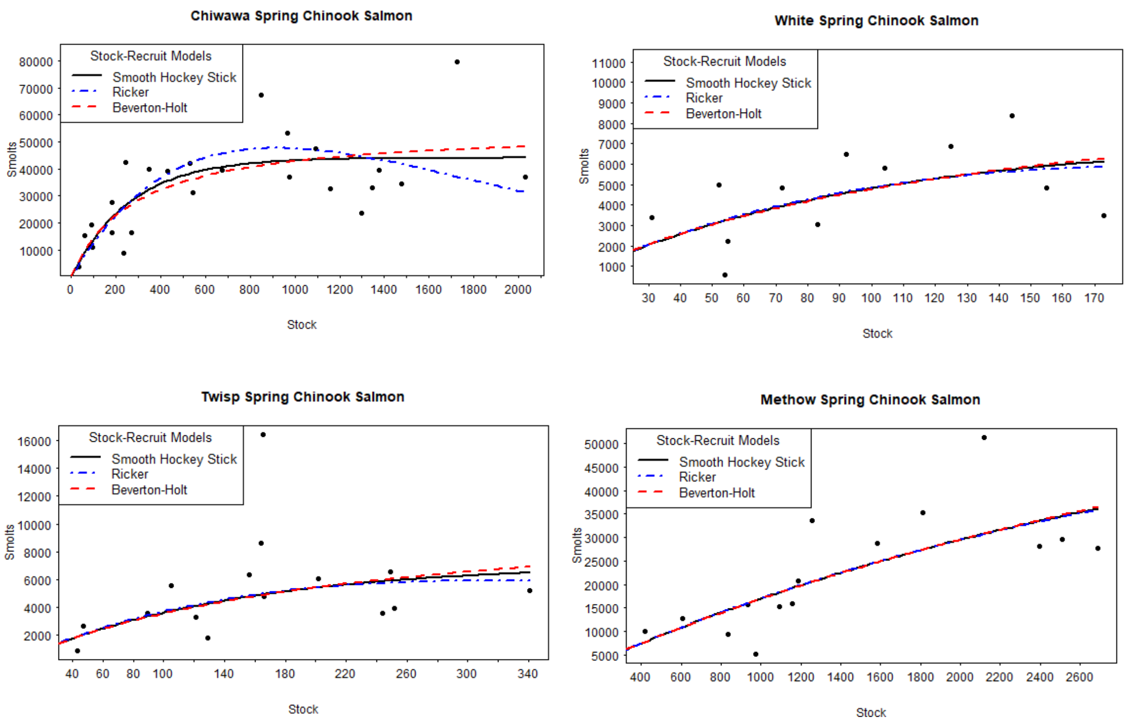


Figure 2. Stock-recruitment models fit to smolt and spawner data for Spring Chinook salmon populations (plot for White population includes 2014 brood year).

Table 2. Fitted stock-recruitment models for smolts and stock (spawner) data for each Spring Chinook salmon population. Confidence intervals were estimated using bootstrap with at least 1,000 bootstrap samples. Correlation = Pearson correlation coefficient between parameter estimates from bootstrap samples. Model equations are defined in Equations (1), (2), and (3). ΔAICc represents change in AICc compared to model with minimum AICc for the population. (Results include 2014 brood year for all populations). *Only the Ricker model could be fit to the Nason Creek data.

Population	Model*	ΔAICc	Parameter[a]	Parameter Estimates	95% CI	Correlation
Chiwawa	Smooth Hockey Stick	0.00	α	168	118.2 – 248.7	α, R∞: -0.39
			R∞	44,090	35,095 – 56,732	
	Beverton-Holt	0.75	α	54,825	40,678 – 77,093	α, β: 0.87
			β	278	134.5 – 559.0	
	Ricker	0.71	α	141	109.2 – 184.3	α, β: 0.80
			β	0.0011	0.0008 – 0.0014	

Population	Model*	ΔAICc	Parameter[a]	Parameter Estimates	95% CI	Correlation
			K	47,760	40,825 – 56,520	
Nason	Smooth Hockey Stick	NA	α	NA	NA	α, R_∞: NA
			R_∞	NA	NA	
	Beverton-Holt	NA	α	NA	NA	α, β: NA
			β	NA	NA	
	Ricker	NA	α	51.1	25.7 –89.2	α, β: 0.89
			β	0.0037	0.0022 – 0.0052	
			K	5,144	3,710 – 7,011	
White	Smooth Hockey Stick	0.08	α	79.7	44.7 – 262.1	α, R_∞: -0.24[b]
			R_∞	7,183	3,516 – 60,989	
	Beverton-Holt	0.14	α	11,011	5,286 – 185,892	α, β: 0.96
			β	130	32 – 3,591	
	Ricker	0.00	α	78.9	35.5 – 180.4	α, β: 0.90
			β	0.0049	< 0.0001 – 0.0137	
			K	5,632	4,571 – 9,125	
Twisp	Smooth Hockey Stick	0.31	α	51.2	30.7 – 146.7	α, R_∞: -0.20[c]
			R_∞	7,104	4,344 – 36,313	
	Beverton-Holt	0.62	α	11,295	6,317 – 101,201	α, β: 0.99
			β	216	75 – 3,103	
	Ricker	0.00	α	51.2	29.7 – 93.6	α, β: 0.88
			β	0.0032	< 0.0001 – 0.0064	
			K	5,926	4,267 – ∞	
Methow	Smooth Hockey Stick	0.02	α	19.7	14.7 – 37.7	α, R_∞: -0.30[d]
			R_∞	65,051	23,577 – 549,603	
	Beverton-Holt	0.04	α	115,394	32,755 – 1,382,406	α, β: 0.99
			β	5,806	785 – 82,314	
	Ricker	0.00	α	19.6	11.6 – 32.7	α, β: 0.88
			β	0.0001	< 0.0001 – 0.0005	
			K	50,572	22,637 – ∞	

a = Estimated maximum recruitment parameters are: R_∞ for the Smooth Hockey Stick model, α for the Beverton-Holt model, and $K = (\alpha/\beta)e^{-1}$ for the Ricker model.

b = Correlation coefficient between α and R_∞ is uninformative because parameter estimates were inversely related. The correlation coefficient between $1/\alpha$ and R_∞ = 0.6241.

c = Correlation coefficient between α and R_∞ is uninformative because parameter estimates were inversely related. The correlation coefficient between $1/\alpha$ and R_∞ = 0.4951.

d = Correlation coefficient between α and R_∞ is uninformative because parameter estimates were inversely related. The correlation coefficient between $1/\alpha$ and R_∞ = 0.7281.

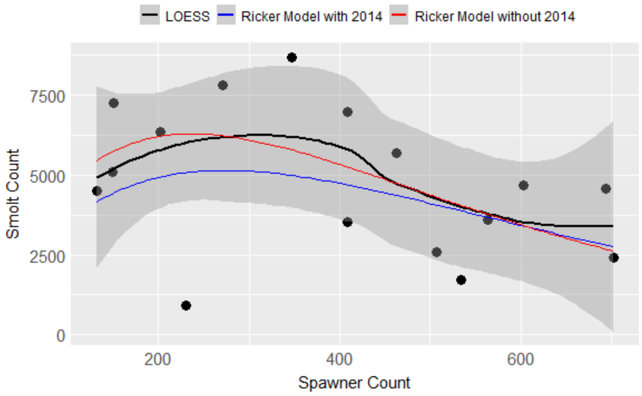
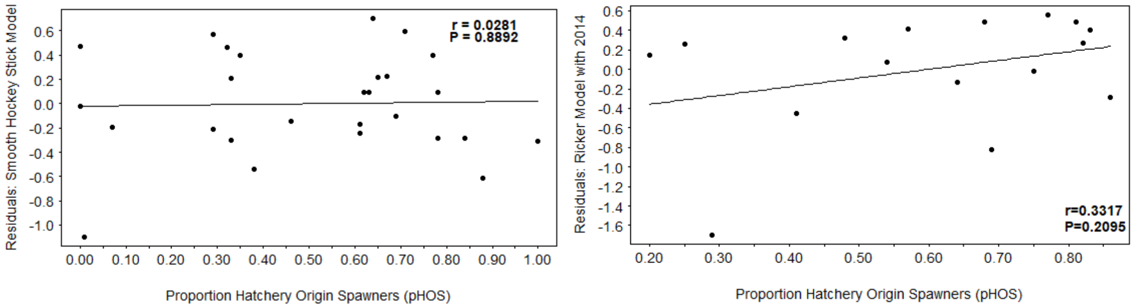


Figure 3. Stock and smolt data with fitted LOESS curve and Ricker Model (with and without data from 2014) for Nason Creek Spring Chinook Salmon, 2002–2017.

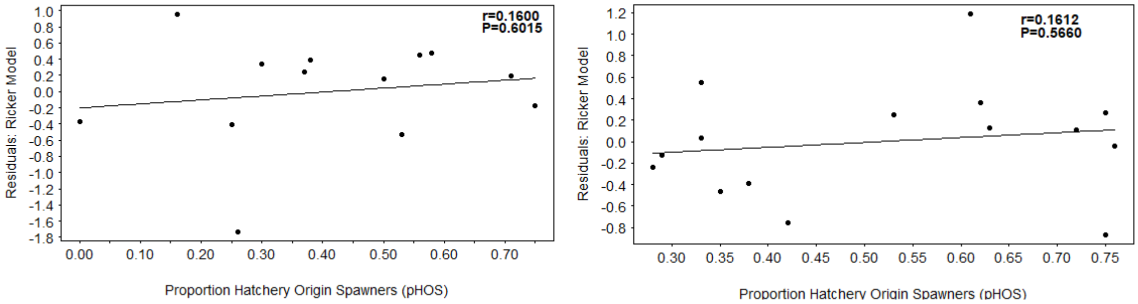
The residuals from all fitted models were compared to pHOS for each population using correlation analysis. Correlation coefficients between residuals and pHOS were not significantly different from 0 for any population (Figure 4). Additionally, likelihood ratio tests of the effect of pHOS on the Beverton-Holt and Ricker models were non-significant for each population (Table 3). Thus, there was no evidence to suggest that higher proportions of hatchery spawners were associated with lower juvenile productivity for spring Chinook Salmon in the populations. When the 2014 brood year was removed from the Nason Creek and White River data sets, model residuals were again uncorrelated with pHOS (r=0.1614, P=0.5655 for Nason Creek; r=-0.0184 to 0.0599, P≥0.8533 for White River) and likelihood ratio tests of the effect of pHOS remained insignificant (Table 3).

There were a number of limitations in the data and analyses for the majority of the populations of Spring Chinook salmon for hypothesis $H0_{2.2.1.1}$. Only the Chiwawa population had as many as 20 years of data; the shorter time series available for the other populations provided lower statistical power to detect an effect of pHOS. Modeling assumptions were not well-supported by the data for some populations. In particular, the assumption of lognormal errors was not supported for Nason Creek or White River when the 2014 brood year was included in the analysis; in both cases, the lognormal assumption was better supported when 2014 was omitted. For the Twisp population, negative autocorrelation in the model residuals at a time lag of 3 years violated the assumption of non-stationarity and suggested that these stock-recruitment models do not adequately account for the population dynamics. For the White, Twisp, and Methow populations, model parameters had wide confidence intervals that included values far beyond the range of the observed data and parameter estimates were highly correlated; both these conditions reflect poor model fit and increase uncertainty in model predictions and the resulting residual analysis. These limitations preclude firm conclusions and it is possible that a relationship may exist between pHOS and juvenile productivity that was not observable using the available data and analyses.



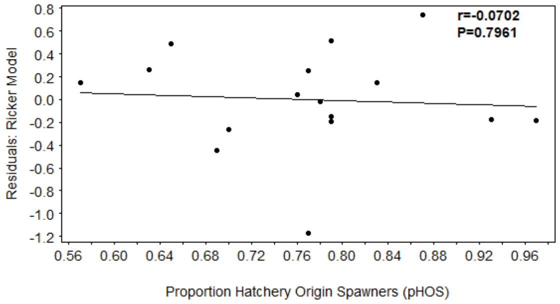
Chiwawa - Smooth Hockey Stick

Nason – Ricker (with 2014)



White – Ricker (with 2014)

Twisp - Ricker



Methow - Ricker

Figure 4. Proportion Hatchery Origin Spawners verses Residuals from stock recruit model. P-value from two-sided t-test and Pearson correlation coefficient (r) are provided in the figure. The stock-recruitment model with the lowest AICc value for each population was chosen for this figure. Plots with the 2014 brood year (possible outlier) are shown for Nason and White.

Table 3. Results from likelihood ratio tests of the effect of pHOS on Beverton-Holt and Ricker Models. Value = P-value from chi-squared test with df = 1.

Population	Beverton-Holt	Ricker
Chiwawa	0.9421	0.8181
Nason	NA	0.1420[a]
White	0.6070[b]	0.5518[b]
Twisp	0.4524	0.5256
Methow	0.7635	0.7645

a = P=0.5092 when brood year 2014 was omitted for Nason Creek.

b = P=0.9492 for the Beverton-Holt model and P=0.8331 for the Ricker model when brood year 2014 was omitted for White river.

Hypothesis $H0_{2.2.1.2}$ Effect of pHOS on Juveniles per Redd:

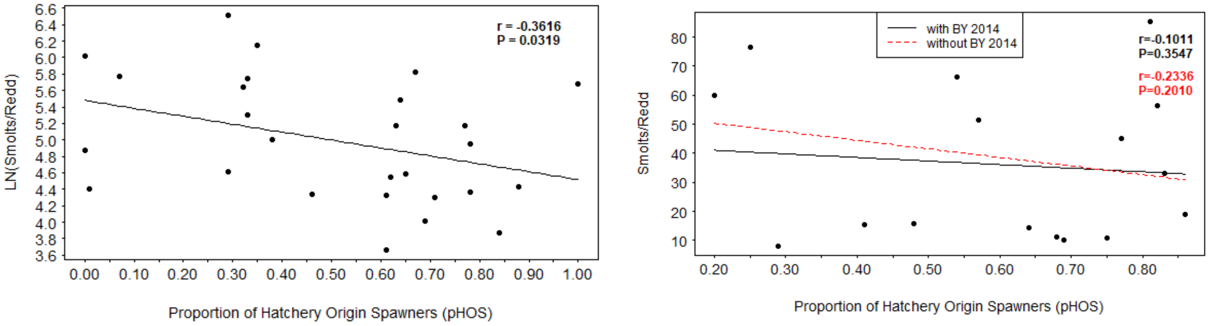
The relationship between average smolts per redd and pHOS was investigated for each Spring Chinook salmon population. A weak negative association was found between smolts per redd and pHOS for Chiwawa River Spring Chinook Salmon (P=0.0319; Figure 5). However, redd count was positively associated with pHOS (P=0.0280) and there was a strong pattern of post-spawning density dependence apparent from examination of the smolts per redd plotted against the redd counts (Figure 6). Thus, it is possible that the negative association between smolts per redd and pHOS may have resulted from the density dependence. The relationship between smolts per redd and pHOS was examined using the Ricker and Beverton-Holt stock-recruitment models in order to account for density dependence effects, with redds used in place of spawner counts. The Beverton-Holt model had considerably better fit than the Ricker model on the basis of AICc rank (ΔAICc = 5.81 compared to Ricker model) and examination of model residuals (not shown). The fitted Beverton-Holt model for smolts per redd was (Table 4):

$$ln(R/S) = ln(55{,}479) - 0.0343P_{HOS} - ln(117 + S).$$

The 95% bootstrap confidence interval for the effect of pHOS (i.e., β_2 in Equation (5)) was (-0.5443, 0.6421). Because this confidence interval included both positive and negative values, we concluded that there is no evidence of a negative association between pHOS and smolts per redd for Chiwawa Spring Chinook Salmon after adjusting for density dependence.

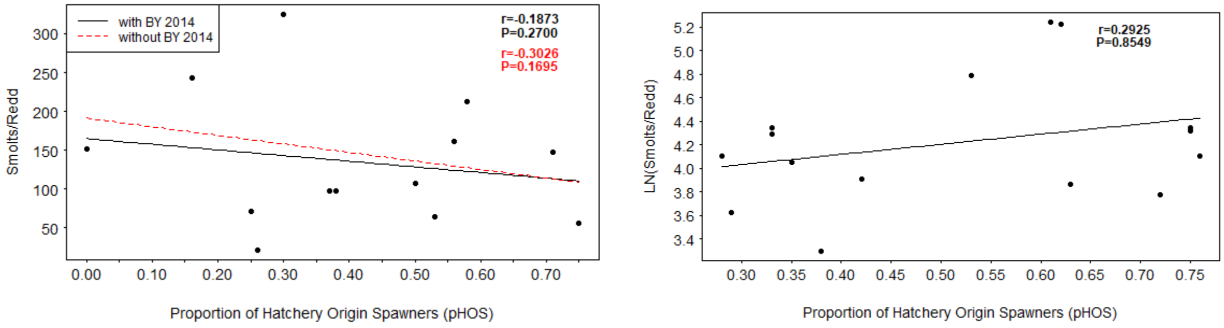
There was no evidence of a negative linear association between smolts per redd and the proportion of hatchery spawners (pHOS) in the other Spring Chinook salmon populations (Figure 5). There was evidence of post-spawning density dependence in Nason and Twisp (Figure 6) and of a linear association of redd count and pHOS in the Methow at the 10% level (P=0.0919). The relationship between smolts per redd and pHOS was examined using the Ricker and Beverton-Holt stock-recruitment models in order to account for any density dependence effects, with redds used in place of spawner counts. In populations where models could be fit to the data, the 95% bootstrap confidence intervals for the effect of pHOS (i.e., β_2) included zero. Because the confidence intervals included both positive and negative values, we concluded that there is no evidence of a negative association between pHOS and smolts per redd for these populations after adjusting for density dependence (Table 4). Results were unchanged whether or not the 2014 brood year was included for the Nason and White populations.

The analysis of the relationship of smolts per redd to pHOS suffered from the same limitations as the analysis of smolts versus pHOS (hypothesis H02.2.1.1). Sample sizes were small for all populations except the Chiwawa, and there was potentially large measurement error in the data for all populations. The modeling assumption of lognormal errors was not supported by the data for Nason Creek, parameter confidence intervals were wide for all models that could be fit for the Nason, White, and Twisp populations, and there was negative autocorrelation observed in the residuals for the Twisp data. Additionally, the Beverton-Holt model could not be fit for the Nason and Methow populations, and the estimated model parameter values were not consistent with their usual interpretation for the White, Twisp, and Methow data sets. These observations reflect poor model fit of the stock-recruitment models for the Nason, White, Twisp, and Methow populations, which results in lower confidence in the estimated model parameters and lower ability to detection any relationship between pHOS and smolts per redd using the available data.



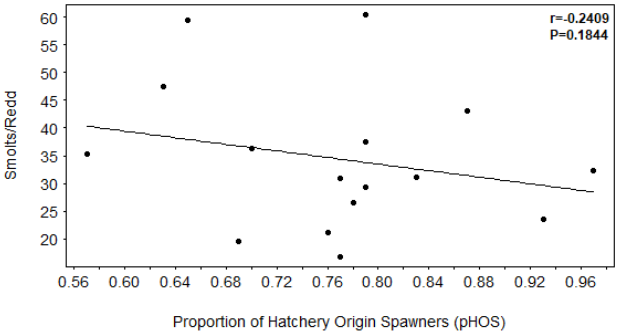
Chiwawa

Nason



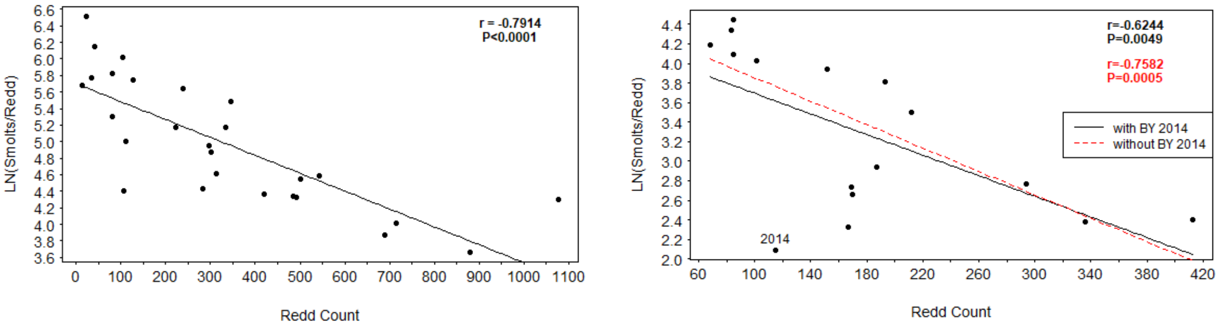
White

Twisp

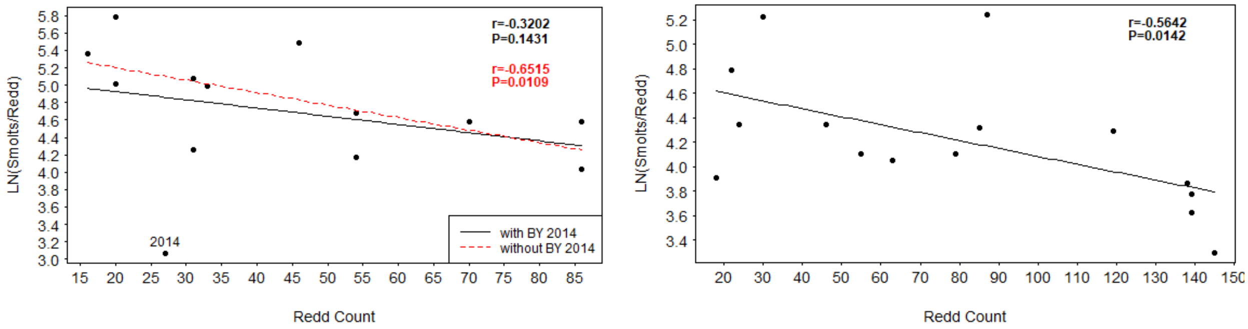


Methow

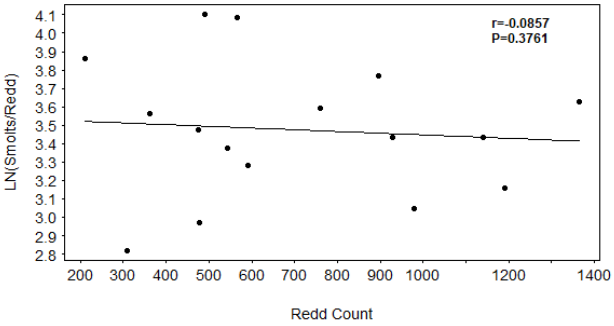
Figure 5. Smolts per redd versus proportion of hatchery origin spawners (pHOS) for each population, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. Plots with and without the 2014 brood year (possible outlier) are shown for Nason and White.



Chiwawa Nason



White Twisp



Methow

Figure 6. Smolts per redd (log scale) versus redd count for each population, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. Negative slope indicates post-spawning density dependence. Plots with and without the 2014 brood year (possible outlier) are shown for Nason and White.

Table 1. Fitted stock-recruitment models for smolts per redd for each Spring Chinook salmon population, including effect (β_2) of proportion of hatchery origin spawners (pHOS). Confidence intervals were estimated using bootstrap with at least 1,000 bootstrap samples. Model equations are defined in Equations (5) and (7). ΔAICc represents change in AICc compared to model with minimum AICc for the population. (Results include 2014 brood year for all populations). *Only the Ricker model could be fit to the Nason Creek and Methow River data.

Population	Model*	ΔAICc	Parameter	Parameter Estimates	95% CI
Chiwawa	Beverton-Holt	0.00	α	55,479	35,197 – 95,959
			β	117	57.9 – 242.2
			β_2	0.0343	-0.5443 – 0.6421
	Ricker	5.81	$\ln(\alpha)$	5.7328	5.2646 – 6.2477
			β	0.0021	0.0014 – 0.0032
			β_2	0.0872	-0.6880 – 0.9010
Nason	Beverton-Holt	NA	α	NA	NA
			β	NA	NA
			β_2	NA	NA
	Ricker	NA	$\ln(\alpha)$	3.8891	2.2758– 4.8782
			β	0.0058	0.0033 – 0.0107
			β_2	-0.7001	-2.7076 – 0.8269
White	Beverton-Holt	0.00	α	9,478	4,270 – 173,640
			β	48.1	12.9 – 1,315
			β_2	-0.0887	-1.6125 – 1.6392
	Ricker	0.10	$\ln(\alpha)$	5.0979	3.5461 – 6.3336
			β	0.0096	-0.0080 – 0.0228
			β_2	-0.0655	-2.2529 – 1.5695
Twisp	Beverton-Holt	0.78	α	8,020	3,952 – 39,818
			β	103	40 – 724
			β_2	-0.7782	-1.9437 – 0.4321
	Ricker	0.00	$\ln(\alpha)$	4.3238	3.6525 – 5.0395
			β	0.0063	0.0011 – 0.0108
			β_2	-0.7621	-2.0433 – 0.1133
Methow	Beverton-Holt	NA	α	NA	NA
			β	NA	NA
			β_2	NA	NA
	Ricker	NA	$\ln(\alpha)$	4.0380	2.6075 – 5.3023
			β	< 0.0001	< 0.0001 – 0.0006
			β_2	0.7383	-1.2657 – 2.3241

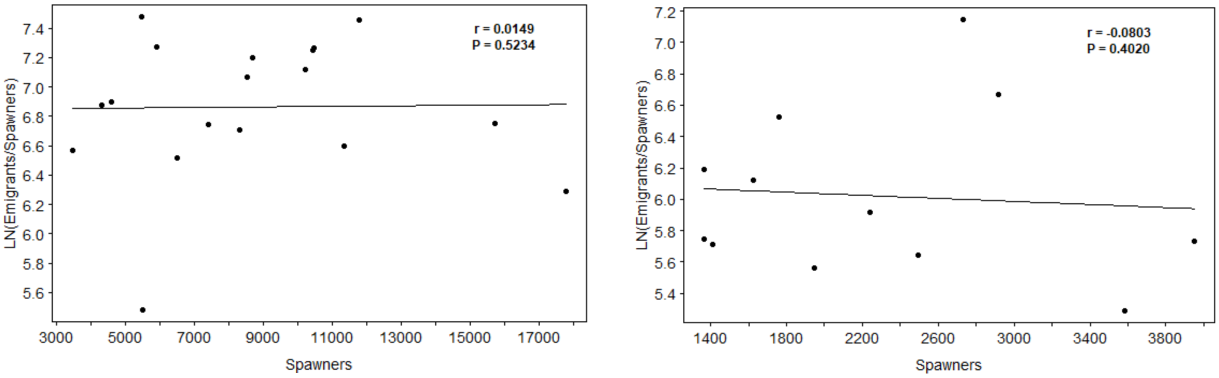
Summer Chinook Salmon

Wenatchee River Summer Chinook adult spawner, emigrant, pHOS, and redd count data were available for the 1999–2018 brood years (no emigrant count for 2010 and 2011). Adult stock abundance (spawners) ranged from 3,473 in 2018 to 17,792 in 2006 and averaged 8,695. Emigrant counts ranged from 1,322,383 in 2000 to 20,426,149 in 2003 and averaged 9,118,268. Redd counts averaged 3,600.5 (range = 1,510 to 8,896), and pHOS averaged 0.176 (range = 0.06 to 0.31). The 2000 and 2003 brood years were identified as possible outliers in emigrant counts, and analysis results were investigated for their sensitivity to inclusion of these brood years.

Methow River Summer Chinook data were available for the 2006–2018 brood years (no emigrant count for 2012). Spawner abundance ranged from 1,364 in 2007 to 3,952 in 2015 and averaged 2,333, and emigrant count ranged from 427,193 in 2017 to 3,465,247 in 2006 and averaged 1,099,370. Redd counts averaged 909.5 (range = 591 to 1,551), and pHOS averaged 0.391 (range = 0.11 to 0.53).

Hypothesis $H0_{2.2.1.1}$ Effect of pHOS on Recruitment:

A positive but non-significant linear relationship was observed between spawners and emigrant count in the Wenatchee population, indicating no evidence of density dependence in mortality between spawner data collection and emigrant data collection (Figure 7). In the Methow population, a slightly negative linear relationship between spawners and emigrant count suggested the presence of density dependence in mortality in one or more life stages between spawner data collection and emigrant data collection, but the relationship was not statistically significant (P=0.4020; (Figure 7).

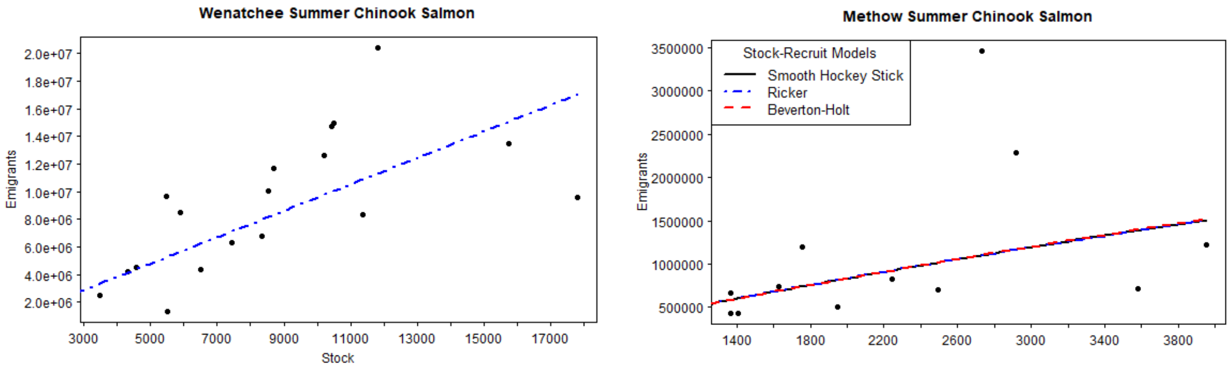


Wenatchee Methow

Figure 7. Emigrants per spawner (log scale) versus spawner abundance for Wenatchee and Methow Rivers Summer Chinook Salmon, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope.

An attempt was made to fit the Smooth Hockey Stick, Beverton-Holt, and Ricker stock-recruitment models to the spawner and emigrant count data from the Wenatchee Summer Chinook salmon populations, but only the Ricker model could be fit when the full data were used (Figure 8; Table 5). The Ricker model residuals were not correlated with pHOS (r=-0.0985, P=0.6973; Figure 9), and the likelihood ratio test of the effect of pHOS on the Ricker model was also non-significant (P=0.6787). When the 2003 brood year was omitted as a possible outlier, all three stock-recruitment models could be fit to the Wenatchee spawner and emigrant data and had common AICc weight (ΔAICc≤0.0072); pHOS was not associated with the residuals from any of the models (P≥0.7155). When the 2000 brood year was omitted as a possible outlier, all three models could be fit to the data and the Ricker model was selected (ΔAICc≤0.1126); model residuals were again not significantly associated with pHOS levels (P≥0.6430), and the likelihood ratio test of the pHOS was also not significant (P≥0.6113). Thus, there was no evidence to suggest that higher proportions of hatchery spawners were associated with lower juvenile productivity for Summer Chinook salmon in the Wenatchee River.

The Smooth Hockey Stick, Beverton-Holt, and Ricker stock-recruitment models were each fit to the spawner and emigrant data for the Methow (Figure 8). There was little difference in the model fits among the three models (ΔAICc≤0.02), but the Ricker model had the lowest AICc value and intermediate correlation between parameter estimates (Table 5). The residuals from each of the three models were not correlated to pHOS (r=-0.0059, P=0.9856 for each model; Figure 9). Additionally, likelihood ratio tests of the effect of pHOS on the Beverton-Holt and Ricker models were non-significant (P≥0.9838). There was no evidence to suggest that higher proportions of hatchery spawners were associated with lower juvenile productivity for Summer Chinook Salmon in the Methow River.



Wenatchee Methow

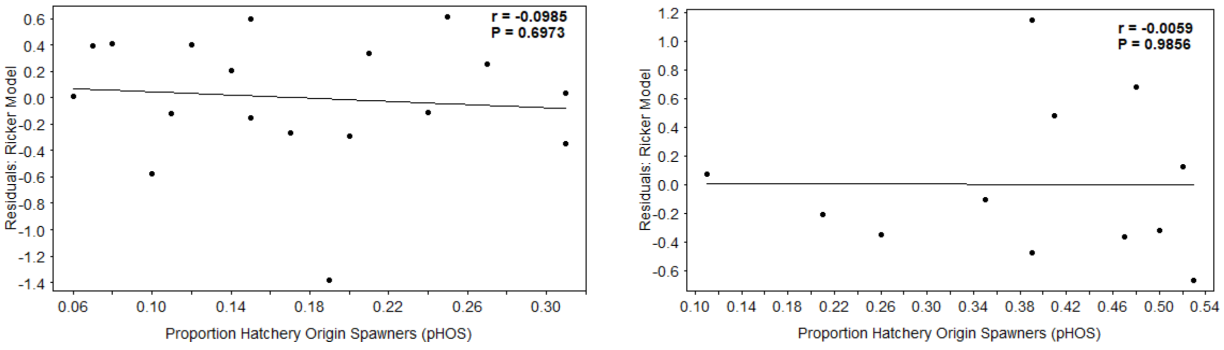
Figure 8. Stock-recruitment models fit to emigrant and spawner data for the Wenatchee and Methow River Summer Chinook Salmon. The Ricker stock-recruitment model is shown for the Wenatchee population.

Table 5. Fitted stock-recruitment models for emigrants and stock (spawner) data from Wenatchee River, 1999–2018 (without 2010, 2011) and Methow River, 2006–2018 (without 2012) Summer Chinook Salmon. Confidence intervals were estimated using bootstrap samples (at least 2,900 Wenatchee and 1,700 Methow). Correlation = Pearson correlation coefficient between parameter estimates from bootstrap samples. Model equations are defined in Equations (1), (2), and (3). ΔAICc represents change in AICc compared to model with minimum AICc for each population. *Only the Ricker model could be fit to the Wenatchee River data.

Population	Model*	ΔAICc	Parameter[a]	Parameter Estimates	95% CI	Correlation
Wenatchee	Smooth Hockey Stick		α	NA	NA	α, R_∞: NA
			R_∞	NA	NA	
	Beverton-Holt		α	NA	NA	α, β: NA
			β	NA	NA	
	Ricker		α	957.3	773.4 – 1609.5	α, β: 0.83
			β	< 0.0001	< 0.0001 – 0.0001	
			K	30,446,537	919,213 - ∞	
Methow	Smooth Hockey Stick	0.01	α	459	352.6 – 1344.6	α, R_∞: -0.23[b]
			R_∞	4,796,000	889,141 – 19,840,304	
	Beverton-Holt	0.02	α	9,817,511	874,870 – 66,701,078	α, β: 0.99
			β	21,552	-26.7 – 16,434.1	
	Ricker	0.00	α	461	331.4 – 1032.5	α, β: 0.88
			β	0.00005	< 0.0001 – 0.0004	
			K	3,457,540	919,213 - ∞	

a = Estimated maximum recruitment parameters are: R_∞ for the Smooth Hockey Stick model, a for the Beverton-Holt model, and $K=(\alpha/\beta)e^{-1}$ for the Ricker model.

b = Correlation coefficient between a and R_∞ is uninformative because parameter estimates are not linearly related.



Wenatchee

Methow

Figure 1. Residuals from Ricker Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using emigrant and spawner data from Wenatchee and Methow Rivers Summer Chinook Salmon. The Wenatchee results included the 2000 and 2003 brood years.

Hypothesis $H0_{2.2.1.2}$ Effect of pHOS on Juveniles per Redd:

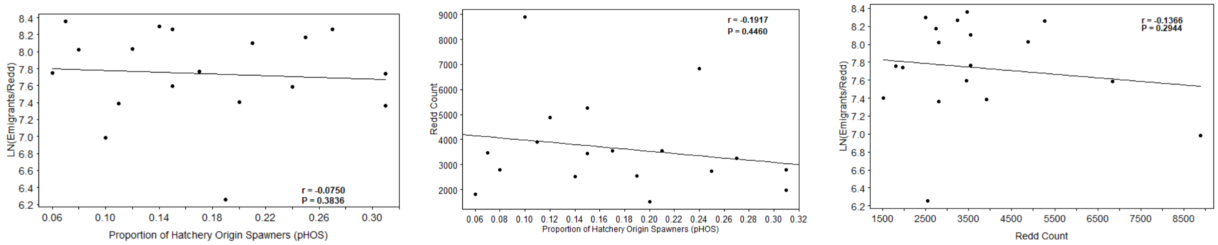
There was a weak but non-significant negative association between emigrants per redd (log scale) and the proportion of hatchery spawners (pHOS) for both populations (P≥0.3836; Figure 10). The redd count was not associated with pHOS in either population and there was no indication of post-spawning density dependence apparent from examination of the emigrants per redd plotted against the redd counts (P≥0.2944, Figure 10). Nevertheless, the relationship between emigrants per redd and pHOS was examined using the Ricker and Beverton-Holt stock-recruitment models in order to account for possible density dependence effects, with redds used in place of spawner counts. Both models were equivalent on the basis of AICc rank (ΔAICc≤0.10) and examination of model residuals for both populations (Table 6). However, for both populations, the Beverton-Holt model could not be fit for the bootstrap samples and the 95% asymptotic confidence intervals for the model parameters α and β included both negative values and values far beyond the range of the observed data; these results indicate a lack of fit for the Beverton-Holt model for the two populations. Thus, the Ricker model was preferred. For the Wenatchee population, the fitted Ricker model for emigrants per redd was (Table 6):

$$ln(R/S) = 8.0322 - 0.7166P_{HOS} - 0.00005 * S.$$

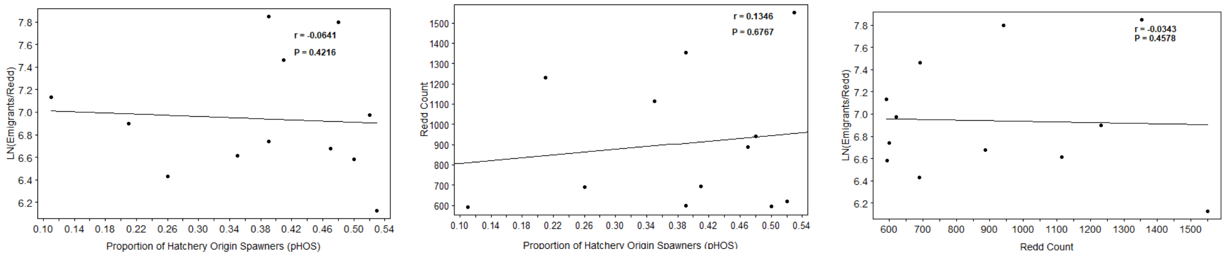
The 95% bootstrap confidence interval for the effect of pHOS (i.e., β_2 in Equation (7)) was (-2.0006 – 3.3638). For the Methow population, the fitted Ricker model for emigrants per redd was:

$$ln(R/S) = 7.0724 - 0.2448P_{HOS} - 0.00004 * S$$

with a 95% bootstrap confidence interval (-3.2640, 2.4357) for the regression coefficient for pHOS. For both populations, the bootstrap confidence interval for the effect of pHOS included both positive and negative values, so we concluded that there is no evidence of a negative association between pHOS and emigrants per redd for Summer Chinook Salmon from either the Wenatchee River or the Methow River. For the Wenatchee population, removing 2000 or 2003 as possible outlier brood years did not significantly change the results.



Wenatchee



Methow

Figure 10. Emigrants per redd (log scale) versus proportion of hatchery origin spawners (pHOS) (left plots), redd count versus proportion of hatchery origin spawners (pHOS) (middle plots), and emigrants per redd versus redd count (right plots) for Wenatchee and Methow River Summer Chinook Salmon, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from t-test of slope (one-sided test of negative slope for left and right plots, two-sided test for middle plots).

Table 6. Fitted stock-recruitment models for emigrants per redd for Wenatchee River 1999–2018 (without 2010, 2011) and Methow River, 2006-2018 (without 2012), Summer Chinook Salmon, including effect (β_2) of proportion of hatchery origin spawners (pHOS). Bootstrap confidence intervals based on 3,000 bootstrap samples (Wenatchee) and 1,000 bootstrap samples (Methow) were provided for the Ricker model, and asymptotic confidence intervals were provided for the Beverton-Holt model. Model equations are defined in Equations (5) and (7). ΔAICc represents change in AICc compared to model with minimum AICc for each population.

Population	Model	ΔAICc	Parameter	Parameter Estimates	95% CI
Wenatchee	Beverton-Holt	0.10	α	69,904,888	- 259,329,930 – 399,139,700
			β	23,464	-105,680 – 9,152,607
			β_2	0.6695	-3.1075 – 4.4465
	Ricker	0.00	ln(α)	8.0322	6.8834 – 8.6882
			β	0.00005	-0.0002 – 0.0001
			β_2	0.7166	-2.0006 – 3.3364
Methow	Beverton-Holt	0.001	α	31,205,045	- 881,383,950 – 943,794,030
			β	26,564	-772,397 – 825,526
			β_2	0.2468	-2.4111 – 2.9046
	Ricker	0.000	ln(α)	7.0724	4.6169 – 8.2810
			β	0.00004	-0.0016 – 0.0010
			β_2	0.2448	-3.2640 – 2.4357

Summer Steelhead

Methow River Summer Steelhead adult spawner, emigrant, pHOS, and redd count data were available for the 2003–2015 brood years. Adult stock abundance (spawners) ranged from 1,105 in 2012 to 3,680 in 2010 and averaged 2,003, and emigrant recruitment ranged from 9,076 in 2003 to 33,739 in 2007 and averaged 18,154. Redd counts averaged 1,084 (range = 591 to 2,019), and pHOS averaged 0.81 (range = 0.58 to 0.89). The 2007 brood year stood out as a possible outlier in emigrant count with a much higher count (33,739) than in the other years (range = 9,076 – 25,845).

Twisp River Summer Steelhead adult spawner, emigrant recruitment, pHOS, and redd count data were available from for the 2003–2015 brood years. Spawners ranged from 143 in 2007 to 1,204 in 2003 and averaged 532, and emigrant recruitment ranged from 3,264 in 2008 to 13,669 in 2007 and averaged 6,133. Redd counts averaged 272 (range = 82 to 696), and pHOS averaged 0.69 (range = 0.48 to 0.89). The 2007 brood year stood out as a possible outlier in emigrant count, with a much higher emigrant count (13,669) than any of the other years (range = 3,264 – 7,467). Additionally, pHOS generally declined over the course of the data collection, partly as a result of a policy change in 2010 to target pHOS values of 0.5.

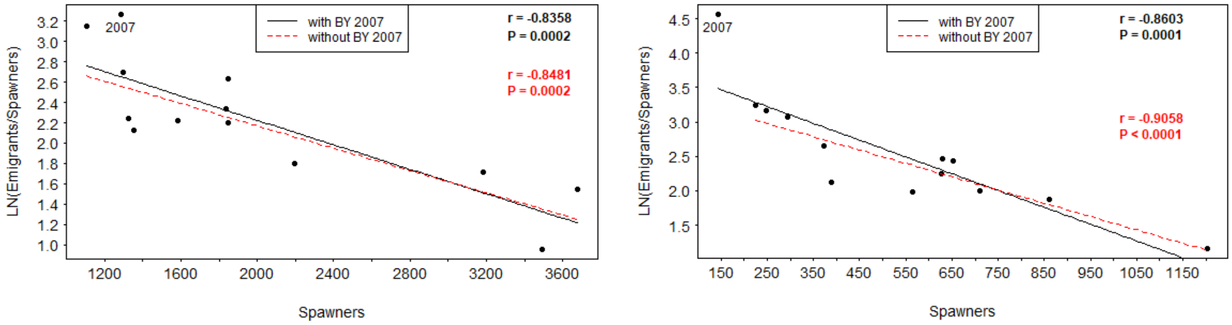
Hypothesis $H0_{2.2.1.1}$ *Effect of pHOS on Recruitment:*

A strong negative linear relationship was observed in both the Methow River and Twisp River between spawners and emigrant recruitment, demonstrating evidence of density dependence in mortality between the spawning and emigrant life stages (Figure 11). Thus, an attempt was made to fit the Smooth Hockey Stick, Beverton-Holt, and Ricker stock-recruitment models to the spawner and emigrant data for each population. However, the Smooth Hockey Stick and Beverton-Holt modeling assumption of asymptotic growth in recruitment as spawner abundance increases was not supported by the data for either population, as demonstrated by the locally smoothed curves (LOESS) in Figure 12, and neither the Smooth Hockey Stick model nor the Beverton-Holt model could be fit to the spawner-recruitment data for these populations. The Ricker model was fit to the data for both populations, and estimated maximum recruitment at approximately 1,662 spawners for the Methow population and approximately 410 spawners for the Twisp population (Figure 12). Although the Ricker model could be fit to the spawner and emigrant data from both populations, in each case there were indications of poor model fit and possible bias. For the Methow data, the model residuals demonstrated negative autocorrelation at a time lag of 1 and 4 years, suggesting that the Ricker model does not adequately account for population dynamics. For the Twisp data, the model residuals did not clearly meet the assumption of lognormal errors. In each case, the model parameter estimates may be biased. Additionally, for both populations there was high correlation observed between the model parameter estimates, which increases uncertainty in the model predictions (Table 7).

For the Methow population, the estimated Pearson correlation coefficient between the Ricker model residuals and pHOS was 0.2222 and was not significantly different from 0 (P=0.4656; Figure 13). Additionally, a likelihood ratio test of the effect of pHOS on the Ricker model was non-significant (P=0.3829). The Beverton-Holt model could not be fit with pHOS as a variable. Analysis that omitted the possible outlier brood year of 2007 resulted in the same findings: only the Ricker model was approximately consistent with the data, and there was no evidence of a negative relationship between pHOS and juvenile productivity of emigrants (Figure 14).

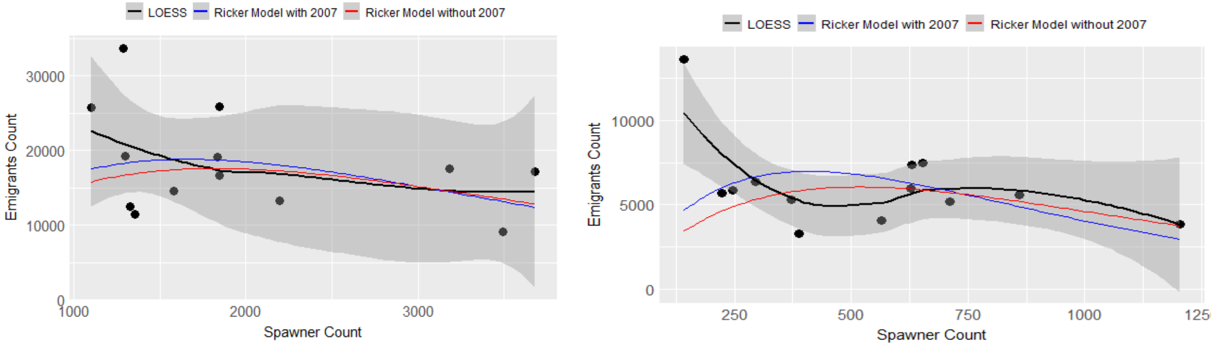
For the Twisp population, the estimated Pearson correlation coefficient between the Ricker model residuals and pHOS (r = 0.2553) was not significantly different from 0 (P=0.3999; Figure 13). A simpler analysis that compared the average Ricker model residuals between the pre-2010 period, when pHOS was not restricted ("control"), and the 2010+ period, when pHOS was targeted at 0.5 ("treatment"), also found no difference in model residuals between the two management periods (*t*-test = -0.4717, df = 11, P = 0.6463; Figure 15). Additionally, a likelihood ratio test of the effect of pHOS on the Ricker model was non-significant (P=0.3071). The Beverton-Holt model could not be fit with pHOS as a variable. When the 2007 brood year was removed as a possible outlier in emigrant count, the results were consistent with the full data set: a non-significant relationship between the Ricker model residuals and pHOS (P=0.2868) and also between the Ricker model residuals and the pHOS management periods (P=0.1728), and the Beverton-Holt and Smooth Hockey Stick models could not be fit to the data (Figure 12, Table 7, Figure 14, Figure 15).

Overall, there was no evidence that to suggest that higher proportions of hatchery spawners were associated with lower juvenile productivity for Summer Steelhead in the Methow or Twisp rivers. However, there were only 13 years of data available for either population and the modeling assumptions were not well supported. Thus, it remains possible that there is a relationship between pHOS and juvenile productivity that is not observable using the available data and analyses.



Methow Twisp

Figure 11. Emigrants per spawner (log scale) versus spawner abundance for Methow and Twisp Rivers Summer Steelhead, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope.



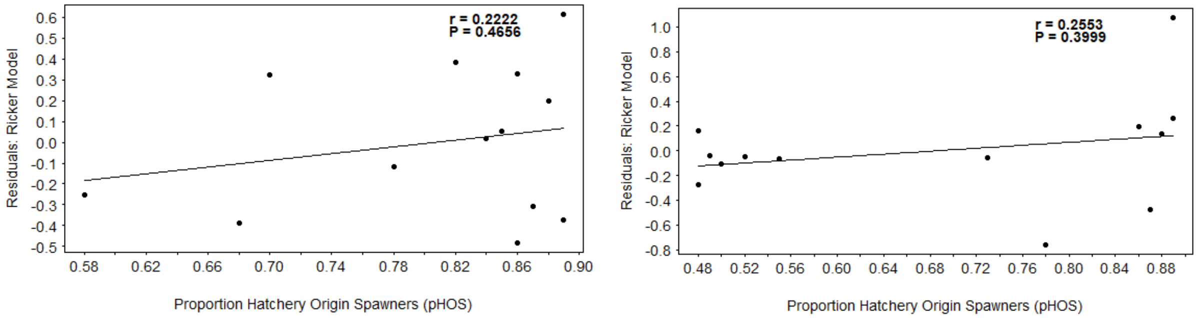
Methow Twisp

Figure 12. Stock and emigrant data with fitted LOESS curve and Ricker Model for Methow and Twisp Rivers Summer Steelhead.

Table 7. Fitted stock-recruitment models for emigrants and stock (spawner) data from Summer Steelhead in the Methow and Twisp rivers, 2003–2015. Confidence intervals were estimated using bootstrap with at least 2,000 bootstrap samples. Correlation = Pearson correlation coefficient between parameter estimates from bootstrap samples. Model equations are defined in Equations (1), (2), and (3). ΔAICc represents change in AICc compared to model with minimum AICc for each population (NA for all models because only one model fit per population). *Only the Ricker model could be fit to the data for Methow and Twisp rivers. The Ricker model was fit both with and without data from the 2007 brood year in the Twisp.

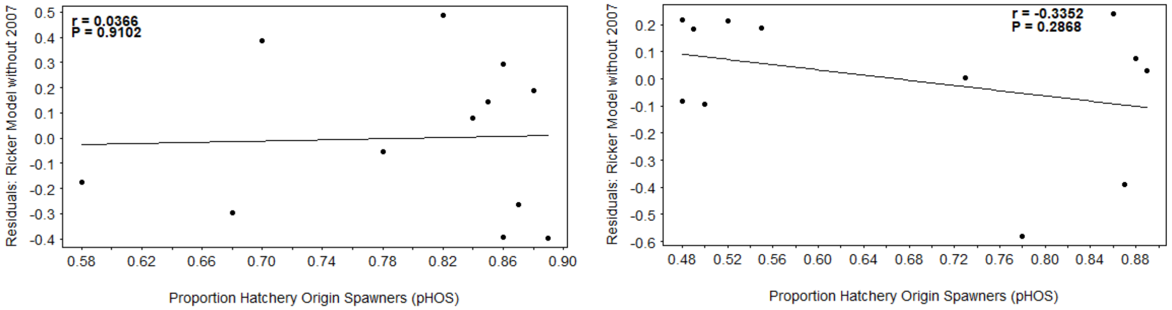
Population	Model*	ΔAICc	Parameter[a]	Parameter Estimates	95% CI	Correlation
Methow	Smooth Hockey Stick	NA	α	NA	NA	α, R_∞: NA
			R_∞	NA	NA	
	Beverton-Holt	NA	α	NA	NA	α, β: NA
			β	NA	NA	
	Ricker with 2007	NA	α	30.8	19.3 – 48.9	α, β: 0.90
			β	0.0006	0.0004 – 0.0008	
			K	18,835	15,830 – 23,693	
	Ricker without 2007	NA	α	26.2	17.1 – 40.7	α, β: 0.91
			β	0.0005	0.0004 – 0.0007	
			K	17,591	14,926 – 21,375	
Twisp	Smooth Hockey Stick	NA	α	NA	NA	α, R_∞: NA
			R_∞	NA	NA	
	Beverton-Holt	NA	α	NA	NA	α, β: NA
			β	NA	NA	
	Ricker with 2007	NA	α	46.3	29.2 – 76.2	α, β: 0.87
			β	0.0024	0.0016 – 0.0032	
			K	6,983	5,667 – 9,221	
	Ricker without 2007	NA	α	31.8	22.9 – 43.1	α, β: 0.90
			β	0.0019	0.0015 – 0.0025	
			K	6,054	5,247 – 6,930	

a = Estimated maximum recruitment parameters are: R_∞ for the Smooth Hockey Stick model, *a* for the Beverton-Holt model, and $K=(\alpha/\beta)e^{-1}$ for the Ricker model.



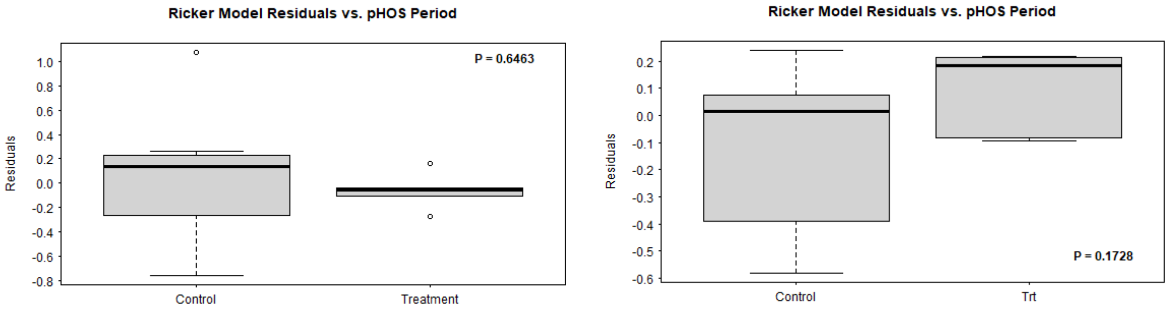
Methow Twisp

Figure 13. Residuals from the Ricker Model versus proportion of hatchery-origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using emigrant and spawner data from Methow and Twisp rivers Summer Steelhead (including 2007).



Methow Twisp

Figure 2. Residuals from the Ricker Model versus proportion of hatchery-origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using emigrant and spawner data from Methow and Twisp rivers Summer Steelhead (without 2007).



Twisp – with 2007 Twisp – without 2007

Figure 15. Distribution of residuals from the Ricker Model categorized by pHOS management period: Control = pre-2010, when pHOS levels were not restricted, and Treatment = 2010–2015, when pHOS levels were targeted at 0.5. Data used were emigrant and spawner counts from Twisp River Summer Steelhead, 2003–2015. P-value is from two-sided t-test: t-test = -0.4717, df = 11 (with brood year 2007), and t-test = 1.4683, df = 10 (without brood year 2007).

Hypothesis $H0_{2.2.1.2}$ *Effect of pHOS on Juveniles per Redd*

There was no evidence of a negative association between emigrants per redd and the proportion of hatchery spawners (pHOS) for Summer Steelhead from either the Methow River or the Twisp River (Figure 16). The linear association between redd count and pHOS was non-significant (P=0.2335) in the Methow but significant at the 10% level (P=0.0723) in the Twisp (Figure 17). Comparison of emigrants per redd with redd count demonstrated strong evidence of post-spawning density dependence in both populations ($P \leq 0.0002$; Figure 18). Thus, the relationship between emigrants per redd and pHOS was examined using stock-recruitment models in order to account for density dependence effects, using redds in place of spawner abundance. In both populations the Beverton-Holt model resulted in a negative (i.e., inadmissible) estimate of the β parameter, confirmed by examination of the likelihood surface. Thus, results are provided only for the Ricker model.

For the Methow population, the residuals from the Ricker model agreed moderately well with model assumptions. The fitted Ricker model for Methow River emigrants per redd was (Table 8):

$$ln(R/S) = 3.3547 + 0.9921 * P_{HOS} - 0.0012 * S,$$

with a 95% bootstrap confidence interval (-3.3407, 2.5691) for the effect of pHOS (i.e., β_2 in Equation (7)). Because the confidence interval for the effect of pHOS included both positive and negative values, we concluded that there was no evidence of a negative association between pHOS and emigrants per redd for Summer Steelhead from the Methow River whether or not an adjustment was made for density dependence. We reached the same conclusion when the possible outlier brood year (2007) was omitted from the data analysis (Figure 19, Table 8). However, the small sample size, low degree of variability in the observed pHOS values, and potentially high level of measurement error in the observed data may have lowered the ability to detect a relationship between pHOS and emigrants per redd.

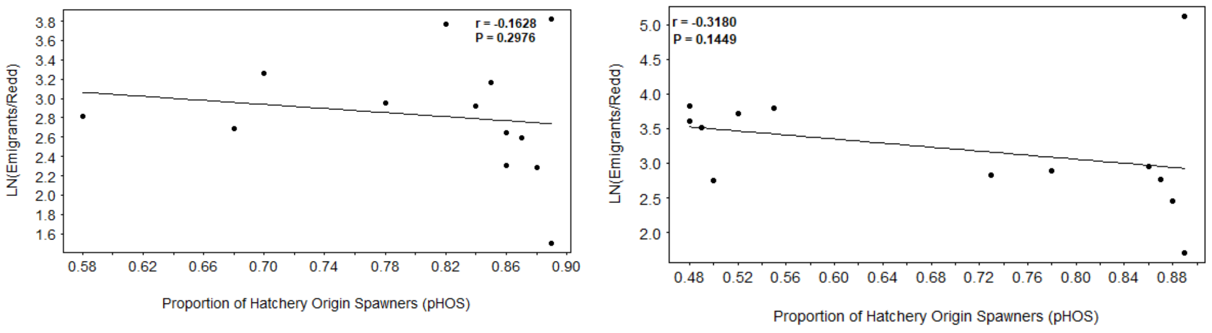
For the Twisp population, the residuals from the Ricker model agreed poorly with the model assumption of lognormal errors. The fitted Ricker model for Twisp River emigrants per redd was (Table 8):

$$ln(R/S) = 3.9305 + 0.7680 * P_{HOS} - 0.0045 * S,$$

with a 95% bootstrap confidence interval of (-2.3366, 2.1443) for the effect of pHOS. Because the confidence interval for the effect of pHOS included both positive and negative values, we concluded that there was no evidence of a negative association between pHOS and emigrants per redd for Summer Steelhead from the Twisp River whether or not an adjustment was made for density dependence. However, the failure to meet the model assumptions demonstrates an overall lack of model fit. The small sample size and potentially high level of measurement error in the observed data may have contributed to the lack of model fit, and likewise may have lowered the ability to detect a relationship between pHOS and emigrants per redd using the available data.

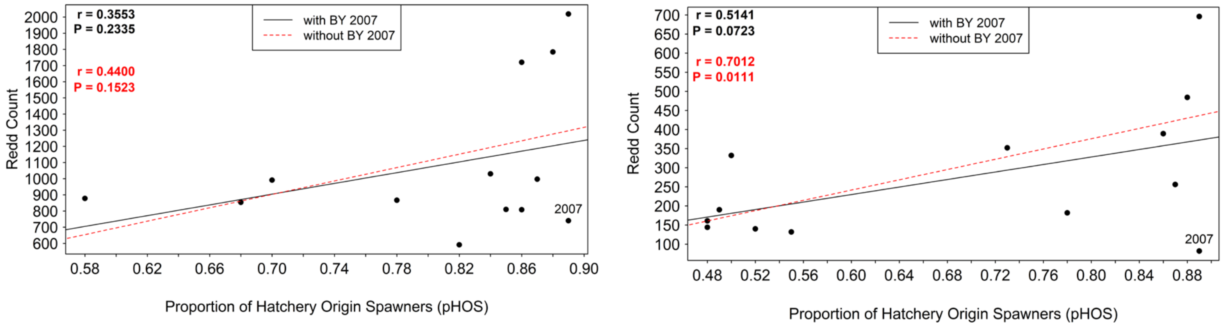
When the potential outlier brood year of 2007 was omitted from the Twisp River data set, there was a negative association between emigrants per redd and pHOS when density dependence was not accounted for (P=0.0009, Figure 19). However, there was significant density dependent mortality observed between the redd count and emigrant count (P<0.0001, Figure 18), which may have accounted for the perceived association between emigrants per redd and pHOS. When analyzed using the Ricker model, which accounts for density dependence, the estimated effect of pHOS on the redd-emigrant relationship was non-significant, with a 95% bootstrap confidence interval of (-2.3915, 1.0898) (Table 8). Without the 2007 brood year, the Beverton-Holt model relating emigrants to redd counts was able to be fit when pHOS was in the model and pHOS was associated with lower emigrants per redd, demonstrated by the 95% bootstrap confidence interval for β_2 that was entirely greater than 0 (i.e., (0.0700, 1.9685); Table 8). However, the bootstrap confidence intervals for the other Beverton-Holt model parameters were notably wide: the confidence interval of the asymptotic maximum recruitment (α) included values 5 times the maximum recruitment observed, and the confidence interval for the redd counts predicted to generate half the maximum recruitment (β) included negative values (Table 8). The apparently poor fit of the Beverton-Holt model raises questions about the validity of its finding of a statistically significant pHOS effect.

Overall, the evidence for a negative association in both populations between the proportion of hatchery origin spawners (pHOS) and juvenile productivity in emigrants was not strong. There was no such evidence for the Methow population or for the Twisp population when based on the full data set that included the 2007 brood year; however, in each case, one of the two stock-recruitment models could not be fit to the data because of misalignment of modeling assumptions with the data, and the data set was small (only 13 brood years). When the 2007 brood year was treated as an outlier and omitted from the Twisp analysis, a negative association was observed between emigrants per redd and pHOS, but it disappeared when density dependence was accounted for using the Ricker model. The alternative stock-recruitment model (Beverton-Holt) maintained an effect of pHOS but did not appear to fit the data well, indicating possible bias in the estimate of the pHOS effect. The small sample size available may have lowered the ability to detect an effect of pHOS on juvenile productivity. Additionally, a negative trend in pHOS from nearly 0.90 in 2003 to nearly 0.50 in 2015 raises the possibility that any pHOS effect actually masks a temporal trend in juvenile productivity.



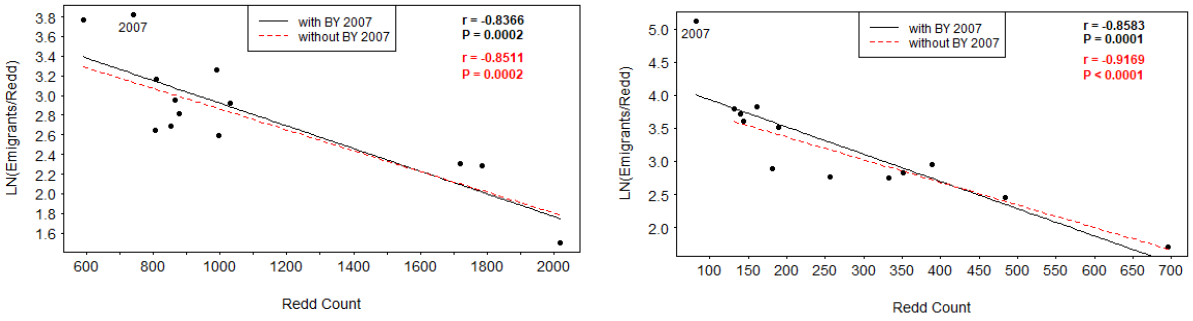
Methow Twisp

Figure 16. Emigrants per redd (log scale) versus proportion of hatchery origin spawners (pHOS) for Methow and Twisp rivers Summer Steelhead, 2003–2015, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope.



Methow Twisp

Figure 17. Redd count versus proportion of hatchery origin spawners (pHOS) for Methow River and Twisp River Summer Steelhead, 2003–2015, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope.



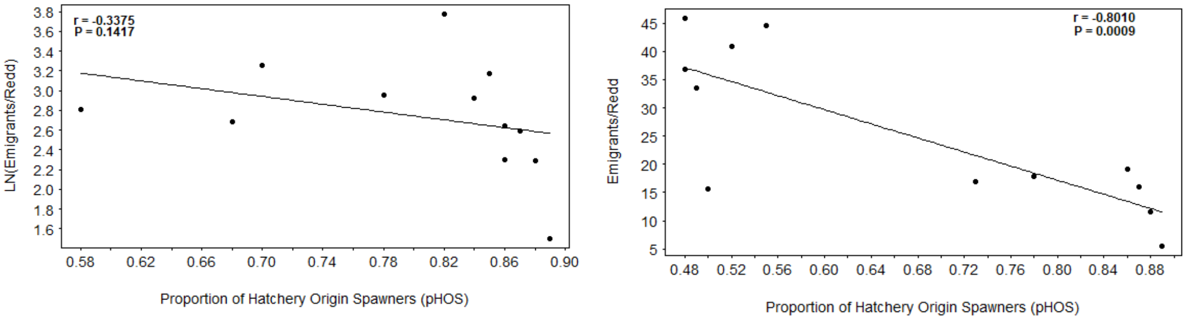
Methow Twisp

Figure 18. Emigrants per redd (log scale) versus redd count for Methow River and Twisp River Summer Steelhead, 2003–2015, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. Negative slope indicates post-spawning density dependence.

Table 2. Fitted stock-recruitment models for emigrants per redd for Methow River and Twisp River Summer Steelhead, 2003–2015, including effect (β_2) of proportion of hatchery origin spawners (pHOS). Confidence intervals were estimated using bootstrap with 3,000 bootstrap samples. Model equations are defined in Equations (5) and (7). ΔAICc represents change in AICc compared to model with minimum AICc for each population and data set (i.e., with or without 2007; NA if only one model fit). *Only the Ricker model could be fit for the Methow data or for the Twisp data when 2007 was included.

Population	Model*	ΔAICc	Parameter	Parameter Estimates	95% CI
Methow	Beverton-Holt	NA	α	NA	NA
			β	NA	NA
			β_2	NA	NA
	Ricker (with 2007)	NA	ln(α)	3.3547	1.5579 – 6.1456
			β	0.0012	0.0006 – 0.0018
			β_2	-0.9921	-3.3407 – 2.5691
	Ricker (without 2007)	NA	ln(α)	3.7302	2.3844 – 6.8984
			β	0.0011	0.0005 – 0.0016
			β_2	-0.2687	-2.2563 – 3.9353
Twisp	Beverton-Holt (with 2007)	NA	α	NA	NA
			β	NA	NA
			β_2	NA	NA
	Ricker (with 2007)	NA	ln(α)	3.9305	3.3009 – 5.0401
			β	0.0045	0.0015 – 0.0067
			β_2	-0.7680	-2.3366 – 2.1443
Twisp	Beverton-Holt (without 2007)	0.24^a	α	12,008	5,158 – 40,066
			β	46.4	-31.2 – 275.2
			β_2	0.9259	0.0700 – 1.9685
	Ricker (without 2007)	0.00^a	ln(α)	4.5239	3.8033 – 5.1740
			β	0.0027	0.0007 – 0.0049
			β_2	1.0323	-2.3915 – 1.0898

a = compare ΔAICc values within Twisp modeling results without 2007 brood year.



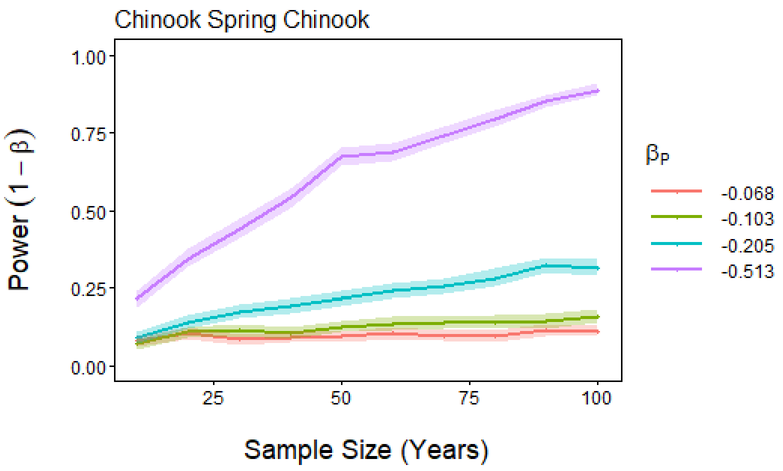
Methow Twisp

Figure 19. Emigrants per redd versus proportion of hatchery origin spawners (pHOS) for Methow and Twisp rivers Summer Steelhead, 2003–2015, omitting brood year 2007, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope.

Power Analysis

Simulated statistical power to detect a negative effect of pHOS was consistently ≤ 0.32 for all sample sizes considered (N≤100 years) and for all but the most extreme pHOS effect sizes considered (i.e., β_P=-0.068 to -0.205), both with and without measurement error (Figure 20). For the largest effect size (β_P=-0.513), simulated power was as high as 0.54 for a sample size of N= 40 years without measurement error, and only slightly lower at 0.52 for N= 40 years when measurement error was incorporated into the simulations. Achieving power of at least 0.70 required as many as N= 70 years of data. Power greater than 0.80 required 90 years of data. These simulations defined detection of a negative effect of pHOS as a 90% bootstrap confidence interval that was entirely less than 0.

(i) Without measurement error



(ii) With measurement error

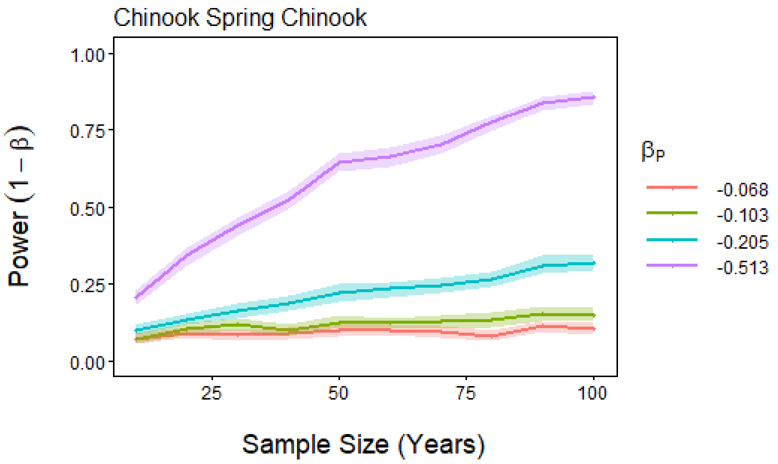


Figure 20. Statistical power of detecting a negative effect of pHOS for various levels of pHOS effect size β_P with (i) and without (ii) measurement error in stock and recruitment data. Power based on 1,000 simulations of stock (spawners) and juvenile recruitment data using Ricker stock-recruitment model fit to data from Chiwawa spring Chinook Salmon, 1991-2017: a = 138, b = 0.0011, σ = 0.4386 (equation (2)). Type I error probability = 0.10. Measurement error (ii) was incorporated into simulated observations of spawner and recruitment data using coefficient of variation (CV): CV=0.07 for HOS, CV=0.06 for NOS, and CV=0.11 for recruitment. Shaded region = 95% bootstrap confidence interval using 300 bootstrap samples from the simulated data.

Discussion

Our investigation of whether a higher proportion of hatchery origin spawners (pHOS) may result in lowered juvenile productivity was largely inconclusive. For most populations studied, no evidence of an effect of pHOS was observed. For the single population that demonstrated a possible negative effect of pHOS on juvenile productivity (Twisp River Summer Steelhead), the evidence was weak: when density dependence was accounted for, the perceived negative association between pHOS and juveniles per redd was no longer observed. Additionally, the significant result was observed only when a possible outlier in emigrant counts was omitted, which may not be justified depending on the cause of the unusual emigrant count for that brood year. Thus, even when some evidence of a negative effect of pHOS was found, the evidence was particularly weak.

The spring Chinook life history type that emigrates from tributaries and upper reaches to presumably rear in the main stem rivers was not analyzed explicitly. However, the life history type would be included as age 1 emigrants captured by the lower river rotary screw traps in the basin level analyses.

Multiple factors combined to lower the ability to detect an effect, should it exist. The most obvious factor was the small size of most of the data sets. Most of the populations had data for fewer than 20 brood years, resulting in lowered opportunity to observe the full range of variability in stock-recruitment dynamics in response to changes in hatchery proportion of spawners and lower statistical power to detect an effect. A complication in assessing the stock-recruitment data for an effect of pHOS is data quality. The stock-recruitment models all assume low levels of measurement error in both spawners or redd counts and smolts or emigrants. The higher the level of measurement error, the lower the ability to model the dynamics well enough to detect an effect. In some populations (e.g., Twisp River Steelhead, Methow River Steelhead), pHOS has declined almost consistently since the start of data collection, which means any perceived effect of pHOS would be entirely confounded with temporal changes in juvenile productivity. This risk is increased by the observational nature of the pHOS data.

Some data sets studied also demonstrated low contrast in the spawner or redd counts observed across brood years. The stock-recruitment models require observations at both low and high levels of spawners. This requirement means that low variability in spawner (or redd count) data reduces the quality of fit of the stock-recruitment models and in some cases makes them impossible to be fit altogether. A lack of data at low spawner levels may have lowered the ability to fit the Smooth Hockey Stick model, which requires data at low spawner levels to estimate the model parameter associated with depensation (α). Examination of the likelihood surface for the Smooth Hockey Stick model for some populations demonstrated moderate information in maximum recruitment but a complete lack of information in the α parameter, interpreted as the slope of the stock-recruitment curve at very low numbers of spawners (for example, see the flat contour curves in the dimension of the α parameter in Figure 21). Then again, several populations failed to demonstrate a stable maximum (or simply high) juvenile recruitment pattern at high levels of spawners, which is assumed by both the Smooth Hockey Stick and Beverton-Holt models. Again, examination of the likelihood surface in these cases indicated either a lack of information in model parameters or else model parameters optimized at inadmissible values (e.g., negative spawner counts necessary to generate half the asymptotic maximum recruitment, Figure 22). Although the Smooth Hockey Stick stock-recruitment model was the preferred analysis framework, it appeared poorly suited to the stock and juvenile recruitment data available for many populations.

For all three stock-recruitment models considered, there was often high uncertainty in model parameter estimates even when the models could be fit to the data. This was indicated by wide confidence intervals that often included maximum smolt or emigrant values far beyond the range of observed data and by high correlation in model parameter estimates. High correlation lowers the ability to distinguish between different model fits and increases uncertainty in the results; it arises from lack of contrast in the data or violation of modeling assumptions.

In most cases there was no evidence of a time lag in juvenile recruitment per spawner as represented by autocorrelation in the residuals from the stock-recruitment models. However, a negative autocorrelation was observed with a time lag of three years for Twisp River Spring Chinook Salmon and a time lag of one and four years for Methow River Summer Steelhead. Such negative autocorrelations may be observed when a high level of recruitment one year is habitually followed by a low level of recruitment after a consistent delay (e.g., 3 years). Such a pattern may be expected for populations with consistent age structure among spawners, paired with density-dependent mortality between spawning and juvenile recruit surveys. In such cases, the Smooth Hockey Stick, Beverton-Holt, and Ricker models are unlikely to adequately represent all important features of the population dynamics; an age-structured model may be required. The value of pHOS may also be affected by such autocorrelation. Thus, such factors should be accounted for in order to detect a true effect of pHOS on juvenile productivity beyond age- and density-dependent components of the population dynamics.

Simulated power to detect a negative effect of pHOS on juvenile recruitment was low for all but the strongest effect sizes and for studies shorter than approximately 70 years. The low power values resulted from the high variability in residuals from the Ricker stock-recruitment model ($\sigma = 0.4386$) estimated from its fit to 27 years of data from the Chiwawa Spring Chinook salmon population (1991–2017).

The Chiwawa data set is the largest of the juvenile productivity data sets available for spring Chinook salmon and steelhead. The alterative data sets either failed to meet the modeling assumptions for the Ricker model (e.g., Methow and Twisp steelhead) or else had higher error variance about the fitted Ricker model (e.g., other spring Chinook salmon populations) than seen for the Chiwawa spring Chinook salmon population. Thus, it is expected that the power to detect a negative effect of pHOS on juvenile productivity would be highest for the Chiwawa spring Chinook population. Low power for this population would be compounded for the other populations with shorter time series or more complex population dynamics. As a consequence, it is unlikely that assessment of stock-recruitment curves similar to the Ricker model will be sufficient to detect a negative effect of pHOS in time to mediate any such effect. Other methods of monitoring and assessment are recommended to evaluate the effect of pHOS on juvenile productivity of anadromous salmonids in the upper Columbia River basin.

Given all the complicating factors identified here, only the most extreme effect of pHOS on juvenile productivity could have been detected. Thus, we caution against concluding that such an effect is truly absent. Future data collection efforts could be substantially improved by increasing the contrast in pHOS levels and including suitable in-basin unsupplemented references. More specifically, a planned experiment using deliberately chosen pHOS levels could be implemented in order to achieve the necessary contrast and remove confounding analyses with temporal and age-structured processes. Appropriate power analyses must be performed on the study design prior to commencing work to ensure that a result may be obtained within an acceptable time frame.

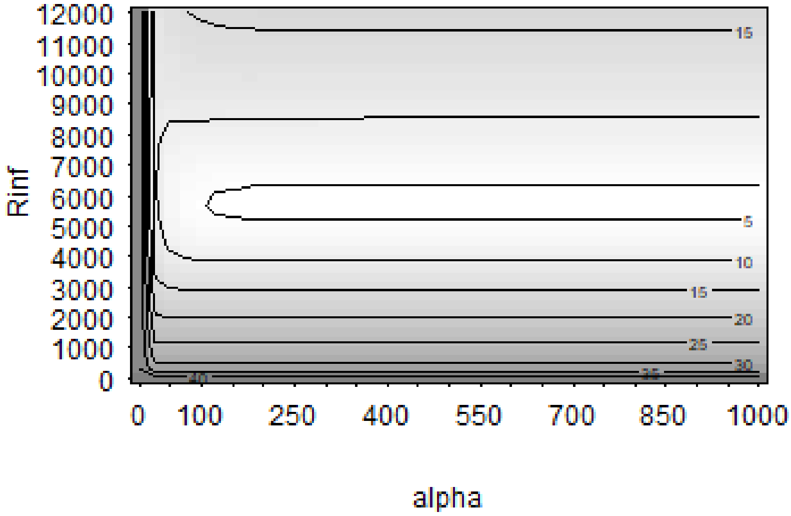


Figure 21. Negative log-likelihood surface and contour curves for the Smooth Hockey Stick model of emigrants and spawner counts. Lighter regions indicate higher likelihood values (lower negative log-likelihood values). The estimated parameter values occur where the negative log-likelihood is minimized. Data set = Twisp River Summer Steelhead, 2003–2015.

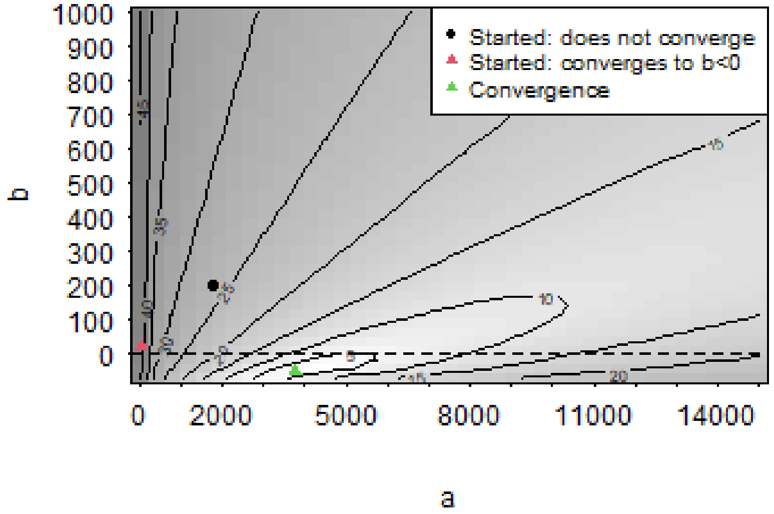


Figure 22. Negative log-likelihood surface and contour curves for Beverton-Holt model of emigrants, redd counts, and pHOS, using $\boldsymbol{\beta_2}$ = -0.1160. Lighter regions indicate higher likelihood values (lower negative log-likelihood values). The estimated parameter values occur where the negative log-likelihood is minimized. The green triangle (falls below b=0 line) indicates the parameter set that optimizes the likelihood. Data set = Twisp River Summer Steelhead, 2003–2015.

Acknowledgments

We thank the many people who collected the data presented in this chapter, notably the field staff from the Washington Department of Wildlife and BioAnalysts. The collection of data, and data analysis and writing of this report were funded by Chelan, Douglas, and Grant counties public utility districts. Tracy Hillman, Charles Snow, Catherine Willard, and Josh Williams assisted in assembling and verifying the data. Todd Pearsons and Tom Kahler reviewed and provided helpful suggestions on earlier drafts of this manuscript. Finally, we thank the Wells, Rocky Reach, and Rock Island HCP Hatchery Committees, and the Priest Rapids Coordinating Committee's Hatchery Subcommittee.

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Appendix A

Investigations into Association between Proportion of Hatchery Spawners and Juvenile Productivity for M&E 2021 Update

COLUMBIA BASIN RESEARCH

Investigations into Association between Proportion of Hatchery Spawners and Juvenile Productivity for M&E 2021 Update

30 April 2021

TO: GREG MACKEY
PUD No. 1 of Douglas County
1151 Valley Mall Parkway, East Wenatchee, Washington 98802

FROM: REBECCA A. BUCHANAN, RICHARD L. TOWNSEND
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Introduction

Conservation hatchery programs implemented in the Wenatchee and Methow river basins are intended to increase the abundance of the target populations. The strategy of the hatchery programs is to return hatchery adults that increase the spawning population, resulting in an increase in the number of offspring that will maintain and recover naturally reproducing populations. The assumption are that 1) increasing the number of spawners will increase the naturally reproducing population abundance in future generations, and 2) hatchery origin spawners have similar fitness to natural origin spawners and will not decrease the productivity of natural spawning fish. Assessment of the production of juvenile offspring prior to entering the ocean provides information on freshwater productivity and avoids ocean effects on the abundance and productivity of the population. However, there is a concern that the hatchery programs may lower the juvenile productivity in supplemented watersheds. The populations are managed under the concept of Proportionate Natural Influence (PNI; Hatchery Scientific Review Group, 2009), a framework that uses genetic modeling to estimate risk of hatchery introgression in natural populations and prescribes management benchmarks intended to allow hatchery programs to operate within an acceptable risk level to the natural population. PNI is composed of two metrics: Proportion of Hatchery Origin Spawners (pHOS; the proportion of hatchery fish in the naturally spawning population), and Proportion of Natural Origin Broodstock (pNOB; the proportion of natural origin fish in a hatchery broodstock). Part of ongoing monitoring and evaluation (M&E) activities is to assess the relationship between pHOS and measures of juvenile productivity including the number of recruits to the smolt or emigrant populations and the average number of juveniles per redd. This report describes the statistical methods and results used to investigate these questions.

Methods

The abundance of spawners and redds was assessed by conducting spawning ground surveys. The number of redds was tabulated and for semelparous species, carcass recoveries were used to estimate the proportions of males and females by origin (hatchery and natural origin). Summer steelhead biological data for gender and origin were obtained at sampling points (various traps). Abundance of semelparous spawners was estimated by expansion of redd counts based on the estimated portions of males to females, by origin, and assuming the number of redds created by a single female. Abundance of steelhead was estimated by adjusting dam and/or trap counts for proportions of fish estimated to return to the various tributaries in the Upper Columbia based on previous radio telemetry studies. Escapement estimates were adjusted to compensate for fall back and re-ascension at dams and to exclude fish removed from the spawning population through harvest and broodstock collection.

Juvenile abundance was estimated using rotary screw traps to sample migrating juveniles. Estimates were generated by conducting trap efficiency trials across a range of river flows, generating a regression model (flow versus trap efficiency), and using the model to predict the number of emigrants based on mean daily flow and daily captures. The daily estimates were summed for each year (season) to estimate the total abundance of emigrating juveniles per population. Juvenile steelhead were parsed into cohorts based on age determined through scales.

Spring chinook juveniles were yearlings assumed to be emigrating to the ocean. Age 0+ spring Chinook migrants were not included in the analysis because their life history and survival are not well understood and we preferred to focus on emigrating fish when possible. Summer Chinook emigrants were subyearlings and assumed to be exhibiting an ocean-type life history. All age classes of steelhead from a cohort were included because of the difficulty in knowing how to parse emigrating fish from those that are not leaving the freshwater system. Therefore steelhead include the entire range of observed age classes for each cohort. For the sake of simplicity, we refer to the steelhead juveniles caught in the screw traps as "emigrants."

Section 3.1 of the monitoring and evaluation plan for the hatchery programs (Hillman et al. 2019) addresses freshwater juvenile productivity and presents two questions, with additional hypotheses to be tested for each question:

Question 1: Has the supplementation program changed the number of juveniles (smolts, parr, and/or emigrants) per redd within the supplemented population?

Question 2: Does the number of juveniles per redd decrease as the proportion of hatchery spawners increases?

The first question could not be assessed because it requires reference populations, which are unavailable for the target populations. Furthermore, estimates of juvenile production are not available in a long enough time series to estimate the juvenile productivity before and after a hatchery program was implemented.

The second question was assessed in this report. The data and methods used to assess Question 2 are described below.

Data

Douglas County PUD provided productivity data for the populations listed in Table 1. The size of the adult spawning stock, number of redds, and proportion of hatchery origin spawners (pHOS) were provided for each brood year, in addition to the number of smolts or emigrants. No data were available for Summer Steelhead from the Wenatchee River.

Table 1. Summary of spawner and recruitment data provided by Douglas County PUD. The size of the adult spawning stock, number of redds, and proportion of hatchery origin spawners (pHOS) were provided for each brood year, in addition to the number of smolts or emigrants.

Species and Run	Population	Brood Years	Smolts	Emigrants[a]	Comment
Spring Chinook	Chiwawa	1991–2017	X		
Spring Chinook	Nason	2002–2017	X		
Spring Chinook	White	2005–2017	X		
Spring Chinook	Twisp	2003–2017	X		
Spring Chinook	Methow	2002–2017	X		
Summer Chinook	Wenatchee	1991–2018		X	No emigrant data: 2010, 2011
Summer Chinook	Methow	2006–2018		X	No emigrant data: 2012
Summer Steelhead	Wenatchee				No data
Summer Steelhead	Methow	2003–2015		X	
Summer Steelhead	Twisp	2003–2015		X	

a = Emigrant data were provided for Spring Chinook Salmon populations from the Chiwawa, Methow, and Twisp rivers but were not used in the analysis.

Statistical Methods

Spawner, redd count, and recruit data were analyzed together with proportion of hatchery spawners to address Objective 2 under Section 3: Juvenile Productivity of the Monitoring and Evaluation Plan for PUD Hatchery Programs: 2019 Update (Hillman et al. 2019):

Objective 2: Determine if the proportion of hatchery fish on the spawning grounds affects the freshwater productivity of supplemented stocks.

Monitoring Question Q2.2.1: Does the number of juveniles per redd decease as the proportion of hatchery spawners increases?

The following statistical hypotheses were investigated:

$H0_{2.2.1.1}$: There is no association between the proportion of hatchery-origin spawners (pHOS) and the residuals from the smooth hockey stick stock-recruitment curve; $\rho = 0$.

$H0_{2.2.1.2}$: The slope between proportion of hatchery spawners and juveniles/redd is ≥ 0.

Three stock-recruitment models were used to account for density dependent mortality in assessment of the two hypotheses. The Smooth Hockey Stick model assumes that recruitment increases quickly at low levels of spawners and asymptotes to a maximum recruitment levels as spawners increase:

$$R = R_{\infty}\left(1 - e^{-\left(\frac{\alpha}{R_{\infty}}\right)S}\right) \tag{1}$$

where R = recruits and S = spawners for a given brood year, R_{∞} is the maximum number of recruits (population carrying capacity), and α is the slope at low levels of spawner abundance (Froese 2008).

The Beverton-Holt model also assumes asymptotic growth to a maximum:

$$R = \frac{\alpha S}{\beta + S} \tag{2}$$

where R = recruits and S = spawners for a given brood year, α is the asymptotic maximum number of recruits (population carrying capacity), and β is the predicted spawner abundance required to produce half the maximum recruits (Hilborn and Walters 1992).

The Ricker model assumes that recruitment increases at lower levels of spawners and declines at higher spawner abundance:

$$R = \alpha S e^{-\beta S} \tag{3}$$

where R = recruits and S = spawners for a given brood year, α is the increase in recruits per spawner at low levels of spawners and β is the intensity of the decrease in recruitment at high levels of spawner abundance (Ricker 1954). The maximum number of recruits is defined as $K = (\alpha/\beta)e^{-1}$.

Modeling assumptions were (based on Hillman et al. 2019):

1. Density-dependent mortality: The brood instantaneous mortality rate is proportional to the number of spawners for the brood year (Ricker 1954).
2. Lognormal errors: The variation in recruitment about the modeled recruitment for a given spawner abundance is lognormally distributed and acts multiplicatively (Quinn and Deriso 1999).
3. Negligible measurement error: Measurement error in spawning stock size and recruitment is small relative to the range of observed spawning stock sizes and variation in recruitment, respectively (Hilborn and Walters 1992).
4. Stationarity: The average stock-recruitment relationship is constant over time, with the possible exception of effects of changes in pHOS (Hilborn and Walters 1992).

The proportion of hatchery origin spawners may have the effect of lowering the maximum recruitment or recruits per spawner. The pHOS variable may be introduced into the Beverton-Holt model to reduce maximum recruitment when pHOS is high as follows:

$$R = \frac{\alpha e^{-\beta_2 P_{HOS}} S}{\beta + S} \tag{4}$$

or equivalently

$$ln(R/S) = ln(\alpha) - ln(\beta + S) - \beta_2 P_{HOS} \tag{5}$$

In Equations (4) and (5), the maximum number of recruits per brood year is α when pHOS is 0 and decreases asymptotically to $\alpha e^{-\beta_2}$ when pHOS is 1.

The pHOS variable may be introduced into the Ricker model in such a way as to lower the slope in the spawner-recruitment curve at low levels of spawner abundance as follows:

$$R = \alpha e^{-\beta_2 P_{HOS}} S e^{-\beta S} \tag{6}$$

or equivalently

$$ln(R/S) = ln(\alpha) - \beta_2 P_{HOS} - \beta S. \tag{7}$$

Alternatively, if higher levels of pHOS are expected to increase the intensity of the decrease in recruitment at high spawner levels, then pHOS may be incorporated as follows:

$$R = \alpha S e^{-(\beta + \beta_2 P_{HOS})S} \tag{8}$$

or equivalently

$$ln(R/S) = ln(\alpha) - (\beta + \beta_2 P_{HOS})S. \tag{9}$$

Both models in Equation (6) and Equation (8) result in lower maximum recruitment for higher pHOS if $\beta_2 > 0$.

Hypothesis H0$_{2.2.1.1}$

Hypothesis H0$_{2.2.1.1}$ was investigated by fitting a stock-recruitment model to the available data and regressing the residuals from the model against pHOS. The Smooth Hockey Stick model, Beverton-Holt model, and Ricker model were considered.

Modeling assumption 1 was assessed by investigating the linear relationship between the log of recruits per spawner with the number of spawners; a negative relationship was consistent with density-dependent mortality. Modeling assumption 2 was assessed via quantile-quantile plots and Shapiro-Wilk tests (Shapiro and Wilk 1965) performed on the residuals from the fitted stock-recruitment model on the log scale. Modeling assumption 4 was assessed by plotting model residuals versus brood year and examining for autocorrelation. The available data did not allow for assessment of assumption 3; violation of assumption 3 would result in lower ability to detect a relationship between spawner abundance and recruitment (Hilborn and Walters 1992).

The fits of the three stock-recruitment models in Equations (1), (2), and (3) to the data were ranked using AICc (Burnham and Anderson 2002). Models with ΔAICc≤2 compared to the minimum observed AICc were used to assess the association between residuals and pHOS. The Smooth Hockey Stick model was included regardless of its AICc rank. Additionally, bias, uncertainty, and correlation in estimates of model parameters were estimated using bootstrapping with at least 1,000 bootstrap samples. Point estimates, 95% bootstrap confidence intervals, and bootstrap correlation coefficients between model parameters were reported for each model. In the event that bootstrapping failed, asymptotic (normal theory) confidence intervals and correlation coefficients were provided. Bias and correlation were considered in assessment of model fit.

For a given model, the residual for brood year i $(i = 1, \ldots, n)$ was defined as

$$r_i = R_i - \hat{R}_i, \tag{10}$$

where R_i is the observed number of recruits for brood year i, and $\hat{R}_i$ is the predicted number of recruits from the model for brood year i. The association between the residuals r_i $(i = 1, \dots, n)$ and pHOS was investigated using the Pearson correlation coefficient and visual inspection of the fitted linear model

$$r_i = \beta_0 + \beta_1 pHOS_i + \epsilon_i, \tag{11}$$

for regression coefficients β_0 and β_1 and random error $\epsilon_i \sim N(0, \sigma_r^2)$. Hypothesis H02.2.1.1 was rejected if the Pearson correlation coefficient between r_i and pHOS was negative and significantly different from 0 ($P<0.05$). In this event, we concluded that there was evidence that hatchery fish may be reducing the productivity of the wild population.

An additional assessment of the effect of pHOS on juvenile productivity was performed by fitting the pHOS-enhanced stock-recruitment models in Equations (4), (6), and (8) and testing whether $\beta_2 = 0$ using likelihood ratio tests.

Hypothesis $H0_{2.2.1.2}$

Hypothesis H02.2.1.2 was investigated in two ways. First, the ratio of recruits per redd was modeled using pHOS in a linear model:

$$\frac{R_i}{S_i} = \beta_0 + \beta_1 pHOS_i + \epsilon_i, \tag{12}$$

where R_i is the observed number of recruits for brood year i, S_i is the observed number of redds for brood year i, β_0 and β_1 are regression coefficients, and $\epsilon_i \sim N(0, \sigma_r^2)$. The estimated regression coefficient $\hat{\beta}_1$ was tested against 0 using a one-sided t-test. If $\hat{\beta}_1$ was significantly <0 ($P<0.05$) (equivalently, significant negative Pearson correlation coefficient), we rejected hypothesis H02.2.1.2 and concluded there was evidence that hatchery fish may be reducing the productivity of the wild population. Modeling assumptions were that the error terms ϵ_i $(i = 1, \dots, n)$ are independent normal random variables with mean 0 and common variance (σ_r^2). The observed error terms from the fitted model in Equation (12) were examined for non-normality using quantile-quantile plots and Shapiro-Wilk tests (Shapiro and Wilk 1965). Heteroscedasticity was examined using plots of $\hat{\epsilon}_i$ against fitted values of R_i/S_i. In the event of heteroscedasticity and non-normal errors, R_i/S_i was log-transformed in Equation (12).

The approach described above assumes that there is no density dependence in recruits per redd, that is, that any density dependence observed in analysis of hypothesis H02.2.1.1 occurs during spawning rather than during incubation and rearing. This assumption was assessed by inspection of recruits per redd compared to redd counts: a negative association (i.e., negative Pearson correlation coefficient) was interpreted as evidence of density dependence after spawning. In this event, an additional assessment was implemented in which we modeled recruits per redd as a function of both redd counts and pHOS using the Beverton-Holt model in Equation (5) and the Ricker model in Equation (7), using redd counts in place of spawner counts. A negative association between pHOS and juveniles per redd was assessed by the 95% bootstrap confidence interval for β_2 using at least 1,000 bootstrap samples. In the event that bootstrapping failed, asymptotic (normal theory) confidence intervals and correlation coefficients were provided. If the 95% confidence interval was entirely >0, it was concluded that there was a negative association between pHOS and juveniles per redd, and that hatchery fish may result in lowered juvenile productivity of naturally spawning fish.

Results

Chiwawa River Spring Chinook Salmon

Adult spawner, smolt recruitment, pHOS, and redd count data were available for the 1991–2017 brood years. Adult stock abundance (spawners) ranged from 33 in 1995 to 2,032 in 2011 and averaged 723, and smolt recruitment ranged from 3,830 in 1995 to 82,845 in 2002 and averaged 36,318 (Figure 1, Figure 2). Redd counts averaged 328.2 (range = 13 to 1,078), and pHOS averaged 0.508 (range = 0.00 to 1.00).

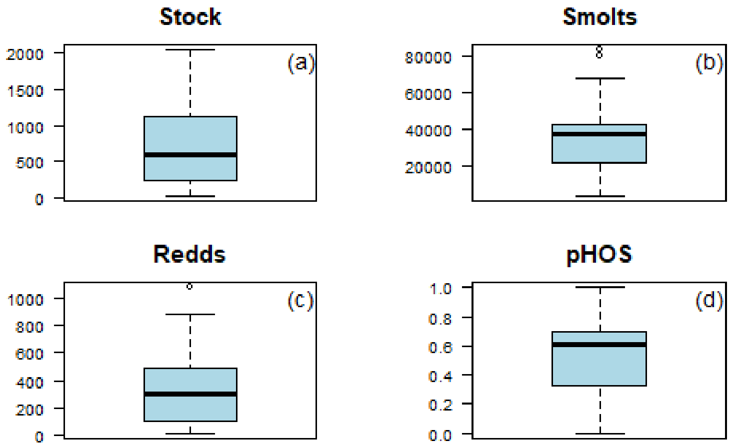


Figure 1. Chiwawa River Spring Chinook Salmon boxplots for Stock (spawner abundance), Smolts, Redd counts, and proportion of hatchery origin spawners (pHOS), 1991–2017. Box indicates interquartile range and thick horizontal bar is median. Whiskers indicate quartile ± 1.5×interquartile range.

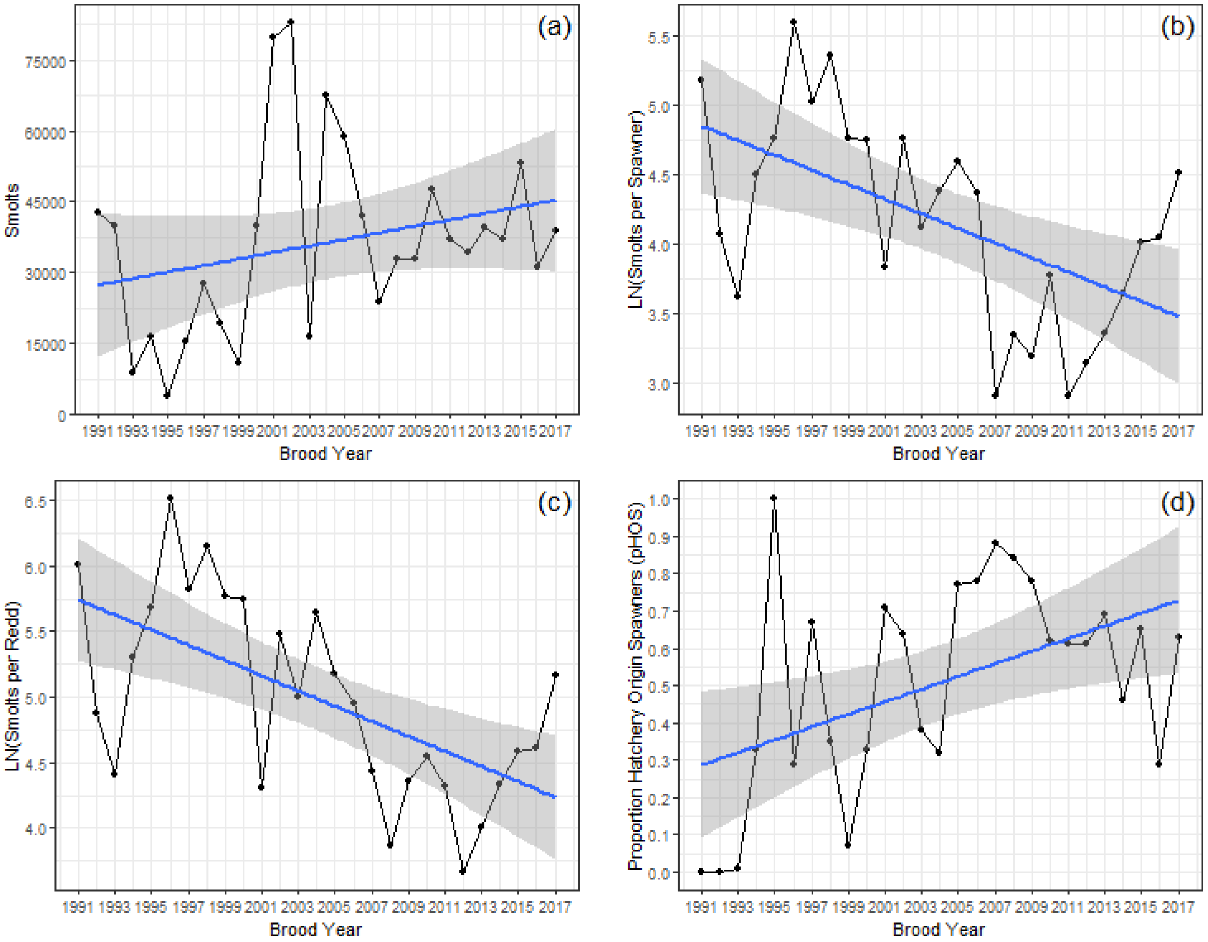


Figure 2. Chiwawa River Spring Chinook Salmon annual Smolt counts, Smolt/Spawner (log scale), Smolt/Redd (log scale), and proportion of hatchery origin spawners (pHOS), 1991–2017. Line indicates the linear trend. Shaded area is the estimated 95% confidence interval of the line.

Hypothesis H02.2.1.1

A negative linear relationship between spawners and smolt recruitment indicated the presence of density dependence in mortality in one or more life stages between spawner data collection and smolt data collection (Figure 3). Thus, the Smooth Hockey Stick, Beverton-Holt, and Ricker stock-recruitment models were each fit to the spawner and smolt data (Figure 4). There was little difference in the model fits among the three models (ΔAICc ≤ 0.75), but the Smooth Hockey Stock model had the lowest AICc value and the lowest correlation between parameter estimates (Table 2). The residuals from all three models were compared to pHOS using correlation analysis. Correlation coefficients between residuals and pHOS ranged from −0.0132 to 0.0396; none was significantly different from 0 ($P \geq 0.8445$; Figure 5–Figure 7). Additionally, likelihood ratio tests of the effect of pHOS on the Beverton-Holt and Ricker models were non-significant ($P \geq 0.8181$). Thus, there was no evidence to suggest that higher proportions of hatchery spawners were associated with lower juvenile productivity for spring Chinook Salmon in the Chiwawa River.

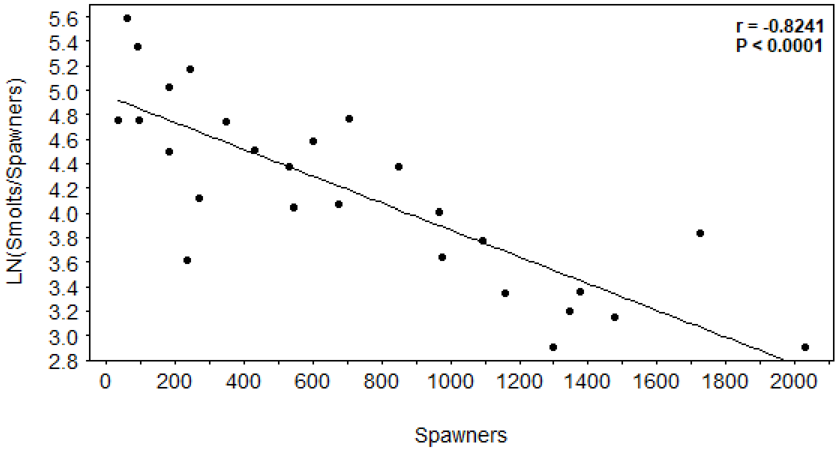


Figure 3. Smolts per spawner (log scale) versus spawner abundance for Chiwawa River Spring Chinook Salmon, 1991–2017, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope.

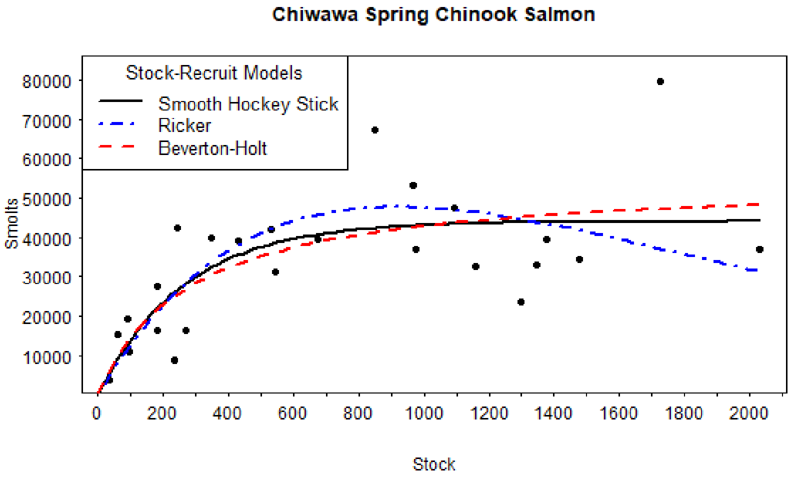


Figure 4. Stock-recruitment models fit to smolt and spawner data for Chiwawa River Spring Chinook Salmon, 1991–2017.

Table 2. Fitted stock-recruitment models for smolts and stock (spawner) data from Chiwawa River Spring Chinook Salmon, 1991–2017. Confidence intervals were estimated using bootstrap with 3,000 bootstrap samples. Correlation = Pearson correlation coefficient between parameter estimates from bootstrap samples. Model equations are defined in Equations (1), (2), and (3). ΔAICc represents change in AICc compared to model with minimum AICc.

Model	AICc	ΔAICc	Parameter[a]	Parameter Estimates	95% CI	Correlation
Smooth Hockey Stick	35.32	0.00	α	168	118.2 – 248.7	α, R_∞: -0.39
			R_∞	44,090	35,095 – 56,732	
Beverton-Holt	36.07	0.75	α	54,825	40,678 – 77,093	α, β: 0.87
			β	278	134.5 – 559.0	
Ricker	36.03	0.71	α	141	109.2 – 184.3	α, β: 0.80
			β	0.0011	0.0008 – 0.0014	
			K	47,760	40,825 – 56,520	

a = Estimated maximum recruitment parameters are: R_∞ for the Smooth Hockey Stick model, α for the Beverton-Holt model, and $K = (\alpha/\beta)e^{-1}$ for the Ricker model.

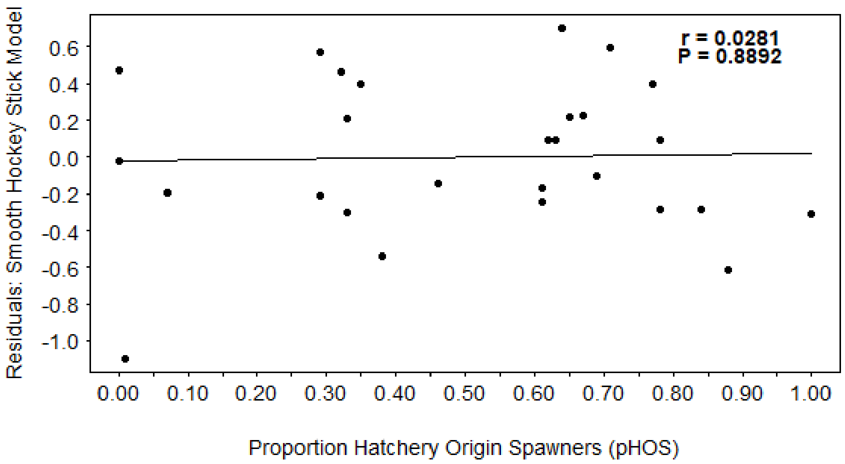


Figure 5. Residuals from Smooth Hockey Stick Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Chiwawa River Chinook Salmon, 1991–2017. R^2=0.0008.

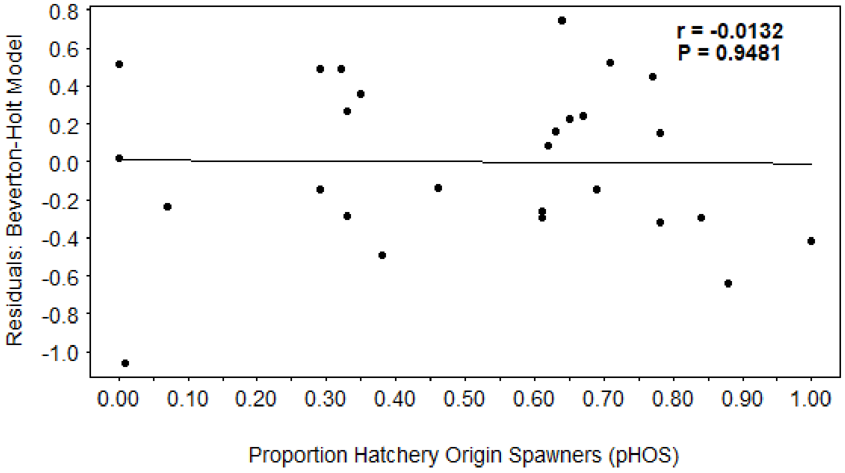


Figure 6. Residuals from Beverton-Holt Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Chiwawa River Chinook Salmon, 1991–2017. R^2=0.0002.

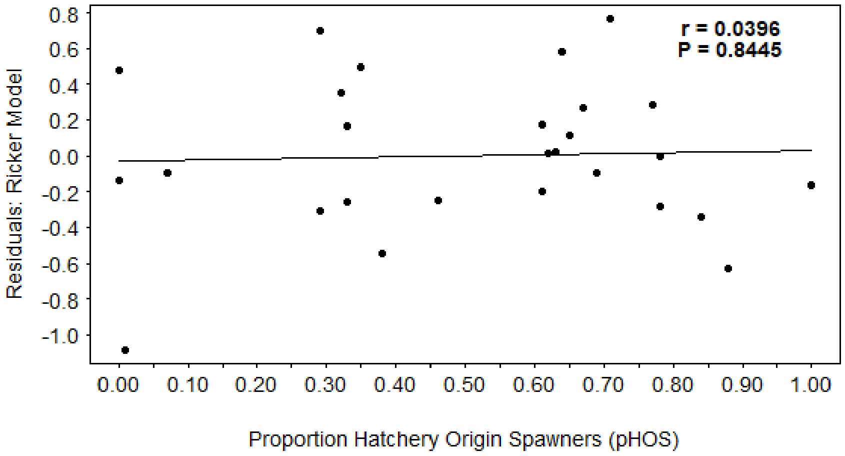


Figure 7. Residuals from Ricker Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Chiwawa River Chinook Salmon, 1991–2017. R^2=0.0016.

Hypothesis H02.2.1.2

There was a weak negative association between smolts per redd and the proportion of hatchery spawners (pHOS) for Chiwawa River Spring Chinook Salmon (Pearson correlation coefficient r=-0.3616, P=0.0319) (Figure 8). However, redd count was positively associated with pHOS (P=0.0280, Figure 9) and there was a strong pattern of post-spawning density dependence apparent from examination of the smolts per redd plotted against the redd counts (Figure 10). Thus, it is possible that the negative association between smolts per redd and pHOS may have resulted from the density dependence. The relationship between smolts per redd and pHOS was examined using the Ricker and Beverton-Holt stock-recruitment models in order to account for density dependence effects, with redds used in place of spawner counts. The Beverton-Holt model had considerably better fit than the Ricker model on the basis of AICc rank (ΔAICc = 5.81 compared to Ricker model) and examination of model residuals (Table 3; Figure A9 to Figure A13). The fitted Beverton-Holt model for smolts per redd was (Table 3):

$$ln(R/S) = ln(55{,}479) - 0.0343P_{HOS} - ln(117 + S).$$

The 95% bootstrap confidence interval for the effect of pHOS (i.e., β_2 in Equation (5)) was (-0.5443, 0.6421). Because this confidence interval included both positive and negative values, we concluded that there is no evidence of a negative association between pHOS and smolts per redd for Chiwawa Spring Chinook Salmon after adjusting for density dependence.

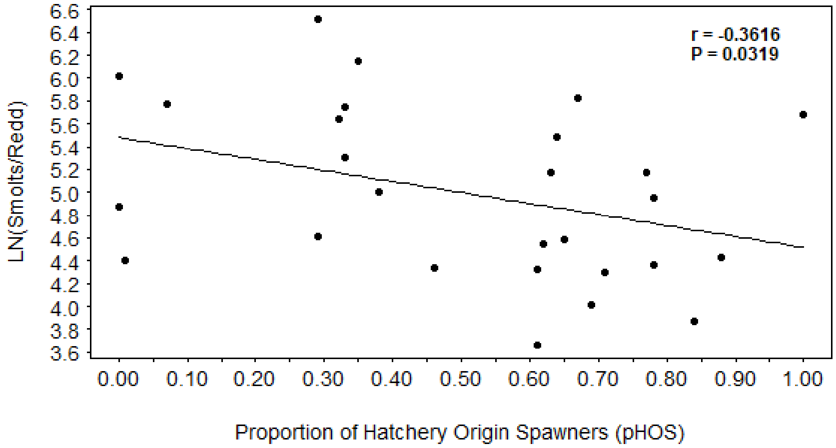


Figure 8. Smolts per redd (log scale) versus proportion of hatchery origin spawners (pHOS) for Chiwawa River Spring Chinook Salmon, 1991–2017, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. $R^2 = 0.1256$.

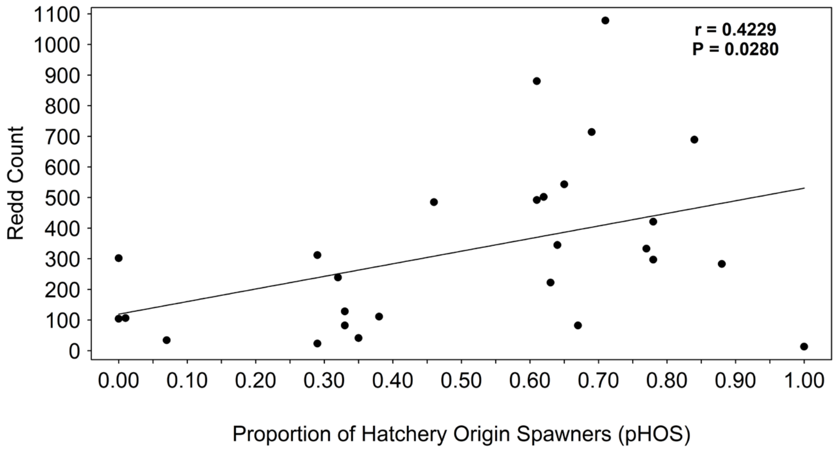


Figure 9. Redd count versus proportion of hatchery origin spawners (pHOS) for Chiwawa River Spring Chinook Salmon, 1991–2017, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope.

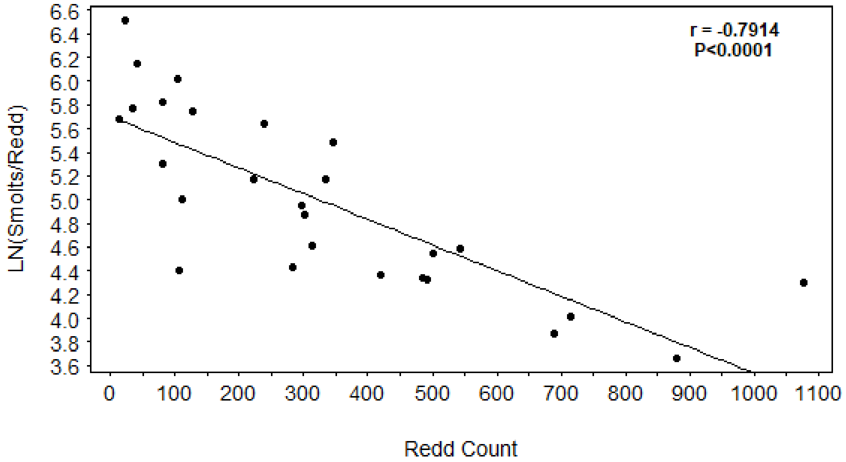


Figure 10. Smolts per redd versus redd count for Chiwawa River Spring Chinook Salmon, 1991–2017, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. Negative slope indicates post-spawning density dependence.

Table 3. Fitted stock-recruitment models for smolts per redd for Chiwawa River Spring Chinook Salmon, 1991–2017, including effect (β_2) of proportion of hatchery origin spawners (pHOS). Confidence intervals were estimated using bootstrap with 3,000 bootstrap samples. Model equations are defined in Equations (5) and (7). ΔAICc represents change in AICc compared to model with minimum AICc.

Model	AICc	ΔAICc	Parameter	Parameter Estimates	95% CI
Beverton-Holt	37.72	0.00	α	55,479	35,197 – 95,959
			β	117	57.9 – 242.2
			β_2	0.0343	-0.5443 – 0.6421
Ricker	43.54	5.81	$ln(\alpha)$	5.7328	5.2646 – 6.2477
			β	0.0021	0.0014 – 0.0032
			β_2	0.0872	-0.6880 – 0.9010

Nason Creek Spring Chinook Salmon

Adult spawner, smolt recruitment, pHOS, and redd count data were available for the 2002–2017 brood years. Adult stock abundance (spawners) ranged from 132 in 2017 to 702 in 2011 and averaged 398, and smolt recruitment ranged from 930 in 2014 to 8,696 in 2005 and averaged 4,774 (Figure 11, Figure 12). Redd counts averaged 176.9 (range = 68 to 413), and pHOS averaged 0.599 (range = 0.20 to 0.86). The analysis was performed with and without the low smolt count of 930 from the 2014 brood year.

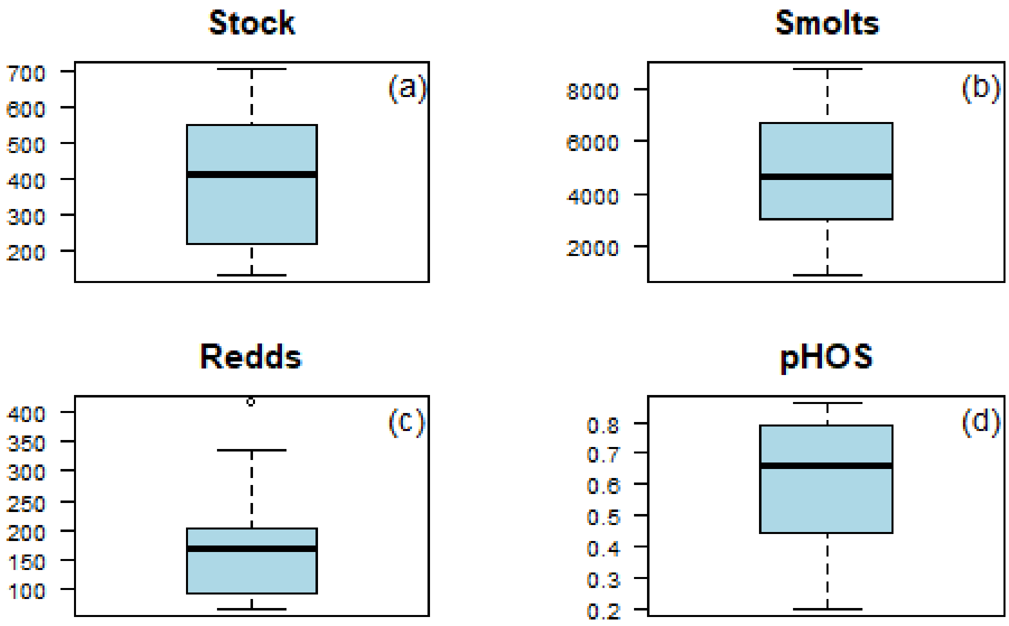


Figure 11. Nason Creek Spring Chinook Salmon boxplots for Stock (spawner abundance), Smolts, Redd counts, and proportion of hatchery origin spawners (pHOS), 2002–2017. Box indicates interquartile range and thick horizontal bar is median. Whiskers indicate quartile ± 1.5×interquartile range.

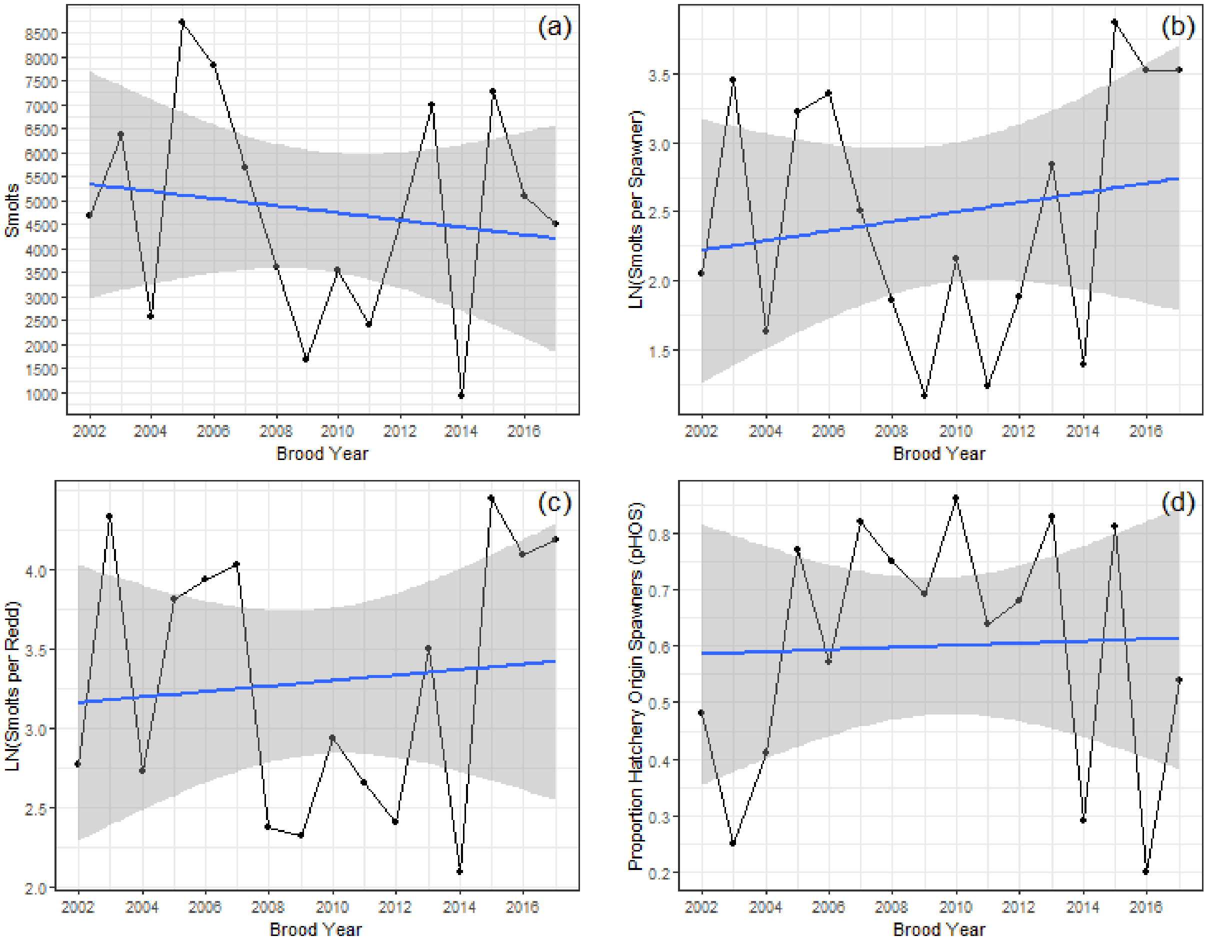


Figure 12. Nason Creek Spring Chinook Salmon annual Smolt counts, Smolt/Spawner (log scale), Smolt/Redd (log scale), and proportion of hatchery origin spawners (pHOS), 2002–2017. Line indicates the linear trend. Shaded area is the estimated 95% confidence interval of the line.

Hypothesis H02.2.1.1

A negative linear relationship between spawners and smolt recruitment indicated the presence of density dependence in mortality in one or more life stages between spawner data collection and smolt data collection (Figure 13). The low smolt count from 2014 had little effect on the detection of density dependence. An attempt was made to fit the Smooth Hockey Stick, Beverton-Holt, and Ricker stock-recruitment models to the spawner and smolt data. However, the Smooth Hockey Stick and Beverton-Holt modeling assumption of asymptotic growth in recruitment as spawner abundance increases was not supported by the data, as demonstrated by the locally smoothed curve (LOESS) in Figure 14, and neither the Smooth Hockey Stick model nor the Beverton-Holt model could be fit for the Nason Creek spawner-recruitment data. The Ricker model was fit to the Nason Creek data and demonstrated a maximum predicted recruitment at around 274 spawners (Figure 14), but the residuals demonstrated violation of modeling assumption 2 (lognormal errors) (Figure B1). The residuals from the Ricker model were compared to pHOS using correlation analysis. The estimated Pearson correlation coefficient between the Ricker model residuals and pHOS was 0.3317 and was not significantly different from 0 (P=0.2095; Figure 15). Additionally, a likelihood ratio test of the effect of pHOS on the Ricker model was non-significant, (P=0.1420). The Beverton-Holt model could not be fit with pHOS as a variable.

The Ricker model was refit without data from year 2014, the year that generated the very large negative residual apparent in Figure 14. Residuals from this model fit appeared to meet the modeling assumption of lognormal errors (Figure B3). The correlation between the Ricker model residuals and pHOS remained non-significant even without the 2014 brood year data (r=0.1614, P=0.5655; Figure 16). A likelihood ratio test of the effect of pHOS on the Ricker model was non-significant (P=0.5092) when the 2014 brood year was excluded. Even excluding data from 2014, the Smooth Hockey Stick model and the Beverton-Holt model could not be fit for the Nason Creek data set.

Overall, there was no evidence to suggest that higher proportions of hatchery spawners were associated with lower juvenile productivity for spring Chinook Salmon in the Nason Creek. However, the data did not satisfy the modeling assumptions well, and there may be a relationship that was not observable using the current analysis methods and data quality.

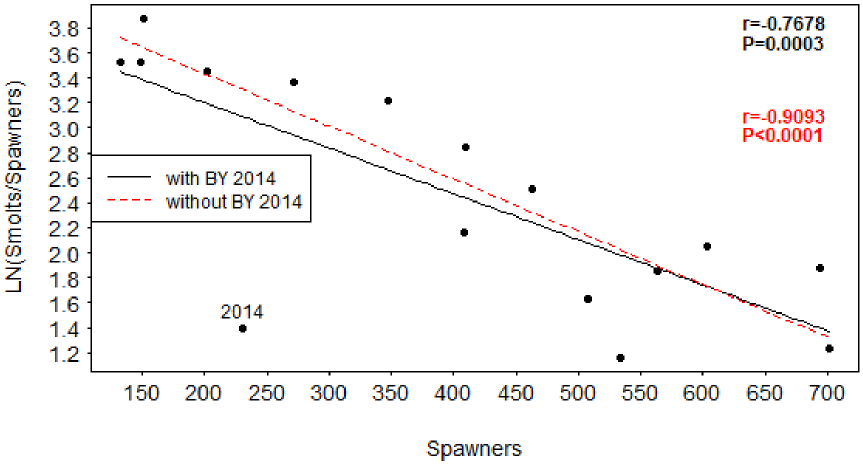


Figure 13. Smolts per spawner (log scale) versus spawner abundance for Nason Creek Spring Chinook Salmon, 2002–2017, with and without brood year 2014, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope.

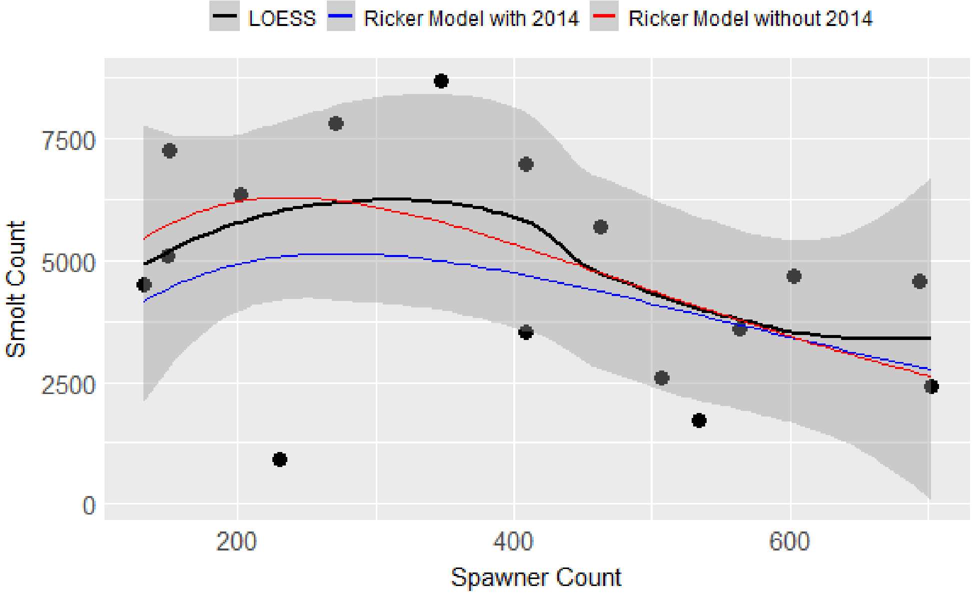


Figure 14. Stock and smolt data with fitted LOESS curve and Ricker Model (with and without data from 2014) for Nason Creek Spring Chinook Salmon, 2002–2017.

Table 4. Fitted stock-recruitment models for smolts and stock (spawner) data from Nason Creek Spring Chinook Salmon, 2002–2017. Confidence intervals were estimated using bootstrap with at least 3,000 bootstrap samples. Correlation = Pearson correlation coefficient between parameter estimates from bootstrap samples. Model equations are defined in Equations (1), (2), and (3). ΔAICc represents change in AICc compared to model with minimum AICc. *Only the Ricker model could be fit for Nason Creek data. The Ricker model was fit both with and without data from the 2014 brood year. AICc should not be compared between the two Ricker models.

Model*	AICc	ΔAICc	Parameter[a]	Parameter Estimates	95% CI	Correlation
Smooth Hockey Stick	NA	NA	α	NA	NA	α, R_∞: NA
			R_∞	NA	NA	
Beverton-Holt	NA	NA	α	NA	NA	α, β: NA
			β	NA	NA	
Ricker with 2014	35.52	NA	α	51.1	25.7 –89.2	α, β: 0.89
			β	0.0037	0.0022 – 0.0052	
			K	5,144	3,710 – 7,011	
Ricker without 2014	20.44	NA	α	72.1	44.7 – 108.1	α, β: 0.90
			β	0.0042	0.0032 – 0.0005	
			K	6,286	4,942 – 7,995	

a = Estimated maximum recruitment parameters are: R_∞ for the Smooth Hockey Stick model, α for the Beverton-Holt model, and $K = (\alpha/\beta)e^{-1}$ for the Ricker model.

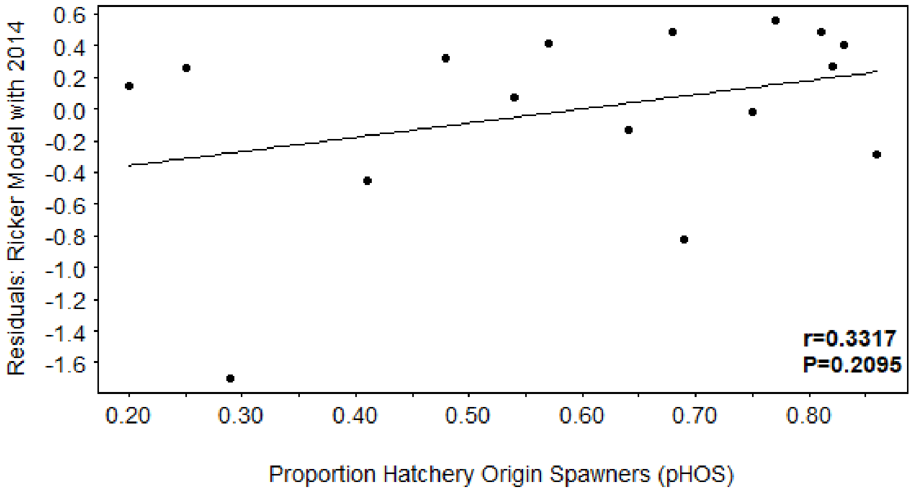


Figure 15. Residuals from the Ricker model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Nason Creek Chinook Salmon, 2002–2017 (including brood year 2014). R^2=0.1100.

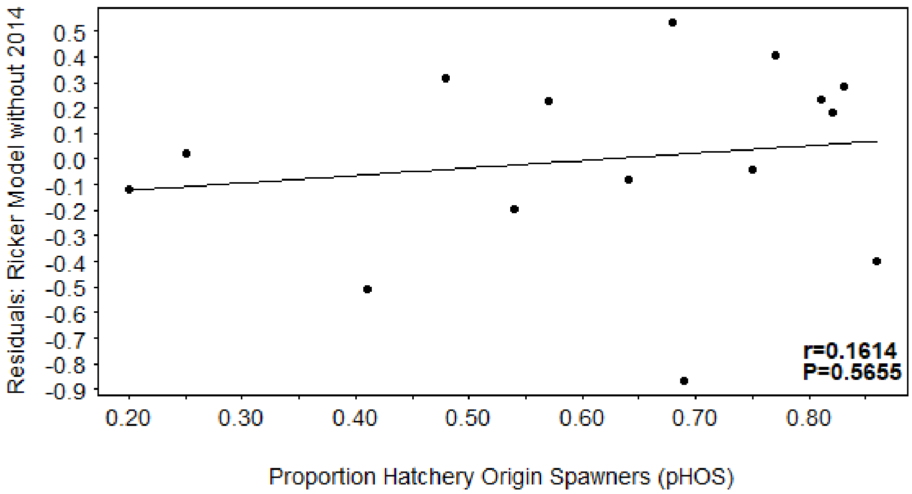


Figure 16. Residuals from the Ricker model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Nason Creek Chinook Salmon, 2002–2017 without brood year 2014. R^2=0.0261.

Hypothesis H02.2.1.2

There was no evidence of a negative association between smolts per redd and the proportion of hatchery spawners (pHOS) for Nason Creek Spring Chinook Salmon (Pearson correlation coefficient r=-0.1011, P=0.3547) (Figure 17). Additionally, the linear association between redd count and pHOS was non-significant (P=0.2278; Figure 18). Nevertheless, there was weak evidence of post-spawning density dependence based on comparison of smolts per redd versus redd counts using data from all brood years, including 2014 (P=0.0049; Figure 19). Thus, the relationship between smolts per redd and pHOS was examined using the Ricker stock-recruitment model in order to account for density dependence effects, using redds in place of spawner abundance. Similar to the modeling using spawner abundance, the Beverton-Holt model could not be fit using redd counts.

The fitted Ricker model (including brood year 2014) was (Table 5):

$$ln(R/S) = 3.8891 + 0.7001P_{HOS} - 0.0058S.$$

The 95% bootstrap confidence interval for the effect of pHOS (i.e., β_2 in Equation (7)) was (-2.7076, 0.8269). When the 2014 brood year was omitted, the regression model was

$$ln(R/S) = 4.4479 + 0.0084P_{HOS} - 0.0060S,$$

and the 95% bootstrap confidence interval for the effect of pHOS was (-1.6065, 1.1149).

Whether or not the 2014 brood year was included, the 95% confidence interval included both positive and negative values for the effect of pHOS, providing no evidence of a negative association between pHOS and smolts per redd for Nason Creek Chinook Salmon after adjusting for density dependence. However, analysis of residuals from the Ricker model with and without 2014 demonstrated poor agreement with the assumption of lognormal errors and poor model fit (Figures B6, B8), which is also demonstrated by the wide 95% bootstrap confidence intervals for the model parameters (Table 5). This pattern results in lower confidence in the estimated model parameters and lowered ability to detect a relationship between pHOS and smolts per redd using the available data.

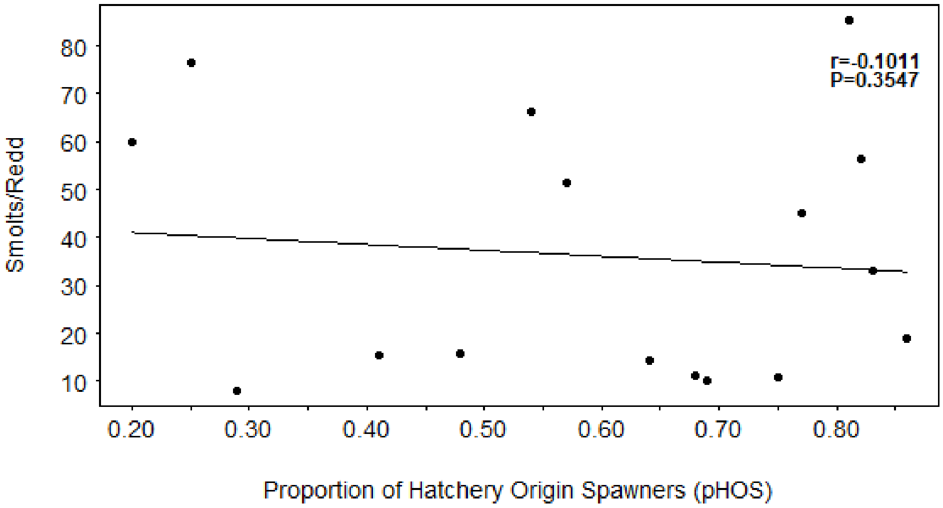


Figure 17. Smolts per redd versus proportion of hatchery origin spawners (pHOS) for Nason Creek Spring Chinook Salmon, 2002–2017, including brood year 2014, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. $R^2 = 0.0102$.

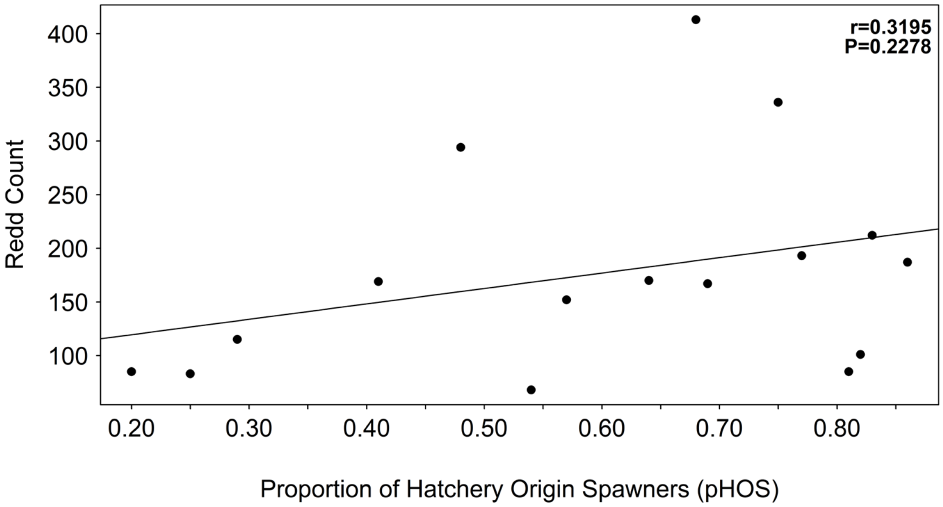


Figure 18. Redd count versus proportion of hatchery origin spawners (pHOS) for Nason Creek Spring Chinook Salmon, 2002–2017, including brood year 2014, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope.

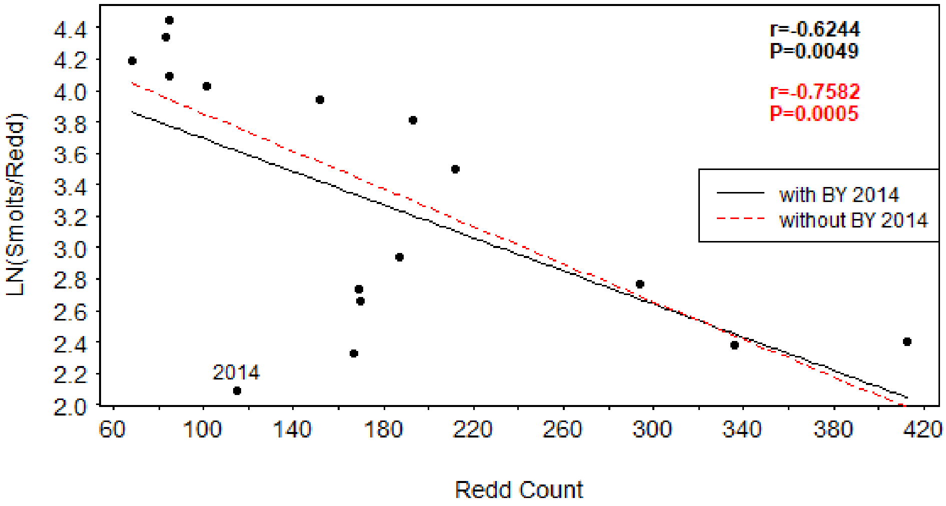


Figure 19. Smolts per redd (log scale) versus redd count for Nason Creek Spring Chinook Salmon, 2002–2017, with and without 2014, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. Negative slope indicates post-spawning density dependence.

Table 5. Fitted stock-recruitment models for smolts per redd for Nason Creek Spring Chinook Salmon, 2002–2017 (including brood year 2014), including effect (β_2) of proportion of hatchery origin spawners (pHOS). Confidence intervals were estimated using bootstrap with 3,000 bootstrap samples. Model equations are defined in Equations (5) and (7). ΔAICc represents change in AICc compared to model with minimum AICc. *Only the Ricker model could be fit for Nason Creek data. The Ricker model was fit both with and without data from the 2014 brood year. AICc should not be compared between the two Ricker models.

Model*	AICc	ΔAICc	Parameter	Parameter Estimates	95% CI
Beverton-Holt	NA	NA	α	NA	NA
			β	NA	NA
			β_2	NA	NA
Ricker with 2014	41.22	NA	$ln(\alpha)$	3.8891	2.2758– 4.8782
			β	0.0058	0.0033 – 0.0107
			β_2	-0.7001	-2.7076 – 0.8269
Ricker without 2014	33.64	NA	$ln(\alpha)$	4.4479	3.1832 – 5.0293
			β	0.0060	0.0037 – 0.0100
			β_2	-0.0084	-1.6065 – 1.1149

White River Spring Chinook Salmon

Adult spawner, smolt recruitment, pHOS, and redd count data were available for the 2005–2017 brood years. Adult stock abundance (spawners) ranged from 31 in 2017 to 173 in 2009 and averaged 94, and smolt recruitment ranged from 580 in 2014 to 11,170 in 2016 and averaged 5,079 (Figure 20, Figure 21). Redd counts averaged 44.1 (range = 16 to 86), and pHOS averaged 0.412 (range = 0.00 to 0.75).

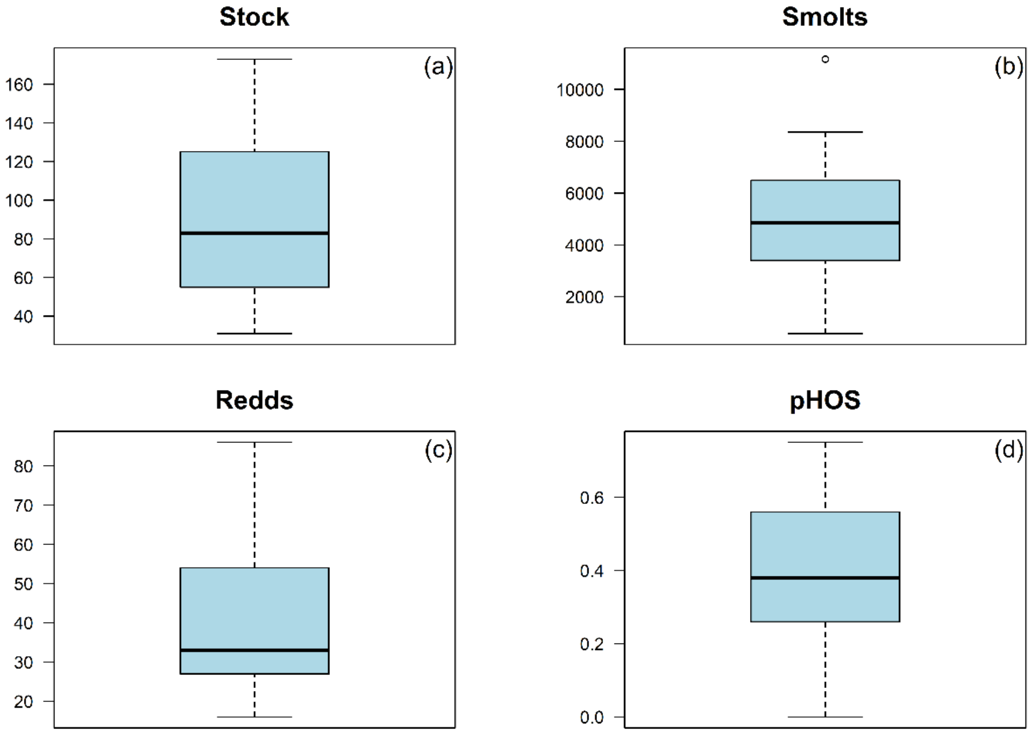


Figure 20. White River Spring Chinook Salmon boxplots for Stock (spawner abundance), Smolts, Redd counts, and proportion of hatchery origin spawners (pHOS), 2005–2017. Box indicates interquartile range and thick horizontal bar is median. Whiskers indicate quartile ± 1.5×interquartile range.

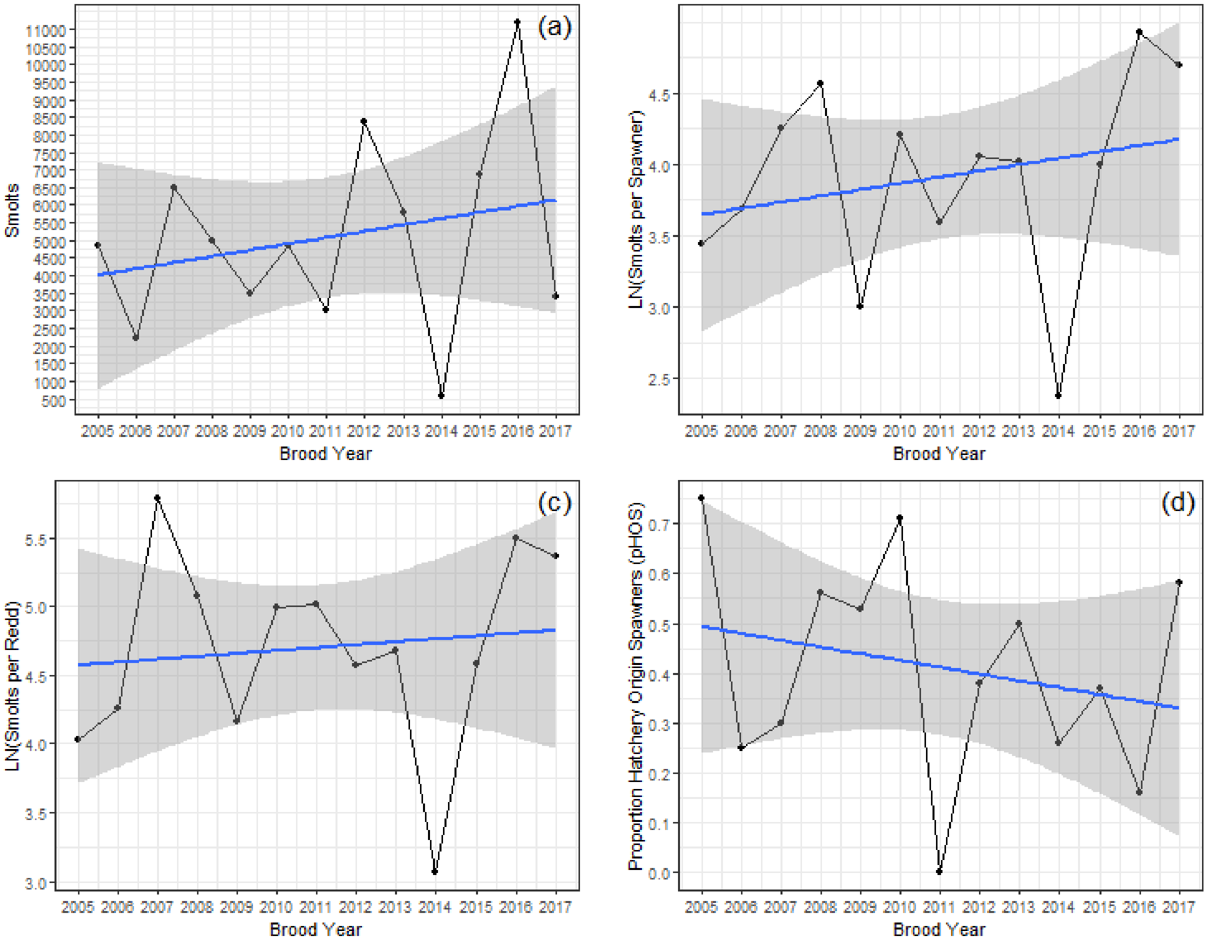


Figure 21. White River Spring Chinook Salmon annual Smolt counts, Smolt/Spawner (log scale), Smolt/Redd (log scale), and proportion of hatchery origin spawners (pHOS), 2005–2017. Line indicates the linear trend. Shaded area is the estimated 95% confidence interval of the line.

Hypothesis H02.2.1.1

A weak negative linear relationship was observed between White River spring Chinook Salmon spawners and smolt recruitment, but it was non-significant, providing inconclusive evidence of density dependence in mortality between the spawning and smolt life stages (P=0.1550; Figure 22). The very low smolt count from 2014 influenced the perceived relationship; without the 2014 brood year, there was a strong negative relationship between spawners and smolt recruitment (P=0.0084). Thus, the Smooth Hockey Stick, Beverton-Holt, and Ricker stock-recruitment models were fit to the spawner and smolt data.

When the 2014 brood year was included in the analysis, there was essentially no difference in the fits among the three stock-recruitment models (Figure 23, Table 6). Correlation coefficients between residuals from those models and pHOS ranged from 0.1408 to 0.1600; none was significantly different from 0 (P≥0.6015; Figure 24 – Figure 26). Additionally, likelihood ratio tests of the effect of pHOS on the Beverton-Holt and Ricker models were non-significant (P≥0.5518). However, tests of the modeling assumption of lognormal errors were inconclusive for all three models (Figures C1, C7, and C11), and model parameters were highly correlated (Table 6, Figure C3). Additionally, the 95% bootstrap confidence intervals for maximum recruitment included smolt recruitment levels far beyond the maximum observed smolt recruitment of 11,170. Thus, results based on these three stock-recruitment models should be interpreted with caution.

Removing the 2014 brood year from the analysis had little effect on the comparisons among the three models (Figure 27, Table 7), although the residuals were more consistently lognormally distributed. There remained high correlation in the model parameters observed from the bootstrap samples (Table 7, Figure C6). The 95% bootstrap confidence intervals again included maximum recruitment estimates beyond the observed data, but they were considerably lower than when 2014 was included. Nevertheless, even without the 2014 brood year, the residuals were not correlated with pHOS for any of the three models (P≥0.8533; Figure 28–Figure 30). Likelihood ratio tests of the effect of pHOS on the Beverton-Holt and Ricker models were also non-significant (P≥0.7763).

Overall, there was no evidence to suggest that higher proportions of hatchery spawners were associated with lower juvenile productivity for spring Chinook Salmon in the White River. However, there were only 13 years of data including the 2014 brood year, and some of the modeling assumptions were not well supported. It is possible that there is a relationship between pHOS and juvenile productivity that was not observable using the available data.

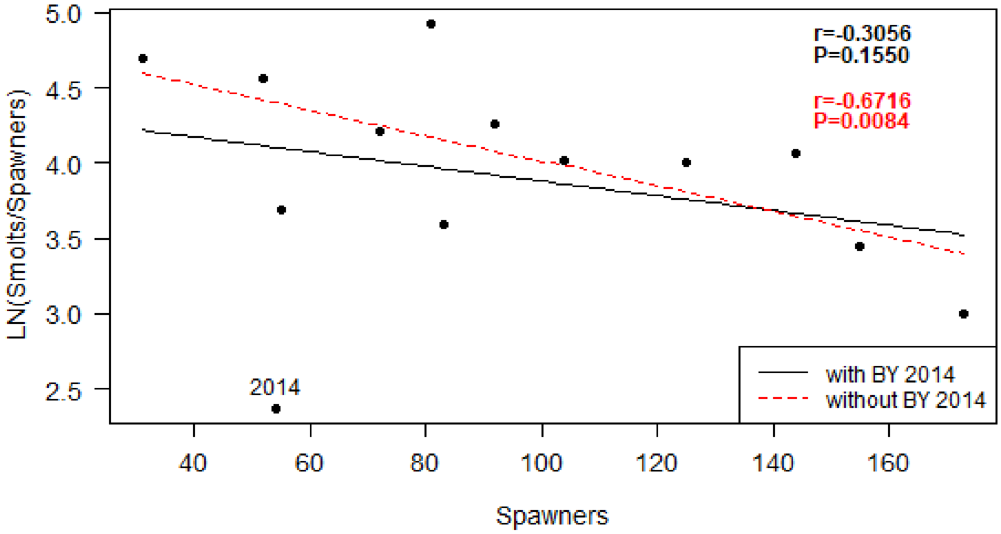


Figure 22. Smolts per spawner (log scale) versus spawner abundance for White River Spring Chinook Salmon, 2005–2017, with and without brood year 2014, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope.

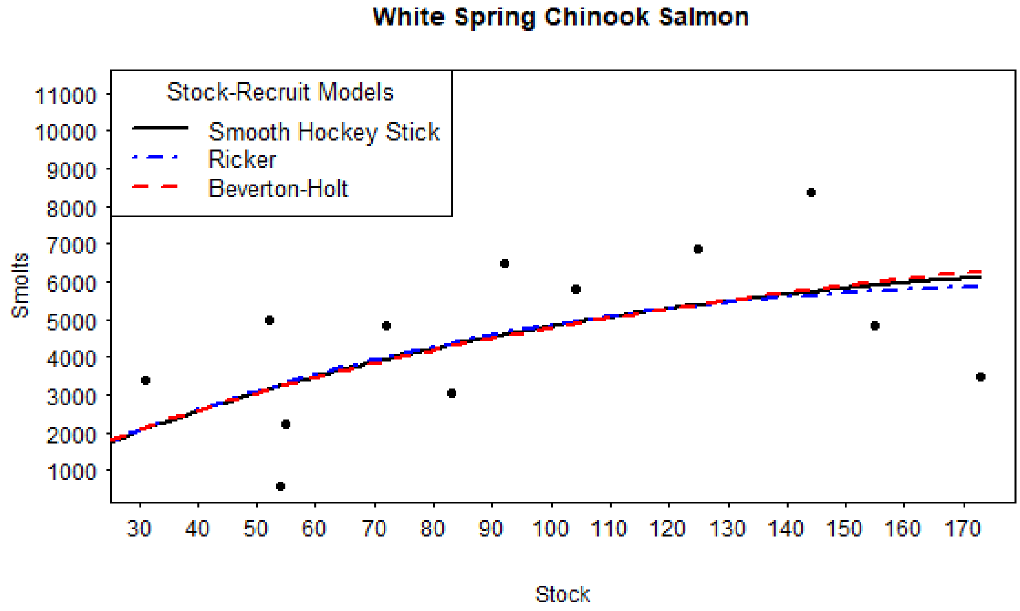


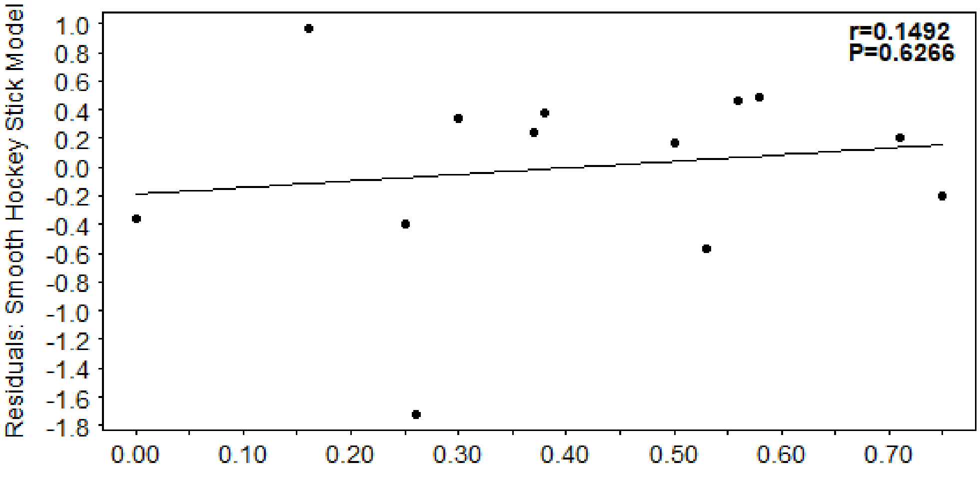
Figure 23. Stock-recruitment models fit to smolt and spawner data for White River Spring Chinook Salmon, 2005–2017, including brood year 2014.

Table 6. Fitted stock-recruitment models for smolts and stock (spawner) data from White River Spring Chinook Salmon, 2005–2017, including brood year 2014. Confidence intervals were estimated using bootstrap with at least 1,000 bootstrap samples. Correlation = Pearson correlation coefficient between parameter estimates from bootstrap samples. Model equations are defined in Equations (1), (2), and (3). ΔAICc represents change in AICc compared to model with minimum AICc.

Model	AICc	ΔAICc	Parameter[b]	Parameter Estimates	95% CI	Correlation
Smooth Hockey Stick	34.06	0.08	α	79.7	44.7 – 262.1	α, R_∞: -0.24[a]
			R_∞	7,183	3,516 – 60,989	
Beverton-Holt	34.12	0.14	α	11,011	5,286 – 185,892	α, β: 0.96
			β	130	32 – 3,591	
Ricker	33.98	0.00	α	78.9	35.5 – 180.4	α, β: 0.90
			β	0.0049	< 0.0001 – 0.0137	
			K	5,961	3,595 – ∞	

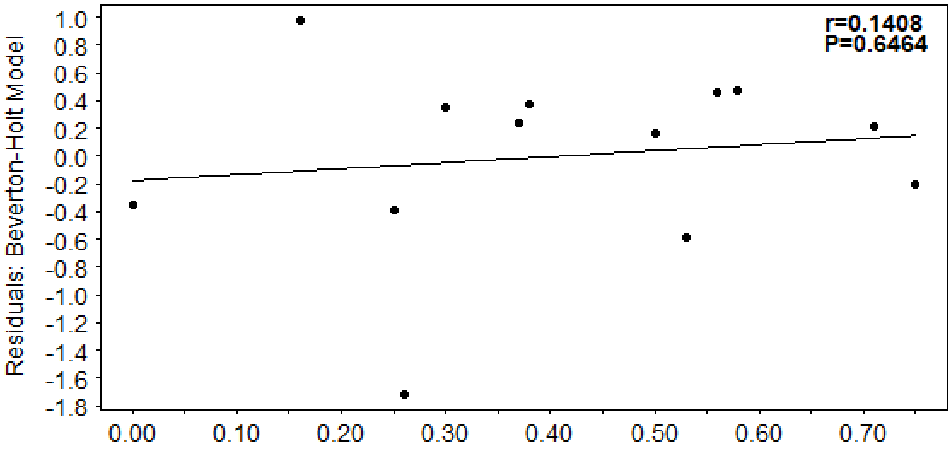
a = Correlation coefficient between α and R_∞ is uninformative because parameter estimates are not linearly related; see Figure C3. The correlation coefficient between $1/\alpha$ and R_∞ = 0.6241.

b = Estimated maximum recruitment parameters are: R_∞ for the Smooth Hockey Stick model, α for the Beverton-Holt model, and $K = (\alpha/\beta)e^{-1}$ for the Ricker model.



Proportion Hatchery Origin Spawners (pHOS)

Figure 24. Residuals from Smooth Hockey Stick Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from White River Spring Chinook Salmon, 2005–2017, including brood year 2014. R^2=0.0223.



Proportion Hatchery Origin Spawners (pHOS)

Figure 25. Residuals from the Beverton-Holt Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from White River Spring Chinook Salmon, 2005–2017, including brood year 2014. R^2=0.0198.

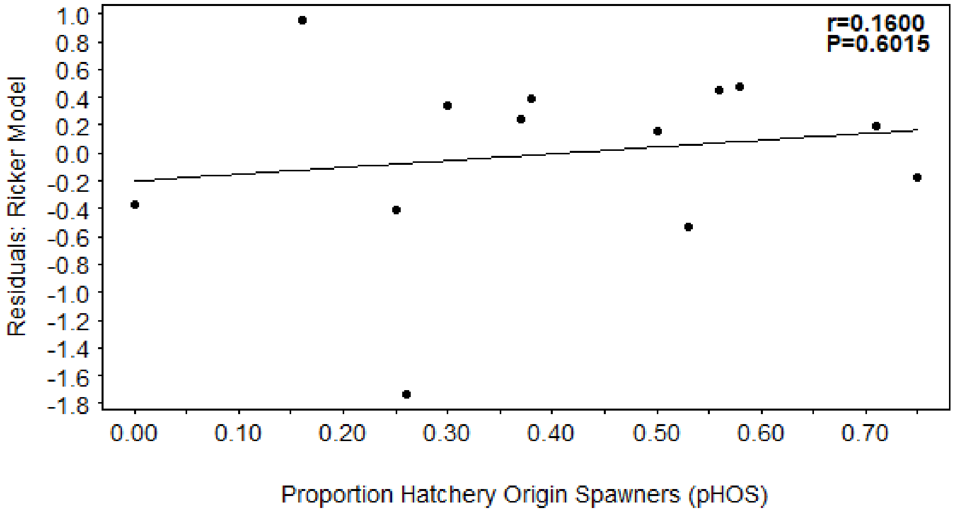


Figure 26. Residuals from the Ricker Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from White River Spring Chinook Salmon, 2005–2017, including brood year 2014. R^2=0.0256.

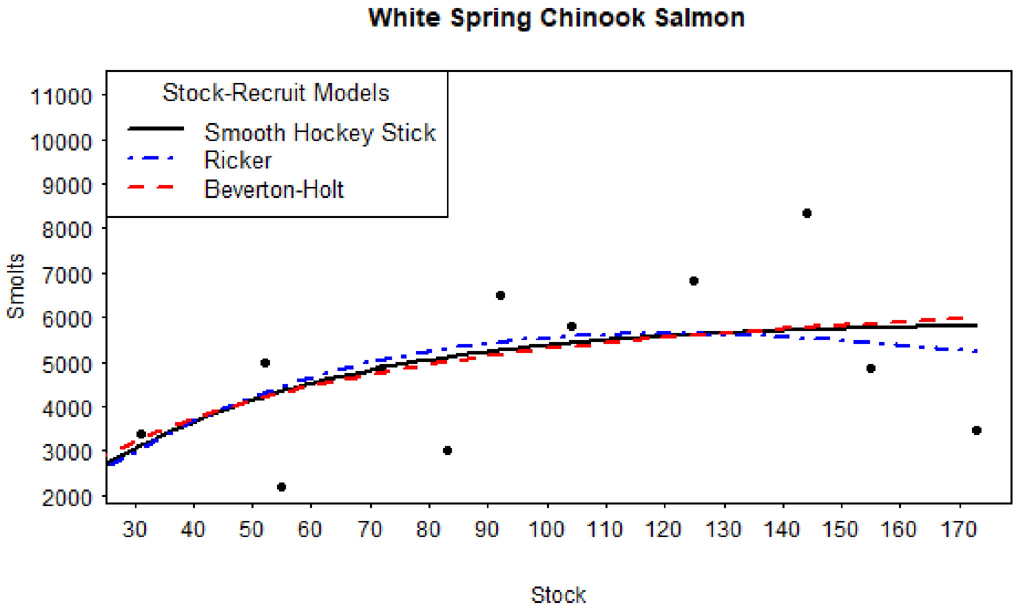


Figure 27. Stock-recruitment models fit to smolt and spawner data for White River Spring Chinook Salmon, 2005–2017, without brood year 2014.

Table 7. Fitted stock-recruitment models for smolts and stock (spawner) data from White River Spring Chinook Salmon, 2005–2017, without brood year 2014. Confidence intervals were estimated using bootstrap with at least 3,000 bootstrap samples. Correlation = Pearson correlation coefficient between parameter estimates from bootstrap samples. Model equations are defined in Equations (1), (2), and (3). ΔAICc represents change in AICc compared to model with minimum AICc.

Model	AICc	ΔAICc	Parameter[b]	Parameter Estimates	95% CI	Correlation
Smooth Hockey Stick	20.72	0.60	α	142.8	73.0 – 364.0	α, R_∞: -0.38[a]
			R_∞	5,903	4,348 – 12,940	
Beverton-Holt	20.97	0.85	α	7,320	4,574 – 24,921	α, β: 0.99
			β	38.4	0.08 – 340.1	
Ricker	20.12	0.00	α	128	73.2 – 219.4	α, β: 0.90
			β	0.0084	0.0032 – 0.0135	
			K	5,632	4,571 – 9,125	

a = Correlation coefficient between α and R_∞ is uninformative because parameter estimates are not linearly related; see Figure C6. The correlation coefficient between $1/\alpha$ and R_∞ = 0.5703.

b = Estimated maximum recruitment parameters are: R_∞ for the Smooth Hockey Stick model, α for the Beverton-Holt model, and $K = (\alpha/\beta)e^{-1}$ for the Ricker model.

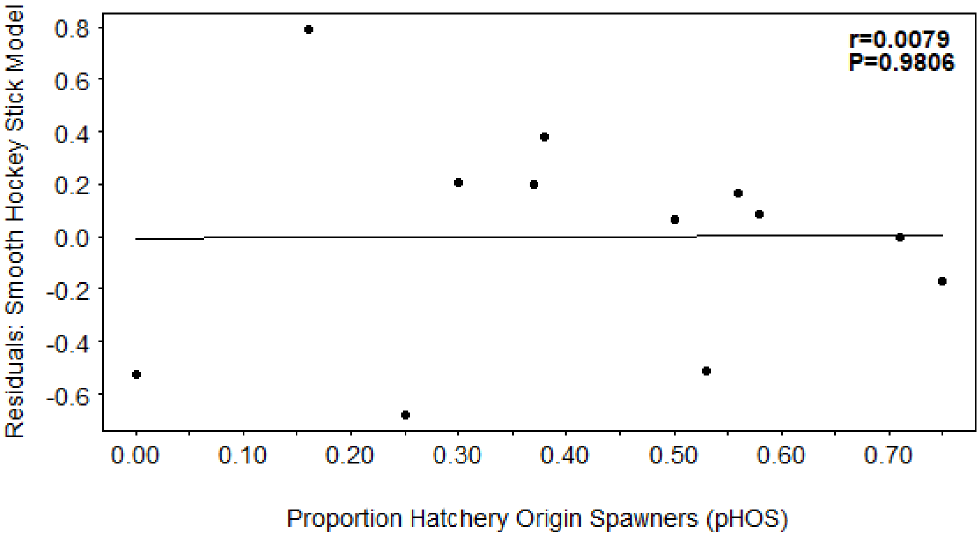


Figure 28. Residuals from Smooth Hockey Stick Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from White River Spring Chinook Salmon, 2005–2017, without brood year 2014. R^2=0.0001.

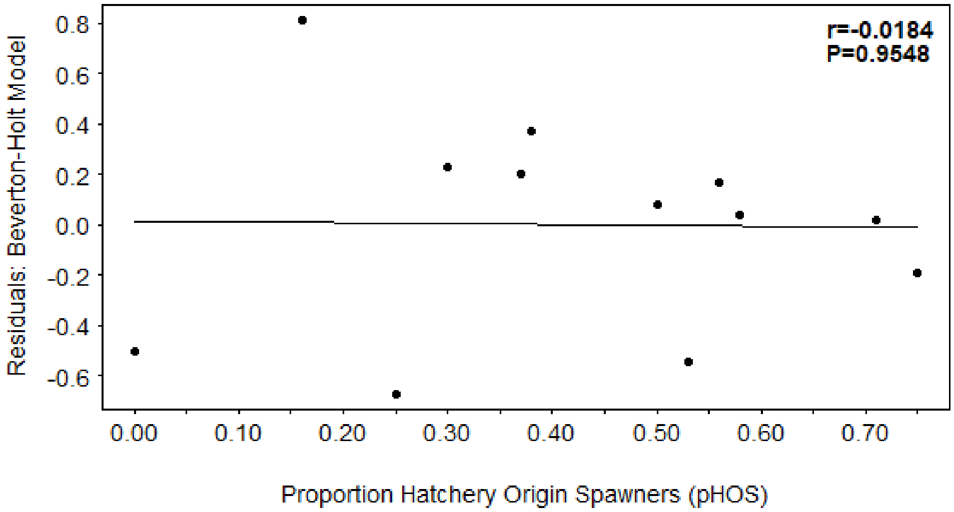


Figure 29. Residuals from the Beverton-Holt Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from White River Spring Chinook Salmon, 2005–2017, without brood year 2014. R^2=0.0003.

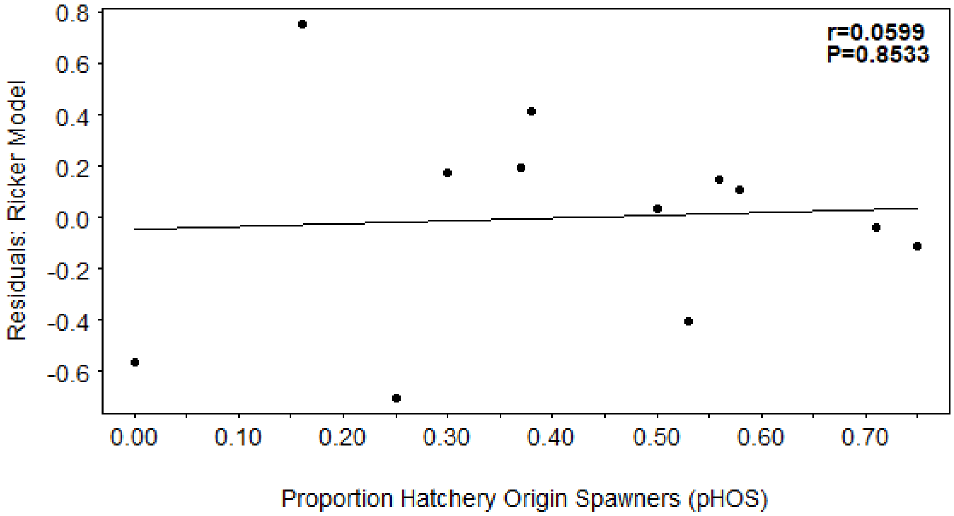


Figure 30. Residuals from the Ricker Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from White River Spring Chinook Salmon, 2005–2017, without brood year 2014. R^2=0.0036.

Hypothesis H02.2.1.2

There was no evidence of a negative association between smolts per redd and the proportion of hatchery spawners (pHOS) for White River Spring Chinook Salmon (Pearson correlation coefficient r=-0.1873, P=0.2700) (Figure 31). Additionally, the linear association between redd count and pHOS was non-significant (P=0.2795; Figure 32). There was no evidence of post-spawning density dependence based on comparison of smolts per redd versus redd counts using data from all brood years, including 2014 (P=0.1431; Figure 33). However, when the 2014 brood year was omitted, density dependence was more apparent (P=0.0109). Thus, the relationship between smolts per redd and pHOS was examined using the Ricker and Beverton-Holt stock-recruitment models in order to account for density dependence effects, using redds in place of spawner abundance. The model fits and assessment of residuals were very similar (Table 8, Figure C16 – Figure C23). The fitted Beverton-Holt model for smolts per redd was (including the 2014 brood year; Table 8):

$$ln(R/S) = ln(9{,}478) + 0.0887P_{HOS} - ln(48.1 + S).$$

The 95% bootstrap confidence interval for the effect of pHOS (i.e., β_2 in Equation (5)) was (-1.6125, 1.6392). The fitted Ricker model for smolts per redd was:

$$ln(R/S) = 5.0979 + 0.0655P_{HOS} - 0.0096S.$$

The 95% bootstrap confidence interval for the effect of pHOS (i.e., β_2 in Equation (7)) was (-2.2529, 1.5695). Similar results were observed when the models were fit without the 2014 brood year (Table 9).

Because the confidence intervals for the effect of pHOS included both positive and negative values regardless of the model and whether the 2014 brood year was included, we concluded that there was no evidence of a negative association between pHOS and smolts per redd for White River Spring Chinook Salmon after adjusting for density dependence. However, the bootstrap confidence intervals for the model parameters were wide and included maximum recruitment levels beyond the range of the observed data (Table 8,

Table 9), demonstrating an overall lack of fit. The small sample size may have contributed to the lack of model fit, and likewise may lower the ability to detect a relationship between pHOS and smolts per redd using the available data.

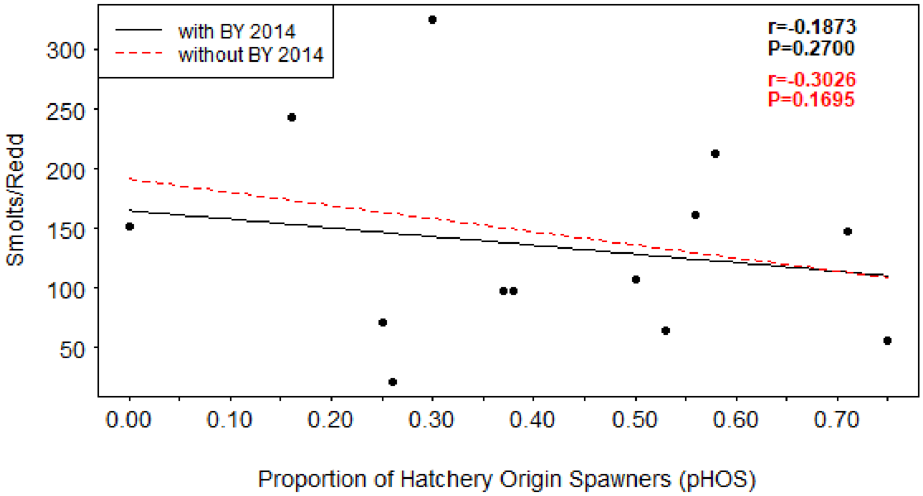


Figure 31. Smolts per redd versus proportion of hatchery origin spawners (pHOS) for White River Spring Chinook Salmon, 2005–2017, with and without brood year 2014, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. R^2 = 0.0351 with BY 2014 and R^2 = 0.0916 without BY 2014.

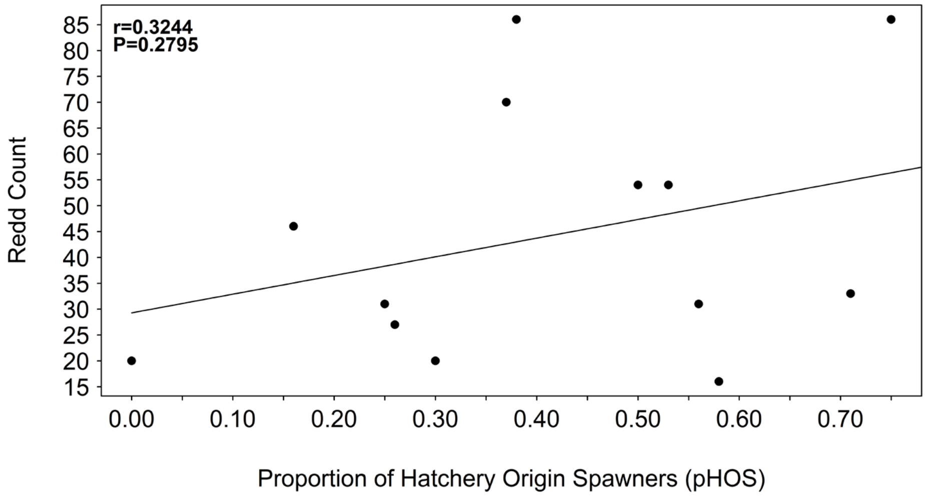


Figure 32. Redd count versus proportion of hatchery origin spawners (pHOS) for White River Spring Chinook Salmon, 2005–2017, including 2014 brood year, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope.

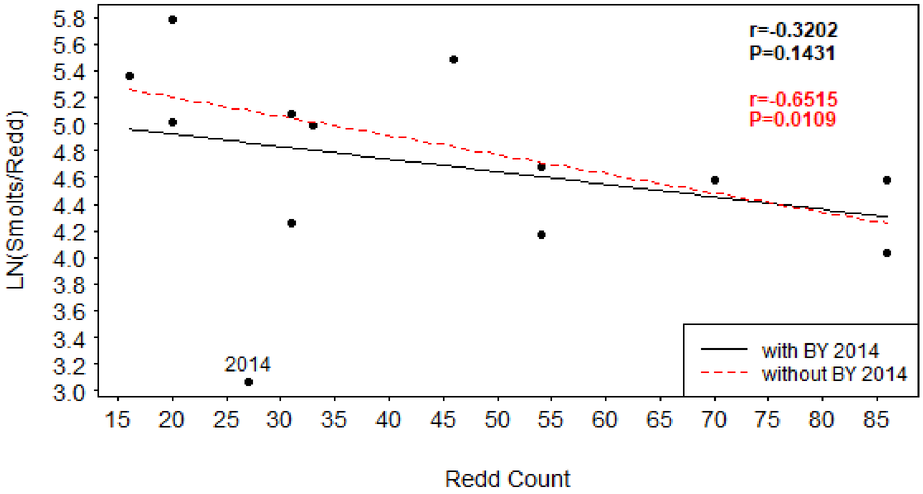


Figure 33. Smolts per redd (log scale) versus redd count for White River Spring Chinook Salmon, 2005–2017, with and without the 2014 brood year, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. Negative slope indicates post-spawning density dependence.

Table 8. Fitted stock-recruitment models for smolts per redd for White River Spring Chinook Salmon, 2005–2017, including brood year 2014, including effect (β_2) of proportion of hatchery origin spawners (pHOS). Confidence intervals were estimated using bootstrap with 3,000 bootstrap samples. Model equations are defined in Equations (5) and (7). ΔAICc represents change in AICc compared to model with minimum AICc.

Model	AICc	ΔAICc	Parameter	Parameter Estimates	95% CI
Beverton-Holt	38.71	0.00	α	9,478	4,270 – 173,640
			β	48.1	12.9 – 1,315
			β_2	-0.0887	-1.6125 – 1.6392
Ricker	38.82	0.10	$ln(\alpha)$	5.0979	3.5461 – 6.3336
			β	0.0096	-0.0080 – 0.0228
			β_2	-0.0655	-2.2529 – 1.5695

Table 9. Fitted stock-recruitment models for smolts per redd for White River Spring Chinook Salmon, 2005–2017, omitting brood year 2014, including effect (β_2) of proportion of hatchery origin spawners (pHOS). Confidence intervals were estimated using bootstrap with 3,000 bootstrap samples. Model equations are defined in Equations (5) and (7). ΔAICc represents change in AICc compared to model with minimum AICc.

Model	AICc	ΔAICc	Parameter	Parameter Estimates	95% CI
Beverton-Holt	24.87	0.00	α	9,680	4,671 – 39,360
			β	24.9	3.0 – 175.3
			β_2	0.3364	-0.6880 – 1.3979
Ricker	25.26	0.38	$ln(\alpha)$	5.5953	4.7824 – 6.5861
			β	0.0135	0.0030 – 0.0237
			β_2	0.3455	-0.8663 – 1.8240

Twisp River Spring Chinook Salmon

Adult spawner, smolt recruitment, pHOS, and redd count data were available for the 2003–2017 brood years. Adult stock abundance (spawners) ranged from 43 in 2003 to 341 in 2004 and averaged 165, and smolt recruitment ranged from 900 in 2003 to 16,415 in 2006 and averaged 5,295 (Figure 34, Figure 35). Redd counts averaged 79.3 (range = 18 to 145), and pHOS averaged 0.52 (range = 0.28 to 0.76).

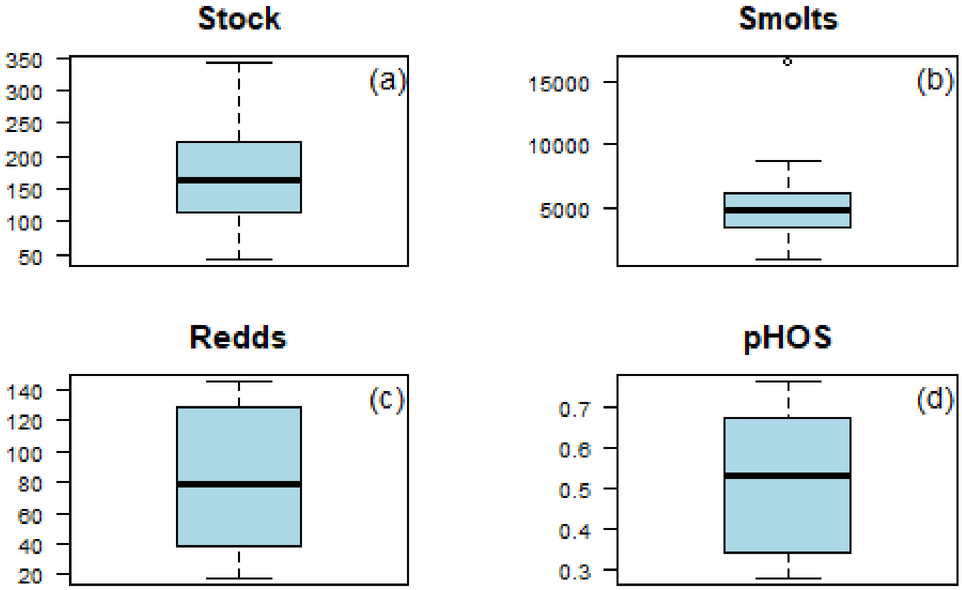


Figure 34. Twisp River Spring Chinook Salmon boxplots for Stock (spawner abundance), Smolts, Redd counts, and proportion of hatchery origin spawners (pHOS), 2003–2017. Box indicates interquartile range and thick horizontal bar is median. Whiskers indicate quartile ± 1.5×interquartile range.

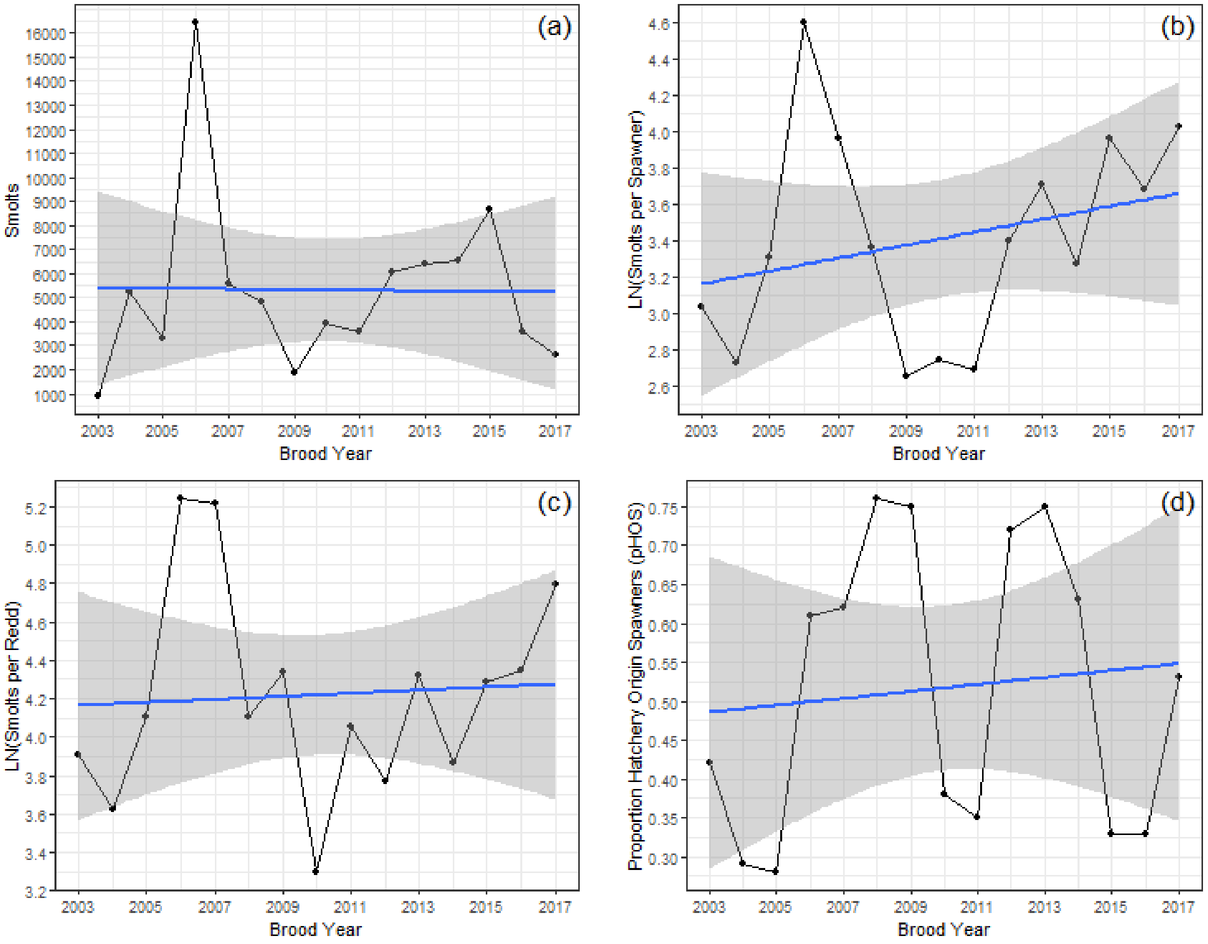


Figure 35. Twisp River Spring Chinook Salmon annual Smolt counts, Smolt/Spawner (log scale), Smolt/Redd (log scale), and proportion of hatchery origin spawners (pHOS), 2002–2017. Line indicates the linear trend. Shaded area is the estimated 95% confidence interval of the line.

Hypothesis H02.2.1.1

A weak negative linear relationship was observed between Twisp River Spring Chinook Salmon spawners and smolt recruitment, providing evidence of density dependence in mortality between the spawning and smolt life stages (P=0.0463; Figure 36). Thus, the Smooth Hockey Stick, Beverton-Holt, and Ricker stock-recruitment models were fit to the spawner and smolt data.

There was little difference in the model fits among the three stock-recruitment models, with the only perceptible differences in model predictions observed for spawner abundance greater than approximately 240 (Figure 37). The Ricker model had the lowest AICc value but the Beverton-Holt and Smooth Hockey Stick models both had ΔAICc$\leq$0.62 (Table 10). However, all three models produced wide bootstrap confidence intervals for the model parameters. The maximum recruitment estimates in particular had confidence intervals that extended far beyond the maximum observed smolt recruitment (16,415). High correlation was observed between the model parameter estimates, increasing uncertainty in the model predictions (Table 10, Figure D3). Additionally, analysis of residuals from each of the models demonstrated a negative autocorrelation at a time lag of 3 years (Figure D2, Figure D5, Figure D7), further suggesting that these models do not adequately account for the population dynamics and that the model parameters may be biased.

Correlation analysis found no association between the residuals from these stock-recruitment models and pHOS, with correlation coefficients ranging from 0.1612 to 0.1921 (P$\geq$0.4927; Figure 38 – Figure 40).

Additionally, likelihood ratio tests of the effect of pHOS on the Beverton-Holt and Ricker models were non-significant (P≥0.4470). Thus, there was no evidence to suggest that higher proportions of hatchery spawners were associated with lower juvenile productivity for spring Chinook Salmon in the Twisp River. However, there were only 15 years of data available, and the modeling assumptions were not well supported. Thus, it remains possible that there is a relationship between pHOS and juvenile productivity that are not observable using the available data and analyses.

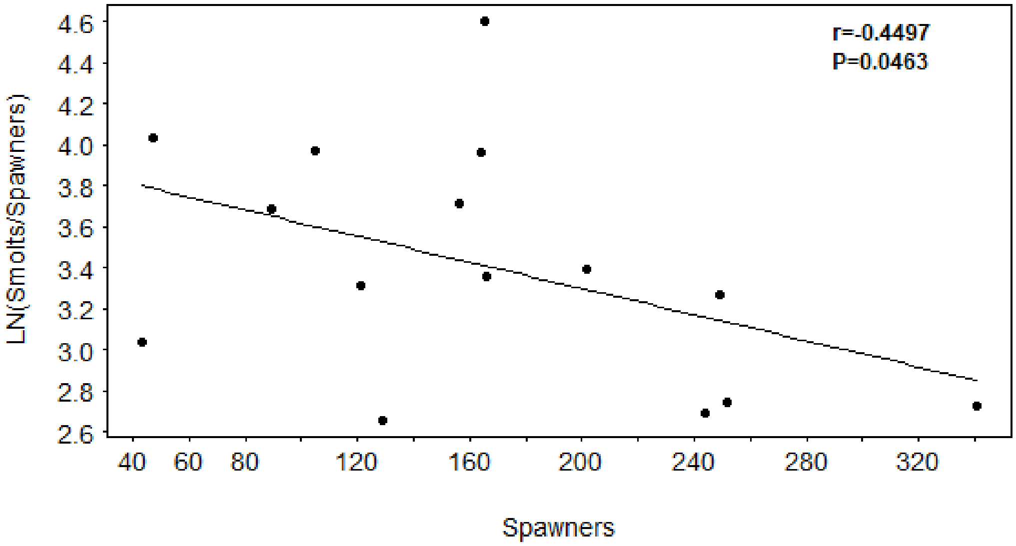


Figure 36. Smolts per spawner (log scale) versus spawner abundance for Twisp River Spring Chinook Salmon, 2003–2017, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope.

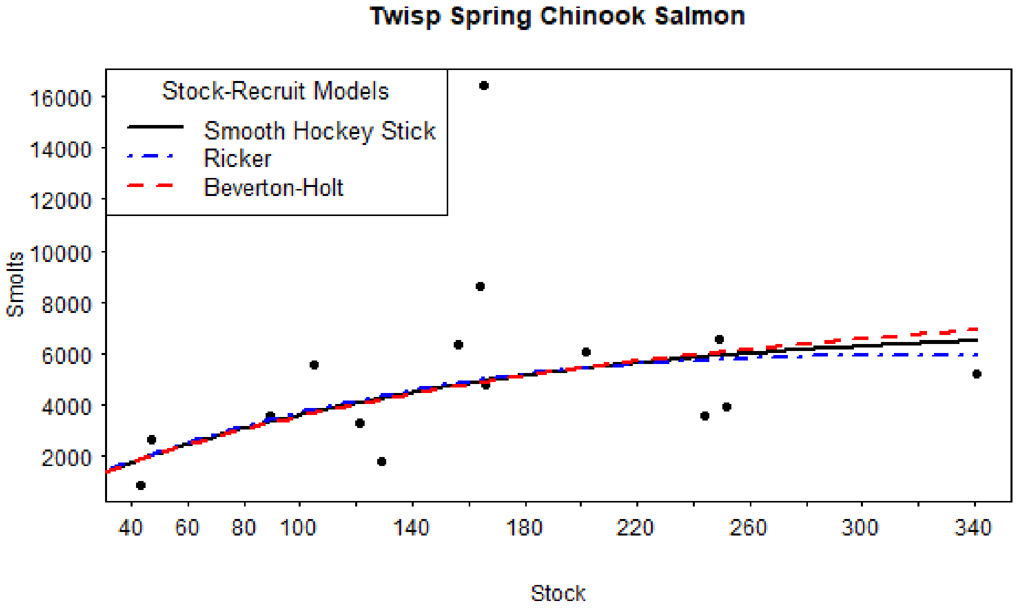


Figure 37. Stock-recruitment models fit to smolt and spawner data for Twisp River Spring Chinook Salmon, 2003–2017.

Table 10. Fitted stock-recruitment models for smolts and stock (spawner) data from Twisp River Spring Chinook Salmon, 2003–2017. Confidence intervals were estimated using bootstrap with at least 2,000 bootstrap samples. Correlation = Pearson correlation coefficient between parameter estimates from bootstrap samples. Model equations are defined in Equations (1), (2), and (3). ΔAICc represents change in AICc compared to model with minimum AICc.

Model	AICc	ΔAICc	Parameter[b]	Parameter Estimates	95% CI	Correlation
Smooth Hockey Stick	30.39	0.31	α	51.2	30.7 – 146.7	α, R_∞: -0.20[a]
			R_∞	7,104	4,344 – 36,313	
Beverton-Holt	30.69	0.62	α	11,295	6,317 – 101,201	α, β: 0.99
			β	216	75 – 3,103	
Ricker	30.07	0.00	α	51.2	29.7 – 93.6	α, β: 0.88
			β	0.0032	< 0.0001 – 0.0064	
			K	5,926	4,267 – ∞	

a = Correlation coefficient between α and R_∞ is uninformative because parameter estimates are not linearly related; see Figure D3. The correlation coefficient between $1/\alpha$ and R_∞ = 0.4951.

b = Estimated maximum recruitment parameters are: R_∞ for the Smooth Hockey Stick model, α for the Beverton-Holt model, and $K = (\alpha/\beta)e^{-1}$ for the Ricker model.

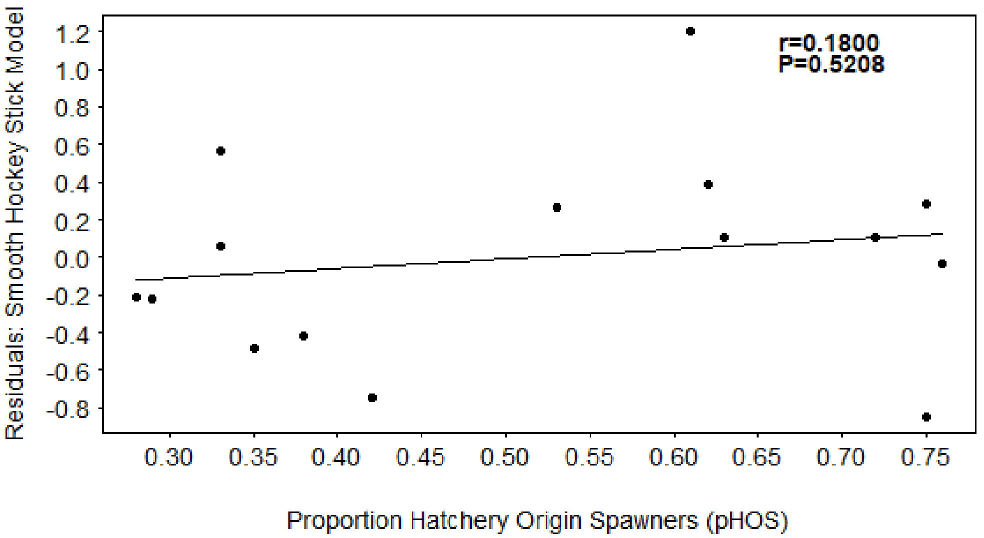


Figure 38. Residuals from Smooth Hockey Stick Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Twisp River Spring Chinook Salmon, 2003–2017. R^2=0.0324.

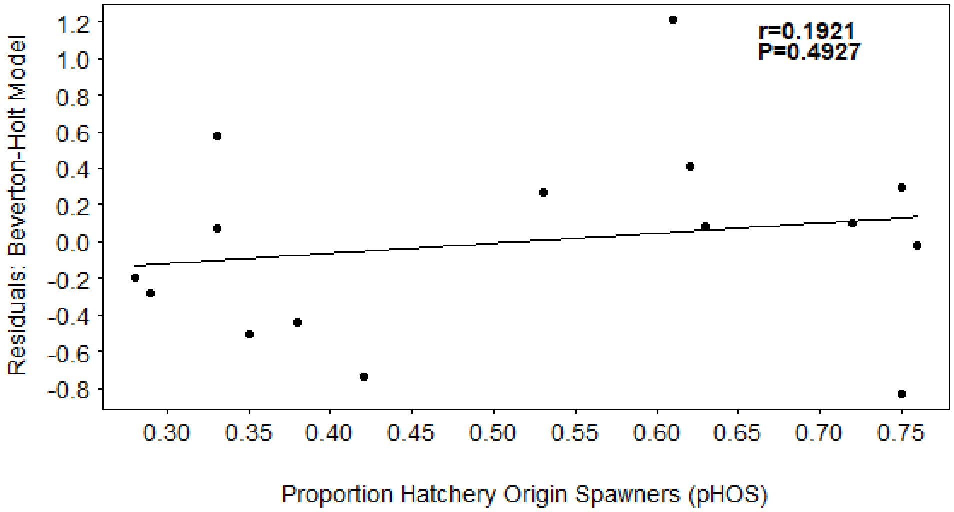


Figure 39. Residuals from the Beverton-Holt Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Twisp River Spring Chinook Salmon, 2003–2017. R^2=0.0369.

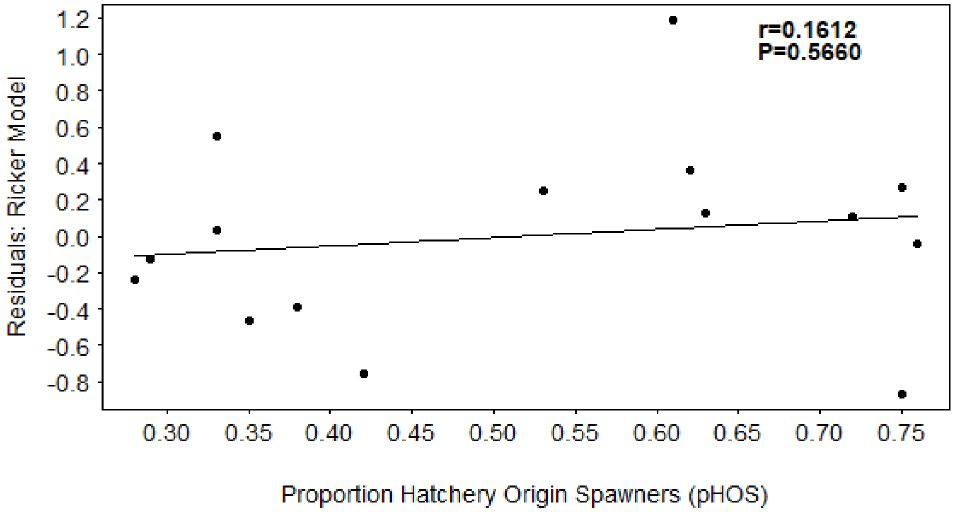


Figure 40. Residuals from the Ricker Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Twisp River Spring Chinook Salmon, 2003–2017. R^2=0.0260.

Hypothesis H02.2.1.2

There was no evidence of a negative association between smolts per redd and the proportion of hatchery spawners (pHOS) for Twisp River Spring Chinook Salmon (Pearson correlation coefficient r=0.2925, P=0.8549) (Figure 41). Additionally, the linear association between redd count and pHOS was non-significant (P=0.8313; Figure 42). However, comparison of smolts per redd with redd count demonstrated evidence of post-spawning density dependence (P=0.0142; Figure 43). Thus, the relationship between smolts per redd and pHOS was examined using the Ricker and Beverton-Holt stock-recruitment models in order to account for density dependence effects, using redds in place of spawner abundance. The model fits and assessment of residuals were very similar (Table 11, Figure D9 – Figure D13). The fitted Beverton-Holt model for smolts per redd was (Table 11):

$$ln(R/S) = ln(8{,}020) + 0.7782P_{HOS} - ln(103 + S).$$

The 95% bootstrap confidence interval for the effect of pHOS (i.e., β_2 in Equation (5)) was (-1.9437, 0.4321). The fitted Ricker model for smolts per redd was:

$$ln(R/S) = 4.3238 + 0.7621P_{HOS} - 0.0063S.$$

The 95% bootstrap confidence interval for the effect of pHOS (i.e., β_2 in Equation (7)) was (-2.0433, 0.1133).

Because the confidence intervals for the effect of pHOS included both positive and negative values regardless of the model, we concluded that there was no evidence of a negative association between pHOS and smolts per redd for Twisp River Spring Chinook Salmon after adjusting for density dependence. However, the bootstrap confidence intervals for the model parameters were wide and included maximum recruitment levels beyond the range of the observed data (Table 11), demonstrating an overall lack of fit. There was moderate evidence of autocorrelation in the residuals (Figure D11, Figure D13), suggesting a failure to account for some feature of the population dynamics. The small sample size may have contributed to the lack of model fit, and likewise may lower the ability to detect a relationship between pHOS and smolts per redd using the available data.

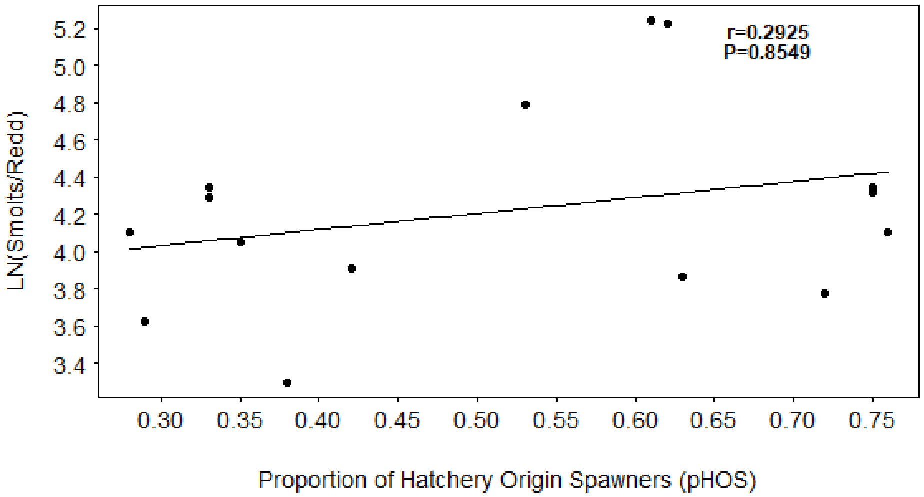


Figure 41. Smolts per redd (log scale) versus proportion of hatchery origin spawners (pHOS) for Twisp River Spring Chinook Salmon, 2003–2017, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. $R^2 = 0.0855$.

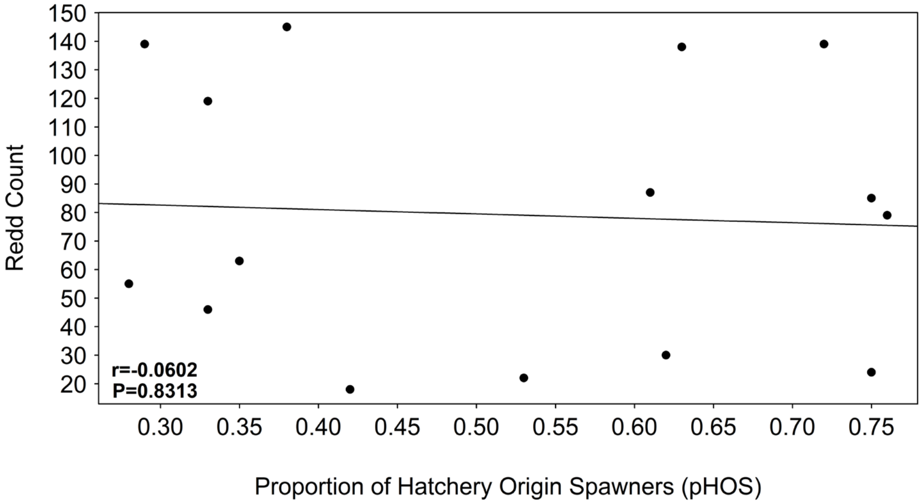


Figure 42. Redd count versus proportion of hatchery origin spawners (pHOS) for Twisp River Spring Chinook Salmon, 2003–2017, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope.

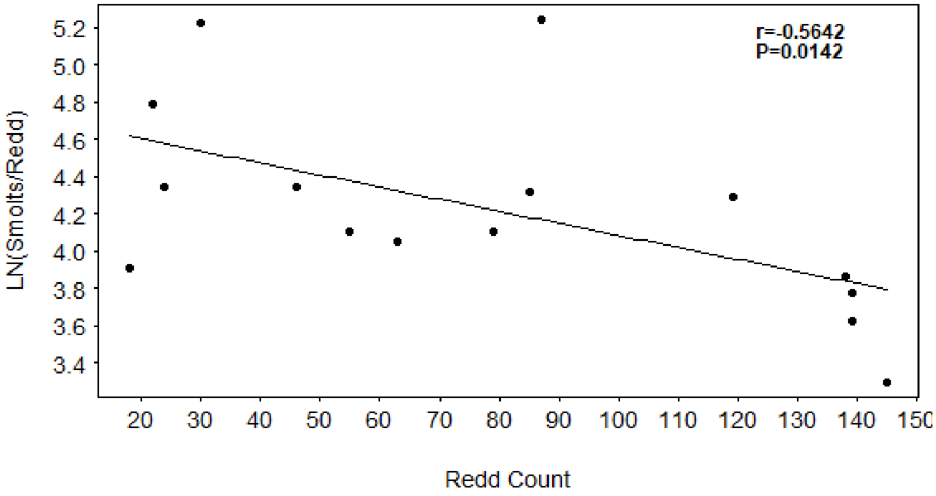


Figure 43. Smolts per redd (log scale) versus redd count for Twisp River Spring Chinook Salmon, 2003–2017, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. Negative slope indicates post-spawning density dependence.

Table 11. Fitted stock-recruitment models for smolts per redd for Twisp River Spring Chinook Salmon, 2003–2017, including effect (β_2) of proportion of hatchery origin spawners (pHOS). Confidence intervals were estimated using bootstrap with 3,000 bootstrap samples. Model equations are defined in Equations (5) and (7). ΔAICc represents change in AICc compared to model with minimum AICc.

Model	AICc	ΔAICc	Parameter	Parameter Estimates	95% CI
Beverton-Holt	28.58	0.78	α	8,020	3,952 – 39,818
			β	103	40 – 724
			β_2	-0.7782	-1.9437 – 0.4321
Ricker	27.79	0.00	$ln(\alpha)$	4.3238	3.6525 – 5.0395
			β	0.0063	0.0011 – 0.0108
			β_2	-0.7621	-2.0433 – 0.1133

Methow River Spring Chinook Salmon

Adult spawner, smolt recruitment, pHOS, and redd count data from spring Chinook Salmon were available from the Methow River for the 2002–2017 brood years. Adult stock abundance (spawners) ranged from 417 in 2017 to 2,692 in 2011 and averaged 1,417, and smolt recruitment ranged from 5,163 in 2007 to 51,325 in 2010 and averaged 23,624 (Figure 44, Figure 45). Redd counts averaged 705 (range = 210 to 1,366), and pHOS averaged 0.77 (range = 0.57 to 0.97).

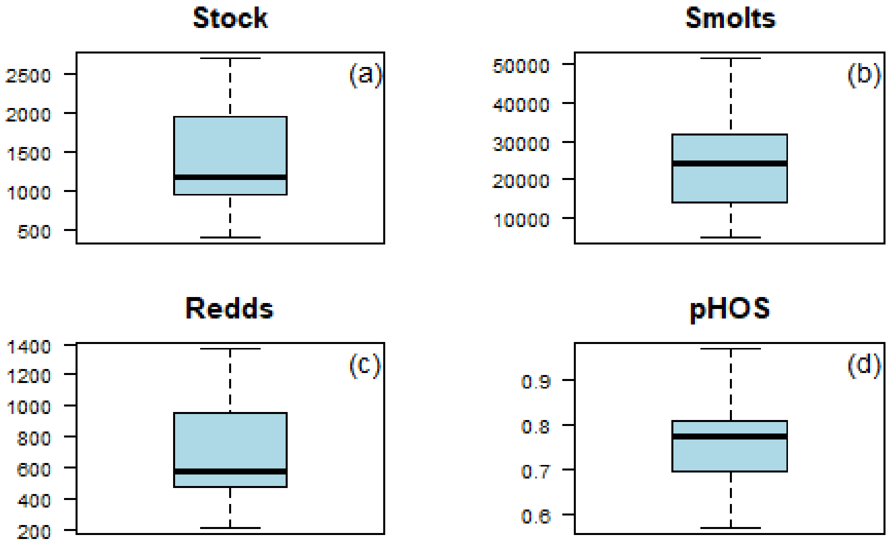


Figure 44. Methow River Spring Chinook Salmon boxplots for Stock (spawner abundance), Smolts, Redd counts, and proportion of hatchery origin spawners (pHOS), 2002–2017. Box indicates interquartile range and thick horizontal bar is median. Whiskers indicate quartile ± 1.5×interquartile range.

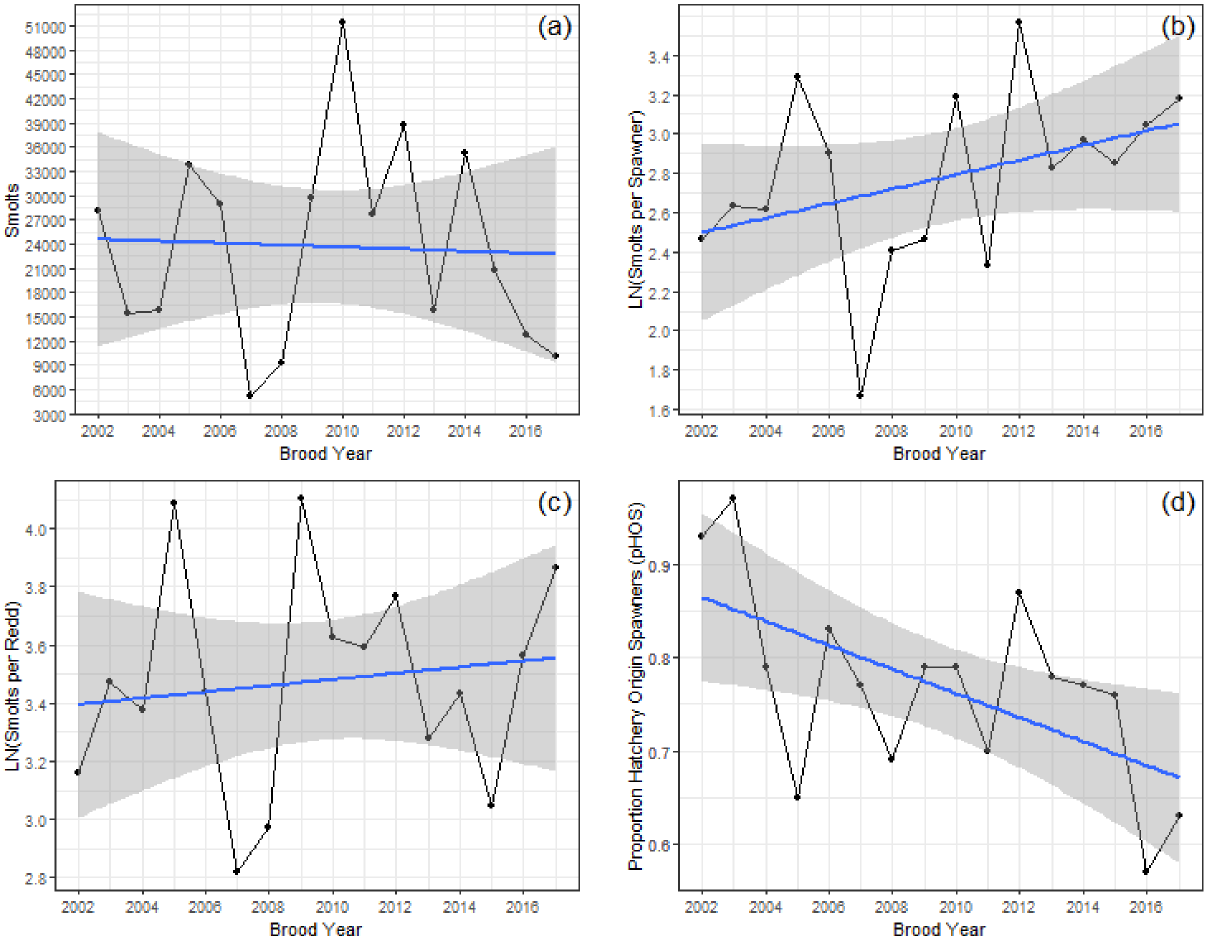


Figure 45. Methow River Spring Chinook Salmon annual Smolt counts, Smolt/Spawner (log scale), Smolt/Redd (log scale), and proportion of hatchery origin spawners (pHOS), 2002–2017. Line indicates the linear trend. Shaded area is the estimated 95% confidence interval of the line.

Hypothesis H02.2.1.1

A weak negative linear relationship was observed between Methow River Spring Chinook Salmon spawners and smolt recruitment but it was non-significant, providing inconclusive evidence of density dependence in mortality between the spawning and smolt life stages (P=0.2101; Figure 46). Nevertheless, the Smooth Hockey Stick, Beverton-Holt, and Ricker stock-recruitment models were fit to the spawner and smolt data.

There was little difference in the model fits among the three stock-recruitment models, with no perceptible difference in model predictions for any range of observed spawner abundance (Figure 47). The Ricker model had the lowest AICc value but ΔAICc≤0.04 for all models (Table 12). Despite the agreement in model predictions among the three models, all models showed considerable uncertainty in the estimated parameters, with particularly wide confidence intervals. The maximum recruitment estimates in particular had confidence intervals that extended far beyond the maximum observed smolt recruitment (51,325). High correlation was observed between the model parameter estimates, increasing uncertainty in the model predictions (Table 12, Figure E3). However, there was no severe violation of the assumption of lognormal errors and no evidence of lack of stationarity or autocorrelation. (Figures E1, E2, Figure E4 – Figure E7).

Correlation analysis found no association between the residuals from these stock-recruitment models and pHOS, with correlation coefficients ranging from 0.0697 to 0.0704 (P≥0.7955; Figure 48 – Figure 50). Additionally, likelihood ratio tests of the effect of pHOS on the Beverton-Holt and Ricker models were non-significant (P≥0.7635). Thus, there was no evidence to suggest that higher proportions of hatchery spawners were associated with lower juvenile productivity for spring Chinook Salmon in the Methow River. However, there were only 16 years of data available, and the modeling assumptions were not well supported. Thus, it remains possible that there is a relationship between pHOS and juvenile productivity that are not observable using the available data and analyses.

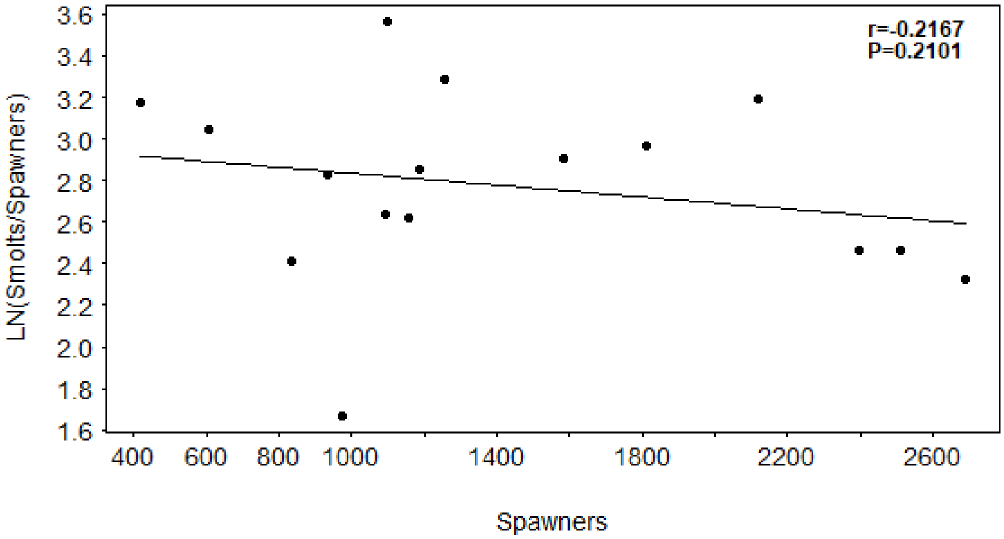


Figure 46. Smolts per spawner (log scale) versus spawner abundance for Methow River Spring Chinook Salmon, 2002–2017, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope.

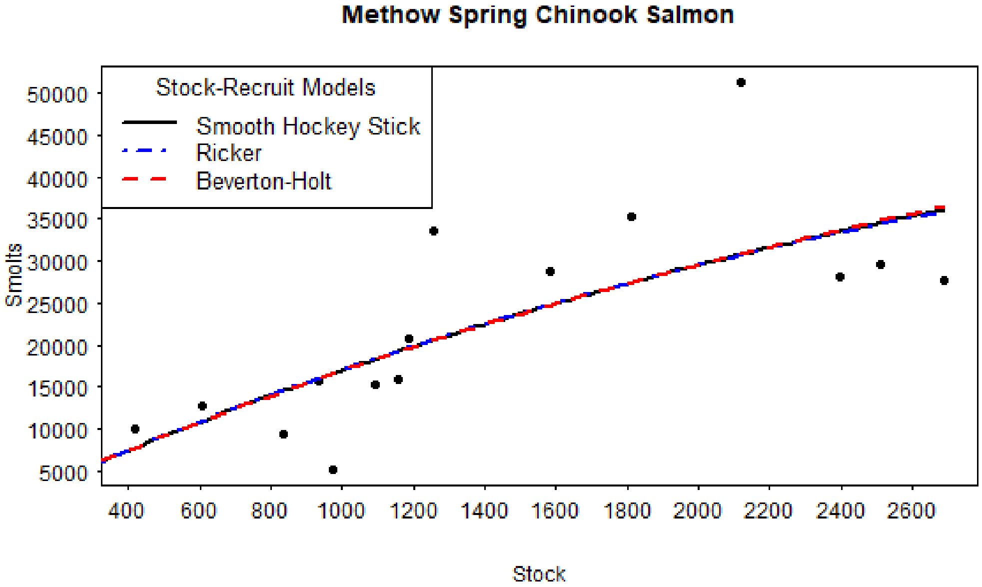


Figure 47. Stock-recruitment models fit to smolt and spawner data for Methow River Spring Chinook Salmon, 2002–2017.

Table 12. Fitted stock-recruitment models for smolts and stock (spawner) data from Methow River Spring Chinook Salmon, 2002–2017. Confidence intervals were estimated using bootstrap with at least 2,000 bootstrap samples. Correlation = Pearson correlation coefficient between parameter estimates from bootstrap samples. Model equations are defined in Equations (1), (2), and (3). ΔAICc represents change in AICc compared to model with minimum AICc.

Model	AICc	ΔAICc	Parameter[b]	Parameter Estimates	95% CI	Correlation
Smooth Hockey Stick	26.64	0.02	α	19.7	14.7 – 37.7	α, R_∞: -0.30[a]
			R_∞	65,051	23,577 – 549,603	
Beverton-Holt	26.66	0.04	α	115,394	32,755 – 1,382,406	α, β: 0.99
			β	5,806	785 – 82,314	
Ricker	26.62	0.00	α	19.6	11.6 – 32.7	α, β: 0.88
			β	0.0001	< 0.0001 – 0.0005	
			K	50,572	22,637 – ∞	

a = Correlation coefficient between α and R_∞ is uninformative because parameter estimates are not linearly related; see Figure D3. The correlation coefficient between $1/\alpha$ and R_∞ = 0.7281.

b = Estimated maximum recruitment parameters are: R_∞ for the Smooth Hockey Stick model, α for the Beverton-Holt model, and $K = (\alpha/\beta)e^{-1}$ for the Ricker model.

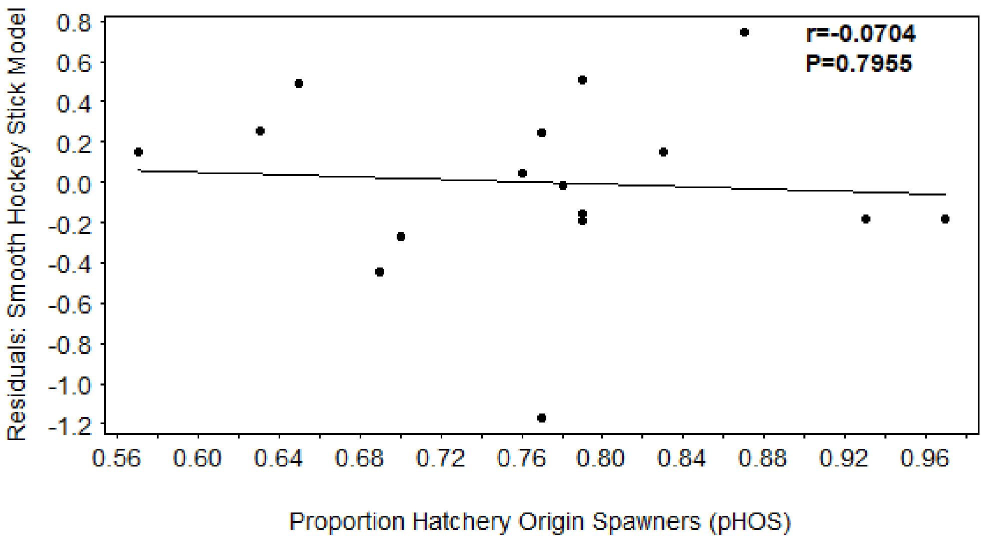


Figure 48. Residuals from Smooth Hockey Stick Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Methow River Spring Chinook Salmon, 2002–2017. R^2=0.0050.

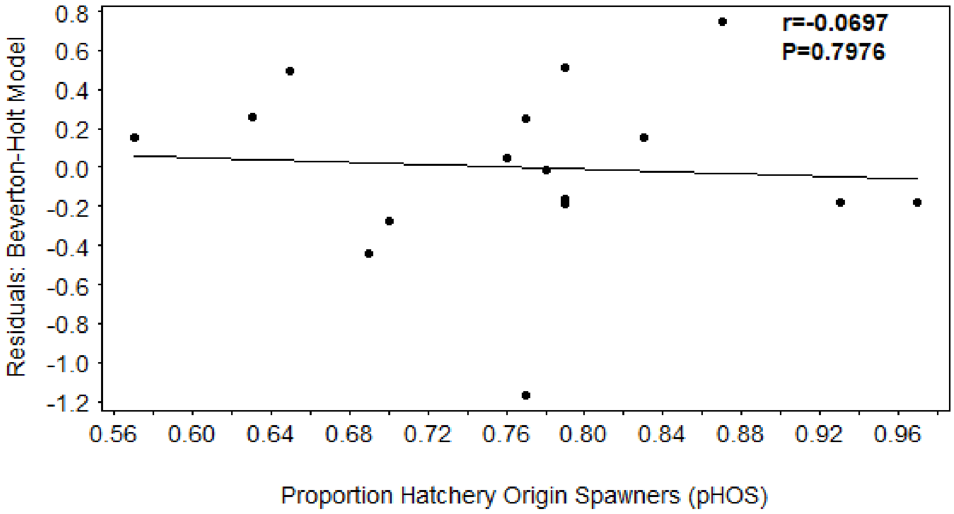


Figure 49. Residuals from the Beverton-Holt Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Methow River Spring Chinook Salmon, 2003–2017. R^2=0.0049.

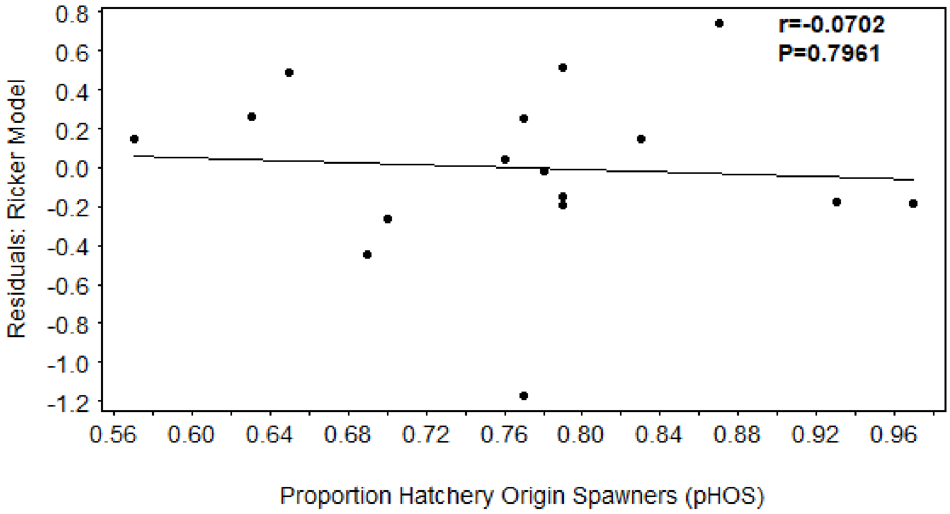


Figure 50. Residuals from the Ricker Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Methow River Spring Chinook Salmon, 2002–2017. R^2=0.0049.

Hypothesis H02.2.1.2

There was no evidence of a negative association between smolts per redd and the proportion of hatchery spawners (pHOS) for Methow River Spring Chinook Salmon (Pearson correlation coefficient r=-0.2409, P=0.1844) (Figure 51). Although the linear association between redd count and pHOS was significant at the 10% level (P=0.0919; Figure 52), comparison of smolts per redd with redd count demonstrated no evidence of post-spawning density dependence (P=0.3761, Figure 53). Nevertheless, the relationship between smolts per redd and pHOS was examined using stock-recruitment models in order to account for density dependence effects, using redds in place of spawner abundance. The Beverton-Holt model could not be fit to the data; examination of the likelihood indicated a flat likelihood surface and high correlation between the α and β model parameter estimates which could not be overcome when pHOS was included in the model. The Ricker model was able to be fit and the residuals agreed moderately well with model assumptions (Figures E9, Figure E10); however, the estimate for the β parameter was essentially 0, which is not consistent with interpretation of model parameters (Table 13). The fitted Ricker model for smolts per redd was:

$$ln(R/S) = 4.0380 - 0.7383 * P_{HOS} + (< 0.0001) * S.$$

The 95% bootstrap confidence interval for the effect of pHOS (i.e., β_2 in Equation (7)) was -1.2657 – 2.3241). Because the confidence interval for the effect of pHOS included both positive and negative values, we concluded that there was no evidence of a negative association between pHOS and smolts per redd for Methow River Spring Chinook Salmon whether or not an adjustment was made for density dependence. However, the model parameters were not consistent with their usual interpretation, demonstrating an overall lack of fit. The small sample size, low degree of variability in the observed pHOS values, and potentially high level of measurement error in the observed data may have contributed to the lack of model fit, and likewise may lower the ability to detect a relationship between pHOS and smolts per redd using the available data.

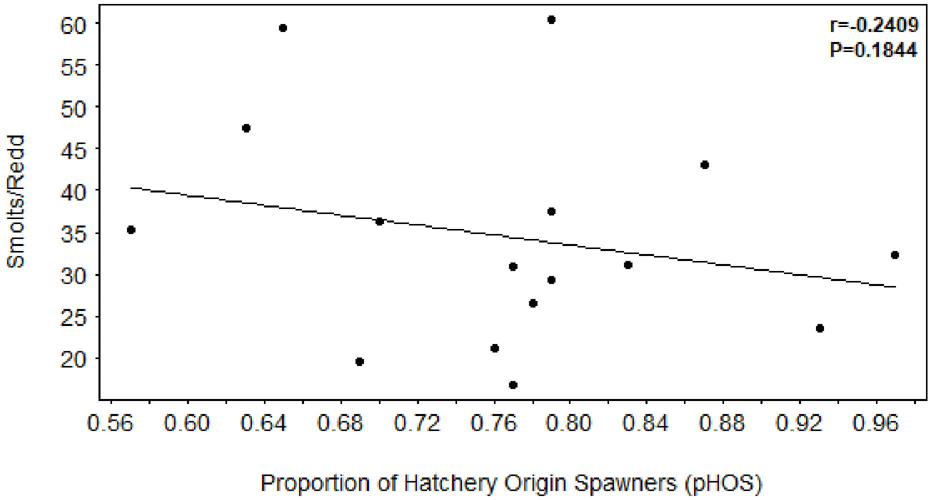


Figure 51. Smolts per redd versus proportion of hatchery origin spawners (pHOS) for Methow River Spring Chinook Salmon, 2002–2017, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. $R^2 = 0.0580$.

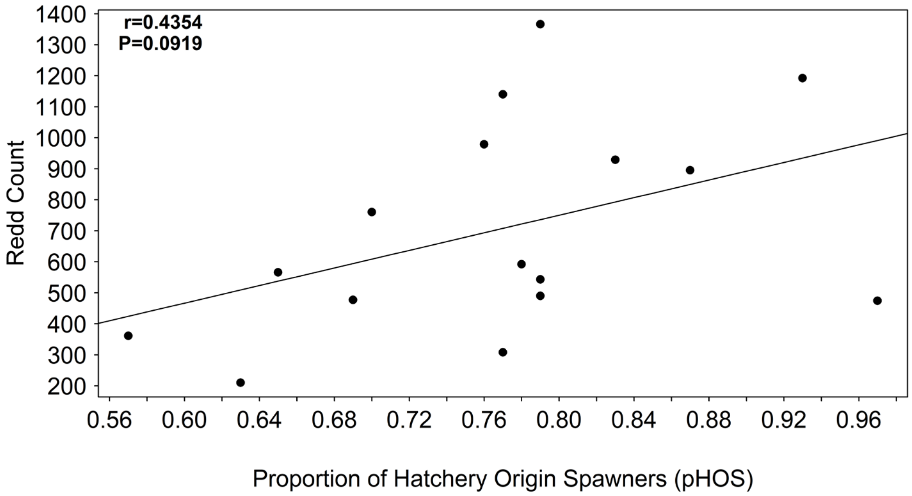


Figure 52. Redd count versus proportion of hatchery origin spawners (pHOS) for Methow River Spring Chinook Salmon, 2002–2017, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope.

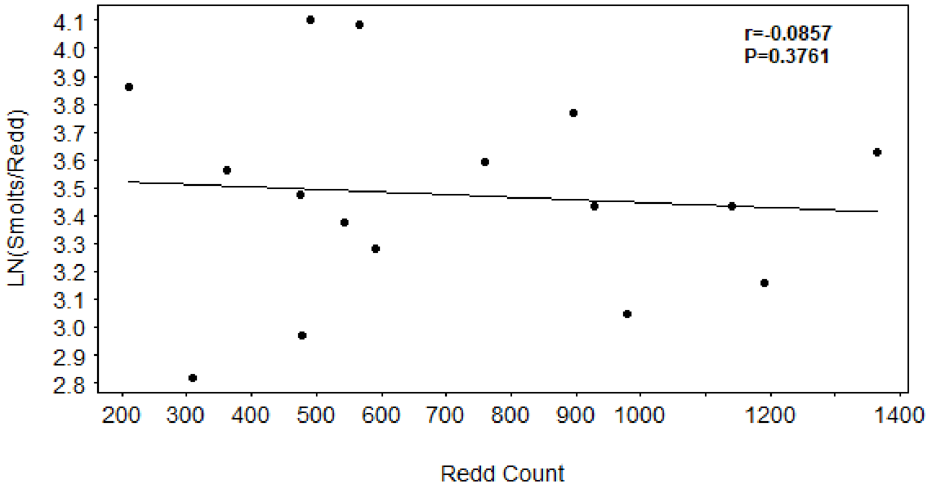


Figure 53. Smolts per redd (log scale) versus redd count for Methow River Spring Chinook Salmon, 2002–2017, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. Negative slope indicates post-spawning density dependence.

Table 13. Fitted stock-recruitment models for smolts per redd for Methow River Spring Chinook Salmon, 2002–2017, including effect (β_2) of proportion of hatchery origin spawners (pHOS). Confidence intervals were estimated using bootstrap with at least 2,000 bootstrap samples. Model equations are defined in Equations (5) and (7). ΔAICc represents change in AICc compared to model with minimum AICc. *Only the Ricker model could be fit for Methow River Spring Chinook Salmon data.

Model*	AICc	ΔAICc	Parameter	Parameter Estimates	95% CI
Beverton-Holt	NA	NA	α	NA	NA
			β	NA	NA
			β_2	NA	NA
Ricker	23.56	NA	$ln(\alpha)$	4.0380	2.6075 – 5.3023
			β	< 0.0001	< 0.0001 – 0.0006
			β_2	0.7383	-1.2657 – 2.3241

Wenatchee River Summer Chinook Salmon

Adult spawner, emigrant, pHOS, and redd count data were available for the 1999–2018 brood years (no emigrant count for 2010 and 2011). Adult stock abundance (spawners) ranged from 3,473 in 2018 to 17,792 in 2006 and averaged 8,695. Emigrant counts ranged from 1,322,383 in 2000 to 20,426,149 in 2003 and averaged 9,118,268 (Figure 54, Figure 55). Redd counts averaged 3,600.5 (range = 1,510 to 8,896), and pHOS averaged 0.176 (range = 0.06 to 0.31). The 2000 and 2003 brood years were identified as possible outliers in emigrant counts (Figure 55), and analysis results were investigated for their sensitivity to inclusion of these brood years.

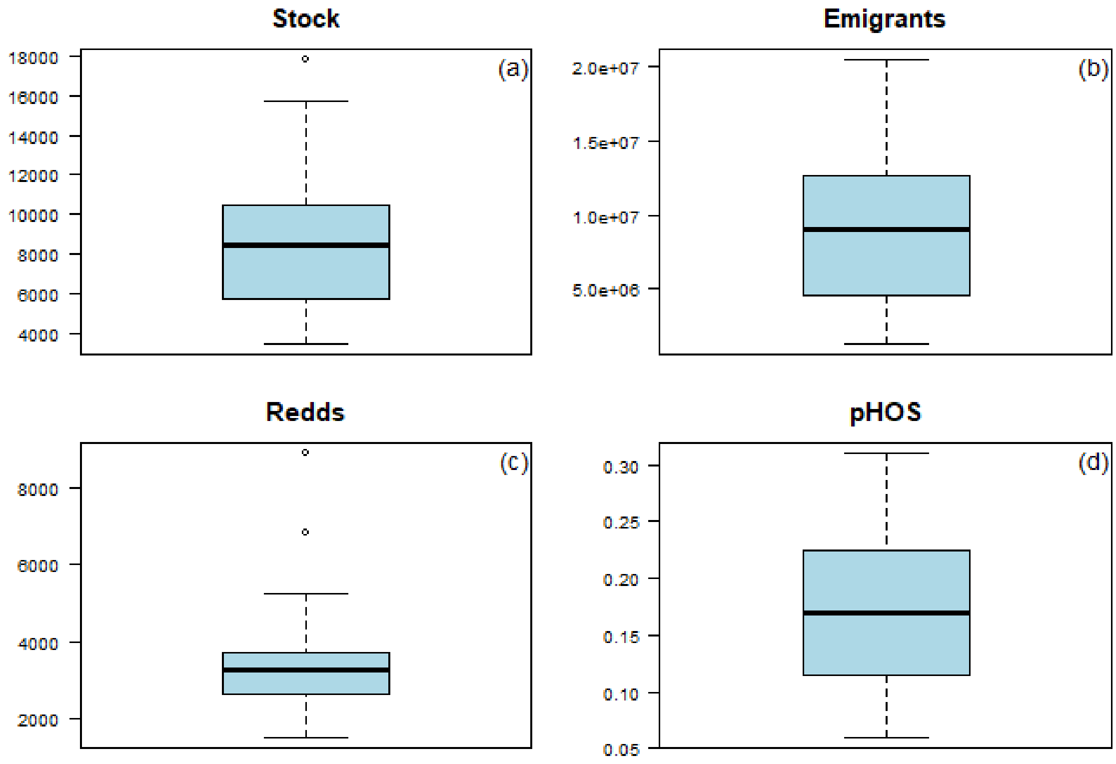


Figure 54. Wenatchee River Summer Chinook Salmon boxplots for Stock (spawner abundance), Emigrant counts, Redd counts, and proportion of hatchery origin spawners (pHOS), 1999–2018, without 2010 and 2011. Box indicates interquartile range and thick horizontal bar is median. Whiskers indicate quartile ± 1.5 × interquartile range.

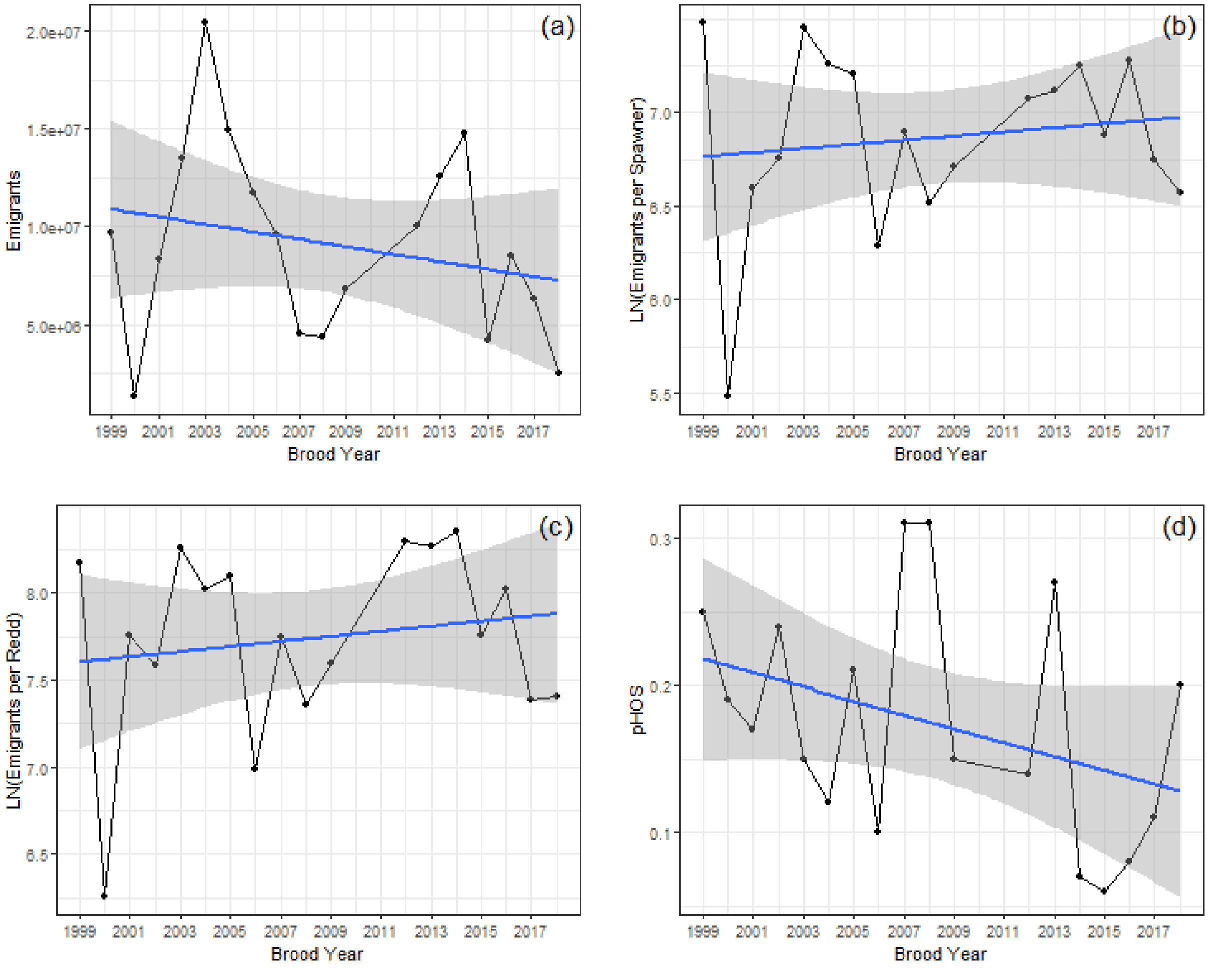


Figure 55. Wenatchee River Summer Chinook Salmon annual Emigrant counts, Emigrant/Spawner (log scale), Emigrant/Redd (log scale), and proportion of hatchery origin spawners (pHOS), 1999–2018 (without 2010, 2011). Line indicates the linear trend. Shaded area is the estimated 95% confidence interval of the line.

Hypothesis H02.2.1.1

A positive but non-significant linear relationship was observed between spawners and emigrant count, indicating no evidence of density dependence in mortality between spawner data collection and emigrant data collection (Figure 56). The Smooth Hockey Stick and Beverton-Holt stock-recruitment models could not be fit to the spawner and emigrant data, so only the Ricker model is presented (Figure 57 with parameter estimates (Table 14). The residuals from the Ricker model was compared to pHOS using correlation analysis. The correlation coefficient between residuals and pHOS was -0.0985 and was not significantly different from 0 (P=0.6973; Figure 58). Additionally, the likelihood ratio test of the effect of pHOS on the Ricker model was non-significant (P=0.6787). There was no evidence to suggest that higher proportions of hatchery spawners were associated with lower juvenile productivity for Summer Chinook Salmon in the Wenatchee River.

When the 2003 brood year was omitted as a possible outlier, the Smooth Hockey Stick and Beverton-Holt models could be fit to the spawner and emigrant data but had equivalent weight with the Ricker model (ΔAICc≤0.0072); pHOS was not associated with the residuals from any of the models (P≥0.7155). When the 2000 brood year was omitted as a possible outlier, all three models could be fit to the data but the Ricker model was again selected (ΔAICc≤0.1126). Model residuals were again not significantly associated with pHOS levels without the 2000 brood year (P≥0.6430; Figure F3 – Figure F6), and the likelihood ratio test of the pHOS was also not significant (P≥0.6113).

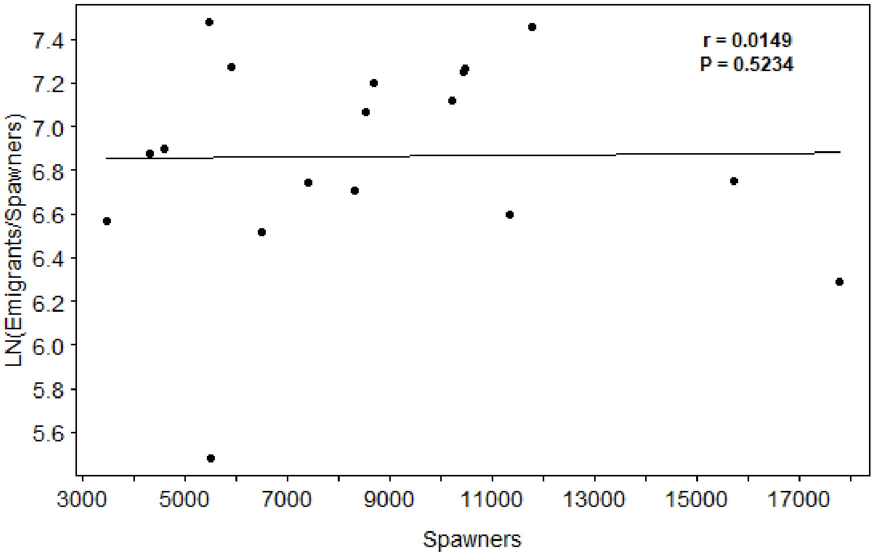


Figure 56. Emigrants per spawner (log scale) versus spawner abundance for Wenatchee River Summer Chinook Salmon, 1999–2018 (without 2010, 2011), with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope.

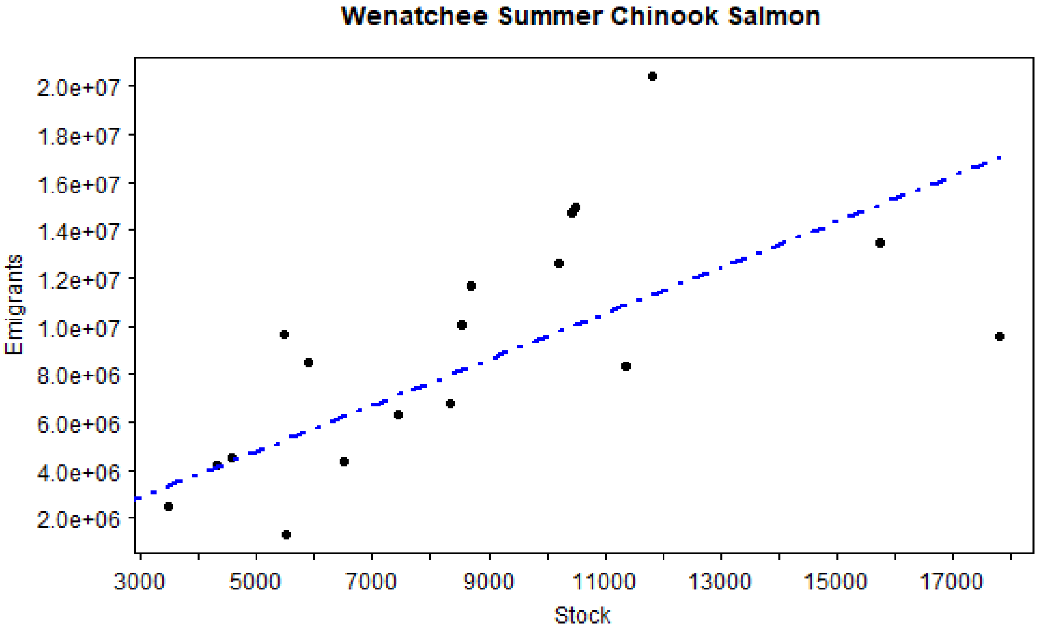


Figure 57. The Ricker stock-recruitment model fit to emigrants and spawner data for Wenatchee River Summer Chinook Salmon, 1999–2018 (without 2010, 2011).

Table 14. Fitted stock-recruitment models for emigrants and stock (spawner) data from Wenatchee River Summer Chinook Salmon, 1999–2018 (without 2010, 2011). Confidence intervals were estimated using bootstrap with at least 2,900 bootstrap samples. Correlation = Pearson correlation coefficient between parameter estimates from bootstrap samples. Model equations are defined in Equations (1), (2), and (3). ΔAICc represents change in AICc compared to model with minimum AICc. *Only the Ricker model could be fit to the Wenatchee River data.

Model*	AICc	ΔAICc	Parameter[a]	Parameter Estimates	95% CI	Correlation
Smooth Hockey Stick			α	NA	NA	α, R_∞: NA
			R_∞	NA	NA	
Beverton-Holt			α	NA	NA	α, β: NA
			β	NA	NA	
Ricker	31.72		α	957.3	773.4 – 1609.5	α, β: 0.83
			β	< 0.0001	< 0.0001 – 0.0001	
			K	30,446,537	919,213 - ∞	

a = Estimated maximum recruitment parameters are: R_∞ for the Smooth Hockey Stick model, a for the Beverton-Holt model, and $K=(\alpha/\beta)e^{-1}$ for the Ricker model.

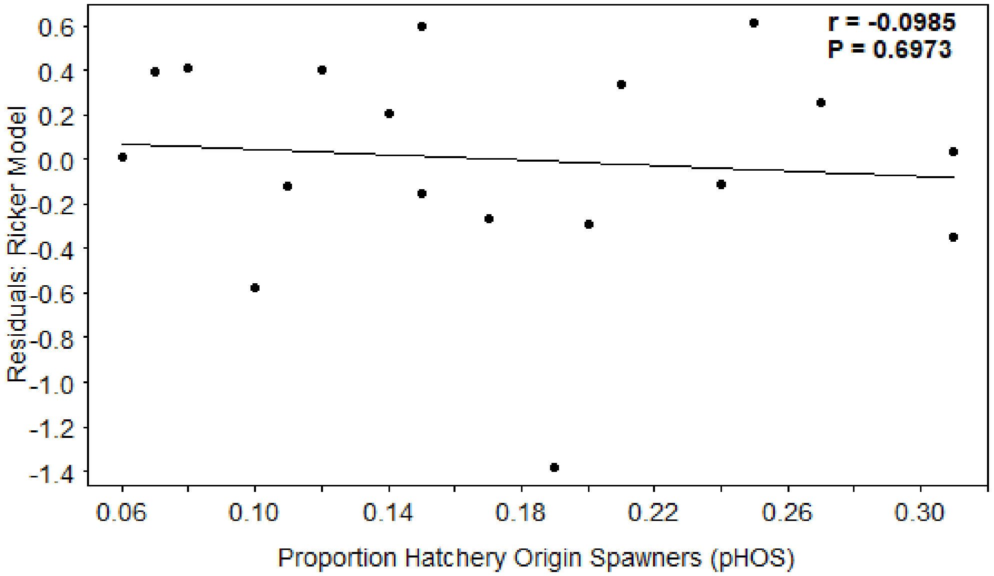


Figure 58. Residuals from Ricker Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using emigrant and spawner data from Wenatchee River Summer Chinook Salmon, 1999–2018 (without 2010, 2011). R^2 =0.0097.

Hypothesis H02.2.1.2

There was a weak and non-significant negative association between emigrants per redd (log scale) and the proportion of hatchery spawners (pHOS) for Wenatchee River Summer Chinook Salmon (Pearson correlation coefficient r= -0.0750, P=0.3836) (Figure 59). The redd count was not associated with pHOS (P=0.4460, Figure 60) and there was no indication of post-spawning density dependence apparent from examination of the emigrants per redd plotted against the redd counts (Figure 61). Nevertheless, the relationship between emigrants per redd and pHOS was examined using the Ricker and Beverton-Holt stock-recruitment models in order to account for density dependence effects, with redds used in place of spawner counts. Both models were equivalent on the basis of AICc rank (ΔAICc = 0.01 compared to Ricker model) and examination of model residuals (Table 15; Figure F8 – Figure F12). However, the Beverton-Holt model could not be fit for the bootstrap samples and the 95% asymptotic confidence intervals for the model parameters α and β included both negative values and values far beyond the range of the observed data; both these results indicate a lack of fit for the Beverton-Holt model. Thus, the Ricker model was preferred. The fitted Ricker model for emigrants per redd was (Table 15):

$$ln(R/S) = 8.0322 - 0.7166P_{HOS} - 0.00005 * S$$

The 95% bootstrap confidence interval for the effect of pHOS (i.e., β_2 in Equation (7)) was (-2.0006 – 3.3638). Because this confidence interval included both positive and negative values, we concluded that there is no evidence of a negative association between pHOS and emigrants per redd for Wenatchee Summer Chinook Salmon after adjusting for density dependence. Removing 2000 or 2003 as possible outlier brood years did not significantly change the results (e.g., Figure F13).

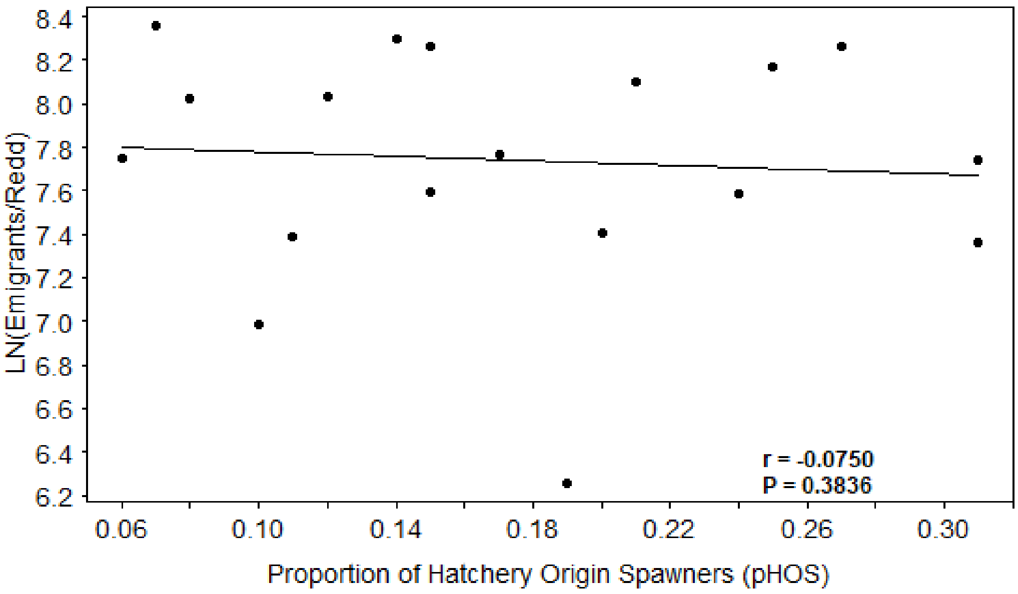


Figure 59. Emigrants per redd (log scale) versus proportion of hatchery origin spawners (pHOS) for Wenatchee River Summer Chinook Salmon, 1999–2018 (without 2010, 2011), with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. $R^2 = 0.0056$.

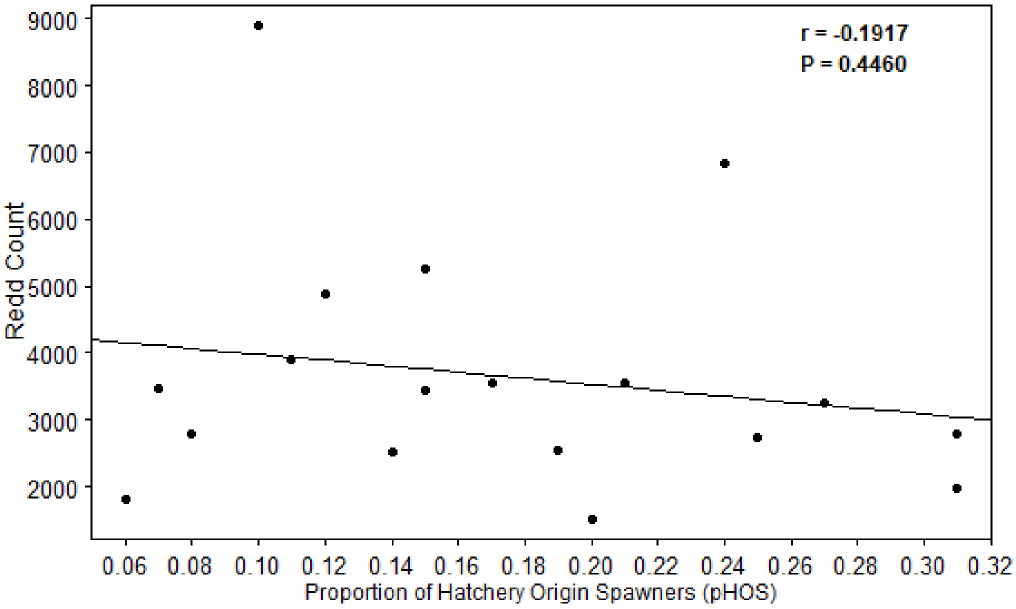


Figure 60. Redd count versus proportion of hatchery origin spawners (pHOS) for Wenatchee River Summer Chinook Salmon, 1999–2018 (without 2010, 2011), with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope.

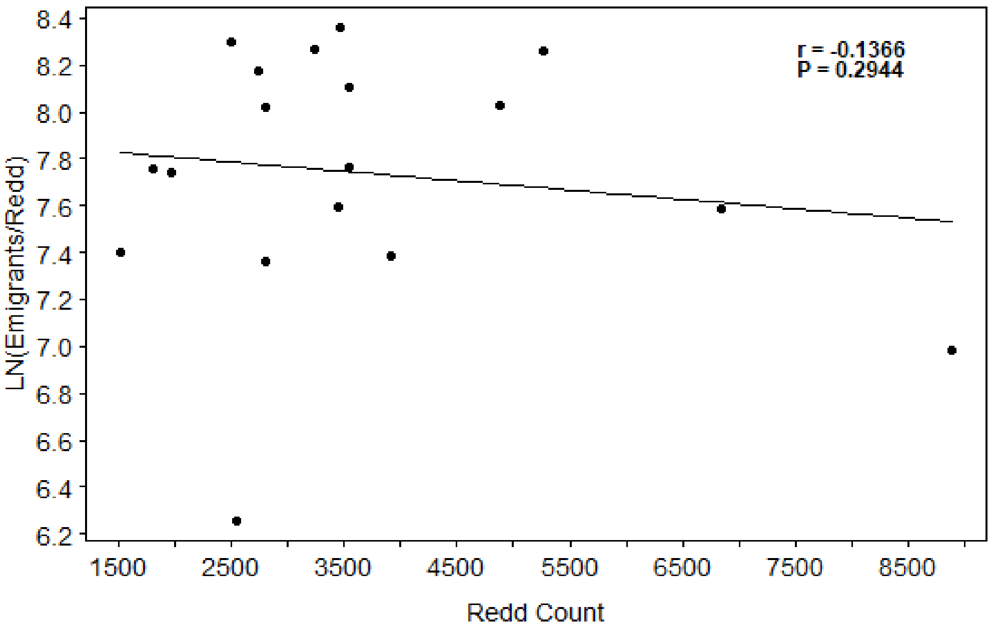


Figure 61. Emigrants per redd versus redd count for Wenatchee River Summer Chinook Salmon, 1999–2018 (without 2010, 2011), with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. Negative slope indicates post-spawning density dependence.

Table 15. Fitted stock-recruitment models for emigrants per redd for Wenatchee River Summer Chinook Salmon, 1999–2018 (without 2010, 2011), including effect (β_2) of proportion of hatchery origin spawners (pHOS). Bootstrap confidence intervals based on 3,000 bootstrap samples were provide for the Ricker model, and asymptotic confidence intervals were provided for the Beverton-Holt model. Model equations are defined in Equations (5) and (7). ΔAICc represents change in AICc compared to model with minimum AICc.

Model	AICc	ΔAICc	Parameter	Parameter Estimates	95% CI
Beverton-Holt	38.41	0.10	α	69,904,888	- 259,329,930 – 399,139,700
			β	23,464	-105,680 – 9,152,607
			β_2	0.6695	-3.1075 – 4.4465
Ricker	38.31	0.00	$ln(\alpha)$	8.0322	6.8834 – 8.6882
			β	0.00005	-0.0002 – 0.0001
			β_2	0.7166	-2.0006 – 3.3638

Methow River Summer Chinook Salmon

Adult spawner, emigrant, pHOS, and redd count data were available for the 2006–2018 brood years (no emigrant count for 2012). Adult stock abundance (spawners) ranged from 1,364 in 2007 to 3,952 in 2015 and averaged 2,333, and emigrant count ranged from 427,193 in 2017 to 3,465,247 in 2006 and averaged 1,099,370 (Figure 62, Figure 63). Redd counts averaged 909.5 (range = 591 to 1,551), and pHOS averaged 0.391 (range = 0.11 to 0.53).

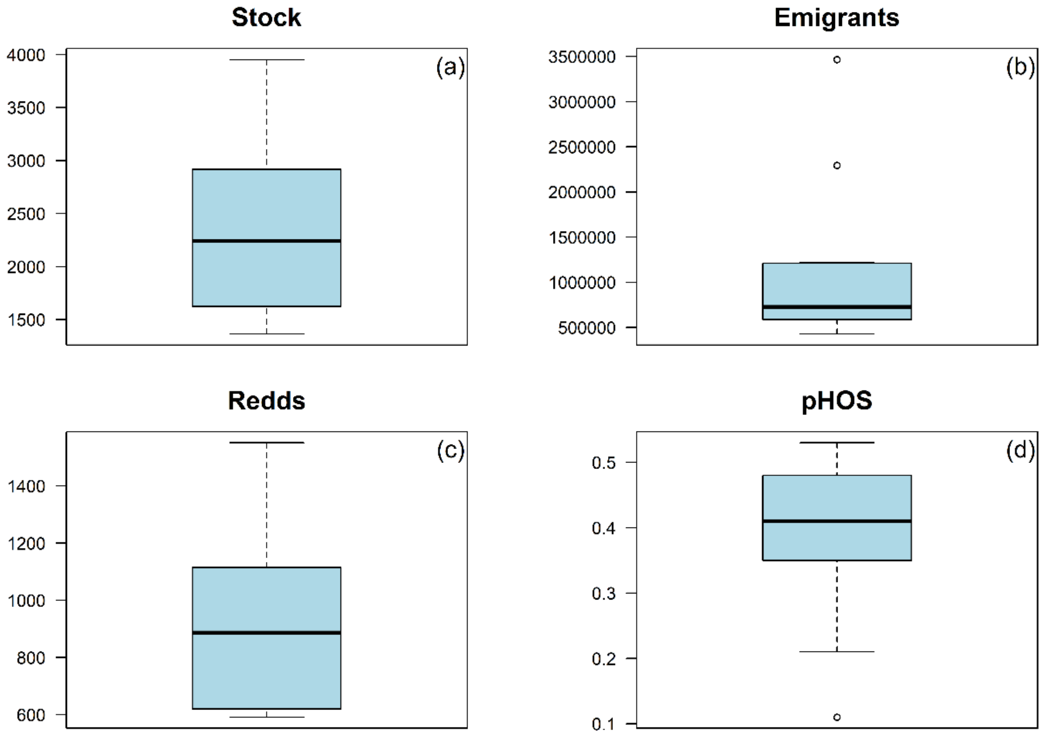


Figure 62. Methow River Summer Chinook Salmon boxplots for Stock (spawner abundance), Emigrant counts, Redd counts, and proportion of hatchery origin spawners (pHOS), 2006–2018. Box indicates interquartile range and thick horizontal bar is median. Whiskers indicate quartile ± 1.5 × interquartile range.

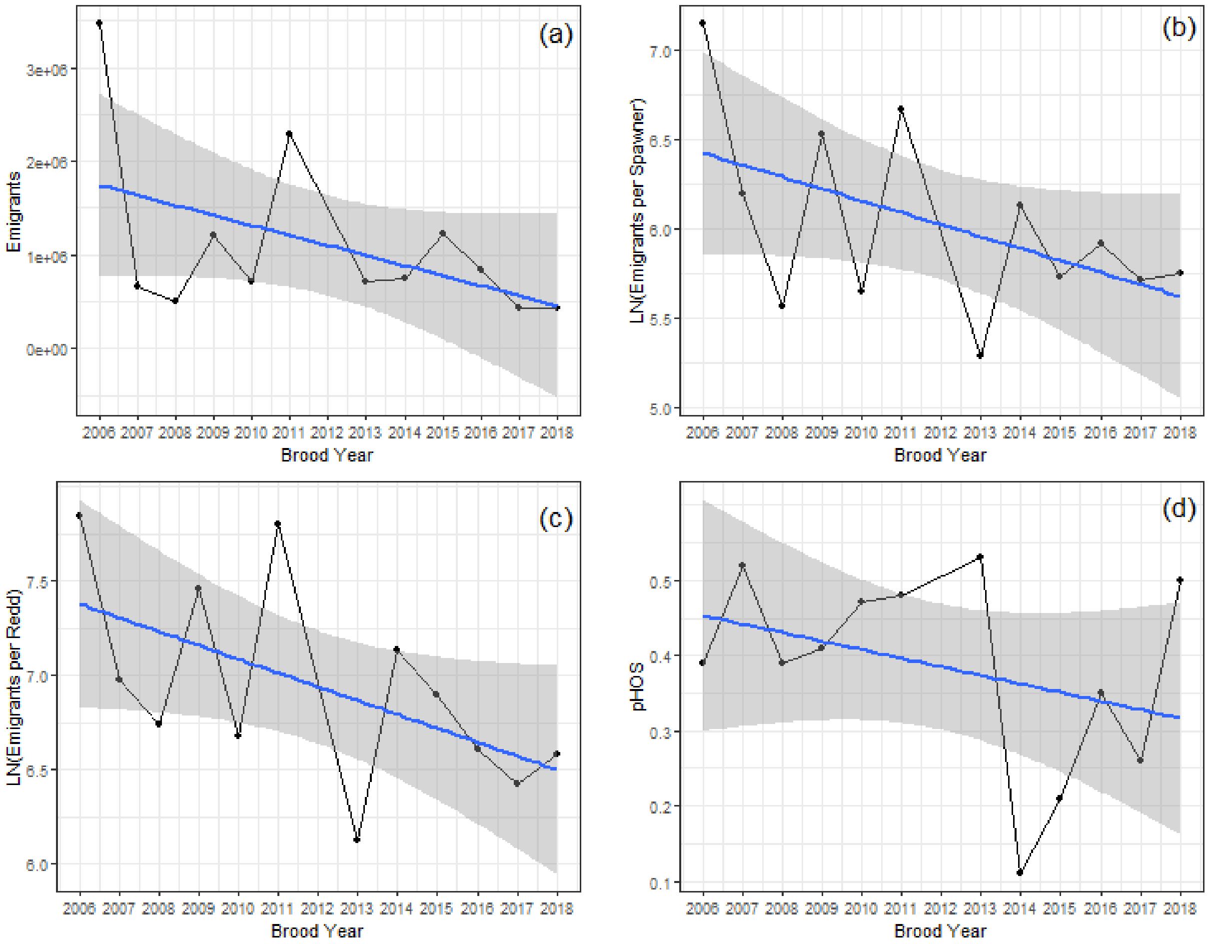


Figure 63. Methow River Summer Chinook Salmon annual Emigrant counts, Emigrant/Spawner (log scale), Emigrant/Redd (log scale), and proportion of hatchery origin spawners (pHOS), 2006–2018 (without 2012). Line indicates the linear trend. Shaded area is the estimated 95% confidence interval of the line.

Hypothesis H02.2.1.1

A slightly negative linear relationship between spawners and emigrant count indicated the presence of density dependence in mortality in one or more life stages between spawner data collection and emigrant data collection (Figure 64). Thus, the Smooth Hockey Stick, Beverton-Holt, and Ricker stock-recruitment models were each fit to the spawner and emigrant data (Figure 65). There was little difference in the model fits among the three models (ΔAICc $\leq$ 0.02), but the Ricker model had the lowest AICc value and the intermediate correlation between parameter estimates (Table 16). The residuals from all three models were compared to pHOS using correlation analysis. Correlation coefficients between residuals and pHOS were all non-significant (r=-0.0059, P=0.9856 for each model; Figure 66 – Figure 68). Additionally, likelihood ratio tests of the effect of pHOS on the Beverton-Holt and Ricker models were non-significant (P≥0.9838). There was no evidence to suggest that higher proportions of hatchery spawners were associated with lower juvenile productivity for Summer Chinook Salmon in the Methow River.

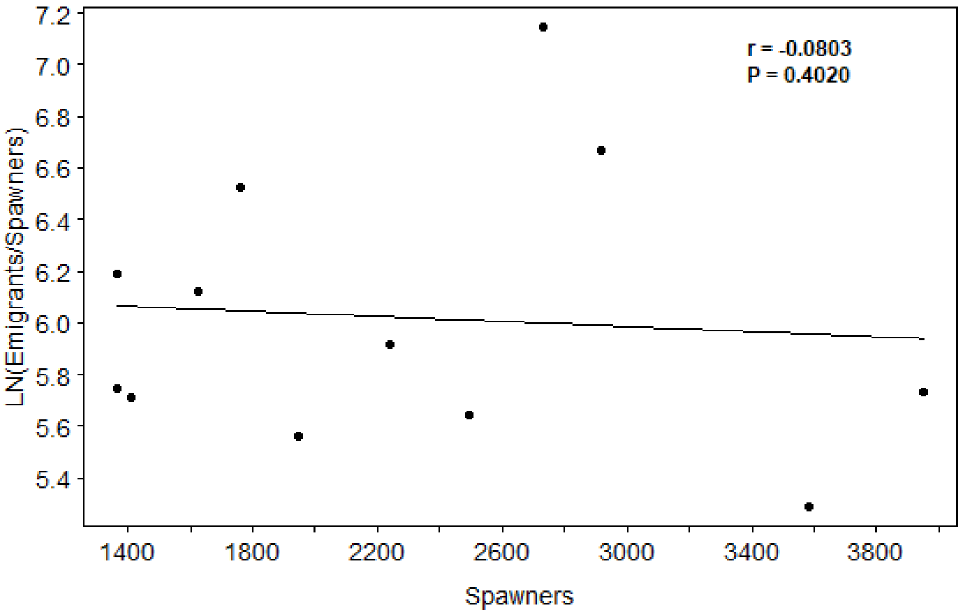


Figure 64. Emigrants per spawner (log scale) versus spawner abundance for Methow River Summer Chinook Salmon, 2006–2018 (without 2012), with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope.

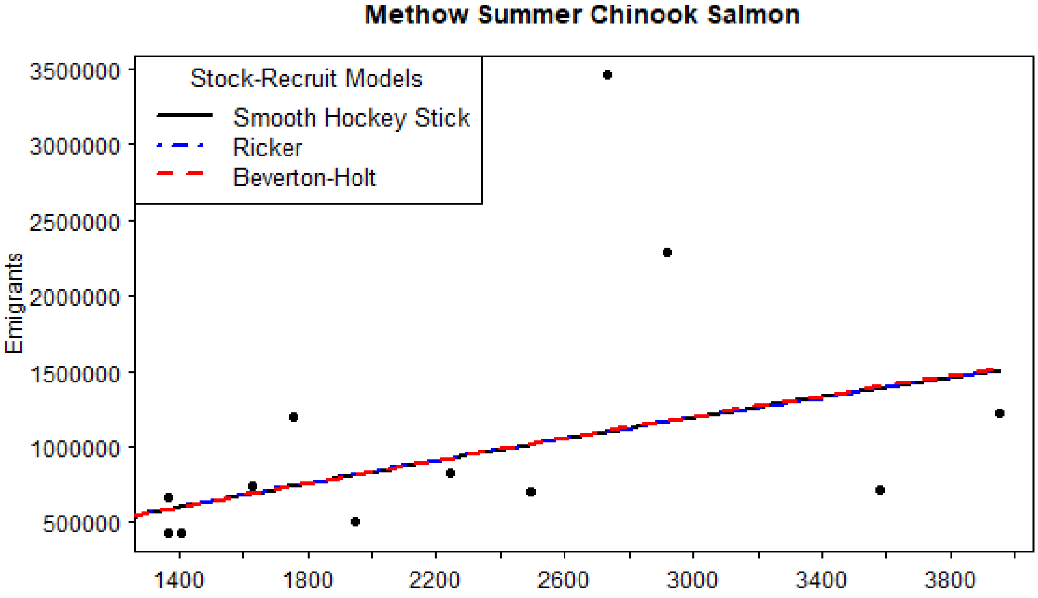


Figure 65. Stock-recruitment models fit to emigrants and spawner data for Methow River Summer Chinook Salmon, 2006–2018 (without 2012).

Table 16. Fitted stock-recruitment models for emigrants and stock (spawner) data from Methow River Summer Chinook Salmon, 2006–2018 (without 2012). Confidence intervals were estimated using bootstrap with at least 1700 bootstrap samples. Correlation = Pearson correlation coefficient between parameter estimates from bootstrap samples. Model equations are defined in Equations (1), (2), and (3). ΔAICc represents change in AICc compared to model with minimum AICc.

Model	AICc	ΔAICc	Parameter[b]	Parameter Estimates	95% CI	Correlation
Smooth Hockey Stick	26.85	0.01	α	459	352.6 – 1344.6	α, R_∞: -0.23[a]
			R_∞	4,796,000	889,141 – 19,840,304	
Beverton-Holt	26.86	0.02	α	9,817,511	874,870 – 66,701,078	α, β: 0.99
			β	21,552	-26.7 – 16,434.1	
Ricker	26.84	0.00	α	461	331.4 – 1032.5	α, β: 0.88
			β	0.00005	< 0.0001 – 0.0004	
			K	3,457,540	919,213 - ∞	

a = Correlation coefficient between *a* and R_∞ is uninformative because parameter estimates are not linearly related; see Figure D3. The correlation coefficient between $1/\alpha$ and $R_\infty = 0.2984$.

b = Estimated maximum recruitment parameters are: R_∞ for the Smooth Hockey Stick model, *a* for the Beverton-Holt model, and $K=(\alpha/\beta)e^{-1}$ for the Ricker model.

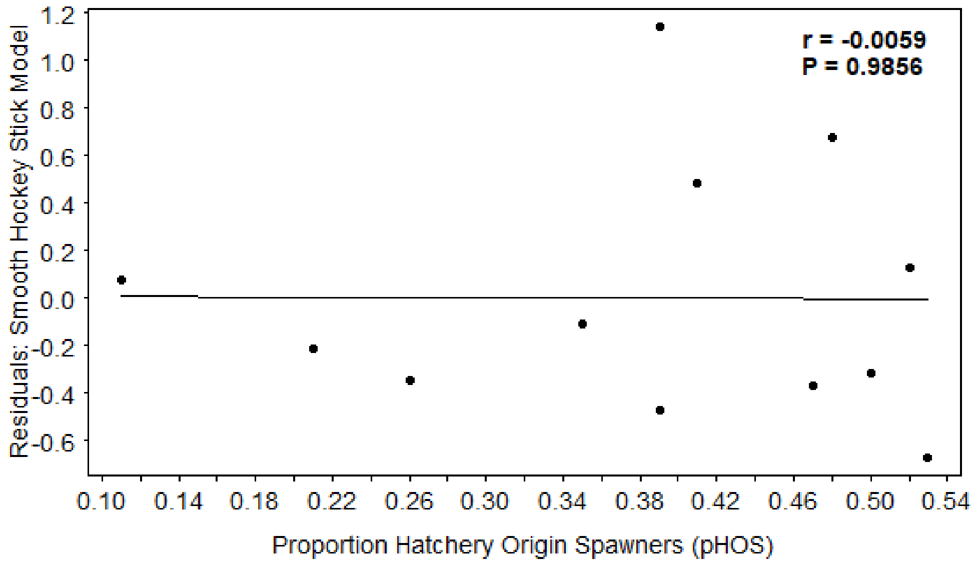


Figure 66. Residuals from Smooth Hockey Stick Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using emigrant and spawner data from Methow River Summer Chinook Salmon, 2006–2018 (without 2012). $R^2 < 0.0001$.

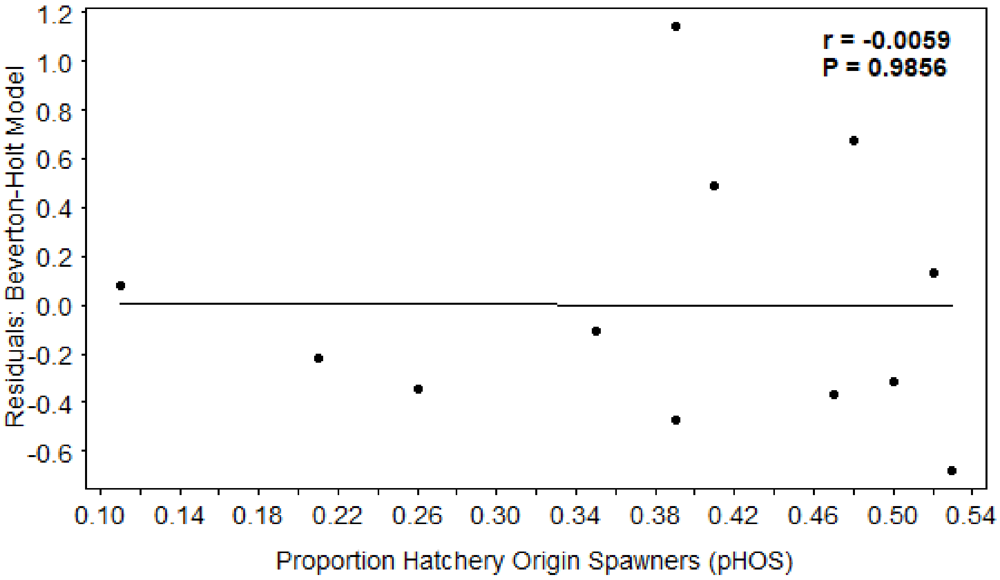


Figure 67. Residuals from Beverton-Holt Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using emigrant and spawner data from Methow River Summer Chinook Salmon, 2006–2018 (without 2012). $R^2 < 0.0001$.

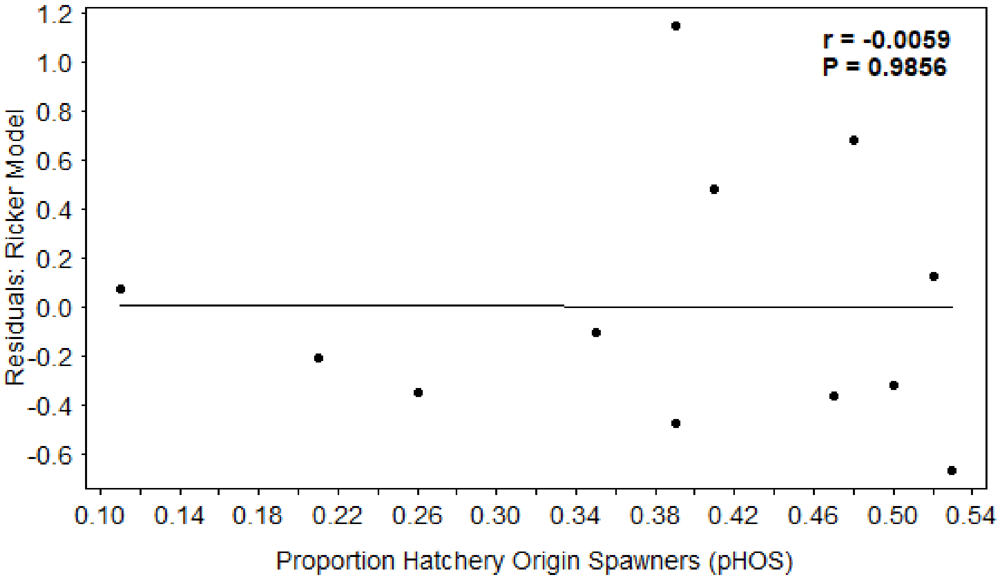


Figure 68. Residuals from Ricker Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using emigrant and spawner data from Methow River Summer Chinook Salmon, 2006–2018 (without 2012). $R^2 < 0.0001$.

Hypothesis H02.2.1.2

There was a very weak and non-significant negative association between ln(emigrants per redd) and the proportion of hatchery spawners (pHOS) for Methow River Summer Chinook Salmon (Pearson correlation coefficient r= -0.0641, P=0.4216) (Figure 69). The redd count was not associated with pHOS (P=0.6767, Figure 70) and there was no indication of post-spawning density dependence apparent from examination of the emigrants per redd plotted against the redd counts (Figure 71). Nevertheless, the relationship between emigrants per redd and pHOS was examined using the Ricker and Beverton-Holt stock-recruitment models in order to account for density dependence effects, with redds used in place of spawner counts. Both models were equivalent on the basis of AICc rank (ΔAICc = 0.001 compared to Ricker model) and examination of model residuals (Table 17; Figure G8 – Figure G12). However, the Beverton-Holt model fit was not robust to variability in the data, as demonstrated by the inability to fit it to bootstrap samples and the wide and inadmissible asymptotic confidence intervals on the model parameters (Table 17). Thus, the Ricker model was preferred. The fitted Ricker model for emigrants per redd was (Table 17):

$$ln(R/S) = 7.0724 - 0.2448P_{HOS} - 0.00004 * S$$

The 95% bootstrap confidence interval for the regression coefficient for pHOS (i.e., β_2 in Equation (7)) was (-3.2640, 2.4357). Because this confidence interval included both positive and negative values, we concluded that there is no evidence of a negative association between pHOS and emigrants per redd for Methow Summer Chinook Salmon after adjusting for density dependence.

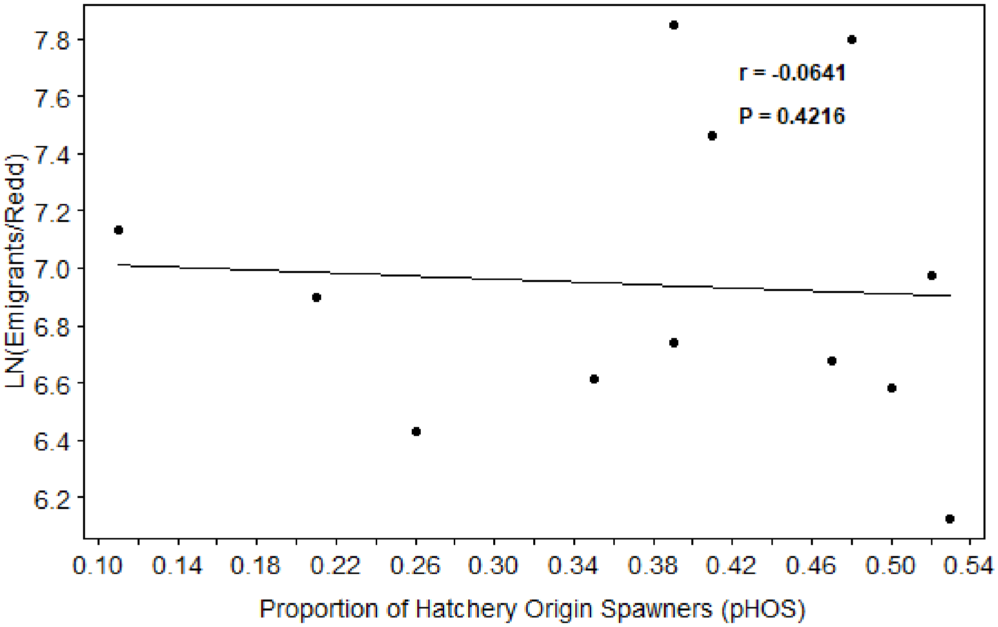


Figure 69. Emigrants per redd (log scale) versus proportion of hatchery origin spawners (pHOS) for Methow River Summer Chinook Salmon, 2006–2018 (without 2012), with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. $R^2 = 0.0041$.

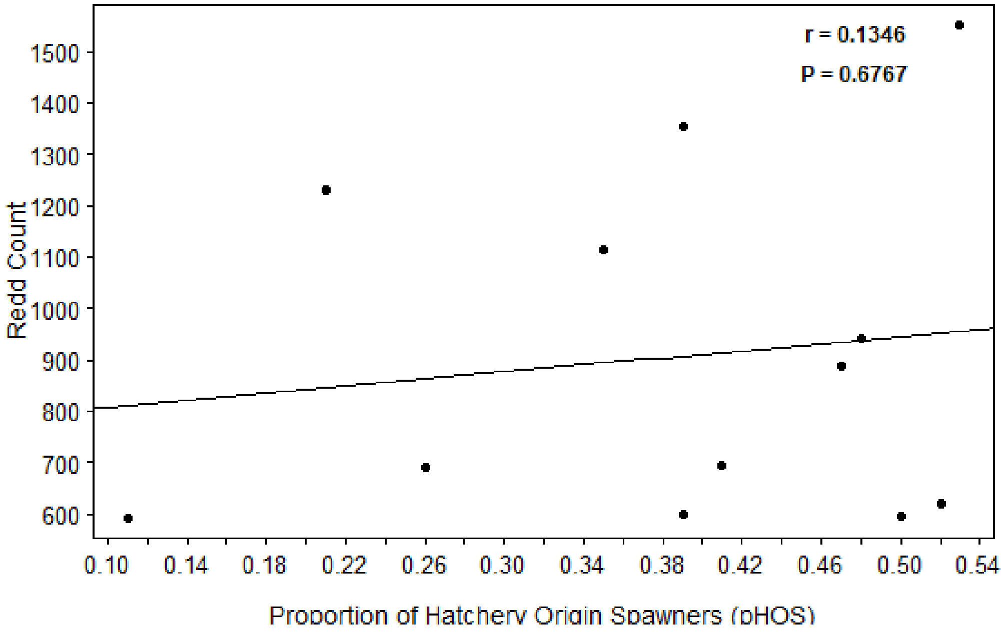


Figure 70. Redd count versus proportion of hatchery origin spawners (pHOS) for Methow River Summer Chinook Salmon, 2006–2018 (without 2012), with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope.

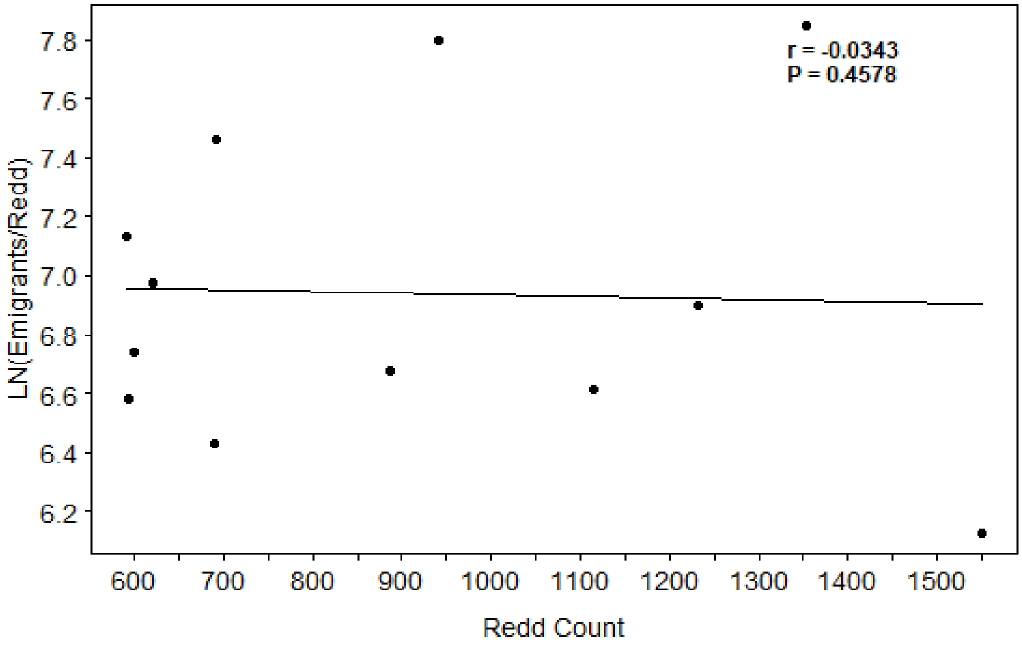


Figure 71. Emigrants per redd versus redd count for Methow River Summer Chinook Salmon, 2006–2018 (without 2012), with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. Negative slope indicates post-spawning density dependence.

Table 17. Fitted stock-recruitment models for emigrants per redd for Methow River Summer Chinook Salmon, 2006–2018 (without 2012), including effect (β_2) of proportion of hatchery origin spawners (pHOS). Bootstrap confidence intervals based on ≥1,000 bootstrap samples were provide for the Ricker model, and asymptotic confidence intervals were provided for the Beverton-Holt model. Model equations are defined in Equations (5) and (7). ΔAICc represents change in AICc compared to model with minimum AICc.

Model	AICc	ΔAICc	Parameter	Parameter Estimates	95% CI
Beverton-Holt	31.64	0.001	α	31,205,045	- 881,383,950 – 943,794,030
			β	26,564	-772,397 – 825,526
			β_2	0.2468	-2.4111 – 2.9046
Ricker	31.64	0.000	$ln(\alpha)$	7.0724	4.6169 – 8.2810
			β	0.00004	-0.0016 – 0.0010
			β_2	0.2448	-3.2640 – 2.4357

Methow River Summer Steelhead

Adult spawner, emigrant recruitment, pHOS, and redd count data from Summer Steelhead were available from the Methow River for the 2003–2015 brood years. Adult stock abundance (spawners) ranged from 1,105 in 2012 to 3,680 in 2010 and averaged 2,003, and emigrant recruitment ranged from 9,076 in 2003 to 33,739 in 2007 and averaged 18,154 (Figure 72, Figure 73). Redd counts averaged 1,084 (range = 591 to 2,019), and pHOS averaged 0.81 (range = 0.58 to 0.89). The 2007 brood year stood out as a possible outlier in emigrant count with a much higher count (33,739) than in the other years (range = 9,076 – 25,845) (Figure 73a).

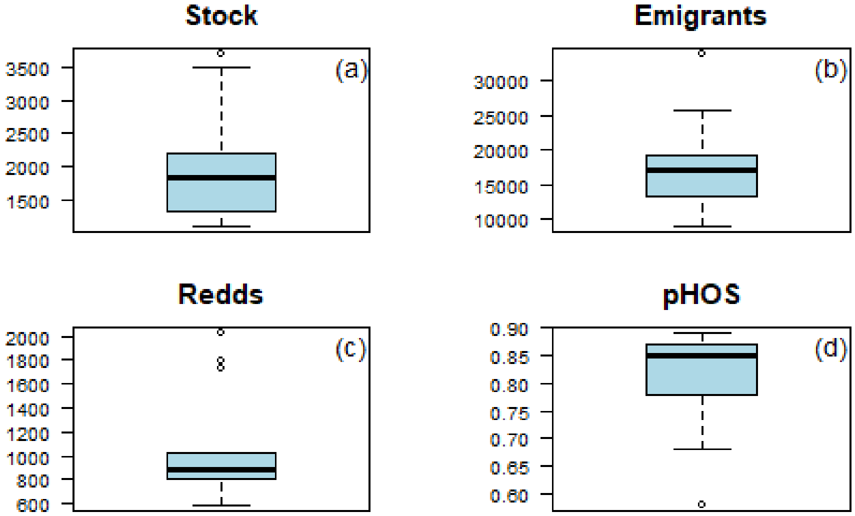


Figure 72. Methow River Summer Steelhead boxplots for Stock (spawner abundance), Emigrants, Redd counts, and proportion of hatchery origin spawners (pHOS), 2003–2015. Box indicates interquartile range and thick horizontal bar is median. Whiskers indicate quartile ± 1.5×interquartile range.

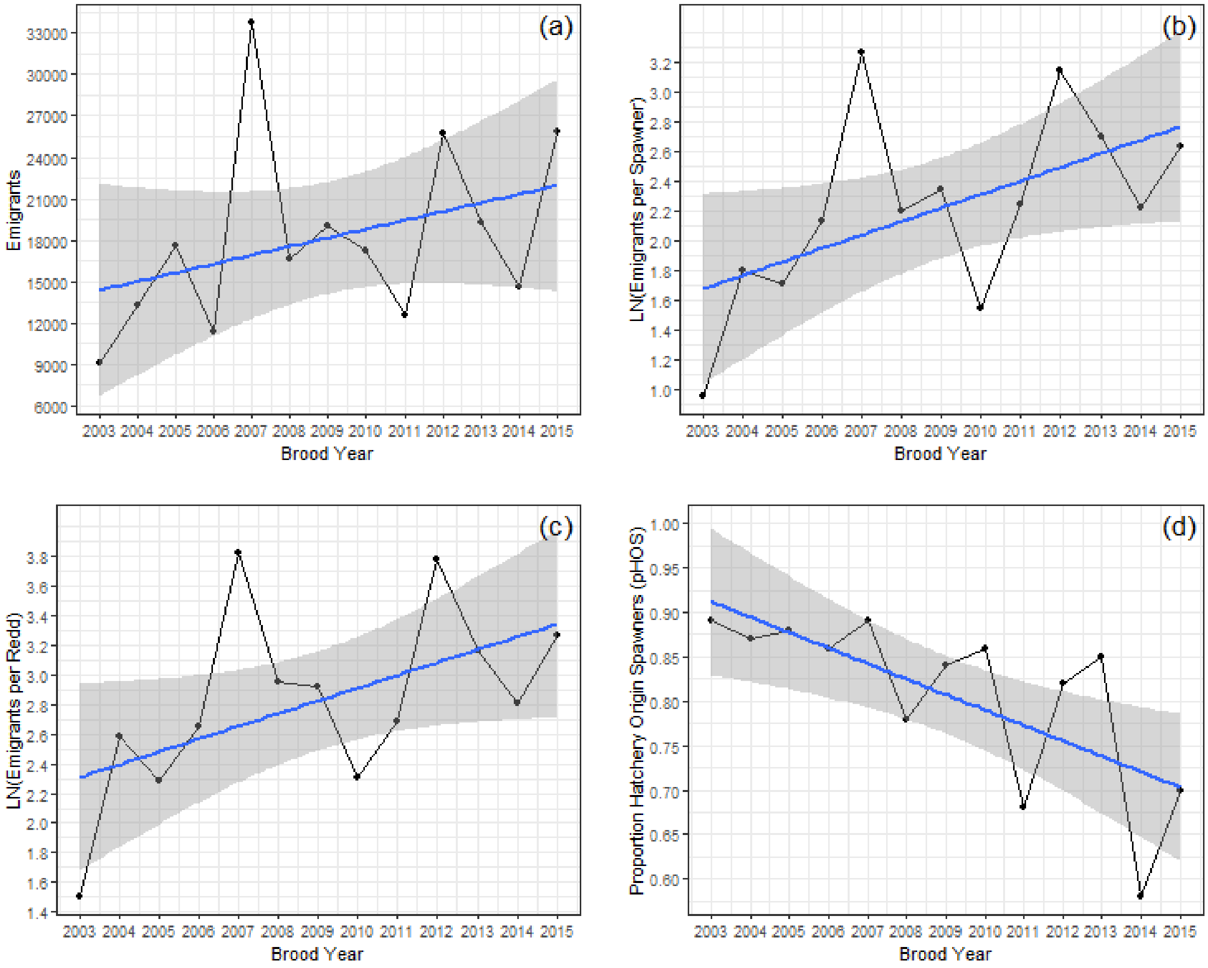


Figure 73. Methow River Summer Steelhead annual Emigrant counts, Emigrant/Spawner (log scale), Emigrant/Redd (log scale), and proportion of hatchery origin spawners (pHOS), 2003–2015. Line indicates the linear trend. Shaded area is the estimated 95% confidence interval of the line.

Hypothesis H02.2.1.1

A strong negative linear relationship was observed between Methow River Summer Steelhead spawners and emigrant recruitment, demonstrating evidence of density dependence in mortality between the spawning and emigrant life stages (P=0.0002; Figure 74). Thus, an attempt was made to fit the Smooth Hockey Stick, Beverton-Holt, and Ricker stock-recruitment models to the spawner and emigrant data. However, the Smooth Hockey Stick and Beverton-Holt modeling assumption of asymptotic growth in recruitment as spawner abundance increases was not supported by the data, as demonstrated by the locally smoothed curve (LOESS) in Figure 75, and neither the Smooth Hockey Stick model nor the Beverton-Holt model could be fit for the Methow River spawner-recruitment data. The Ricker model was fit to the Methow River data and estimated maximum recruitment at approximately 1,662 spawners (Figure 75). Although the Ricker stock-recruitment model could be fit to the Methow River spawner and emigrant data, the model residuals demonstrated negative autocorrelation at a time lag of 1 and 4 years (Figure H2), suggesting that the Ricker model does not adequately account for the population dynamics and that the model parameters may be biased. Additionally, high correlation was observed between the model parameter estimates, increasing uncertainty in the model predictions (Table 18).

The residuals from the Ricker model were compared to pHOS using correlation analysis. The estimated Pearson correlation coefficient between the Ricker model residuals and pHOS was 0.2222 and was not significantly different from 0 (P=0.4656; Figure 76). Additionally, a likelihood ratio test of the effect of pHOS on the Ricker model was non-significant (P=0.3829). The Beverton-Holt model could not be fit with pHOS as a variable. Analysis that omitted the possible outlier brood year of 2007 resulted in the same findings: only the Ricker model was approximately consistent with the data, and there was no evidence of a negative relationship between pHOS and juvenile productivity of emigrants.

Overall, there was no evidence that to suggest that higher proportions of hatchery spawners were associated with lower juvenile productivity for Summer Steelhead in the Methow River. However, there were only 13 years of data available, and the modeling assumptions were not well supported. Thus, it remains possible that there is a relationship between pHOS and juvenile productivity that are not observable using the available data and analyses.

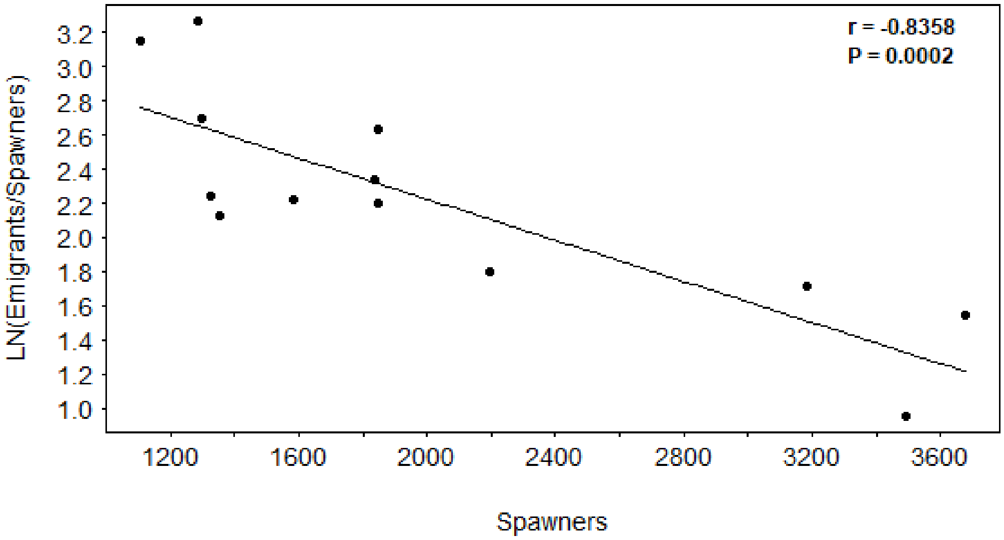


Figure 74. Emigrants per spawner (log scale) versus spawner abundance for Methow River Summer Steelhead, 2003–2015, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope.

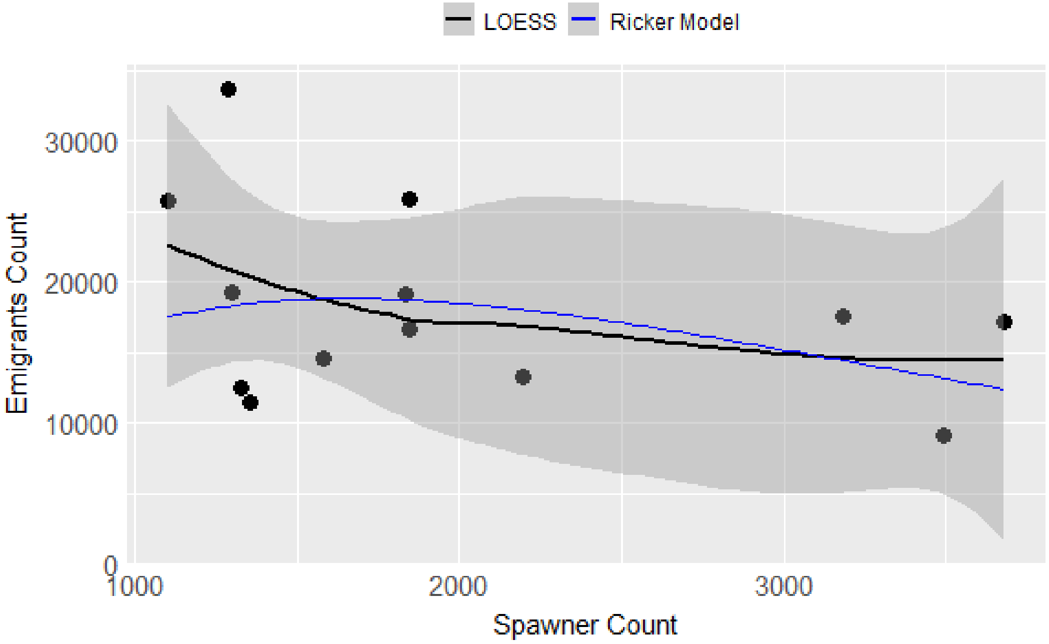


Figure 75. Stock and emigrant data with fitted LOESS curve and Ricker Model for Methow River Summer Steelhead, 2003–2015.

Table 18. Fitted stock-recruitment models for emigrants and stock (spawner) data from Methow River Summer Steelhead, 2003–2015. Confidence intervals were estimated using bootstrap with 3,000 bootstrap samples. Correlation = Pearson correlation coefficient between parameter estimates from bootstrap samples. Model equations are defined in Equations (1), (2), and (3). ΔAICc represents change in AICc compared to model with minimum AICc. *Only the Ricker model could be fit for Methow River data.

Model*	AICc	ΔAICc	Parameter[a]	Parameter Estimates	95% CI	Correlation
Smooth Hockey Stick	NA	NA	α	NA	NA	α, R_∞: NA
			R_∞	NA	NA	
Beverton-Holt	NA	NA	α	NA	NA	α, β: NA
			β	NA	NA	
Ricker	17.22	NA	α	30.8	19.3 – 48.9	α, β: 0.90
			β	0.0006	0.0004 – 0.0008	
			K	18,835	15,830 – 23,693	

a = Estimated maximum recruitment parameters are: R_∞ for the Smooth Hockey Stick model, α for the Beverton-Holt model, and $K = (\alpha/\beta)e^{-1}$ for the Ricker model.

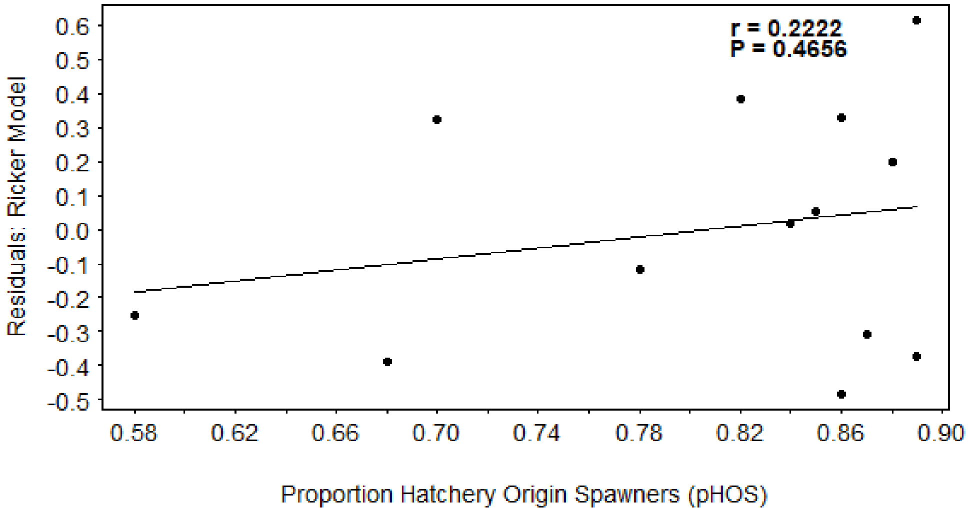


Figure 76. Residuals from the Ricker Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using emigrant and spawner data from Methow River Summer Steelhead, 2003–2015. R^2=0.0494.

Hypothesis H02.2.1.2

There was no evidence of a negative association between emigrants per redd and the proportion of hatchery spawners (pHOS) for Methow River Summer Steelhead (Pearson correlation coefficient r=-0.1628, P=0.2976) (Figure 77). Also, the linear association between redd count and pHOS was non-significant (P=0.2335; Figure 78). However, comparison of emigrants per redd with redd count demonstrated strong evidence of post-spawning density dependence (P=0.0002, Figure 79). Thus, the relationship between emigrants per redd and pHOS was examined using stock-recruitment models in order to account for density dependence effects, using redds in place of spawner abundance. The Beverton-Holt model resulted in an inadmissible (i.e., negative) estimate of the β parameter, confirmed by examination of the likelihood surface. Thus, no results are provided for the Beverton-Holt model. The Ricker model was able to be fit and the residuals agreed moderately well with model assumptions (Figure H4, Figure H5). The fitted Ricker model for emigrants per redd was (Table 19):

$$ln(R/S) = 3.3547 + 0.9921 * P_{HOS} - 0.0012 * S.$$

The 95% bootstrap confidence interval for the effect of pHOS (i.e., β_2 in Equation (7)) was (-3.3407, 2.5691). Because the confidence interval for the effect of pHOS included both positive and negative values, we concluded that there was no evidence of a negative association between pHOS and emigrants per redd for Methow River Summer Steelhead whether or not an adjustment was made for density dependence. We came to the same conclusion when the possible outlier brood year (2007) was omitted from the data analysis. However, the small sample size, low degree of variability in the observed pHOS values, and potentially high level of measurement error in the observed data may have lowered the ability to detect a relationship between pHOS and emigrants per redd.

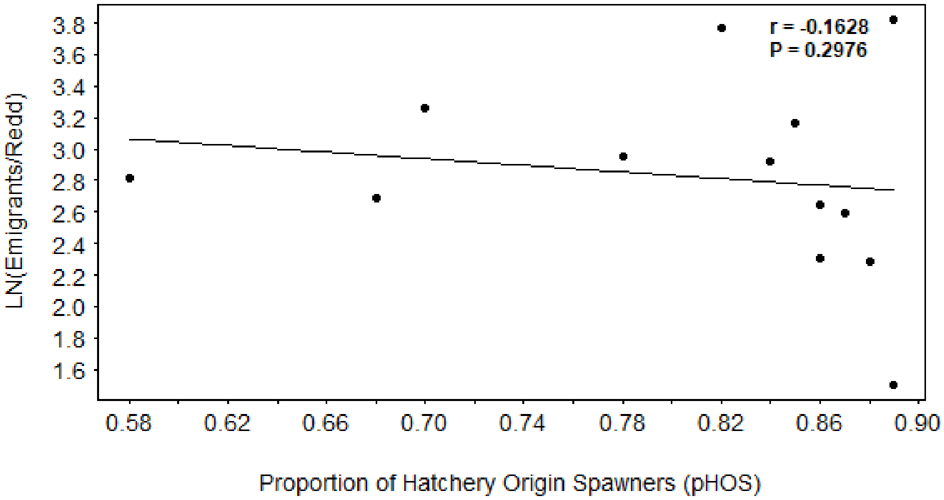


Figure 77. Emigrants per redd (log scale) versus proportion of hatchery origin spawners (pHOS) for Methow River Summer Steelhead, 2003–2015, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. $R^2 = 0.0265$.

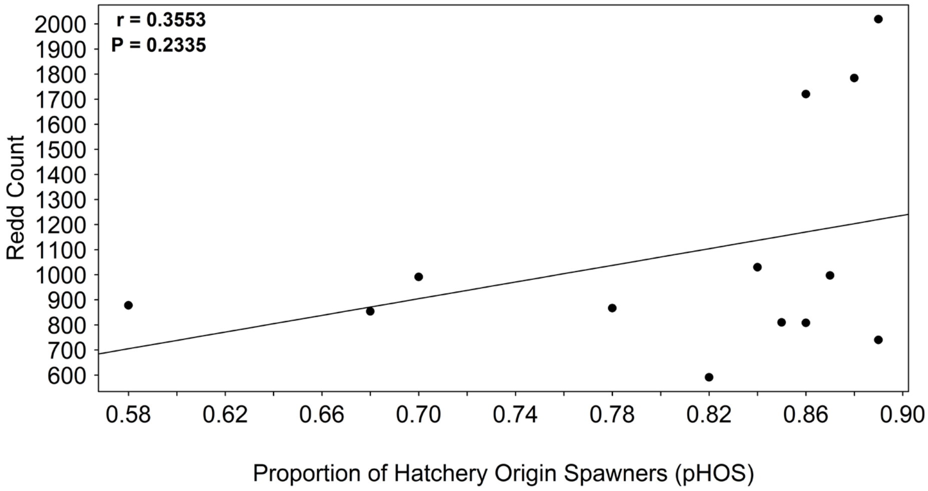


Figure 78. Redd count versus proportion of hatchery origin spawners (pHOS) for Methow River Summer Steelhead, 2003–2015, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope.

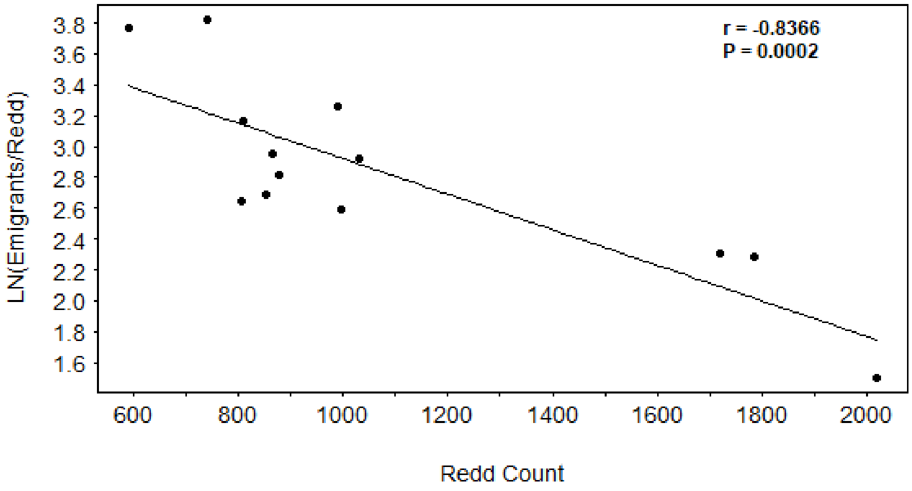


Figure 79. Emigrants per redd (log scale) versus redd count for Methow River Summer Steelhead, 2003–2015, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. Negative slope indicates post-spawning density dependence.

Table 19. Fitted stock-recruitment models for emigrants per redd for Methow River Summer Steelhead, 2003–2015, including effect (β_2) of proportion of hatchery origin spawners (pHOS). Confidence intervals were estimated using bootstrap with 3,000 bootstrap samples. Model equations are defined in Equations (5) and (7). ΔAICc represents change in AICc compared to model with minimum AICc. *Only the Ricker model could be fit for Methow River Summer Steelhead data.

Model*	AICc	ΔAICc	Parameter	Parameter Estimates	95% CI
Beverton-Holt	NA	NA	α	NA	NA
			β	NA	NA
			β_2	NA	NA
Ricker	19.92	NA	$ln(\alpha)$	3.3547	1.5579 – 6.1456
			β	0.0012	0.0006 – 0.0018
			β_2	-0.9921	-3.3407 – 2.5691

Twisp River Summer Steelhead

Adult spawner, emigrant recruitment, pHOS, and redd count data from Summer Steelhead were available from the Twisp River for the 2003–2015 brood years. Adult stock abundance (spawners) ranged from 143 in 2007 to 1,204 in 2003 and averaged 532, and emigrant recruitment ranged from 3,264 in 2008 to 13,669 in 2007 and averaged 6,133 (Figure 80, Figure 81). Redd counts averaged 272 (range = 82 to 696), and pHOS averaged 0.69 (range = 0.48 to 0.89). The 2007 brood year stood out as a possible outlier in emigrant count, with a much higher emigrant count (13,669) than any of the other years (range = 3,264 – 7,467) (Figure 81a). Additionally, pHOS generally declined over the course of the data collection, partly as a result of a policy change in 2010 to target pHOS values of 0.5 (Figure 81d).

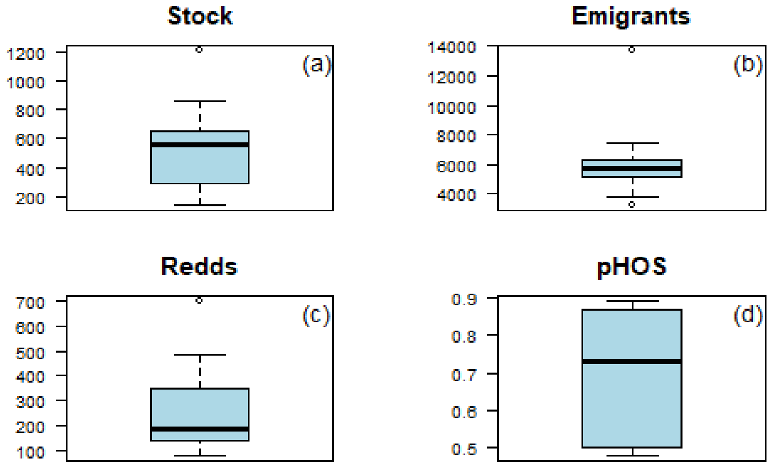


Figure 80. Twisp River Summer Steelhead boxplots for Stock (spawner abundance), Emigrants, Redd counts, and proportion of hatchery origin spawners (pHOS), 2003–2015. Box indicates interquartile range and thick horizontal bar is median. Whiskers indicate quartile ± 1.5×interquartile range.

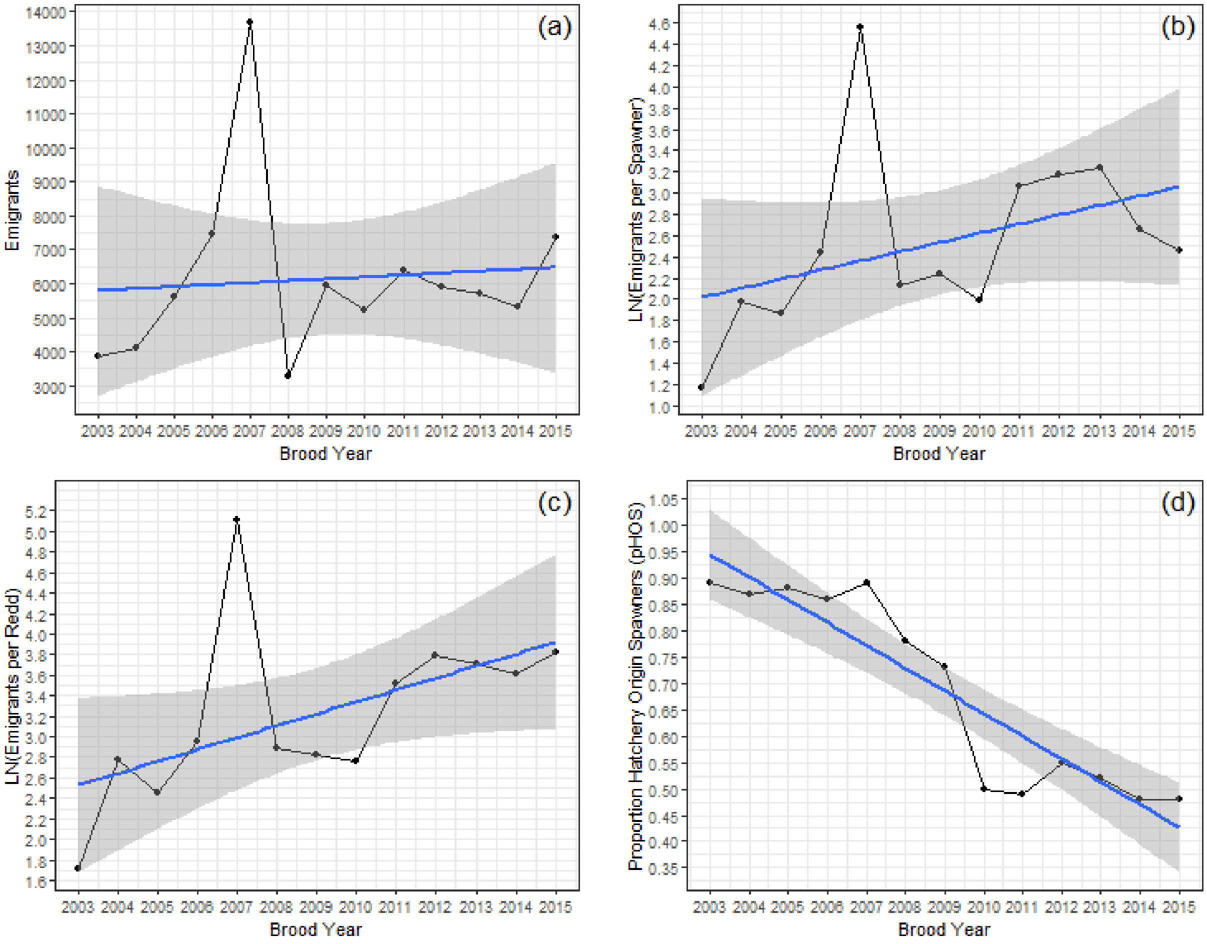


Figure 81. Twisp River Summer Steelhead annual Emigrant counts, Emigrant/Spawner (log scale), Emigrant/Redd (log scale), and proportion of hatchery origin spawners (pHOS), 2003–2015. Line indicates the linear trend. Shaded area is the estimated 95% confidence interval of the line.

Hypothesis H02.2.1.1

A strong negative linear relationship was observed between Twisp River Summer Steelhead spawners and emigrant recruitment, providing evidence of density dependence in mortality between the spawning and emigrant life stages (P=0.0001; Figure 82). Thus, an attempt was made to fit the Smooth Hockey Stick, Beverton-Holt, and Ricker stock-recruitment models to the spawner and emigrant data. However, the Smooth Hockey Stick and Beverton-Holt modeling assumption of asymptotic growth in recruitment as spawner abundance increases was not supported by the data, as demonstrated by the locally smoothed curve in Figure 83, and neither the Smooth Hockey Stick model nor the Beverton-Holt model could be fit for the Twisp River spawner-recruitment data. The Ricker model was fit to the Twisp River data and estimated maximum recruitment at approximately 410 spawners (Figure 83). Although the Ricker stock-recruitment model could be fit to the Twisp River spawner and emigrant data, the model residuals did not clearly meet the assumption of lognormal errors (Figure I1), suggesting that the model parameters may be biased.

The residuals from the Ricker model were compared to pHOS using correlation analysis. The estimated Pearson correlation coefficient between the Ricker model residuals and pHOS (r = 0.2553) was not significantly different from 0 (P=0.3999; Figure 84). A simpler analysis that compared the average Ricker model residuals between the pre-2010 period, when pHOS was not restricted (“control”), and the 2010+ period, when pHOS was targeted at 0.5 (“treatment”), also found no difference in model residuals between the two management periods (*t*-test = -0.4717, df = 11, P = 0.6463; Figure 85). Additionally, a likelihood ratio test of the effect of pHOS on the Ricker model was non-significant (P=0.3071). The Beverton-Holt model could not be fit with pHOS as a variable.

The 2007 brood year was noted as a possible outlier in emigrant count, so the analysis was redone without the 2007 brood year. The results from the Ricker model were consistent with the full data set (i.e., non-significant relationship between residuals and pHOS, P=0.2868, and also between residuals and pHOS management periods, P=0.1728), and the Beverton-Holt and Smooth Hockey Stick models could not be fit to the data (Figure 83, Table 20, Figure 86, Figure 87).

Overall, there was no evidence that to suggest that higher proportions of hatchery spawners were associated with lower juvenile productivity for Summer Steelhead in the Twisp River. However, with only 13 years of data, it remains possible that there is a relationship between pHOS and juvenile productivity that are not observable using the available data and analyses.

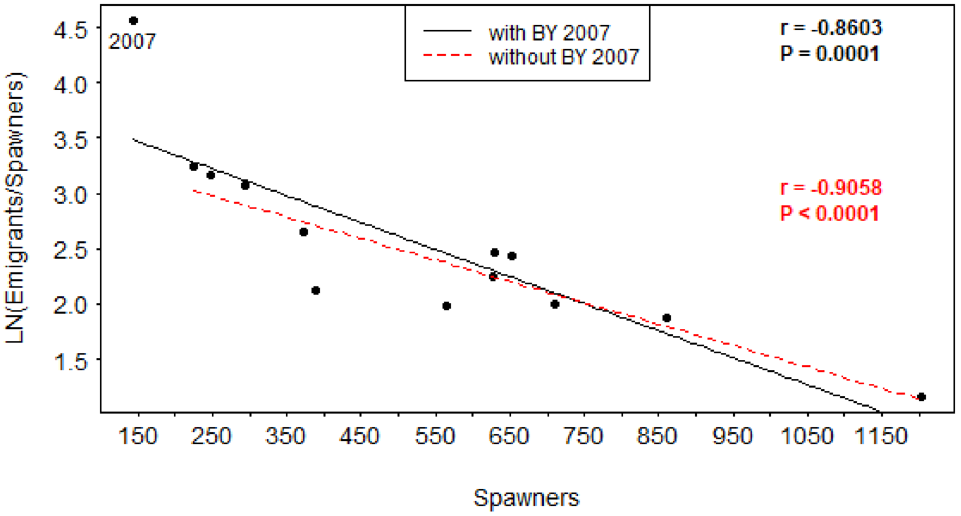


Figure 82. Emigrants per spawner (log scale) versus spawner abundance for Twisp River Summer Steelhead, 2003–2015, with and without brood year 2007, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope.

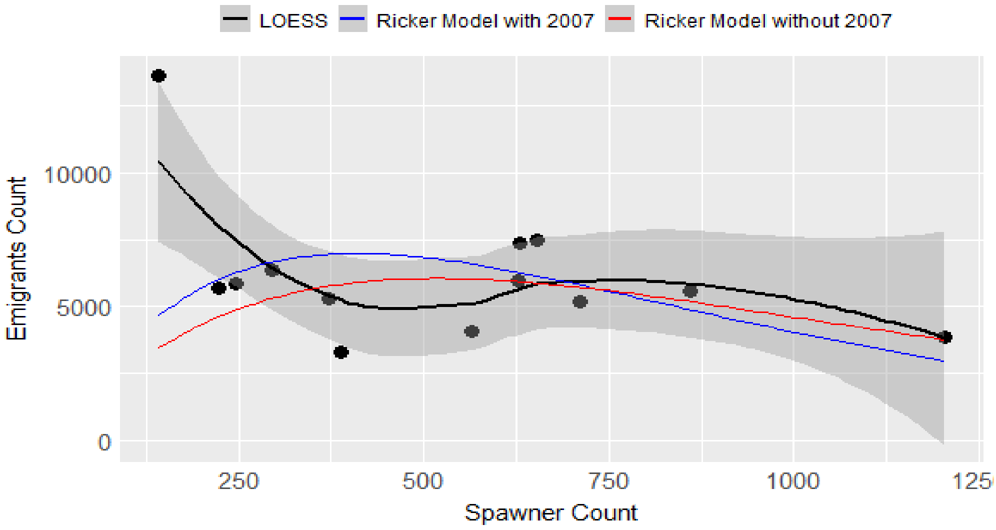


Figure 83. Stock and emigrant data with fitted LOESS curve and Ricker Model for Twisp River Summer Steelhead, 2003–2015, with and without brood year 2007.

Table 20. Fitted stock-recruitment models for emigrants and stock (spawner) data from Twisp River Summer Steelhead, 2003–2015. Confidence intervals were estimated using bootstrap with at least 2,000 bootstrap samples. Correlation = Pearson correlation coefficient between parameter estimates from bootstrap samples. Model equations are defined in Equations (1), (2), and (3). ΔAICc represents change in AICc compared to model with minimum AICc. *Only the Ricker model could be fit for Twisp River data. The Ricker model was fit both with and without data from the 2007 brood year. AICc should not be compared between the two Ricker models.

Model*	AICc	ΔAICc	Parameter[a]	Parameter Estimates	95% CI	Correlation
Smooth Hockey Stick	NA	NA	α	NA	NA	α, R_∞: NA
			R_∞	NA	NA	
Beverton-Holt	NA	NA	α	NA	NA	α, β: NA
			β	NA	NA	
Ricker with 2007	22.50	NA	α	46.3	29.2 – 76.2	α, β: 0.87
			β	0.0024	0.0016 – 0.0032	
			K	6,983	5,667 – 9,221	
Ricker without 2007	9.44	NA	α	31.8	22.9 – 43.1	α, β: 0.90
			β	0.0019	0.0015 – 0.0025	
			K	6,054	5,247 – 6,930	

a = Estimated maximum recruitment parameters are: R_∞ for the Smooth Hockey Stick model, α for the Beverton-Holt model, and $K = (\alpha/\beta)e^{-1}$ for the Ricker model.

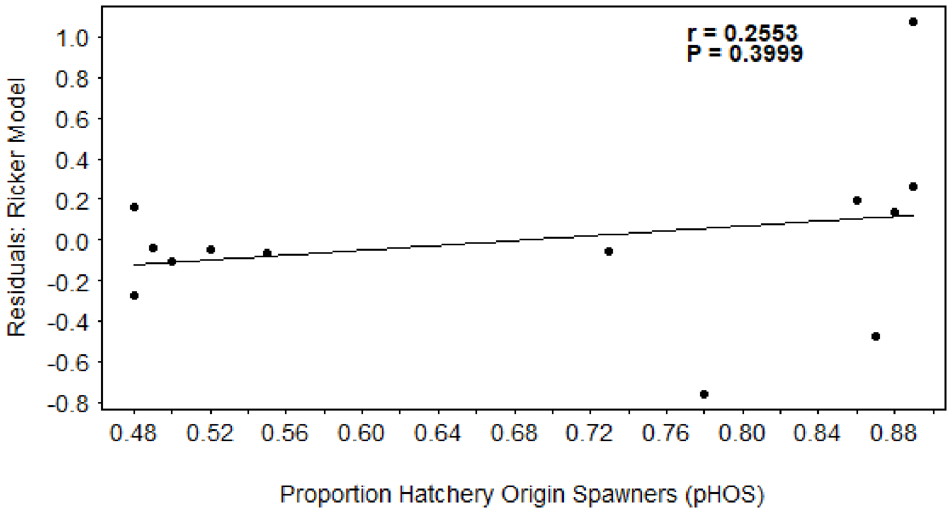


Figure 84. Residuals from the Ricker Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using emigrant and spawner data from Twisp River Summer Steelhead, 2003–2015, including brood year 2007. R^2=0.0652.

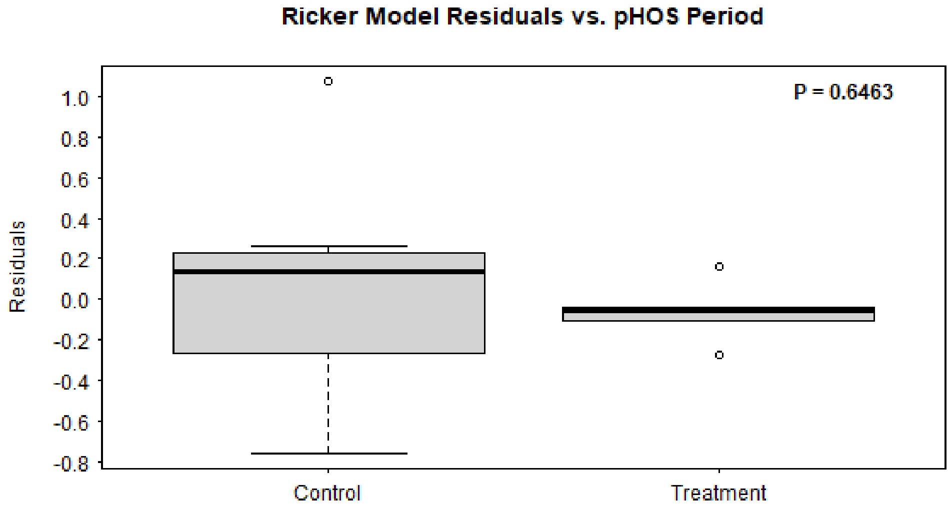


Figure 85. Distribution of residuals from the Ricker Model categorized by pHOS management period: Control = pre-2010, when pHOS levels were not restricted, and Treatment = 2010–2015, when pHOS levels were targeted at 0.5. P-value is from two-sided t-test: *t*-test = -0.4717, df = 11. Data used were emigrant and spawner counts from Twisp River Summer Steelhead, 2003–2015, including brood year 2007.

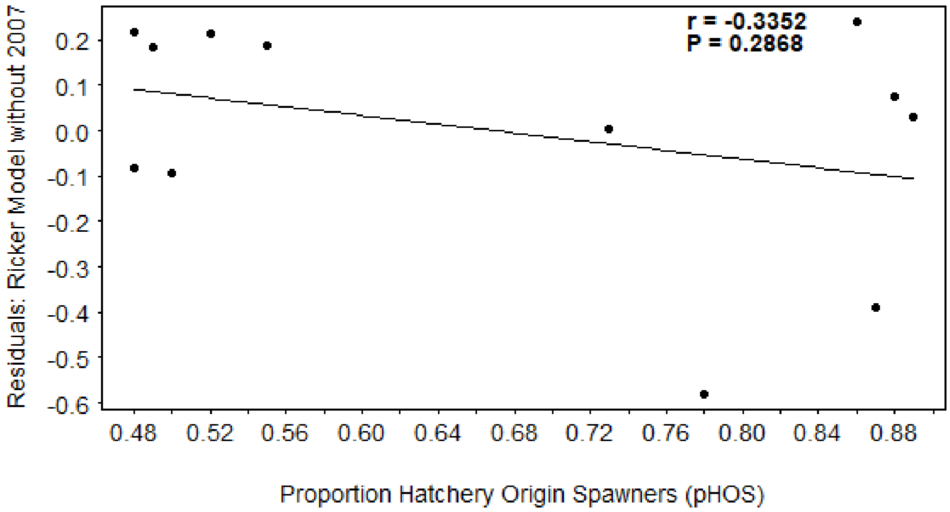


Figure 86. Residuals from the Ricker Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using emigrant and spawner data from Twisp River Summer Steelhead, 2003–2015, without brood year 2007. R^2=0.1124.

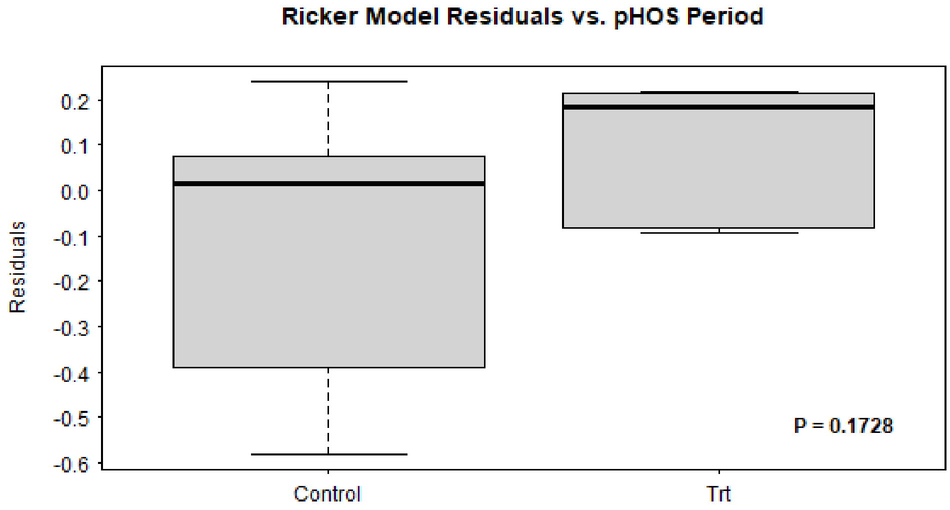


Figure 87. Distribution of residuals from the Ricker Model categorized by pHOS management period: Control = pre-2010, when pHOS levels were not restricted, and Treatment = 2010–2015, when pHOS levels were targeted at 0.5. P-value is from two-sided t-test: *t*-test = 1.4683, df = 10. Data used were emigrant and spawner counts from Twisp River Summer Steelhead, 2003–2015, without brood year 2007.

Hypothesis H02.2.1.2

There was no evidence of a negative association between emigrants per redd and the proportion of hatchery spawners (pHOS) for Twisp River Summer Steelhead using the full data set that included brood year 2007 (Pearson correlation coefficient r=-0.3180, P=0.1449) (Figure 88). The linear association between redd count and pHOS was significant at the 10% level (P=0.0723; Figure 89), and comparison of emigrants per redd with redd count demonstrated strong evidence of post-spawning density dependence (P=0.0001,

Figure 90). The relationship between emigrants per redd and pHOS was examined using stock-recruitment models in order to account for density dependence effects, using redds in place of spawner abundance. The Beverton-Holt model could not be fit to the data; examination of the likelihood indicated an optimum model fit for a negative value of the β model parameter, which is inconsistent with model interpretation (Figure I6). The Ricker model was able to be fit but the residuals agreed poorly with model assumptions (Figure I4, Figure I5). The fitted Ricker model for emigrants per redd was (Table 21):

$$ln(R/S) = 3.9305 + 0.7680 * P_{HOS} - 0.0045 * S.$$

The 95% bootstrap confidence interval for the effect of pHOS (i.e., β_2 in Equation (7)) was (-2.3366, 2.1443). Because the confidence interval for the effect of pHOS included both positive and negative values, we concluded that there was no evidence of a negative association between pHOS and emigrants per redd for Twisp River Summer Steelhead whether or not an adjustment was made for density dependence. However, the model assumptions were not well met, demonstrating an overall lack of fit. The small sample size and potentially high level of measurement error in the observed data may have contributed to the lack of model fit, and likewise may have lowered the ability to detect a relationship between pHOS and emigrants per redd using the available data.

When the potential outlier brood year of 2007 was omitted from the data set, there was a negative association between emigrants per redd and pHOS when density dependence was not accounted for (P=0.0009, Figure 91). However, there was significant density dependent mortality observed between the redd count and emigrant count (P<0.0001, Figure 90), which may have accounted for the association between emigrants per redd and pHOS. The Ricker model estimated that the effect of pHOS on the redd-emigrant relationship was non-significant, with a 95% bootstrap confidence interval of (-2.3915, 1.0898) (Table 22). Without the 2007 brood year, the Beverton-Holt model relating emigrants to redd counts was able to be fit when pHOS was in the model and pHOS was associated with lower emigrants per redd, demonstrated by the 95% bootstrap confidence interval for β_2 that was entirely greater than 0 (i.e., (0.0700, 1.9685); Table 22). However, the bootstrap confidence intervals for the other Beverton-Holt model parameters were notably wide: the confidence interval of the asymptotic maximum recruitment (α) included values 5 times the maximum recruitment observed, and the confidence interval for the redd counts predicted to generate half the maximum recruitment (β) included negative values (Table 22). The apparently poor fit of the Beverton-Holt model raises questions about the validity of its finding of a statistically significant pHOS effect.

Overall, the evidence for a negative association between the proportion of hatchery origin spawners (pHOS) and juvenile productivity in emigrants was not strong. There was no such evidence based on the full data set that included the 2007 brood year; however, one of the two stock-recruitment models could not be fit to the data because of misalignment of modeling assumptions with the data, and the data set was small (only 13 brood years). When the 2007 brood year was treated as an outlier and omitted from analysis, a negative association was observed between emigrants per redd and pHOS, but it disappeared when density dependence was accounted for using the Ricker model. The alternative stock-recruitment model (Beverton-Holt) maintained an effect of pHOS but did not appear to fit the data well, indicating possible bias in the estimate of the pHOS effect. The small sample size available may have lowered the ability to detect an effect of pHOS on juvenile productivity. Additionally, a negative trend in pHOS from nearly 0.90 in 2003 to nearly 0.50 in 2015 raises the possibility that any pHOS effect actually masks a temporal trend in juvenile productivity (Figure 81).

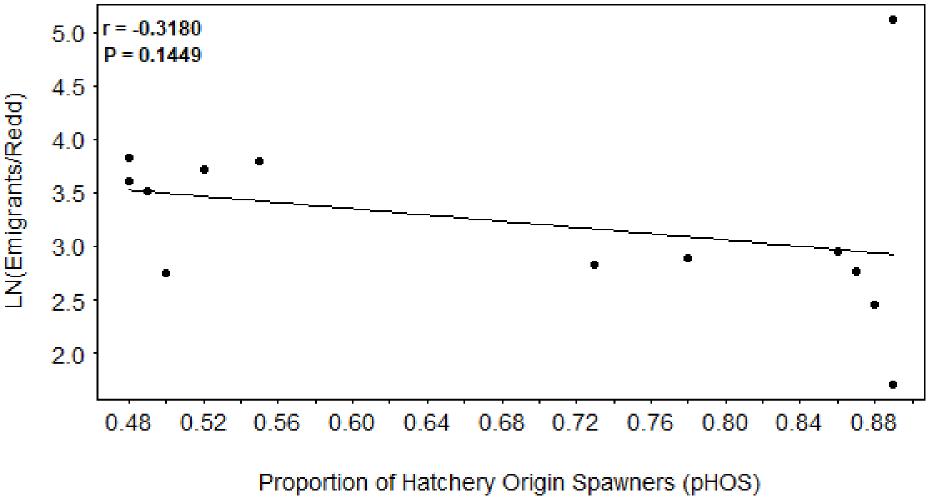


Figure 88. Emigrants per redd (log scale) versus proportion of hatchery origin spawners (pHOS) for Twisp River Summer Steelhead, 2003–2015, including brood year 2007, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. $R^2 = 0.1011$.

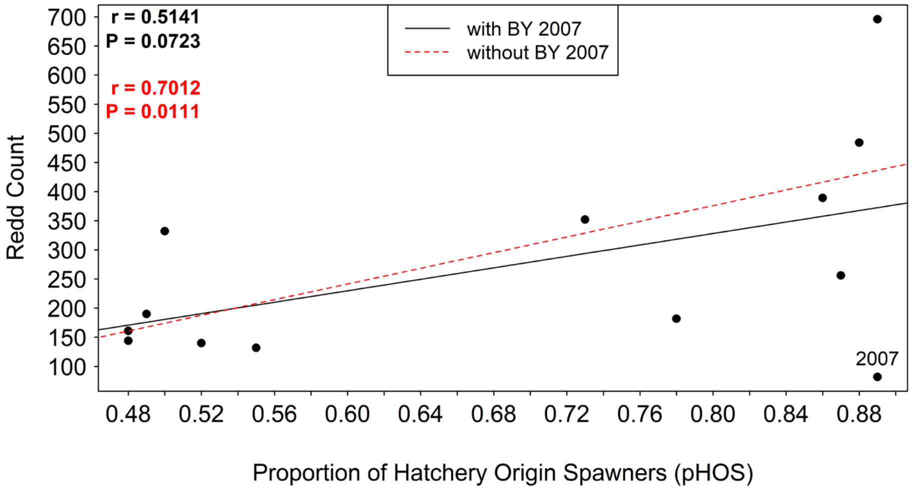


Figure 89. Redd count versus proportion of hatchery origin spawners (pHOS) for Twisp River Summer Steelhead, 2003–2015, with and without brood year 2007, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope.

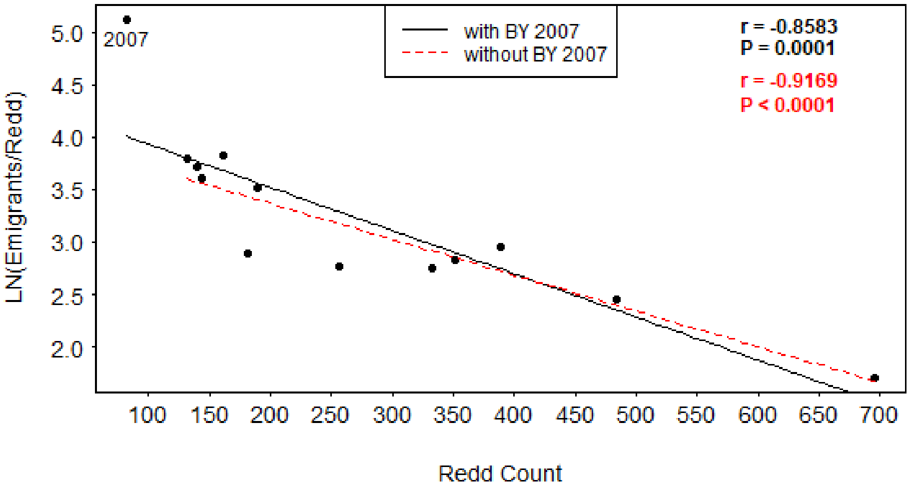


Figure 90. Emigrants per redd (log scale) versus redd count for Twisp River Summer Steelhead, 2003–2015, with and without brood year 2007, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. Negative slope indicates post-spawning density dependence.

Table 21. Fitted stock-recruitment models for emigrants per redd for Twisp River Summer Steelhead, 2003–2015, including brood year 2007 and the effect (β_2) of proportion of hatchery origin spawners (pHOS). Confidence intervals were estimated using bootstrap with 3,000 bootstrap samples. Model equations are defined in Equations (5) and (7). ΔAICc represents change in AICc compared to model with minimum AICc. *Only the Ricker model could be fit for Twisp River Summer Steelhead data.

Model*	AICc	ΔAICc	Parameter	Parameter Estimates	95% CI
Beverton-Holt	NA	NA	α	NA	NA
			β	NA	NA
			β_2	NA	NA
Ricker	25.81	NA	$ln(\alpha)$	3.9305	3.3009 – 5.0401
			β	0.0045	0.0015 – 0.0067
			β_2	-0.7680	-2.3366 – 2.1443

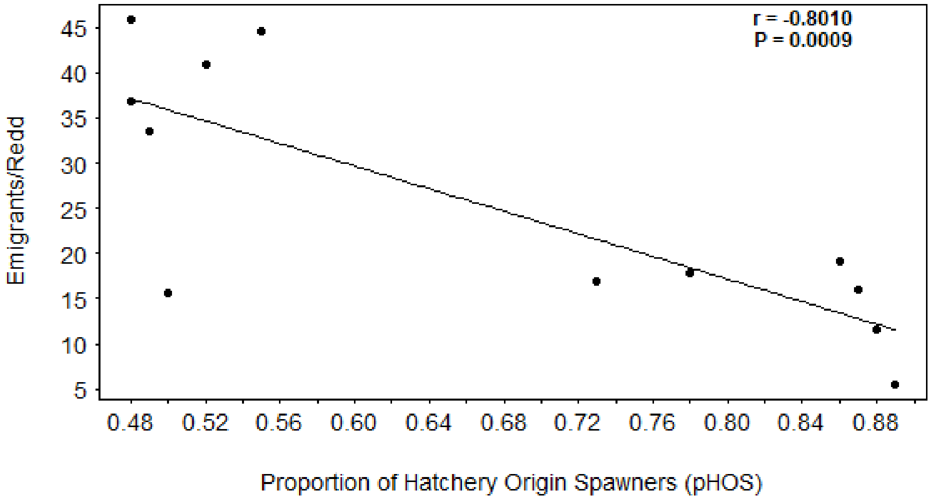


Figure 91. Emigrants per redd versus proportion of hatchery origin spawners (pHOS) for Twisp River Summer Steelhead, 2003–2015, omitting brood year 2007, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. $R^2 = 0.6417$.

Table 22. Fitted stock-recruitment models for emigrants per redd for Twisp River Summer Steelhead, 2003–2015, omitting brood year 2007 and including the effect (β_2) of proportion of hatchery origin spawners (pHOS). Confidence intervals were estimated using bootstrap with 3,000 bootstrap samples. Model equations are defined in Equations (5) and (7). ΔAICc represents change in AICc compared to model with minimum AICc.

Model	AICc	ΔAICc	Parameter	Parameter Estimates	95% CI
Beverton-Holt	10.55	0.24	α	12,008	5,158 – 40,066
			β	46.4	-31.2 – 275.2
			β_2	0.9259	0.0700 – 1.9685
Ricker	10.31	NA	$ln(\alpha)$	4.5239	3.8033 – 5.1740
			β	0.0027	0.0007 – 0.0049
			β_2	1.0323	-2.3915 – 1.0898

Discussion

Our investigation of whether a higher proportion of hatchery origin spawners (pHOS) may result in lowered juvenile productivity was largely inconclusive. For most populations studied, no evidence of an effect of pHOS was observed. For the single population that demonstrated a possible negative effect of pHOS on juvenile productivity (Twisp River Summer Steelhead), the evidence was weak: when density dependence was accounted for, the perceived negative association between pHOS and juveniles per redd was no longer observed. Additionally, the significant result was observed only when a possible outlier in emigrant counts was omitted, which may not be justified depending on the cause of the unusual emigrant count for that brood year. Thus, even when some evidence of a negative effect of pHOS was found, the evidence was particularly weak.

The lack of an observed effect of pHOS does not necessarily mean that such an effect does not exist, however. Multiple factors combined to lower the ability to detect an effect, should it exist. The most obvious factor was the small size of most of the data sets. Most of the populations had data for fewer than 20 brood years, resulting in lowered opportunity to observe the full range of variability in stock-recruitment dynamics in response to changes in hatchery proportion of spawners and lower statistical power to detect an effect. Then too, many populations showed low contrast in the observed pHOS values. A wider range of hatchery proportion values would make detecting an effect more feasible. In some populations (e.g., Twisp River Steelhead, Methow River Steelhead), pHOS has declined almost consistently since the start of data collection, which means any perceived effect of pHOS would be entirely confounded with temporal changes in juvenile productivity. This risk is increased by the observational nature of the pHOS data. An experiment that purposely manages hatchery origin spawners at planned pHOS levels would improve the ability to detect an effect on juvenile productivity.

Some data sets studied also demonstrated low contrast in the spawner or redd counts observed across brood years. The stock-recruitment models require observations at both low and high levels of spawners. This requirement means that low variability in spawner (or redd count) data reduces the quality of fit of the stock-recruitment models and in some cases makes them impossible to be fit altogether. A lack of data at low spawner levels may have lowered the ability to fit the Smooth Hockey Stick model, which requires data at low spawner levels to estimate the model parameter associated with depensation (α). Examination of the likelihood surface for the Smooth Hockey Stick model for some populations demonstrated moderate information in maximum recruitment but a complete lack of information in the α parameter, interpreted as the slope of the stock-recruitment curve at very low numbers of spawners (for example, see the flat contour curves in the dimension of the α parameter in Figure 92). Then again, several populations failed to demonstrate a stable maximum (or simply high) juvenile recruitment pattern at high levels of spawners, which is assumed by both the Smooth Hockey Stick and Beverton-Holt models. Again, examination of the likelihood surface in these cases indicated either a lack of information in model parameters or else model parameters optimized at inadmissible values (e.g., negative spawner counts necessary to generate half the asymptotic maximum recruitment, Figure 93). Although the Smooth Hockey Stick stock-recruitment model was the preferred analysis framework, it appeared poorly suited to the stock and juvenile recruitment data available for many populations.

For all three stock-recruitment models considered, there was often high uncertainty in model parameter estimates even when the models could be fit to the data. This was indicated by wide confidence intervals that often included maximum smolt or emigrant values far beyond the range of observed data and by high correlation in model parameter estimates. High correlation lowers the ability to distinguish between different model fits and increases uncertainty in the results; it arises from lack of contrast in the data or violation of modeling assumptions.

In most cases there was no evidence of a time lag in juvenile recruitment per spawner as represented by autocorrelation in the residuals from the stock-recruitment models. However, a negative autocorrelation was observed with a time lag of three years for Twisp River Spring Chinook Salmon and a time lag of one and four years for Methow River Summer Steelhead. Such negative autocorrelations may be observed when a high level of recruitment one year is habitually followed by a low level of recruitment after a consistent delay (e.g., 3 years). Such a pattern may be expected for populations with consistent age structure among spawners, paired with density-dependent mortality between spawning and juvenile recruit surveys. In such cases, the Smooth Hockey Stick, Beverton-Holt, and Ricker models are unlikely to adequately represent all important features of the population dynamics; an age-structured model may be required. The value of pHOS may also be affected by such autocorrelation. Thus, such factors should be accounted for in order to detect a true effect of pHOS on juvenile productivity beyond age- and density-dependent components of the population dynamics.

A final complication in assessing the stock-recruitment data for an effect of pHOS is data quality. The stock-recruitment models all assume low levels of measurement error in both spawners or redd counts and smolts or emigrants. The higher the level of measurement error, the lower the ability to model the dynamics well enough to detect an effect. Given all the complicating factors identified here, only the most extreme effect of pHOS on juvenile productivity could have been detected. Thus, we caution against concluding that such an effect is truly absent. Instead, we recommend that future data collection efforts attempt to minimize measurement error and increase the contrast in pHOS levels. We recommend that a planned experiment using deliberately chosen pHOS levels be implemented in order to achieve the necessary contrast and remove confounding with temporal and age-structured processes. Finally, we recommend that additional stock-recruitment models be considered that may better match the observed patterns in stock and juvenile recruitment data for populations of Chinook Salmon and Steelhead in tributaries affected by hatchery origin spawners.

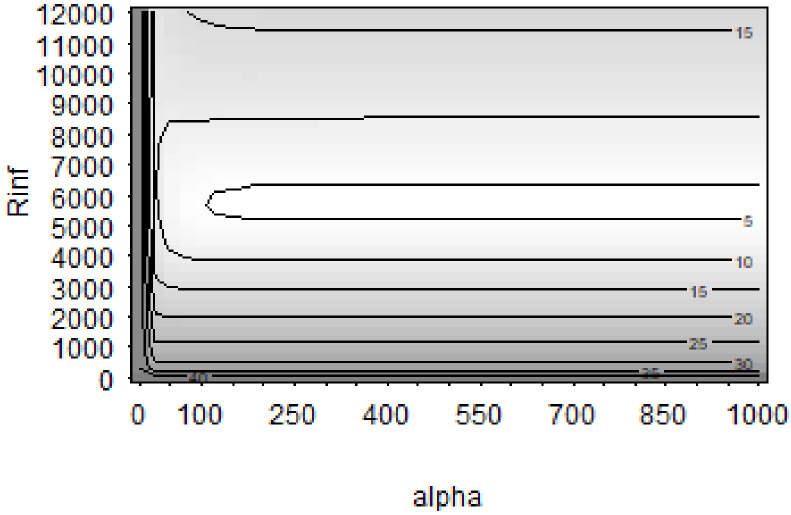


Figure 92. Negative log-likelihood surface and contour curves for the Smooth Hockey Stick model of emigrants and spawner counts. Lighter regions indicate higher likelihood values (lower negative log-likelihood values). The estimated parameter values occur where the negative log-likelihood is minimized. Data set = Twisp River Summer Steelhead, 2003–2015.

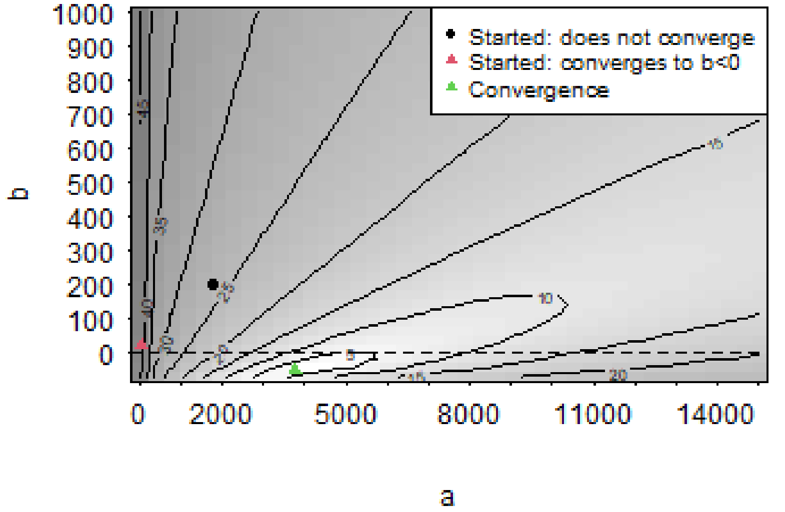


Figure 93. Negative log-likelihood surface and contour curves for Beverton-Holt model of emigrants, redd counts, and pHOS, using β_2 = -0.1160. Lighter regions indicate higher likelihood values (lower negative log-likelihood values). The estimated parameter values occur where the negative log-likelihood is minimized. The green triangle (falls below b=0 line) indicates the parameter set that optimizes the likelihood. Data set = Twisp River Summer Steelhead, 2003–2015.

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Appendices: Evaluation of Modeling Assumptions

Appendix A: Chiwawa River Spring Chinook Salmon

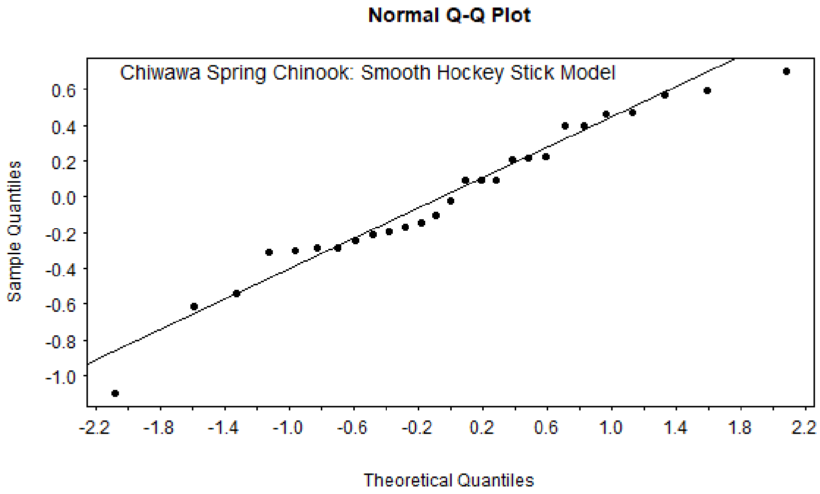

Figure A1. Normal quantile-quantile plot of residual from Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for Chiwawa River Spring Chinook, 1991–2017. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.9643, P=0.4604.

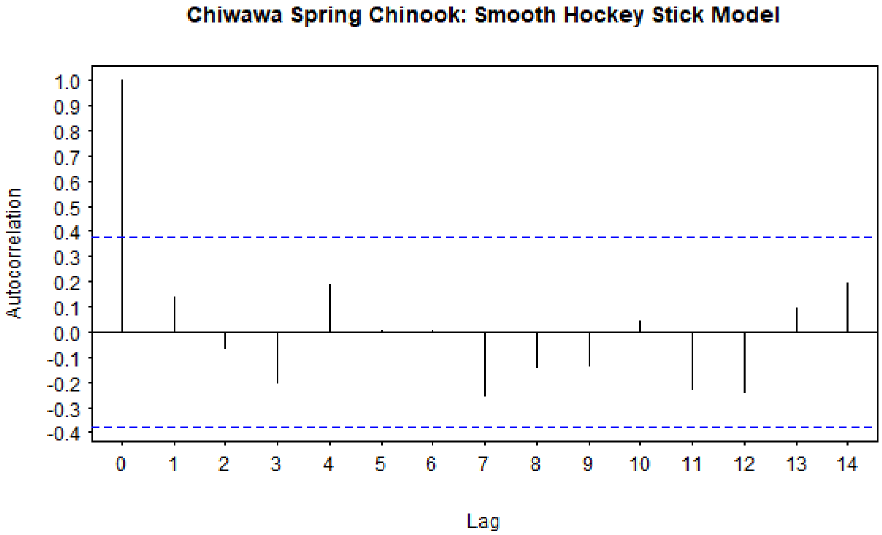

Figure A2. Autocorrelation plot of residuals for Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for Chiwawa River Spring Chinook, 1991–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

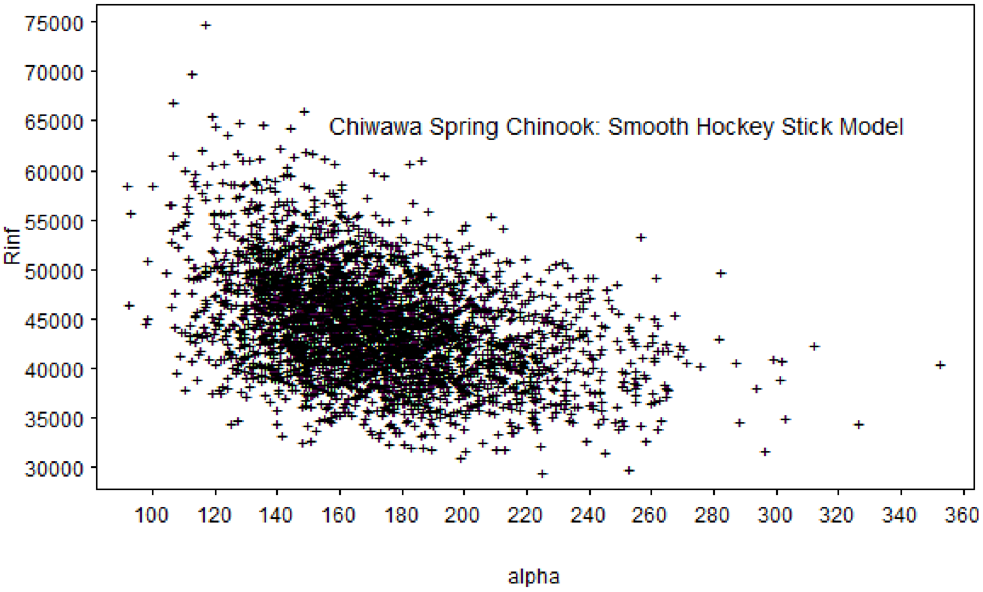

Figure A3. Correlation plot of bootstrap parameter estimates from the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for Chiwawa River Spring Chinook, 1991–2017, based on 3,000 bootstrap samples.

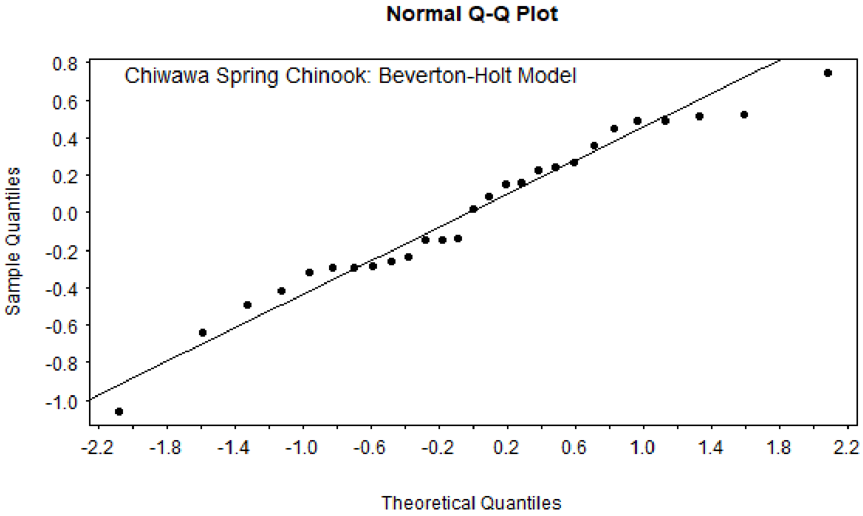

Figure A4. Normal quantile-quantile plot of residual from Beverton-Holt model of smolt recruitment as a function of spawner abundance (stock) for Chiwawa River Spring Chinook, 1991–2017. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.9672, P=0.5293.

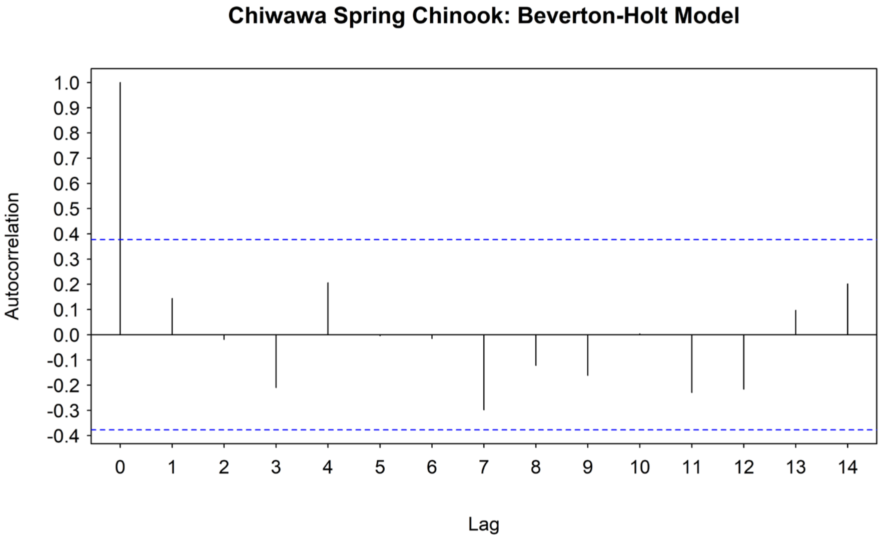

Figure A5. Autocorrelation plot of residuals for Beverton-Holt model of smolt recruitment as a function of spawner abundance (stock) for Chiwawa River Spring Chinook, 1991–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

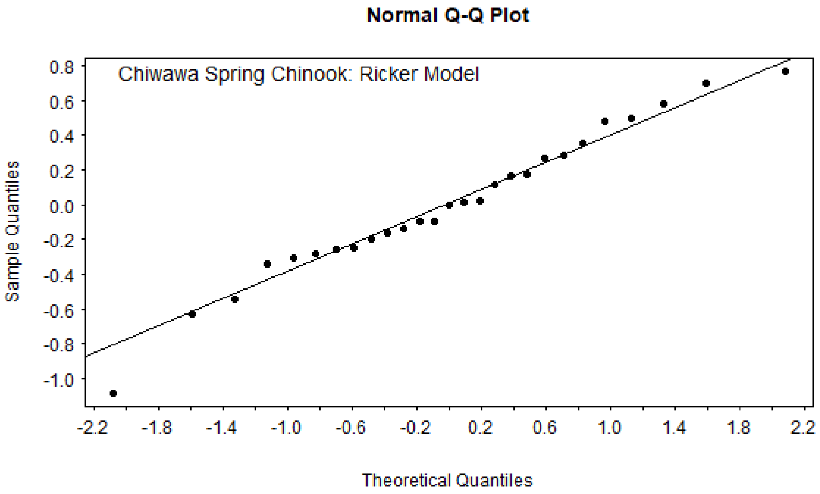

Figure A6. Normal quantile-quantile plot of residual from Ricker model of smolt recruitment as a function of spawner abundance (stock) for Chiwawa River Spring Chinook, 1991–2017. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.9788, P=0.8347.

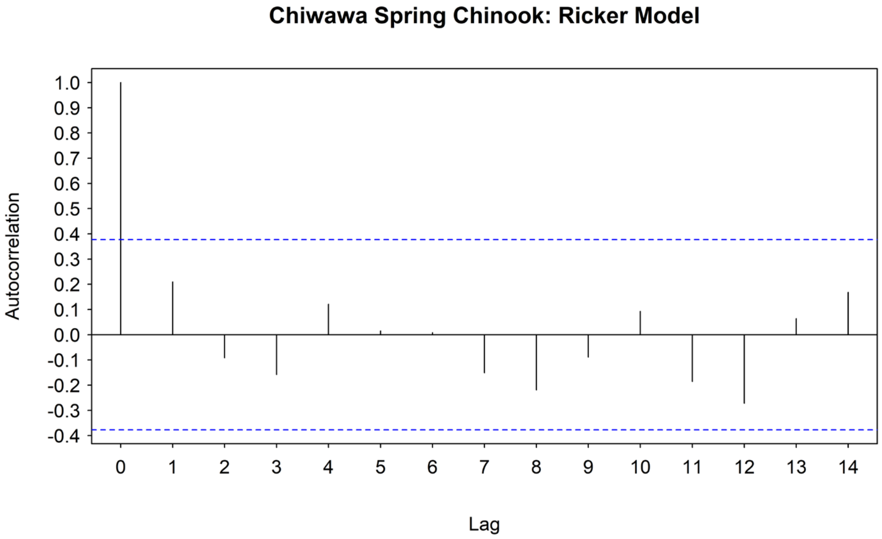

Figure A7. Autocorrelation plot of residuals for Ricker model of smolt recruitment as a function of spawner abundance (stock) for Chiwawa River Spring Chinook, 1991–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

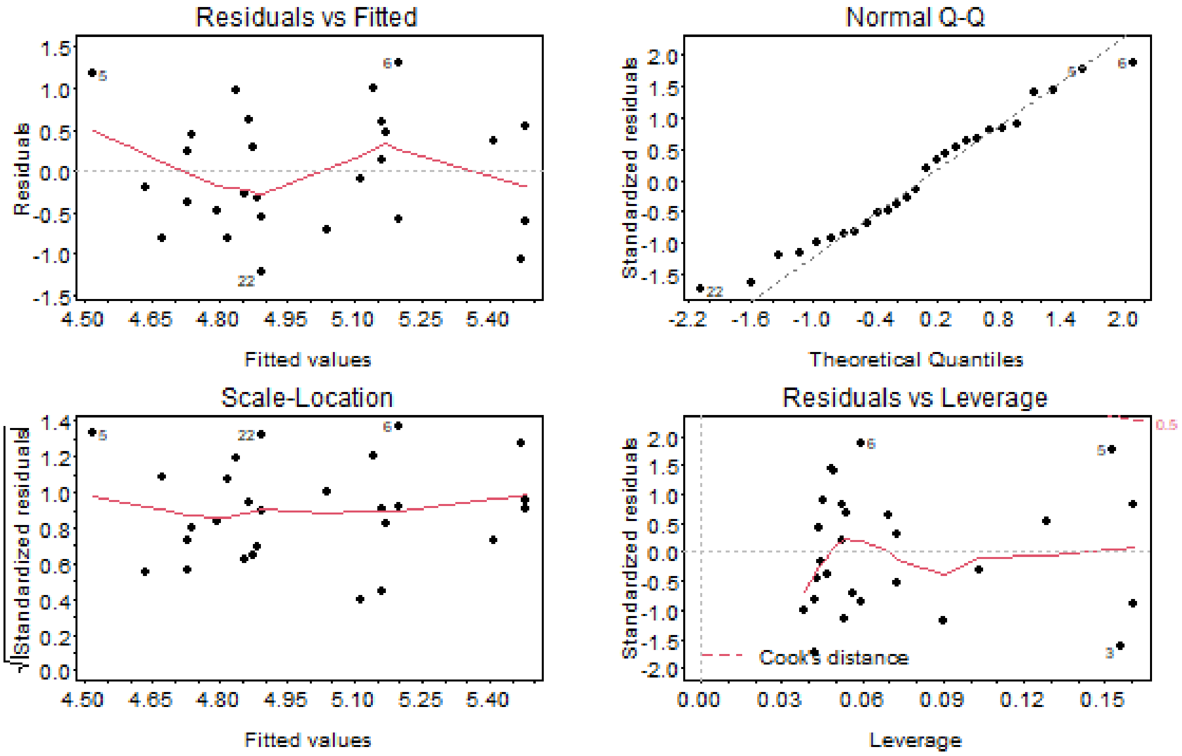

Figure A8. Residual plots for linear model of smolts per redd as a function of pHOS for Chiwawa River Spring Chinook, 1991–2017. Shapiro-Wilk test of normality of residuals: W=0.9672, P=0.5302.

Table A1. Pearson correlation coefficient (below diagonal) and two-sided P-value (above diagonal) for Beverton-Holt stock-recruitment model of smolts per redd for Chiwawa River Spring Chinook, 1991–2017. Model form is: $ln(R/S) = ln(\alpha) - \beta_2 P_{HOS} - ln(\beta + S)$. Correlation computed from bootstrap (3,000 bootstrap samples).

Parameter	α	β	β_2
α		<0.0001	<0.0001
β	0.7954		<0.0001
β_2	0.7776	0.3714	

Table A2. Pearson correlation coefficient (below diagonal) and two-sided P-value (above diagonal) for Ricker stock-recruitment model of smolts per redd for Chiwawa River Spring Chinook, 1991–2017. Model form is: $ln(R/S) = \beta_0 - \beta S - \beta_2 P_{HOS}$. Correlation computed from bootstrap (3,000 bootstrap samples).

Parameter	β_0	β	β_2
β_0		<0.0001	<0.0001
β	0.3198		<0.0001
β_2	0.7427	-0.3097	

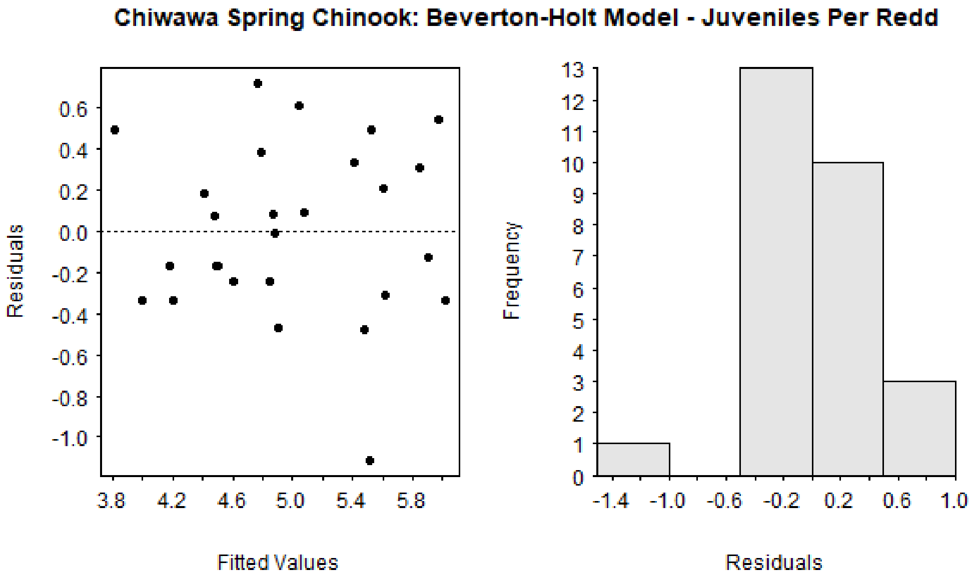

Figure A9. Residual plots for Beverton-Holt model of smolts per redd as a function of redd count and pHOS for Chiwawa River Spring Chinook, 1991–2017. Shapiro-Wilk test of normality of residuals: W=0.9608, P=0.3864.

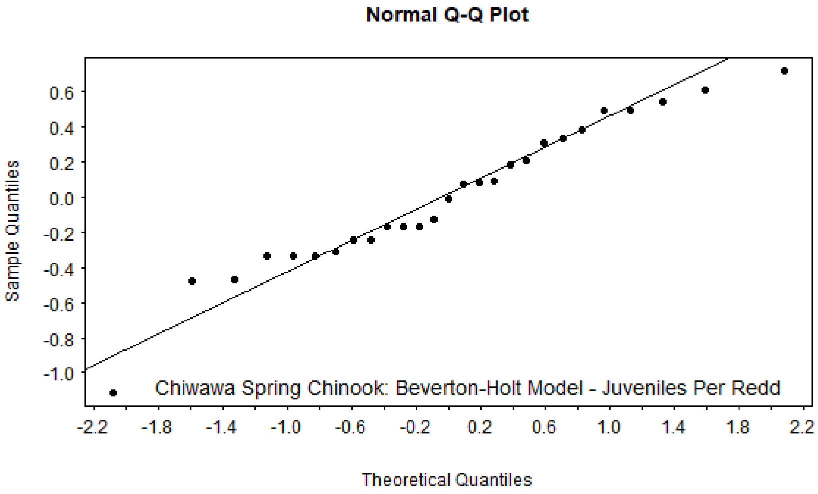

Figure A10. Normal quantile-quantile plot of residual from Beverton-Holt model of smolts per redd as a function of redd count and pHOS for Chiwawa River Spring Chinook, 1991–2017. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.9608, P=0.3864.

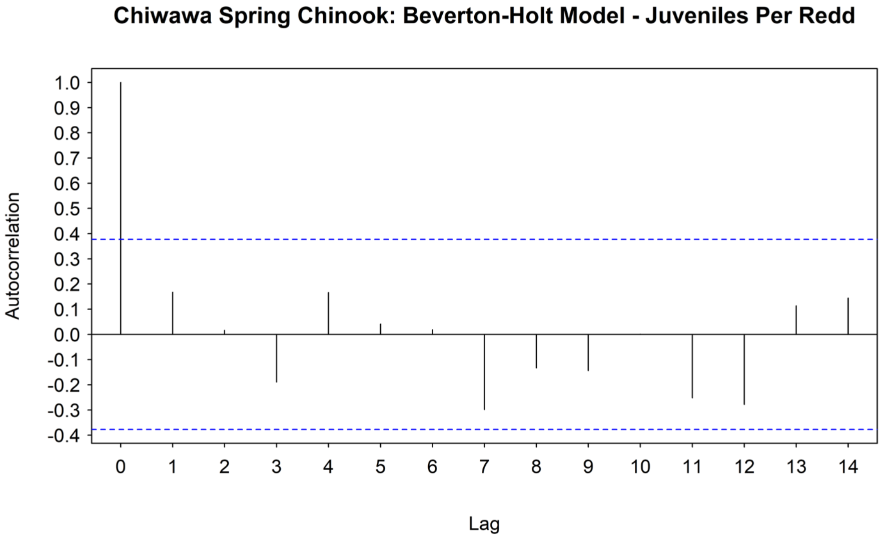

Figure A11. Autocorrelation plot of residuals for Beverton-Holt model of smolts per redd as a function of redd count and pHOS for Chiwawa River Spring Chinook, 1991–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

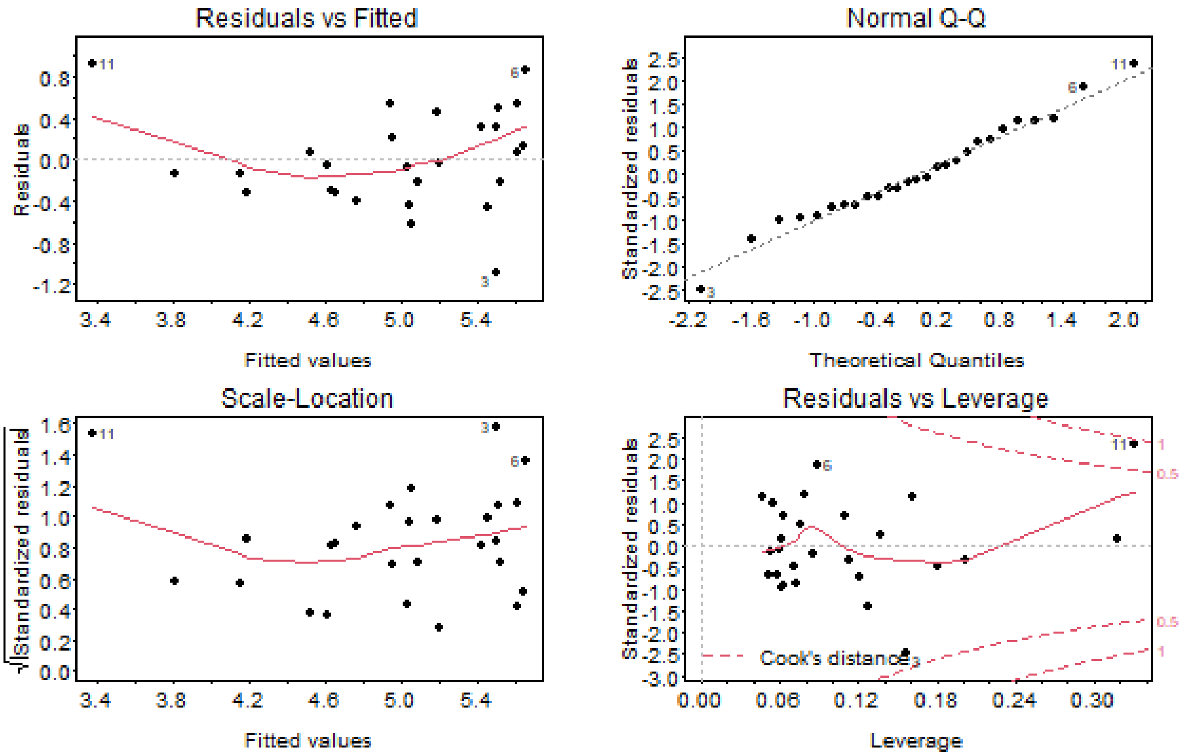

Figure A12. Residual plots for Ricker model of smolts per redd as a function of redd count and pHOS for Chiwawa River Spring Chinook, 1991–2017. Shapiro-Wilk test of normality of residuals: W=0.9801, P=0.8656.

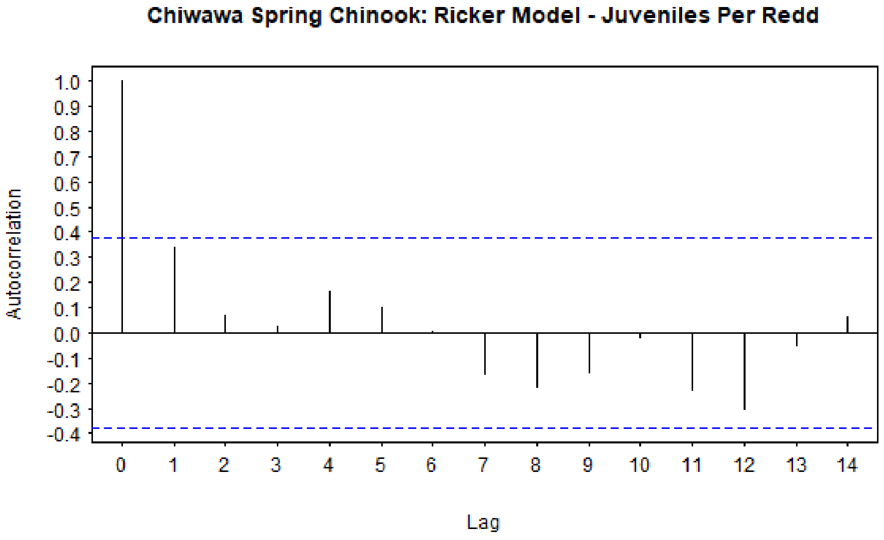

Figure A13. Autocorrelation plot of residuals for Ricker model of smolts per redd as a function of redd count and pHOS for Chiwawa River Spring Chinook, 1991–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

Appendix B: Nason Creek Spring Chinook Salmon

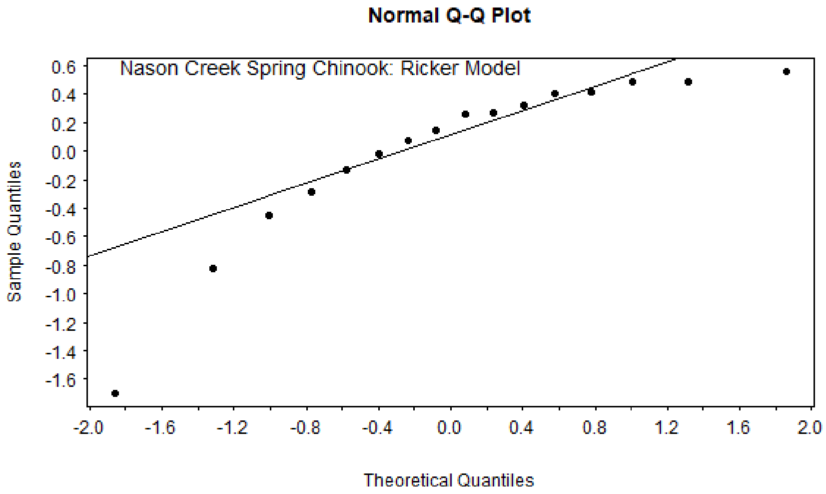

Figure B1. Normal quantile-quantile plot of residual from Ricker model of smolt recruitment as a function of spawner abundance (stock) for Nason Creek Spring Chinook, 2002–2017, including brood year 2014. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.8152, P=0.0044.

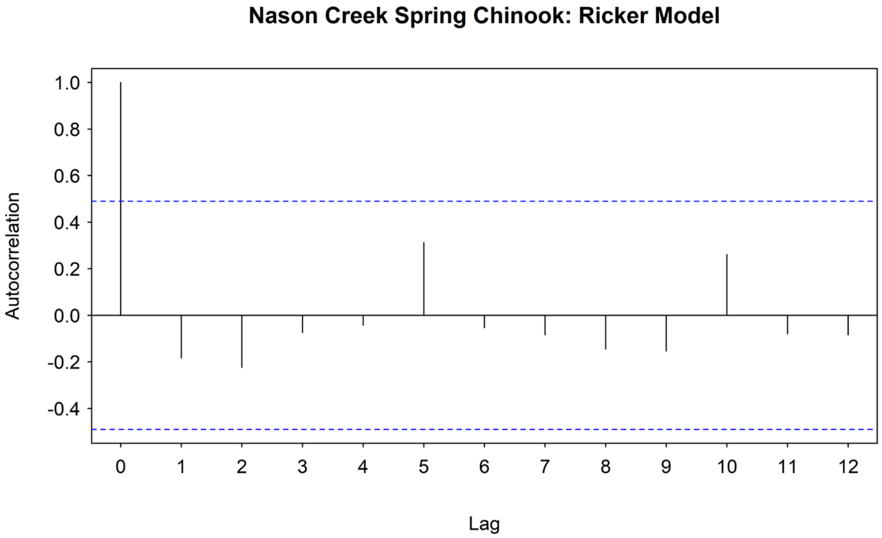

Figure B2. Autocorrelation plot of residuals for Ricker model of smolt recruitment as a function of spawner abundance (stock) for Nason Creek Spring Chinook, 2002–2017, including brood year 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

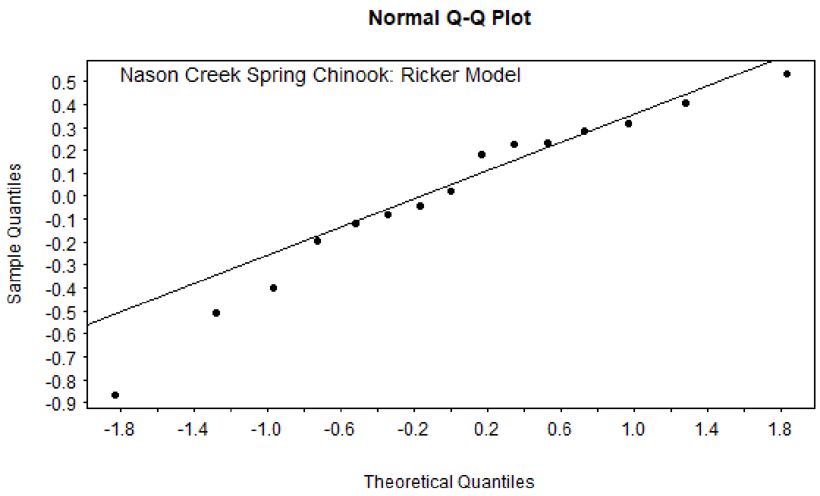

Figure B3. Normal quantile-quantile plot of residual from Ricker model of smolt recruitment as a function of spawner abundance (stock) for Nason Creek Spring Chinook, 2002–2017 without brood year 2014. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.9478, P=0.4906.

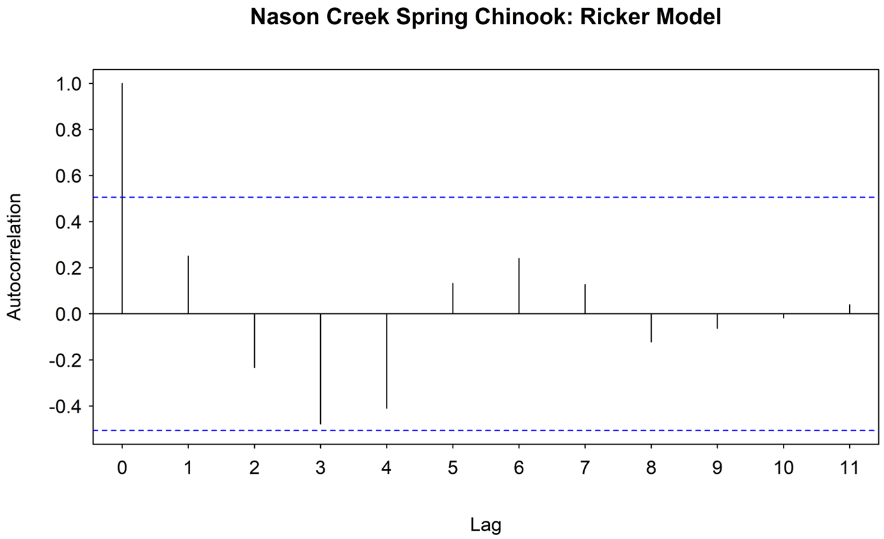

Figure B4. Autocorrelation plot of residuals for Ricker model of smolt recruitment as a function of spawner abundance (stock) for Nason Creek Spring Chinook, 2002–2017 without brood year 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

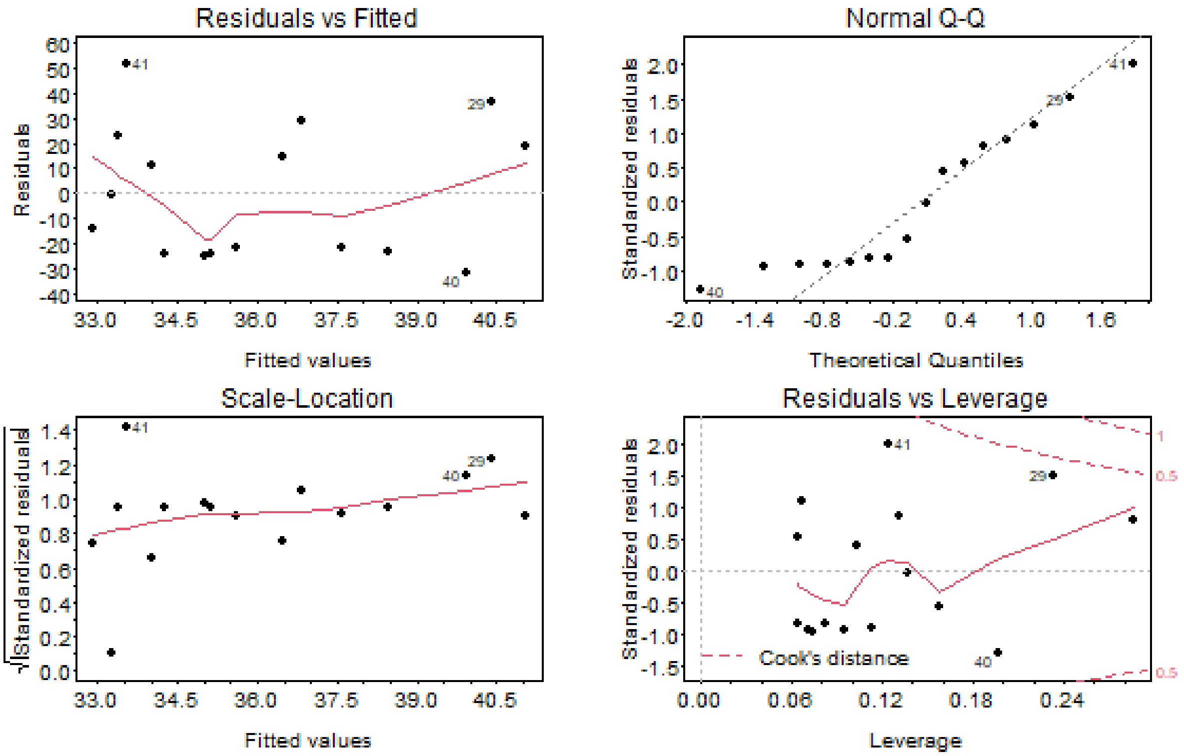

Figure B5. Residual plots for linear model of smolts per redd as a function of pHOS for Nason Creek Spring Chinook, 2002–2017 (including brood year 2014). Shapiro-Wilk test of normality of residuals: W=0.8923, P=0.0606.

Table B1. Pearson correlation coefficient (below diagonal) and two-sided P-value (above diagonal) for Ricker stock-recruitment model of smolts per redd for Nason Creek Spring Chinook, 2002–2017, with and without brood year 2014. Model form is: $ln(R/S) = \beta_0 - \beta S - \beta_2 P_{HOS}$. Correlation computed from bootstrap (3,000 bootstrap samples).

With BY 2014			
Parameter	β_0	β	β_2
β_0		<0.0001	<0.0001
β	0.3600		<0.0001
β_2	0.8629	-0.0925	
Without BY 2014			
Parameter	β_0	β	β_2
β_0		<0.0001	<0.0001
β	0.3509		<0.0001
β_2	0.7692	-0.2354	

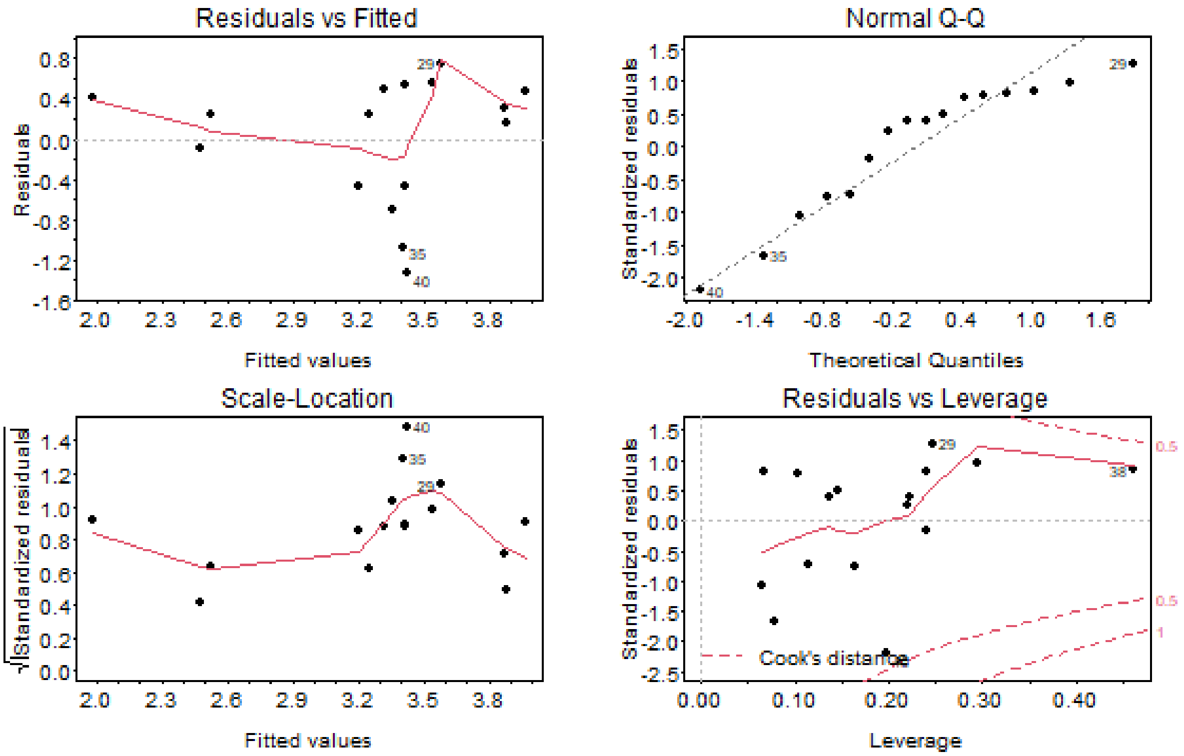

Figure B6. Residual plots for Ricker model of smolts per redd as a function of redd count and pHOS for Nason Creek Spring Chinook, 1991–2017, with brood year 2014. Shapiro-Wilk test of normality of residuals: W=0.8831, P=0.0434.

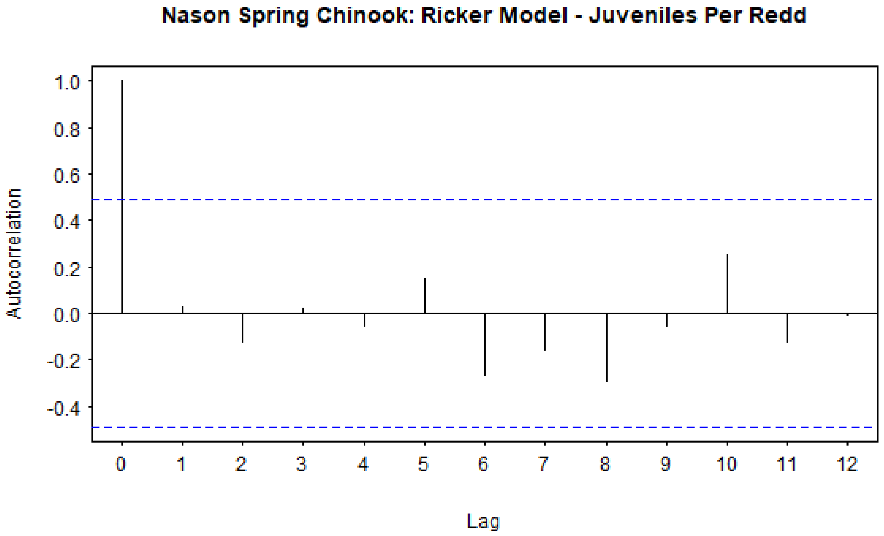

Figure B7. Autocorrelation plot of residuals for Ricker model of smolts per redd as a function of redd count and pHOS for Nason Creek Spring Chinook, 2002–2017, with brood year 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

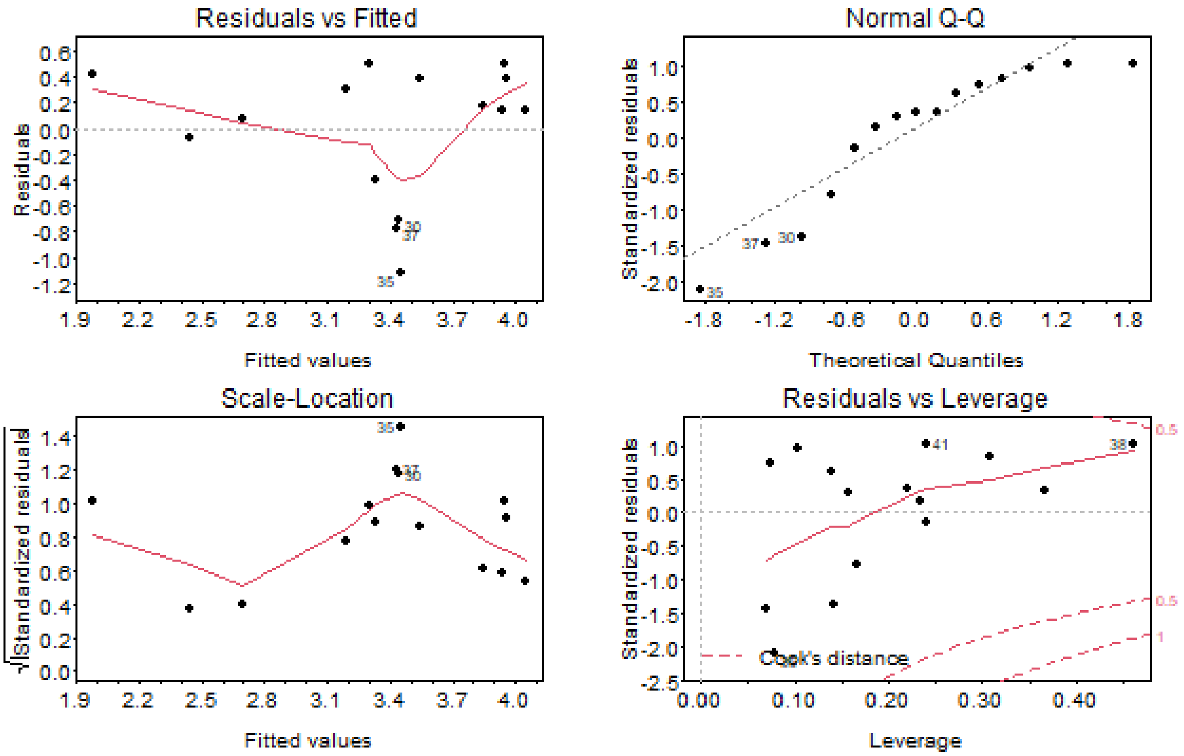

Figure B8. Residual plots for Ricker model of smolts per redd as a function of redd count and pHOS for Nason Creek Spring Chinook, 1991–2017, without brood year 2014. Shapiro-Wilk test of normality of residuals: W=0.8533, P=0.0193.

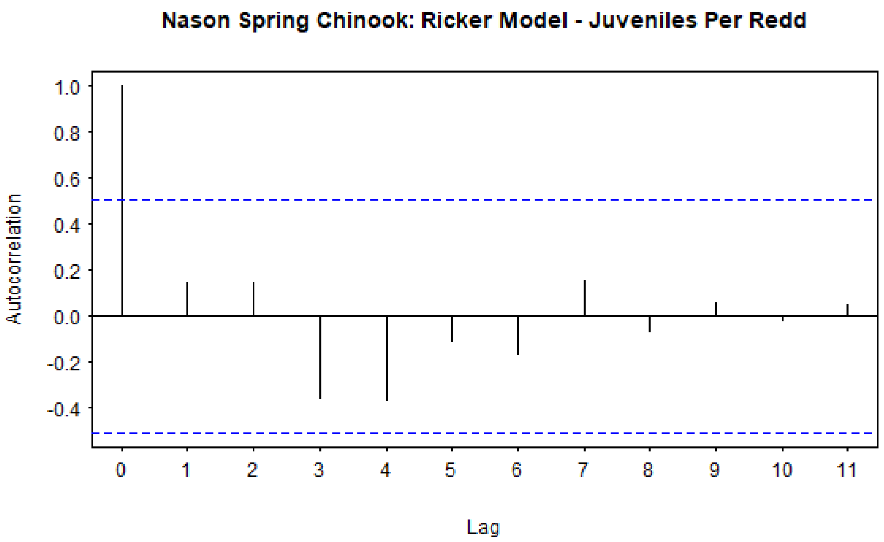

Figure B9. Autocorrelation plot of residuals for Ricker model of smolts per redd as a function of redd count and pHOS for Nason Creek Spring Chinook, 2002–2017, without brood year 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

Appendix C: White River Spring Chinook Salmon

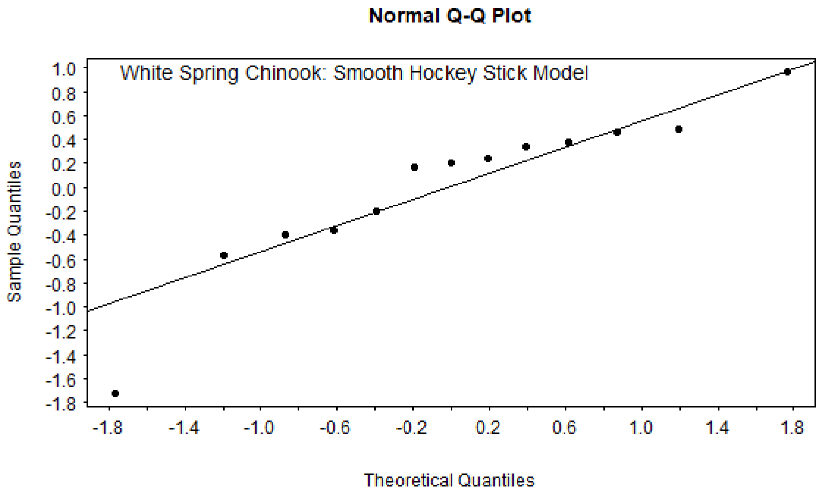

Figure C1. Normal quantile-quantile plot of residual from the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017, including brood year 2014. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.8887, P=0.0936.

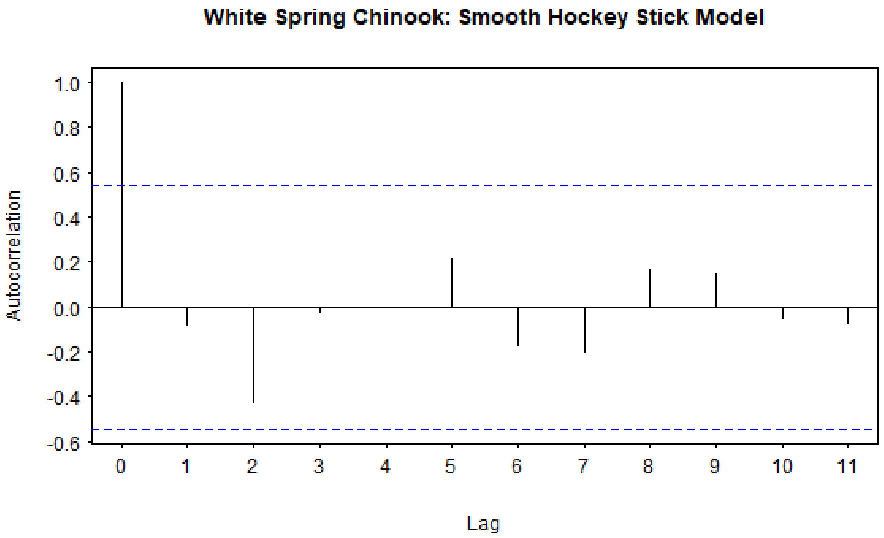

Figure C2. Autocorrelation plot of residuals for the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017, including brood year 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

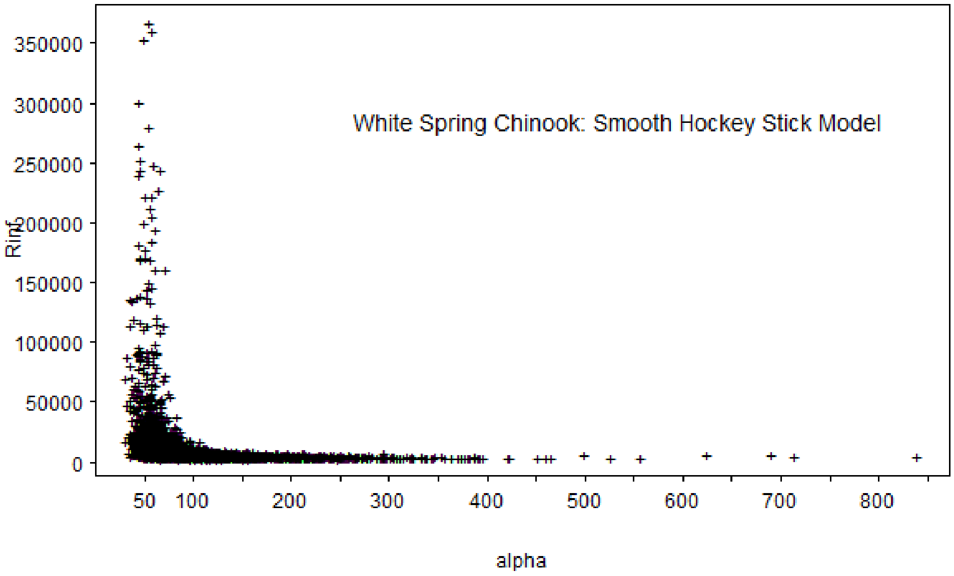

Figure C3. Correlation plot of bootstrap parameter estimates from the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017, including brood year 2014, based on 3,291 bootstrap samples.

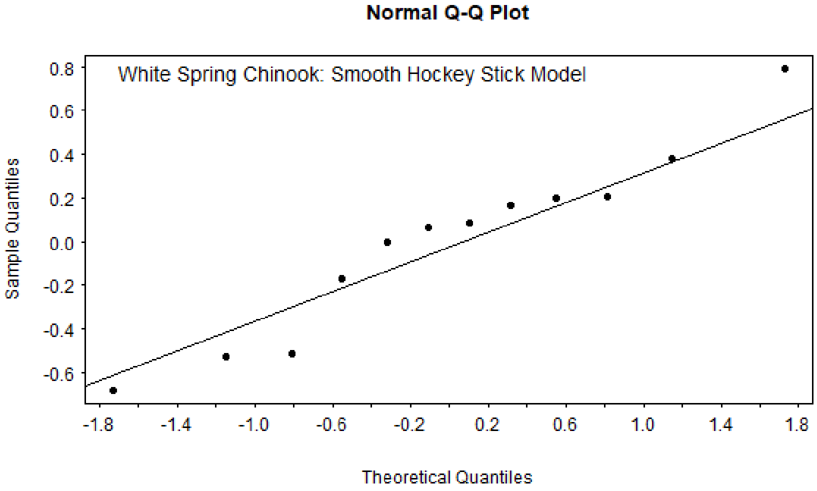

Figure C4. Normal quantile-quantile plot of residual from the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017 without brood year 2014. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.9484, P=0.6144.

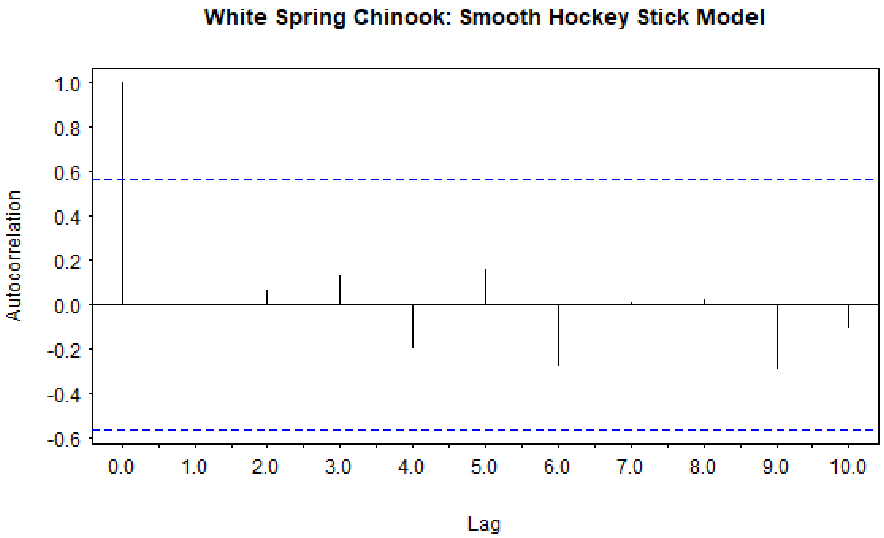

Figure C5. Autocorrelation plot of residuals for the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017 without brood year 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

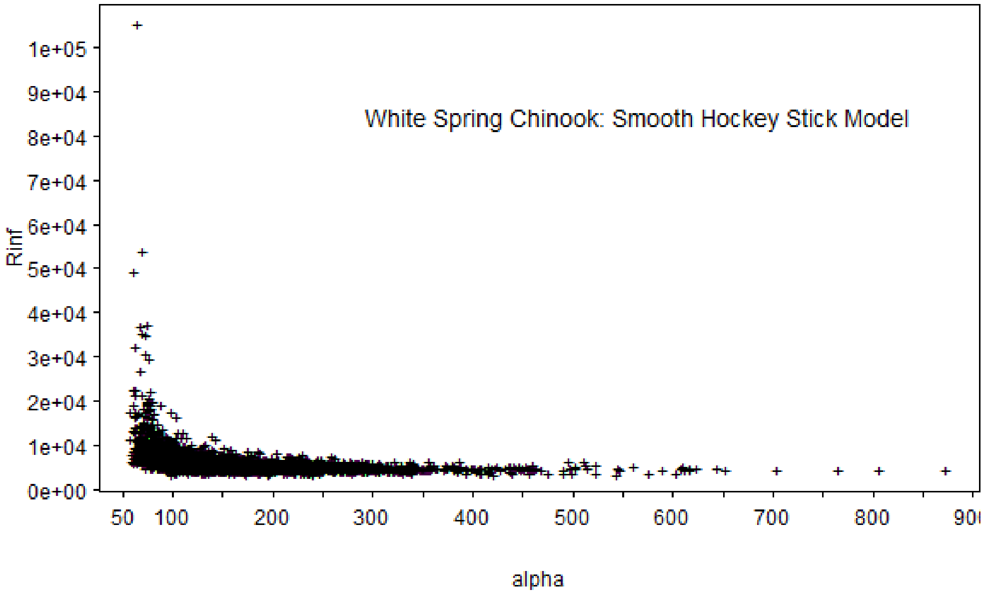

Figure C6. Correlation plot of bootstrap parameter estimates from the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017, without brood year 2014, based on 3,618 bootstrap samples.

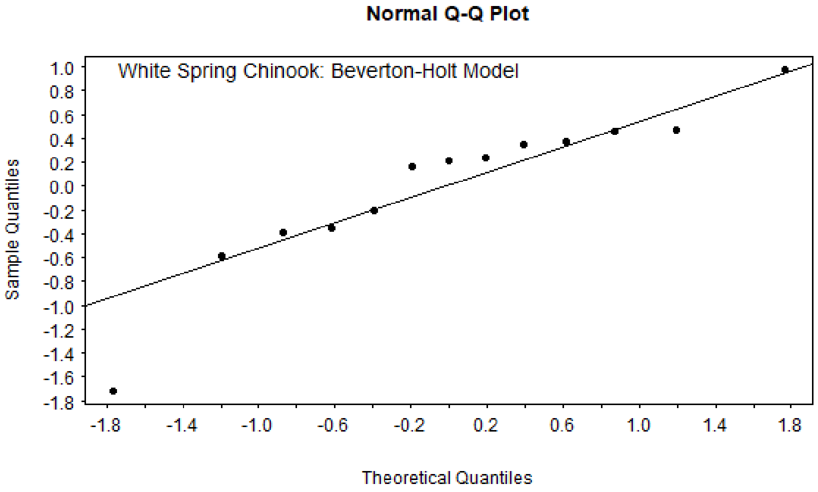

Figure C7. Normal quantile-quantile plot of residual from Beverton-Holt model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017, including brood year 2014. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.8893, P=0.0954.

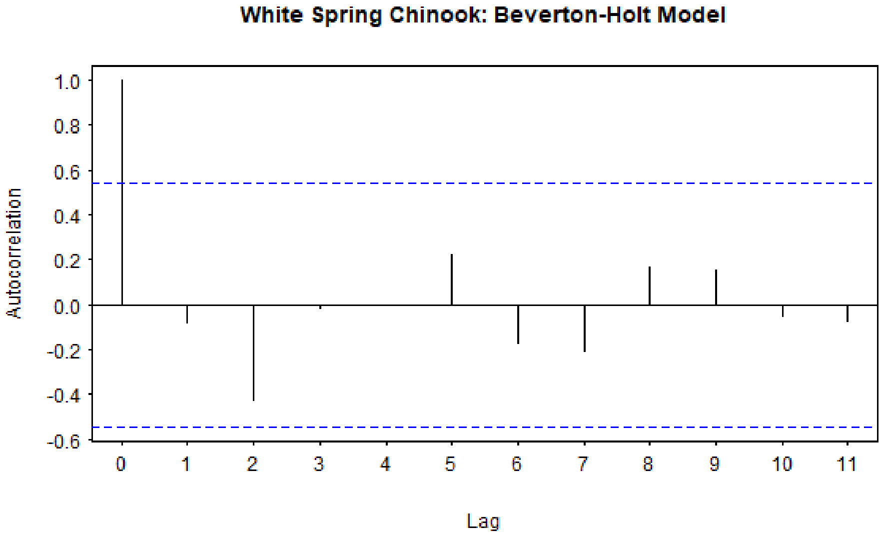

Figure C8. Autocorrelation plot of residuals for Beverton-Holt model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017, including brood year 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

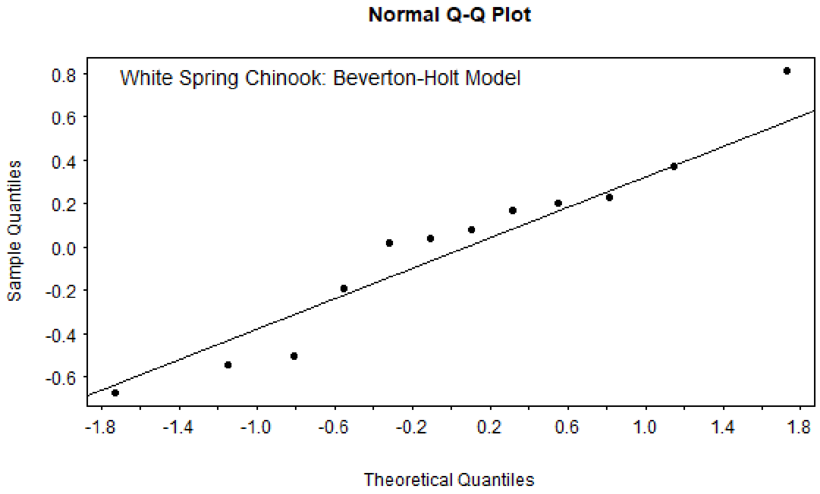

Figure C9. Normal quantile-quantile plot of residual from Beverton-Holt model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017 without brood year 2014. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.9501, P=0.6384.

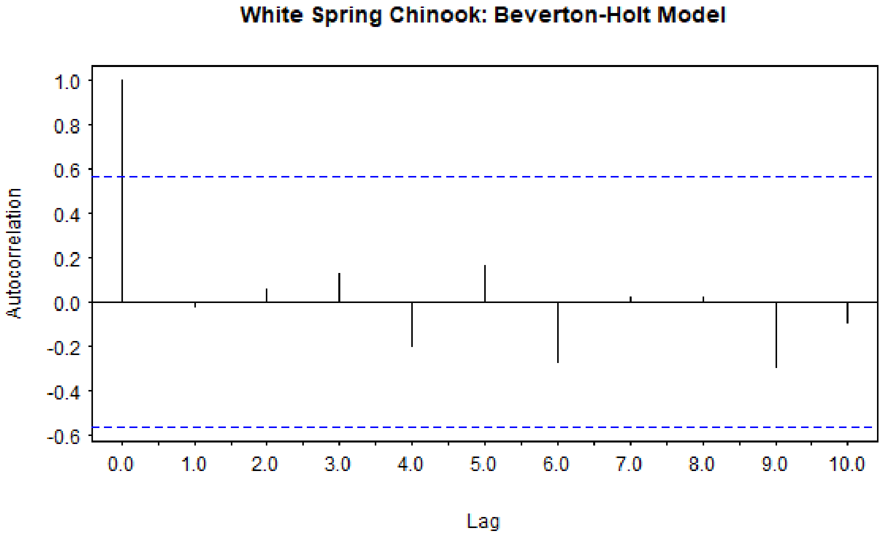

Figure C10. Autocorrelation plot of residuals for Beverton-Holt model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017 without brood year 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

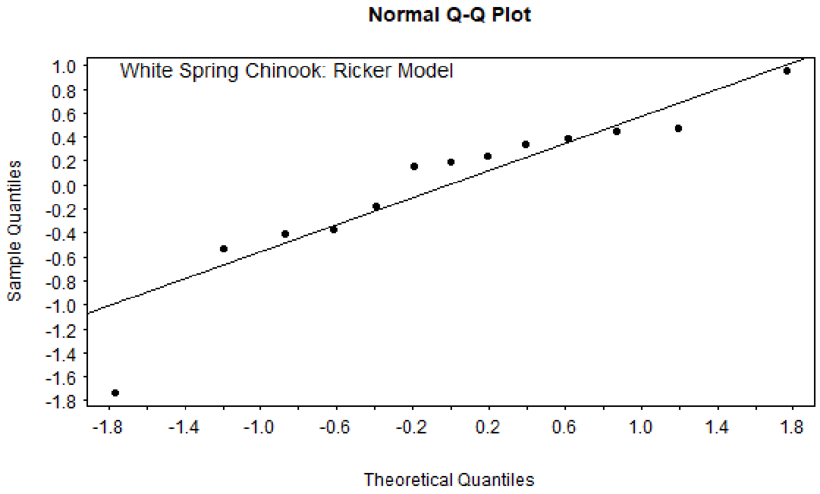

Figure C11. Normal quantile-quantile plot of residual from Ricker model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017, including brood year 2014. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.8826, P=0.0774.

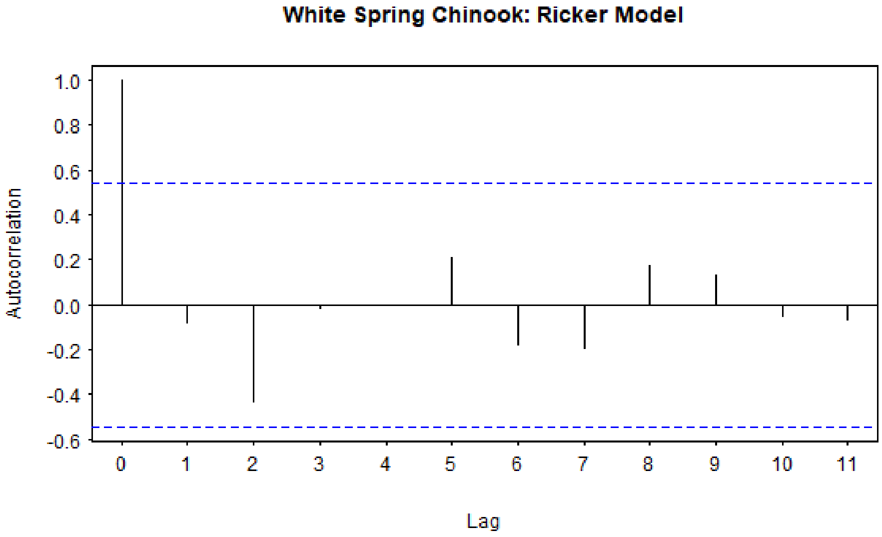

Figure C12. Autocorrelation plot of residuals for Ricker model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017, including brood year 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

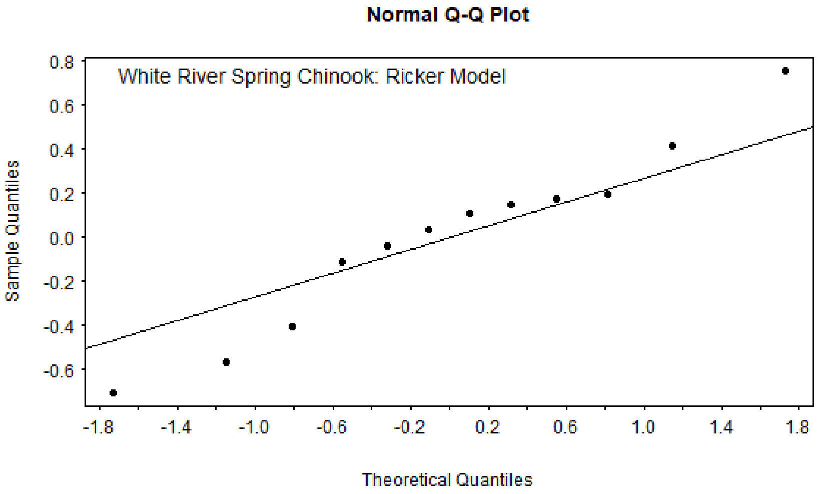

Figure C13. Normal quantile-quantile plot of residual from Ricker model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017 without brood year 2014. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.9632, P=0.8287.

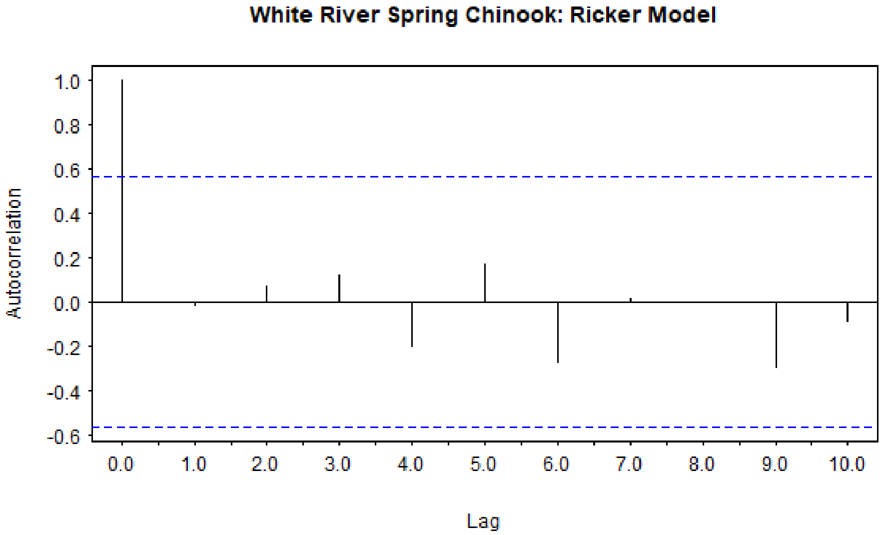

Figure C14. Autocorrelation plot of residuals for Ricker model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017 without brood year 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

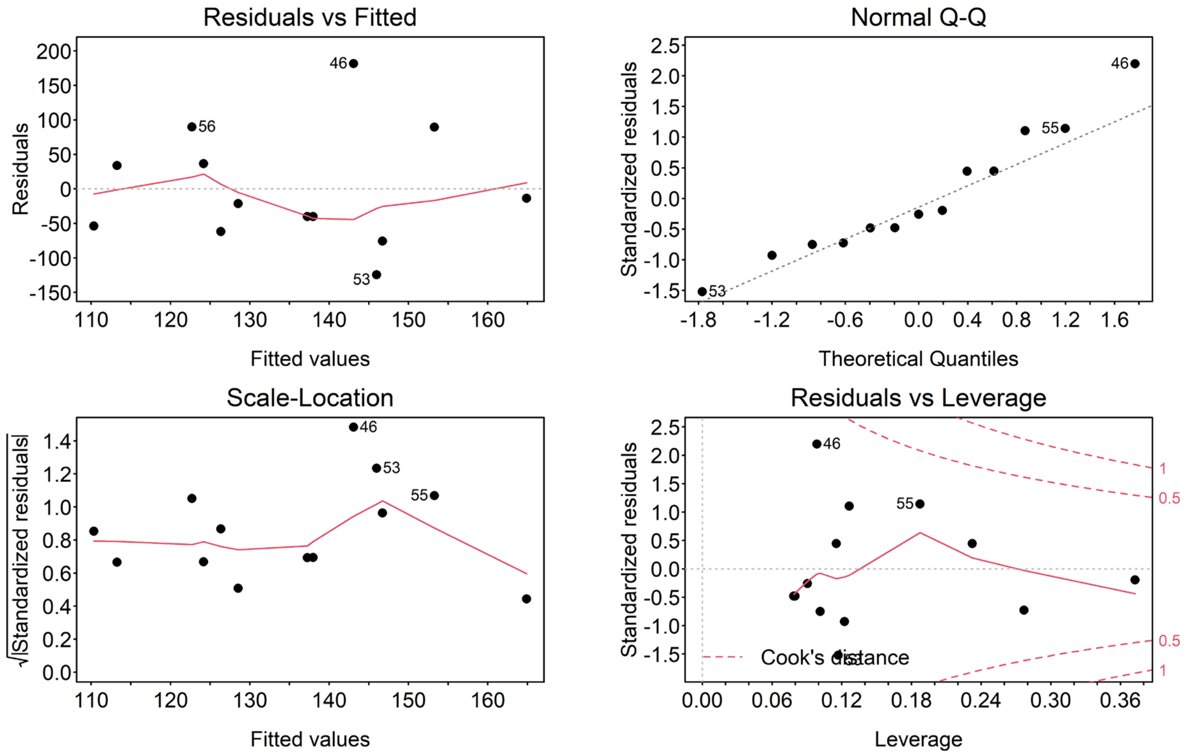

Figure C15. Residual plots for linear model of smolts per redd as a function of pHOS for White River Spring Chinook, 2005–2017 (including brood year 2014). Shapiro-Wilk test of normality of residuals: W=0.9443, P=0.5150.

Table C1. Pearson correlation coefficient (below diagonal) and two-sided P-value (above diagonal) for Beverton-Holt stock-recruitment model of smolts per redd for White River Spring Chinook, 2005–2017, with and without brood year 2014. Model form is: $ln(R/S) = ln(\alpha) - \beta_2 P_{HOS} - ln(\beta + S)$. Correlation computed from bootstrap (≥3,000 bootstrap samples).

With BY 2014			
Parameter	α	β	β_2
α		<0.0001	<0.0001
β	0.9107		0.3015
β_2	0.1240	0.0175	
Without BY 2014			
Parameter	α	β	β_2
α		<0.0001	<0.0001
β	0.9669		<0.0001
β_2	0.2922	0.1259	

Table C2. Pearson correlation coefficient (below diagonal) and two-sided P-value (above diagonal) for Ricker stock-recruitment model of smolts per redd for White River Spring Chinook, 2005–2017, with and without brood year 2014. Model form is: $ln(R/S) = \beta_0 - \beta S - \beta_2 P_{HOS}$. Correlation computed from bootstrap (≥3,000 bootstrap samples).

With BY 2014			
Parameter	β_0	β	β_2
β_0		<0.0001	<0.0001
β	0.6155		0.0003
β_2	0.7044	-0.0652	
Without BY 2014			
Parameter	β_0	β	β_2
β_0		<0.0001	<0.0001
β	0.5568		<0.0001
β_2	0.7439	-0.0755	

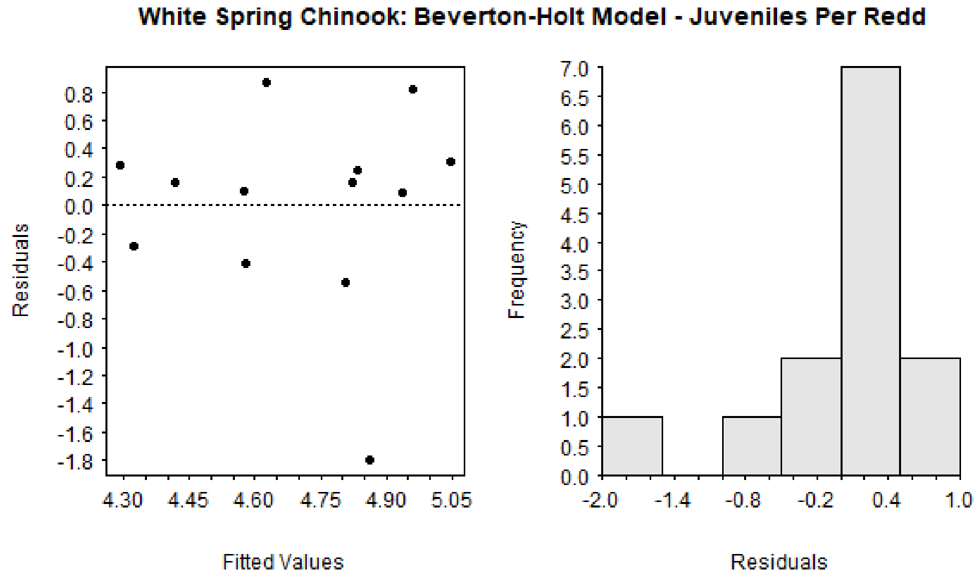

Figure C16. Residual plots for Beverton-Holt model of smolts per redd as a function of redd count and pHOS for White River Spring Chinook, 2005–2017, with 2014. Shapiro-Wilk test of normality of residuals: W=0.8585, P=0.3681.

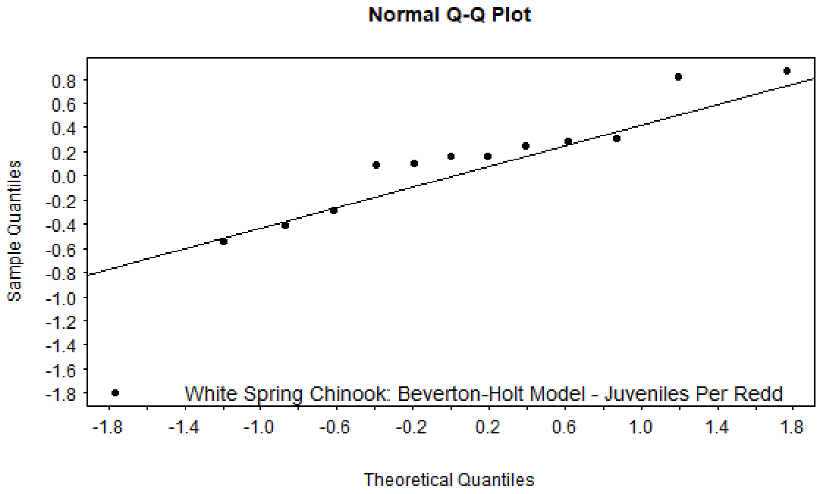

Figure C17. Normal quantile-quantile plot of residual from Beverton-Holt model of smolts per redd as a function of redd count and pHOS for White River Spring Chinook, 2005–2017, with 2014. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.8585, P=0.3681.

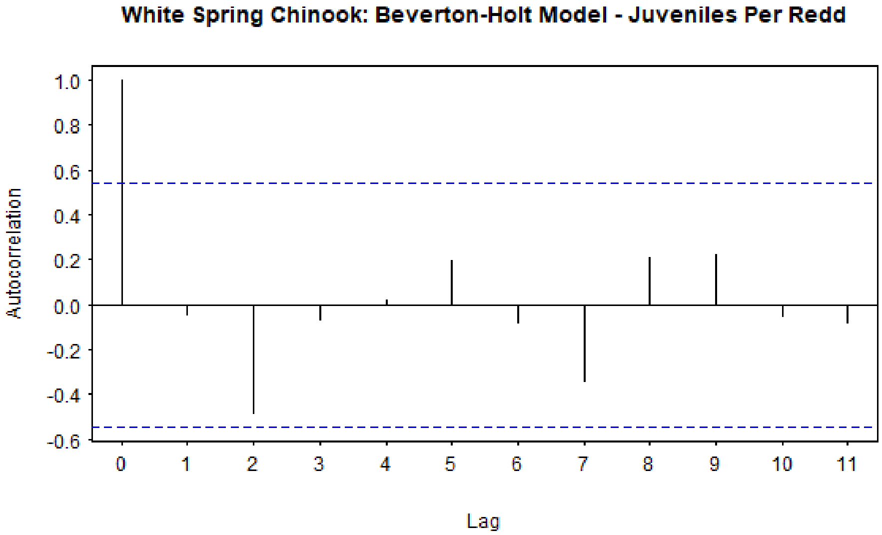

Figure C18. Autocorrelation plot of residuals for Beverton-Holt model of smolts per redd as a function of redd count and pHOS for White River Spring Chinook, 2005–2017, with 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

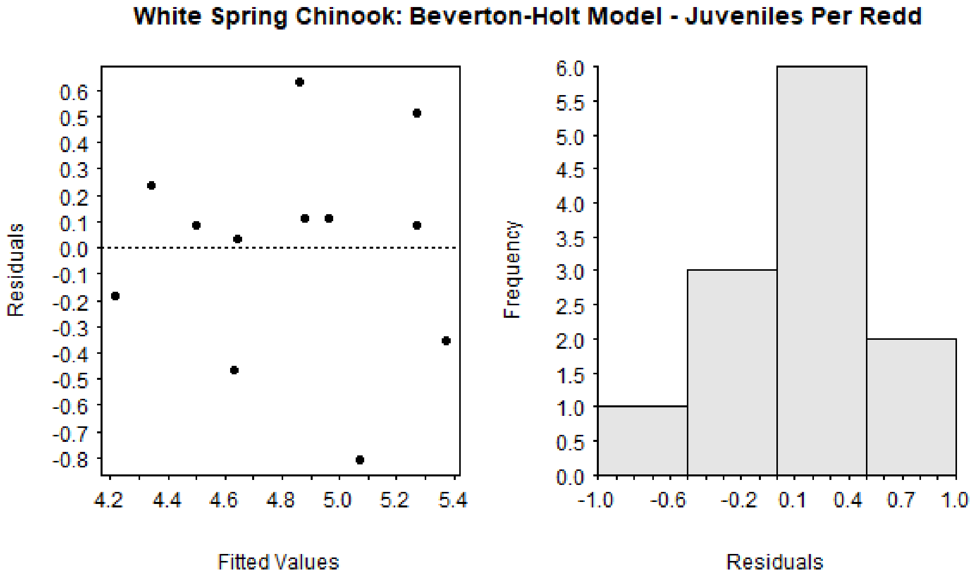

Figure C19. Residual plots for Beverton-Holt model of smolts per redd as a function of redd count and pHOS for White River Spring Chinook, 2005–2017, without 2014. Shapiro-Wilk test of normality of residuals: W=0.9549, P=0.7099.

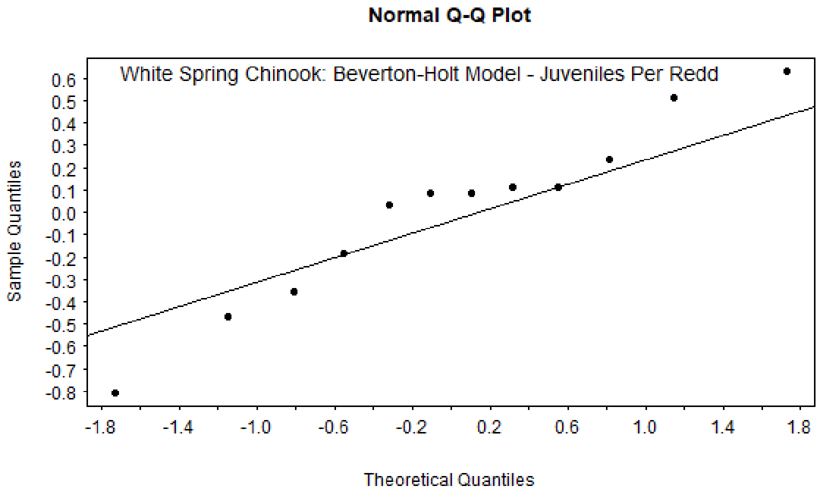

Figure C20. Normal quantile-quantile plot of residual from Beverton-Holt model of smolts per redd as a function of redd count and pHOS for White River Spring Chinook, 2005–2017, without 2014. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.9549, P=0.7099.

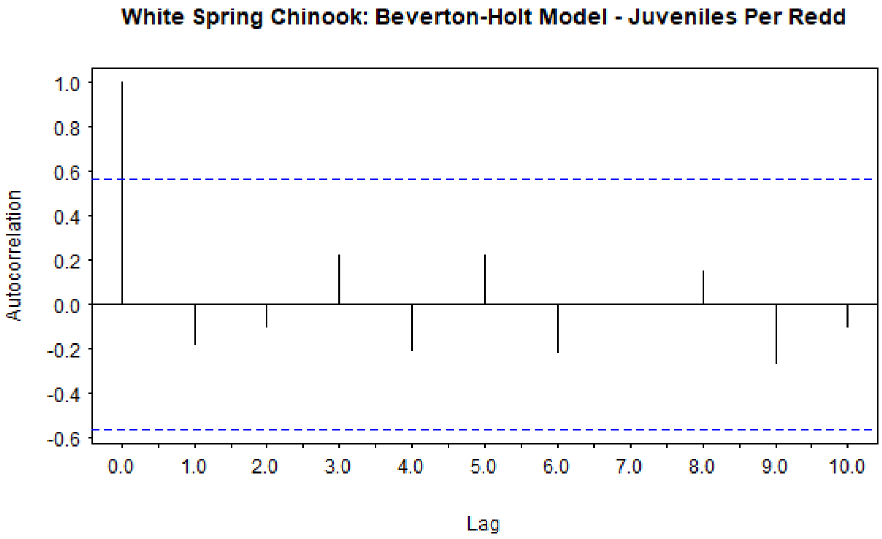

Figure C21. Autocorrelation plot of residuals for Beverton-Holt model of smolts per redd as a function of redd count and pHOS for White River Spring Chinook, 2005–2017, without 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

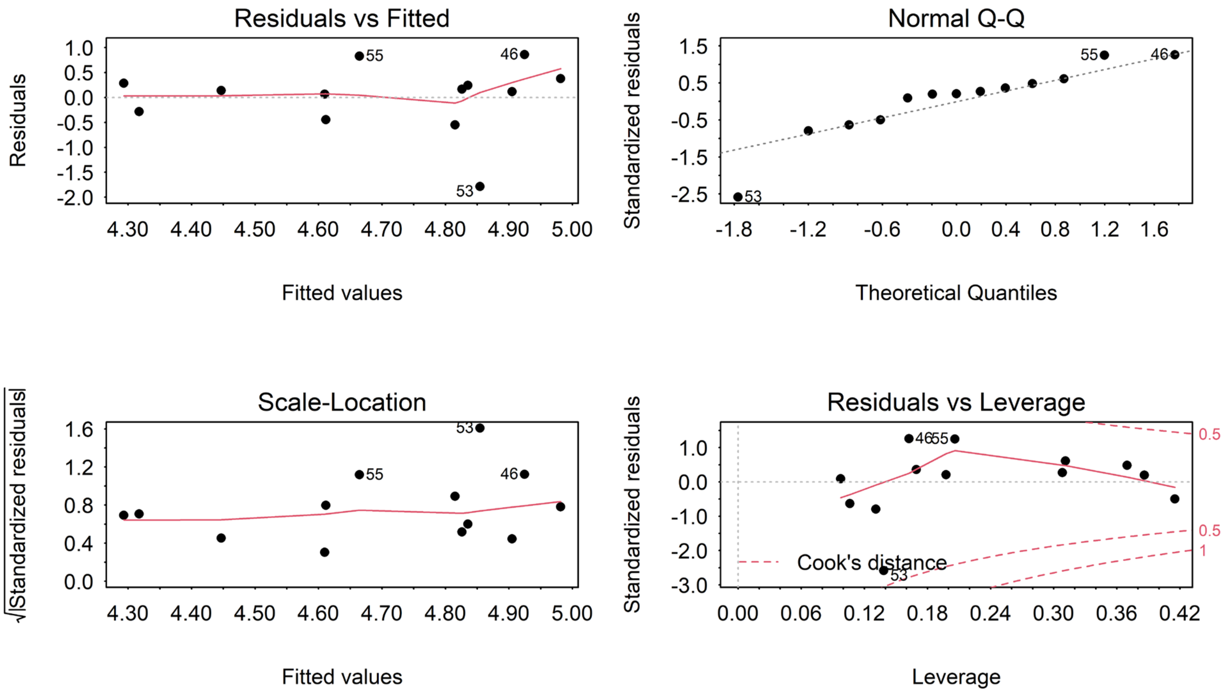

Figure C22. Residual plots for Ricker model of smolts per redd as a function of redd count and pHOS for White River Spring Chinook, 2005–2017, including brood year 2014. Shapiro-Wilk test of normality of residuals: W=0.8682, P=0.0495.

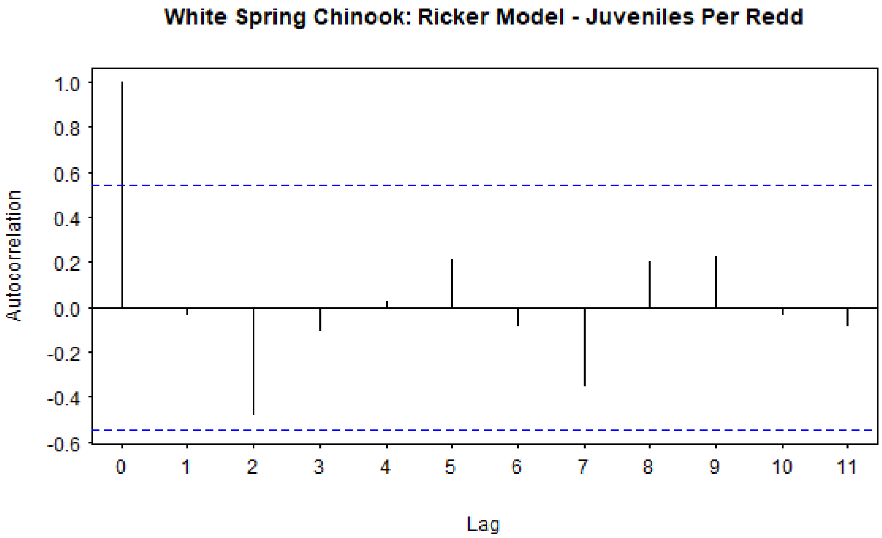

Figure C23. Autocorrelation plot of residuals for Ricker model of smolts per redd as a function of redd count and pHOS for White River Spring Chinook, 2005–2017, including brood year 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

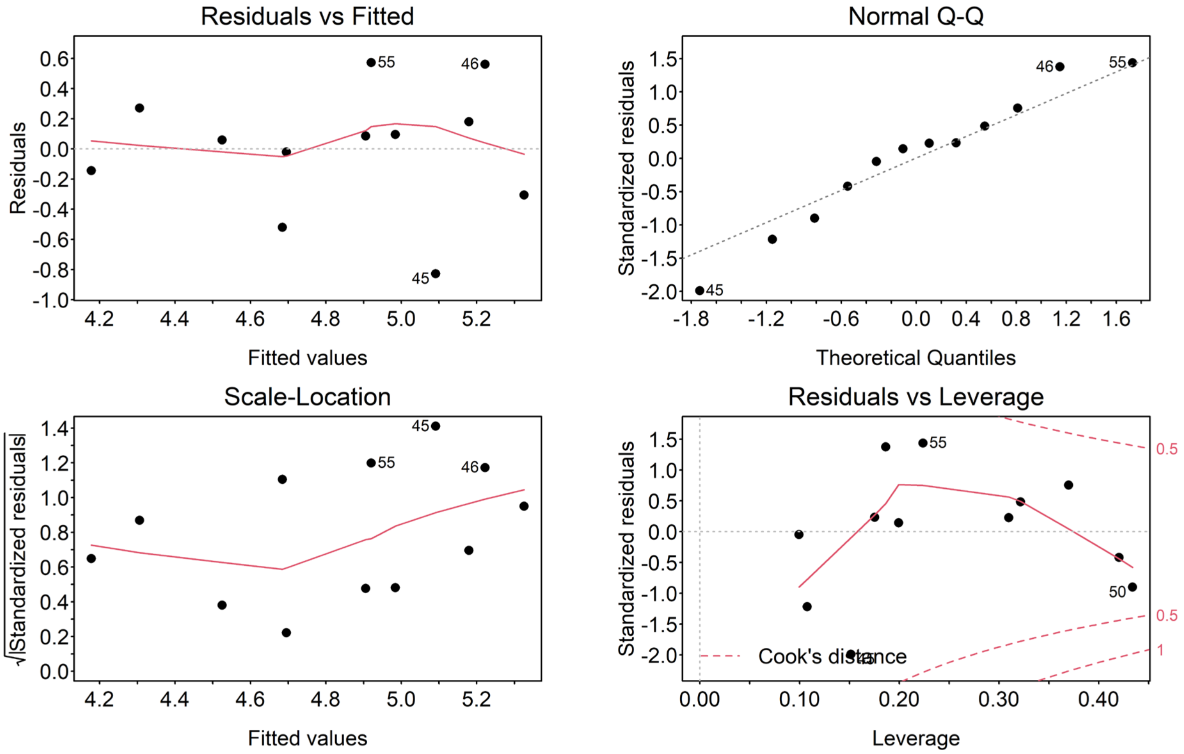

Figure C24. Residual plots for Ricker model of smolts per redd as a function of redd count and pHOS for White River Spring Chinook, 2005–2017, omitting brood year 2014. Shapiro-Wilk test of normality of residuals: W=0.9540, P=0.6956.

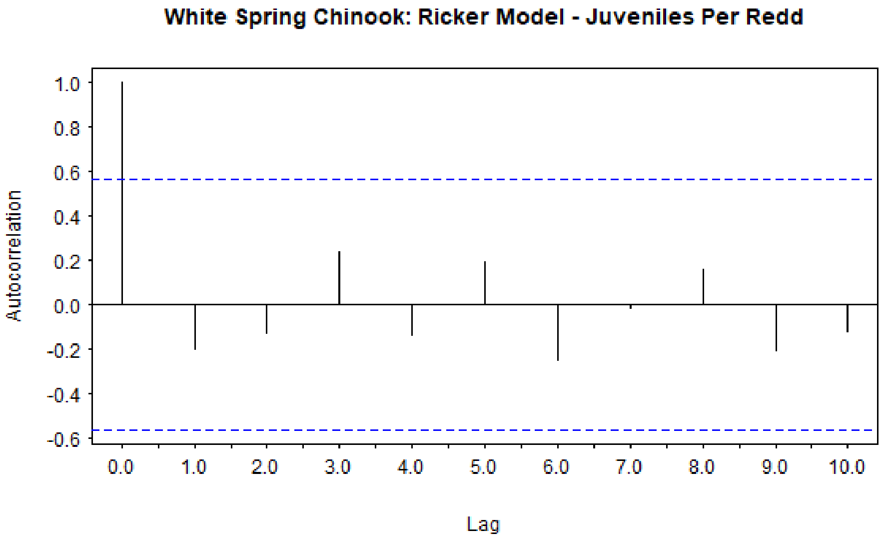

Figure C25. Autocorrelation plot of residuals for Ricker model of smolts per redd as a function of redd count and pHOS for White River Spring Chinook, 2005–2017, omitting brood year 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

Appendix D: Twisp River Spring Chinook Salmon

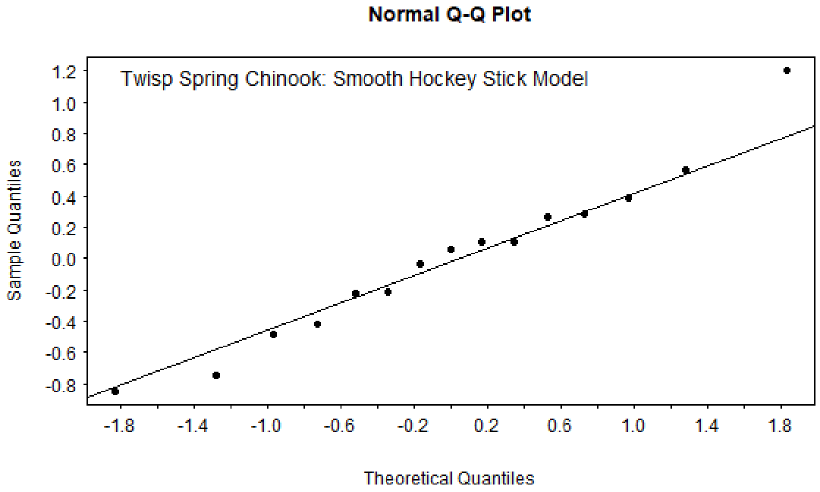

Figure D1. Normal quantile-quantile plot of residual from the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for Twisp River Spring Chinook, 2003–2017. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.9707, P=0.8678.

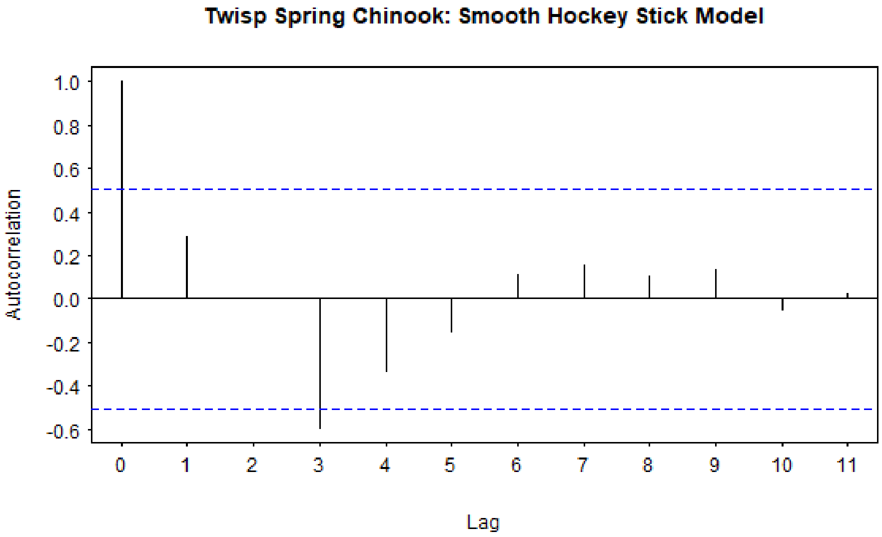

Figure D2. Autocorrelation plot of residuals for the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for Twisp River Spring Chinook, 2003–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

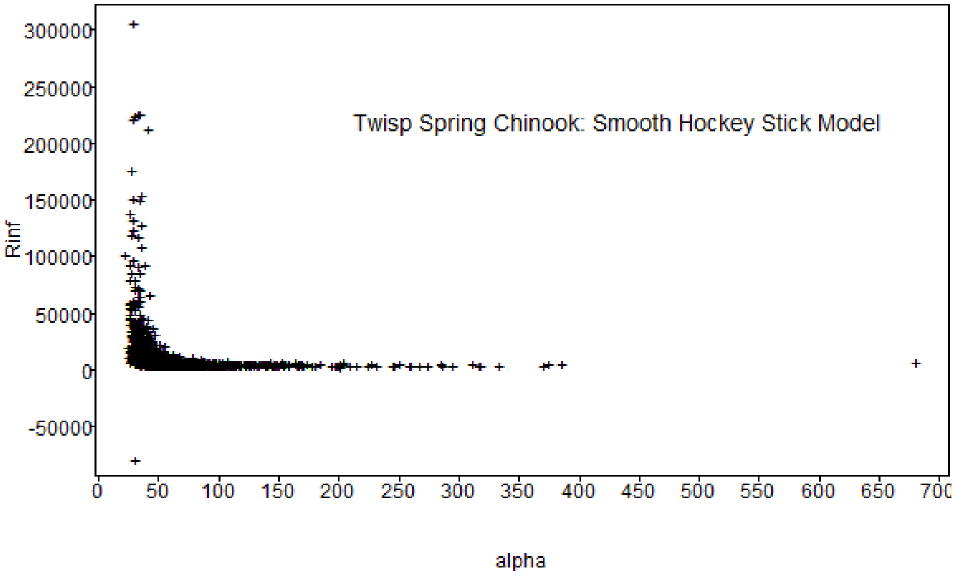

Figure D3. Correlation plot of bootstrap parameter estimates from the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for Twisp River Spring Chinook, 2003–2017, based on 2,813 bootstrap samples.

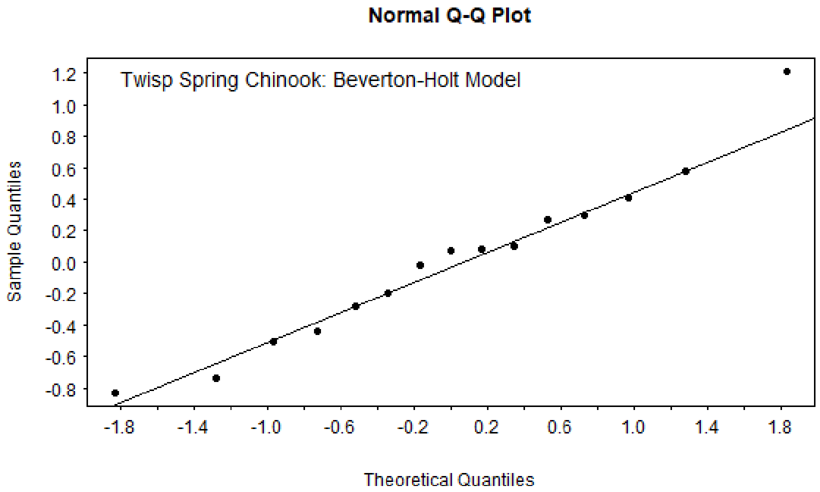

Figure D4. Normal quantile-quantile plot of residual from Beverton-Holt model of smolt recruitment as a function of spawner abundance (stock) for Twisp River Spring Chinook, 2003–2017. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.9700, P=0.8579.

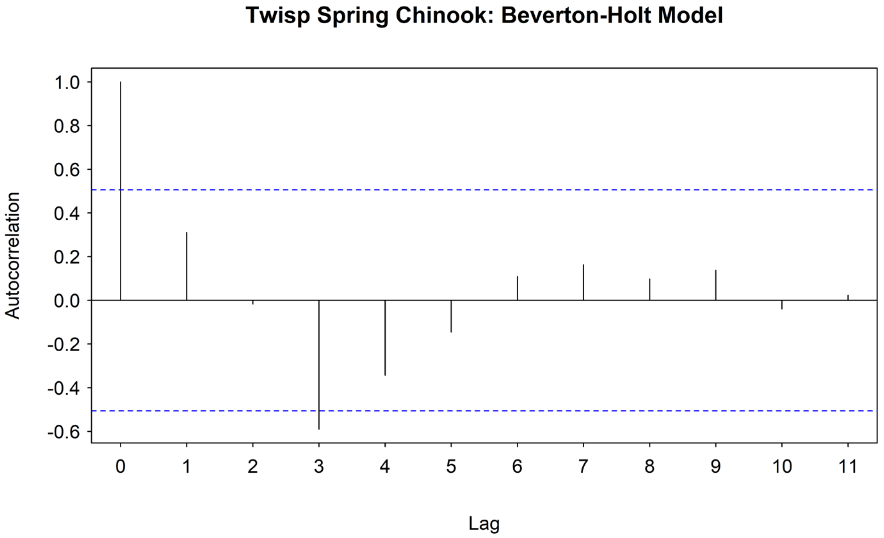

Figure D5. Autocorrelation plot of residuals for Beverton-Holt model of smolt recruitment as a function of spawner abundance (stock) for Twisp River Spring Chinook, 2003–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

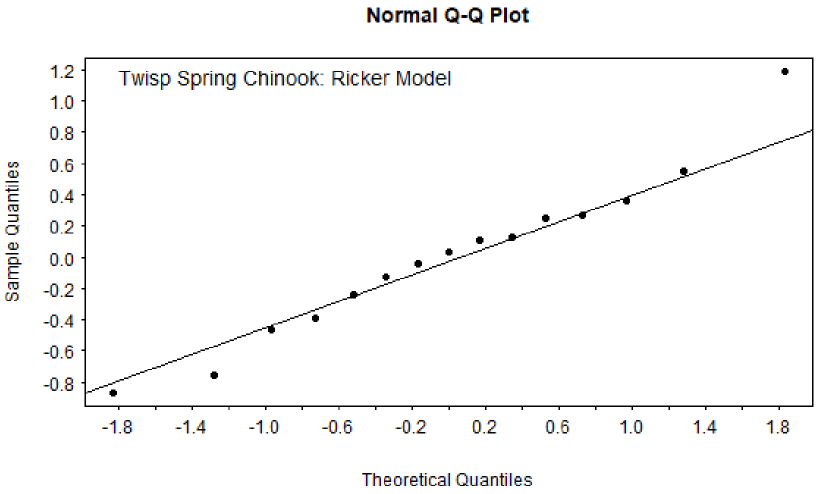

Figure D6. Normal quantile-quantile plot of residual from Ricker model of smolt recruitment as a function of spawner abundance (stock) for Twisp River Spring Chinook, 2003–2017. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.9815, P=0.8831.

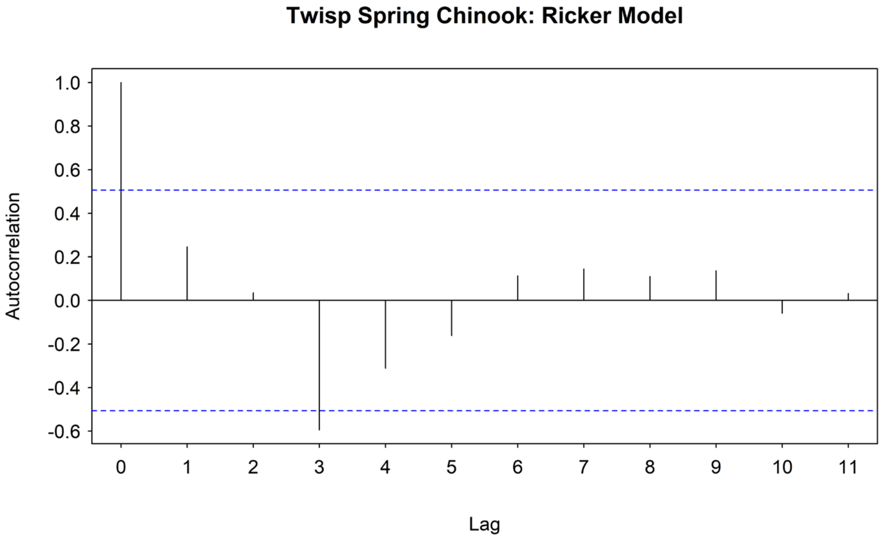

Figure D7. Autocorrelation plot of residuals for Ricker model of smolt recruitment as a function of spawner abundance (stock) for Twisp River Spring Chinook, 2003–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

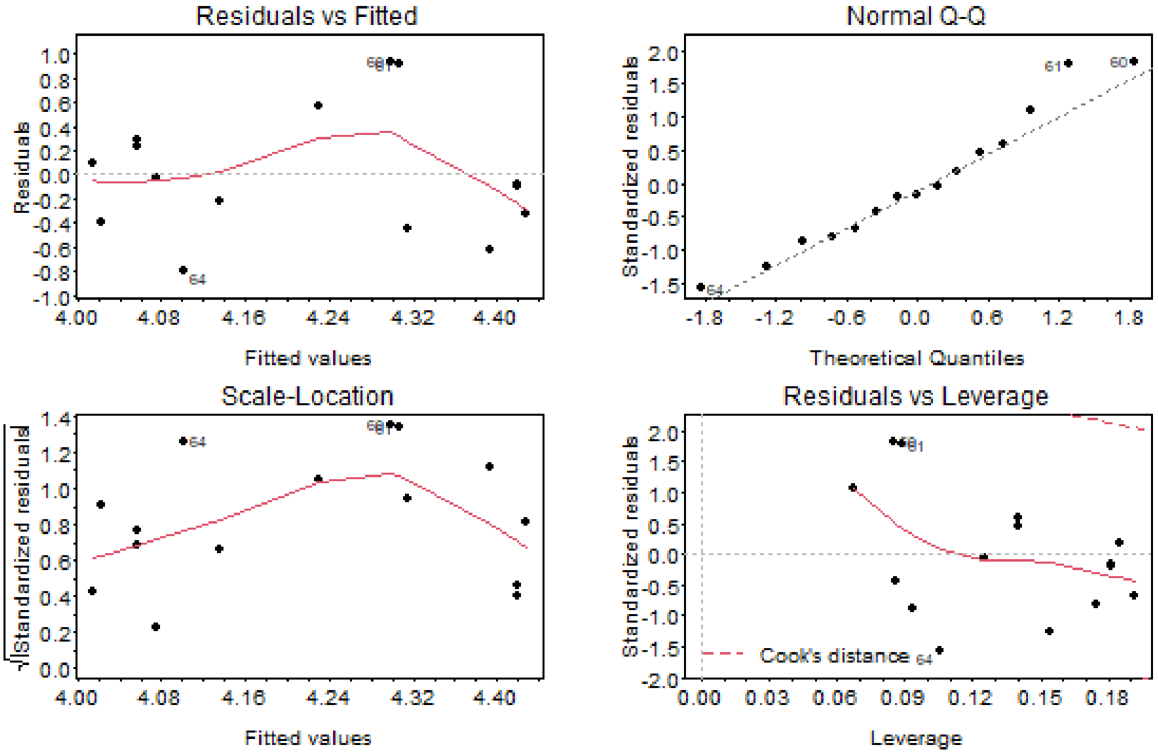

Figure D8. Residual plots for linear model of smolts per redd (log scale) as a function of pHOS for Twisp River Spring Chinook, 2003–2017. Shapiro-Wilk test of normality of residuals: W=0.9575, P=0.6489.

Table D1. Pearson correlation coefficient (below diagonal) and two-sided P-value (above diagonal) for Beverton-Holt stock-recruitment model of smolts per redd for Twisp River Spring Chinook, 2003–2017. Model form is: $ln(R/S) = ln(\alpha) - \beta_2 P_{HOS} - ln(\beta + S)$. Correlation computed from bootstrap (2,798 bootstrap samples).

Parameter	α	β	β_2
α		<0.0001	<0.0001
β	0.9153		0.3039
β_2	0.1298	-0.0194	

Table D2. Pearson correlation coefficient (below diagonal) and two-sided P-value (above diagonal) for Ricker stock-recruitment model of smolts per redd for Twisp River Spring Chinook, 2003–2017. Model form is: $ln(R/S) = \beta_0 - \beta S - \beta_2 P_{HOS}$. Correlation computed from bootstrap (3,000 bootstrap samples).

Parameter	β_0	β	β_2
β_0		<0.0001	<0.0001
β	0.5750		0.0418
β_2	0.7243	-0.0372	

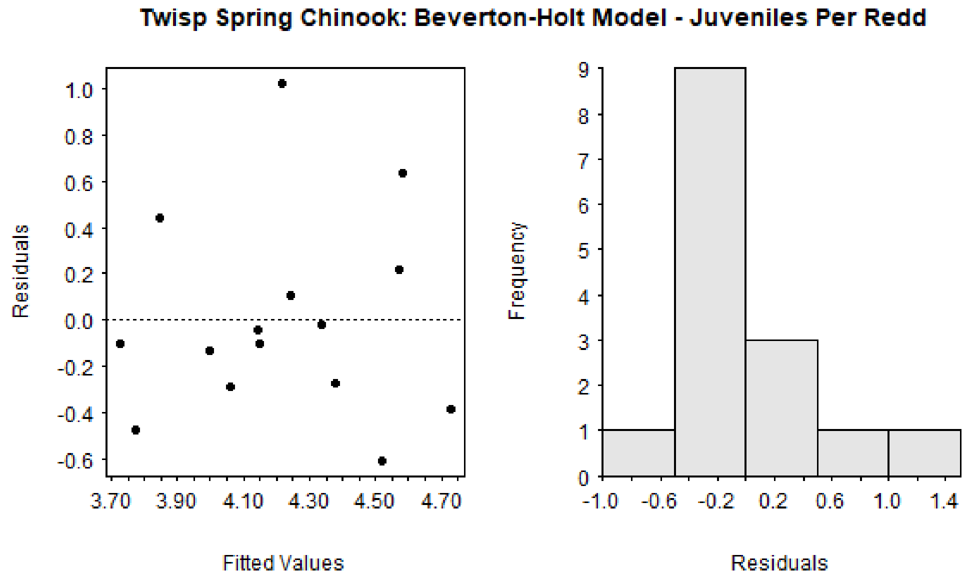

Figure D9. Residual plots for Beverton-Holt model of smolts per redd as a function of redd count and pHOS for Twisp River Spring Chinook, 2003–2017. Shapiro-Wilk test of normality of residuals: W=0.9345, P=0.3185.

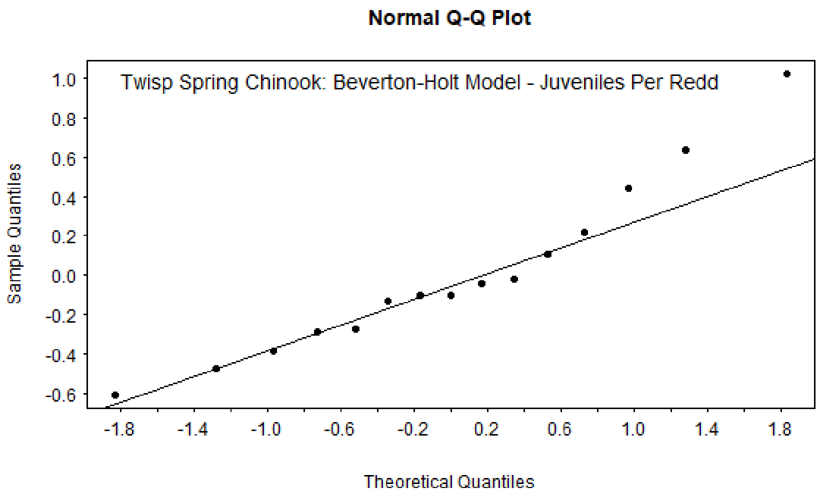

Figure D10. Normal quantile-quantile plot of residual from Beverton-Holt model of smolts per redd as a function of redd count and pHOS for Twisp River Spring Chinook, 2003–2017. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.9345, P=0.3185.

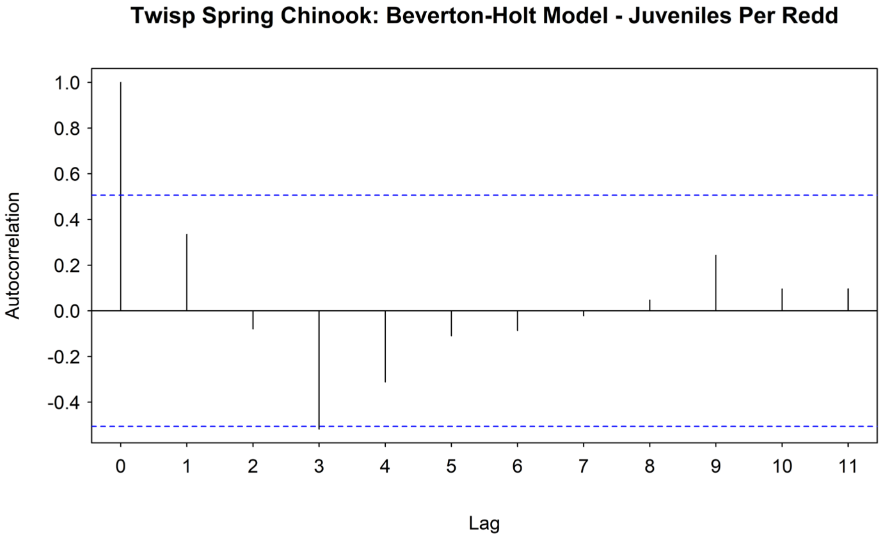

Figure D11. Autocorrelation plot of residuals for Beverton-Holt model of smolts per redd as a function of redd count and pHOS for Twisp River Spring Chinook, 2003–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

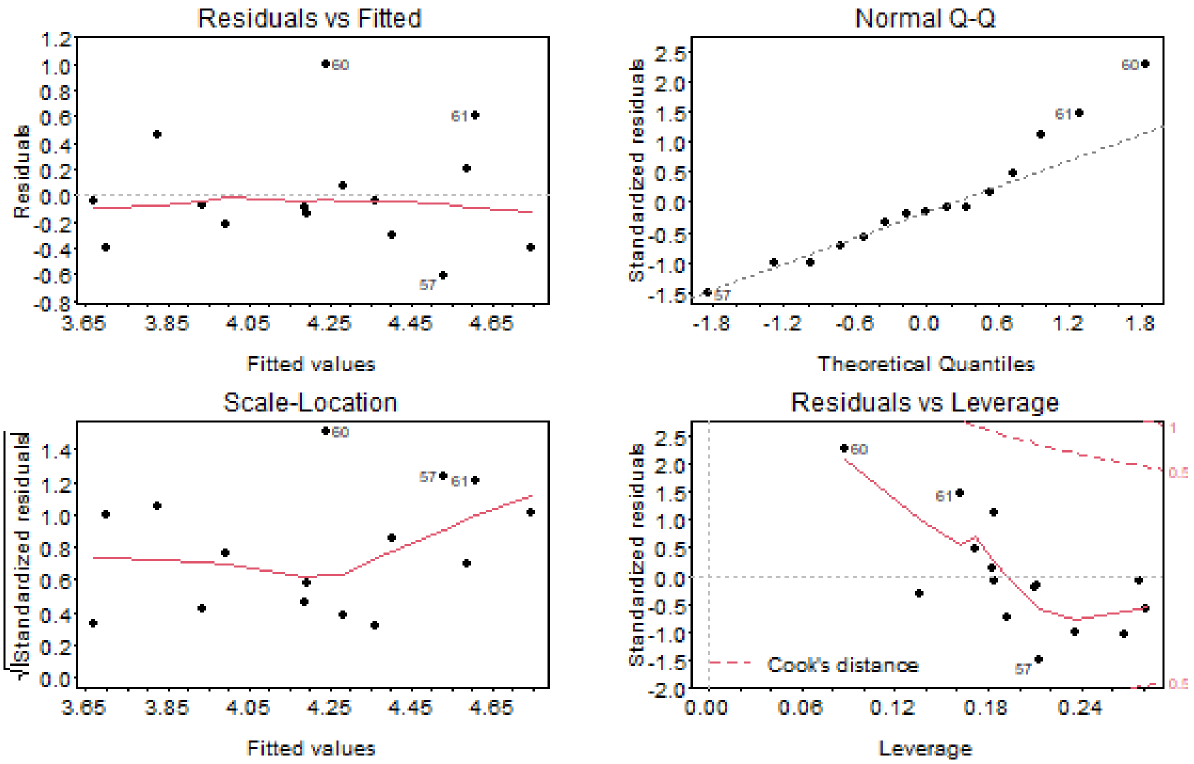

Figure D12. Residual plots for Ricker model of smolts per redd as a function of redd count and pHOS for Twisp River Spring Chinook, 2003–2017. Shapiro-Wilk test of normality of residuals: W=0.9284, P=0.2587.

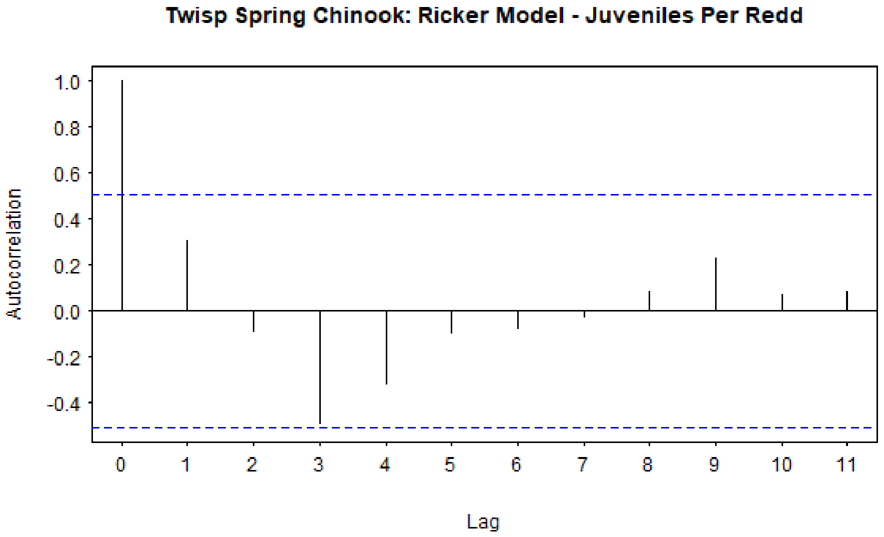

Figure D13. Autocorrelation plot of residuals for Ricker model of smolts per redd as a function of redd count and pHOS for Twisp River Spring Chinook, 2003–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

Appendix E: Methow River Spring Chinook Salmon

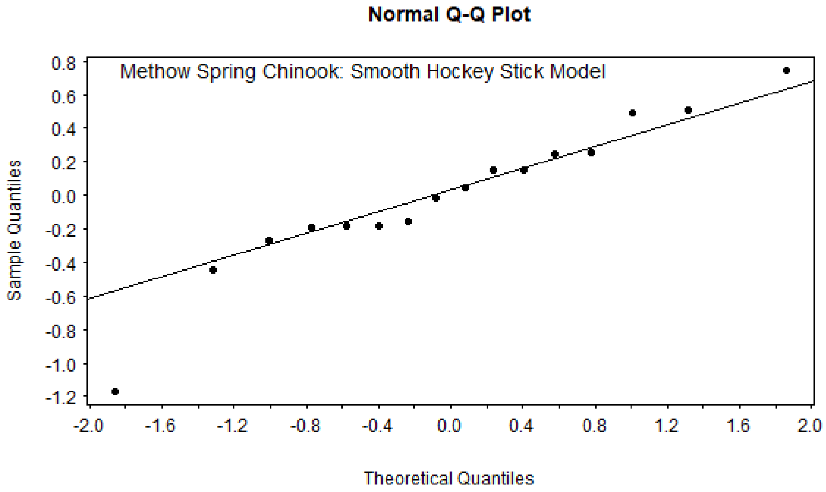

Figure E1. Normal quantile-quantile plot of residual from the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for Methow River Spring Chinook, 2002–2017. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.9376, P=0.3202.

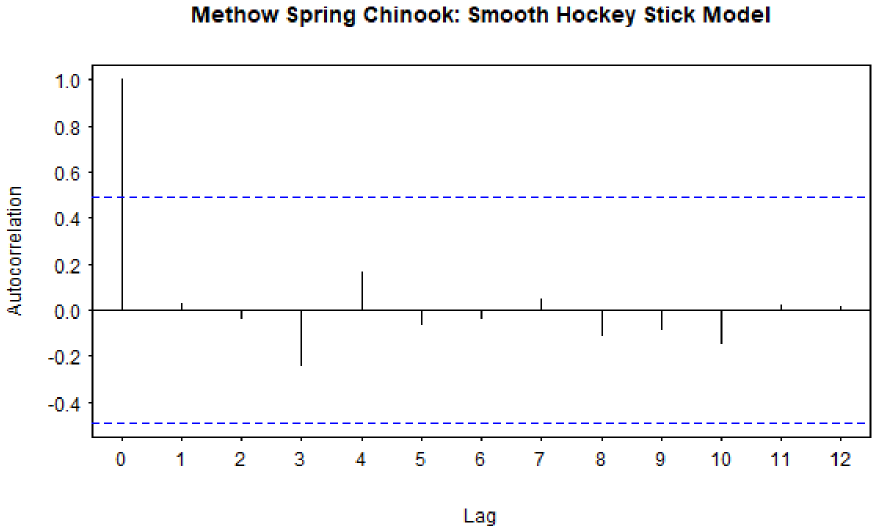

Figure E2. Autocorrelation plot of residuals for the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for Methow River Spring Chinook, 2002–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

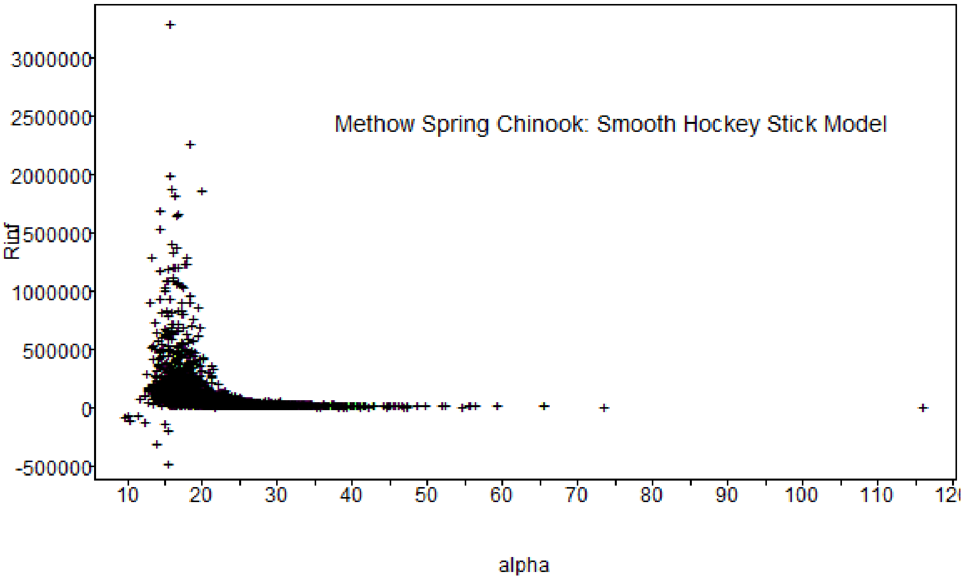

Figure E3. Correlation plot of bootstrap parameter estimates from the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for Methow River Spring Chinook, 2002–2017, based on 3,182 bootstrap samples.

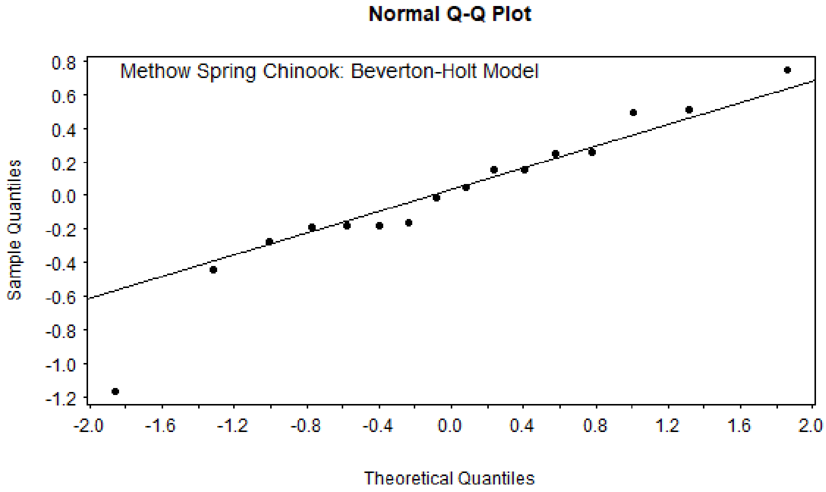

Figure E4. Normal quantile-quantile plot of residual from Beverton-Holt model of smolt recruitment as a function of spawner abundance (stock) for Methow River Spring Chinook, 2002–2017. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.9382, P=0.3275.

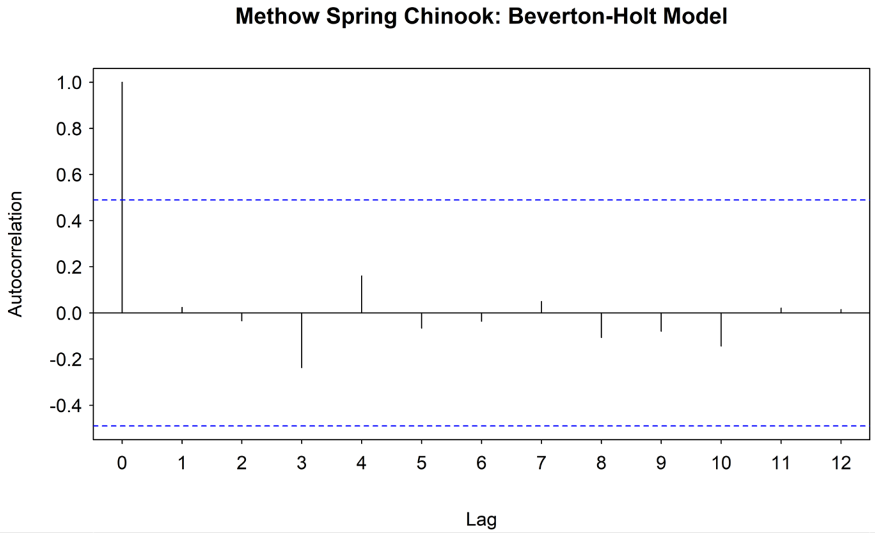

Figure E5. Autocorrelation plot of residuals for Beverton-Holt model of smolt recruitment as a function of spawner abundance (stock) for Methow River Spring Chinook, 2002–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

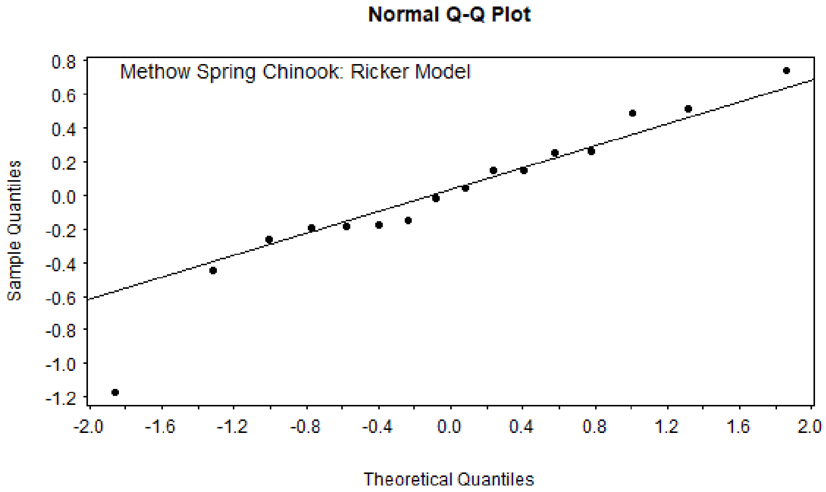

Figure E6. Normal quantile-quantile plot of residual from Ricker model of smolt recruitment as a function of spawner abundance (stock) for Methow River Spring Chinook, 2002–2017. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.9370, P=0.3135.

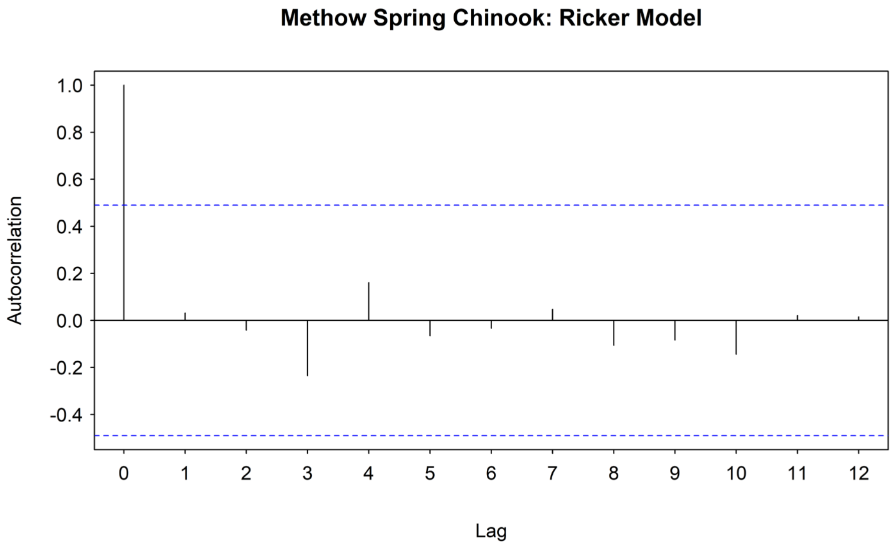

Figure E7. Autocorrelation plot of residuals for Ricker model of smolt recruitment as a function of spawner abundance (stock) for Methow River Spring Chinook, 2002–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

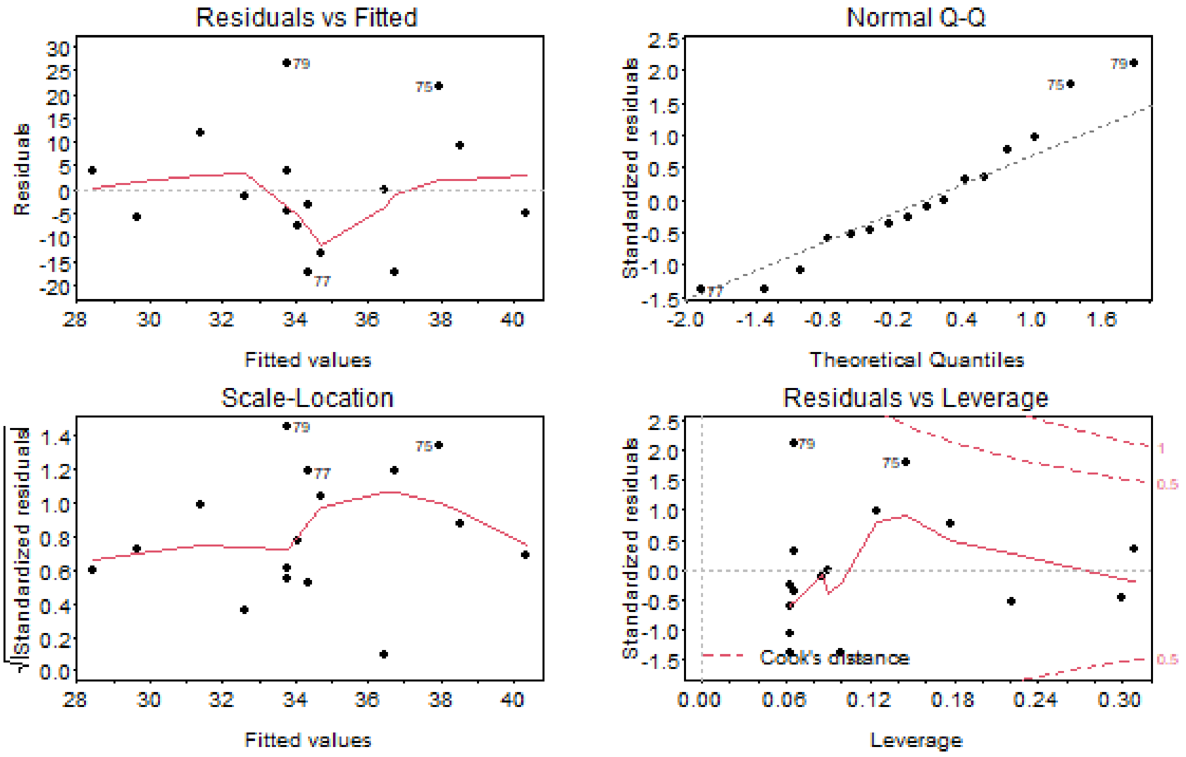

Figure E8. Residual plots for linear model of smolts per redd as a function of pHOS for Methow River Spring Chinook, 2002–2017. Shapiro-Wilk test of normality of residuals: W=0.9467, P=0.4400.

Table E1. Pearson correlation coefficient (below diagonal) and two-sided P-value (above diagonal) for Ricker stock-recruitment model of smolts per redd for Methow River Spring Chinook, 2002–2017. Model form is: $ln(R/S) = \beta_0 - \beta S - \beta_2 P_{HOS}$. Correlation computed from bootstrap (3,000 bootstrap samples).

Parameter	β_0	β	β_2
β_0		<0.0001	<0.0001
β	-0.2102		<0.0001
β_2	0.9366	-0.5241	

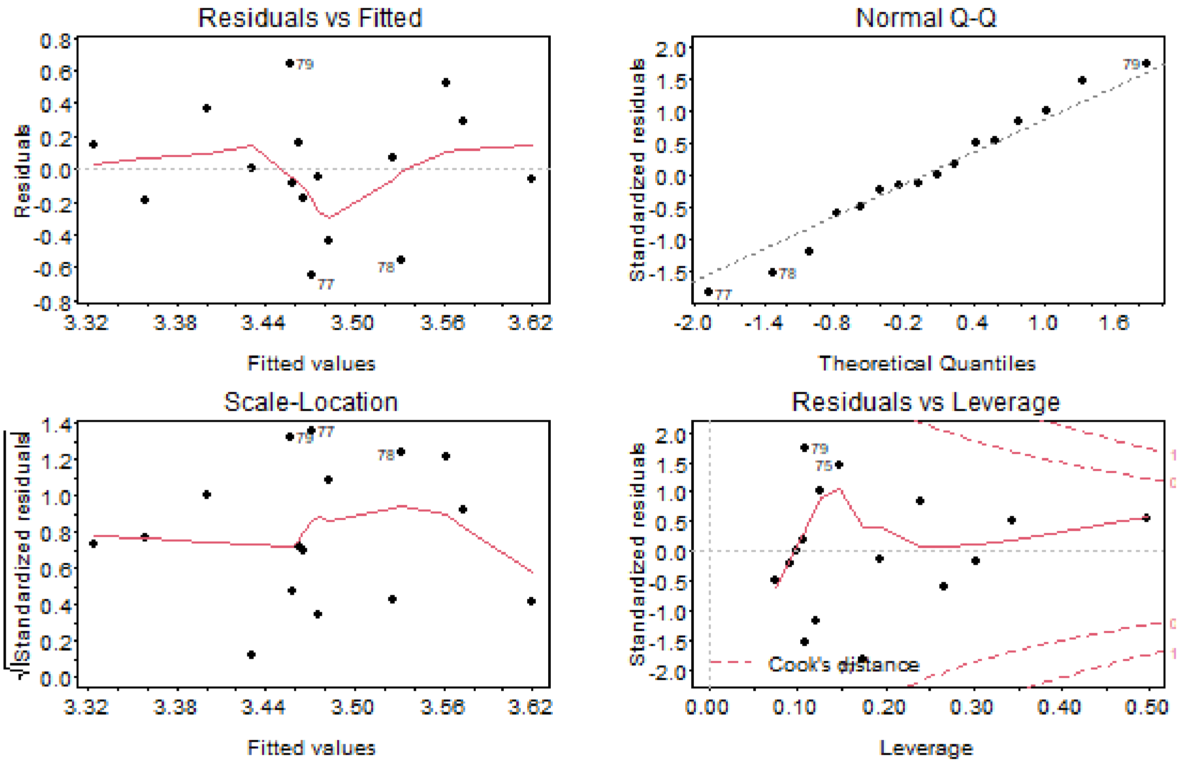

Figure E9. Residual plots for Ricker model of smolts per redd as a function of redd count and pHOS for Methow River Spring Chinook, 2002–2017. Shapiro-Wilk test of normality of residuals: W=0.9794, P=0.9589.

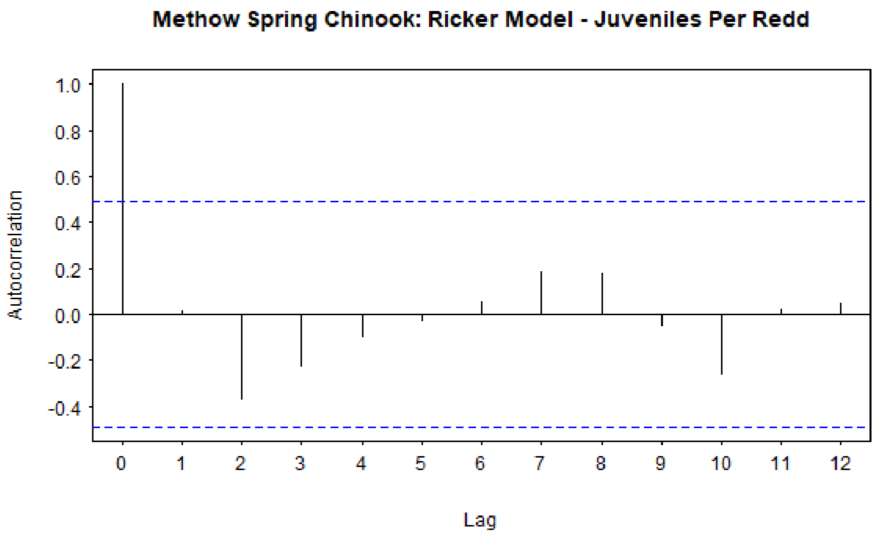

Figure E10. Autocorrelation plot of residuals for Ricker model of smolts per redd as a function of redd count and pHOS for Methow River Spring Chinook, 2002–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

Appendix F: Wenatchee River Summer Chinook Salmon

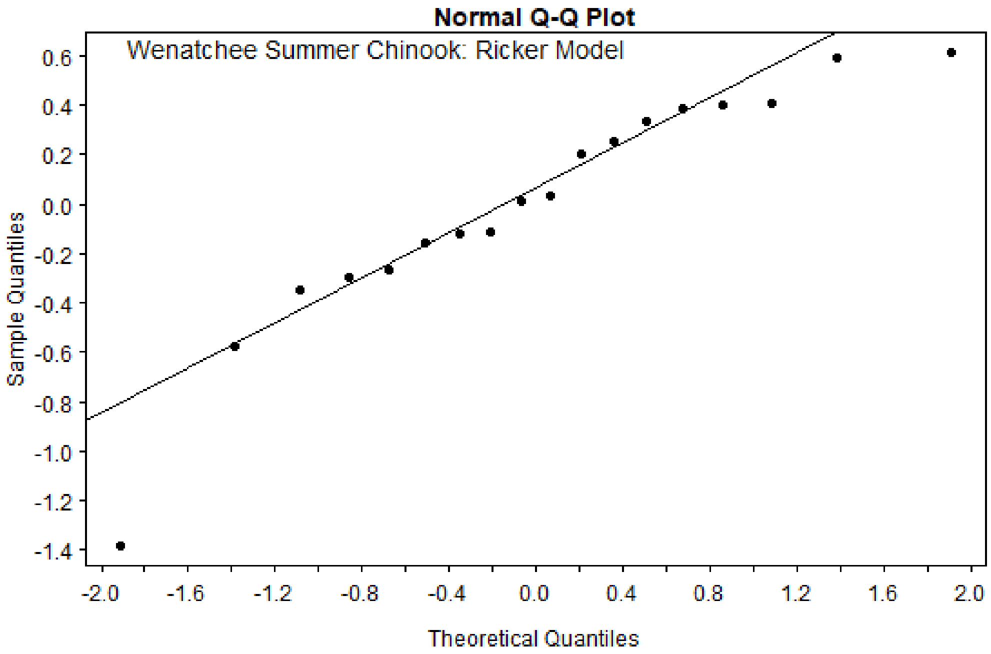

Figure F1. Normal quantile-quantile plot of residual from Ricker model of emigrant count as a function of spawner abundance (stock) for Wenatchee River Summer Chinook, 1999–2018 (without 2010, 2011). Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.9015, P=0.0611.

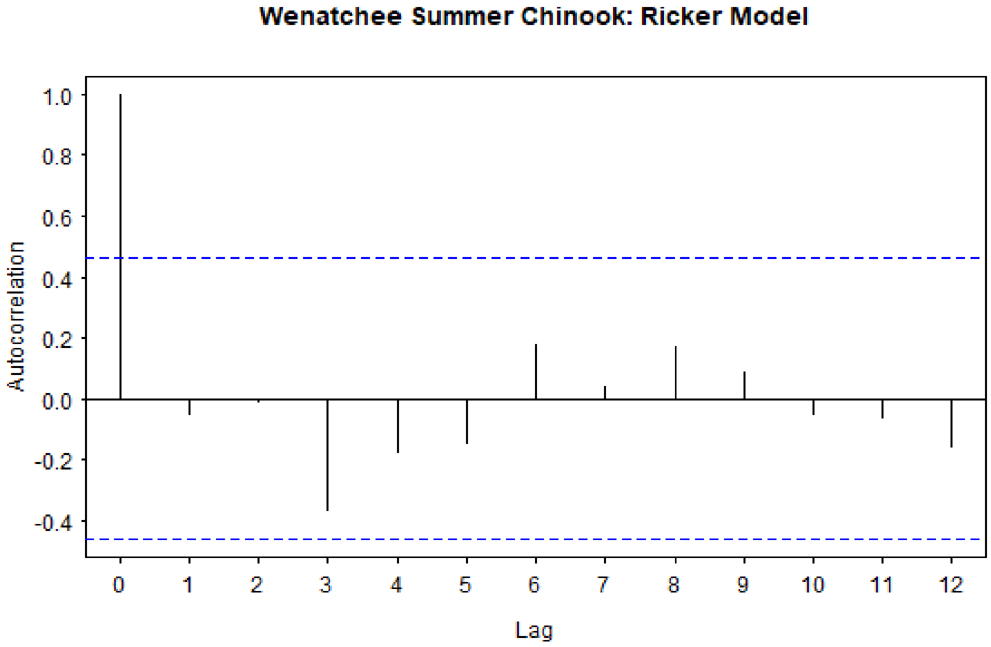

Figure F2. Autocorrelation plot of residuals for Ricker model of smolt recruitment as a function of spawner abundance (stock) for Wenatchee River Summer Chinook, 1999–2018 (without 2010, 2011). Blue lines mark 95% confidence interval under assumption of no autocorrelation.

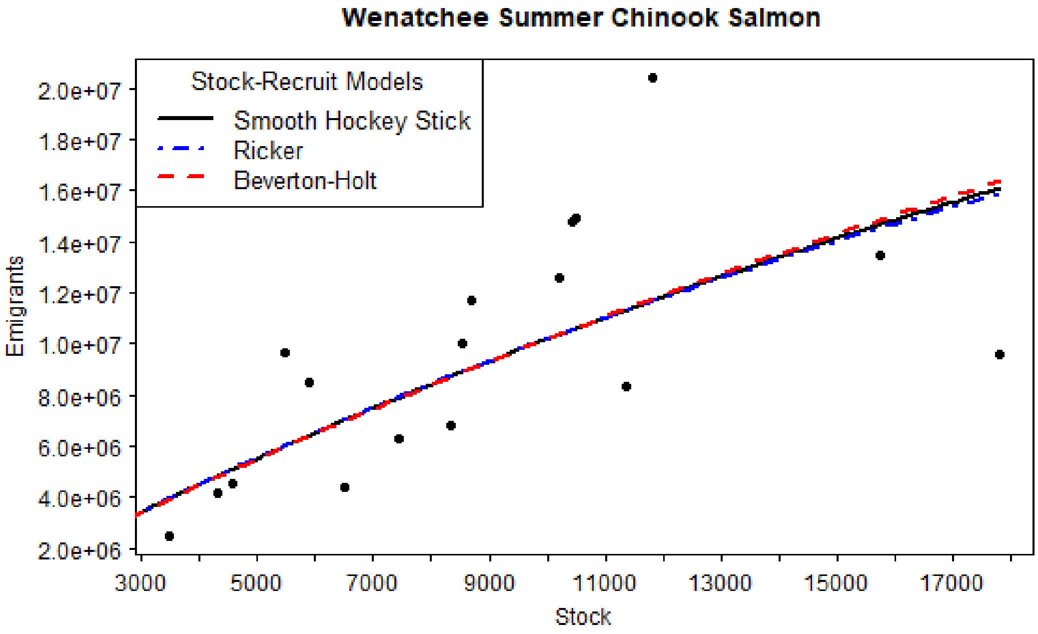

Figure F3. The Smooth Hockey Stick, Beverton-Holt, and Ricker stock-recruitment model fit to emigrants and spawner data for Wenatchee River Summer Chinook Salmon, 1999–2018 (without 2000, 2010, 2011).

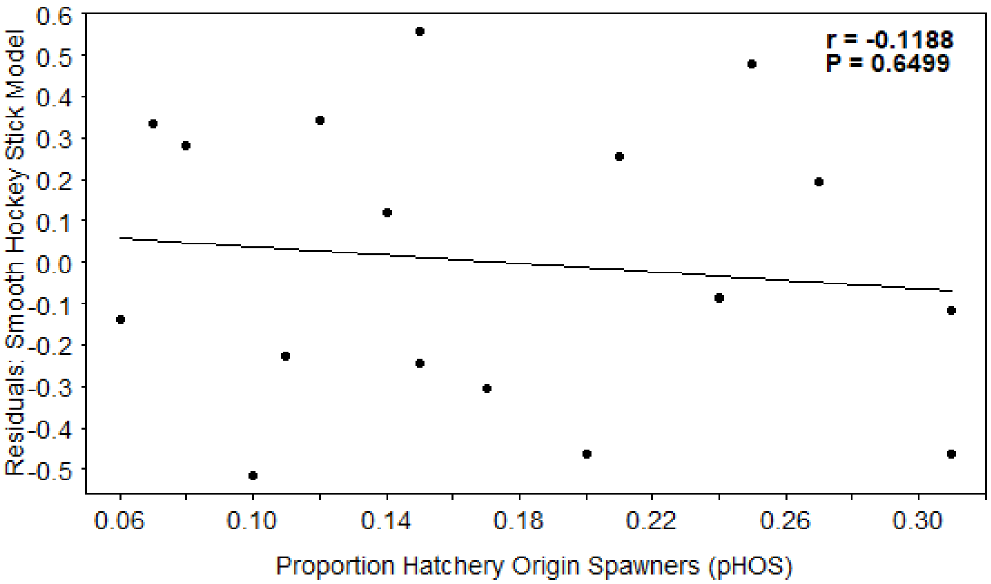

Figure F4. Residuals from the Smooth Hockey Stick Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Wenatchee River Summer Chinook Salmon, 1999–2018 (without 2000, 2010, 2011). R^2 =0.0141.

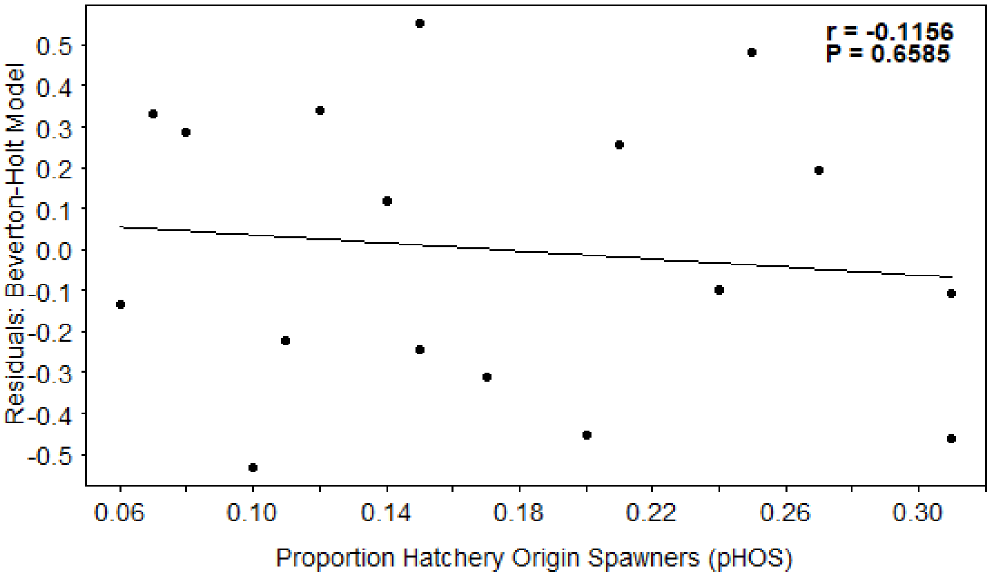

Figure F5. Residuals from the Beverton-Holt Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Wenatchee River Summer Chinook Salmon, 1999–2018 (without 2000, 2010, 2011). R^2 =0.0134.

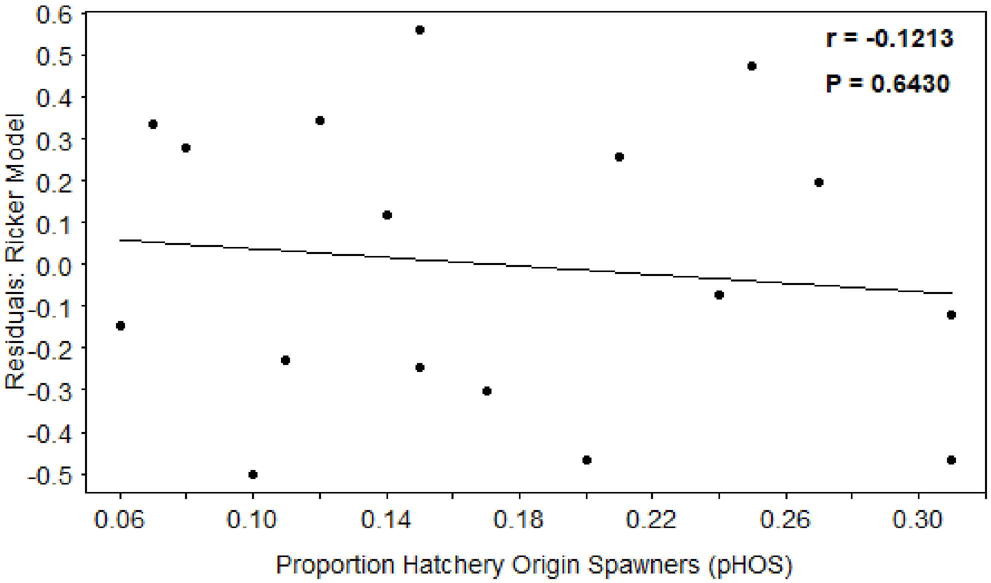

Figure F6. Residuals from Ricker Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Wenatchee River Summer Chinook Salmon, 1999–2018 (without 2000, 2010, 2011). R^2 =0.0147.

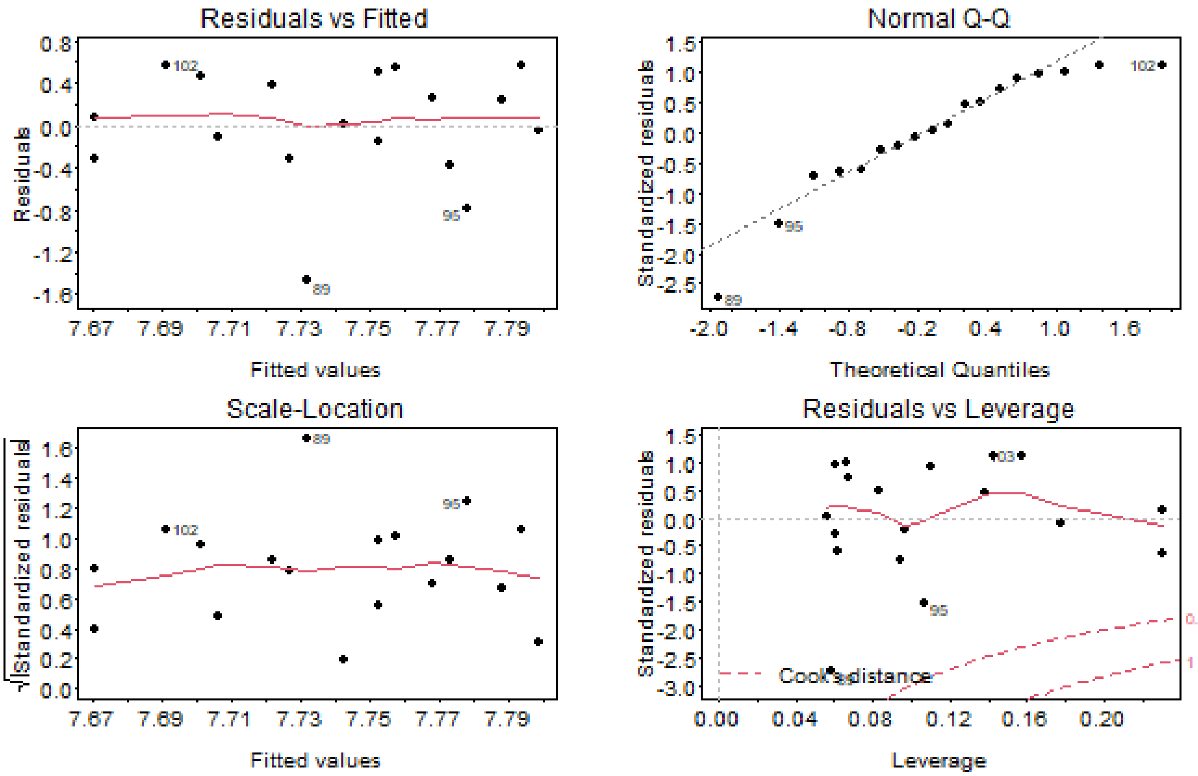

Figure F7. Residual plots for linear model of emigrants (log scale) per redd as a function of pHOS for Wenatchee River Summer Chinook, 1999–2018 (without 2010, 2011). Shapiro-Wilk test of normality of residuals: W=0.8877, P=0.0353.

Table F1. Pearson correlation coefficient (below diagonal) for Beverton-Holt stock-recruitment model of smolts per redd for Wenatchee River Summer Chinook, 1999–2018 (without 2010, 2011). Attempts to bootstrap for variance failed, and correlation significance could not be estimated. Model form is: $ln(R/S) = ln(\alpha) - \beta_2 P_{HOS} - ln(\beta + S)$. Correlation computed from Hessian matrix from nonlinear model fitting.

Parameter	α	β	β_2
α			
β	0.9887		
β_2	- 0.0548	- 0.1913	

Table F2. Pearson correlation coefficient (below diagonal) and two-sided P-value (above diagonal) for Ricker stock-recruitment model of smolts per redd for Methow River Summer Chinook, 1999–2018 (without 2010, 2011). Model form is: $ln(R/S) = \beta_0 + \beta_1 S - \beta_2 P_{HOS}$. Correlation computed from bootstrap (>3000 bootstrap samples).

Parameter	β_0	β_1	β_2
β_0		< 0.0001	< 0.0001
β_1	- 0.8055		< 0.0001
β_2	0.4975	0.3896	

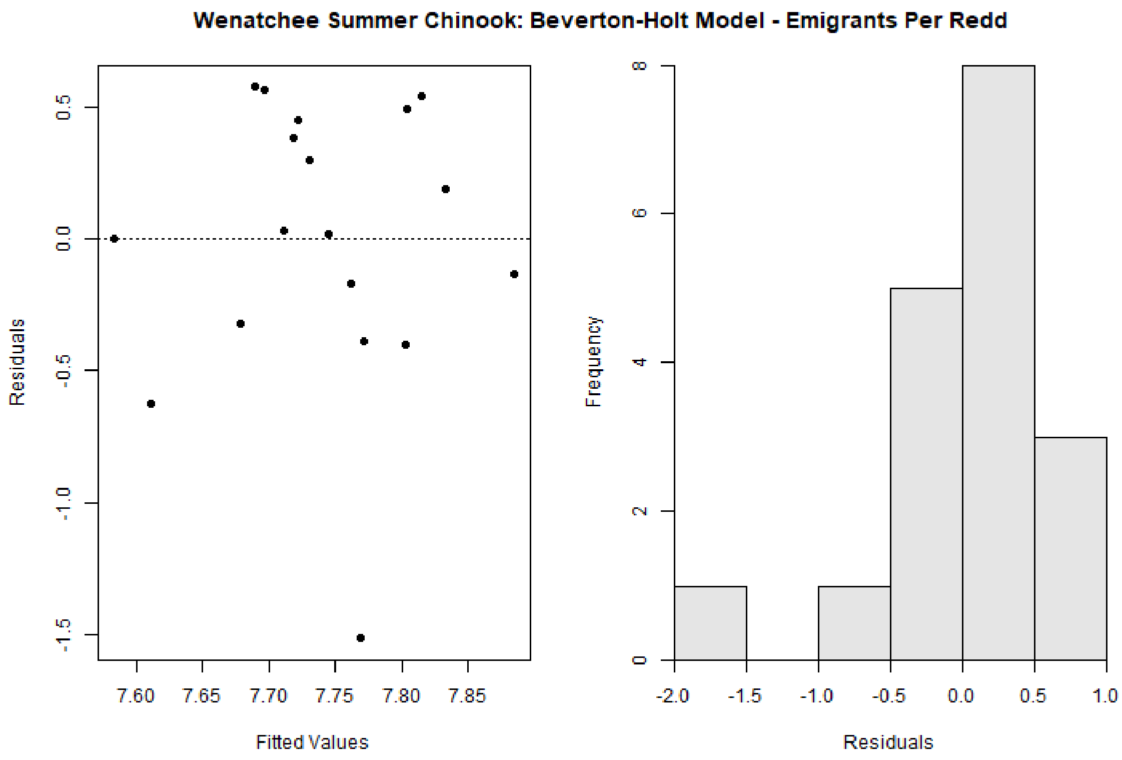

Figure F8. Residual plots for Beverton-Holt model of emigrants per redd as a function of redd count and pHOS for Wenatchee River Summer Chinook, 1999–2018 (without 2010, 2011). Shapiro-Wilk test of normality of residuals: W=0.8845, P=0.0311.

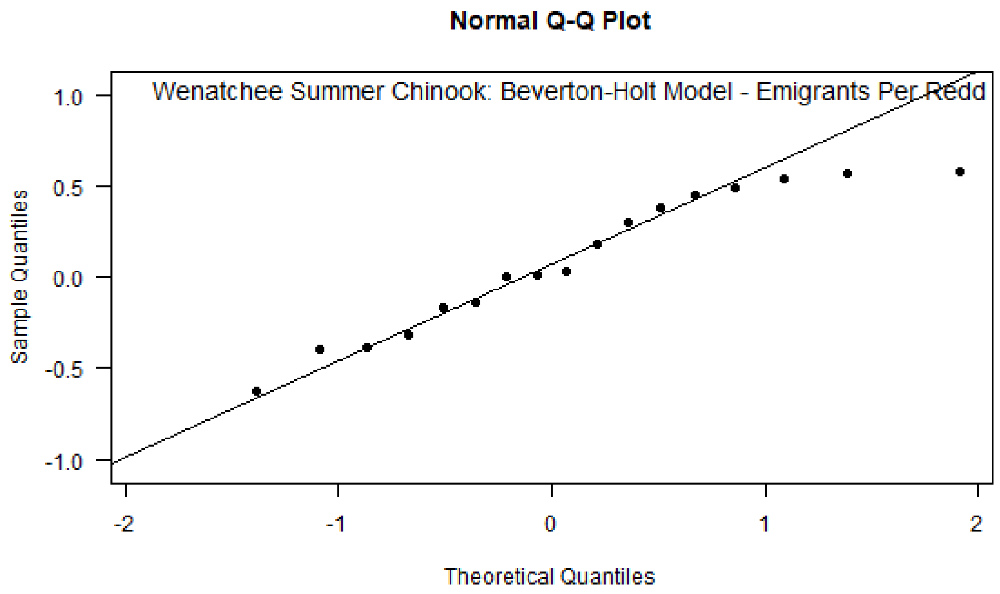

Figure F9. Normal quantile-quantile plot of residual from Beverton-Holt model of emigrants per redd as a function of redd count and pHOS for Wenatchee River Summer Chinook, 1999–2018 (without 2010, 2011). Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.8845, P=0.0311.

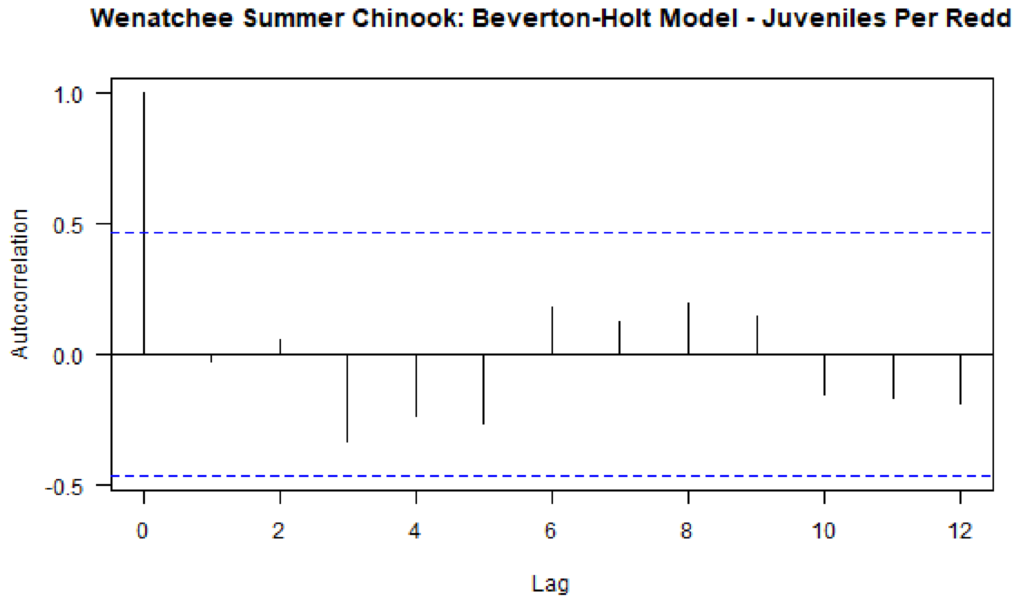

Figure F10. Autocorrelation plot of residuals for Beverton-Holt model of emigrants per redd as a function of redd count and pHOS for Wenatchee River Summer Chinook, 1999–2018 (without 2010, 2011). Blue lines mark 95% confidence interval under assumption of no autocorrelation.

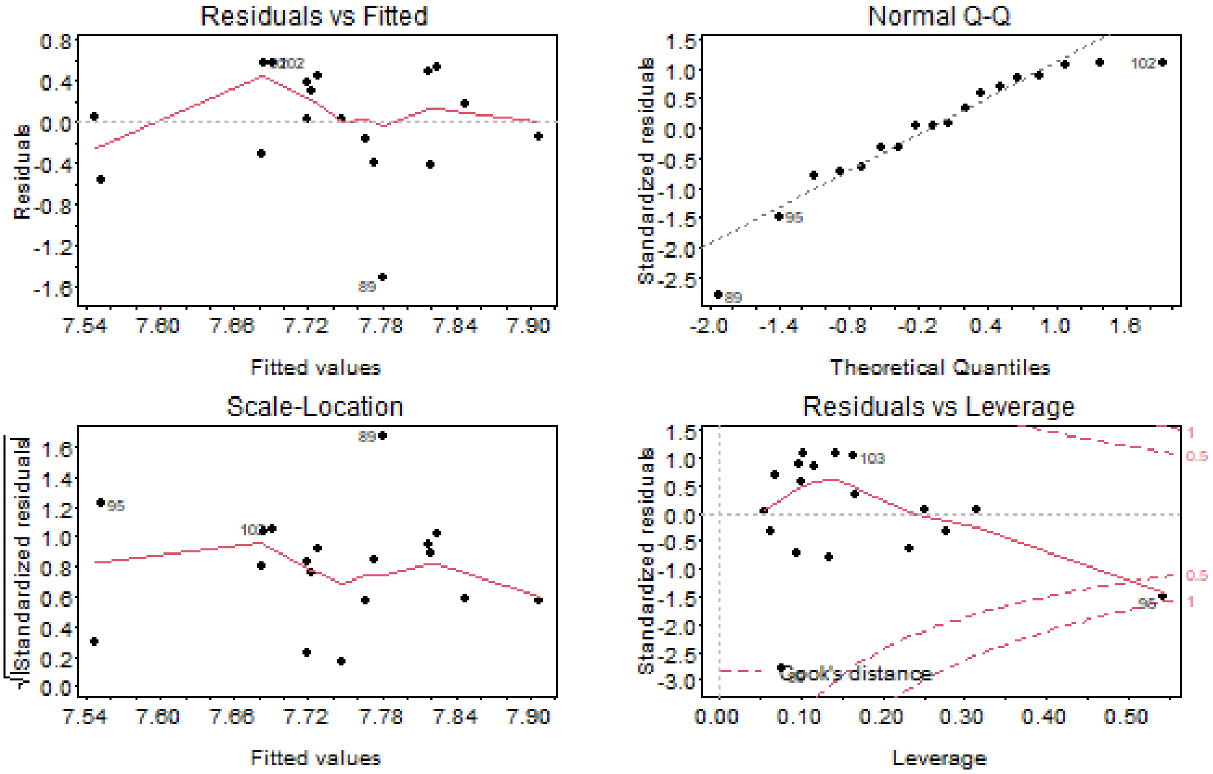

Figure F11. Residual plots for Ricker model of emigrants per redd as a function of redd count and pHOS for Wenatchee River Summer Chinook, 1999–2018 (without 2010, 2011). Shapiro-Wilk test of normality of residuals: W=0.8822, P=0.0284.

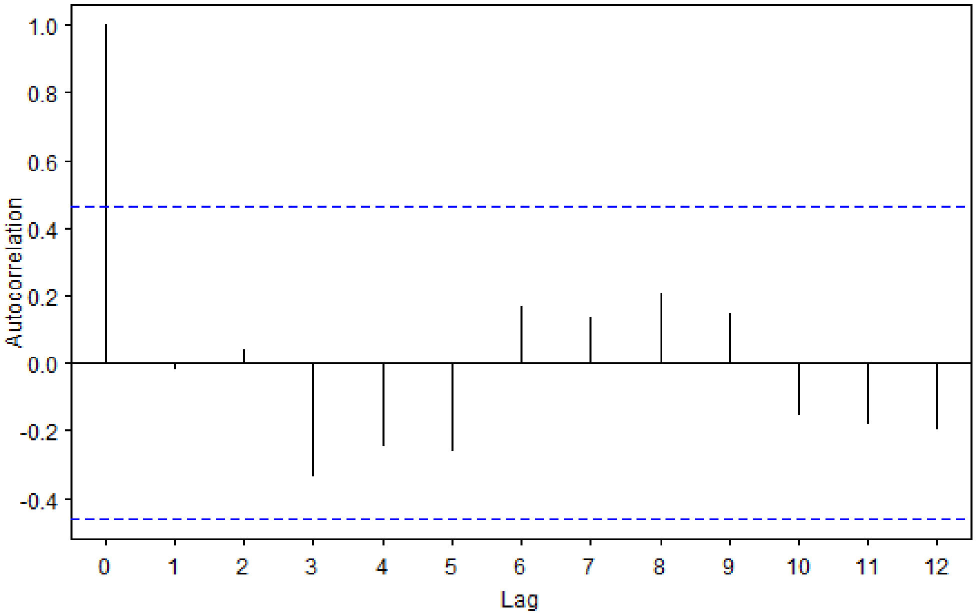

Figure F12. Autocorrelation plot of residuals for Ricker model of smolts per redd as a function of redd count and pHOS for Wenatchee River Summer Chinook, 1999–2018 (without 2010, 2011). Blue lines mark 95% confidence interval under assumption of no autocorrelation.

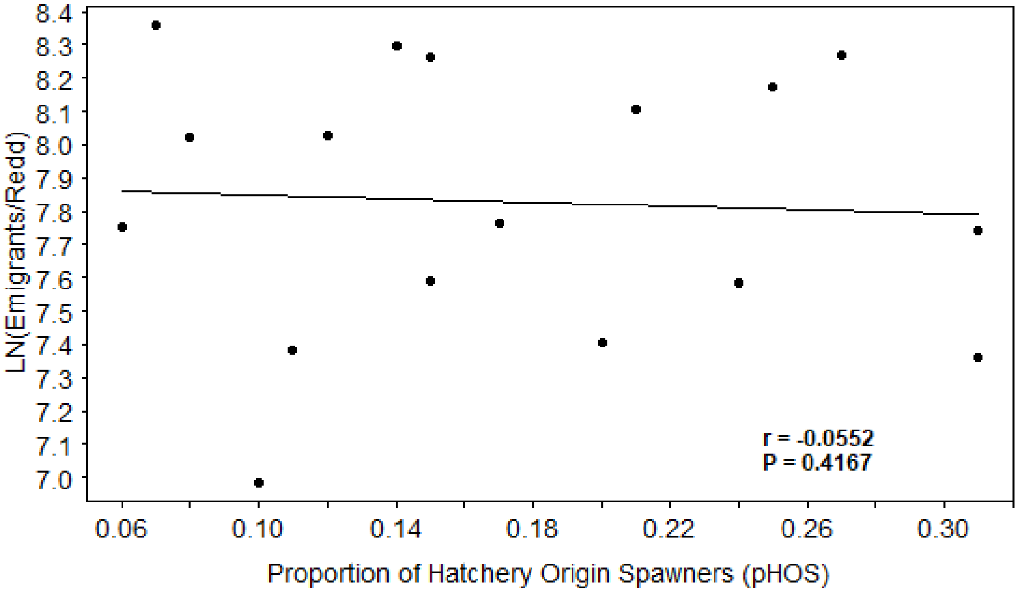

Figure F13. Emigrants per redd (log scale) versus proportion of hatchery origin spawners (pHOS) for Wenatchee River Summer Chinook Salmon, 1999–2018 (without 2000, 2010, 2011), with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. $R^2 = 0.0030$.

Appendix G: Methow River Summer Chinook Salmon

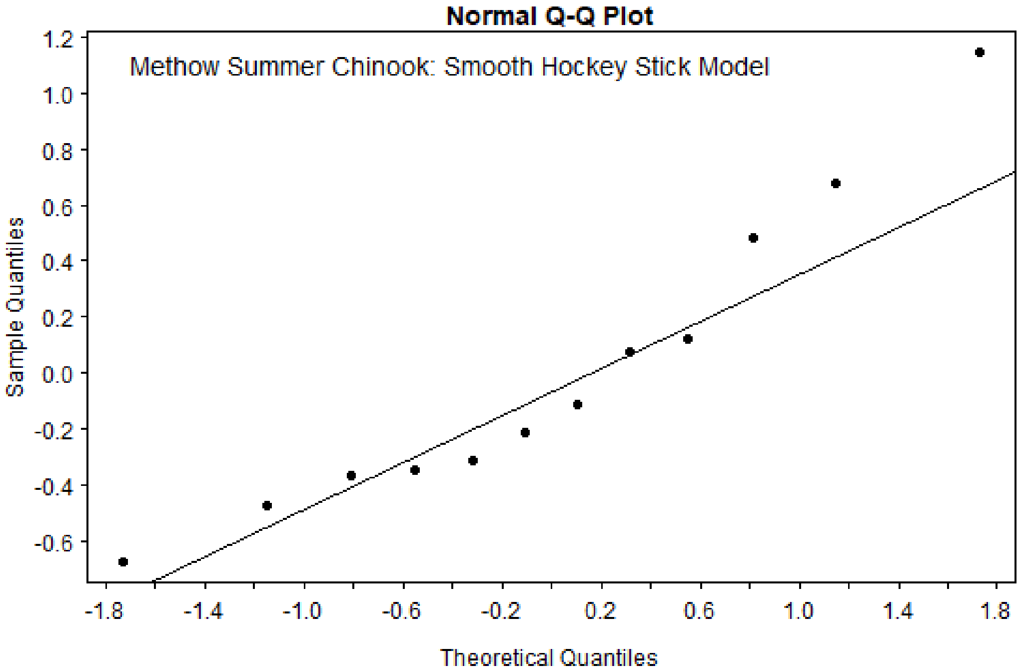

Figure G1. Normal quantile-quantile plot of residual from Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for Methow River Summer Chinook, 2006–2018 (without 2012). Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.9192, P=0.2793.

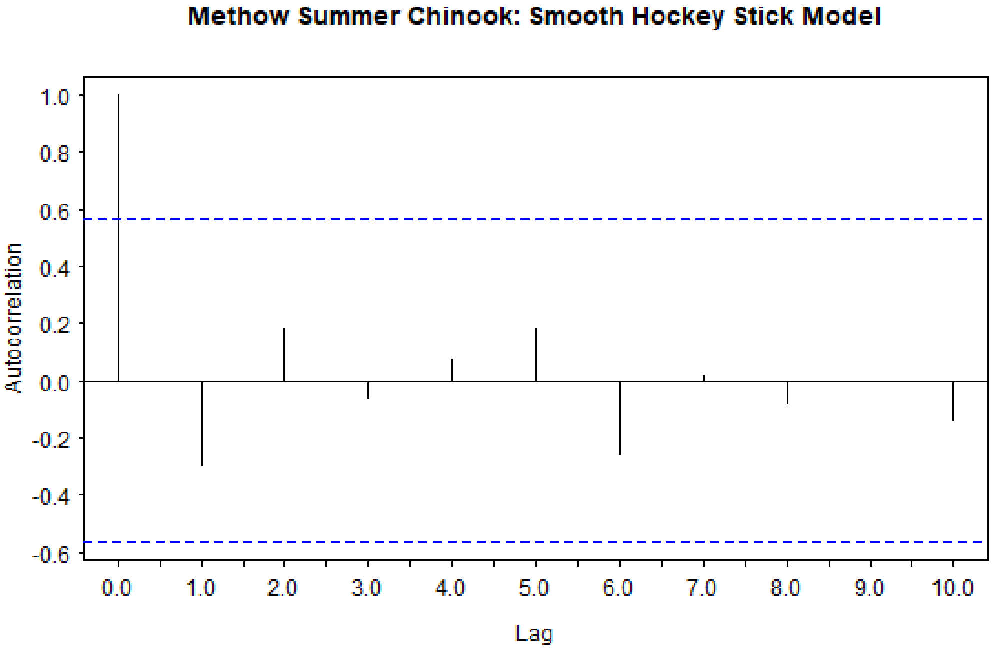

Figure G2. Autocorrelation plot of residuals for Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for Methow River Summer Chinook, 2006–2018 (without 2012). Blue lines mark 95% confidence interval under assumption of no autocorrelation.

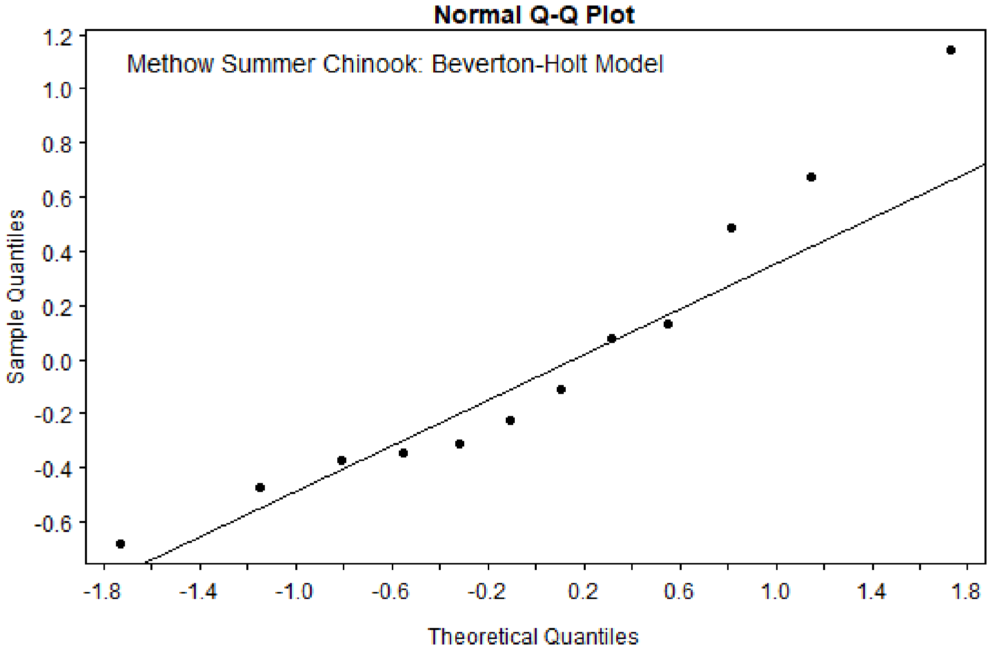

Figure G3. Normal quantile-quantile plot of residual from Beverton-Holt model of emigrant count as a function of spawner abundance (stock) for Methow River Summer Chinook, 2006–2018 (without 2012). Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.9206, P=0.2910.

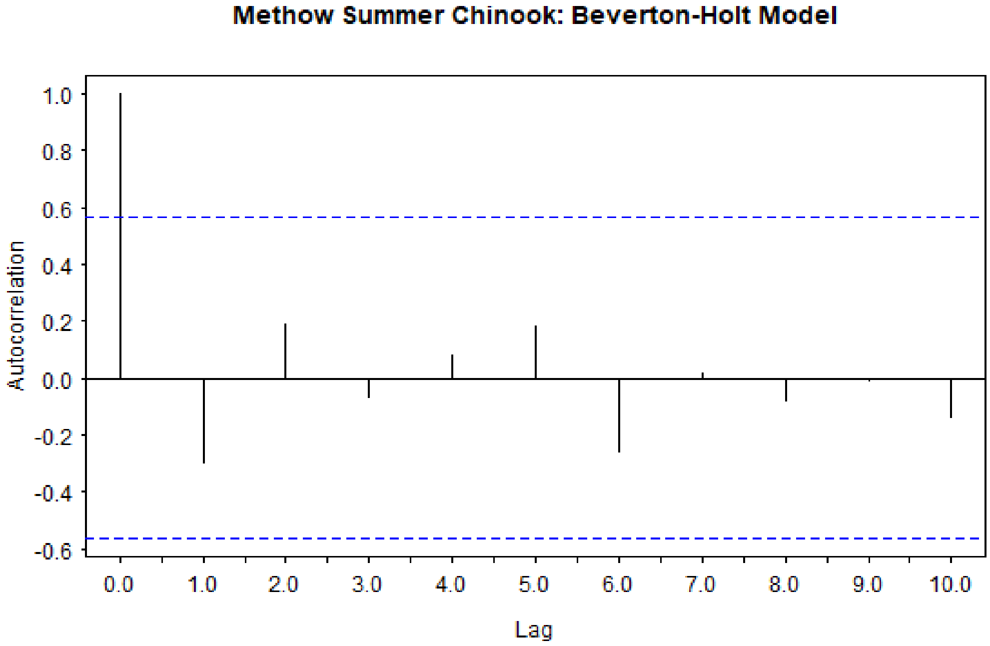

Figure G4. Autocorrelation plot of residuals for Beverton-Holt model of smolt recruitment as a function of spawner abundance (stock) for Methow River Summer Chinook, 2006–2018 (without 2012). Blue lines mark 95% confidence interval under assumption of no autocorrelation.

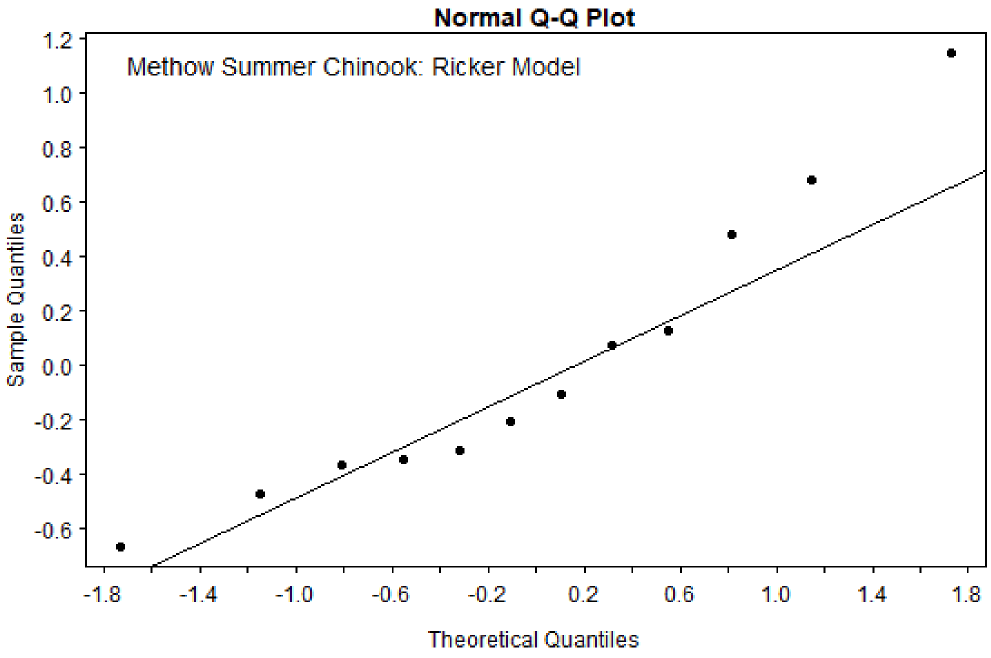

Figure G5. Normal quantile-quantile plot of residual from Ricker model of emigrant count as a function of spawner abundance (stock) for Methow River Summer Chinook, 2006–2018 (without 2012). Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.9181, P=0.2707.

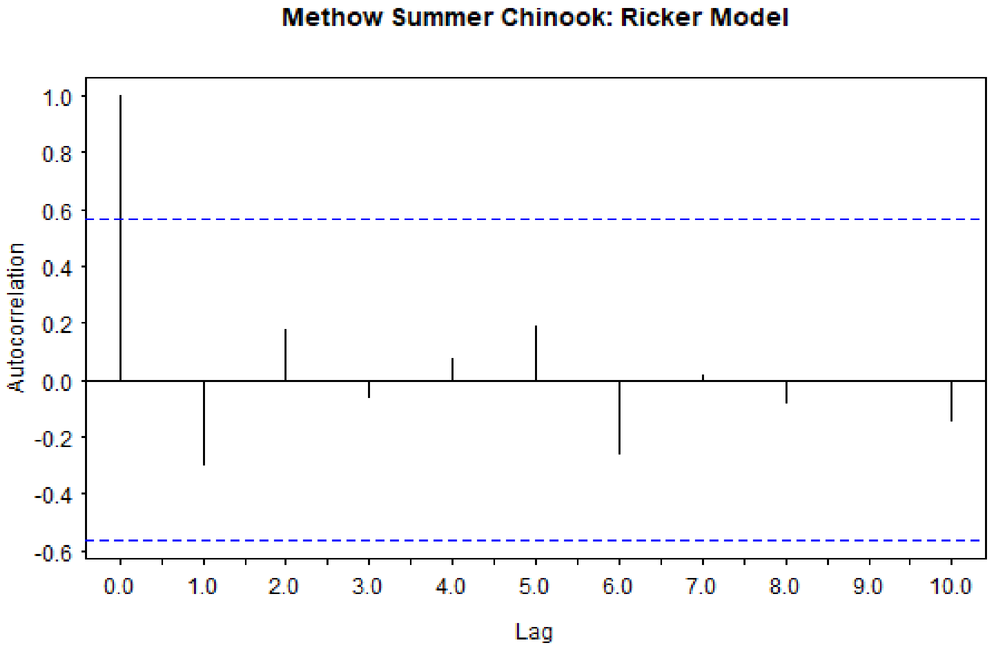

Figure G6. Autocorrelation plot of residuals for Ricker model of smolt recruitment as a function of spawner abundance (stock) for Methow River Summer Chinook, 2006–2018 (without 2012). Blue lines mark 95% confidence interval under assumption of no autocorrelation.

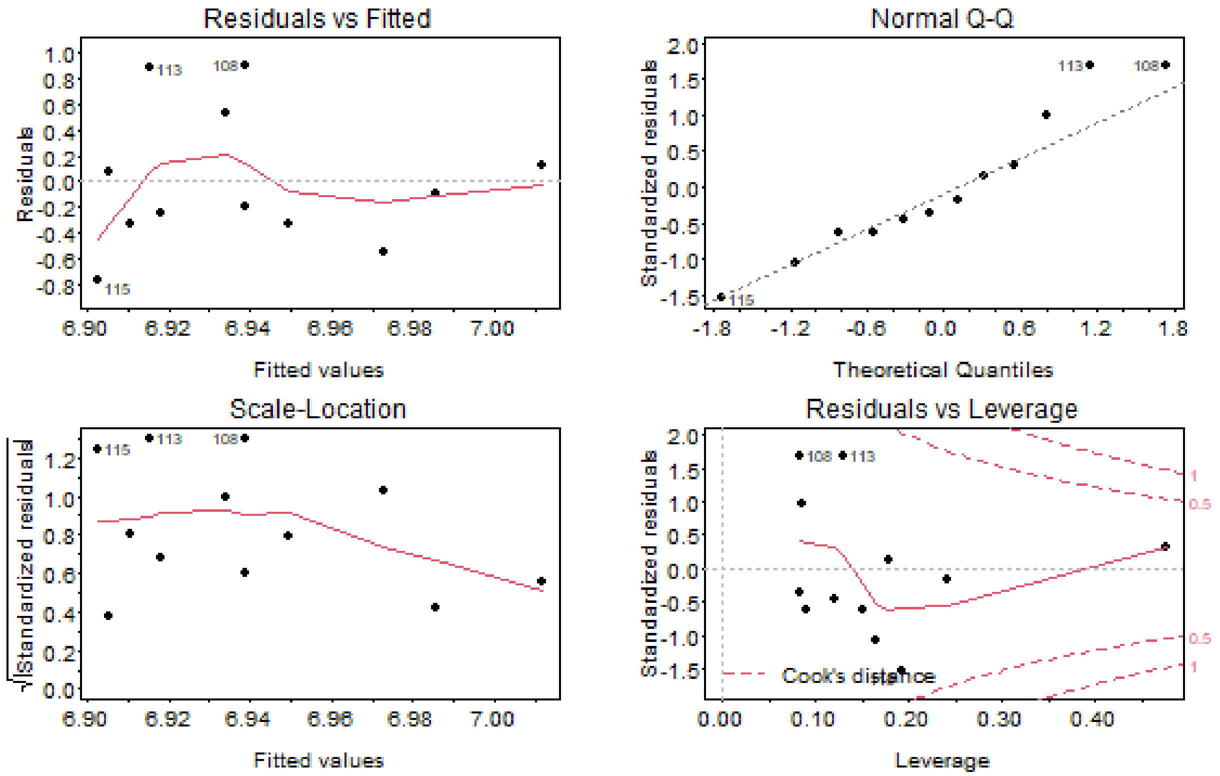

Figure G7. Residual plots for linear model of smolts per redd as a function of pHOS for Methow River Summer Chinook, 2006–2018 (without 2012). Shapiro-Wilk test of normality of residuals: W=0.9284, P=0.3632.

Table G1. Pearson correlation coefficient (below diagonal) and two-sided P-value (above diagonal) for Beverton-Holt stock-recruitment model of smolts per redd for Methow River Summer Chinook, 2006–2018 (without 2012). Model form is: $ln(R/S) = ln(\alpha) - \beta_2 P_{HOS} - ln(\beta + S)$. Correlation computed from Hessian matrix from nonlinear model fitting.

Parameter	α	β	β_2
α		NA	NA
β	0.9993		NA
β_2	0.1676	0.1333	

Table G2. Pearson correlation coefficient (below diagonal) and two-sided P-value (above diagonal) for Ricker stock-recruitment model of smolts per redd for Methow River Summer Chinook, 2006–2018 (without 2012). Model form is: $ln(R/S) = \beta_0 + \beta_1 S - \beta_2 P_{HOS}$. Correlation computed from bootstrap (> 1500 bootstrap samples).

Parameter	β_0	β_1	β_2
β_0		< 0.0001	< 0.0001
β_1	- 0.7893		< 0.0001
β_2	0.8198	- 0.3334	

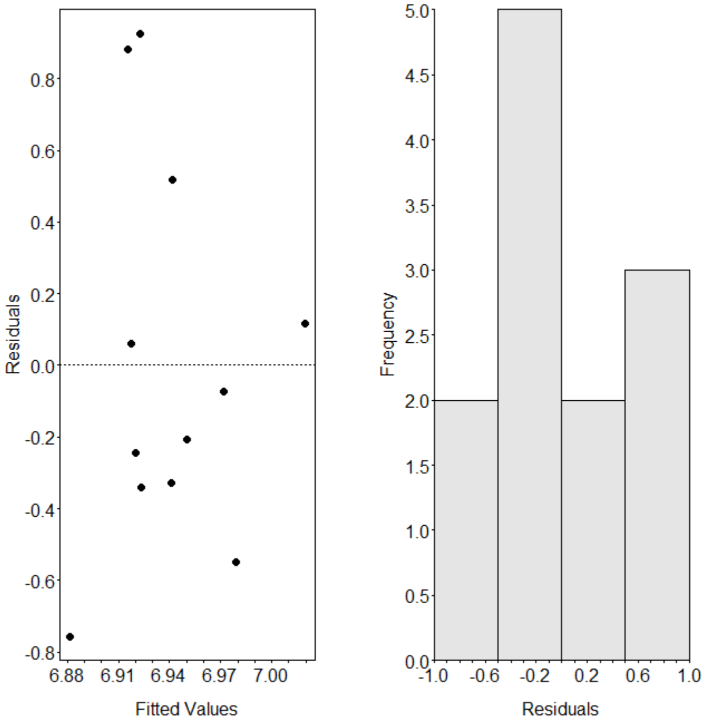

Figure G8. Residual plots for Beverton-Holt model of emigrants per redd as a function of redd count and pHOS for Methow River Summer Chinook, 2006–2018 (without 2012). Shapiro-Wilk test of normality of residuals: W=0.9255, P=0.3352.

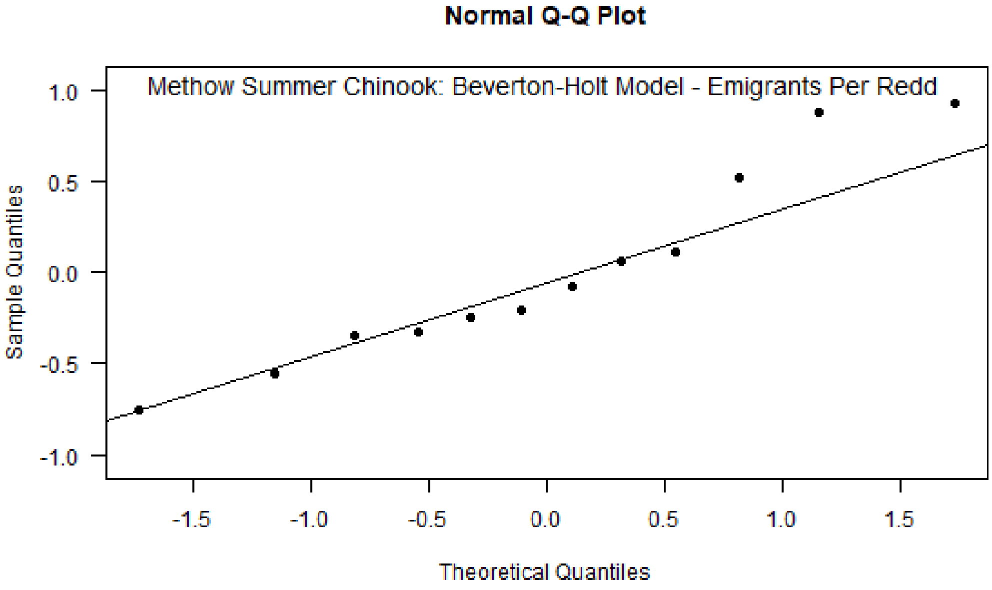

Figure G9. Normal quantile-quantile plot of residual from Beverton-Holt model of emigrants per redd as a function of redd count and pHOS for Methow River Summer Chinook, 2006–2018 (without 2012). Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.9255, P=0.3352.

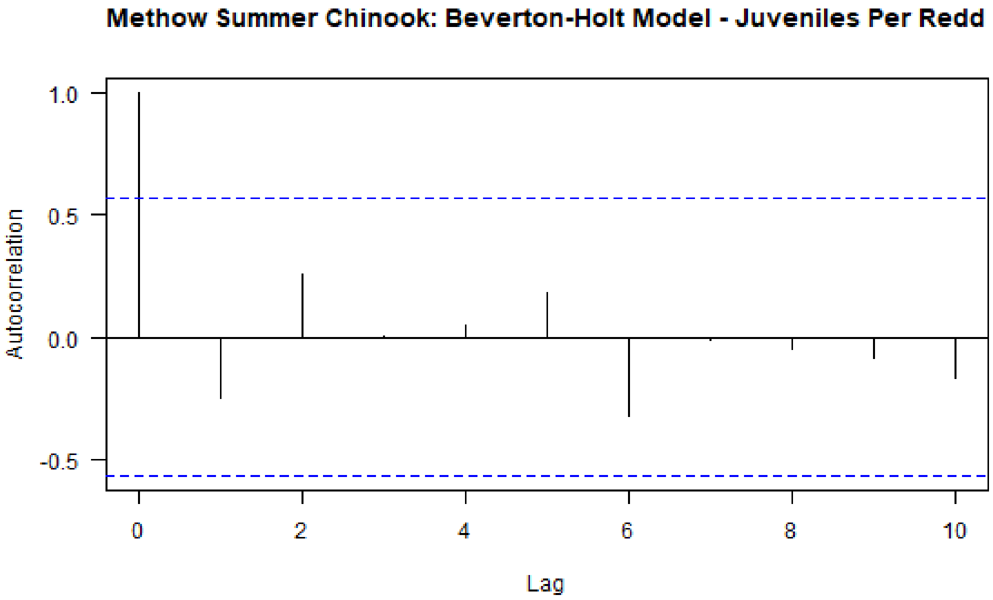

Figure G10. Autocorrelation plot of residuals for Beverton-Holt model of emigrants per redd as a function of redd count and pHOS for Methow River Summer Chinook, 2006–2018 (without 2012). Blue lines mark 95% confidence interval under assumption of no autocorrelation.

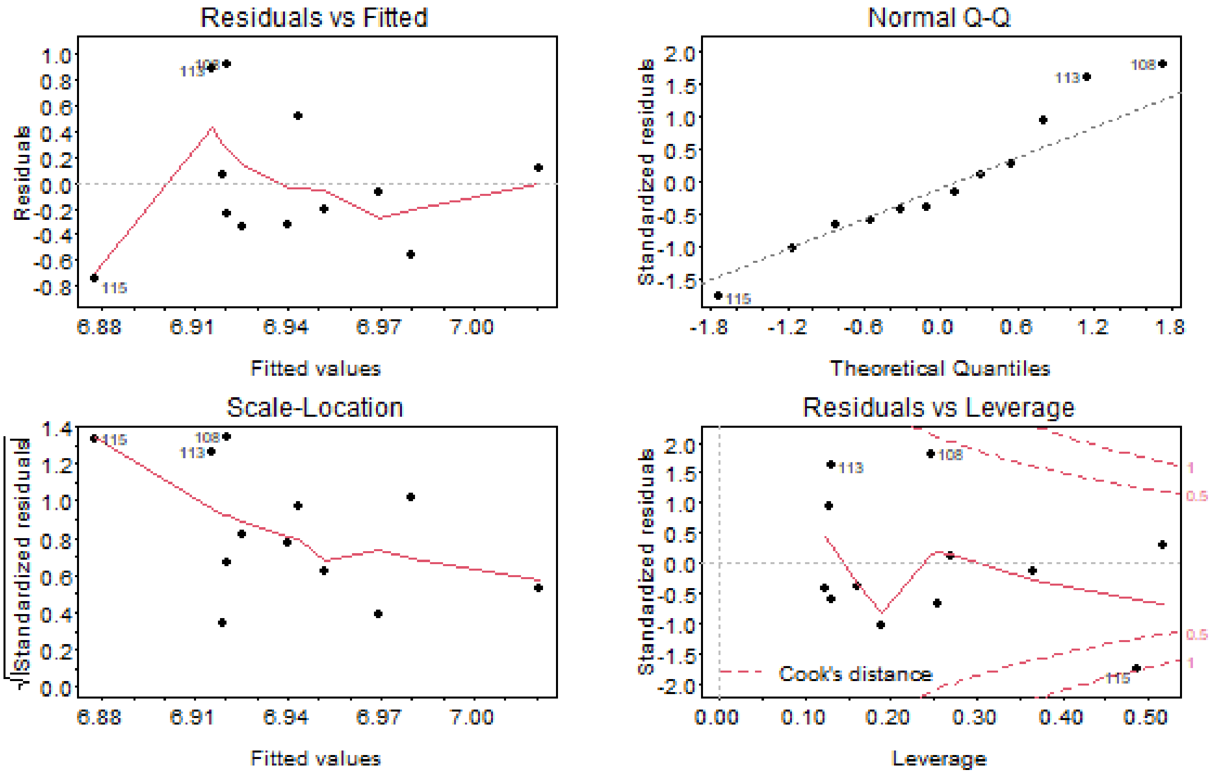

Figure G11. Residual plots for Ricker model of emigrants per redd as a function of redd count and pHOS for Methow River Summer Chinook, 2006–2018 (without 2012). Shapiro-Wilk test of normality of residuals: W=0.9251, P=0.3313.

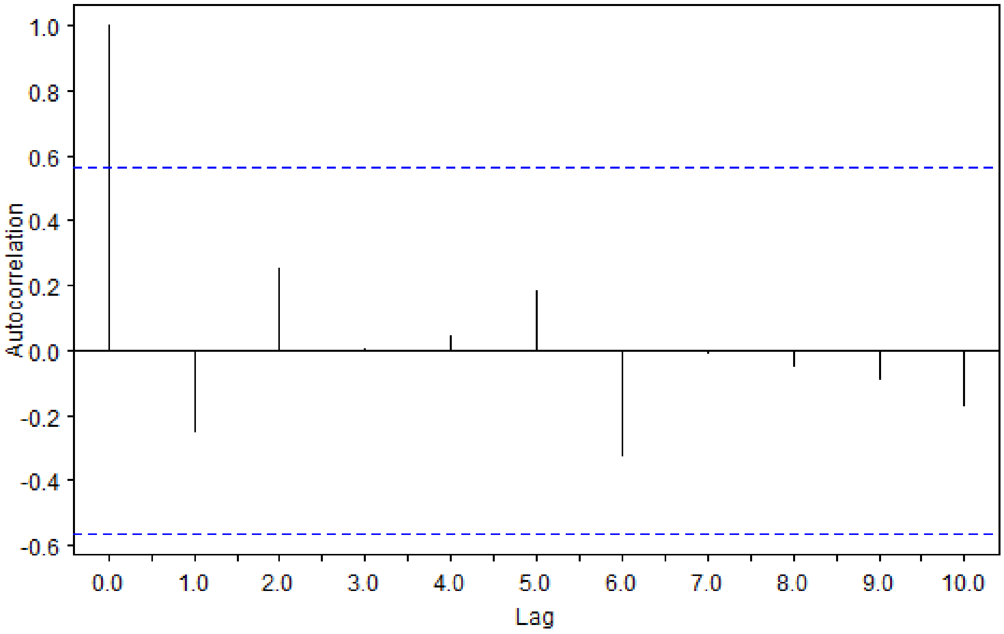

Figure G12. Autocorrelation plot of residuals for Ricker model of smolts per redd as a function of redd count and pHOS for Methow River Summer Chinook, 2006–2018 (without 2012). Blue lines mark 95% confidence interval under assumption of no autocorrelation.

Appendix H: Methow River Summer Steelhead

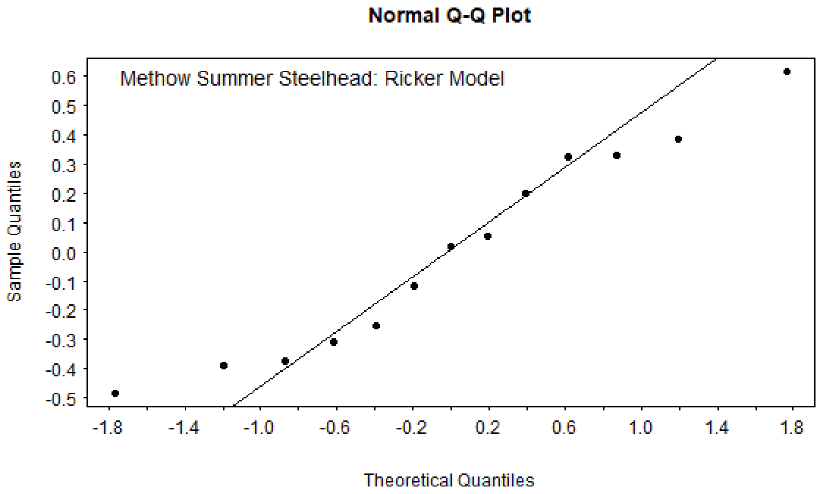

Figure H1. Normal quantile-quantile plot of residual from Ricker model of emigrant recruitment as a function of spawner abundance (stock) for Methow River Summer Steelhead, 2003–2015. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.9445, P=0.5183.

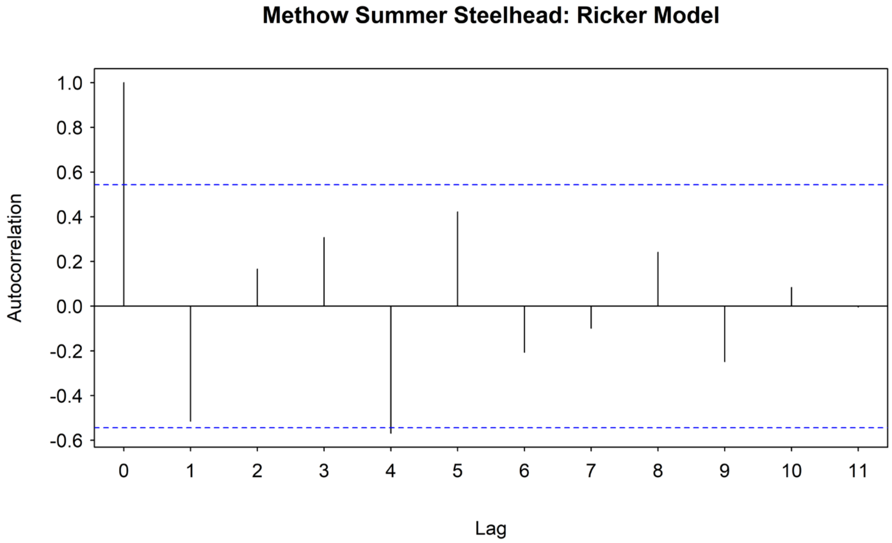

Figure H2. Autocorrelation plot of residuals for Ricker model of emigrant recruitment as a function of spawner abundance (stock) for Methow River Summer Steelhead, 2003–2015. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

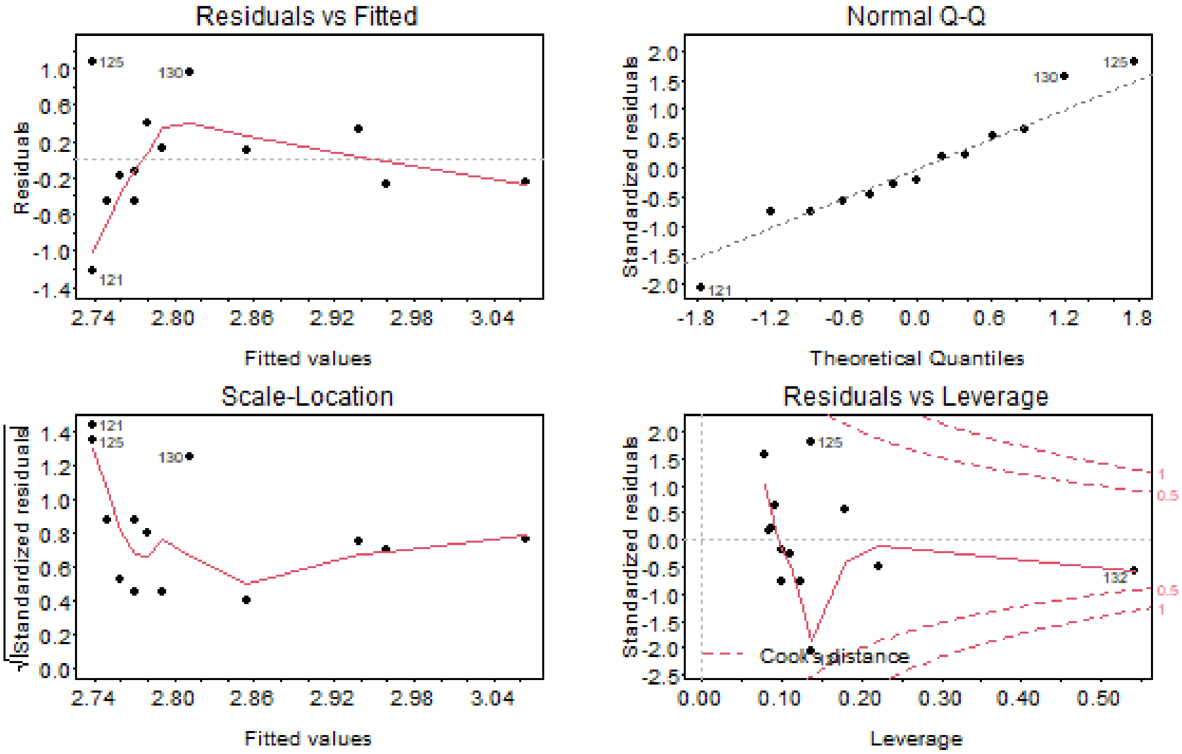

Figure H3. Residual plots for linear model of emigrants per redd (log scale) as a function of pHOS for Methow River Summer Steelhead, 2003–2015. Shapiro-Wilk test of normality of residuals: W=0.9579, P=0.7205.

Table H1. Pearson correlation coefficient (below diagonal) and two-sided P-value (above diagonal) for Ricker stock-recruitment model of emigrants per redd for Methow River Summer Steelhead, 2003–2015. Model form is: $ln(R/S) = \beta_0 - \beta S - \beta_2 P_{HOS}$. Correlation computed from bootstrap (3,000 bootstrap samples).

Parameter	β_0	β	β_2
β_0		0.0003	<0.0001
β	-0.0656		<0.0001
β_2	0.9637	-0.3156	

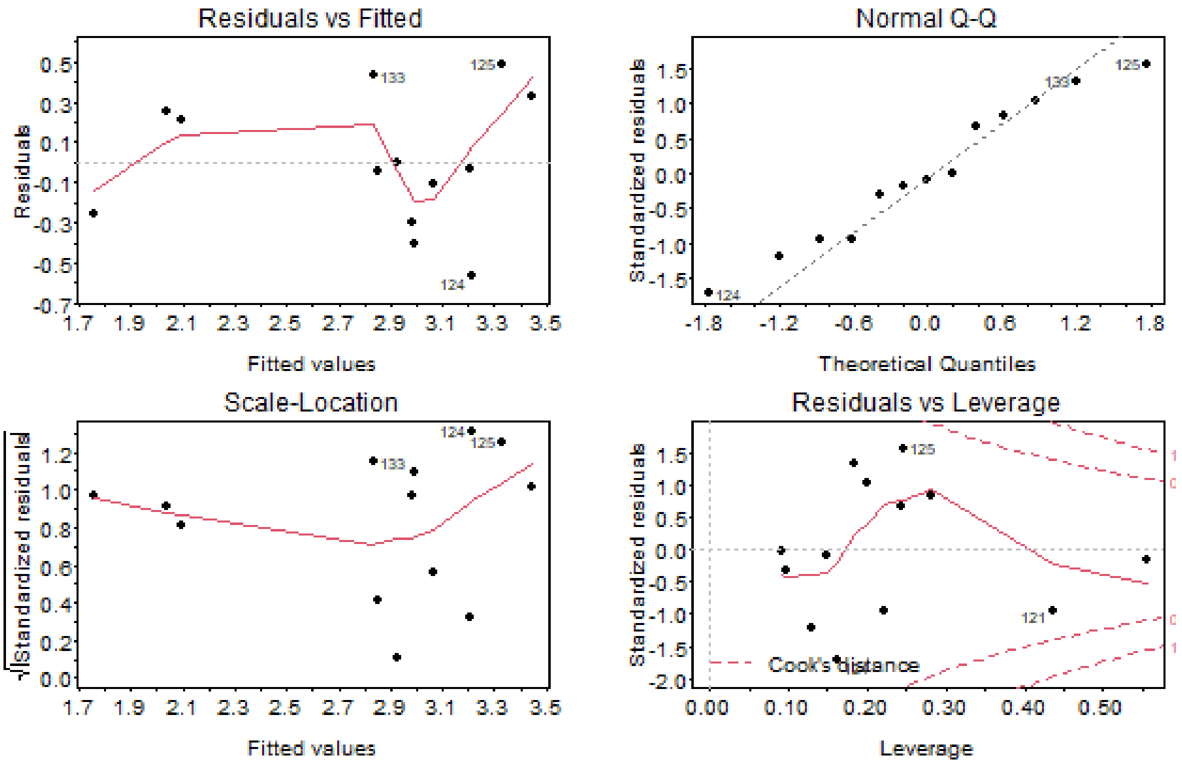

Figure H4. Residual plots for Ricker model of emigrants per redd as a function of redd count and pHOS for Methow River Summer Steelhead, 2003–2015. Shapiro-Wilk test of normality of residuals: W=0.9671, P=0.8578.

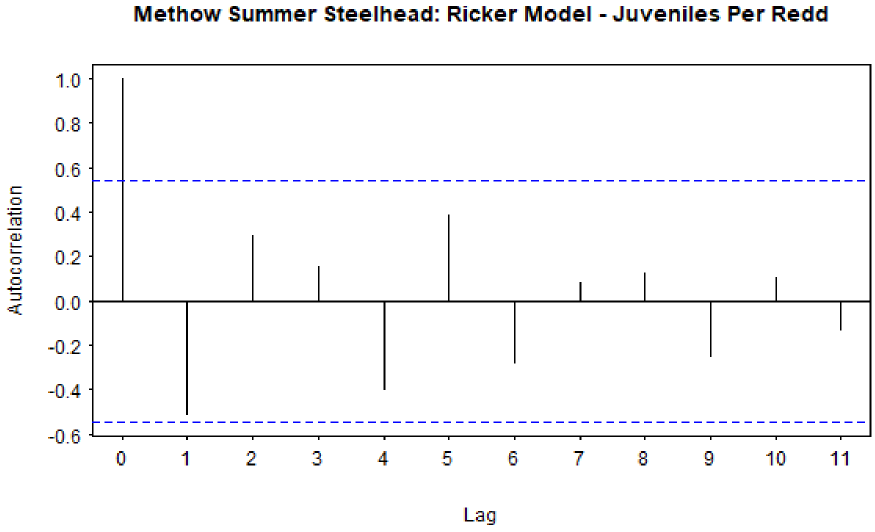

Figure H5. Autocorrelation plot of residuals for Ricker model of emigrants per redd as a function of redd count and pHOS for Methow River Summer Steelhead, 2003–2015. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

Appendix I: Twisp River Summer Steelhead

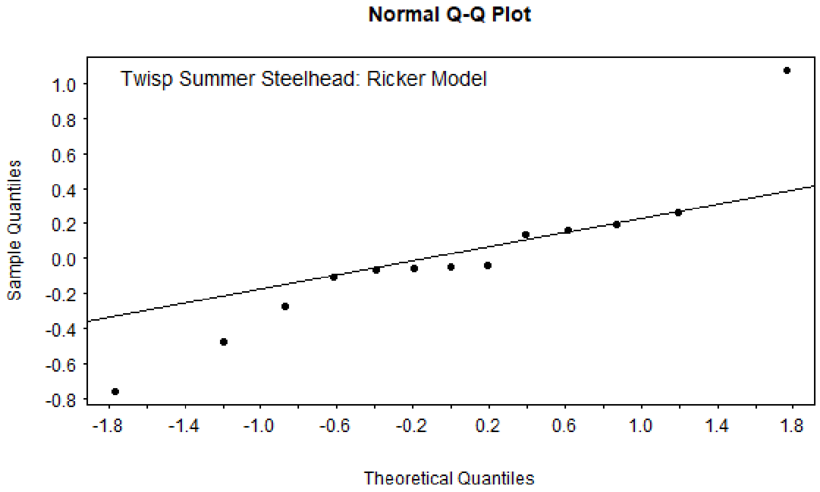

Figure I1. Normal quantile-quantile plot of residual from Ricker model of emigrant recruitment as a function of spawner abundance (stock) for Twisp River Summer Steelhead, 2003–2015, including brood year 2007. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.9011, P=0.1383.

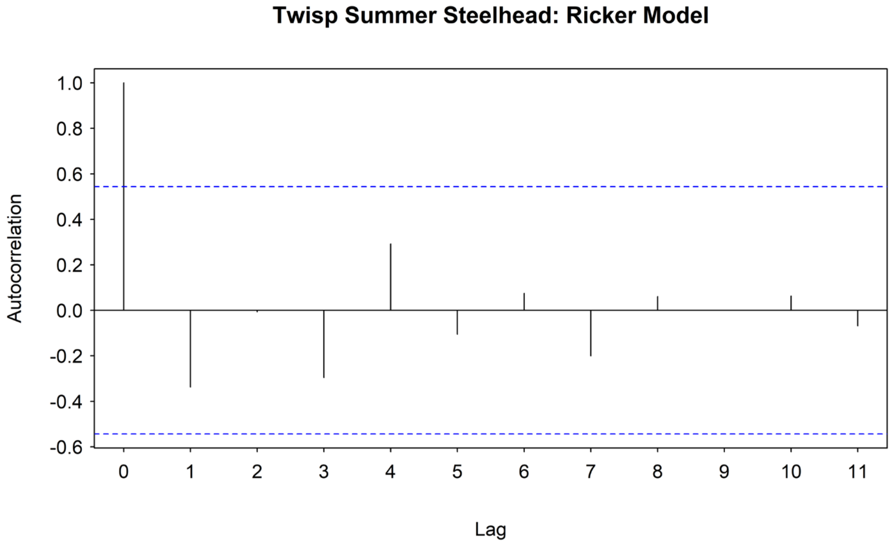

Figure I2. Autocorrelation plot of residuals for Ricker model of emigrant recruitment as a function of spawner abundance (stock) for Twisp River Summer Steelhead, 2003–2015, including brood year 2007. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

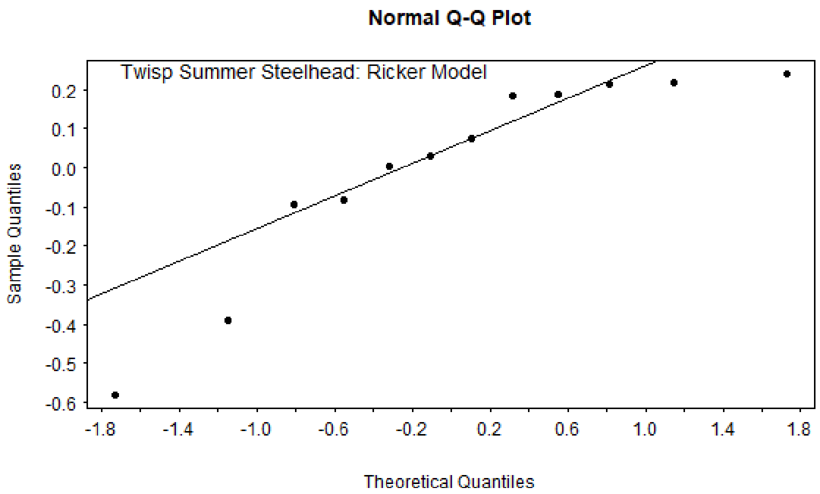

Figure I3. Normal quantile-quantile plot of residual from Ricker model of emigrant recruitment as a function of spawner abundance (stock) for Twisp River Summer Steelhead, 2003–2015, without brood year 2007. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.8429, P=0.0300.

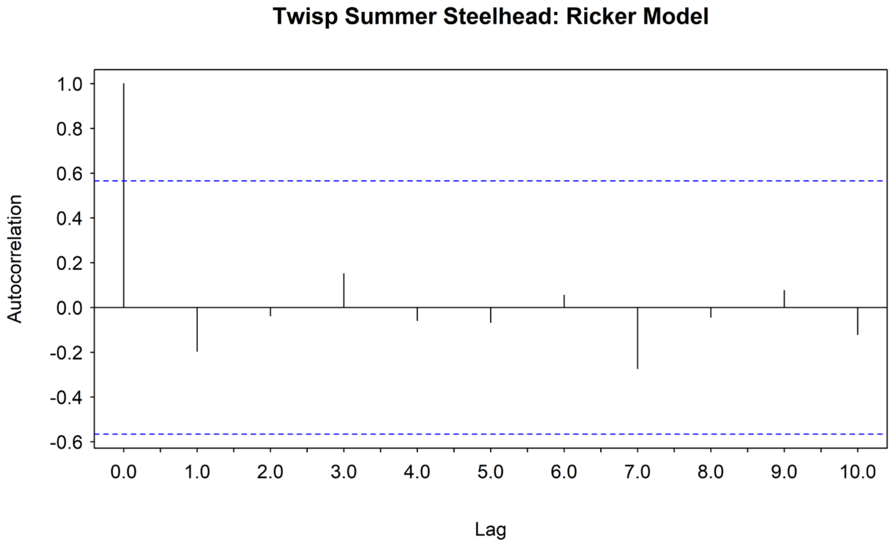

Figure I4. Autocorrelation plot of residuals for Ricker model of emigrant recruitment as a function of spawner abundance (stock) for Twisp River Summer Steelhead, 2003–2015, without brood year 2007. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

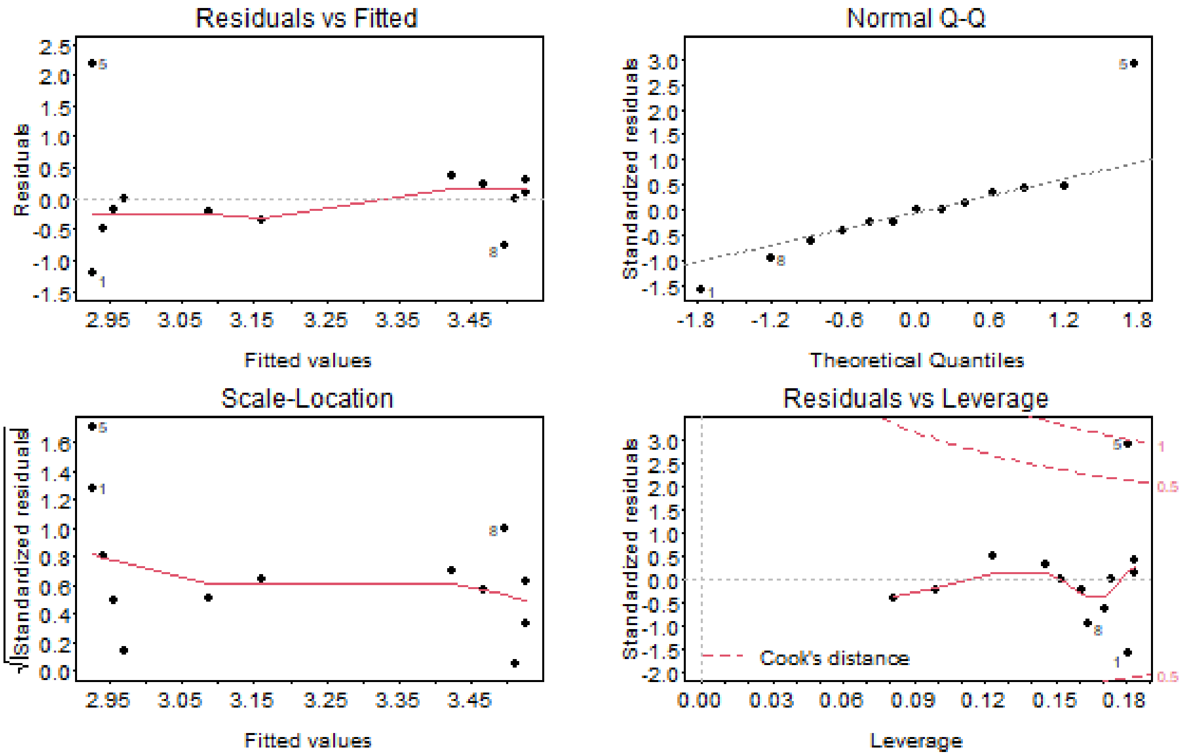

Figure I5. Residual plots for linear model of emigrants per redd (log scale) as a function of pHOS for Twisp River Summer Steelhead, 2003–2015, including brood year 2007. Shapiro-Wilk test of normality of residuals: W=0.8461, P=0.0254.

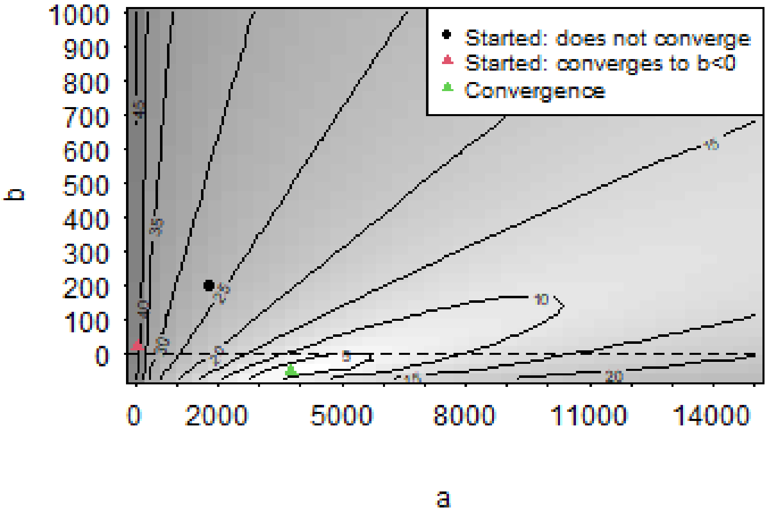

Figure I6. Negative log-likelihood surface and contour curves for Beverton-Holt model of emigrants, redd counts, and pHOS, using $\beta_2 = -0.1160$. Lighter regions indicate higher likelihood values. The green triangle (falls below b=0 line) indicates the parameter set that optimizes the likelihood. Data set = Twisp River Summer Steelhead, 2003–2015, including brood year 2007.

Table I1. Pearson correlation coefficient (below diagonal) and two-sided P-value (above diagonal) for Ricker stock-recruitment model of emigrants per redd for Twisp River Summer Steelhead, 2003–2015, including 2007. Model form is: $ln(R/S) = \beta_0 - \beta S - \beta_2 P_{HOS}$. Correlation computed from bootstrap (3,000 bootstrap samples).

Parameter	β_0	β	β_2
β_0		<0.0001	<0.0001
β	-0.6298		<0.0001
β_2	0.9280	-0.8606	

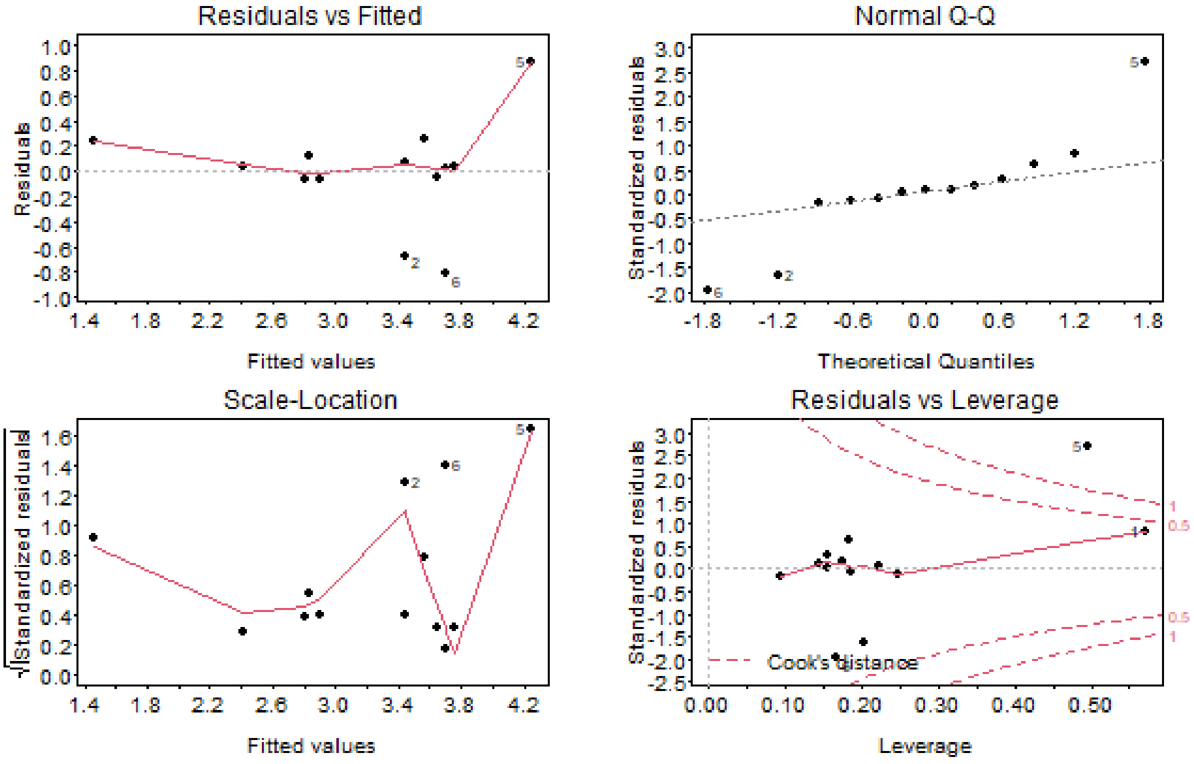

Figure I7. Residual plots for Ricker model of emigrants per redd as a function of redd count and pHOS for Twisp River Summer Steelhead, 2003–2015, including 2007. Shapiro-Wilk test of normality of residuals: W=0.8740, P=0.0592.

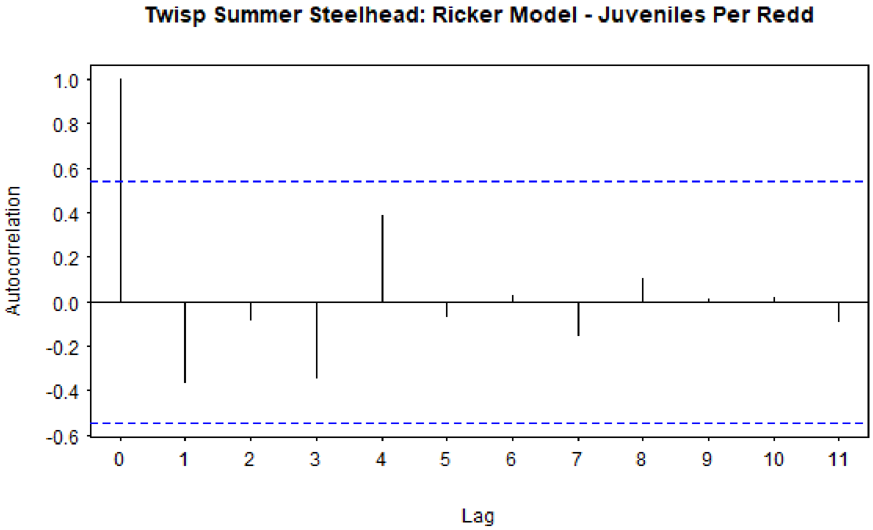

Figure I8. Autocorrelation plot of residuals for Ricker model of emigrants per redd as a function of redd count and pHOS for Twisp River Summer Steelhead, 2003–2015, including 2007. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

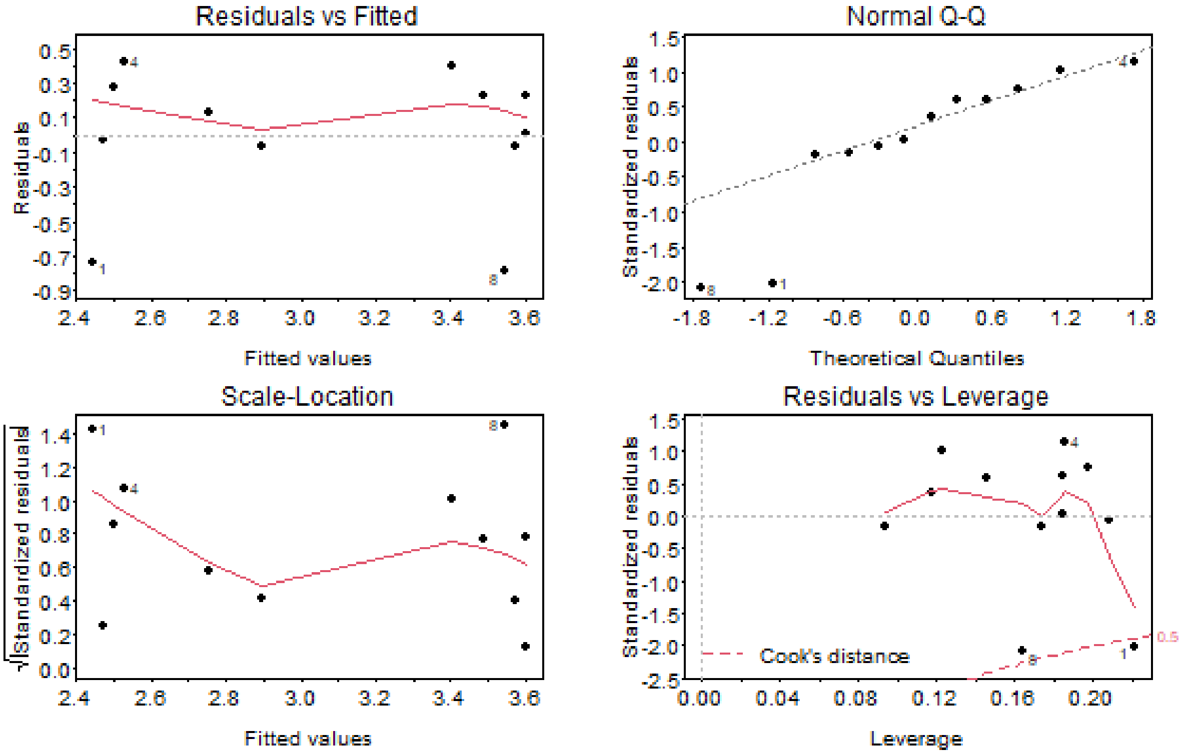

Figure I9. Residual plots for linear model of emigrants per redd as a function of pHOS for Twisp River Summer Steelhead, 2003–2015, omitting brood year 2007. Shapiro-Wilk test of normality of residuals: W=0.9230, P=0.3116.

Table I2. Pearson correlation coefficient (below diagonal) and two-sided P-value (above diagonal) for Beverton-Holt stock-recruitment model of smolts per redd for Twisp River Summer Steelhead, 2003–2015, omitting brood year 2007. Model form is: $ln(R/S) = ln(\alpha) - \beta_2 P_{HOS} - ln(\beta + S)$. Correlation computed from bootstrap (2,909 bootstrap samples).

Parameter	α	β	β_2
α		<0.0001	<0.0001
β	0.8976		<0.0001
β_2	0.8437	0.6772	

Table I3. Pearson correlation coefficient (below diagonal) and two-sided P-value (above diagonal) for Ricker stock-recruitment model of emigrants per redd for Twisp River Summer Steelhead, 2003–2015, omitting brood year 2007. Model form is: $ln(R/S) = \beta_0 - \beta S - \beta_2 P_{HOS}$. Correlation computed from bootstrap (3,000 bootstrap samples).

Parameter	β_0	β	β_2
β_0		<0.0001	<0.0001
β	-0.6094		<0.0001
β_2	0.9213	-0.8469	

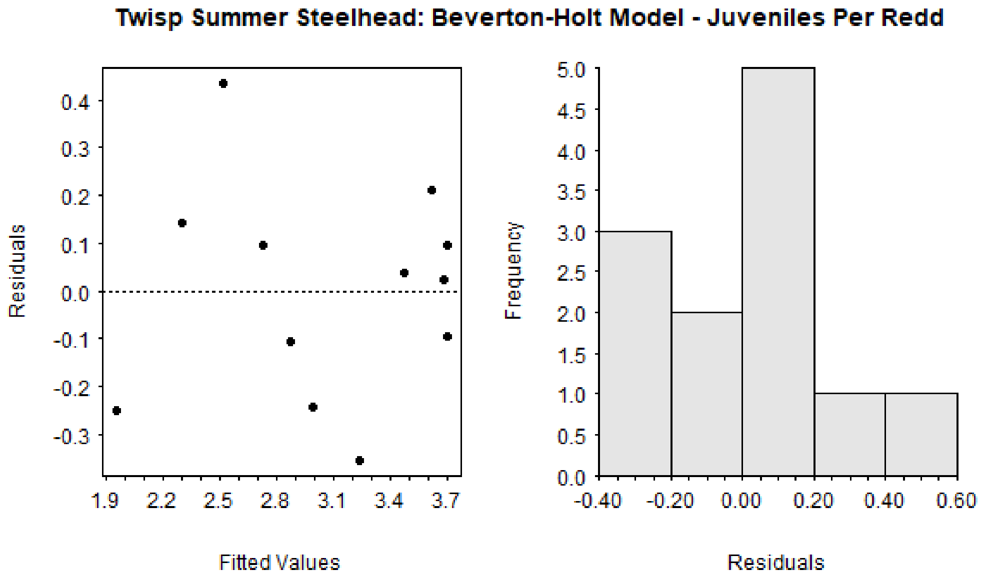

Figure I10. Residual plots for Beverton-Holt model of smolts per redd as a function of redd count and pHOS for Twisp River Summer Steelhead, 2003–2015, omitting brood year 2007. Shapiro-Wilk test of normality of residuals: W=0.9728, P=0.9377.

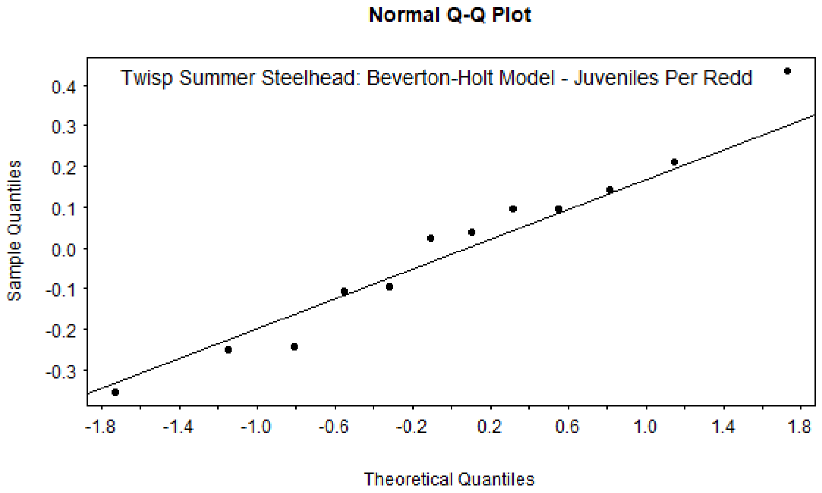

Figure I11. Normal quantile-quantile plot of residual from Beverton-Holt model of smolts per redd as a function of redd count and pHOS for Twisp River Summer Steelhead, 2003–2015, omitting brood year 2007. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: W=0.9728, P=0.9377.

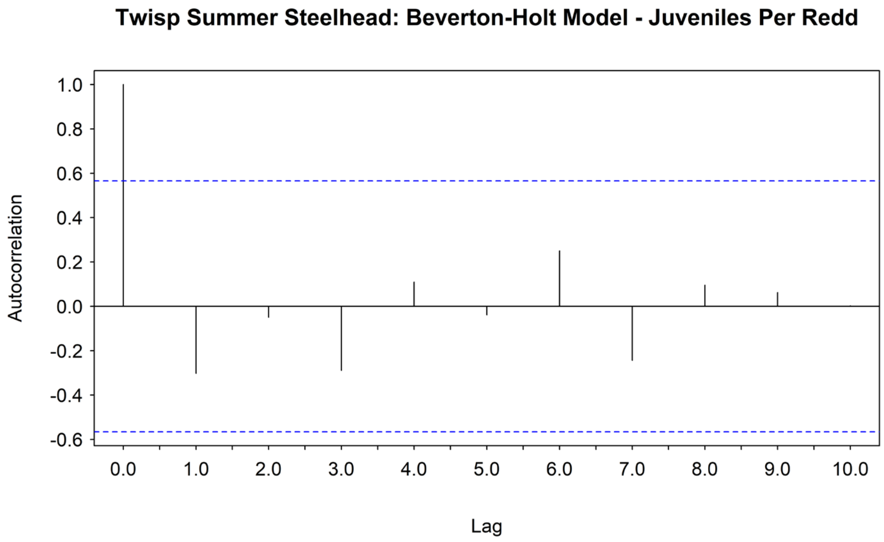

Figure I12. Autocorrelation plot of residuals for Beverton-Holt model of smolts per redd as a function of redd count and pHOS for Twisp River Summer Steelhead, 2003–2015, omitting brood year 2007. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

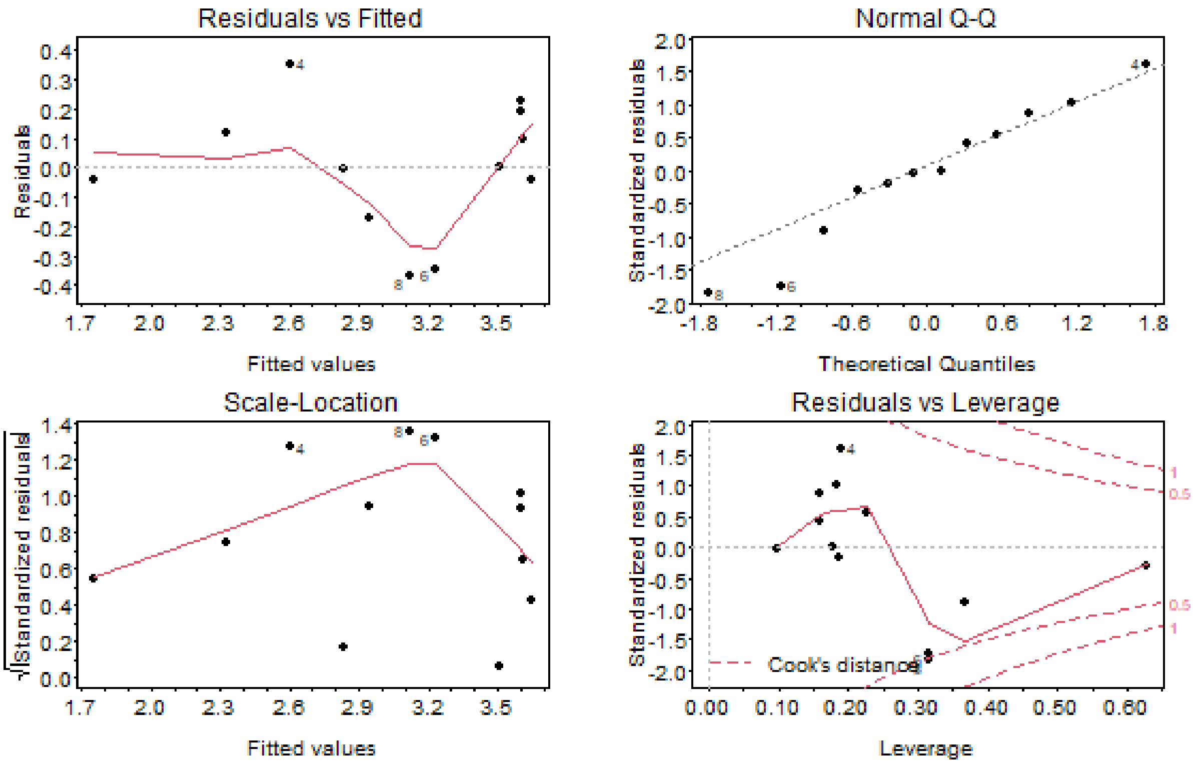

Figure I13. Residual plots for Ricker model of emigrants per redd as a function of redd count and pHOS for Twisp River Summer Steelhead, 2003–2015, omitting brood year 2007. Shapiro-Wilk test of normality of residuals: W=0.9588, P=0.7658.

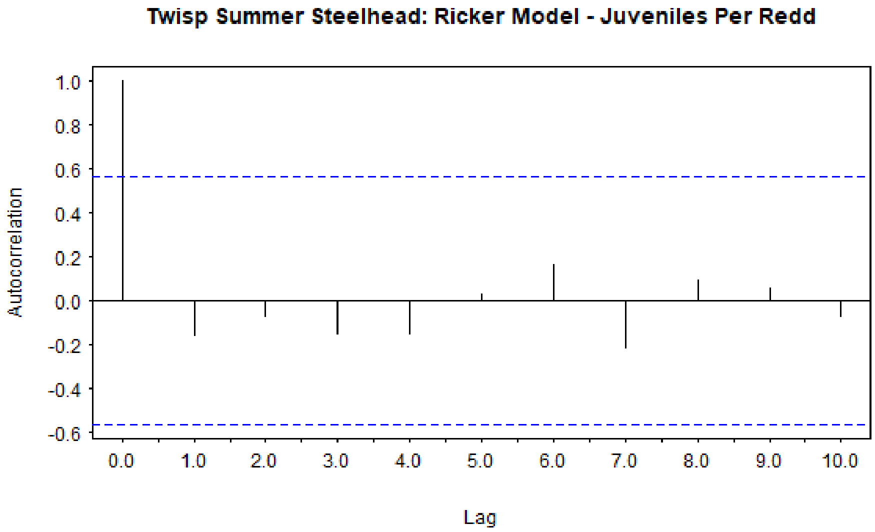

Figure I14. Autocorrelation plot of residuals for Ricker model of emigrants per redd as a function of redd count and pHOS for Twisp River Summer Steelhead, 2003–2015, omitting brood year 2007. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

Appendix B

Power Analysis for Effect of pHOS on Juvenile Productivity

COLUMBIA BASIN RESEARCH

Power Analysis for effect of pHOS on juvenile productivity

5 August 2021

TO: GREG MACKEY
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1325 Fourth Avenue, Suite 1515, Seattle, Washington 98101-2540

Introduction

There is concern that a higher proportion of hatchery-origin spawners (pHOS) on the spawning grounds may have a negative effect on juvenile productivity. Analysis of existing data has shown little to no evidence of a negative effect for Chinook Salmon and steelhead in the Upper Columbia tributaries but is limited by short time series and high observation error. A power analysis is warranted to determine the ability to detect a negative effect of pHOS, should it exist, and how many years of data collection are expected to achieve a useful level of power.

Statistical Methods

The statistical power was computed to detect a reduction in mean juvenile recruitment with Type I error probability of $\alpha = 0.10$ when the actual reduction in mean recruitment associated with a change in the pHOS level was 5%. Power was computed at varying sample sizes, where sample size = number of years of observations, and both with and without measurement error in the number of spawners and pHOS. The stock-recruitment model was a Ricker model with parameters taken from the Chiwawa River spring Chinook Salmon population. The Chiwawa population was selected because it has the longest time series of stock and juvenile recruitment data of the populations available and the stock recruitment curves have fit the juvenile productivity from this population relatively well (Buchanan and Townsend 2021). Power was calculated for sampling sizes from $N = 5$ to $N = 100$ years for varying levels of pHOS effect size, β_P.

Ricker Stock-Recruitment Model

The effect of pHOS is assessed after accounting for density dependence by either regressing the residuals from a stock-recruitment curve onto pHOS or else incorporating pHOS as a term in a stock-recruitment model. For the purposes of this power analysis, we used the latter approach and incorporated pHOS into the Ricker model as follows:

$$R = ae^{\beta_P P_{HOS}} \times Se^{-bS} \qquad (1)$$

where R = recruits, S = spawner abundance, a = increase in recruits per spawner at low levels of spawners, and b = intensity of the decrease in recruitment at high levels of spawners, and lognormal errors are assumed. The parameter β_P is the fixed effect of pHOS on recruitment. The maximum number of recruits is defined as $K = (a/b)e^{-1}e^{\beta_P P_{HOS}}$. This formulation of the model assumes that pHOS may lower the slope of the spawner-recruitment curve at low levels of spawner abundance if $\beta_P < 0$, which will also result in a lower maximum recruitment. Model (1) may be rewritten as a linear model as follows:

$$Y = ln(a) - bS + \beta_P P_{HOS} + \varepsilon \qquad (2)$$

where $Y = ln(R/S)$ and $\varepsilon \sim N(0, \sigma^2)$. A negative effect of pHOS is consistent with $\beta_P < 0$ and may be concluded when the upper limit of the $(1 - \alpha) \times 100\%$ bootstrap confidence interval is < 0 (i.e., the confidence interval is entirely below 0) for α = probability of a Type I error. Power was computed using simulations. Briefly, the number of spawners (S), pHOS, and smolt recruits were simulated from model (2) according to the existing data for the Chiwawa River spring Chinook Salmon population and for a specific value of the pHOS effect (β_P). Measurement error was added to the spawners and pHOS values, and the Ricker model in model (2) was fit to the resulting simulated data set. Statistical power was computed by the proportion of the simulated data sets that yielded a 90% bootstrap confidence interval that was completely < 0. One thousand (1,000) simulations were used. Details and results are provided below.

Simulations

For each simulation $i = 1, \ldots, 1000$, the total number of spawners S_{iy} and the number of natural origin spawners NOS_{iy} were simulated for each year y $(y = 1, \ldots, N)$ from independent negative binomial distributions whose parameters were estimated from observed Chiwawa spring Chinook Salmon data from 1991–2017 (Table 1 and Figure 1):

$$S_{iy} \sim NBin(n = 1.30, \mu\ = 722.81)$$

$$NOS_{iy} \sim NBin(n = 1.36, \mu\ = 287.57)$$

where μ is the mean and n is the dispersion parameter. Any simulated NOS value > S was replaced by a new simulation to ensure $NOS_{iy} \leq S_{iy}$ for each year y and simulation i. For each simulation i and year y, the simulated pHOS value was calculated as $pHOS_{iy} = {}^{HOS_{iy}}\!/\!_{S_{iy}}$, where $HOS_{iy} = (1 - NOS_{iy})S_{iy}$ is the simulated number of hatchery origin spawners.

For a given value of the pHOS effect β_P, the number of juvenile recruits was calculated according to

$$R_{iy} = S_{iy} \times exp\big(ln(a) - bS_{iy} + \beta_P P_{HOS,iy} + \varepsilon_{iy}\big) \tag{3}$$

where $\varepsilon_{iy} \sim N(0, \sigma^2)$. The parameters a, b, and σ^2 were estimated from the Chiwawa spring Chinook salmon population data from 1991–2017: $a = 138$, $b = 0.0011$, and $\sigma^2 = 0.1924$.

Measurement error was incorporated to the data set by simulating the size of measurement error for each component and adding it to the simulated "true" value. The data collected each year consisted of the number of natural origin spawners (NOS) and the number of hatchery origin spawners (HOS); the data reported are $S = NOS + HOS$ and $pHOS = HOS/S$. Thus, measurement error was simulated for NOS and HOS using reported precision levels of coefficient of variation (CV) = 0.07 for HOS and CV = 0.06 for NOS, based on Murdoch et al. (2019). Measurement error was also simulated for juvenile recruitment R using CV = 0.11, based on the mean of the stock-averaged CV values reported for spring Chinook Salmon from the Twisp and Methow populations (rotary screw trap data provided by WDFW). This yielded the "observed" values for each simulation i and year y as follows:

Observed NOS: $\widetilde{NOS}_{iy} = NOS_{ij} + e_{NOS,iy}$ where $e_{NOS,iy}$ is randomly generated from the $N\big(0, \sigma^2_{NOS,iy}\big)$ distribution with $\sigma^2_{NOS,iy} = NOS^2_{iy} \times CV^2_{NOS}$

Observed HOS: $\widetilde{HOS}_{iy} = HOS_{ij} + e_{HOS,iy}$ where $e_{HOS,iy}$ is randomly generated from the $N\big(0, \sigma^2_{HOS,iy}\big)$ distribution with $\sigma^2_{HOS,iy} = HOS^2_{iy} \times CV^2_{HOS}$.

Observed S: $\tilde{S}_{iy} = \widetilde{NOS}_{iy} + \widetilde{HOS}_{iy}$

Observed pHOS: $\widetilde{pHOS}_{iy} = \frac{\widetilde{HOS}_{iy}}{\tilde{S}_{iy}}$

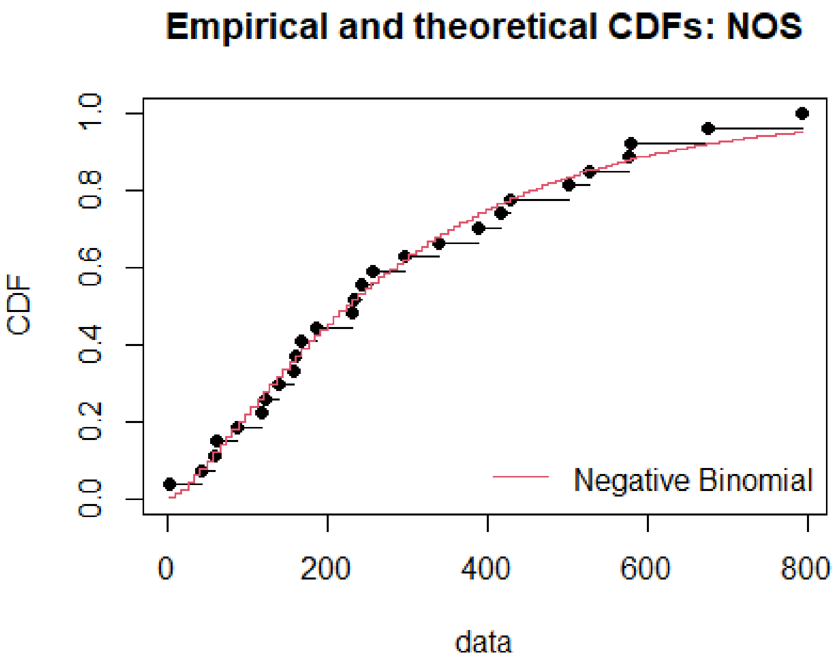
Observed R: $\tilde{R}_{iy} = R_{ij} + e_{R,iy}$ where $e_{R,iy}$ is randomly generated from the $N\big(0, \sigma^2_{R,iy}\big)$ distribution for $\sigma^2_{R,iy} = R^2_{iy} \times CV^2_R$.

For each simulated data set, the Ricker model in equation (2) was fit to the simulated observations of spawner, recruit, and pHOS data both with and without measurement error in the spawners and pHOS values. For each simulation, the bootstrap was used to calculate a 90% bootstrap confidence interval for the pHOS regression coefficient β_P using 1,000 bootstrap samples. The statistical power was computed as the proportion of the simulated data sets for which the upper limit of the 90% bootstrap confidence interval for β_P was <0. Because the power estimates were the result of simulations, the bootstrap was again used on the simulated data sets to generate 95% confidence intervals on the power estimates.

Table 1. Spawner and juvenile recruit data for Chiwawa Spring Chinook Salmon. Value of HOS was calculated as S*pHOS, and value of NOS was calculated as S-HOS.

Brood Year	Spawners (S)	Smolts (R)	pHOS	HOS	NOS
1991	242	42,525	0.00	0	242
1992	676	39,723	0.00	0	676
1993	233	8,662	0.01	2	231
1994	184	16,472	0.33	61	123
1995	33	3,830	1.00	33	0
1996	58	15,475	0.29	17	41
1997	182	27,555	0.67	122	60
1998	91	19,257	0.35	32	59
1999	94	10,931	0.07	7	87
2000	346	39,812	0.33	114	232
2001	1,725	79,814	0.71	1,225	500
2002	707	82,845	0.64	452	255
2003	270	16,559	0.38	103	167
2004	851	67,491	0.32	272	579
2005	599	58,833	0.77	461	138
2006	529	41,951	0.78	413	116
2007	1,296	23,766	0.88	1,140	156
2008	1,158	32,849	0.84	973	185
2009	1,347	32,979	0.78	1,051	296
2010	1,094	47,511	0.62	678	416
2011	2,032	37,185	0.61	1,240	792
2012	1,478	34,334	0.61	902	576
2013	1,378	39,396	0.69	951	427
2014	975	37,170	0.46	449	526
2015	967	53,344	0.65	629	338
2016	546	31,300	0.29	158	388
2017	431	39,015	0.63	272	159

(a) NOS



(b) S

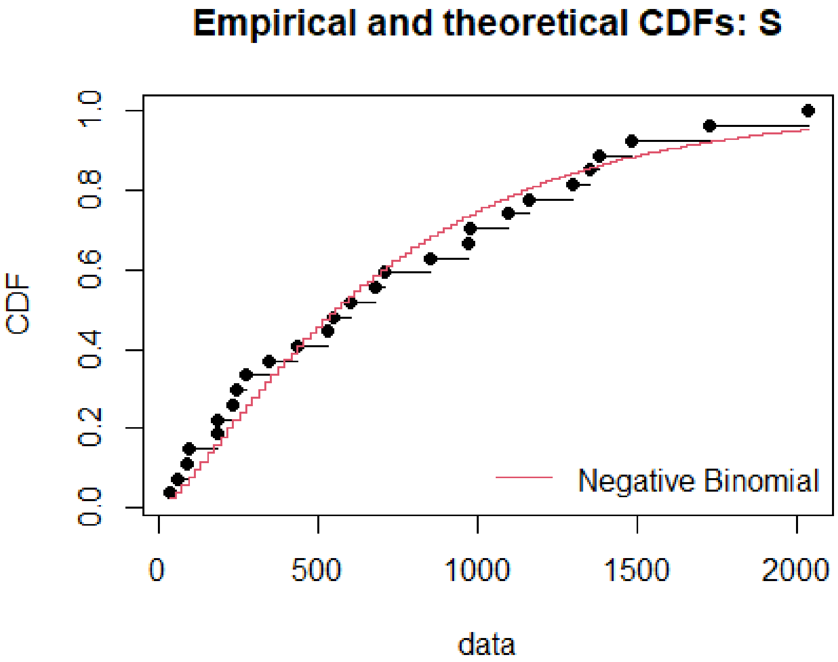


Figure 1. Comparison of empirical and fitted negative binomial cumulative distribution functions (CDFs) for natural origin spawners (NOS) data (a) and total spawners (S) data (b). Black dots represent observed data, and horizontal lines represent the distance between observations in empirical step-wise distribution.

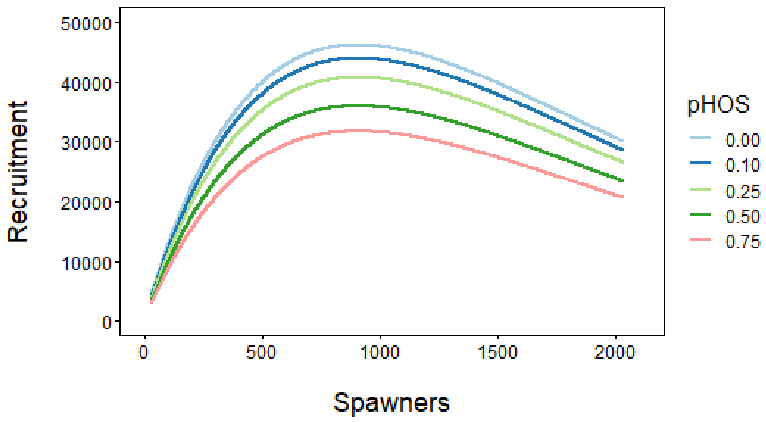
pHOS Effect Size

Figure 2 demonstrates how the value of pHOS is expected to lower predicted recruitment across a wide range of spawner levels for a hypothetical population for two fixed values of the effect size, β_P, according to the model in equation (2). When β_P is farther from 0 (e.g., $\beta_P =$ -0.5, Figure 2a), a small change in pHOS is expected to produce a larger reduction in recruitment than when β_P is closer to 0 (e.g., $\beta_P =$ -0.1, Figure 2b). Larger effects are detectable with smaller sample sizes than smaller effects.

Statistical power is defined in this setting to be the probability of detecting a negative effect of pHOS given that pHOS actually has a negative effect. Calculating it requires specifying both the true effect size, i.e., the true value of β_P, and the change in pHOS value for which the effect is expected to occur. The value of the pHOS effect that is of interest is the effect necessary to reduce recruitment by 5% for a given level of spawners or stock. Over time, such a reduction will result in a smaller population that will be at increased risk of extinction.

Although any reduction in recruitment is a concern, a reduction in recruitment that occurs for a small change in pHOS values will be harder to avoid than the same reduction that occurs only for a large change in pHOS values. Thus, it is also necessary to specify the difference in pHOS values over which the recruitment reduction is expected to occur. For example, a 5% reduction recruitment that is associated with a difference in pHOS of only 0.1 (e.g., an increase in pHOS from 0.2 to 0.3) represents a stronger pHOS effect than a 5% reduction in recruitment associated with a difference in pHOS of 0.5 (e.g., an increase in pHOS from 0.2 to 0.7). Figure 3 demonstrates how the level of pHOS and the size of the effect (β_P) combine to lower the predicted recruitment at a fixed level of spawner. In Figure 3, the predicted recruitment from the Ricker model achieved at $S =$ 1,000 spawners is reduced by 5% from the baseline setting (i.e., no hatchery origin spawners, pHOS=0) at a lower value of pHOS when β_P is more negative, indicated by the colored curves crossing the dashed line. When β_P is closer to 0, it requires a higher value of pHOS to result in a 5% reduction in recruitment from a setting without hatchery origin spawners. Thus, values of β_P that are more negative may be considered more extreme effects of pHOS than values of β_P that are closer to 0.

(a) Predicted Recruitment for β_P = -0.5



(b) Predicted Recruitment for β_P = -0.1

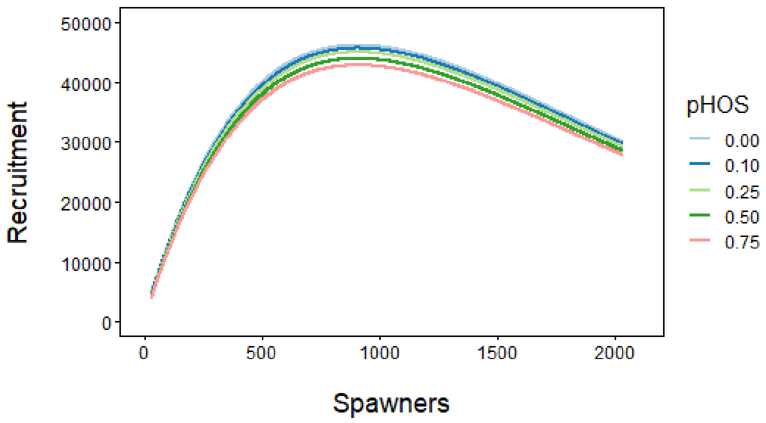


Figure 2. Predicted juvenile recruitment from Ricker model (2) at various levels of spawners S and pHOS for (a) β_P = -0.5 and (b) β_P = -0.1. Ricker model parameters: a = 138, b = 0.0011.

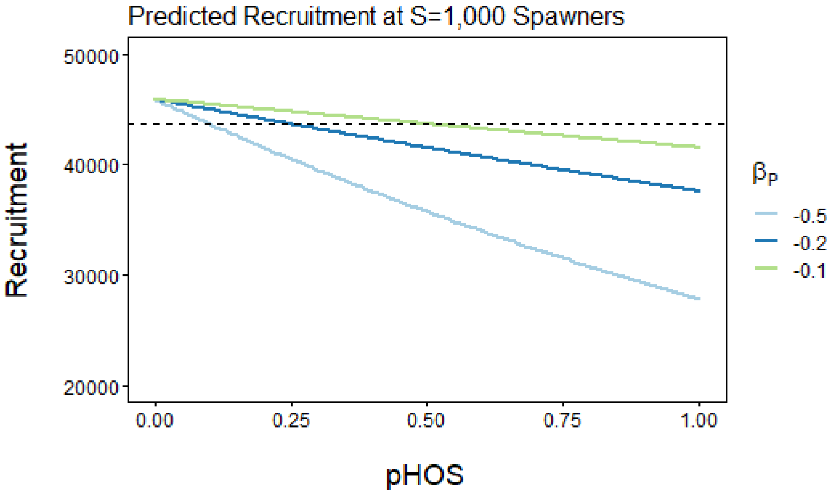


Figure 3. Predicted juvenile recruitment from Ricker model at S=1,000 spawners for various levels of pHOS and β_P, the effect of pHOS on recruitment. Dashed line indicates 5% reduction in recruitment compared to pHOS=0. Ricker model parameters: a = 138, b = 0.0011.

The relationship between the reduction in mean recruitment, the change in pHOS values, and the effect size β_P can be derived as follows: Let R_1 be the mean recruitment for a given number of spawners at a baseline pHOS value of P_1, and R_2 be the mean recruitment for a given number of spawners for a treatment pHOS value of P_2; that is:

$$R_1 = ae^{\beta_P P_1} Se^{-bS}$$

and

$$R_2 = ae^{\beta_P P_2} Se^{-bS}.$$

R_2 can be expressed in terms of R_1 by taking the ratio of R_2/R_1 as follows:

$$\frac{R_2}{R_1} = \frac{ae^{\beta_P P_2} Se^{-bS}}{ae^{\beta_P P_1} Se^{-bS}} = \frac{e^{\beta_P P_2}}{e^{\beta_P P_1}} = e^{\beta_P (P_2 - P_1)}$$

which leads to:

$$R_2 = R_1 e^{\beta_P (P_2 - P_1)}$$

or

$$R_2 = R_1 e^{\beta_P \Delta P_{HOS}}$$

where $\Delta P_{HOS} = P_2 - P_1$. Then if R_2 is a 5% reduction from R_1, we have:

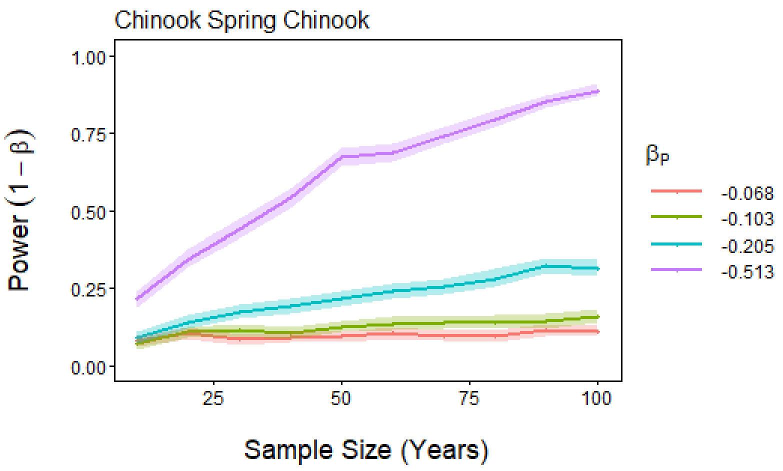
$$\beta_P = \frac{ln(0.95)}{\Delta P_{HOS}}. \tag{6}$$

Thus, for a 5% reduction in recruitment for a change in pHOS of $\Delta P_{HOS} = 0.1$, the pHOS effect size is $\beta_P = -0.513$, whereas for $\Delta P_{HOS} = 0.5$, the pHOS effect size is only $\beta_P = -0.103$. We calculated power to detect a 5% reduction in recruitment for a change in pHOS of $\Delta P_{HOS} = 0.1, 0.25, 0.50$, and 0.75. These settings are consistent with a pHOS effect of $\beta_P = -0.513, -0.205, -0.103$, and -0.068, respectively.

Results

Simulated statistical power to detect a negative effect of pHOS was consistently ≤ 0.32 for all sample sizes considered ($N \leq 100$ years) and for all but the most extreme pHOS effect sizes considered (i.e., $\beta_P = -0.068$ to -0.205), both with and without measurement error (Figure 4). For the largest effect size ($\beta_P = -0.513$), simulated power was as high as 0.54 for a sample size of $N = 40$ years without measurement error, and only slightly lower at 0.52 for $N = 40$ years when measurement error was incorporated into the simulations. Achieving power of at least 0.70 required as many as $N = 70$ years of data. Power greater than 0.80 required 90 years of data. These simulations defined detection of a negative effect of pHOS as a 90% bootstrap confidence interval that was entirely less than 0.

(i) Without measurement error



(ii) With measurement error

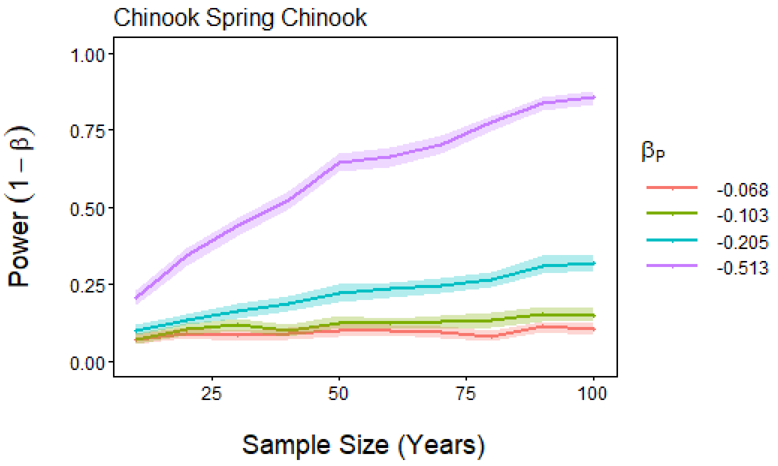


Figure 4. Statistical power of detecting a negative effect of pHOS for various levels of pHOS effect size β_P with (i) and without (ii) measurement error in stock and recruitment data. Power based on 1,000 simulations of stock (spawners) and juvenile recruitment data using Ricker stock-recruitment model fit to data from Chiwawa spring Chinook Salmon, 1991-2017: a = 138, b = 0.0011, σ = 0.4386 (equation (2)). Type I error probability = 0.10. Measurement error (ii) was incorporated into simulated observations of

spawner and recruitment data using coefficient of variation (CV)=0.07 for HOS, CV=0.06 for NOS, and CV=0.11 for recruitment. Shaded region = 95% bootstrap confidence interval using 300 bootstrap samples from the simulated data.

Conclusions

Simulated power to detect a negative effect of pHOS on juvenile recruitment was low for all but the strongest effect sizes and for studies shorter than approximately 70 years. The low power values resulted from the high variability in residuals from the Ricker stock-recruitment model ($\sigma = 0.4386$) estimated from its fit to 27 years of data from the Chiwawa Spring Chinook salmon population (1991–2017).

The Chiwawa data set is the largest of the juvenile productivity data sets available for Chinook salmon and steelhead. The alterative data sets either failed to meet the modeling assumptions for the Ricker model (e.g., Methow and Twisp steelhead) or else had higher error variance about the fitted Ricker model (e.g., other spring Chinook salmon populations) than seen for the Chiwawa spring Chinook salmon population. Thus, it is expected that the power to detect a negative effect of pHOS on juvenile productivity would be highest for the Chiwawa spring Chinook population. Low power for this population would be compounded for the other populations with shorter time series or more complex population dynamics. As a consequence, it is unlikely that assessment of stock-recruitment curves similar to the Ricker model will be sufficient to detect a negative effect of pHOS in time to mediate any such effect. Other methods of monitoring and assessment are recommended to evaluate the effect of pHOS on juvenile productivity of anadromous salmonids in the upper Columbia River basin.

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The Effect of Hatchery Programs on Proportionate Natural Influence (PNI) in the Upper Columbia Basin

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Abstract

Hatchery programs and natural populations in the Wenatchee and Methow subbasins were managed under the Proportionate Natural Influence (PNI) strategy, whereby gene flow between the hatchery and natural populations was manipulated to achieve greater overall genetic influence from the natural population as opposed to the hatchery population. The target PNI value was 0.67. Steelhead programs in the Wenatchee and Methow had PNI averages or medians below 0.67. The new management regime for steelhead in the Methow was not initiated until 2017. Therefore, data in this report do not reflect the future management of the steelhead in the Methow subbasin for gene flow. Spring Chinook Salmon PNI in the Wenatchee Subbasin was below 0.67 for all populations under the contemporary management strategy but exceeded 0.50 in all cases. Methow subbasin spring Chinook PNI was 0.29, and has not increased appreciably in the two years of adult returns following reduction in program sizes in 2013. Wenatchee and Methow summer Chinook both had PNI means that exceeded 0.67. Both of these programs appear successful in meeting PNI objectives with the Wenatchee PNI an impressive 0.87. The results of this analysis indicate that the Spring Chinook and steelhead programs require adjustment to meet the PNI targets. In some cases, the PNI values may improve as new management strategies mature. The Methow steelhead and particularly Methow spring Chinook may require substantial management changes in order to achieve the gene-flow objectives. In general, PNI targets were not met for small populations (spring Chinook Salmon and steelhead) but were for large populations (summer Chinook Salmon).

Introduction

Conservation hatchery programs integrate the spawning of hatchery- and natural-origin fish into a single gene pool. However, the gene flow among origins has the potential to impose genetic risk associated with domestication selection. Hatchery programs and natural populations in the Wenatchee and Methow subbasins were managed under the Proportionate Natural Influence (PNI; HSRG 2009) strategy, whereby gene flow between the hatchery and natural populations is manipulated to achieve greater overall genetic influence from the natural population as opposed to the hatchery population. Two components may be manipulated to achieve a desired PNI: the proportion of hatchery-origin spawners (pHOS) in nature and the proportion of natural-origin broodstock (pNOB) in the hatchery. The PNI is an index of domestication selection that is relatively easy to measure and ranges from 0 to 1. A PNI of 0 indicates that all of the selection is from gene flow among hatchery-origin fish. In contrast, a PNI of 1 indicates that all of the selection is from gene flow among natural-origin fish. Management targets of > 0.67 have been established for PNI for the various programs under the Endangered Species Act and for many unlisted programs of conservation importance (Mobrand et al. 2005; Paquet et al. 2011; Pearsons et al. 2020). These targets are intended to minimize the risk of domestication selection which could decrease the fitness of fish spawning in the natural environment. We estimated PNI for the spring Chinook Salmon, summer Chinook Salmon, and summer steelhead populations and programs in the Wenatchee and Methow subbasins that have PNI targets of 0.67.

Study Area

The study examined PNI values in the Wenatchee and Methow subbasins. In the Wenatchee, PNI for spring Chinook populations in the Chiwawa River, Nason Creek, and White River was estimated separately, plus PNI was estimated for the population upstream of Tumwater Dam. In the Methow Subbasin, PNI for spring Chinook was evaluated at the subbasin level, according to terms in the ESA permits. PNI for summer steelhead was evaluated at the subbasin level in the Wenatchee and Methow subbasins. Similarly, PNI for summer Chinook was evaluated at the subbasin level in the Wenatchee and Methow subbasins.

Methods

Data Collection and Derived Metrics

Information needed to estimate PNI included the number of natural-origin fish in hatchery broodstock (NOB), the number of hatchery-origin fish in hatchery broodstock (HOB), the number of hatchery-origin spawners (HOS), and the number of natural-origin spawners (NOS). From these, we calculated the proportion of natural-origin fish in hatchery broodstock ($pNOB = NOB / (NOB + HOB)$), the proportion of hatchery-origin fish in hatchery broodstock ($pHOB = HOB / (NOB + HOB)$), the proportion of hatchery-origin spawners ($pHOS = HOS / (NOS + HOS)$), and the proportion of natural-origin spawners ($pNOS = NOS / (NOS + HOS)$). For all programs, pNOB and pHOB were estimated based on the total number of adults collected for broodstock.

Methods used to estimate NOS and HOS varied depending on stock. Spawning-ground surveys were used to estimate NOS and HOS for spring and summer Chinook Salmon in the Wenatchee and Methow subbasins. For most stocks, these surveys have been conducted since at least 1981 to determine the abundance, distribution, and origin of spring and summer Chinook Salmon spawners. Field methods were consistent with those described in Gallagher et al. (2007) and Murdoch et al. (2010). Surveyors walked or floated the entire distribution of Chinook Salmon spawning habitat and identified and counted new redds weekly throughout the spawning season. Redds were flagged and locations recorded on a Global-Positioning-System device to avoid recounting in subsequent surveys. Chinook Salmon carcasses were also counted and examined to determine sex, origin (e.g., hatchery or natural origin; nearly all hatchery-origin fish were marked with a tag such as a coded wire tag (CWT) and/or adipose fin clipped prior to release), size, distribution, and other biological characteristics. In addition, scales collected from carcasses were used to determine fish age and confirm origin.

We expanded spawning-ground data into derived estimates of total adult abundance (combined hatchery- and natural-origin adults), NOS abundance, and HOS abundance. We assumed that each female made one redd (Murdoch et al. 2009a), female carcass location was a good surrogate for spawning location by origin (Murdoch et al. 2009b), and that redd counts and carcass data could be used to estimate spawning escapement for hatchery- and natural-origin Chinook Salmon (Murdoch et al. 2010). Total adult spawning abundance was estimated by multiplying redd counts by the male:female sex ratio estimated at Dryden Dam (for Wenatchee River summer Chinook Salmon), Tumwater Dam (for Wenatchee River spring Chinook Salmon), or at Wells Dam (for Methow programs). Adult fish removed from the natural spawning population by gene-flow management and broodstock-collection activities were subtracted from the data used to estimate the sex ratios. NOS and HOS abundances were estimated by multiplying the respective proportion of natural-origin carcasses and hatchery-origin carcasses by the total adult spawning abundance. From these data and the equations described above, we calculated pNOS and pHOS for each Chinook salmon program.

Several methods and combinations of methods have been used to estimate steelhead NOS and HOS abundances within the Wenatchee and Methow subbasins. Within the Wenatchee River Subbasin, spawning escapements have been estimated based on run reconstruction and mark-recapture (Passive Integrated Transponder (PIT) tag) models. Prior to 2014, only run reconstruction was used to estimate steelhead escapements within the Wenatchee River. Steelhead run reconstruction was based on the number of hatchery- and natural-origin steelhead observed at Priest Rapids and Wells dams and apportioned to Upper Columbia subbasins based on previously conducted radio-telemetry studies (English et al. 2001; 2003) and differences in dam counts. Run escapement to each of the subbasins was then adjusted for adult management, harvest, broodstock collection, and an assumed 10% pre-spawn mortality to estimate spawning escapement. Beginning in 2014, steelhead escapements in tributaries were estimated using PIT-tag mark-recapture techniques (Truscott et al. 2017), while observer-efficiency-expanded redd counts were used to estimate escapements in the mainstem Wenatchee River (See 2021). Total redd counts were also used to estimate escapements in the lower portions of the main tributaries (downstream from the PIT-tag interrogation sites). Redd counts were expanded by multiplying redd counts by the male:female sex ratio estimated based on detections of PIT-tagged males and females within the Wenatchee River Subbasin.

Steelhead spawning escapements in the Methow River Subbasin were based on four population components: (1) conservation programs including the Twisp River and Winthrop National Fish Hatchery (WNFH), (2) a safety-net program that included Methow River releases from Wells Hatchery, (3) annual spawning component of the upper Methow River and tributaries (also included Beaver, Gold, and Libby creeks), and (4) annual spawning component of the mainstem Methow River downstream from the Methow Fish Hatchery. Overall NOS and HOS abundances were estimated based on PIT-tag detections at the lower Methow River instream PIT-tag array (LMR) expanded by estimated efficiency of the array and the PIT-tag rate of hatchery- and natural-origin steelhead tagged at Priest Rapids Dam within each return year since 2014. All adipose fin-clipped steelhead lacking a CWT were assumed to be from the Wells safety-net program, while those with a CWT were assumed to be from the WNFH conservation program. Steelhead with a CWT but without an adipose fin-clip were assumed to be from the Twisp River conservation program. Some returning fish from previous marking strategies (e.g., yellow elastomer tags) were included as conservation program fish if their parental origin was greater than or equal to 0.5 natural-origin steelhead. Similarly, known conservation program fish from other subbasins (e.g., Omak Creek in the Okanogan River Subbasin) were pooled with other conservation program returns in the Methow River Subbasin. All other hatchery-origin steelhead were considered safety-net program fish for modeling purposes.

After estimating the total steelhead escapement to the Methow River Subbasin, escapement estimates for the upper Methow River and tributaries were subtracted from the LMR-generated subbasin estimate. This provided a separate escapement estimate for the conservation (upper Methow River and tributaries) and management (lower Methow River mainstem) areas. From the management area estimate, we subtracted all known steelhead removed during broodstock collection or adult-management activities, including sport fisheries, broodstock collections, or management (removal) of excess hatchery-origin fish at the Methow Fish Hatchery and WNFH. From the conservation area estimate, we subtracted all known steelhead removed at the Twisp River weir for broodstock or to reduce escapement of hatchery-origin fish. The proportion of natural-origin steelhead in the broods from which the returning conservation program adults originated in each spawn year was estimated as an average of the pNOB for each returning age class and program (i.e., Twisp 1- and 2-salt, WNFH 1- and 2-salt). The genetic parentage of safety-net program adults was assumed to be 75% safety-net program fish and 25% conservation program fish for broods prior to 2018.

Data Analysis

Although PNI is estimated using pNOB and pHOS, different methods can be used to calculate PNI. According to authorized annual take permits, PNI is calculated using the PNI approximate equation 11 (HSRG 2009). However, in this report, we used Ford's (2002) equations 5 and 6 with a heritability of 0.3 and a selection strength of three standard deviations to calculate PNI for all Wenatchee River stocks. This approach is more accurate than using the PNI approximate equation. For Methow River stocks, PNI was calculated using a multi-population model developed by Busack (2015).

The interpretation of PNI is straightforward. The larger the PNI value, the greater the strength of selection in the natural environment relative to that of the hatchery environment. For the natural environment to dominate selection, PNI should be greater than 0.50, and integrated populations should have a PNI of at least 0.67 (HSRG/WDFW/NWIFC 2004; HSRG 2009; Mobrand et al. 2005; Paquet et al. 2011). For the Wenatchee and Methow River steelhead programs, PNI criteria were implemented in accordance with permits to achieve a subbasin-wide, five-year running average of PNI ≥ 0.67. In years when the natural-origin steelhead escapement is low (i.e., < 500 fish in the Methow and <433 fish in the Wenatchee), the populations will be managed to meet escapement goals rather than PNI.

Results

Wenatchee River Steelhead

As described above, for the Wenatchee River steelhead program, PNI criteria are implemented in accordance with Permit 18583 to achieve a subbasin-wide, five-year running average of PNI ≥ 0.67. In years when the natural-origin escapement is low (i.e., < 433 fish), the Wenatchee River steelhead population will be managed to meet escapement goals rather than PNI.

For brood years 2001-2013, prior to the reduction in smolt production, PNI values were consistently less than 0.67 and the five-year running average ranged from 0.49 to 0.53 (Table 1). For brood years 2014-2018, the period after reduction in smolt production, PNI values were generally less than 0.67 and the five-year running average was 0.55 (Table 1). Because of low escapement in 2017, the Wenatchee steelhead population was managed to meet escapement goals rather than PNI.

Table 1. PNI values for the Wenatchee steelhead supplementation program for brood years 2001-2018. PNI estimates for the period 2001-2013 are based on estimates of spawners upstream from Tumwater Dam; PNI estimates for the period 2014-present are based on mark-recapture modeling for the entire Wenatchee River Subbasin.

Brood Year	Spawners[a]			Broodstock			PNI	PNI (5-yr mean)
	NOS	HOS	pHOS	NOB	HOB	pNOB		
2001	158	127	0.45	51	103	0.33	0.45	--
2002	731	542	0.43	96	64	0.60	0.59	--
2003	355	350	0.50	49	90	0.35	0.43	--
2004	371	445	0.55	75	61	0.55	0.51	--
2005	690	862	0.56	87	104	0.46	0.47	0.49
2006	253	210	0.45	93	69	0.57	0.57	0.51
2007	145	115	0.44	76	58	0.57	0.58	0.51
2008	168	279	0.62	77	54	0.59	0.50	0.53
2009	171	545	0.76	86	73	0.54	0.43	0.51
2010	524	970	0.65	96	75	0.56	0.48	0.51
2011	351	472	0.57	91	70	0.57	0.51	0.50
2012	381	209	0.35	59	65	0.48	0.59	0.50
2013	322	148	0.31	49	68	0.42	0.59	0.52
Average[b]	***355***	***406***	***0.51***	***76***	***73***	***0.51***	***0.52***	***0.51***
Median[b]	***351***	***350***	***0.50***	***77***	***69***	***0.55***	***0.51***	***0.51***
2014	901	477	0.35	62	66	0.48	0.59	--
2015	988	711	0.42	58	52	0.53	0.57	--
2016	587	372	0.39	64	66	0.49	0.57	--
2017	198	232	0.54	56	63	0.47	0.48	--
2018	324	165	0.34	70	75	0.48	0.52	0.55
Average[c]	***524***	***391***	***0.41***	***62***	***64***	***0.49***	***0.55***	***0.55***
Median[c]	***456***	***272***	***0.39***	***62***	***66***	***0.48***	***0.57***	***0.55***

[a] The presence of eroded fins or missing adipose fins was used to distinguish hatchery fish from wild fish during video monitoring at Tumwater Dam. Unknown-origin fish (i.e., undetermined by scale analysis, no elastomer, no CWT, no fin clips, and no additional hatchery marks) were considered naturally produced. Therefore, because not all hatchery fish have eroded fins or missing adipose fins, it is likely we are underestimating WxW-cross hatchery-origin returns based on video monitoring. The PNI estimates are appropriate for steelhead spawning upstream from Tumwater Dam but may not represent PNI for steelhead spawning downstream from Tumwater Dam.

[b] Descriptive statistics using escapements estimated upstream from Tumwater Dam.

[c] Descriptive statistics using escapement estimates based on mark-recapture modeling.

Methow River Steelhead

For the Methow River steelhead program, PNI criteria are implemented in accordance with Permit 23163 to achieve a subbasin-wide, five-year running average of PNI ≥ 0.67 by 2022. The Methow Subbasin is managed in two zones: 1) the upper Methow River and primary tributaries are to achieve pHOS of ≤ 0.25, and 2) the remainder of the subbasin is managed to achieve an overall subbasin PNI of 0.67. Expected PNI from 2018 to 2021 is estimated to be ≥ 0.45 (NMFS, 2017). In years when the natural-origin escapement is low (i.e., < 500 fish), the Methow River steelhead population will be managed to meet 500 total spawners rather than PNI.

For brood years 2014-2018, PNI has been below 0.67 and ranged from 0.43 to 0.59 with a five-year running average of 0.50 (Table 2). The proportion of hatchery-origin spawners within conservation areas has ranged from 0.36 to 0.61, while the proportion of hatchery-origin spawners within management areas has ranged from 0.51 to 0.83.

Table 2. PNI and proportion of hatchery-origin fish on spawning grounds (pHOS) calculated by spawn year in the Methow River conservation and management areas based on expanded PIT-tag observations. PNI was estimated using the model described by Busack (2015) using the proportion of hatchery-origin returns in each area that derive from conservation program returns (HOR-c), safety-net program returns (HOR-sn) and natural-origin returns (NOR). The net proportion of natural-origin fish in the broods from which the HOR-c returns originated (pNOB HOR-c) was calculated as a mean value from contributing adult broods. The genetic contribution of the returning HOR-sn component (not shown) was estimated as being 75% from safety-net adults, and 25% from conservation program adults prior to 2019.

Brood Year	**Conservation areas**				**Management area**				**Overall PNI**	**pNOB HOS-c**
	NOR	**HOR-c**	**HOR-sn**	**pHOS**	**NOR**	**HOR-c**	**HOR-sn**	**pHOS**		
2014	0.61	0.13	0.26	0.39	0.29	0.34	0.36	0.71	0.50	0.53
2015	0.54	0.14	0.32	0.46	0.17	0.11	0.71	0.83	0.46	0.56
2016	0.64	0.14	0.22	0.36	0.35	0.15	0.50	0.65	0.53	0.56
2017	0.39	0.18	0.44	0.61	0.25	0.19	0.56	0.75	0.43	0.71
2018	0.62	0.14	0.24	0.38	0.49	0.46	0.06	0.51	0.59	0.83
Average	***0.56***	***0.15***	***0.30***	***0.44***	***0.31***	***0.25***	***0.44***	***0.69***	***0.50***	***0.64***
Median	***0.61***	***0.14***	***0.26***	***0.39***	***0.29***	***0.19***	***0.50***	***0.71***	***0.50***	***0.56***

Chiwawa River Spring Chinook Salmon

For brood years 1989-2011, prior to the reduction in smolt production, PNI values ranged from 0.26 to 1.00 (Table 3). PNI values for brood years 1989-1994 were greater than or equal to 0.67. For brood years 2012-2018, the period after reduction in smolt production, PNI values were generally less than 0.67, except for brood year 2016, which was 0.68 (Table 3).

Table 3. PNI values for the Chiwawa spring Chinook supplementation program for brood years 1989-2018.

Brood Year	**Spawners**			**Broodstock**			**PNI**[a]
	NOS	**HOS**	**pHOS**	**NOB**	**HOB**	**pNOB**	
1989	713	0	0.00	28	0	1.00	1.00
1990	571	0	0.00	18	0	1.00	1.00
1991	242	0	0.00	27	0	1.00	1.00
1992	676	0	0.00	78	0	1.00	1.00
1993	231	2	0.01	94	0	1.00	0.99
1994	123	61	0.33	8	4	0.67	0.68
1995	0	33	1.00	No Program			
1996	41	17	0.29	8	10	0.44	0.62
1997	60	122	0.67	32	79	0.29	0.32
1998	59	32	0.35	13	34	0.28	0.47
1999	87	7	0.07	No Program			
2000	233	113	0.33	9	21	0.30	0.50
2001	506	1219	0.71	113	259	0.30	0.32
2002	254	453	0.64	20	51	0.28	0.33
2003	168	102	0.38	41	53	0.44	0.55
2004	574	277	0.33	83	132	0.39	0.56
2005	139	460	0.77	91	181	0.33	0.32
2006	114	415	0.78	91	224	0.29	0.29
2007	155	1141	0.88	43	104	0.29	0.27
2008	190	968	0.84	83	220	0.27	0.26
2009	297	1050	0.78	96	111	0.46	0.39
2010	419	675	0.62	77	98	0.44	0.43
2011	801	1231	0.61	80	93	0.46	0.45
2012	574	904	0.61	66	45	0.59	0.50
2013	422	956	0.69	68	2	0.97	0.59
2014	523	452	0.46	58	12	0.83	0.65
2015	337	630	0.65	64	0	1.00	0.61
2016	389	157	0.29	57	42	0.58	0.68
2017	160	271	0.63	50	18	0.74	0.55
2018	166	456	0.73	30	57	0.34	0.34
Average	***307***	***407***	***0.48***	***55***	***66***	***0.57***	***0.56***
Median	***238***	***274***	***0.61***	***58***	***44***	***0.45***	***0.53***

[a] PNI was calculated previously using PNI approximate equation 11 (HSRG 2009; their Appendix A). All PNI values presented here were recalculated by iterating Ford's (2002) equations 5 and 6 to equilibrium using a heritability of 0.3 and a selection strength of three standard deviations. C. Busack, NOAA Fisheries, 21 March 2016, provided the model for calculating PNI.

Nason Creek Spring Chinook Salmon

For brood years 1989-2012, when no brood stock were collected for the Nason Creek Program, the PNI values ranged from 0.28 to 1.00 (Table 4). During this period, PNI values varied over time because of Chiwawa spring Chinook straying into Nason Creek. For brood years 2013-2018, a period when broodstock were collected for the Nason Creek Program, PNI values for the Nason Creek Program ranged from 0.38 to 0.79 (Table 4).

Table 4. PNI values of hatchery spring Chinook spawning in Nason Creek, brood years 1989-2018. See notes below the table for description of each metric.

Brood Year	Spawners					Broodstock			PNI
	NOS	HOS$_{\text{N}}$	HOS$_{\text{S}}$	pHOS$_{\text{N}}$	pHOS$_{\text{N+S}}$	NOB$_{\text{N}}$	HOB$_{\text{N}}$	pNOB	
1989	288	0	0	0.00	0.00	0	0	*1.00*	1.00
1990	235	0	0	0.00	0.00	0	0	*1.00*	1.00
1991	156	0	0	0.00	0.00	0	0	*1.00*	1.00
1992	181	0	0	0.00	0.00	0	0	*1.00*	1.00
1993	430	0	61	0.00	0.12	0	0	*1.00*	0.90
1994	60	0	0	0.00	0.00	0	0	*0.67*	1.00
1995	18	0	0	0.00	0.00	0	0	*0.00*	1.00
1996	58	0	25	0.00	0.30	0	0	*0.44*	0.61
1997	67	0	55	0.00	0.45	0	0	*0.29*	0.42
1998	61	0	3	0.00	0.05	0	0	*0.28*	0.86
1999	22	0	0	0.00	0.00	0	0	*0.00*	1.00
2000	189	0	81	0.00	0.30	0	0	*0.30*	0.52
2001	257	0	341	0.00	0.57	0	0	*0.30*	0.37
2002	313	0	290	0.00	0.48	0	0	*0.28*	0.39
2003	152	0	50	0.00	0.25	0	0	*0.44*	0.65
2004	297	0	210	0.00	0.41	0	0	*0.39*	0.51
2005	81	0	266	0.00	0.77	0	0	*0.33*	0.32
2006	117	0	154	0.00	0.57	0	0	*0.29*	0.36
2007	83	0	380	0.00	0.82	0	0	*0.29*	0.28
2008	139	0	425	0.00	0.75	0	0	*0.27*	0.29
2009	163	0	371	0.00	0.69	0	0	*0.46*	0.42
2010	59	0	349	0.00	0.86	0	0	*0.44*	0.35
2011	250	0	452	0.00	0.64	0	0	*0.46*	0.43
2012	220	0	474	0.00	0.68	0	0	*0.66*	0.50
Average*	***159***	***0***	***166***	***0.00***	***0.36***	***0***	***0***	***0.48***	***0.63***
Median*	***154***	***0***	***71***	***0.00***	***0.36***	***0***	***0***	***0.42***	***0.52***
2013	70	0	339	0.00	0.83	20	5	0.80	0.50
2014	165	0	66	0.00	0.29	21	0	1.00	0.78

Brood Year	Spawners					Broodstock			PNI
	NOS	HOS$_N$	HOS$_S$	pHOS$_N$	pHOS$_{N+S}$	NOB$_N$	HOB$_N$	pNOB	
2015	130	0	21	0.00	0.14	60	63	0.49	0.79
2016	120	11	18	0.07	0.19	70	66	0.51	0.74
2017	61	32	39	0.24	0.54	70	64	0.52	0.51
2018	21	70	78	0.41	0.88	53	54	0.50	0.38
Average**	***95***	***19***	***94***	***0.12***	***0.48***	***49***	***42***	***0.64***	***0.62***
Median**	***95***	***6***	***53***	***0.04***	***0.42***	***57***	***59***	***0.52***	***0.63***

HOS$_N$ = hatchery-origin spawners in Nason Creek from the Nason Creek spring Chinook Supplementation Program.
pHOS$_N$ = proportion of hatchery-origin spawners from Nason Creek spring Chinook Supplementation Program.
HOS$_S$ = stray hatchery-origin spawners in Nason Creek.
pHOS$_S$ = proportion of stray hatchery-origin spawners.
NOB$_N$ = natural-origin broodstock spawned in the Nason Creek spring Chinook Supplementation Program.
HOB$_N$ = hatchery-origin broodstock spawned in the Nason Creek spring Chinook Supplementation Program.
pNOB = proportion of hatchery-origin broodstock. Because of the high incidence of strays to Nason Creek from the Chiwawa River spring Chinook program, pNOB values from the Chiwawa program were used to estimate PNI values during the period from 1989 to 2012 (*italicized*). The weighting for those years was 100% based on the Chiwawa program broodstock selection, because there had been no hatchery returns from the Nason Creek spring Chinook program.
PNI$_N$ = Proportionate Natural Influence for Nason Creek spring Chinook calculated using the gene-flow model for multiple programs.
* Average and median for the period 1989-2012, a period when no brood stock were collected for the Nason Creek Program.
** Average and median for the period 2013-present, a period when brood stock was collected for the Nason Creek Program.

White River Spring Chinook Salmon

For brood years 1989-2000, PNI values ranged from 0.95 to 1.00 (Table 5). For brood years 2001-2013, PNI during the White River Program averaged 0.60 (range, 0.33-1.00) and most of the hatchery spawners originated from the Chiwawa River Hatchery Program (Table 5). The captive brood program ended with brood year 2013.

Table 5. PNI values for hatchery spring Chinook spawning in the White River, brood years 1989-2013. See notes below the table for description of each metric.

Brood Year	Spawners					Broodstock			PNI
	NOS	HOS$_W$	HOS$_S$	pHOS$_W$	pHOS$_S$	NOB$_N$	HOB$_N$	pNOB	
1989	145	0	0	0.00	0.00	0	0	*1.00*	1.00
1990	49	0	0	0.00	0.00	0	0	*1.00*	1.00
1991	49	0	0	0.00	0.00	0	0	*1.00*	1.00
1992	78	0	0	0.00	0.00	0	0	*1.00*	1.00
1993	138	0	7	0.00	0.05	0	0	*0.99*	0.95
1994	7	0	0	0.00	0.00	0	0	*0.67*	1.00
1995	5	0	0	0.00	0.00	0	0	*1.00*	1.00
1996	30	0	0	0.00	0.00	0	0	*0.60*	1.00
1997	33	0	0	0.00	0.00	0	0	*0.30*	1.00
1998	11	0	0	0.00	0.00	0	0	*0.44*	1.00

Brood Year	Spawners					Broodstock			PNI
	NOS	HOS$_W$	HOS$_S$	pHOS$_W$	pHOS$_S$	NOB$_N$	HOB$_N$	pNOB	
1999	3	0	0	0.00	0.00	0	0	*1.00*	1.00
2000	22	0	0	0.00	0.00	0	0	*0.48*	1.00
Average*	***48***	***0***	***1***	***0.00***	***0.00***	***0***	***0***	***0.79***	***1.00***
Median*	***32***	***0***	***0***	***0.00***	***0.00***	***0***	***0***	***1.00***	***1.00***
2001	111	0	55	0.00	0.33	5	0	1.00	0.50
2002	60	0	26	0.00	0.30	18	0	1.00	0.51
2003	31	0	5	0.00	0.14	7	0	1.00	0.77
2004	54	0	12	0.00	0.18	6	0	1.00	0.70
2005	38	11	106	0.07	0.68	103	73	0.59	0.33
2006	41	5	9	0.09	0.16	191	135	0.59	0.61
2007	62	23	7	0.25	0.08	254	6	0.98	0.67
2008	20	2	30	0.04	0.58	116	0	1.00	0.34
2009	81	29	63	0.17	0.36	238	0	1.00	0.53
2010	27	22	23	0.31	0.32	90	0	1.00	0.50
2011	83	0	0	0.00	0.00	306	0	1.00	1.00
2012	89	10	45	0.07	0.31	390	0	1.00	0.73
2013	44	55	5	0.53	0.05	383	0	1.00	0.64
Average**	***57***	***12***	***30***	***0.12***	***0.27***	***162***	***16***	***0.94***	***0.60***
Median**	***54***	***5***	***23***	***0.07***	***0.30***	***116***	***0***	***1.00***	***0.61***

HOS$_W$ = hatchery-origin spawners in White River from the White River spring Chinook Supplementation Program.
pHOS$_W$ = proportion of hatchery-origin spawners from White River spring Chinook Supplementation Program.
HOS$_S$ = stray hatchery-origin spawners in the White River.
pHOS$_S$ = proportion of stray hatchery-origin spawners.
NOB$_W$ = natural origin broodstock spawned for the White River spring Chinook Supplementation Program.
HOB$_W$ = hatchery-origin broodstock spawned in the White River spring Chinook Supplementation Program.
pNOB = proportion of hatchery-origin broodstock. Because of the high incidence of strays to the White River from the Chiwawa River spring Chinook program, pNOB values from the Chiwawa program were used to estimate PNI values during the period from 1989 to 2000 (*italicized*). The weighting for those years was 100% based on the Chiwawa program broodstock selection, because there have been no hatchery returns from the White River spring Chinook program during this period.
PNI = Proportionate Natural Influence for White River spring Chinook calculated using the gene-flow model for multiple programs.
* Average and median for the period 1989-2000.
** Average and median for the period 2001-2013.

Wenatchee Subbasin Spring Chinook Salmon

For brood years 1989-2018, PNI values ranged from 0.34 to 1.00 in the portion of the Wenatchee Subbasin upstream of Tumwater Dam (Table 6; see the sections on Chiwawa River, Nason Creek, and White River for details as to how program changes affected PNI). PNI values for brood years 1989-1994, 2014, and 2016 were greater than or equal to 0.67. However, there were no hatchery origin spawners in brood years 1989-1992 (pre-dated the first hatchery program returns).

Table 6. PNI values for the Wenatchee Subbasin (upstream of Tumwater Dam) spring Chinook supplementation programs for brood years 1989-2018.

Brood Year	Spawners			Broodstock			PNI[a]
	NOS	HOS	pHOS	NOB	HOB	pNOB	
1989	1461	0	0.00	28	0	1.00	1.00
1990	1003	0	0.00	18	0	1.00	1.00
1991	585	0	0.00	27	0	1.00	1.00
1992	1098	0	0.00	78	0	1.00	1.00
1993	935	257	0.22	94	0	1.00	0.82
1994	214	66	0.24	8	4	0.67	0.74
1995	23	36	0.61	0	0	NA	NA
1996	139	43	0.24	8	10	0.44	0.66
1997	211	177	0.46	32	79	0.29	0.41
1998	149	35	0.19	13	34	0.28	0.62
1999	123	10	0.08	0	0	NA	NA
2000	484	278	0.36	9	21	0.30	0.48
2001	979	1977	0.67	118	259	0.31	0.34
2002	732	863	0.54	38	51	0.43	0.46
2003	383	212	0.36	48	53	0.48	0.59
2004	1010	591	0.37	89	132	0.40	0.54
2005	304	1169	0.79	194	254	0.43	0.37
2006	304	636	0.68	282	359	0.44	0.41
2007	388	1619	0.81	297	110	0.73	0.48
2008	362	1778	0.83	199	220	0.47	0.38
2009	585	1610	0.73	334	111	0.75	0.52
2010	539	1220	0.69	167	98	0.63	0.49
2011	1213	1778	0.59	386	93	0.81	0.59
2012	931	1580	0.63	456	45	0.91	0.60
2013	614	1408	0.70	471	7	0.99	0.59
2014	779	575	0.42	79	12	0.87	0.68
2015	616	775	0.56	124	63	0.66	0.55
2016	615	226	0.27	127	108	0.54	0.68
2017	259	369	0.59	120	82	0.59	0.51
2018	221	661	0.75	83	111	0.43	0.38
Average	575	665	0.45	131	77	0.64	0.60
Median	562	472	0.50	86	52	0.61	0.57

[a] PNI was calculated previously using PNI approximate equation 11 (HSRG 2009; their Appendix A). All PNI values presented here were recalculated by iterating Ford's (2002) equations 5 and 6 to equilibrium using a heritability of 0.3 and a selection strength of three standard deviations. C. Busack, NOAA Fisheries, 21 March 2016, provided the model for calculating PNI.

Methow River Spring Chinook Salmon

For brood years 2003-2018, PNI has consistently been below 0.67 and ranged from 0.06 to 0.50 (Table 7). During this time, the mean proportion of natural-origin spring Chinook Salmon on spawning grounds was higher in the Twisp River than in the Methow or Chewuch rivers. However, mean Methow River Subbasin PNI values are low and indicate that most genetic selection pressure on progeny produced from naturally spawning adults comes from the hatchery environment (Table 7).

Table 7. PNI calculated for specific broods of spawning spring Chinook Salmon in the Methow River Subbasin. PNI was calculated using a three-population model incorporating the proportion of hatchery fish from conservation programs (HC; e.g., Methow Hatchery), safety-net programs (HSN; e.g., Winthrop National Fish Hatchery), and natural-origin (Wild) fish on the spawning grounds within each tributary and spawning year. Stray hatchery-origin fish were included in the HC or HSN categories based on the known or assumed parentage of broodstock.

Brood Year	**Chewuch**			**Methow**			**Twisp**			**Methow Subbasin**			
	HC	**HSN**	**Wild**	**HC**	**HSN**	**Wild**	**HC**	**HSN**	**Wild**	**HC**	**HSN**	**Wild**	**PNI**
2003	0.92	0.03	0.05	0.65	0.34	0.01	0.42	0.00	0.58	0.76	0.19	0.05	0.27
2004	0.83	0.03	0.14	0.56	0.20	0.24	0.23	0.06	0.71	0.54	0.13	0.33	0.21
2005	0.52	0.05	0.43	0.56	0.14	0.30	0.28	0.00	0.72	0.52	0.09	0.38	0.50
2006	0.54	0.20	0.26	0.61	0.27	0.12	0.60	0.01	0.39	0.59	0.23	0.19	0.06
2007	0.42	0.31	0.27	0.28	0.50	0.22	0.62	0.00	0.38	0.35	0.41	0.25	0.30
2008	0.37	0.29	0.34	0.30	0.41	0.29	0.76	0.00	0.24	0.39	0.31	0.30	0.28
2009	0.46	0.19	0.35	0.43	0.42	0.15	0.67	0.08	0.25	0.45	0.34	0.21	0.20
2010	0.51	0.18	0.31	0.50	0.32	0.18	0.38	0.00	0.62	0.49	0.25	0.25	0.09
2011	0.42	0.16	0.42	0.50	0.26	0.24	0.16	0.18	0.66	0.45	0.22	0.33	0.19
2012	0.67	0.05	0.28	0.76	0.10	0.14	0.67	0.01	0.32	0.72	0.07	0.20	0.23
2013	0.67	0.05	0.28	0.76	0.06	0.18	0.75	0.00	0.25	0.73	0.05	0.22	0.40
2014	0.53	0.09	0.38	0.63	0.19	0.18	0.62	0.01	0.37	0.60	0.15	0.25	0.40
2015	0.41	0.12	0.47	0.59	0.24	0.17	0.31	0.02	0.67	0.52	0.19	0.29	0.39
2016	0.19	0.19	0.62	0.28	0.36	0.36	0.33	0.00	0.67	0.24	0.30	0.46	0.29
2017	0.38	0.19	0.43	0.32	0.34	0.34	0.40	0.13	0.47	0.35	0.27	0.38	0.38
2018	0.33	0.20	0.47	0.16	0.34	0.50	0.25	0.06	0.69	0.22	0.25	0.53	0.44
Avg.	***0.51***	***0.15***	***0.34***	***0.49***	***0.28***	***0.23***	***0.47***	***0.04***	***0.50***	***0.50***	***0.22***	***0.29***	***0.29***
Median	***0.49***	***0.17***	***0.35***	***0.53***	***0.30***	***0.20***	***0.41***	***0.01***	***0.53***	***0.51***	***0.23***	***0.27***	***0.29***

Wenatchee River Summer Chinook Salmon

For brood years 1989-2018, the PNI value has been greater than 0.67 (Table 8). For those brood years, PNI ranged from 0.68 to 1.00 and averaged 0.87.

Table 8. PNI values for the Wenatchee summer Chinook supplementation program for brood years 1989-2018.

Brood year	Spawners			Broodstock			PNI
	NOS	HOS	pHOS	NOB	HOB	pNOB	
1989	14,331	0	0.00	290	0	1.00	1.00
1990	10,861	0	0.00	57	0	1.00	1.00
1991	10,168	0	0.00	105	0	1.00	1.00
1992	11,652	0	0.00	274	0	1.00	1.00
1993	8,842	608	0.06	406	44	0.90	0.94
1994	8,476	1,678	0.17	333	54	0.86	0.84
1995	6,854	901	0.12	363	16	0.96	0.89
1996	6,000	168	0.03	263	3	0.99	0.97
1997	5,408	505	0.09	205	13	0.94	0.92
1998	4,707	645	0.12	299	78	0.79	0.87
1999	3,997	1,342	0.25	242	236	0.51	0.68
2000	4,466	1,046	0.19	275	180	0.60	0.77
2001	8,356	1,691	0.17	210	136	0.61	0.79
2002	11,846	3,740	0.24	409	10	0.98	0.81
2003	10,064	1,736	0.15	337	7	0.98	0.87
2004	8,044	1,070	0.12	424	2	1.00	0.90
2005	6,869	1,834	0.21	397	3	0.99	0.83
2006	15,405	3,188	0.17	432	4	0.99	0.86
2007	2,764	1,806	0.40	263	3	0.99	0.72
2008	8,061	3,699	0.31	376	71	0.84	0.74
2009	7,754	1,330	0.15	449	8	0.98	0.86
2010	6,253	1,671	0.21	388	5	0.99	0.83
2011	8,107	1,681	0.17	375	7	0.98	0.86
2012	6,963	1,150	0.14	267	1	1.00	0.88
2013	6,798	2,412	0.26	234	2	0.99	0.80
2014	9,901	772	0.07	261	2	0.99	0.94
2015	4,033	240	0.06	248	0	1.00	0.95
2016	5,700	509	0.08	259	0	1.00	0.93
2017	7,620	906	0.11	252	1	1.00	0.90
2018	2,606	656	0.20	205	5	0.98	0.83
Average	***7,764***	***1,233***	***0.14***	***297***	***30***	***0.93***	***0.87***
Median	***7,687***	***1,058***	***0.15***	***275***	***5***	***0.99***	***0.87***

Methow River Summer Chinook Salmon

For brood years 1993-2003, the PNI values were generally less than 0.67 (Table 9). Since brood year 2003, PNI has generally been equal to or greater than 0.67. For the entire time series, PNI has ranged from 0.32 to 1.00 and averaged 0.71.

Table 9. PNI values for the Methow summer Chinook supplementation program for brood years 1989-2018.

Brood year	**Spawners**			**Broodstock**			**PNI**
	NOS	**HOS**	**pHOS**	**NOB**	**HOB**	**pNOB**	
1989	492	0	0.00	1,297	312	0.81	1.00
1990	1,421	0	0.00	828	206	0.80	1.00
1991	566	0	0.00	924	314	0.75	1.00
1992	460	0	0.00	297	406	0.42	1.00
1993	314	194	0.38	681	388	0.64	0.64
1994	596	489	0.45	341	244	0.58	0.58
1995	596	618	0.51	173	240	0.42	0.47
1996	435	180	0.29	290	223	0.57	0.67
1997	529	168	0.24	198	264	0.43	0.71
1998	435	240	0.36	153	211	0.42	0.56
1999	570	415	0.42	224	289	0.44	0.53
2000	862	338	0.28	164	339	0.33	0.56
2001	1,108	1,659	0.60	91	266	0.25	0.32
2002	2,591	2,039	0.44	247	241	0.51	0.55
2003	2,318	1,612	0.41	381	101	0.79	0.67
2004	1,641	548	0.25	506	16	0.97	0.80
2005	1,672	889	0.35	391	9	0.98	0.74
2006	1,685	1,048	0.38	500	10	0.98	0.73
2007	656	708	0.52	456	17	0.96	0.66
2008	1,197	750	0.39	404	41	0.91	0.71
2009	1,044	714	0.41	507	0	1.00	0.72
2010	1,325	1,168	0.47	484	8	0.98	0.68
2011	1,487	1,430	0.49	467	26	0.95	0.67
2012	1,596	1,351	0.46	98	1	0.99	0.69
2013	1,707	1,876	0.52	97	4	0.96	0.66
2014	1,450	175	0.11	96	0	1.00	0.90
2015	3,142	809	0.20	97	1	0.99	0.84
2016	1,466	775	0.35	103	0	1.00	0.75
2017	1,039	369	0.26	111	0	1.00	0.80
2018	675	692	0.51	130	1	0.99	0.67
Average	***1,169***	***708***	***0.34***	***358***	***139***	***0.76***	***0.71***
Median	***1,076***	***655***	***0.38***	***294***	***71***	***0.86***	***0.69***

Discussion

Target PNI values in the upper Columbia Basin were generally not met for species with low population size such as endangered spring Chinook Salmon and threatened steelhead, but were exceeded for populations of summer Chinook Salmon that were relatively large. Recently, PNI targets were exceeded for fall Chinook Salmon in the Hanford Reach, another large upper Columbia population (Pearsons et al. 2020). When hatchery production was large relative to the natural spawning population, then PNI targets were difficult to achieve without significant management of returning adults to control pHOS. In some areas, such as upstream of Tumwater Dam in the Wenatchee Subbasin, the management of hatchery-origin fish was possible. In other areas, such as the Methow Subbasin, the management of hatchery-origin adults was more challenging because it relied upon removal at hatchery traps and recreational angling. It was also difficult to achieve high pNOB when populations were small. Federal Section 10 permits require that the proportion of natural-origin fish that can be collected for hatchery broodstock be less than 33% of the run. When run sizes are small, then the pNOB will be low because a greater proportion of hatchery-origin fish will have to be used for broodstock to meet hatchery production goals. In short, operating large integrated hatchery programs relative to the natural-origin spawning population creates difficult trade-offs and challenges.

Reliance upon adult management to achieve pHOS goals poses risk of mining natural-origin fish from the spawning population, which could pose greater risk to the population than domestication. If hatchery-origin fish were killed to manage pHOS, and natural-origin fish were used as broodstock to produce those hatchery-origin fish, then the natural-origin fish were mined to support the hatchery program. This poses a demographic risk to the population and also removes parental natural-origin fish from contributing to natural production. The risks of mining the natural-origin population could be evaluated relative to the risks of domestication and the size of hatchery programs to determine what is most optimal to achieve program goals.

Straying of non-target hatchery fish is another factor that contributed to lowering PNI of small populations. In some cases, such as in Nason Creek and the White River, strays from other hatcheries influenced PNI more than target hatcheries (Pearsons and Miller, see chapter in this report). Stray hatchery-origin fish increase domestication risk but also pose risk of decreasing between-population genetic variation. Larger populations such as summer Chinook Salmon were able to absorb strays without large increases in PNI that occurred in smaller populations.

Managing to achieve conservation PNI targets could follow guidelines whereby pNOB should be larger than pHOS, but pNOB should not be increased in order to achieve the PNI target. Rather, pHOS should be decreased to the point where the PNI target can be achieved, and should be less than 30% (HSRG 2009; [typically the ESA permitted pHOS upper limit is 25% in conservation programs]). Increasing pNOB above 50% offers minor genetic benefit, while reducing pHOS allows lower pNOB (HSRG 2009). However, controlling pHOS may be difficult or impossible in systems where the opportunity for origin-selective adult removal is limited. Such cases necessitate the re-evaluation of management objectives and program structure to provide a broader suite of approaches for constraining the number of hatchery-origin fish on the spawning ground to a suitable number for meeting the PNI objective. In cases where a population is at risk of functional extirpation, the PNI guidelines described by the HSRG

(2009) may be altered to encourage more fish spawning in the wild. In these cases, clearly defined guidelines could be established and the population carefully monitored (HSRG 2009). In general, pNOB must exceed pHOS (HSRG 2009); however, when pHOS is high, increasing pNOB to compensate risks of mining the natural population of spawners, exacerbating pHOS while continuing to produce more hatchery origin fish than are warranted under a PNI management regime. Management targets have been established for PNI for the various programs listed under the Endangered Species Act. Steelhead programs in the Wenatchee and Methow had PNI averages or medians below 0.67. Assessment of mean PNI can be complicated by management for escapement, as opposed to PNI, when run sizes are small, as happened in the Wenatchee in 2017. The new steelhead management regime in the Methow did not initiate until 2017. Therefore, data in this report do not reflect the current or future management of the Methow River Subbasin for gene flow.

The results of this analyses indicate that the Spring Chinook and steelhead programs would benefit from adjustment to meet the PNI targets. In some cases, the PNI values may improve as the reduction in hatchery release numbers and new management strategies mature. Evaluation of the interaction of adult management, hatchery program size, and stray management could help to achieve PNI targets. Furthermore, assessment of genetic and demographic risks could be evaluated to determine trade-offs between how these factors contribute to long-term fitness. The Methow steelhead and particularly spring Chinook may require substantial management changes in order to achieve the gene flow objectives.

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We thank the many people who collected data that allowed the calculation of PNI in this report. The data collection, analysis, and writing was funded by Grant, Chelan, and Douglas counties public utility districts. Peter Graf, Catherine Willard, and Tom Kahler reviewed and provided helpful suggestions on earlier drafts of this manuscript. Finally, we thank the Wells, Rocky Reach, and Rock Island HCP Hatchery Committees, and the Priest Rapids Coordinating Committee's Hatchery Subcommittee.

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Adult Migration Timing, Spawn Timing, and Spawning Distribution of Spring Chinook Salmon and Summer Chinook Salmon in the Wenatchee and Methow Basins

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Abstract

The migration timing, spawn timing, and spatial spawning distribution of hatchery- and natural-origin salmon in the natural environment can be important metrics in the evaluation of integrated hatchery programs. The timing of migration and spawning of hatchery- and natural-origin spring Chinook Salmon were generally similar in the Wenatchee and Methow sub-basins. Although the difference in arrival timing was small and not statistically significant, the visual observation and PIT-tag data at Tumwater and Wells dams suggests a tendency for hatchery-origin spring Chinook Salmon to arrive later than natural-origin fish. Differences in migration timing between spring Chinook Salmon populations in the Wenatchee versus Methow sub-basins were observed and may result in differences in survival at the adult life-stage. With summer Chinook Salmon, hatchery-origin fish in the Wenatchee sub-basin consistently passed Dryden Dam later than their natural-origin counterparts whereas the migration timing for Methow and Okanogan sub-basin hatchery-origin fish was a near match with natural-origin fish at Wells Dam. Summer Chinook Salmon spawn timing in both Wenatchee and Methow hatchery-origin fish was later than natural-origin fish, with Methow-origin fish having a larger average difference. For spatial distribution of spawning spring Chinook Salmon, differences between hatchery- and natural-origin spawner distribution across the historical survey reaches were observed in all programs except the White River program. In general, hatchery-origin females spawned lower in the watershed. However, the proportion of hatchery-origin fish was high (i.e., greater than 50%) in the majority of survey reaches (33 out of 51), particularly in those reaches that were the primary spawning areas by natural-origin fish. The proportion of hatchery-origin spring Chinook Salmon exceeded 30% in 48 of the 51 survey reaches. The distributions of spawning Wenatchee and Methow hatchery-origin summer Chinook Salmon also differed from the spawner distributions of the natural-origin populations, with hatchery-origin females more often spawning lower in the watershed. This difference in spawning distribution was consistent with management objectives. The proportion of hatchery-origin summer Chinook Salmon was greater than 30% in 6 of the 17 survey reaches.

Introduction

Hatchery programs, through hatchery practices that may induce physiological or behavioral consequences such as unintentional straying, can reduce life-history variability resulting in the reduction of the portfolio effect of multiple aggregate populations (Schindler et al. 2010; Carlson and Satterthwaite 2011). For example, the release timing of juvenile hatchery-origin fish is typically highly condensed in space and time relative to the natural-origin juvenile migration patterns. The condensed release of juvenile hatchery fish, when timed with preferred environmental conditions (e.g., high flows, darkness, low visibility), may increase juvenile survival. However, this artificial narrowing of the emigration temporal window may also reduce the buffering effect of a more widely distributed migration pattern (Kovach et al. 2013). The diversity and variability observed in populations of natural-origin fish is made possible by a combination of genetic, phenotypic, and habitat heterogeneity, all of which can be reduced by both the loss or simplification of habitat and the introduction of hatchery-reared fish. For example, the diversity of Chinook Salmon in the Central Valley of California, the only location where four distinct runs of Chinook Salmon occurred, was reduced first by construction of impassable dams and then by the temporally condensed release of genetically homogeneous hatchery-origin fish in space and time as mitigation for those losses (Carlson and Satterthwaite 2011; Huber and Carlson 2015).

The spatial spawning distribution of hatchery- and natural-origin salmon in the natural environment can be an important metric in the evaluation of integrated hatchery programs (Knudsen et al. 2006; Hoffnagle et al. 2008; Murdoch et al. 2009; Hughes and Murdoch 2017; Hillman et al. 2019). Integrated hatchery programs incorporate naturally produced fish into the hatchery broodstock and hatchery-origin fish are intended to spawn on the spawning grounds with natural-origin fish, with the goal of increasing spawner abundance (Mobrand et al. 2005) and the assumption that this will result in a larger population overall. Spatial similarity in the spawning distributions of hatchery- and naturally produced fish on the spawning grounds indicates effective integration of the spawning population unless assortative mating occurs. Differences in the spatial distribution of spawning hatchery- and naturally produced salmon may simply be an artifact of the low abundance of natural- or hatchery-produced fish (i.e., vacant habitat), sub-optimal smolt release locations (Murdoch et al. 2007; Hoffnagle et al. 2008), or inadequate imprinting and homing of hatchery-origin fish (Murdoch et al. 2007). Alternatively, it can be the result of an intentional management objective where differences in spatial and temporal spawning distribution are desirable (Mackey et al. 2001). Furthermore, strays from other hatchery programs can influence the distribution of hatchery-origin spawners in non-target streams. The Hatchery Scientific Review Group (HSRG) recommends that the proportion of hatchery-origin spawners (pHOS) should not exceed 0.30 for integrated hatchery programs in order to reduce the risk of domestication selection (Mobrand et al. 2005; Paquet et al. 2011).

The spawning distribution objective for the spring Chinook Salmon programs evaluated in these analyses are for hatchery-origin and natural-origin fish to spawn in similar locations, in contrast to the summer Chinook Salmon hatchery programs in which replication of the spawning distribution between hatchery-origin and natural-origin fish is not the objective. The upper range of summer Chinook Salmon spawning distribution has the potential to overlap with ESA-listed spring Chinook Salmon, which may pose an unknown and potentially adverse impact to spring Chinook Salmon; therefore, summer Chinook Salmon acclimation sites are located lower in the sub-basin in an effort to minimize this overlap in the upper range of the spawning distribution of summer Chinook Salmon. Exact replication of the spawning distribution for summer Chinook Salmon is not the management expectation (Hillman et al. 2019).

Using a combination of observational data, we explored qualitative and quantitative differences in migration timing, spawn timing, and spawning distribution between hatchery- and natural-origin spring and summer Chinook Salmon within the Wenatchee Sub-basin and Methow Sub-basin (WA). From these data, we assessed whether the respective hatchery programs are achieving the goal of similar migration and spawn timing of adult hatchery- and natural-origin fish, and whether there is evidence of a temporal shift of migration or spawning timing in either hatchery- or natural-origin fish over time. Additionally, we assessed whether the spatial distribution of redds is similar for hatchery-origin Chinook Salmon compared to natural-origin Chinook Salmon.

Methods

Adult Run Timing

Using PIT-tag recapture data from the PTAGIS database (Pacific States Marine Fisheries Commission, https://www.ptagis.org/), we compared the arrival timing of hatchery- and natural-origin Upper Columbia spring Chinook Salmon populations to various locations within the Columbia Basin. The comparisons included age 3, 4, and 5 fish from return years 2005-2018. The run timing of these fish was evaluated by origin, age, and release location as identified in PTAGIS.

Using data reported from the Public Utility Districts' (PUD) hatchery monitoring and evaluation reports (Hillman et al. 2020; Snow et al. 2020), we evaluated mean arrival timing of hatchery- and natural-origin spring Chinook Salmon from 1998-2018 by calculating mean day of the year (DOY) (days since January 1) that 10%, 50%, and 90% of the fish passed Tumwater Dam (Wenatchee populations) and Wells Dam (Methow populations). All age groups were pooled together in the analysis, because these data were based on video monitoring and trapping. The origin of adults (hatchery or natural) was determined by adipose fin presence or absence or the presence of coded-wire tags. Migration timing at Tumwater Dam was based on video sampling; migration timing at Wells Dam was based on stock-assessment and broodstock trapping in the Wells Dam fishways. Data for 1998 through 2003 were based on video and broodstock trapping and may not reflect the actual number of hatchery-origin spring Chinook Salmon that passed the dams. Most spring Chinook Salmon were visually examined during trapping from 2004 to 2018; however, enumeration errors may still exist because of misidentified run-type assignment (i.e., spring or summer). The mean differences in mean arrival timing were compared with paired t-tests on the 10%, 50% (median), and 90% DOY.

Due to the limited number of natural-origin PIT-tagged summer Chinook Salmon, evaluations of adult run timing for summer Chinook Salmon were limited to visual observations at dam fishways or broodstock collection locations. As with spring Chinook Salmon, we compared the mean migration timing of hatchery- and natural-origin summer Chinook Salmon by comparing the mean DOY on which 10%, 50%, and 90% of the fish passed Dryden Dam and Wells Dam. These data were based on stock assessment and broodstock collection at Dryden Dam (Wenatchee population) and Wells Dam during the migration period 2007-2018. The natural populations observed at Wells Dam consist of fish produced in the Methow and Okanogan sub-basins, plus potentially in the Columbia River. The hatchery populations consist of fish released in the Methow, Okanogan, and Columbia rivers, plus potentially strays from downstream locations.

Spawn Timing

Differences in spawn timing between hatchery- and natural-origin spring Chinook Salmon and summer Chinook Salmon were evaluated by comparing the temporal distributions of female carcasses recovered on the spawning grounds. These data were assessed with all years pooled and year-by-year by sub-basin or major spawning tributary. The mean differences in spawn timing between hatchery- and natural-origin fish were evaluated with paired t-tests on the 10th, 50th, and 90th percentile carcass-recovery date. Additionally, we evaluated the relationship between the DOY and elevation of carcass recoveries. Carcass recovery is an indirect measurement of spawn timing and dependent on several other independent variables that may affect an evaluation of timing. Therefore, the results of differences or similarities in timing should be evaluated in the context of carcass recovery date as a proxy for spawn timing and the relationship between those two metrics.

Spawning Distribution

Differences in the distribution of hatchery- and natural-origin Chinook Salmon spawners were assessed by examining the location (RKm) where female carcasses were observed in spawning streams. The focus was on female carcasses because they are a better indicator of spawning location than are male carcasses (Murdoch et al. 2009). During weekly spawning ground surveys (described in Hillman et al. 2019), crews recorded the location of female carcasses (recorded to the nearest 0.1 RKm) as measured from the confluence (RKm 0.0) of each stream. The entire spawning distribution of Chinook Salmon was inventoried (Hillman et al. 2019).

We evaluated differences in spawning locations at two different spatial scales: at the historical reach scale and at the 0.5-km (in tributaries) or 1.0-km (in mainstem rivers) scale. Historical reaches are the stream reaches defined by individuals conducting redd surveys over the history of the respective monitoring programs and are generally related to river accessibility and the length of stream that one can reasonably survey in given amount of time. At the historical reach scale, we evaluated the proportion of natural- and hatchery-origin spawners among all the reaches and within each reach. That is, we calculated the fraction of all natural- and hatchery-origin spawners within a stream that were observed within each reach of that stream. We also calculated pHOS and pNOS (proportion of natural-origin spawners) within each reach by dividing the number of hatchery-origin or natural-origin spawners within a reach by the total number of hatchery- and natural-origin spawners within that reach. We then constructed frequency-distribution plots to compare the spawning distribution of hatchery- and natural-origin fish within and among reaches. We performed two-way Yates' Chi-square tests on count data to determine whether there were statistical differences in spawning distributions between hatchery- and natural-origin fish at the historical-reach scale. We were unable to evaluate differences in distribution of hatchery- and natural-origin fish "before" and "after" a reduction in Chinook Salmon hatchery production. Based on the year when the last age-5 fish return from the "before" period would provide at most only two years of "after" data. Two years of "after" data are too few to make reasonable comparisons.

Results

Migration Timing of Wenatchee and Methow Spring Chinook Salmon

Adult Upper Columbia River spring Chinook Salmon typically began arriving at Bonneville Dam by April and their migration continued through July (Figure 1). Generally, fish from the Leavenworth National Fish Hatchery and the Methow River sub-basin were the earliest to arrive. From 2005-2018, the median arrival date to Bonneville Dam of natural-origin fish from the Methow Sub-basin was approximately 15 days earlier than natural-origin fish from the Chiwawa River (Figure 1). The arrival timing of hatchery-origin fish to Bonneville Dam followed the same pattern as natural-origin fish; fish from the Methow Sub-basin arrived earlier than Wenatchee Sub-basin fish and the median passage date of fish from the Methow Hatchery was approximately 20 days earlier than fish released from the Chiwawa Acclimation Facility.

In the Wenatchee Sub-basin, the arrival timing at Tumwater Dam of PIT-tagged hatchery- and natural-origin spring Chinook Salmon was nearly identical with some variability due to small sample sizes (Figure 2). The mean arrival DOY of natural-origin fish was 182 versus 184 for hatchery-origin fish (median = 183 vs 185). Similarly, at Wells Dam, PIT-tagged natural-origin and hatchery-origin spring Chinook Salmon from the Methow Sub-basin arrived at similar times (average = 151 for natural-origin, versus 150 for hatchery-origin, median = 148 vs 149, respectively; Figure 3). Both the Methow and Wenatchee sub-basins were consistent in the pattern of return date by age where age-3 fish returned later than age-4 and age-5 fish (Figure 4).

The observed patterns described above were consistent with cumulative frequency plots of migration timing of PIT-tagged hatchery- and natural-origin fish (Figure 5) and statistical tests of differences between hatchery- and natural-origin fish visually observed at Tumwater Dam and Wells Dam (Table 1). In the evaluation of PIT-tag returns, hatchery- and natural-origin arrival timing are a near match at both sampling locations (Figure 5). At Wells Dam, hatchery-origin fish arrived slightly earlier during the second half of the return distribution (e.g., 6 days earlier at the 75th percentile).

PIT-tag-based, within-year data are limited by sample size, particularly for natural-origin PIT-tagged fish; however, we provide Figure 6 as an example of the variability in migration timing that may occur on a year-by-year basis. Even with this variability, the general trends discussed above (i.e., hatchery- and natural-origin overlap and later arriving age-3 fish) are evident.

Based on visual observations, arrival timing at both dams showed similar results with only slight differences from the PIT-tag based evaluation. The differences in arrival timing between hatchery- and natural-origin fish at the 10th, 50th, and 90th percentiles were again minor (range = -2.28-1.14 days). The paired differences were significant on the 10th percentile (P-value = 0.0228) at Tumwater Dam and the 10th (P-value = 0.0179) and 50th percentile (P-value = 0.0206) at Wells Dam; however, the magnitude of the differences was small and in a different temporal direction than the differences observed with PIT-tag data. As described above, where there was a difference in the PIT-tagged fish evaluation, hatchery-origin fish arrived earlier than natural-origin fish. Using visual observations, hatchery-origin fish consistently arrived slightly later than natural-origin fish. In either case, the differences were small relative to the variability observed within and between years.

When viewed year-by-year, the differences between hatchery- and natural-origin arrival timing in the visual observation data show that hatchery-origin fish arrived later than natural-origin fish in most years (Figure 7). However, the temporal trend in differences at both Tumwater Dam and Wells Dam is generally towards no difference and the only significant trend was at Wells Dam for the 50th percentile arrival date.

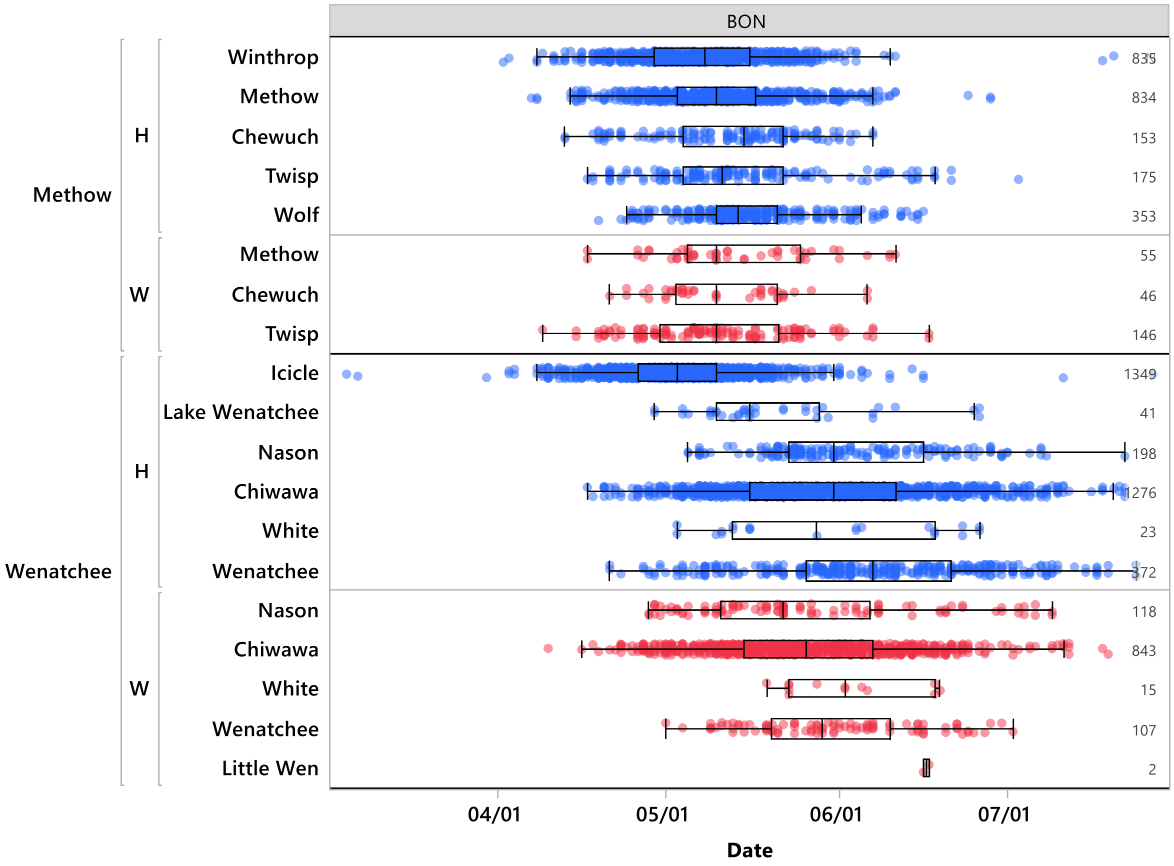


Figure 1. Return timing of PIT-tagged natural-origin (W, red) and hatchery-origin (H, blue) spring Chinook Salmon (age-3, 4, and 5) from the Methow and Wenatchee sub-basins to Bonneville Dam, return years 2006-2018. Data grouped by basin, origin, and river or tributary of release.

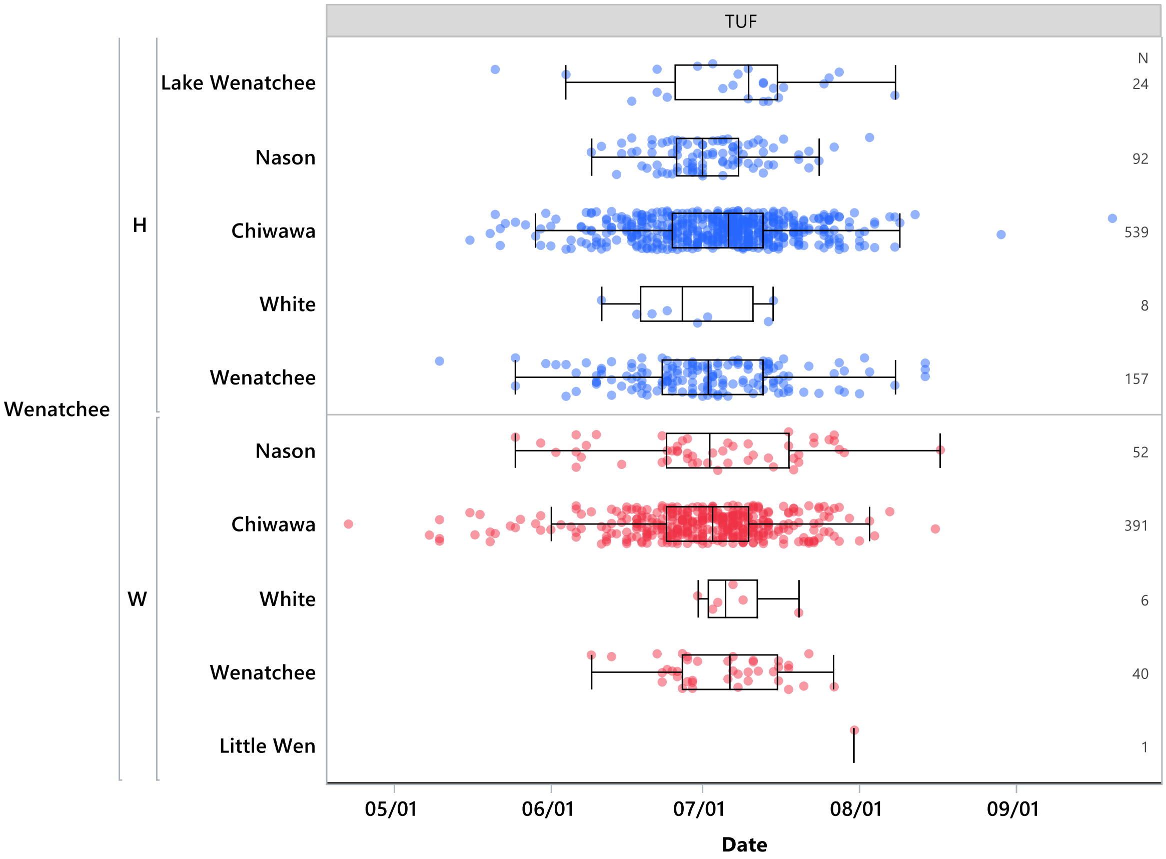


Figure 2. Return timing to Tumwater Dam of PIT-tagged natural-origin (W, red) and hatchery-origin (H, blue) spring Chinook Salmon (age-3, 4, and 5) from the Wenatchee Sub-basin tagged upstream from Tumwater Dam, return years 2006-2018. Data grouped by basin, origin, and river or tributary of release.

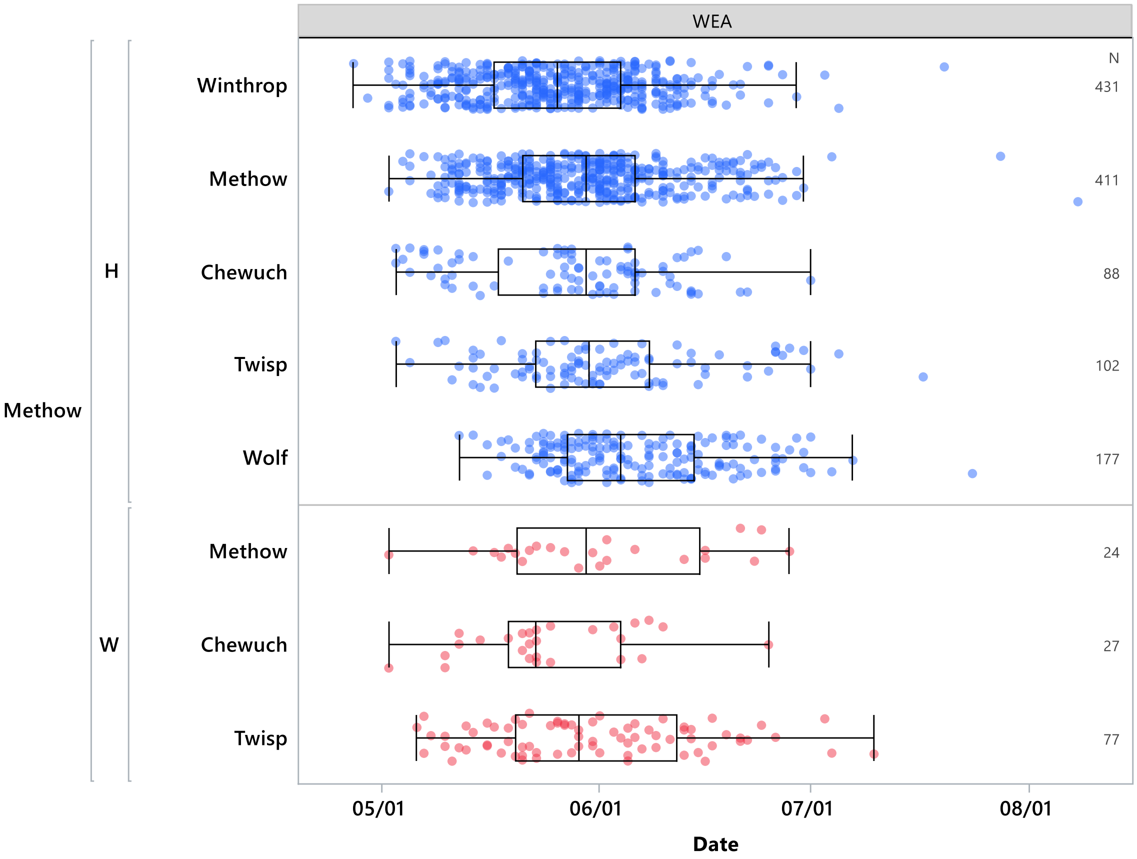


Figure 3. Return timing of PIT-tagged natural-origin (W, red) and hatchery-origin (H, blue) spring Chinook Salmon (age-3, 4, and 5) from the Methow Sub-basin to Wells Dam, return years 2006-2018. Data grouped by basin, origin, and river or tributary of release.

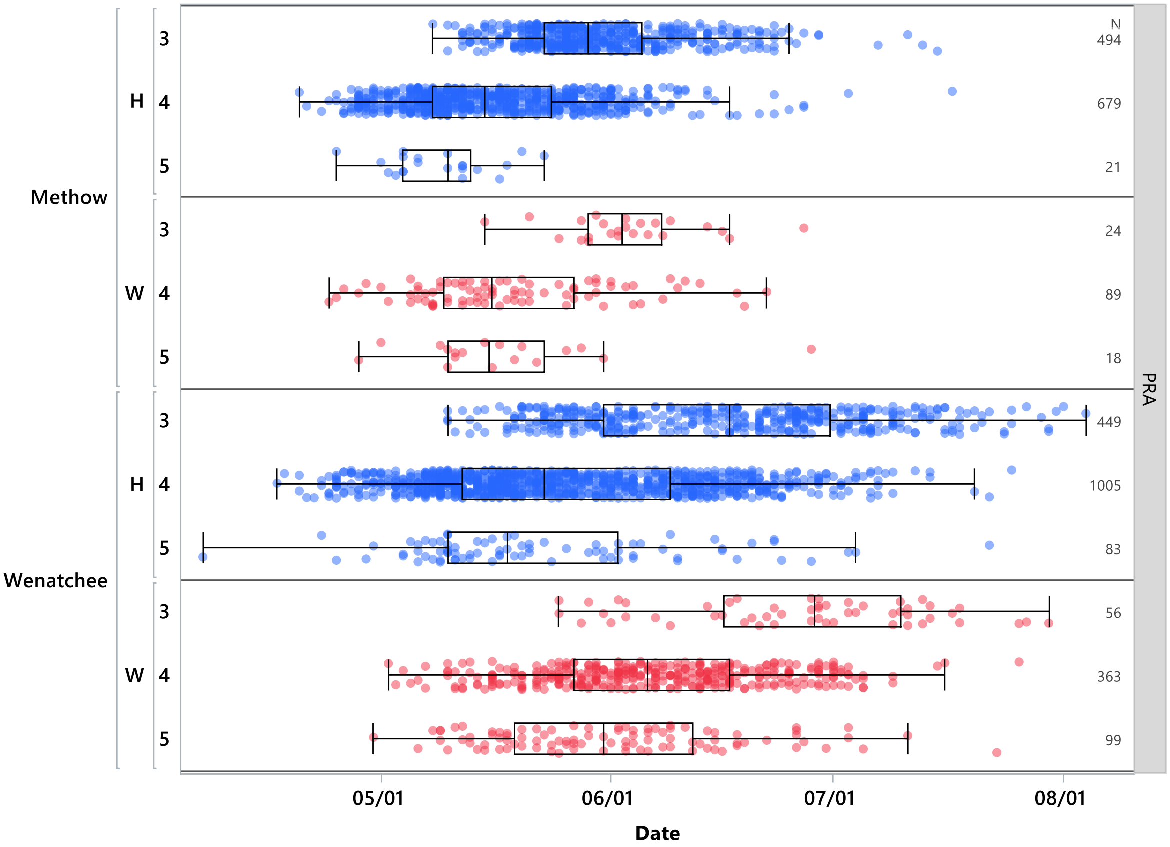


Figure 4. Return timing of PIT-tagged natural-origin (W, red) and hatchery-origin (H, blue) spring Chinook Salmon by age at return from the Methow and Wenatchee sub-basins to Priest Rapids Dam, return years 2006-2018. Data grouped by basin, origin, and river or tributary of release.

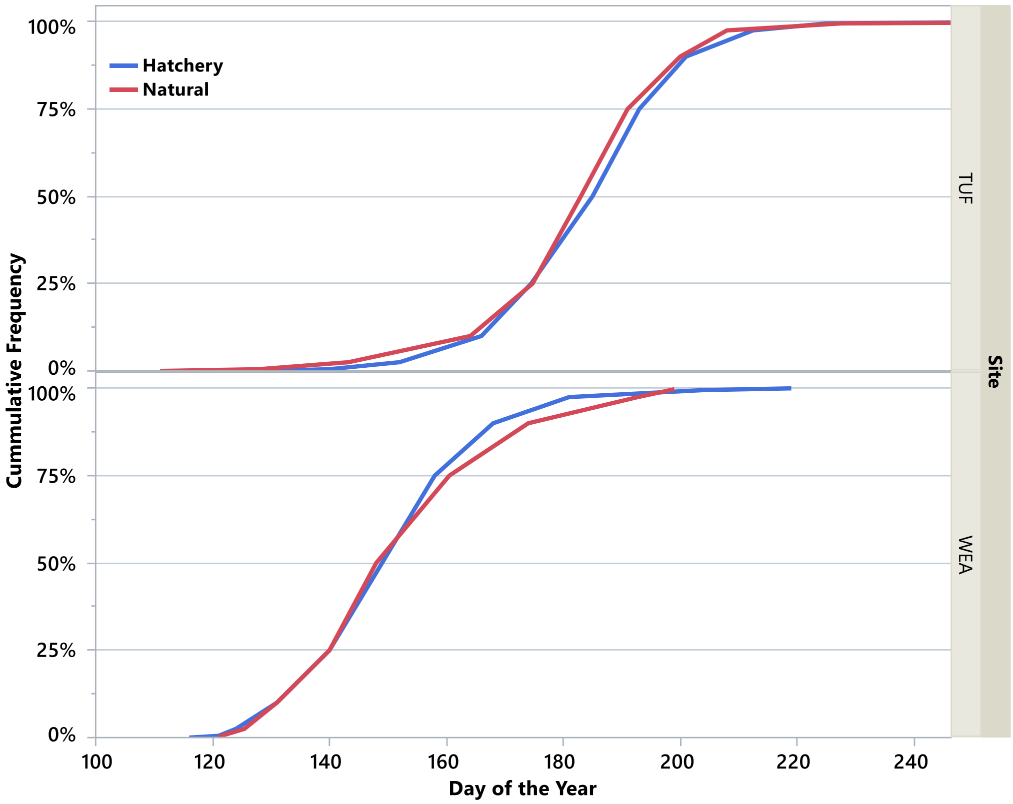


Figure 5. Cumulative frequency plots of migration timing of adult hatchery- and natural-origin spring Chinook Salmon passing Tumwater Dam (TUF) and Wells Dam (WEA). Migration timing was based on PIT-tagged fish detected during 2005-2018 migration years. Sample sizes at Tumwater Dam were 821 hatchery-origin and 490 natural-origin fish, and at Wells Dam 1,258 hatchery- and 137 natural-origin fish.

Table 1. Results of paired t-tests and 95% confidence limits on the 10%, 50% (median), and 90% day of the year that hatchery- and natural-origin spring Chinook Salmon migrated over Tumwater Dam (1998-2018) and Wells Dam (2006-2018). Migration timing was based on video monitoring and visual observations at both dams.

Location	Statistic	10th percentile	50th percentile	90th percentile
Tumwater Dam	Mean Difference	-2.00	-1.19	1.14
	Upper 95% Mean	-0.31	0.22	3.14
	Lower 95% Mean	-3.69	-2.60	-0.85
	N	21	21	21
	Test Statistic	-2.47	-1.76	1.19
	Prob > |t|	0.023	0.093	0.246
Wells Dam	Mean Difference	-2.48	-1.88	-0.75
	Upper 95% Mean	-0.51	-0.34	1.17
	Lower 95% Mean	-4.46	-3.43	-2.66
	N	13	13	13
	Test Statistic	-2.74	-2.66	-0.84
	Prob > |t|	0.018	0.021	0.412

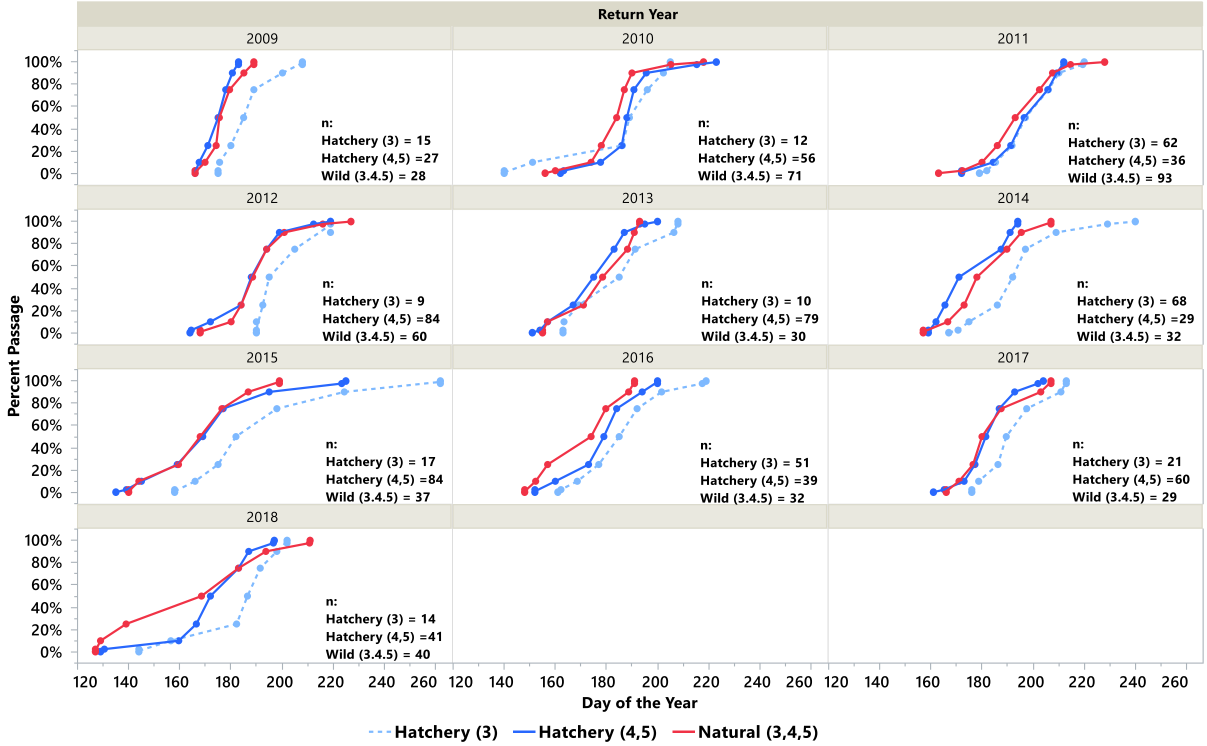


Figure 6. Return timing of PIT-tagged natural-origin (W, red) and hatchery-origin (H, blue) spring Chinook Salmon by age at return from the Wenatchee Sub-basin to Tumwater Dam by year (2009-2018).

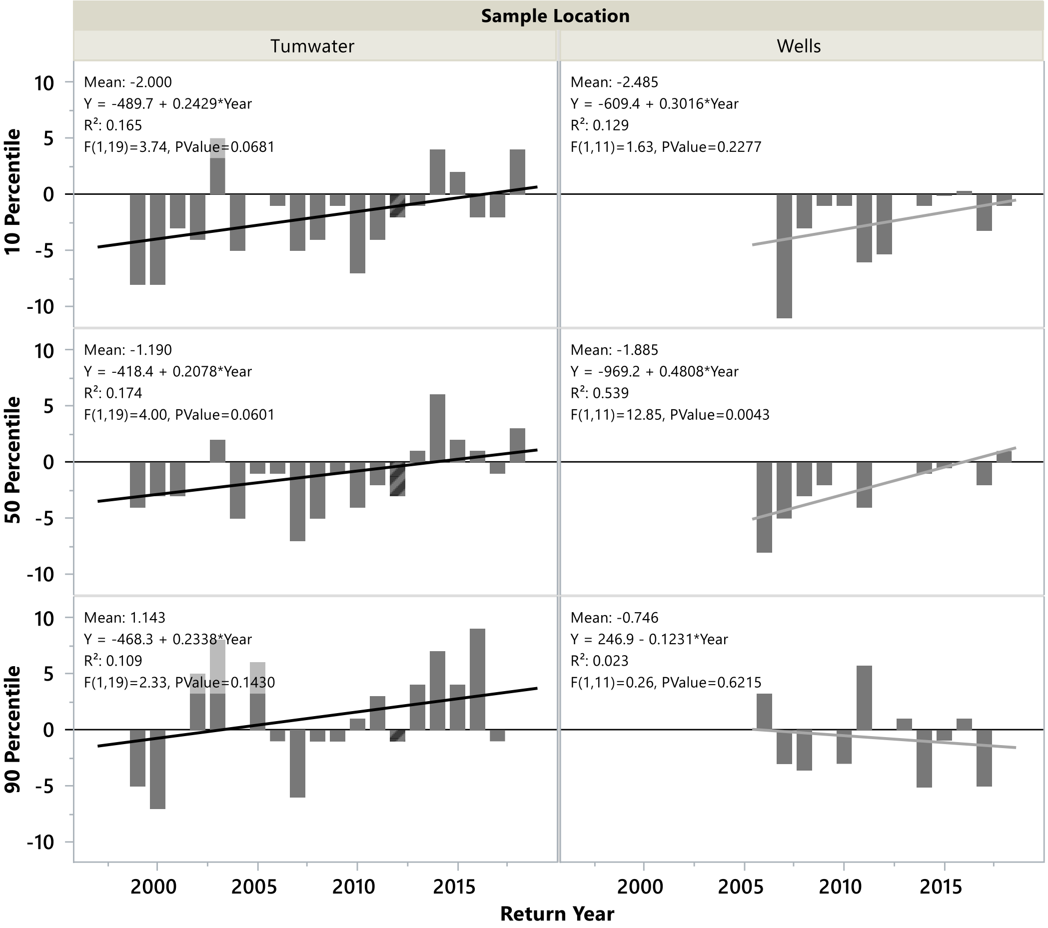


Figure 7. The difference in days (natural-origin minus hatchery-origin) that 10%, 50% (median), and 90% of natural-origin and hatchery-origin spring Chinook Salmon passed Tumwater Dam (1998-2018) and Wells Dam (2006-2018) and the mean difference and trend of that time period. Negative values indicate that hatchery-origin fish passed later in the year. Passage timing was based on visual observations at each dam (data from Table 1, used for paired t-test).

Spawn Timing (Carcass Recovery) of Spring Chinook Salmon in the Wenatchee and Methow Sub-basins

From 1992-2018, carcass recovery of female spring Chinook Salmon in the Wenatchee and Methow sub-basins generally began in early August and extended to early October (Figure 8). Across their range in both sub-basins, hatchery- and natural-origin fish generally had similar and overlapping spawn timing. Across all years, spawn timing was consistent with median carcass recovery dates generally varying between one and two weeks over more than 20 years of sampling (Figure 9). On a year-by-year basis, hatchery-origin fish generally matched the timing of natural-origin spawning (Figure 9 and Figure 10).

The means of paired differences at the 10th, 50th, and 90th timing percentile were small relative to the variation in natural-origin spawn timing within years and, in most cases, not significant at the 0.05 level (Table 2 and Table 3). At the 50th percentile (median), only the Twisp River had a significant difference between hatchery- and natural-origin spawning. However, this analysis and deriving percentiles from distributions was limited by small sample sizes (Table 2 and 3.). For example, in years with fewer than ten fish, percentile metrics (e.g., 10th, 50th, and 90th) should be viewed with caution. Similar limitations exist in the White River. In the Chiwawa River, at the 10th percentile hatchery-origin fish spawned on average 3.29 days earlier than natural-origin fish and this difference was significant. Figure 9 illustrates this difference, and the annual variation associated with it.

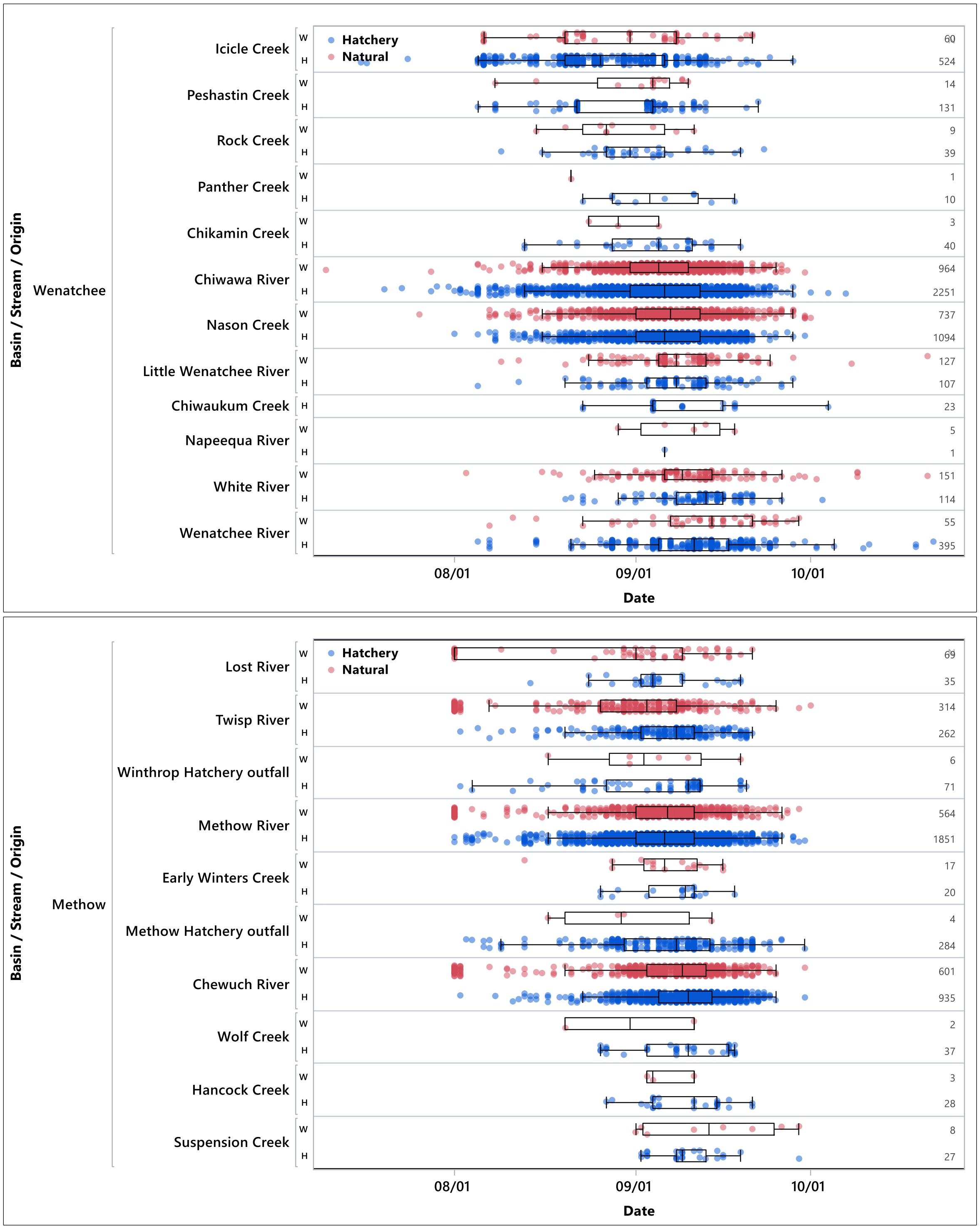
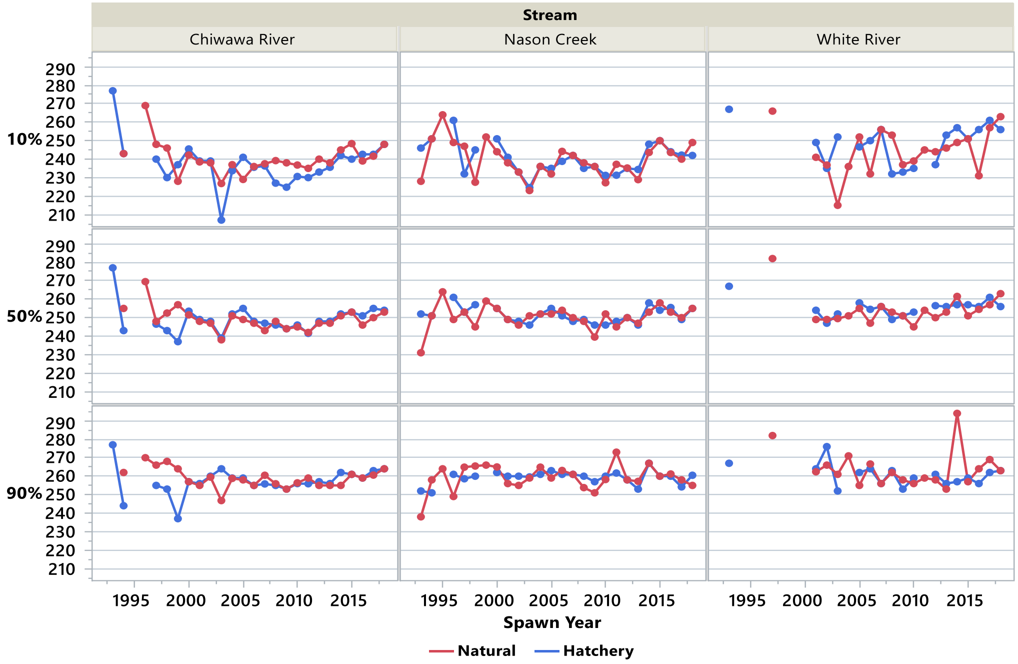


Figure 8. Spawn timing of hatchery- (H, blue) and natural-origin (W, red) female spring Chinook Salmon in the Wenatchee (top, 1992-2018) and Methow (bottom, 1993-2018) sub-basins by stream or tributary. Spawn timing was based on the day of the year that female carcasses were recovered on the spawning grounds. Each dot represents one female. Boxes cover the 25-75% percentile; dots beyond the whiskers are outliers. Sample sizes on right border.



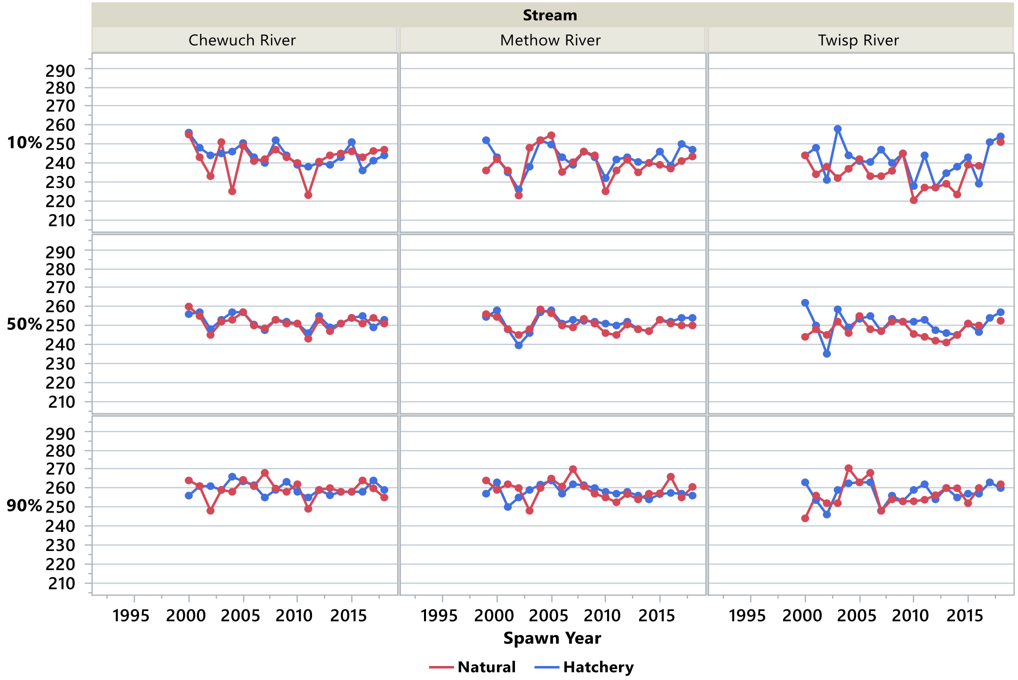


Figure 9. The 10th, 50th (median), and 90th percentile spring Chinook Salmon spawn day of the year in the Wenatchee (top) and Methow (bottom) sub-basins by year and stream. Estimates are based on recovery of female carcasses on spawning grounds.

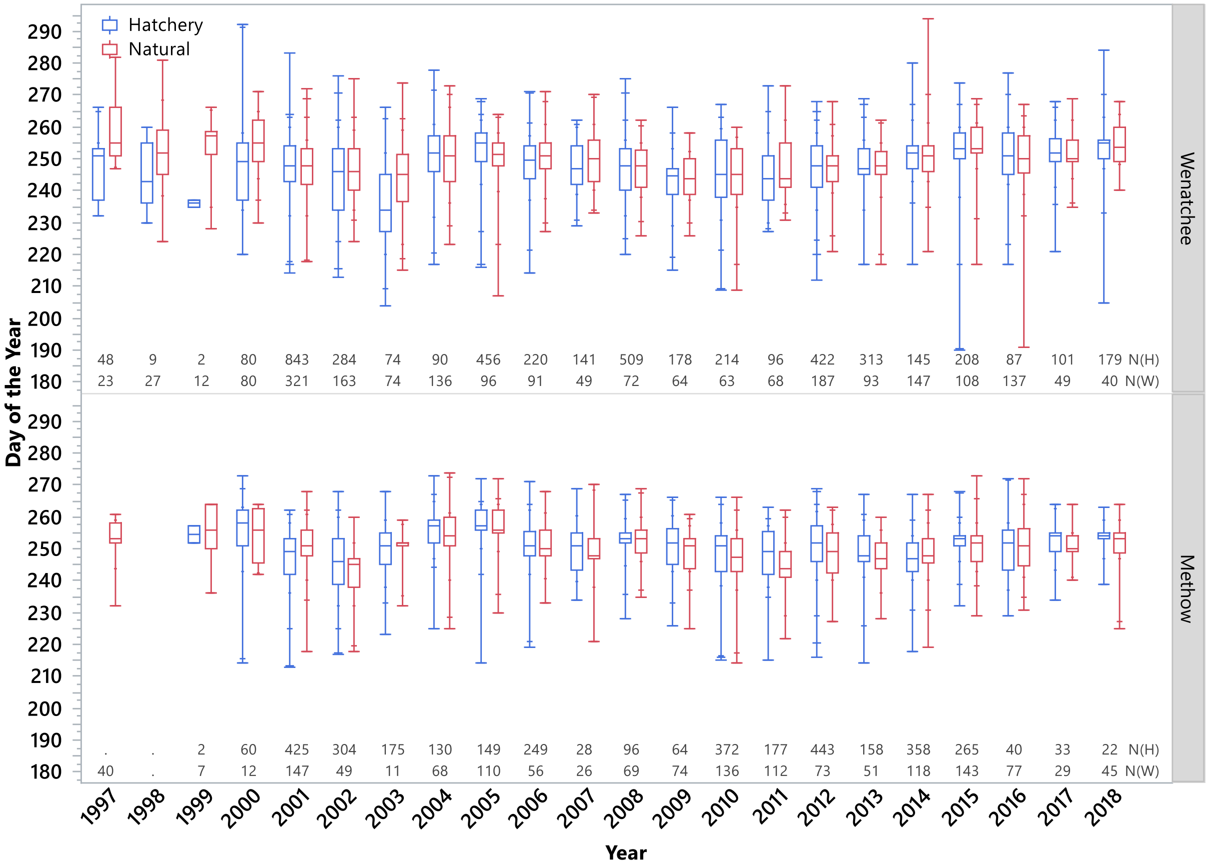


Figure 10. The distributions of spawn timing of hatchery- and natural-origin spring Chinook Salmon by year in the Wenatchee (top) and Methow (bottom) sub-basins based on female carcass recovery. Sample size by origin above the x-axis. Boxes span the 25-75th percentiles. Line inside box = 50th percentile (median). Dashes outside of boxes = 10th/90th, 2.5th/97.5th, and minimum/maximum.

Table 2. Results of paired t-tests and 95% CIs on the 10%, 50% (median), and 90% day of spawn timing (based on female carcass recovery) of hatchery- and natural-origin spring Chinook Salmon in the Wenatchee Sub-basin during the period 1993-2018.

Location	Statistic	10th percentile	50th percentile	90th percentile
Chiwawa River	Mean Difference	3.29	0.59	2.08
	Upper 95% Mean	6.55	3.11	5.87
	Lower 95% Mean	0.04	-1.93	-1.71
	N	23	23	23
	Test Statistic	2.09	0.48	1.13
	Prob > |t|	0.048	0.634	0.268
Nason Creek	Mean Difference	-1.75	-1.92	-0.45
	Upper 95% Mean	1.28	0.62	2.05
	Lower 95% Mean	-4.79	-4.45	-2.95
	N	24	24	24
	Test Statistic	-1.20	-1.56	-0.37
	Prob > |t|	0.244	0.132	0.714
White River	Mean Difference	-3.55	-1.84	2.38
	Upper 95% Mean	3.88	0.54	8.03
	Lower 95% Mean	-10.98	-4.23	-3.28
	N	16	16	16
	Test Statistic	-1.02	-1.65	0.90
	Prob > |t|	0.324	0.120	0.385

Table 3. Results of paired t-tests and 95% CIs on the 10%, 50% (median), and 90% day of spawn timing (based on female carcass recovery) of hatchery- and natural-origin spring Chinook Salmon in the Methow Sub-basin during the period 1999-2018.

Location	Statistic	10th percentile	50th percentile	90th percentile
Chewuch River	Mean Difference	-1.87	-0.76	-0.25
	Upper 95% Mean	1.64	0.37	2.60
	Lower 95% Mean	-5.39	-1.89	-3.10
	N	19	19	19
	Test Statistic	-1.12	-1.42	-0.18
	Prob > |t|	0.277	0.174	0.858
Methow River	Mean Difference	-2.53	-1.00	1.02
	Upper 95% Mean	0.07	0.26	3.58
	Lower 95% Mean	-5.13	-2.26	-1.55
	N	20	20	20
	Test Statistic	-2.03	-1.66	0.83
	Prob > |t|	0.056	0.113	0.417
Twisp River	Mean Difference	-5.95	-2.97	-0.76
	Upper 95% Mean	-1.58	-0.06	2.44
	Lower 95% Mean	-10.32	-5.89	-3.96
	N	18	18	18
	Test Statistic	-2.87	-2.15	-0.50
	Prob > |t|	0.011	0.046	0.622

Spawning Distribution of Spring Chinook Salmon in the Chiwawa River

Both hatchery- and natural-origin spring Chinook Salmon spawned throughout the Chiwawa River and within each reach; however, there was a significant difference in the distribution of hatchery- and natural-origin spawners among historical survey reaches for years 1993-2018 (Yates' Chi-square = 371.914; P= 0.000; Effect Size = 0.342) (Figures 11 and 12). The proportion of natural-origin spawners (pNOS) was highest within reaches C3 through C6 (pNOS = 0.30-0.56); the proportion of hatchery-origin spawners (pHOS) was highest within reaches C1 (pHOS = 0.89), C2 (pHOS = 0.70), and C7 (pHOS = 0.75) (Figure 13). In all reaches, pHOS exceeded 0.30 and it exceeded 0.50 within five of the seven reaches. When comparing spawn distribution at the 0.5-RKm scale, the greatest proportion of hatchery-origin spring Chinook Salmon spawned in the lower 25 km of the river, while the greatest proportion of natural-origin fish spawned between km 30 and 55 (Figure 14).

Spawning Distribution of Spring Chinook Salmon in Nason Creek

The Nason Creek Hatchery Program began producing adult returns in 2016. Prior to 2016, hatchery-origin spring Chinook Salmon that spawned in Nason Creek were strays, mainly from the Chiwawa spring Chinook Salmon Hatchery Program. Hatchery- and natural-origin spring Chinook Salmon spawned throughout Nason Creek; however, there was a significant difference in the distribution of hatchery- and natural-origin spawners among historical survey reaches for years 1993-2018 (Yates' Chi-square = 158.721; P= 0.000; Effect Size = 0.296) (Figures 11 and 15). The pHOS exceeded 0.30 in all reaches and was highest within reaches N1 (pHOS = 0.79) and N2 (pHOS = 0.61). The pHOS and pNOS were close to equal within reaches N3 and N4 where pHOS = 0.46 and pNOS = 0.54 for both reaches (Figure 13). When comparing spawn distribution at the 0.5-RKm scale, the highest proportion of hatchery-origin spring Chinook Salmon spawned in the lower 7 km of Nason Creek; the highest proportion of natural-origin spring Chinook Salmon spawned upstream from RKm 16 (Figure 14).

Spawning Distribution of Spring Chinook Salmon in the White River

There are three historical reaches (H2, H3, and H4) in the White River and most of the hatchery and natural-origin Chinook Salmon spawned in reach H3. Many of the hatchery-origin spawners were strays from the Chiwawa Hatchery program. There was no significant difference in the distribution of hatchery- and natural-origin spawners among the three historical survey reaches for years 1993-2018 (Yates' Chi-square = 0.155; P= 0.925; Effect Size = 0.49) (Figures 11 and 16). The pNOS was higher than pHOS within all three reaches and pNOS was highest in the uppermost reach (pNOS = 0.71) (Figure 13). The pHOS exceeded 0.30 in two of the three reaches. When comparing spawn distribution at the 0.5-RKm scale, the highest proportion of hatchery- and natural-origin spring Chinook Salmon spawned between RKm 20 and 24 (Figure 14).

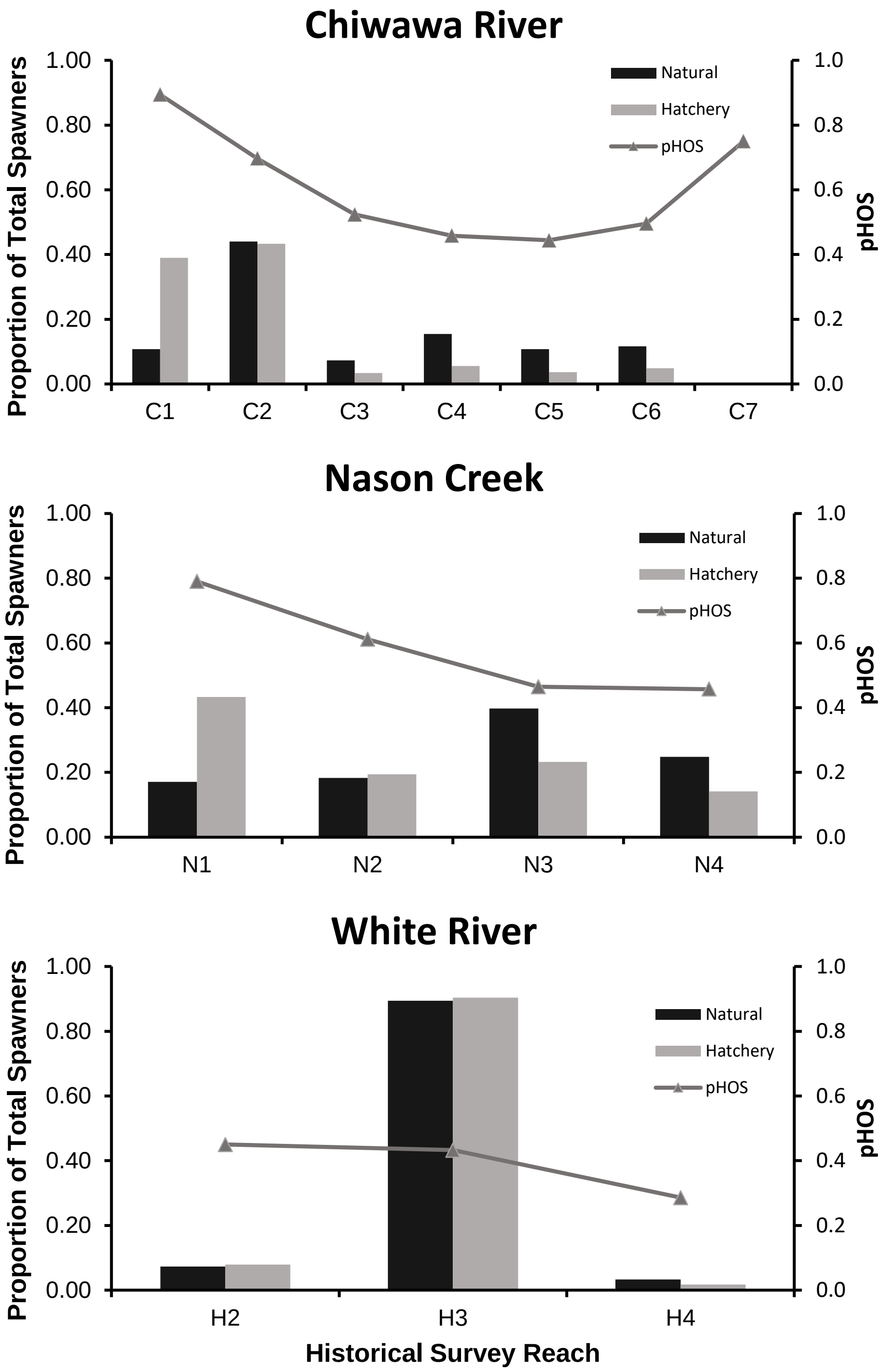


Figure 11. Proportion of hatchery- and natural-origin spring Chinook Salmon spawners within a stream that were observed within each historical reach on the Chiwawa River (top), Nason Creek (middle), and on the White River (bottom) during the period 1993-2018. Here, the proportion of natural-origin or hatchery-origin spawners across historical reaches sum to “1.00.” The line represents the proportion of hatchery-origin spawners within each historical reach.

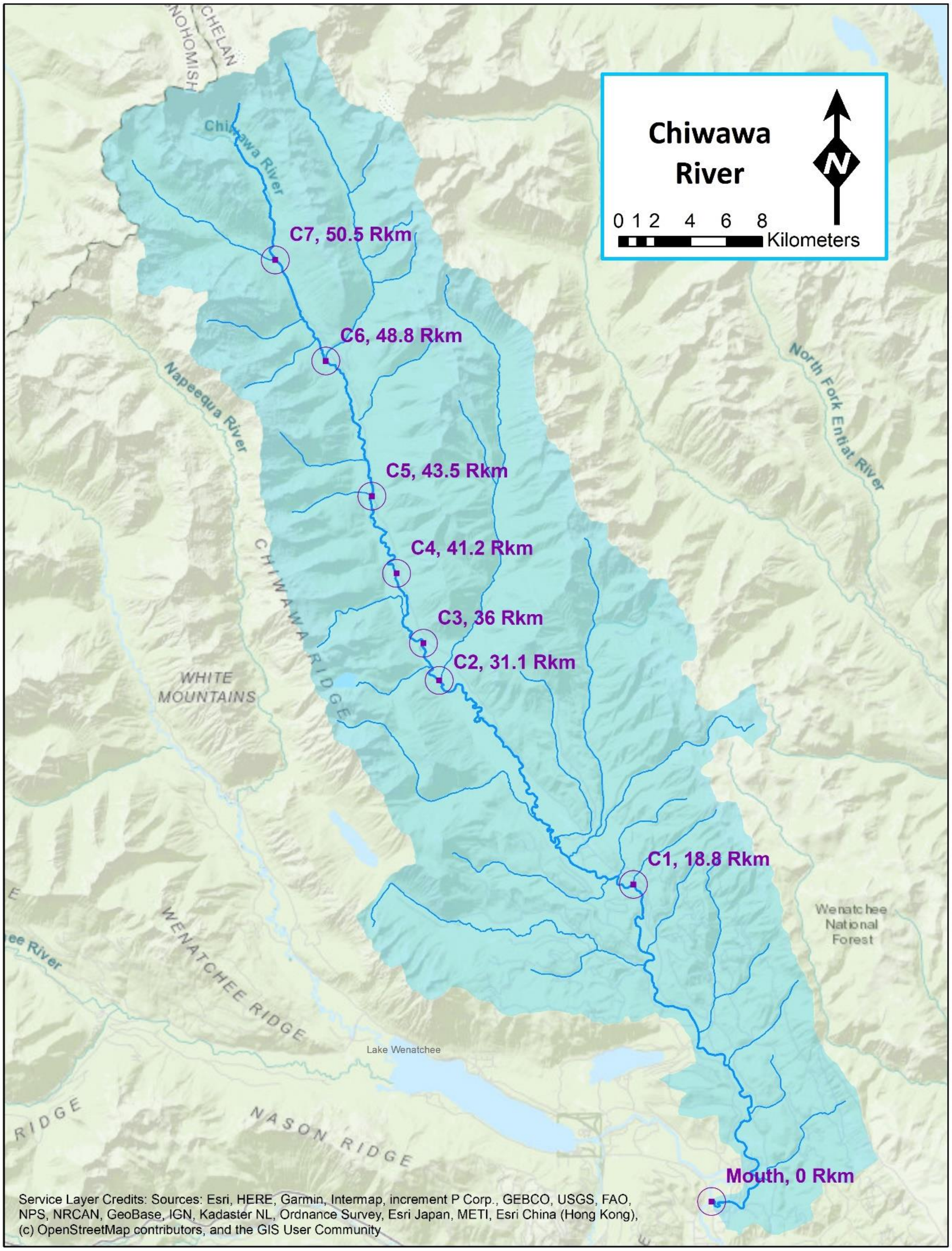


Figure 12. Map of the Chiwawa River showing locations of historical spring Chinook Salmon survey reaches.

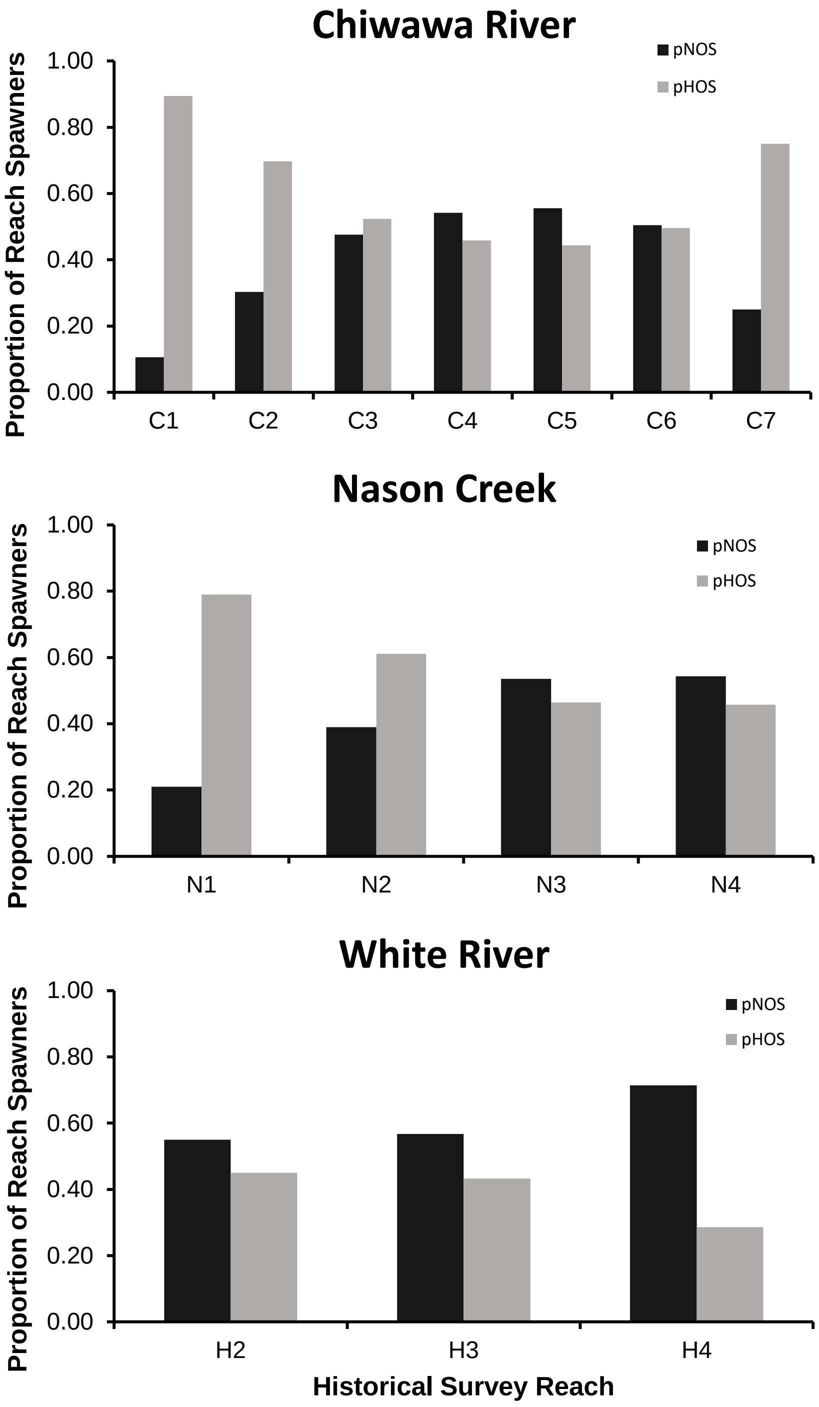


Figure 13. Proportion of hatchery- and natural-origin spring Chinook Salmon spawners within each of the historical sampling reaches on the Chiwawa River (top), Nason Creek (middle), and the White River (bottom) during the period 1993-2018. Here, pNOS and pHOS sum to "1.00" within each reach.

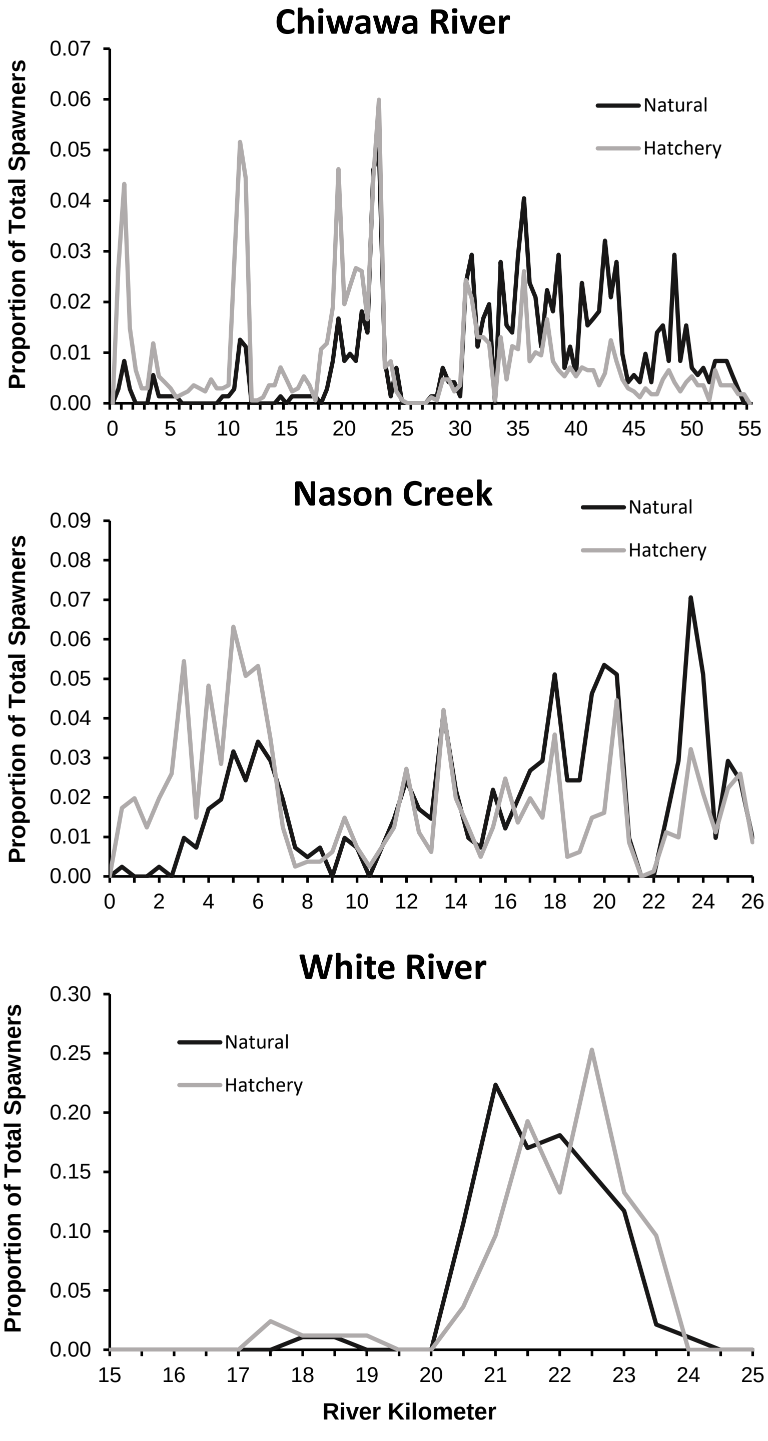


Figure 14. Proportion of natural- and hatchery-origin spring Chinook Salmon spawners distributed along the length of the Chiwawa River (top), Nason Creek (middle), and White River (bottom) during the period 1993-2018. Distribution was based on 0.5-km-long reaches. Chiwawa River sample sizes = 716 natural- and 1,686 hatchery-origin fish, Nason Creek sample sizes = 411 natural- and 808 hatchery-origin fish, and White River sample sizes = 94 natural- and 83 hatchery-origin fish.

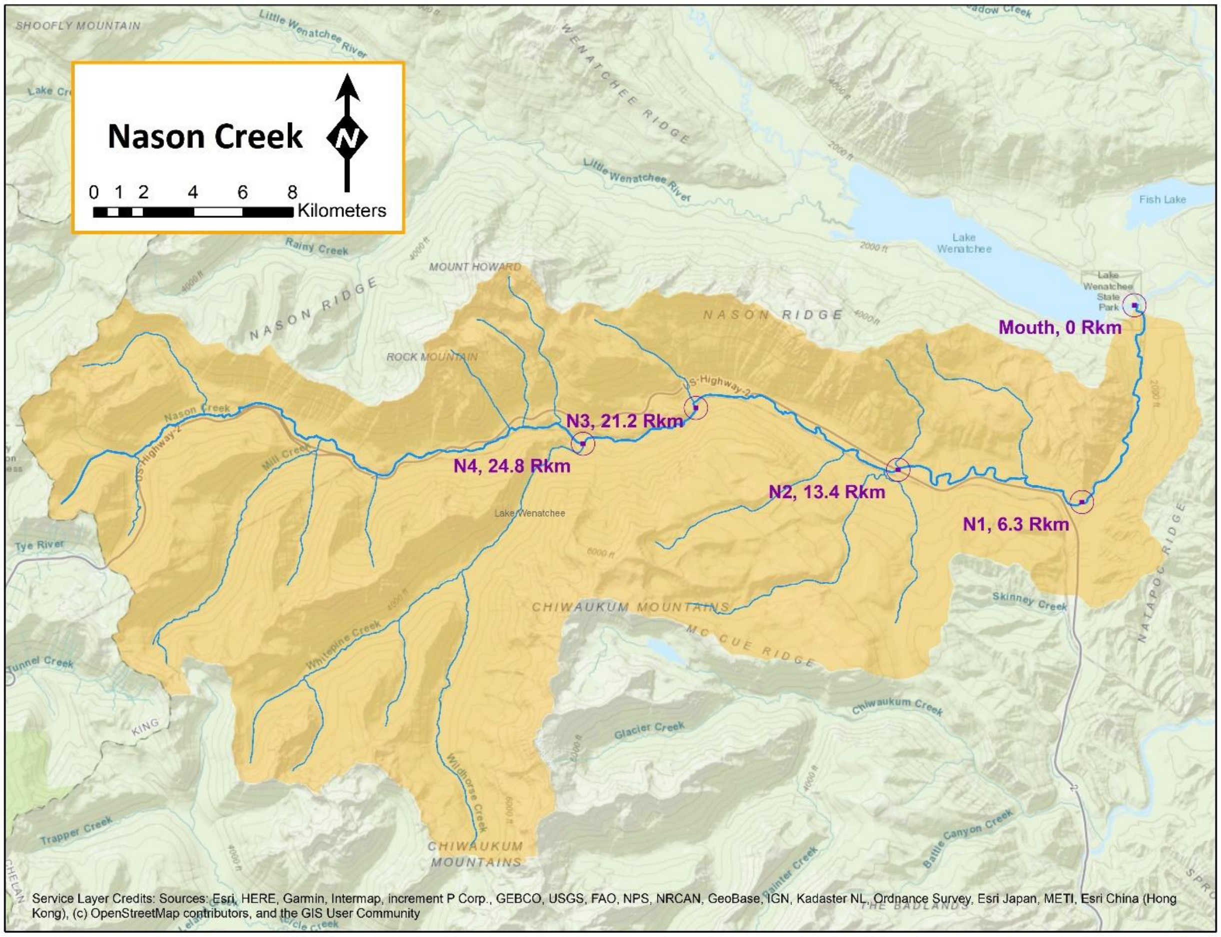


Figure 15. Map of Nason Creek showing locations of historical spring Chinook Salmon survey reaches.

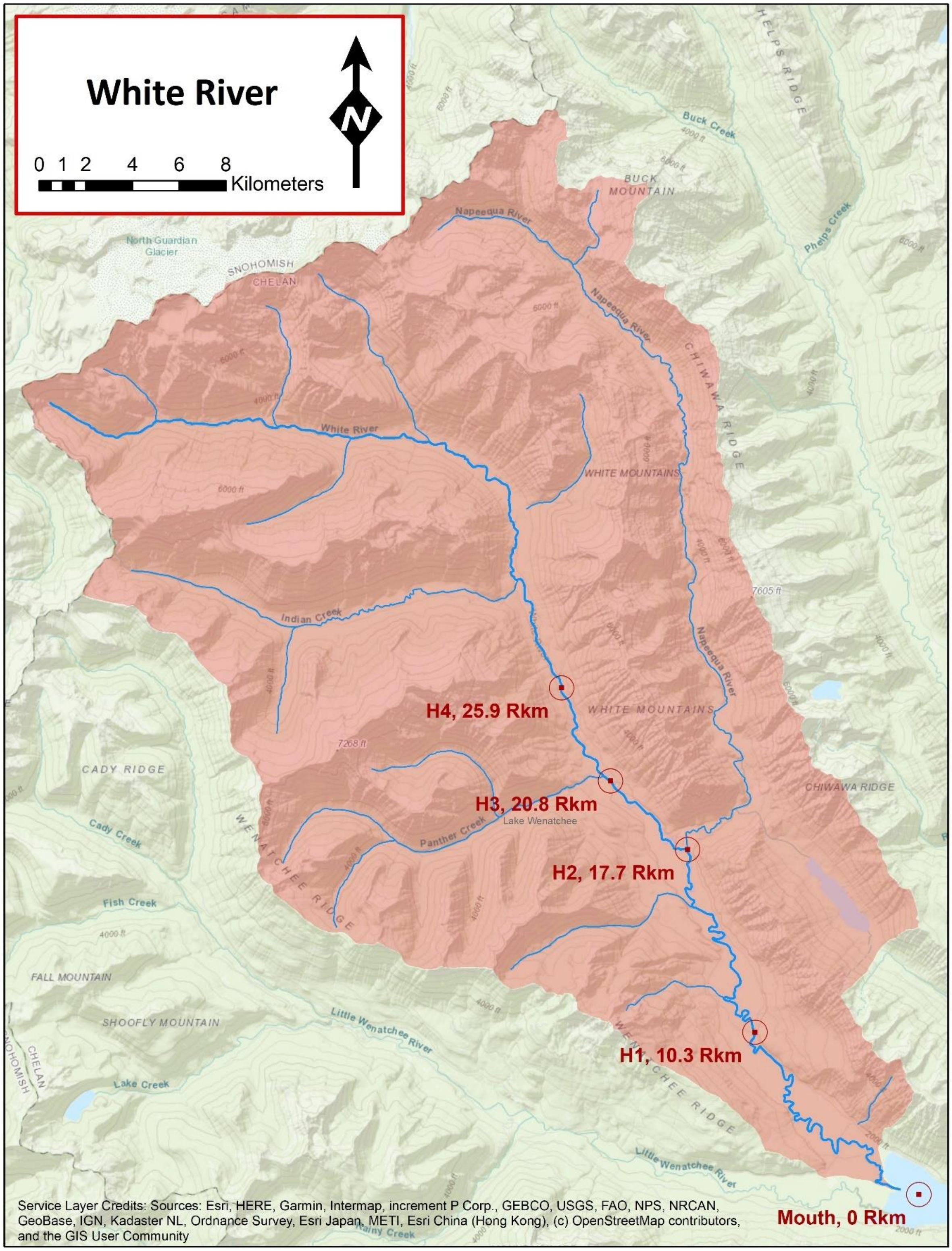


Figure 16. Map of the White River showing locations of historical spring Chinook Salmon survey reaches.

Spawning Distribution of Spring Chinook Salmon in the Chewuch River

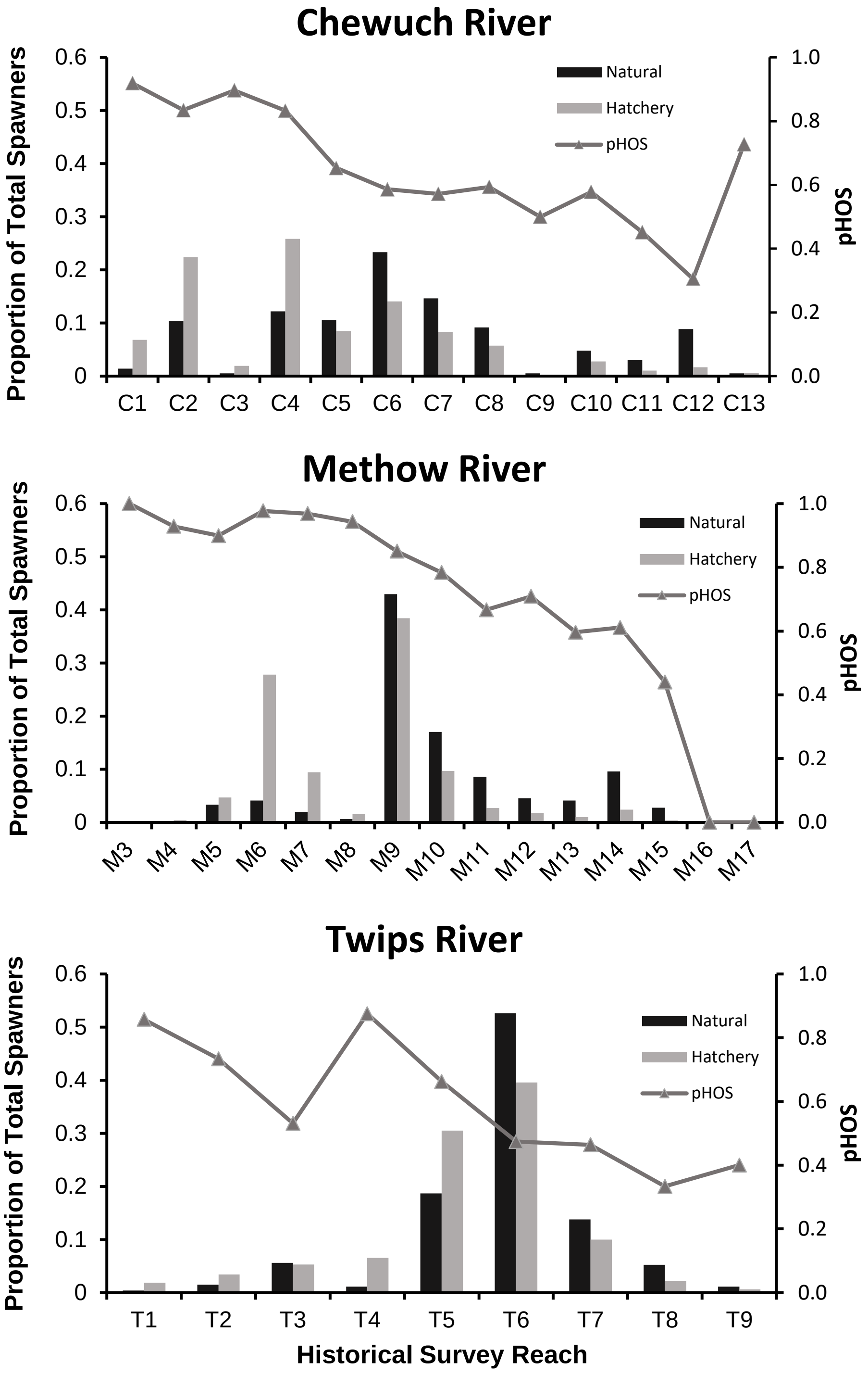
Both hatchery- and natural-origin spring Chinook Salmon spawned throughout the Chewuch River and within each reach; however, there was a significant difference in the distribution of hatchery- and natural-origin spawners among historical survey reaches for years 1996-2018 (Yates' Chi-square = 205.772; P= 0.000; Effect Size = 0.329) (Figures 17 and 18). The pHOS was higher than or equal to the pNOS within 10 out of 13 reaches (Figure 19) and, in general, pHOS declined in an upstream direction. The pHOS was greater than 0.30 in all reaches (pHOS range = 0.31-0.92). When comparing spawn distribution at the 0.5-RKm scale, the highest proportions of both hatchery- and natural-origin spring Chinook Salmon spawned in the lower 55 km of the Chewuch River (Figure 20). A greater proportion of hatchery-origin spring Chinook Salmon spawned in the lower 20 km of the river, while a larger proportion of natural-origin spring Chinook Salmon spawned upstream from RKm 25.

Spawning Distribution of Spring Chinook Salmon in the Methow River

Both hatchery- and natural-origin spring Chinook Salmon spawned throughout the Methow River and within each reach; however, there was a significant difference in the distribution of hatchery- and natural-origin spawners among historical survey reaches for years 1996-2018 (Yates' Chi-square = 370.839; P= 0.000; Effect Size = 0.314) (Figures 17 and 21). The pHOS was higher than the pNOS within 12 of the 15 reaches (Figure 19). The pHOS exceeded 0.30 in 13 of the 15 reaches. When comparing spawning distribution at the 0.5-RKm scale, a larger proportion of hatchery-origin fish spawned between RKm 80 and 90, while a larger proportion of natural-origin fish spawned upstream from RKm 90 (Figure 20).

Spawning Distribution of Spring Chinook Salmon in the Twisp River

Both hatchery- and natural-origin spring Chinook Salmon spawned throughout the Twisp River and within each reach; however, there was a significant difference in the distribution of hatchery- and natural-origin spawners among historical survey reaches for years 1996-2018 (Yates' Chi-square = 29.803; P= 0.000; Effect Size = 0.244) (Figures 17 and 22). The pHOS was higher than the pNOS within reaches T1-T5 and lower within reaches T6-T9 (Figure 19). The pHOS exceeded 0.30 in all reaches. When comparing spawn distribution at the 0.5-RKm scale, a larger proportion of hatchery-origin fish spawned downstream from RKm 25, while a larger proportion of natural-origin fish spawned upstream from RKm 20 (Figure 20).


Chewuch River

Methow River

Twips River

Figure 17. Proportion of hatchery- and natural-origin spring Chinook Salmon spawners within a stream that were observed within each historical reach on the Chewuch River (top), the Methow River (middle), and the Twisp River (bottom) during the period 1996-2018. Here, the proportion of natural-origin or hatchery-origin spawners across historical reaches sum to "1.00." The line represents the proportion of hatchery-origin spawners within each historical reach.

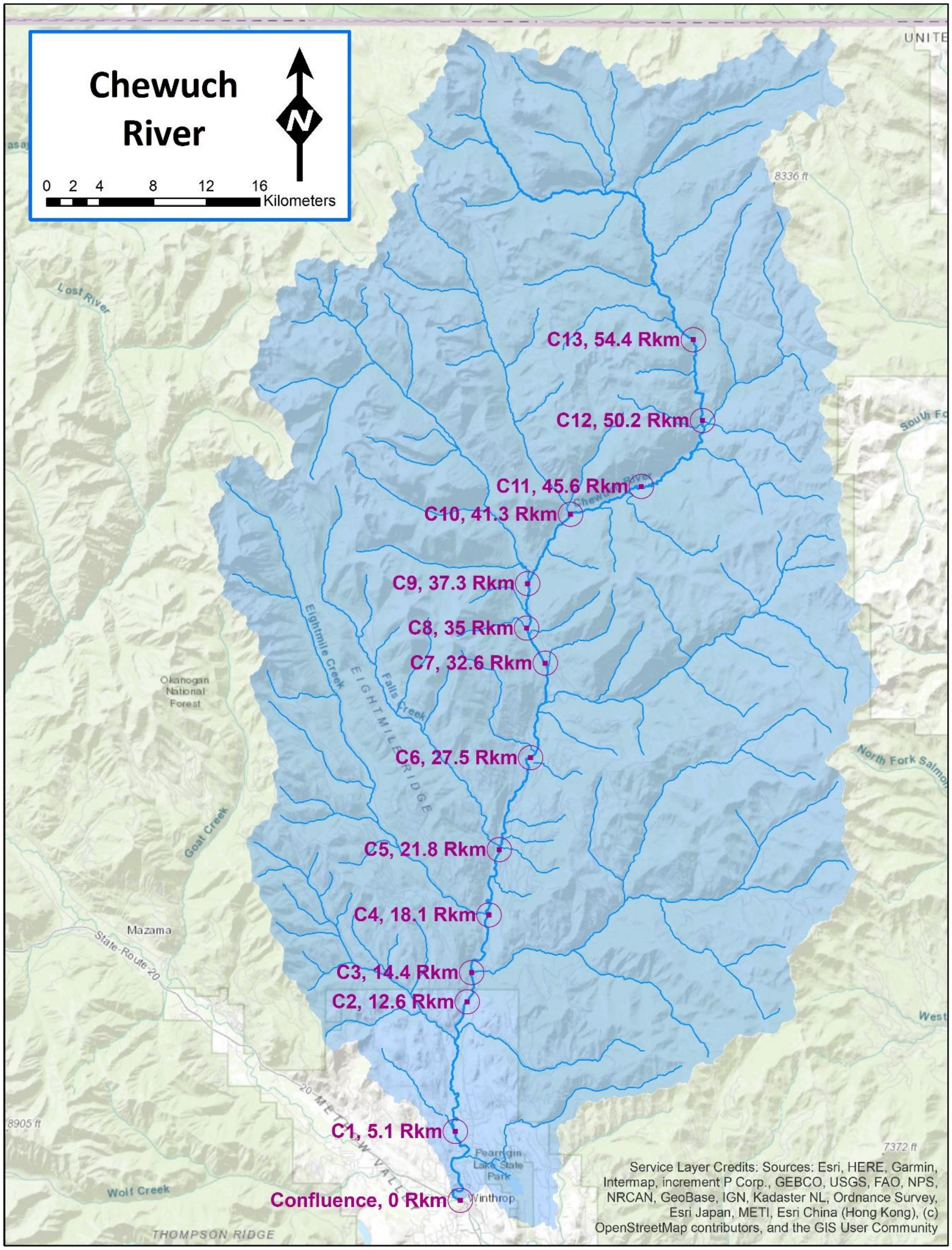


Figure 18. Map of the Chewuch River showing locations of historical spring Chinook Salmon survey reaches.

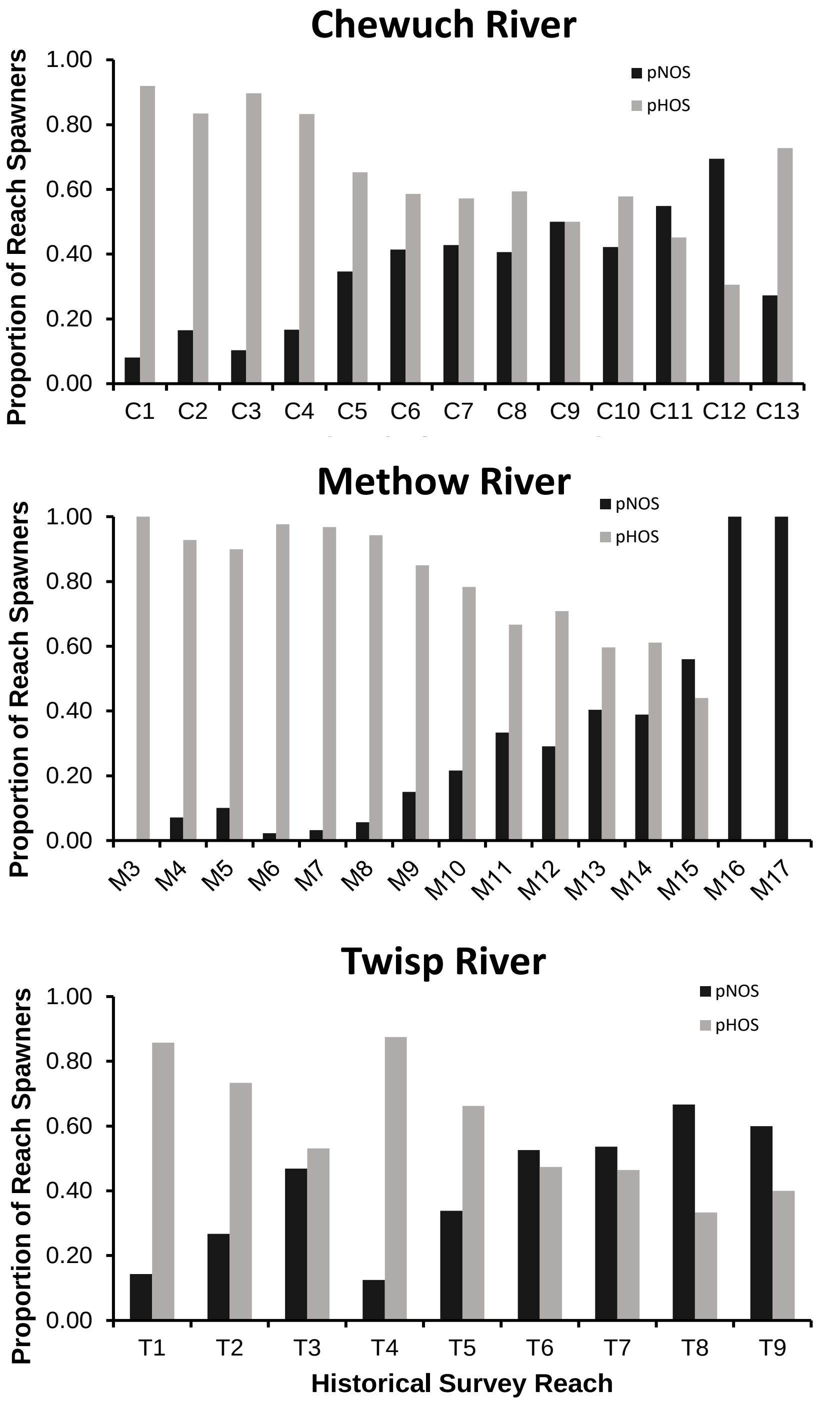


Figure 19. Proportion of hatchery- and natural-origin spring Chinook Salmon spawners within each of the historical sampling reaches on the Chewuch River (top), Methow River (middle), and the Twisp River (bottom) during the period 1996-2018. Here, pNOS and pHOS sum to “1.00” within each reach.

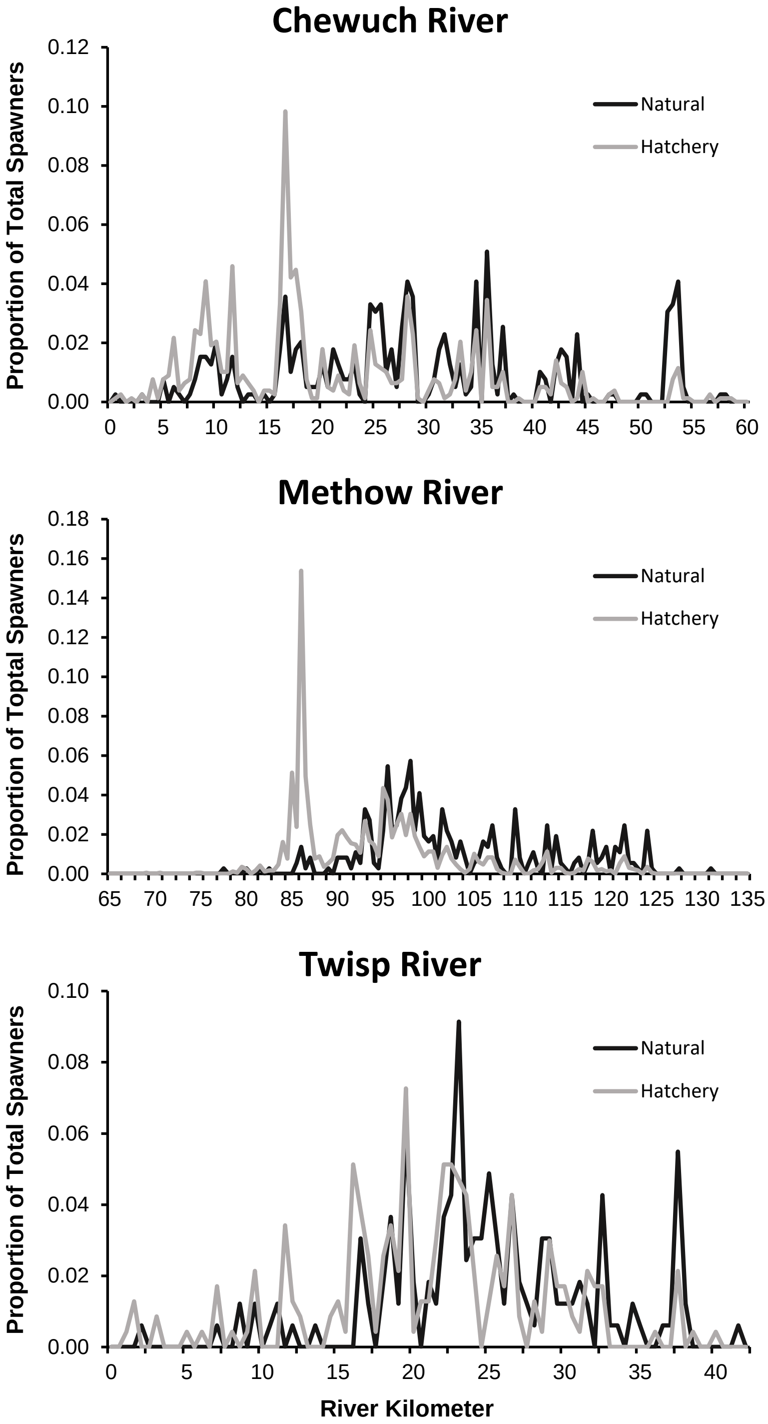


Figure 20. Proportion of natural- and hatchery-origin spring Chinook Salmon spawners distributed along the length of the Chewuch River (top), Methow River (middle), and Twisp River (bottom) during the period 1996-2018. Distribution was based on 0.5-km-long reaches. Chewuch River sample sizes = 393 natural- and 782 hatchery-origin fish, Methow River sample sizes = 366 natural- and 1,677 hatchery-origin fish, and Twisp River sample sizes = 164 natural- and 234 hatchery-origin fish.

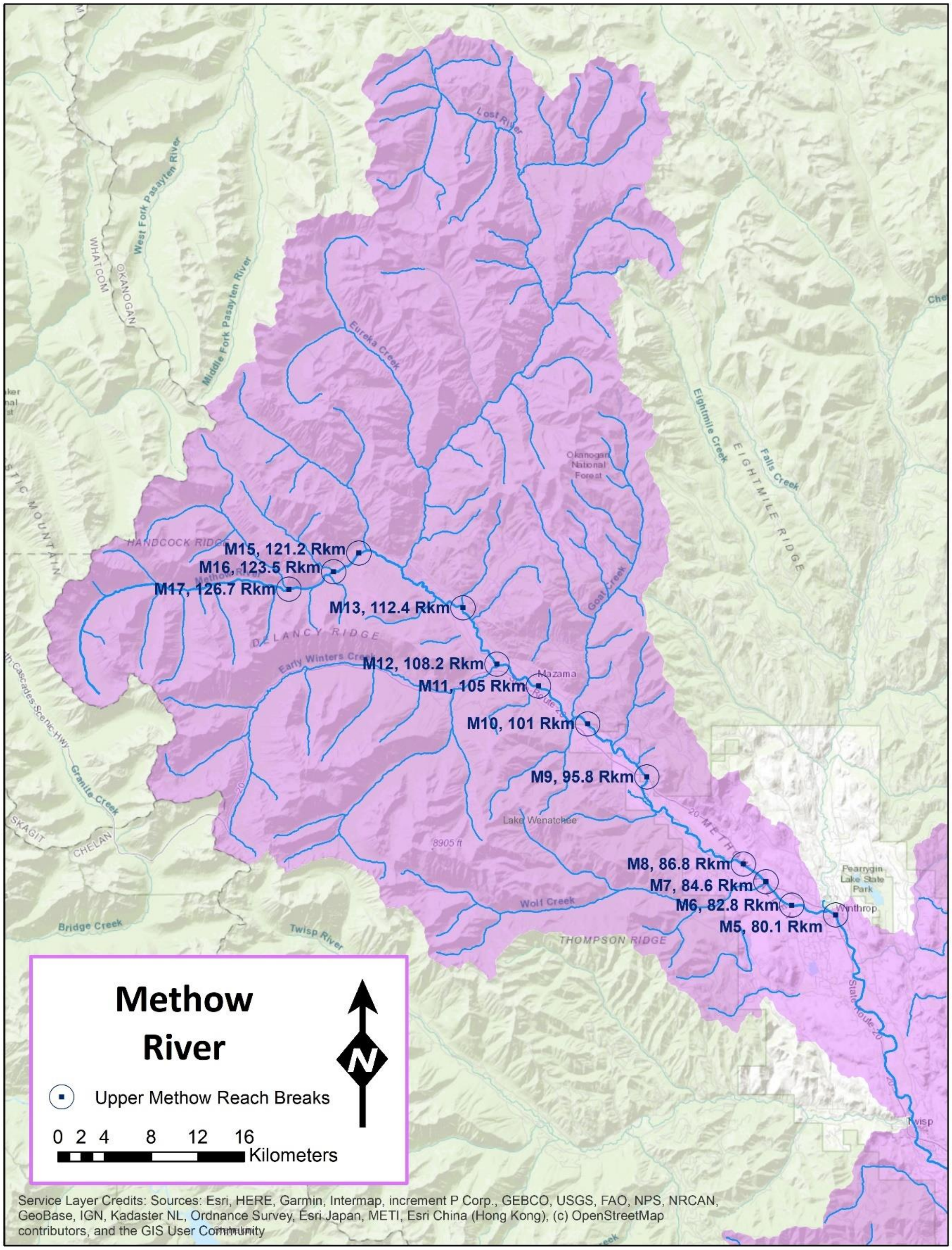


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Figure 21. Map of the Upper Methow River showing locations of historical spring Chinook Salmon survey reaches.

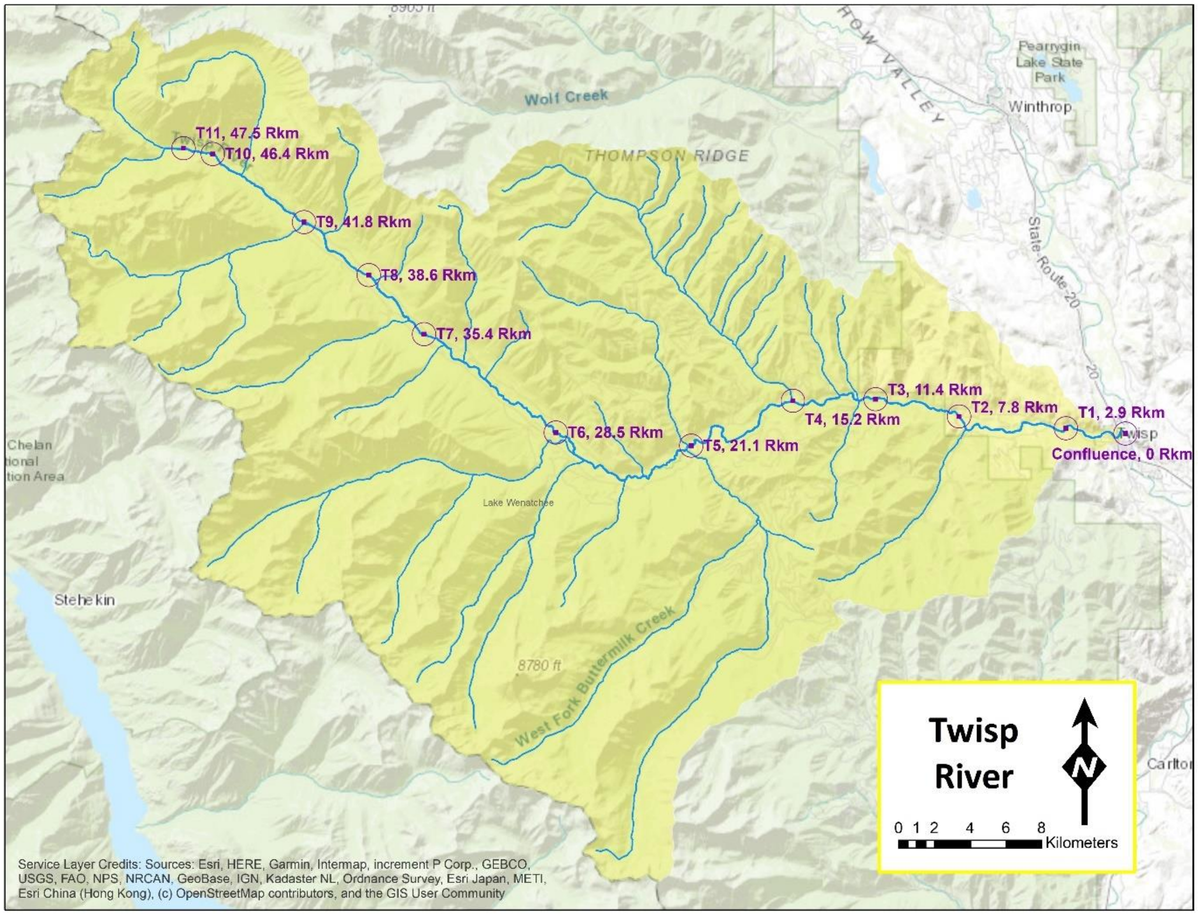

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Figure 22. Map of the Twisp River showing locations of historical spring Chinook Salmon survey reaches.

Migration Timing of Wenatchee and Methow Summer Chinook Salmon

At Dryden Dam, based on 12 years of sampling, there were significant differences in the migration timing of hatchery- and natural-origin summer Chinook Salmon at the 10th and 50th percentiles (Table 4). At most, the average difference in migration timing between hatchery- and natural-origin fish was 2.5 weeks. This later arrival date of hatchery-origin fish at Dryden Dam was generally consistent year-by-year and throughout the arrival distribution (Figure 23). At Wells Dam, migration timing between hatchery- and natural-origin fish were a near match; only at the tail end of the migration (90th percentile) was there a small measurable difference (1 week) and this was not significant. However, the run of hatchery-origin summer Chinook at Wells Dam consists of a mix of fish released in the Methow sub-basin, Okanogan sub-basin, and Columbia River, plus stray fish from downstream locations.

Table 4. Results of paired t-tests and 95% CIs on the 10%, 50% (median), and 90% day of migration timing (weeks) of hatchery- and natural-origin summer Chinook Salmon at Dryden Dam and Wells Dam during the period 2007-2018.

Location	Statistic	10th percentile	50th percentile	90th percentile
Dryden Dam	Mean Difference	-1.08	-2.50	-0.91
	Upper 95% Mean	-0.13	-0.61	1.17
	Lower 95% Mean	-2.04	-4.39	-2.99
	N	12	12	12
	Test Statistic	-2.49	-2.92	-0.96
	Prob > |t|	0.030	0.014	0.358
Wells Dam	Mean Difference	-0.18	0.08	1.00
	Upper 95% Mean	0.20	0.51	2.33
	Lower 95% Mean	-0.53	-0.34	-0.33
	N	12	12	12
	Test Statistic	-1.00	0.432	1.66
	Prob > |t|	0.339	0.674	0.126

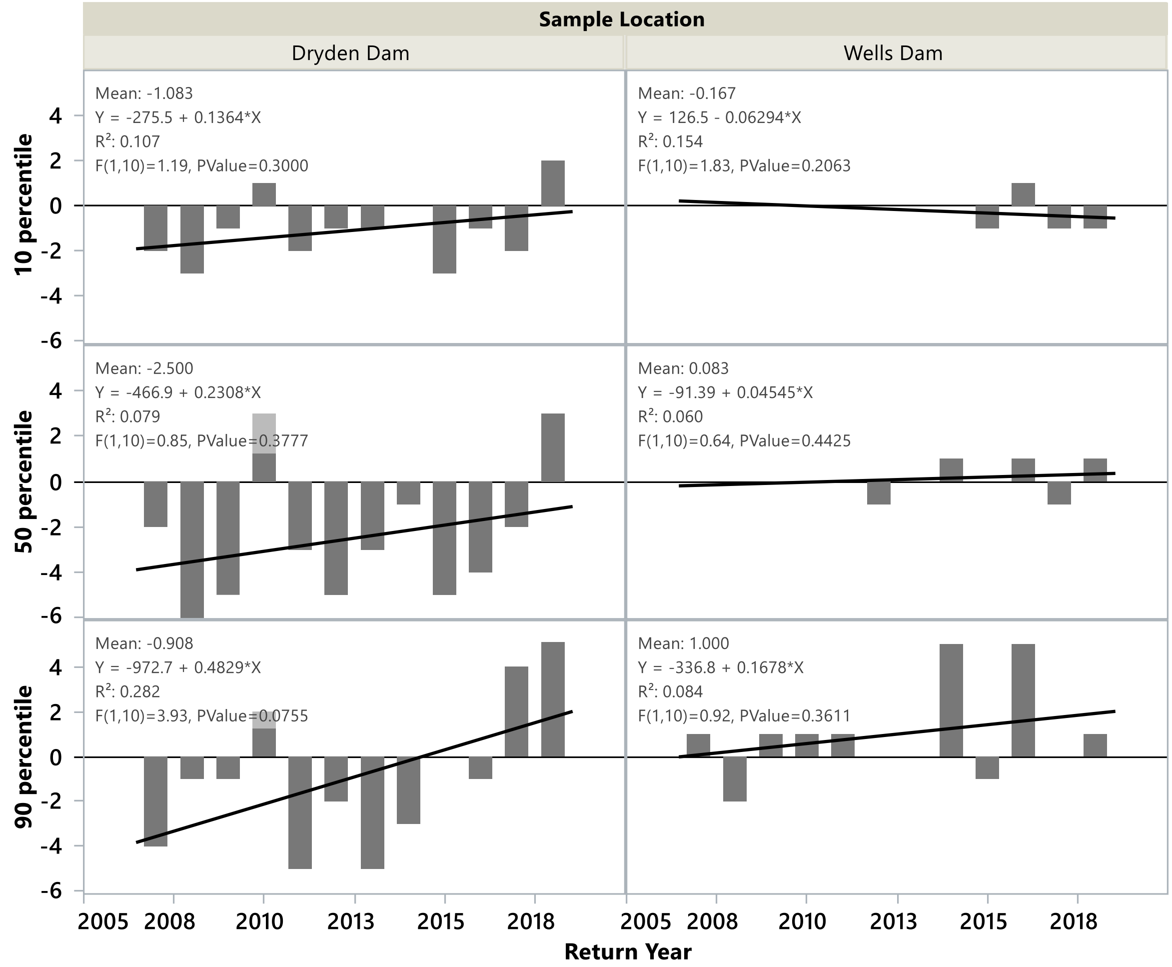


Figure 23. The difference in weeks (natural-origin minus hatchery-origin) that 10%, 50% (median), and 90% of natural-origin and hatchery-origin summer Chinook Salmon passed Dryden Dam and Wells Dam from 2007-2018 and the mean difference of that time period. Negative values indicate that hatchery-origin fish passed later in the year. Passage timing was based on run composition sampling and broodstock collection.

Spawn Timing (Carcass Recovery) of Summer Chinook Salmon in the Wenatchee and Methow Sub-basins

From 1993-2018, female carcass recovery of summer Chinook Salmon in the Wenatchee and Methow sub-basins generally began in mid-September and extended to mid-November (Figure 24). Summer Chinook Salmon in the Wenatchee Sub-basin generally spawned earlier than fish in the Methow Sub-basin and in both sub-basins hatchery-origin fish consistently spawned later than natural-origin fish (Figure 24). However, the difference in timing between hatchery- and natural-origin fish was generally small (seven days or less 90% of the time at the 50th percentile spawn date) and hatchery-origin fish generally followed the timing pattern of natural-origin fish at the 10th, 50th, and 90th percentiles (Figure 25).

The mean of paired differences at the 10th, 50th, and 90th timing percentile reflected the consistent later date of spawning of hatchery-origin fish in both sub-basins (Table 5). In the Wenatchee Sub-basin, hatchery-origin fish spawned significantly later then natural-origin fish at the 50th and 90th percentile with a mean difference of -2.4 days at the 50th percentile. In the Methow Sub-basin, hatchery-origin fish were significantly later statistically at all three levels of measurement with a mean difference of -3.6 days at the 50th percentile. There was no significant directional temporal trend in the differences between hatchery- and natural-origin fish in either sub-basin (Figure 26); however, over the period of data collection, spawn timing for both hatchery- and natural-origin fish shifted to significantly earlier in the year (Figure 27).

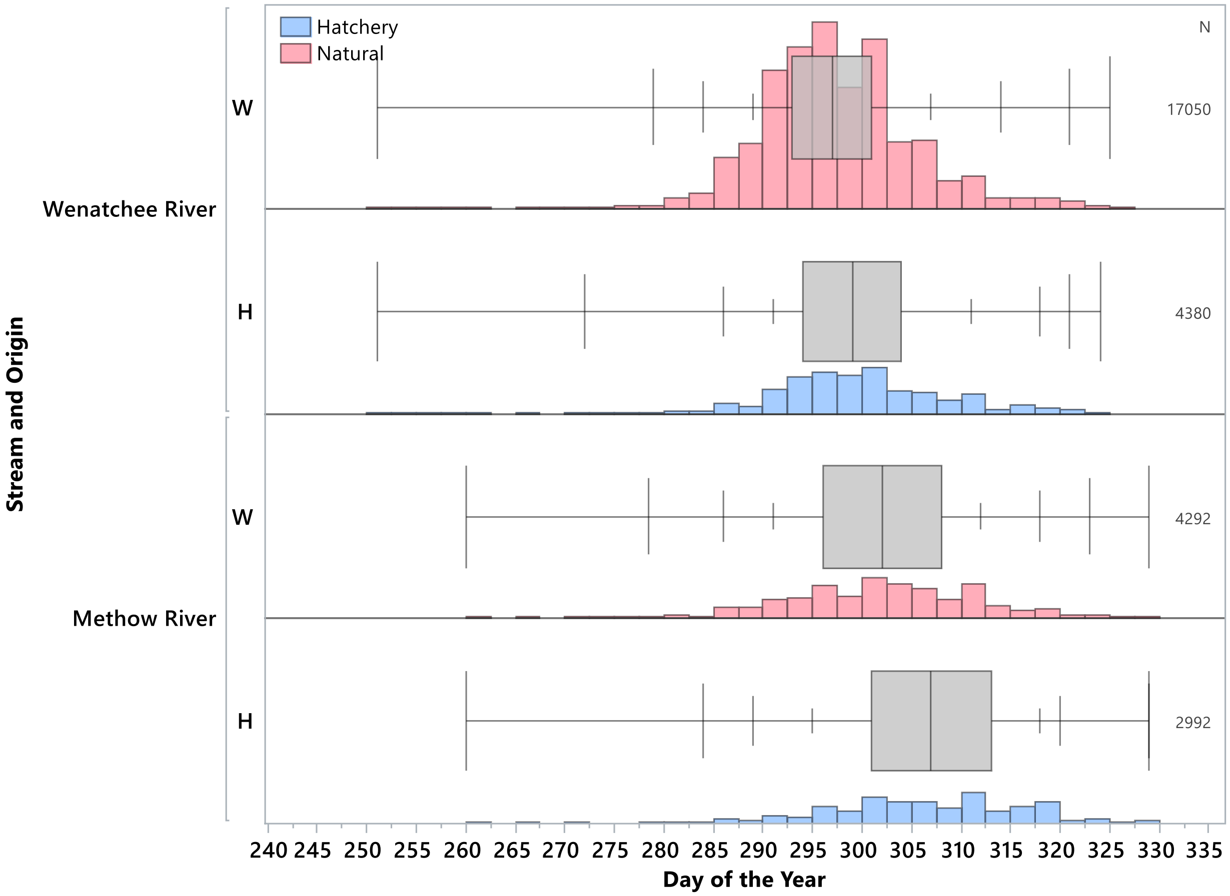
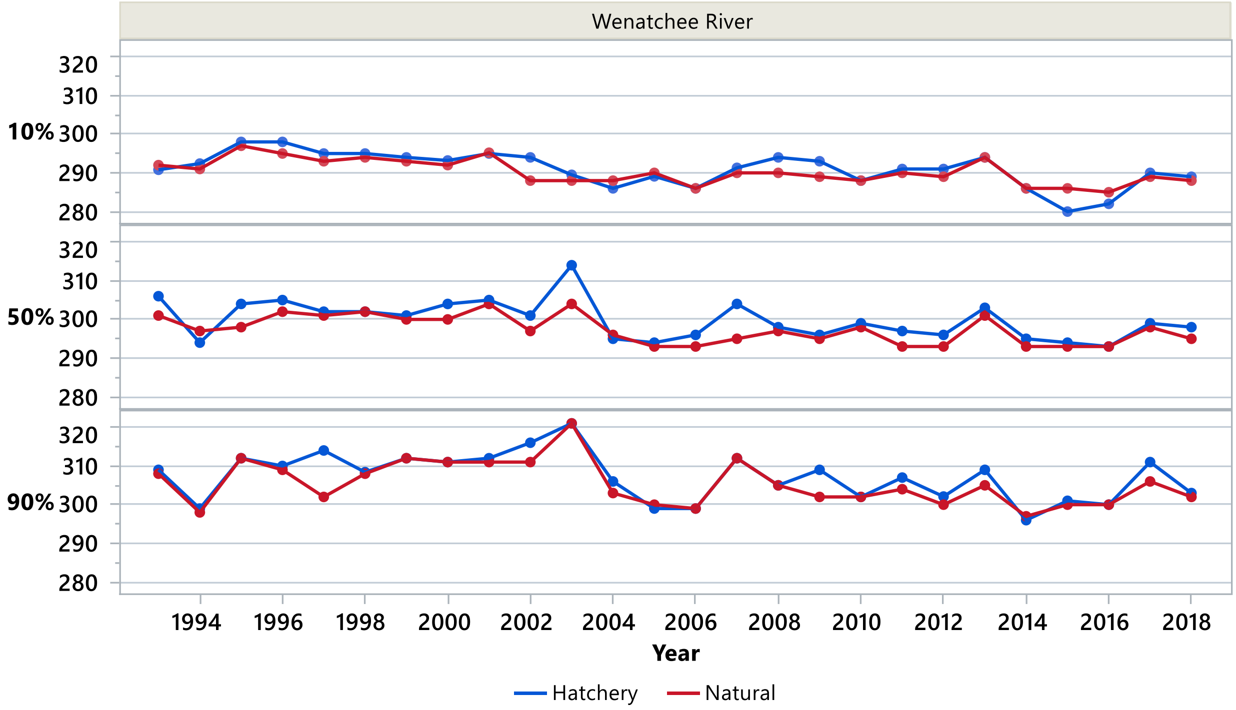


Figure 24. The temporal distribution of spawn timing of summer Chinook Salmon in the Wenatchee and Methow sub-basins from 1993-2018. Sample size by sub-basin and origin on right margin. Boxes span the 25-75th percentiles. Line inside box = 50th percentile (median). Dashes outside of boxes = 10th/90th, 2.5th/97.5th, and minimum/maximum.



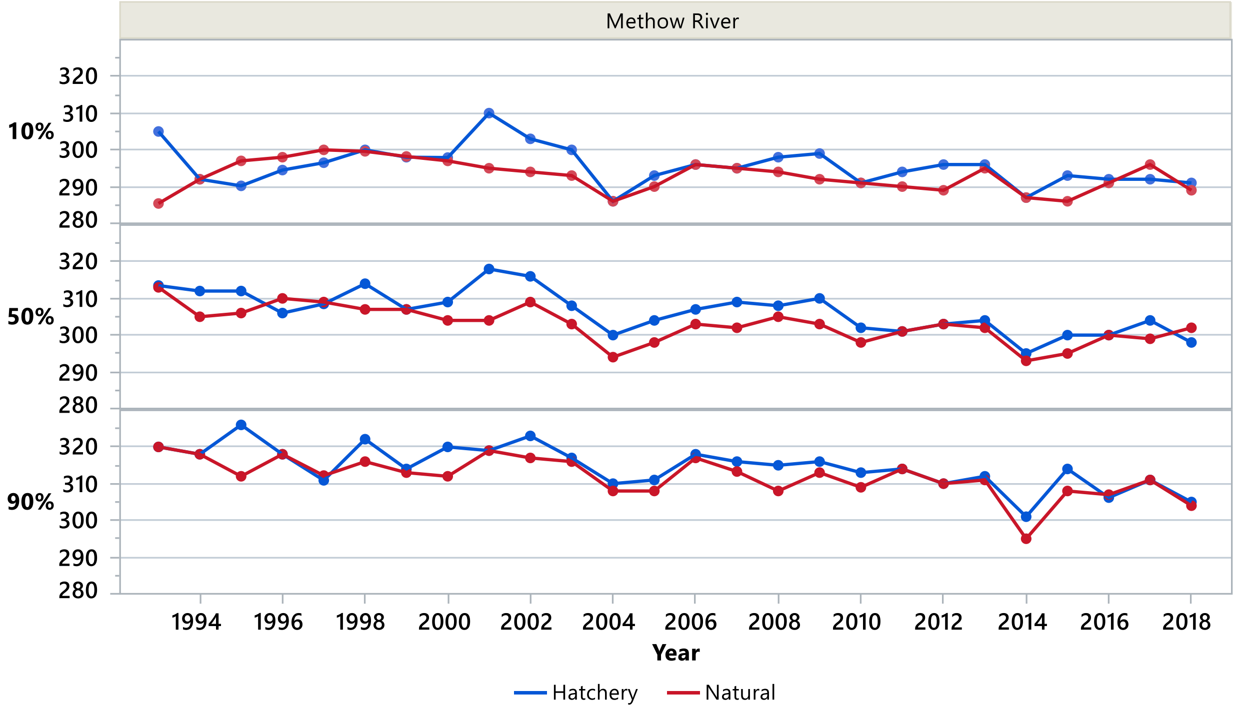


Figure 25. The 10th, 50th (median), and 90th percentile spawn day of the year of summer Chinook Salmon in the Wenatchee (top) and Methow (bottom) sub-basins by year.

Table 5. Results of paired t-tests and 95% CIs on the 10%, 50% (median), and 90% day of spawn timing of hatchery- and natural-origin summer Chinook Salmon in the Wenatchee and Methow sub-basins during the period 1993-2018.

Location	**Statistic**	**10th percentile**	**50th percentile**	**90th percentile**
Wenatchee Sub-basin	Mean Difference	-0.73	-2.42	-1.75
	Upper 95% Mean	0.20	-1.28	-0.580
	Lower 95% Mean	-1.68	-3.57	-2.92
	N	26	26	26
	Test Statistic	-1.60	-4.36	-3.078
	Prob > |t|	0.120	0.000	0.005
Methow Sub-basin	Mean Difference	-2.69	-3.62	-2.72
	Upper 95% Mean	-0.36	-2.02	-1.29
	Lower 95% Mean	-5.02	-5.21	-4.15
	N	26	26	26
	Test Statistic	-2.37	-4.66	-3.91
	Prob > |t|	0.0255	0.000	0.001

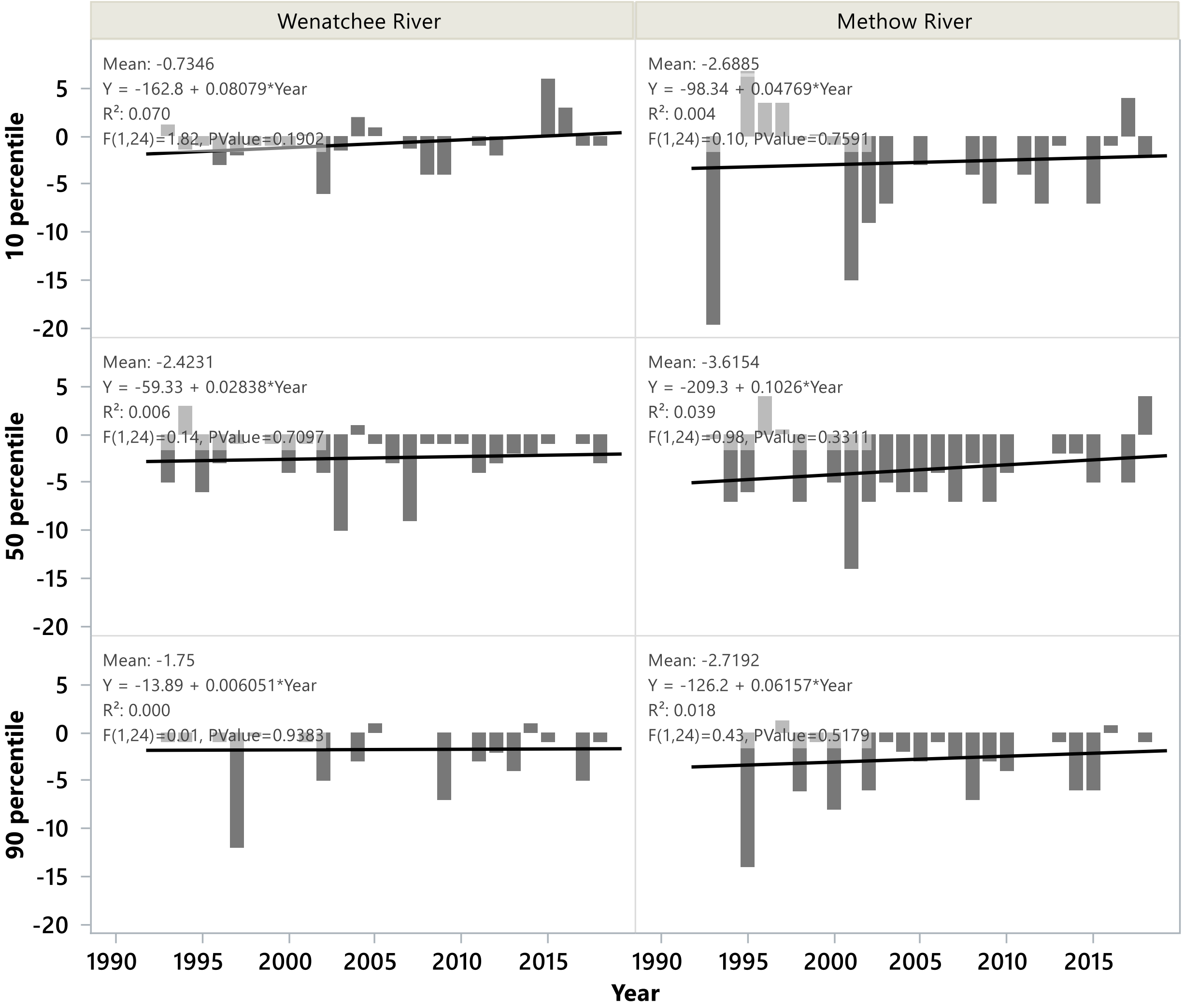


Figure 26. The difference in day (natural-origin minus hatchery-origin) that 10%, 50% (median), and 90% of hatchery- and natural-origin summer Chinook Salmon spawned from 1993-2018 and the mean difference of that time period. Negative values indicate that hatchery-origin fish spawned later in the year. Spawn timing was based on carcass recovery date.

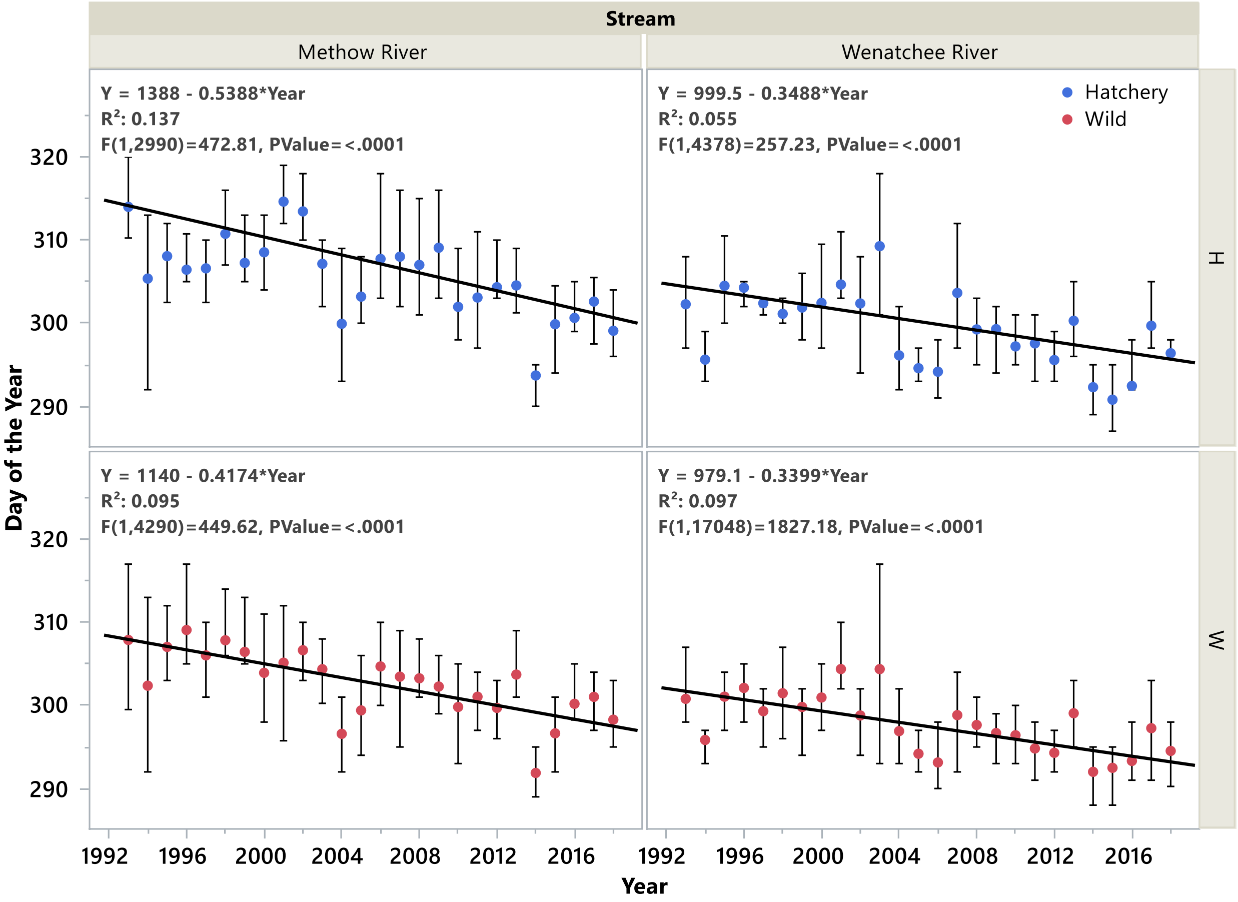


Figure 27. The mean, interquartile range, and trend of summer Chinook Salmon carcass recoveries in the Wenatchee and Methow sub-basins by year.

Spawning Distribution of Summer Chinook Salmon in the Wenatchee River

Both hatchery- and natural-origin summer Chinook Salmon spawned throughout the Wenatchee River and within each reach; however, there was a significant difference in the distribution of hatchery- and natural-origin spawners among historical survey reaches for years 1993-2018 (Yates' Chi-square = 2551.446; P= 0.000; Effect Size = 0.345) (Figures 28 and 29). The pNOS was higher than the pHOS in all 10 reaches (Figures 30). The pHOS exceed 0.30 in 3 of the 10 reaches. When comparing spawn distribution at the 1.0-RKm scale, the highest proportions of hatchery-origin summer Chinook Salmon spawned in the lower 45 km of the Wenatchee River, while the highest proportions of natural-origin summer Chinook Salmon spawned upstream from RKm 35 (Figure 31).

Spawning Distribution of Summer Chinook Salmon in the Methow River

Both hatchery- and natural-origin summer Chinook Salmon spawned throughout the Methow River and within each reach; however, there was a significant difference in the distribution of hatchery- and natural-origin spawners among historical survey reaches for years 1993-2018 (Yates' Chi-square = 829.375; P= 0.000; Effect Size = 0.339) (Figures 28 and 32). The pNOS was higher than the pHOS within six of seven reaches (Figure 30). The pHOS exceeded 0.30 in three of the seven reaches. When comparing spawn distribution at the 1.0-RKm scale, the highest proportions of hatchery-origin summer Chinook Salmon spawned in the lower 65 km of the Methow River, while the highest proportion of natural-origin fish spawned upstream from RKm 60 (Figure 31).

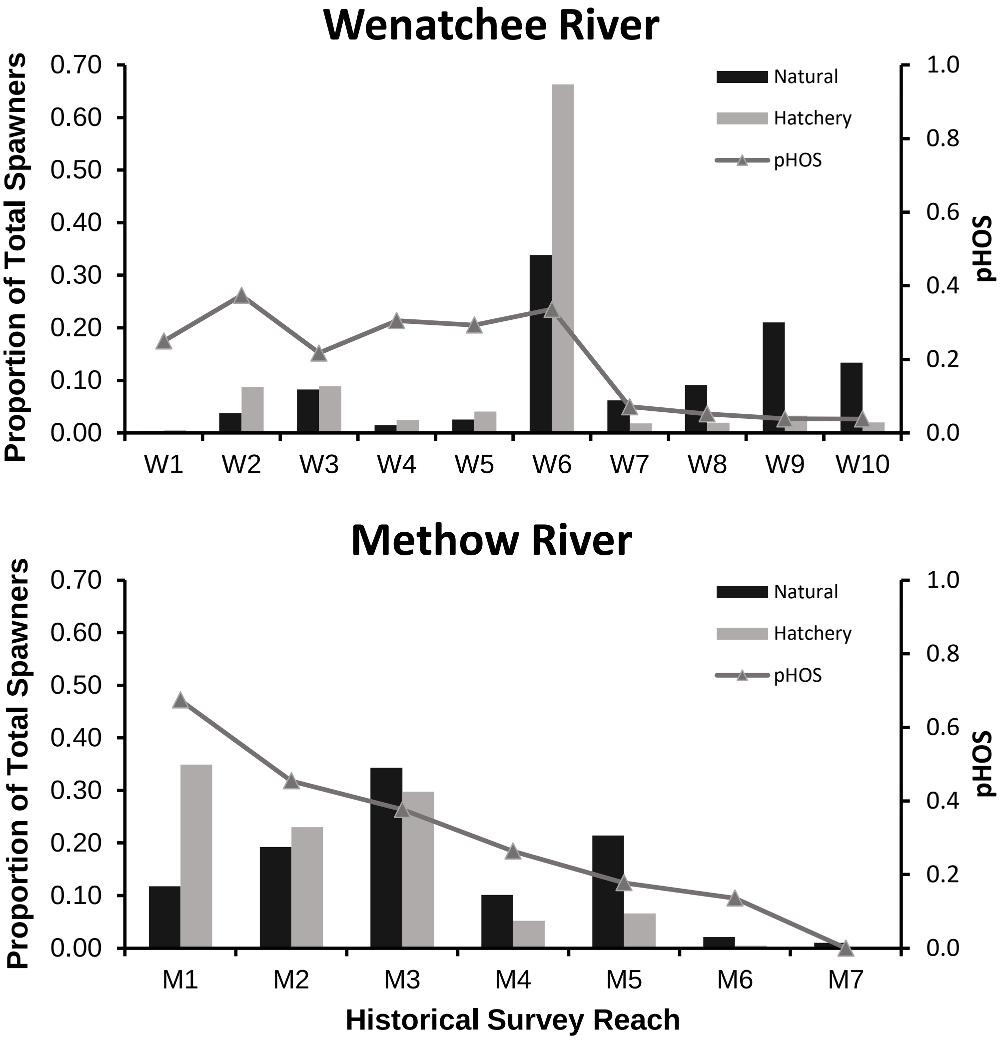
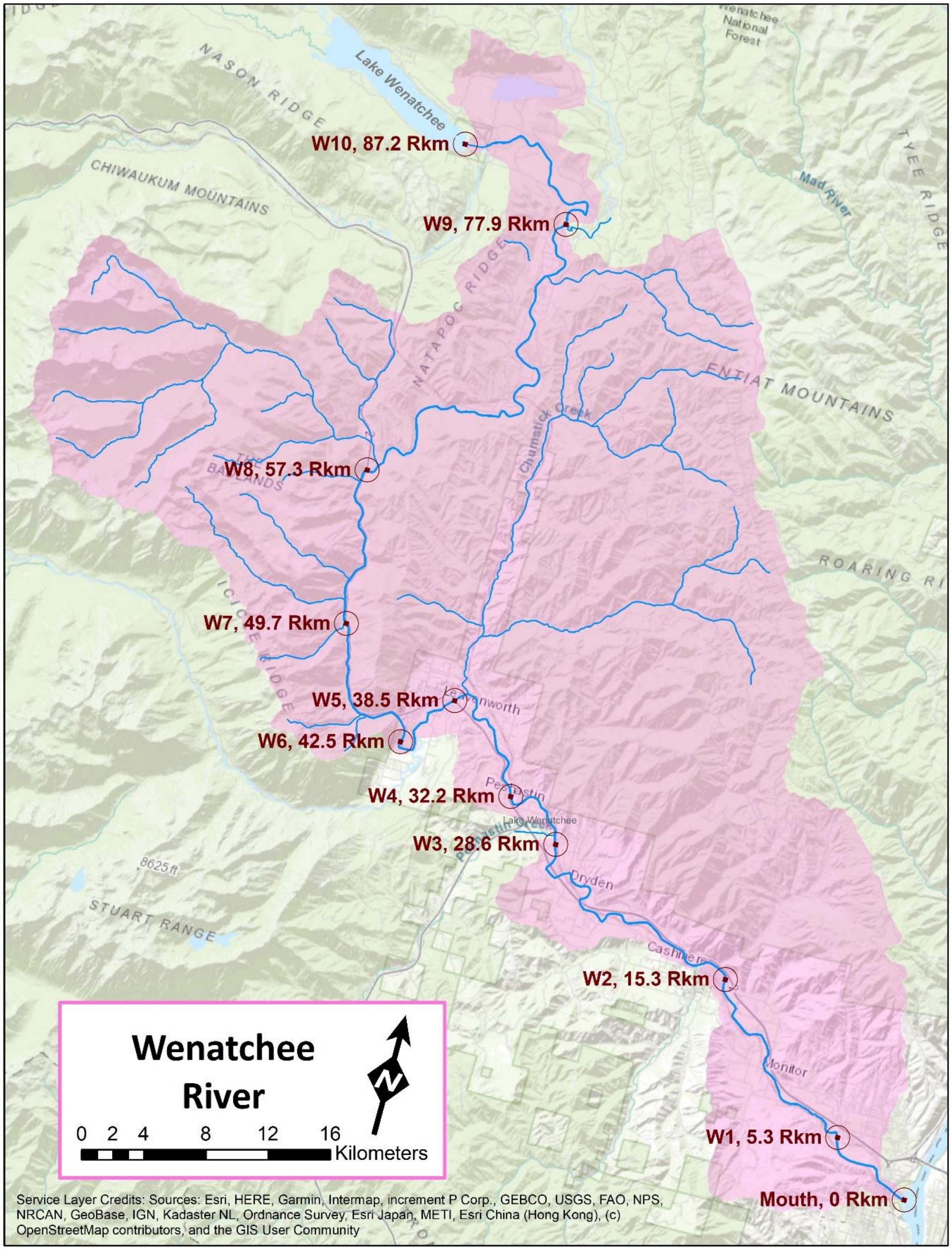


Figure 28. Proportion of hatchery- and natural-origin summer Chinook Salmon spawners within a river that were observed within each historical reach on the Wenatchee River (top) and Methow River (bottom) during the period 1993-2018. Here, the proportion of natural-origin or hatchery-origin spawners across historical reaches sum to "1.00." The line represents the proportion of hatchery-origin spawners within each historical reach.



Service Layer Credits: Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), (c) OpenStreetMap contributors, and the GIS User Community

Figure 29. Map of the Wenatchee River showing locations of historical summer Chinook Salmon survey reaches.

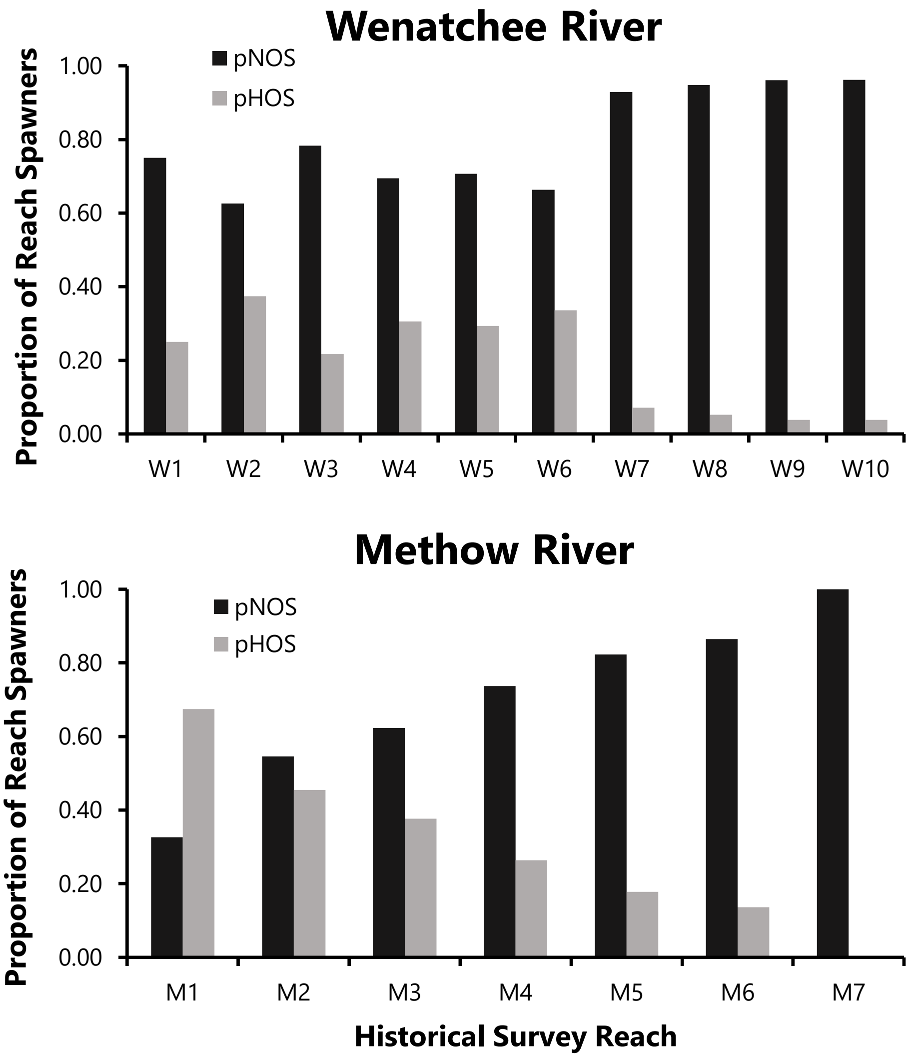


Figure 30. Proportion of hatchery- and natural-origin summer Chinook Salmon spawners within each of the historical sampling reaches on the Wenatchee River (top) and Methow River (bottom) during the period 1993-2018. Here, pNOS and pHOS sum to "1.00" within each reach.

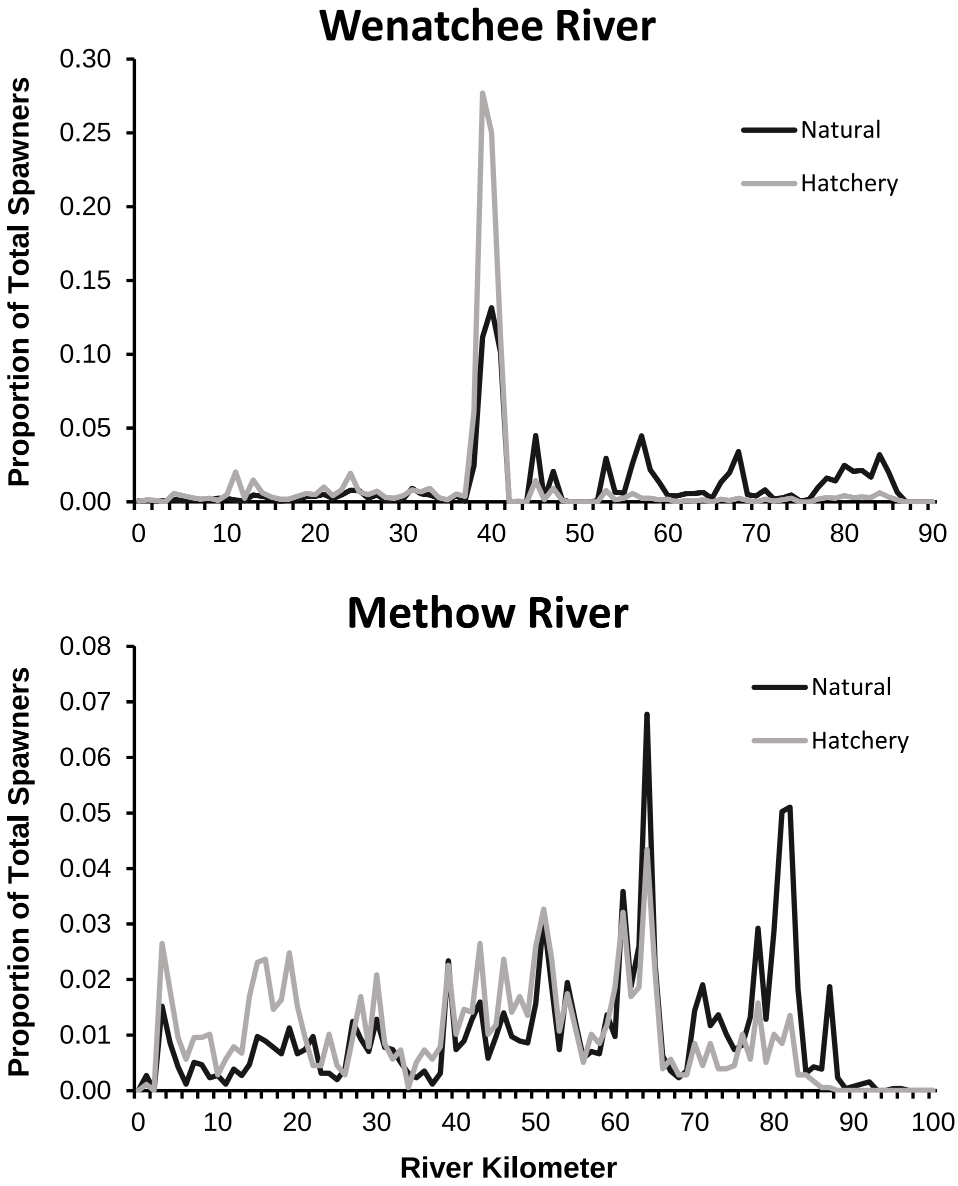


Figure 31. Proportion of natural- and hatchery-origin summer Chinook Salmon spawners distributed along the length of the Wenatchee River (top) and Methow River (bottom) during the period 1993-2018. Distribution was based on 1.0-km-long reaches. Wenatchee River sample sizes = 8,044 natural- and 2,073 hatchery-origin fish and Methow River sample sizes = 2,567 natural- and 1,774 hatchery-origin fish.

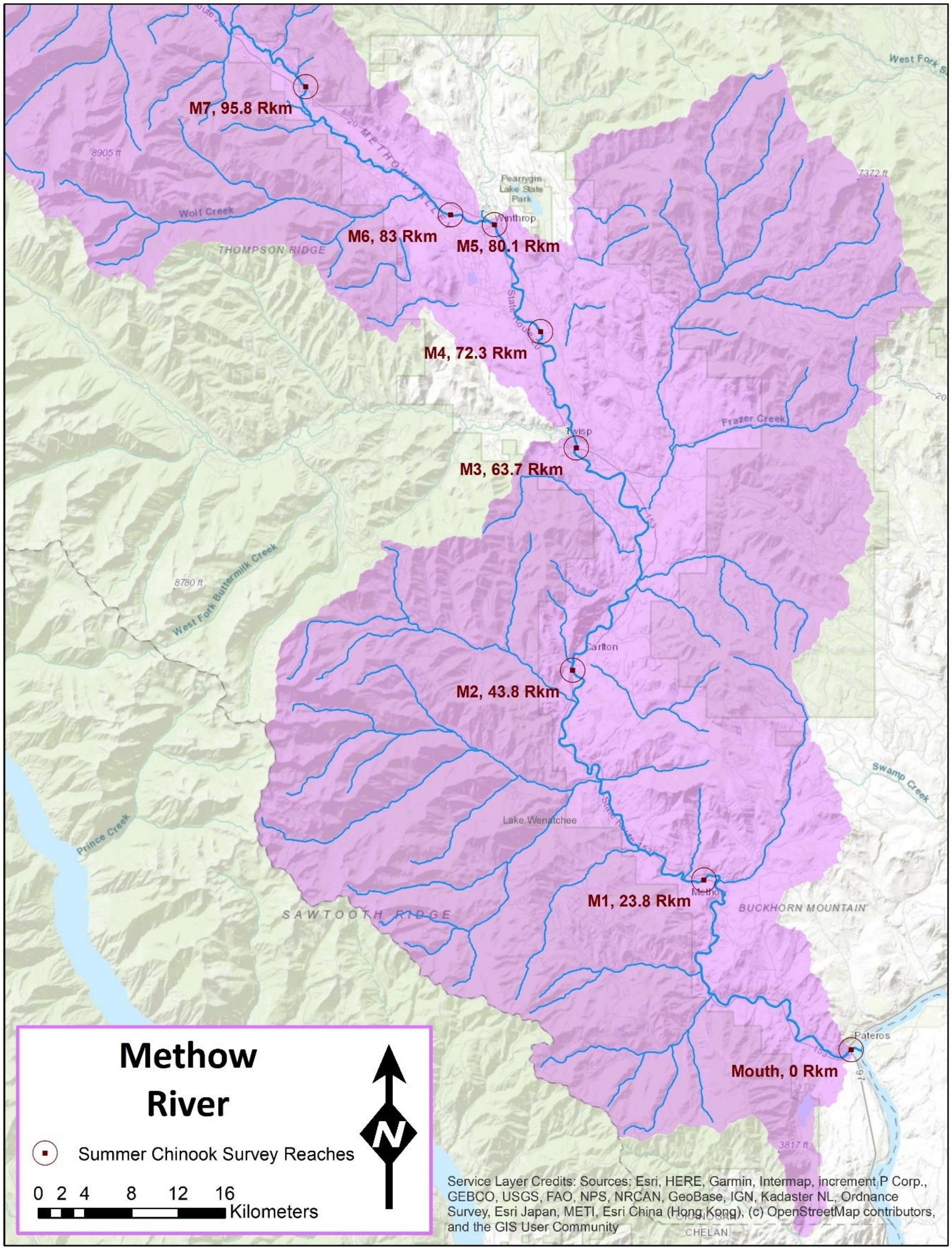


Figure 32. Map of the Methow River showing locations of historical summer Chinook Salmon survey reaches.

Discussion

The timing of migration and spawning of hatchery- and natural-origin spring Chinook Salmon were generally similar in the Wenatchee and Methow subbasins. In both sub-basins, the differences between hatchery- and natural-origin fish were small relative to the inter- and intra-annual variability of natural-origin migration and spawn timing. Although the difference in arrival timing was small and not statistically significant, the visual observation data at Tumwater and Wells dams suggest a tendency for hatchery-origin spring Chinook Salmon to arrive later than natural-origin fish. Such differences could be explained by differences in age distribution between the two groups; hatchery-origin fish tend to mature at younger ages (Graf et al. 2020; Knudsen et al. 2008) and, as observed in Figure 4 and Figure 6, younger fish tend to arrive later. In addition, spring Chinook Salmon generally spawn earlier at higher elevations and hatchery-origin fish generally spawn at lower elevations than natural-origin fish (Williamson et al. 2010; Fast et al. 2015). Spawner distribution may also explain differences in spawn timing. As we described, the distribution of hatchery-origin fish is strongly influenced by the location of acclimation facilities which are located at lower elevations, thus resulting in an elevation-caused spawn timing difference as well. If migration timing is correlated with spawn timing, then this could be another mechanism explaining the small difference in migration timing. Overall, from these data, it is likely that hatchery- and natural-origin fish are generally experiencing similar selective pressures during their adult freshwater migration period and during spawning.

Conversely, the differences in migration timing between spring Chinook Salmon populations in the Wenatchee versus Methow sub-basins likely has resulted in differences in survival at the adult life-stage. Mortality events such as predation and harvest are uneven within a year, and in the case of predation by pinnipeds downstream from Bonneville Dam, earlier arriving fish experience higher mortality rates (Wargo Rub et al. 2019). Based on PIT-tag arrival timing at Bonneville Dam, this suggests that fish from the Methow Hatchery, Winthrop National Fish Hatchery, and Leavenworth National Fish Hatchery may have experienced the highest rates of predation by pinnipeds (Sorel et al. 2020).

Differences in hatchery- and natural-origin summer Chinook migration timing varied between the Wenatchee and Methow/Okanogan sub-basins. Hatchery-origin fish observed at Wells Dam include fish released in the Methow and Okanogan sub-basins, plus the Columbia River. Natural populations consist of the Methow and Okanogan sub-basins, plus fish produced in the Columbia River. Thus, the comparison at Wells Dam consists of mixed stocks of both hatchery- and natural-origin fish. Differences in spawn timing of summer Chinook also varied between the Wenatchee and Methow sub-basins. For migration timing, hatchery-origin fish in the Wenatchee sub-basin consistently passed Dryden Dam later than their natural-origin counterparts; whereas, the migration timing for Methow/Okanagon hatchery-origin fish were a near match with natural-origin fish at Wells Dam. Conversely, spawn timing in both Wenatchee and Methow hatchery-origin fish was later than natural-origin fish, with Methow-origin fish having a larger average difference. This pattern of arrival timing differences at Dryden Dam versus Wells Dam may be due to the relative proximity of the sampling location to the spawning grounds. In both sub-basins, hatchery- and natural-origin summer Chinook Salmon have different spawning spatial distributions where natural-origin fish tend to spawn farther upstream. This spatial difference likely manifests in a temporal difference at Dryden Dam, where hatchery-origin fish have nearly ‘arrived’ at their spawning destination. The consistent later spawn date of Wenatchee and Methow hatchery-origin fish may also be explained by differences in spawning spatial distribution. Environmental conditions higher in the sub-basin (e.g., colder temperatures and lower river flows in later summer) may be driving earlier spawn timing of natural-origin fish. Lastly, hatchery- and natural-origin summer Chinook Salmon from both sub-basins have trended towards earlier spawn dates. This consistent signal may suggest regional environmental conditions that are driving or favoring earlier spawn dates (e.g., lower flows in later summer and/or warmer river temperatures). Should this trend continue, temporal segregation of summer and spring Chinook Salmon spawning populations will diminish, increasing opportunity for these populations to mix.

Hatchery-origin spring Chinook Salmon spawned throughout the range of natural-origin spring Chinook Salmon and generally spawned in the reaches where most natural-origin fish spawned. However, differences between hatchery- and natural-origin spawner distribution across historical survey reaches were observed during some years in all spring Chinook Salmon programs except the White River program. In general, hatchery-origin females spawned farther downstream than natural-origin females, which is consistent with Hughes and Murdoch (2017), who concluded that over a 10-year period, a greater proportion of hatchery-origin females spawned in lower reaches of the Chiwawa River which is likely the result of the acclimation facilities being located in the lower survey reaches. Nevertheless, the greater abundance of hatchery-origin relative to natural-origin fish resulted in exceedances of HSRG recommended pHOS objectives for reducing the risk of domestication selection (Mobrand et al. 2005; Paquet et al. 2011) in nearly every spawning reach (13 of 14 reaches in the Wenatchee Sub-basin; 35 of 37 reaches in the Methow Sub-basin). Thus, even though more hatchery-origin fish spawned lower in each sub-basin than natural-origin fish, returns of hatchery-origin fish to each sub-basin were sufficient to dominate or substantially influence nearly the entire spawning distribution.

The distribution of hatchery-origin fish is likely strongly influenced by the location of acclimation facilities. For example, in the Chiwawa River, juvenile hatchery-origin spring Chinook Salmon are overwinter acclimated at the Chiwawa Acclimation Facility and released volitionally into the river. Most of the returns of hatchery-origin fish released from this facility spawn within the lower reaches of the Chiwawa River. Hughes and Murdoch (2017) found that hatchery-origin fish that spawned farther downstream in the Chiwawa River sub-basin near the program's overwinter acclimation site had lower relative reproductive success compared to natural-origin spring Chinook Salmon. Hughes and Murdoch (2017) believe the mechanism for the reduced relative reproductive success between hatchery- and natural-origin Chiwawa spring Chinook Salmon is related to the lower-quality spawning habitat used by hatchery-origin females in the lower reaches of the Chiwawa River compared to the middle and upper reaches. The Upper Columbia Regional Technical Team of the Upper Columbia Salmon Recovery Board ranked the lower Chiwawa River reaches as high-priority reaches for restoring reach functions to improve spawning and rearing habitat (Upper Columbia Salmon Recovery Board 2021).

The spawning distribution of spring Chinook Salmon in Nason Creek was likely influenced by strays from the Chiwawa Hatchery program, the reduction in hatchery smolt production in the Chiwawa River, and the initiation of the Nason Creek Hatchery program. Prior to the Nason Hatchery program, strays from the Chiwawa Hatchery program spawned mostly in the downstream sections of Nason Creek whereas greater proportions of the natural-origin fish spawned upstream. At the time the Nason hatchery program started, the number of strays from the Chiwawa program decreased as a result of lowered production and this resulted in fewer fish spawning in lower reaches. At the same time, returns from the Nason Creek hatchery program returned to upstream areas and the spawning distribution more closely matched that of the natural-origin distribution. The difference in distribution of the Chiwawa and Nason hatchery-origin fish was likely a result of the locations of the acclimation sites; with the Nason Creek Acclimation Facility located upstream in Nason Creek and the Chiwawa Acclimation Facility located downstream in the Chiwawa River.

The spawning distribution of natural- and hatchery-origin spring Chinook Salmon in the White River was mainly confined to the middle spawning reach. Hatchery-origin fish from the White River captive broodstock program and strays from the Chiwawa Hatchery program all spawned primarily in the reach that was used most by the natural-origin fish and this reach was upstream of where both of these hatchery-origin groups were acclimated. Hatchery-origin fish migrated past portions of the lower White River presumably because spawning habitat was unsuitable in lower reaches. A similar phenomenon was observed for spring Chinook Salmon in the upper Yakima River where habitat suitability was low adjacent to the Clark Flats acclimation site (Cram et al. 2013).

The spawning distributions of spring Chinook Salmon in the Chewuch, Methow, and Twisp rivers were likely influenced by the location of acclimation sites. In all three streams, the distribution of spawning spring Chinook Salmon differed significantly between natural- and hatchery-origin fish with more hatchery-origin fish spawning within the lower survey reaches than natural-origin fish. A greater proportion of natural-origin fish spawned in the upper survey reaches in all three streams. On the Methow River, a large proportion of hatchery-origin spring Chinook Salmon spawned between RKms 83 and 87, which is where the Methow Salmon Hatchery is located. Most of the natural-origin spring Chinook Salmon on the Methow River spawned upstream of RKm 90.

The proportion of hatchery-origin spawners was high within nearly all spring Chinook Salmon survey reaches on Nason Creek and the Chiwawa, White, Chewuch, Methow, and Twisp rivers. The pHOS exceeded 50% within 33 of the 51 survey reaches. The HSRG recommended pHOS below 30% for integrated populations (Mobrand et al. 2005; Paquet et al. 2011), but this recommendation was met in only 3 of the 51 spring Chinook Salmon survey reaches. Although the HSRG recommendation for pHOS is at the population scale, we evaluated pHOS at a reach base scale to better understand pHOS distribution within each of the spawning reaches. Managing for pHOS while managing for similar spawn distribution between hatchery- and natural-origin fish can create competing management objectives. In the majority of the lower and middle reaches, pHOS is too high (i.e., greater than 50%). Implementing adult management can likely reduce pHOS at both the population and reach levels; however, due to the recent years of low adult returns, the requirements to implement adult management have not been met. Increasing homing of hatchery-origin spawners to the upper reaches, where they are often limited, compared to natural-origin spawners, would increase the similarity of the spawner distributions. However, concurrently, pHOS would likely increase to greater than 50% in all reaches because the number of natural-origin spawners in the upper reaches is so low, that an increase of only a few hatchery-origin spawners would dramatically elevate pHOS in those reaches. Furthermore, because the natural-origin abundance is so low in the upper reaches and thus able to accommodate only very few additional hatchery-origin fish and still maintain pHOS less than 30%, we cannot expect that increasing abundance of hatchery-origin fish in those upstream reaches would increase natural production appreciably. Increasing natural-origin spawners in all reaches would improve overall and reach-level pHOS values and provide scope for extending the distribution of hatchery-origin spawners into underutilized spawning reaches.

As stated earlier, the management objective for the summer Chinook Salmon hatchery programs analyzed was hatchery-origin spawners to not replicate the spawning distribution of natural-origin fish. Returns from both Wenatchee summer Chinook Salmon and Methow summer Chinook Salmon hatchery programs achieved this objective by exhibiting spawner distributions significantly different than natural-origin spawners; the hatchery-origin fish spawned lower in the rivers than the natural-origin fish. It is also important that the hatchery programs do not create overlap in the spawning distributions of spring and summer Chinook Salmon. In the Entiat River, summer Chinook Salmon superimposed spring Chinook Salmon redds and some inbreeding occurred (Fraser et al. 2020; Fraser and Cooper 2022).

The pNOS was higher in 16 of the 17 Wenatchee and Methow summer Chinook Salmon spawn survey reaches, which is likely the result of the large number of natural-origin spawners and a popular recreational fishery that targets hatchery-origin summer Chinook Salmon. The pHOS exceeded 30% in 6 of the 17 summer Chinook Salmon survey reaches and exceeded 50% in only one reach.

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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%).

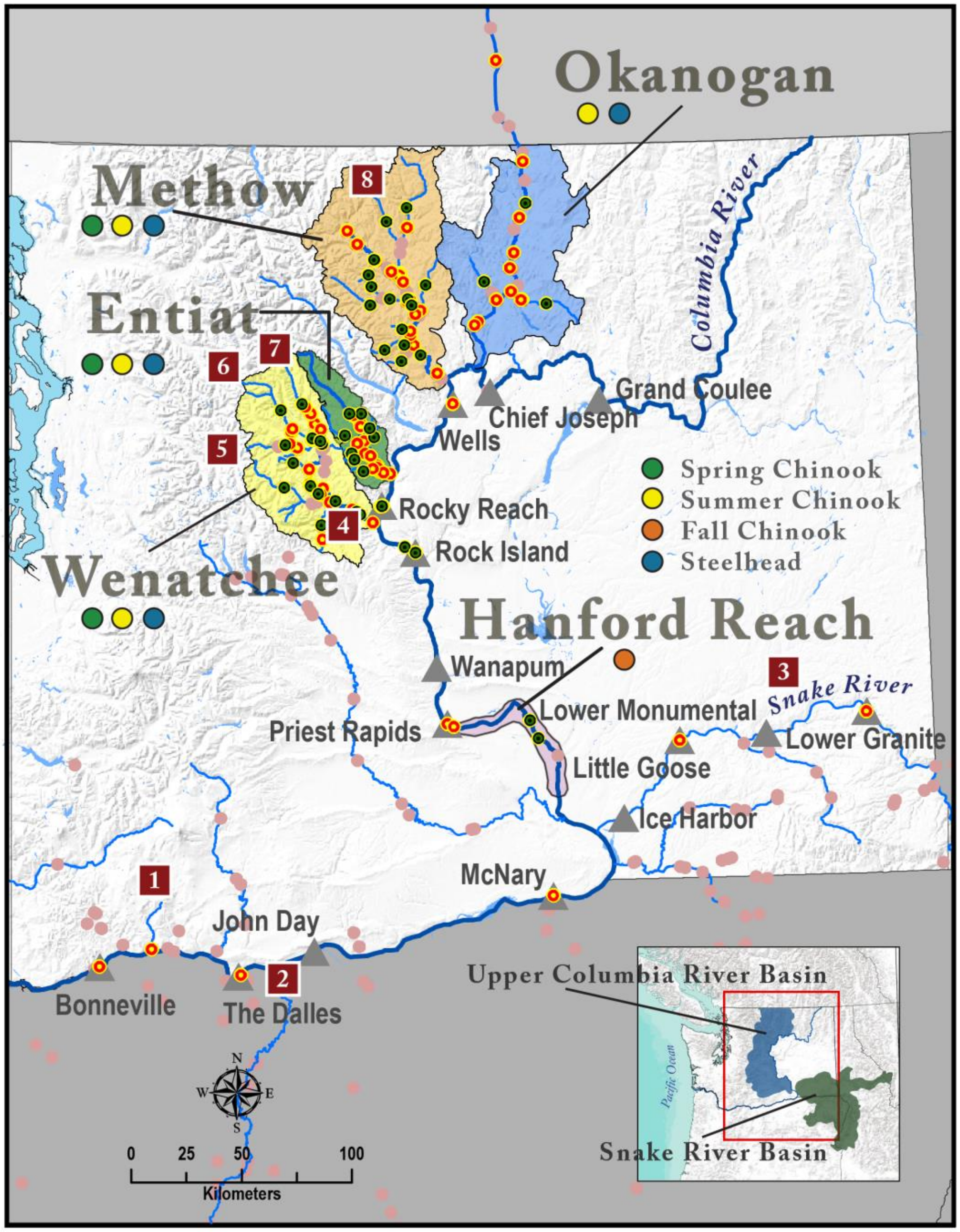

FIGURE 1. Release locations (green bullseye) and final PIT tag detection locations (yellow bullseye) of Chinook Salmon and steelhead originating from the upper Columbia River Basin. Other PIT tag detection sites are displayed as shaded dots for reference. Hydropower dams are denoted with triangles. The 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.

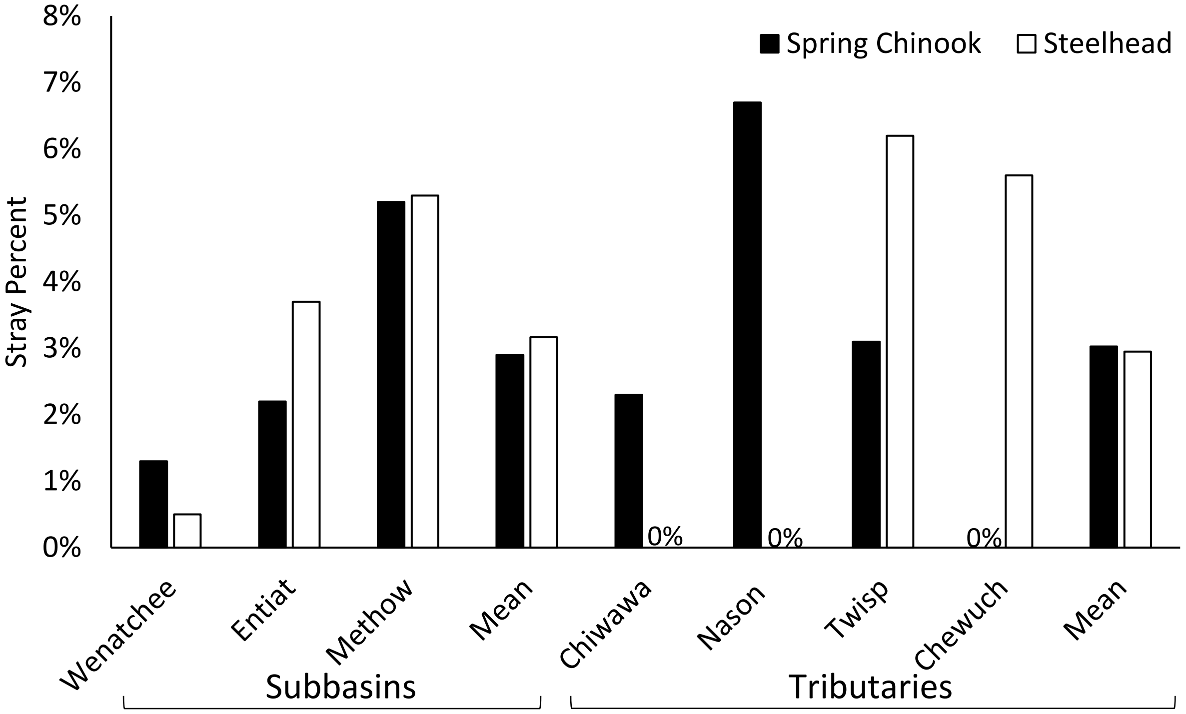

Figure 2. The percent of PIT-tagged natural-origin spring Chinook Salmon and steelhead that strayed away from their subbasins and tributaries of origin.

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*,

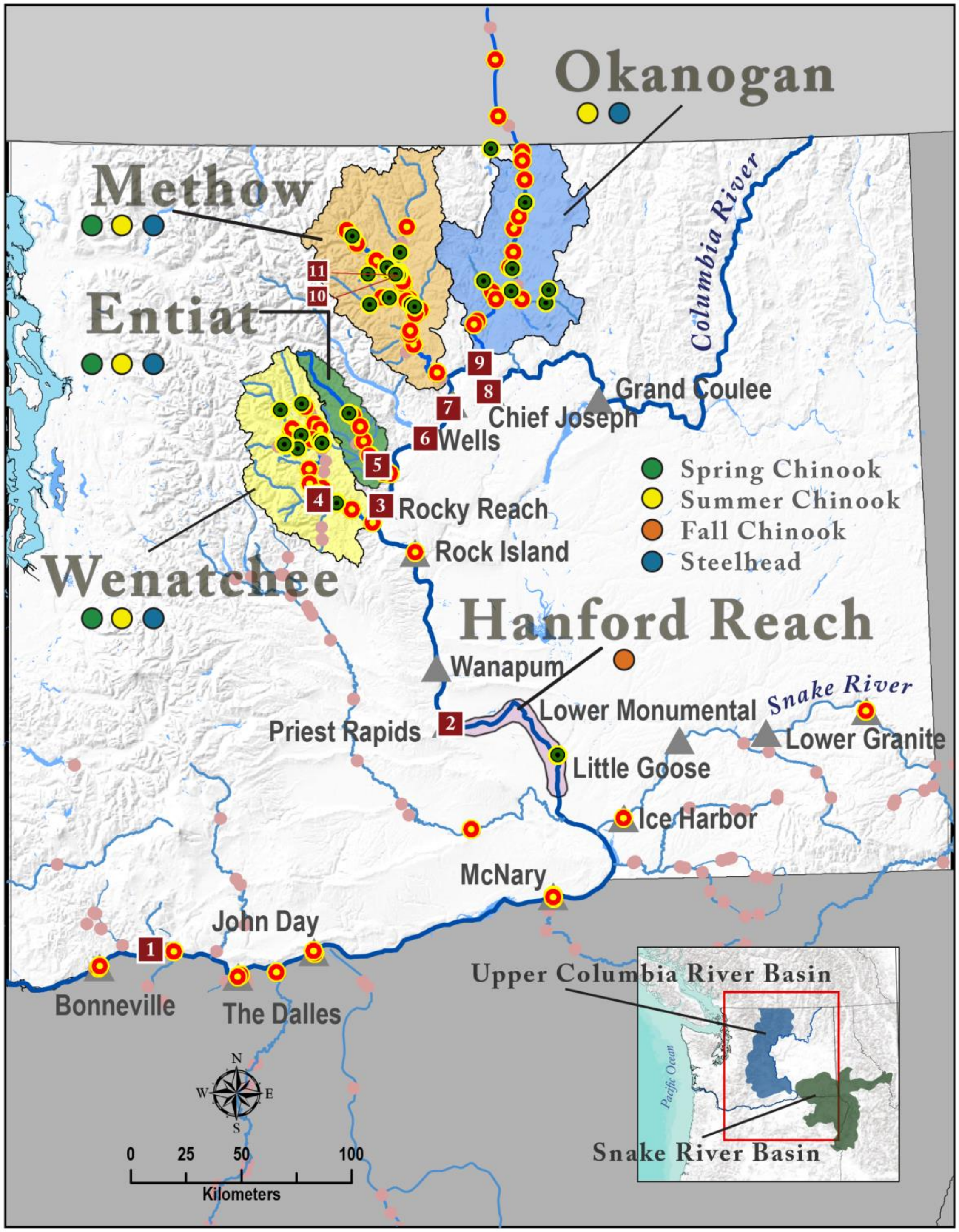

Figure 1. Release locations (green bullseye) and final detection locations (orange bullseye) of spring, summer, and fall Chinook Salmon and steelhead from the upper Columbia River Basin. Other points along rivers indicate PIT tag detection arrays. Numbered boxes represent locations of subject hatcheries 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.

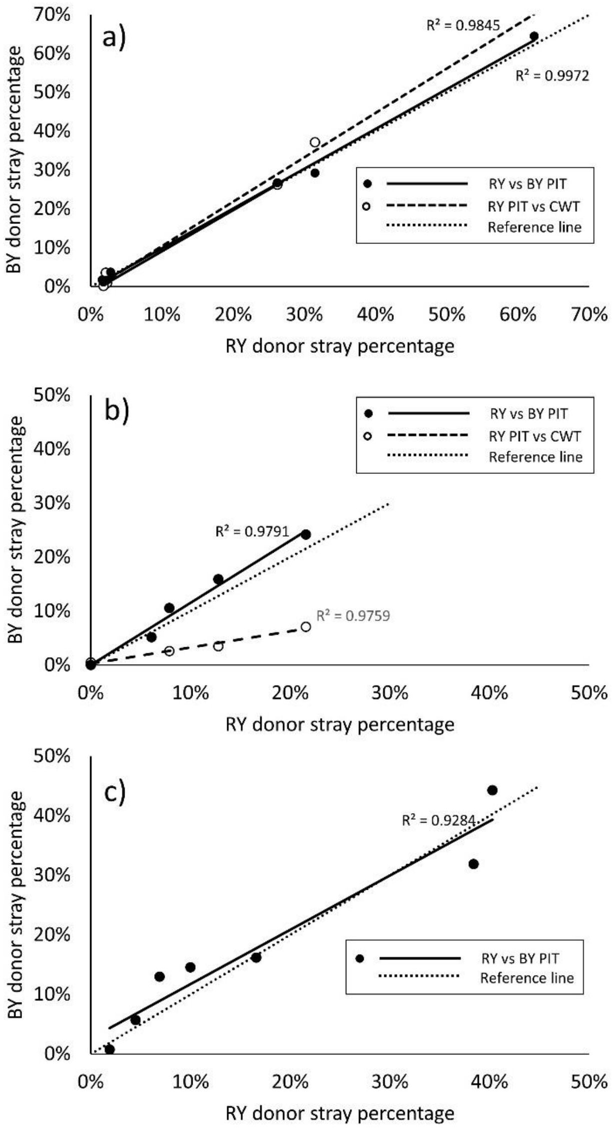

Figure 2. PIT-tag-based return-year (RY, spawn year) stray estimates versus brood-year (BY) stray estimates using either PIT tags or BY coded wire tags (CWT) for upper Columbia watershed a) spring Chinook Salmon, b) summer Chinook Salmon, and c) steelhead.

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).

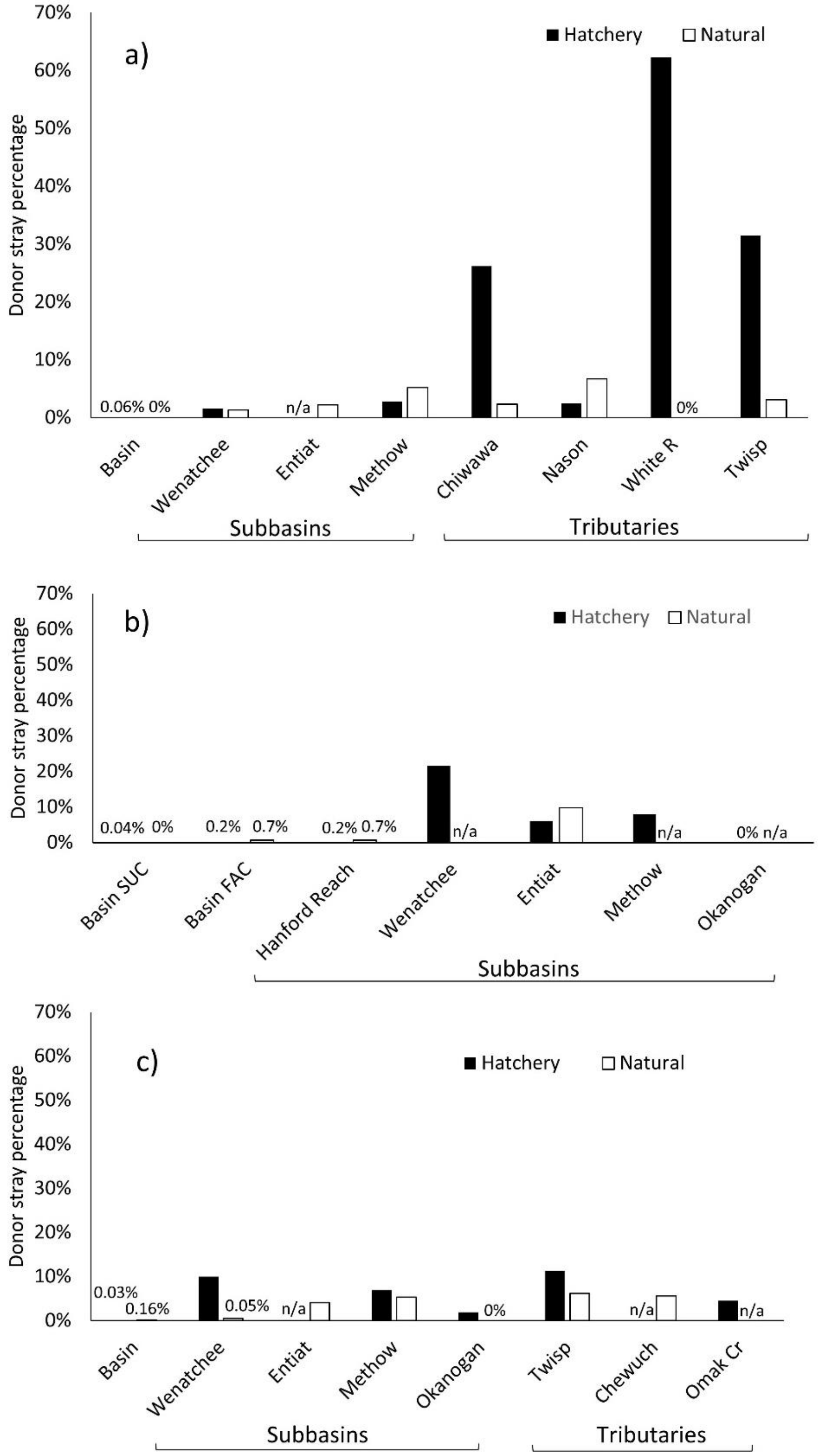

Figure 3. Donor stray percentages of hatchery- and natural-origin a) spring Chinook Salmon, b) summer Chinook Salmon (SUC) and fall Chinook Salmon, (FAC) and c) steelhead at basin, subbasin, and tributary scales.

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.

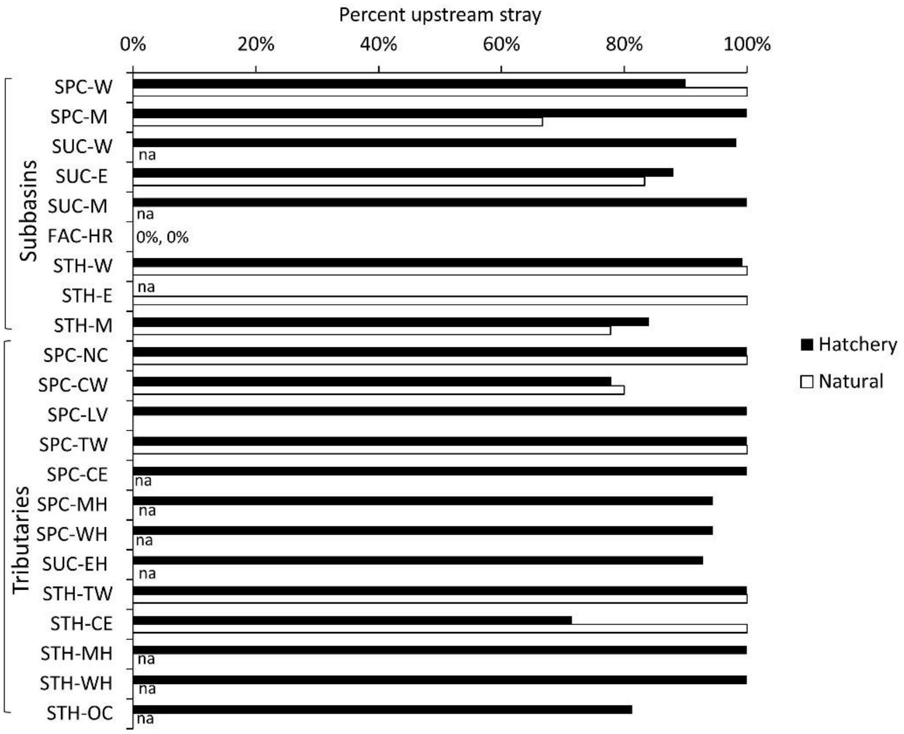

Figure 4. Direction of hatchery- and natural-origin straying. Abbreviations: SPC spring Chinook Salmon, SUC summer Chinook Salmon, FAC fall Chinook Salmon, STH steelhead. W Wenatchee River, M Methow River, E Entiat River, HR Hanford Reach, NC Nason Creek, CW Chiwawa River, LV Leavenworth Nation Fish 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).

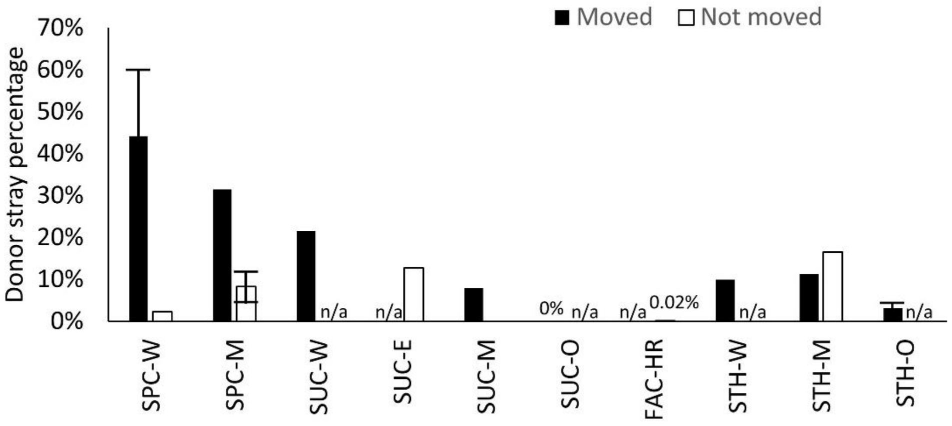

Figure 5. Mean donor stray percentages of hatchery-origin fish that were moved as juveniles among facilities prior to release (moved) or those that were incubated, reared, acclimated and released from a single facility (not moved). Error bars represent the range of values when more than one value was 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).

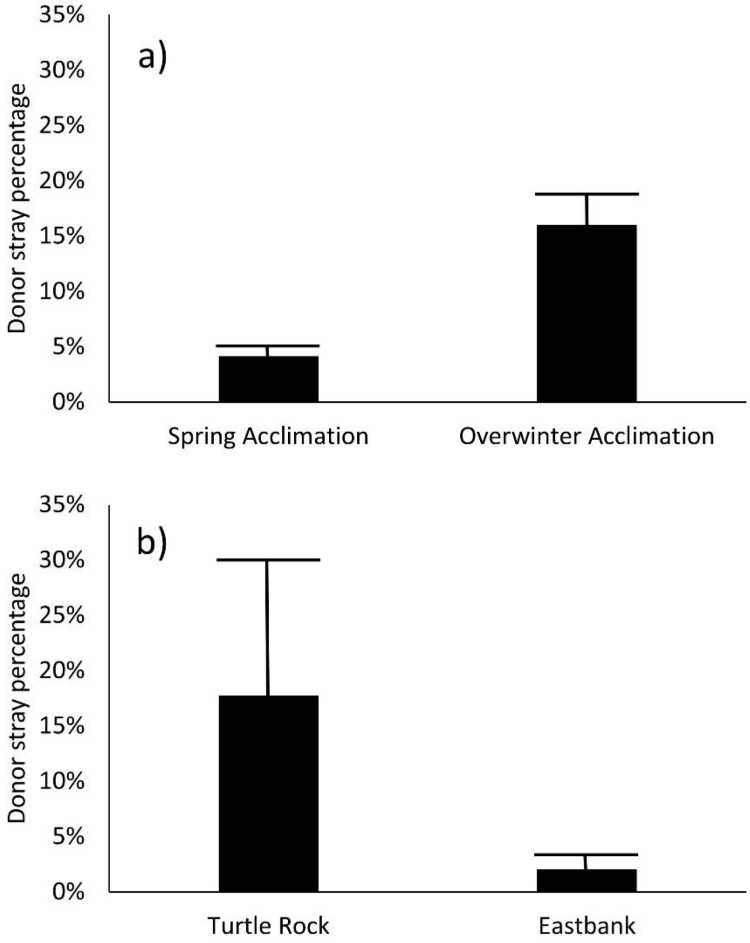

Figure 6. Mean donor stray percentages in periods of differing management regimes for a) summer Chinook Salmon released from the Carlton Acclimation Facility on the Methow River, and b) steelhead released into the Wenatchee River after being raised at either Turtle Rock or Eastbank Hatchery. Bars represent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

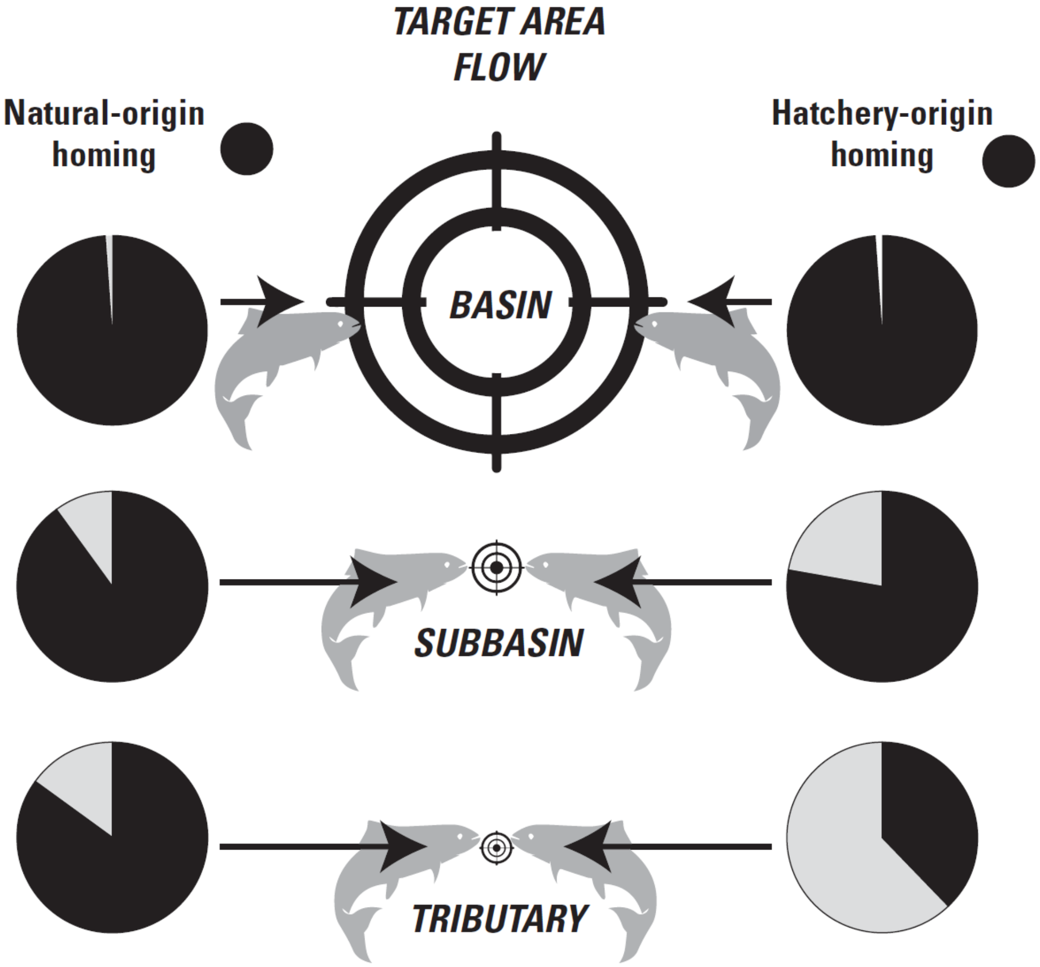

Figure 7. Comparisons of homing rates (minimums in black) and straying (maximums in grey) between hatchery- and natural-origin Salmon and steelhead at three spatial scales in the upper Columbia subregion. The size of the targets was scaled to the fall discharges of the upper Columbia River (basin), the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

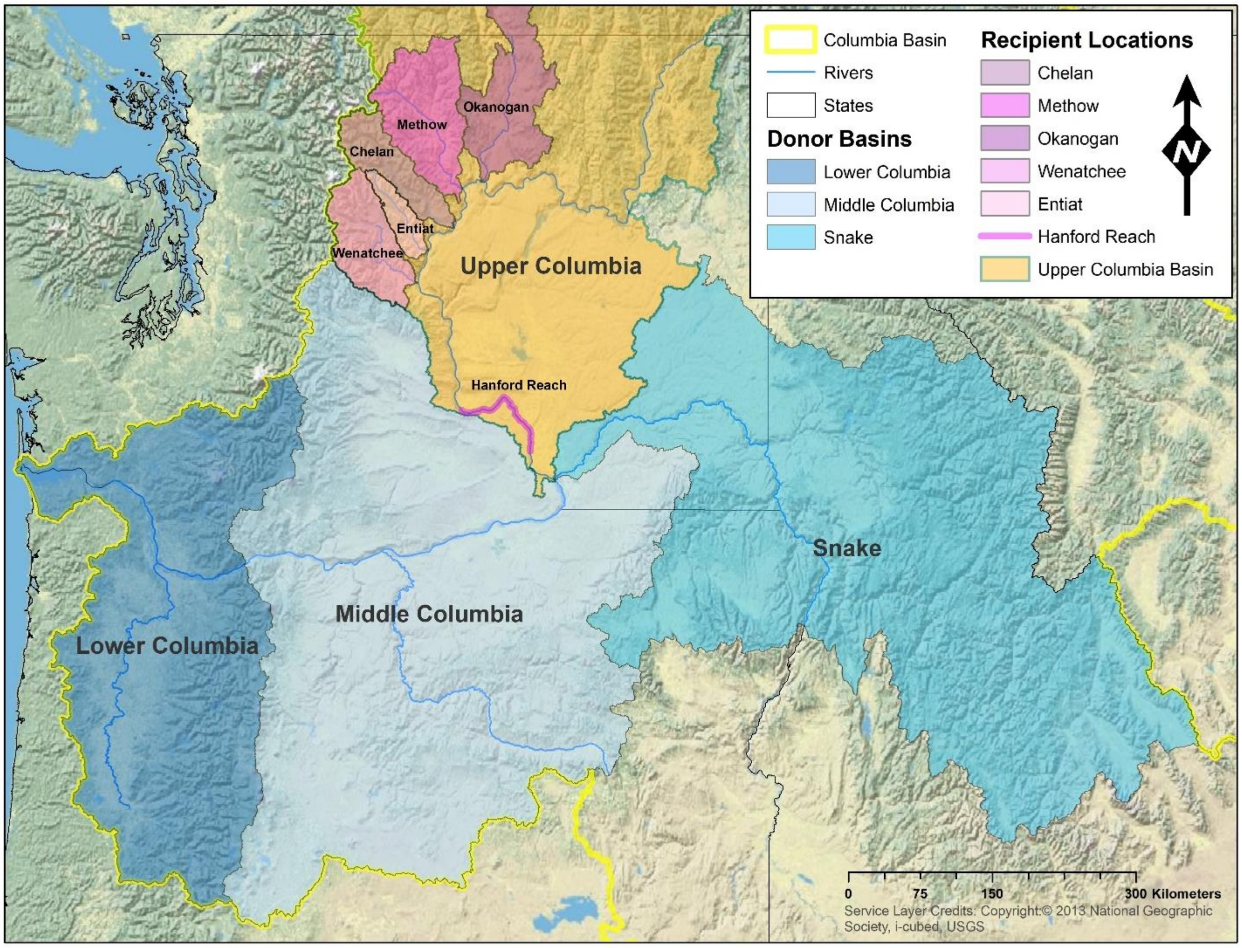

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Figure 1. Map of the study area of the upper Columbia Basin and areas outside of the upper Columbia Basin that contributed strays to recipient populations within the upper Columbia Basin.

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.

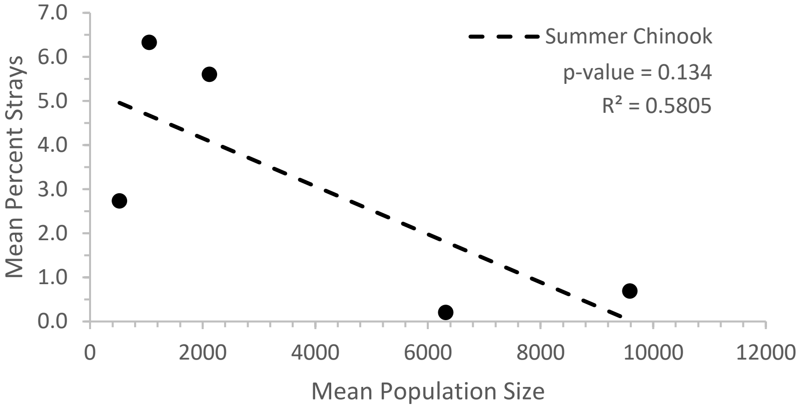
				Target		Non-target strays	
	Subbasin	Natural-origin recruits		Hatchery-origin		Hatchery-origin	
Spawn year	escapement	Number	Percent	Number	Percent	Number	Percent
Wenatchee Spring Chinook Salmon							
Mean (1999-2018)	1,740	644	37.83	1,084	61.53	12	0.65
Mean (2009-2018)	1,876	747	39.28	1,123	60.45	6	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

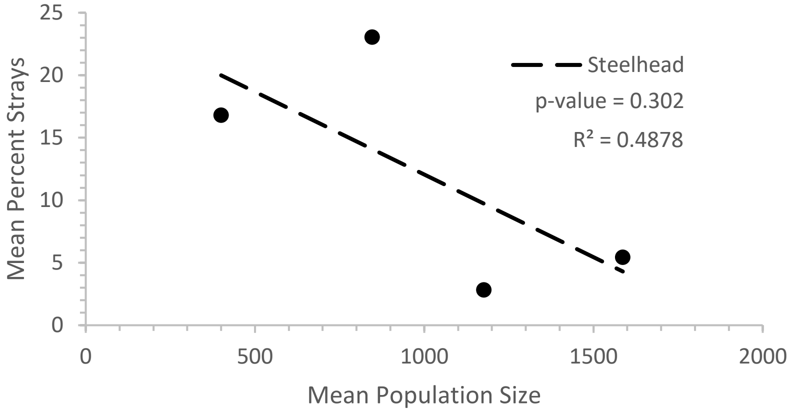
Methow Steelhead							
Mean (2013-2018)	1,574	674	42.89	778	49.42	123	7.69
Mean (2014-2018)	1,587	713	45.15	784	49.40	90	5.45
Okanogan Steelhead							
Mean (2013-2018)	752	248	32.69	328	43.25	175	24.06
Mean (2014-2018)	846	274	30.66	378	46.29	194	23.04

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
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
0
2000
4000
6000
8000
10000
12000
Mean Population Size


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

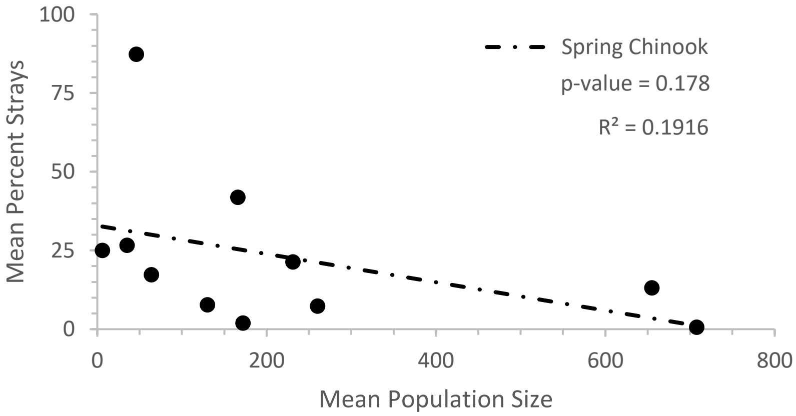

Spring Chinook
p-value = 0.178
R² = 0.1916
Mean Percent Strays
100
75
50
25
0
0
200
400
600
800
Mean Population Size

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).

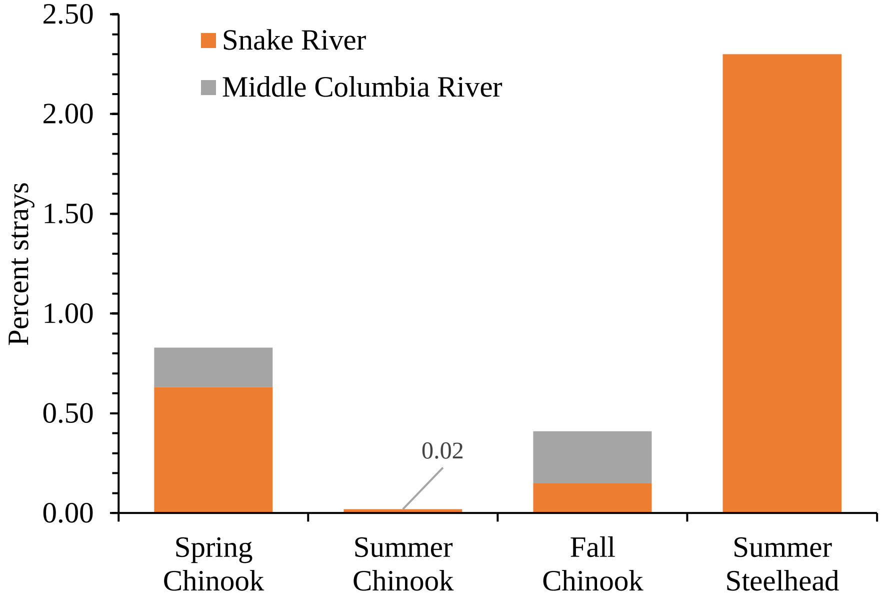


Figure 3. Mean percent hatchery stray Chinook Salmon and steelhead observed in the Upper Columbia River Basin from other regions of the Columbia River Basin from 2014 to 2018.

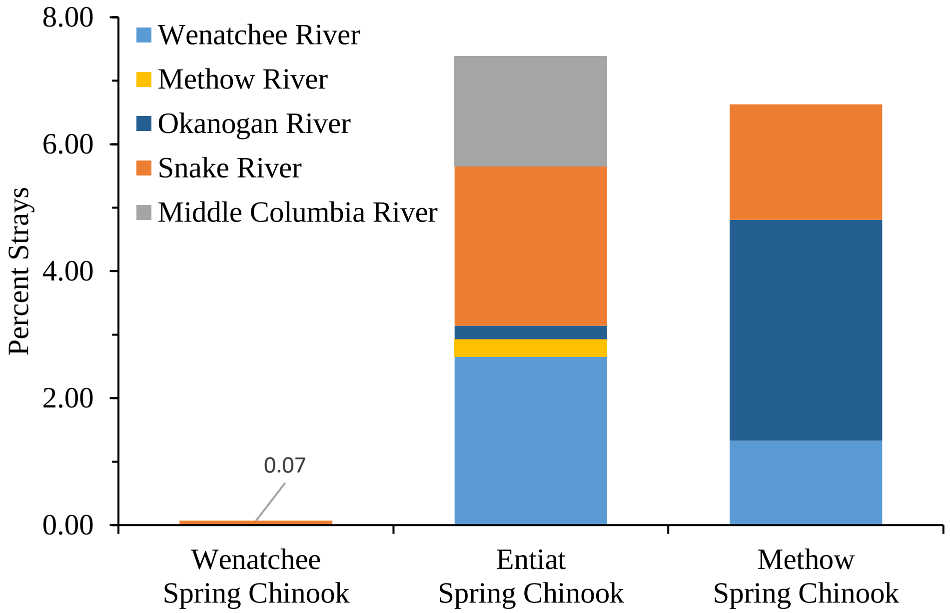


Figure 4. Mean percent hatchery stray spring Chinook Salmon observed in the Upper Columbia River subbasins from other regions of the Columbia River Basin from 2014 to 2018. The management target is <5%.

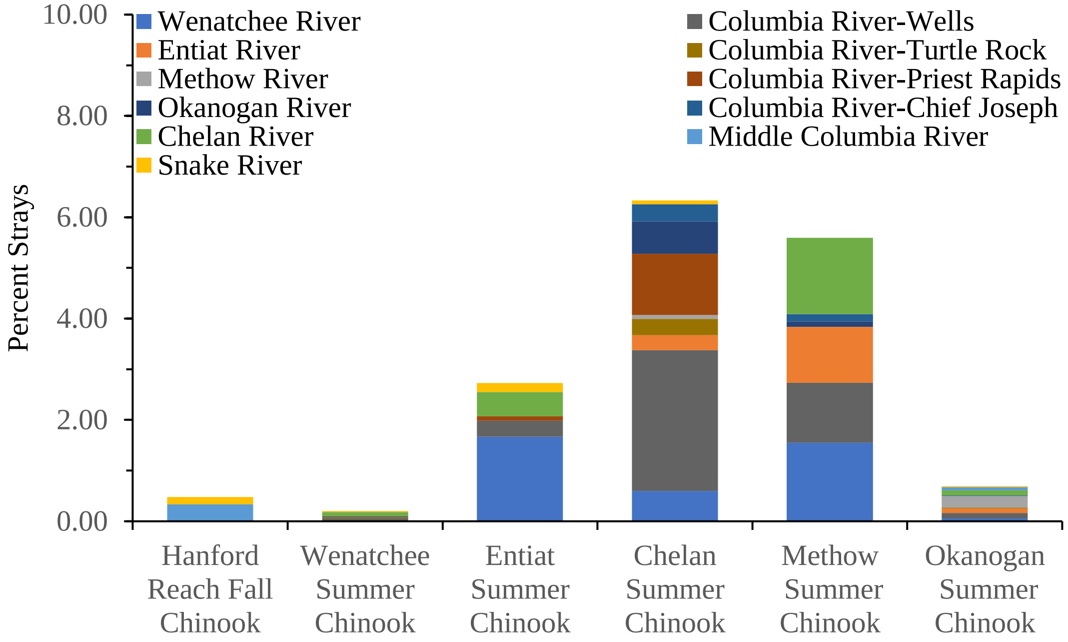


Figure 5. Mean percent hatchery stray summer and fall Chinook Salmon observed in subbasins of the Upper Columbia River basin from 2014 to 2018. The management target is <5%.

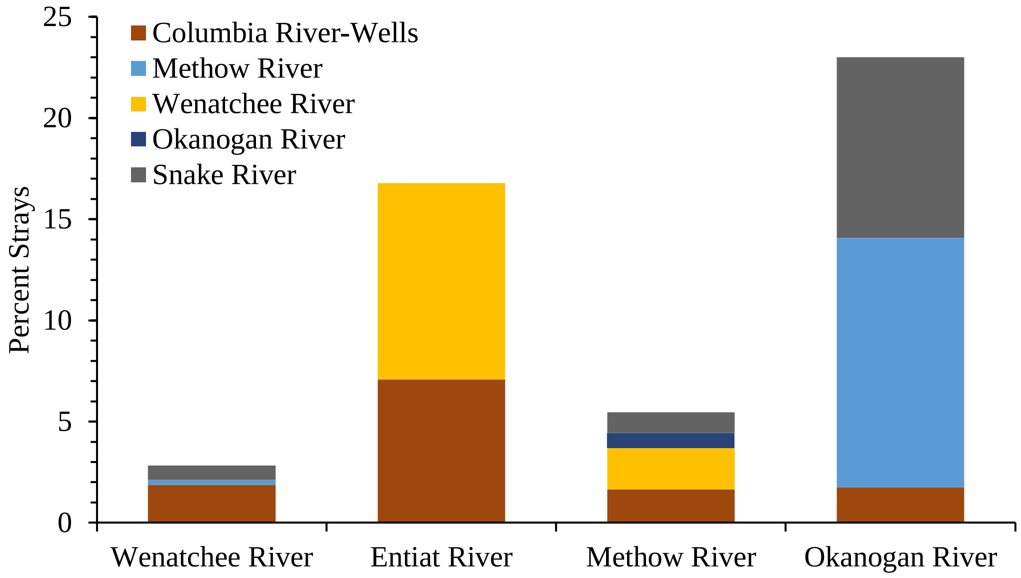


Figure 6. Mean percent hatchery stray steelhead observed in subbasins of the Upper Columbia River basin from 2014 to 2018. The management target is <5%.

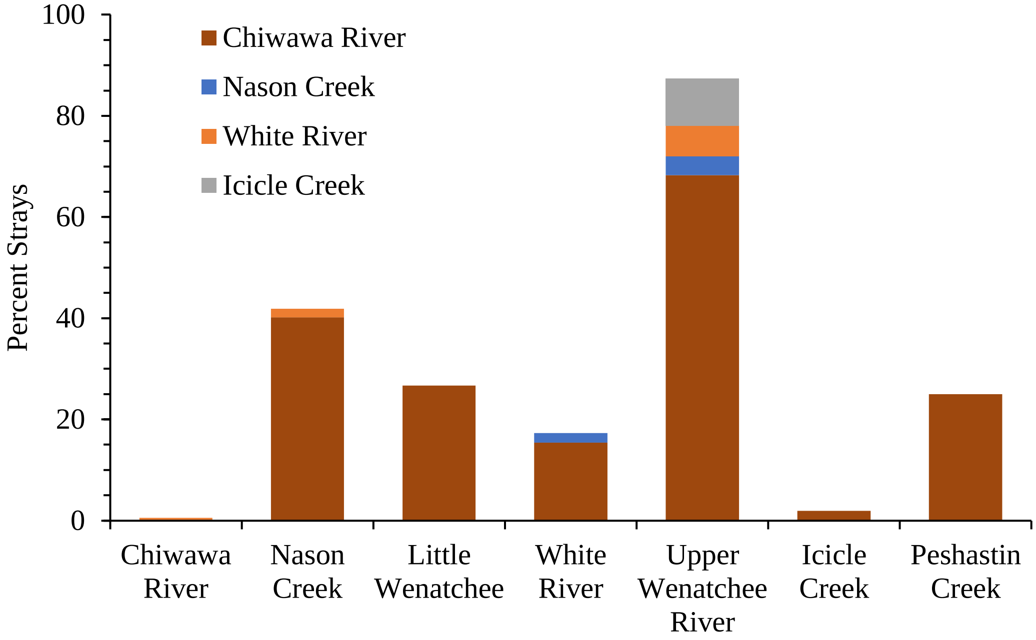


Figure 7. Mean percent hatchery stray spring Chinook Salmon observed in tributaries of the Wenatchee subbasin from 2014 to 2018. The management target is <10%.

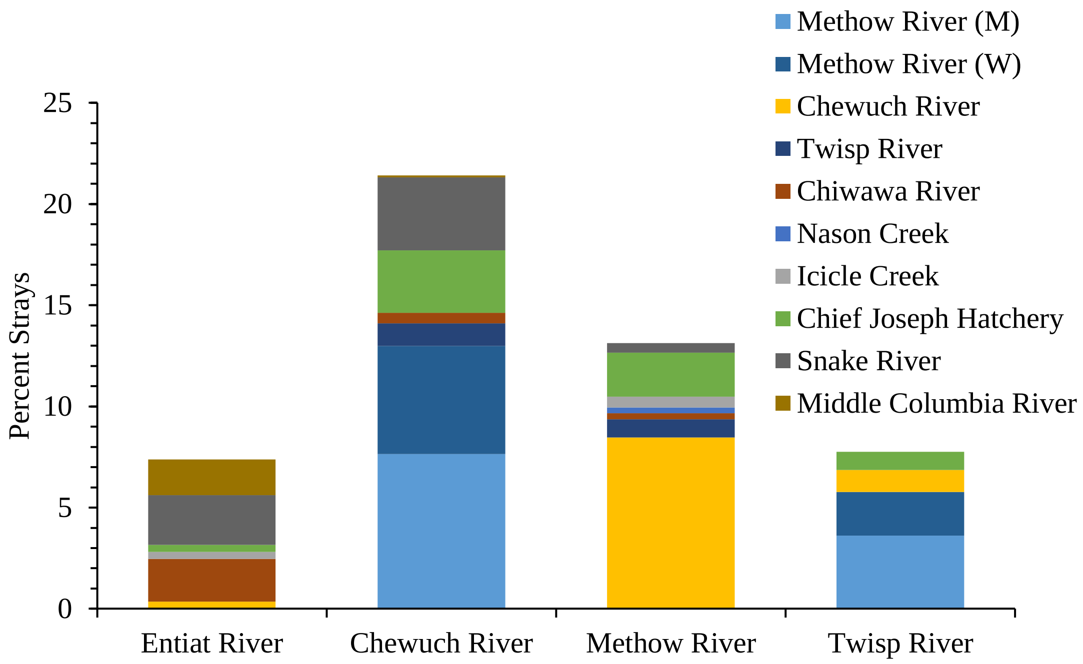


Figure 8. Mean percent hatchery stray spring Chinook Salmon observed in the Entiat River and Methow River and tributaries (Chewuch and Twisp rivers) from 2014 to 2018. The management target is <10% except for the Entiat River which is <5%.

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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Evaluating Genetic Metrics of Adult Natural- and Hatchery-Origin Spring Chinook Salmon in the Upper Columbia Basin

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Abstract

In 1999, the upper Columbia River spring Chinook Salmon evolutionarily significant unit (ESU), was listed as endangered under the Endangered Species Act (ESA). Hatchery programs already underway were used to supplement wild populations in the Wenatchee and Methow rivers for conservation and fishery benefits. Hatchery-origin spring Chinook Salmon that spawn with conspecifics in the natural environment may decrease short- and long-term fitness of natural populations through genetic mechanisms such as domestication selection and loss of within- and among-population genetic variation. Using genetic data from baseline and contemporary collections of hatchery- and natural-origin samples we evaluated the impact of hatchery propagation on within and among population genetic diversity of upper Columbia River spring Chinook Salmon, as required by a monitoring and evaluation plan. The DNA from the earliest available tissue collections, in some locations prior to the onset of local hatchery programs (1989-1993), constituted the baselines and were compared to DNA from tissues collected from contemporary samples (2017, 2018). Analysis indicated genetic changes among spawning aggregates over time. Among the Wenatchee collections the baseline Chiwawa, Nason and White collections were different from each other while the contemporary collections for these populations, along with the Little Wenatchee, were indistinguishable from each other. This is in contrast to Blankenship et al. (2007) who found that the contemporary (in 2006) and baseline collections were undifferentiated. A similar pattern was observed among the Methow collections, where the baseline Twisp, Chewuch and Methow collections were different from each other while the contemporary Chewuch and Methow natural collections were indistinguishable from each other and barely distinguishable from the contemporary Twisp natural collection. Similar to Small et al. (2007) there were differences between baseline and contemporary (in 2006) samples in both the Wenatchee and Methow rivers. It is likely that the management decisions to create composite spawning aggregates, straying hatchery-origin fish, and genetic drift from low effective numbers of breeders contributed to the patterns we observed.

Introduction

The spring Chinook Salmon of the Upper Columbia River (UCR), which comprises spring Chinook Salmon in the Wenatchee, Entiat, Methow, and Okanogan river basins, was listed as endangered under the Endangered Species Act (ESA) in 1999 (endangered status reaffirmed in 2005 and 2014). Included in this listing were several hatchery programs including the Twisp River Program, Chief Joseph spring Chinook Hatchery Program (Okanogan release), Methow Program/Winthrop National Fish Hatchery Program, Chiwawa River Program, White River Program, and Nason Creek Program. The 1999 spring Chinook Salmon status review identified several areas of concern for this ESU including the risk of genetic homogenization due to hatchery practices and the high proportion (65% for the Wenatchee River, 81% for the Methow River) of hatchery-origin fish present on the spawning grounds (Good et al. 2005).

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 hatchery fish interbreeding with natural fish, which may erode local adaptation in naturally spawning populations (Ford 2002; Mobrand et al. 2005; Paquet et al. 2011). Interbreeding can change the genetic profile 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 (Cuenco et al. 1993; 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; Pearsons and O'Connor 2020; Pearsons and O'Connor and Pearsons and Miller chapters in this report). Despite the long-term risks of interbreeding between hatchery- and natural-origin salmon, we are unaware of standardized methods for long-term monitoring of the effects of hatcheries on naturally spawning populations.

The long-term fitness of populations is assumed to depend on maintaining the genetic diversity of natural populations. However, hatchery programs select a subset of individuals from the population to pass on genetic material to the next generation. This is often a relatively small number of individuals that produce a large number of offspring and can result in changes in allele frequencies and reduce the effective population size (Ryman and Laikre 1991). Therefore, it is important to monitor the genetic status of natural populations to determine whether there are signs of changes in genetic distance among populations, changes in allele frequencies and/or linkage disequilibrium from baseline conditions, and to estimate effective population size. Additionally, genetic status of hatchery-origin returns should be monitored to further evaluate potential genetic risks to the natural population.

We endeavored to determine whether genetic diversity, population structure, and effective population size have changed in natural spawning populations as a result of hatchery programs, and to assess genetic changes of hatchery-origin returns. More specifically, we sought to answer the following questions: Is the contemporary allele frequency of natural-origin fish and hatchery-origin fish similar to the baseline allele frequency of natural-origin? (Lacking collections that pre-date hatchery intervention, for the purposes of this study we refer to the earliest available collections as "baseline" collections providing a point in time to estimate whether parameters have changed over time since the "baseline" sample was collected.) Is the contemporary allele frequency of hatchery-origin broodstock similar to the baseline allele frequency of hatchery-origin broodstock? Is contemporary linkage disequilibrium (LD) of natural-origin and hatchery-origin fish similar to the baseline LD of natural-origin fish? Is contemporary LD of hatchery-origin broodstock similar to the baseline LD of hatchery-origin broodstock? Does the genetic distance among supplemented subpopulations (where applicable) and populations remain the same over time? Is the ratio of effective population size (N_e) to spawning population size (N) constant or increasing over time? Beginning with brood years 2017 and 2018 (and then at subsequent ten-year intervals), we will test statistical hypotheses associated with genetic components of the monitoring plan with natural-origin baseline samples (the earliest genetic samples available for each program), natural-origin contemporary samples, and hatchery-origin contemporary samples.

An earlier evaluation attempted to address similar genetic questions but used microsatellite DNA techniques to assess the questions (Blankenship et al. 2007, Small et al. 2007). Blankenship et al. (2007) found that the contemporary (in 2006) and baseline collections of Wenatchee basin Spring Chinook Salmon were undifferentiated. Small et al. (2007) found similar results for Methow River Spring Chinook Salmon prior to 2007 that the Twisp spring Chinook Salmon were differentiated from those in the Methow and Chewuch and that the Methow and Chewuch spring Chinook Salmon became more similar after the hatchery program that combined fish from the two rivers. This evaluation extends the length of the evaluation by 12 years to 2018 and uses single nucleotide polymorphisms instead of microsatellites.

The intent of this project was to fulfill Objective 7 of the monitoring and evaluation plan (Hillman et al. 2019) to determine whether genetic diversity, population structure, and effective population size have changed in naturally spawning spring Chinook Salmon populations in the upper Columbia River as a result of the conservation and safety-net hatchery programs, and to assess genetic changes of hatchery-origin returns. To accomplish this, 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

Background

Spring Chinook Salmon that spawn in the upper Columbia River Basin have persisted despite a variety of challenges in their history. The numbers of spring Chinook Salmon were already dramatically low in the early 1900s. Aside from the typical patterns of overharvest and of habitat alteration from beaver removal, dams, channelization, and deforestation that contributed to declines of spring Chinook Salmon throughout the Columbia River Basin (Lichatowich 2001), upper Columbia spring Chinook Salmon were also uniquely managed because of the construction of Grand Coulee Dam. Between 1939 and 1943, all returning adult upper Columbia spring Chinook Salmon were collected at Rock Island Dam on the Columbia River and transported and released into Nason Creek, a tributary to the Wenatchee River, to spawn as part of the Grand Coulee Fish Maintenance Program (Fish and Hanavan 1948). Transported adults were contained in Nason Creek by weirs with the objective that they would stay and spawn there. Additional hatchery programs were initiated following the transplanting of adult spring Chinook Salmon into Nason Creek. Ultimately, Grand Coulee Dam, and later Chief Joseph Dam, became the upstream limits of spring Chinook Salmon distribution because there was no fish passage at these dams. The historical and ongoing degradations to productivity described by Lichatowich (2001) combined with the transplantation, early artificial propagation, and habitat blockage associated with the construction of Grand Coulee Dam resulted in the low abundance of natural-origin spring Chinook Salmon in the upper Columbia Basin in recent times (McClure et al. 2008).

The Public Utility Districts (PUDs) of Chelan, Douglas, and Grant counties agreed to implement hatchery programs to mitigate for habitat loss caused by construction and unavoidable mortality associated with operation of hydroelectric projects on the Columbia River. Initial hatchery program sizes were negotiated with fisheries managers and later refined using empirical estimates of mortality caused by hydropower projects and survival of hatchery-origin fish. Committees consisting of a representative from the United States Fish and Wildlife Service, National Marine Fisheries Service, Washington State Department of Fish and Wildlife, Yakama Nation, Colville Confederated Tribes, and each Public Utility District 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.

Spring Chinook Salmon in the upper Columbia form an ESU that was listed as Endangered in 1999 when abundance was extremely low (McClure et al. 2008). The ESU consists of three populations that correspond to the Wenatchee, Entiat, and Methow subbasins. The Wenatchee population consists of five major spawning aggregates (Chiwawa, Nason, White, Little Wenatchee, and upper Wenatchee River), the Entiat population consists of one major spawning aggregate, and the Methow population consists of three major spawning aggregates (Twisp, Methow, and Chewuch) (Figure 1). A recovery plan identifies criteria for abundance, productivity, spatial structure, and diversity necessary for the delisting of the upper Columbia spring Chinook Salmon ESU (McClure et al. 2008).

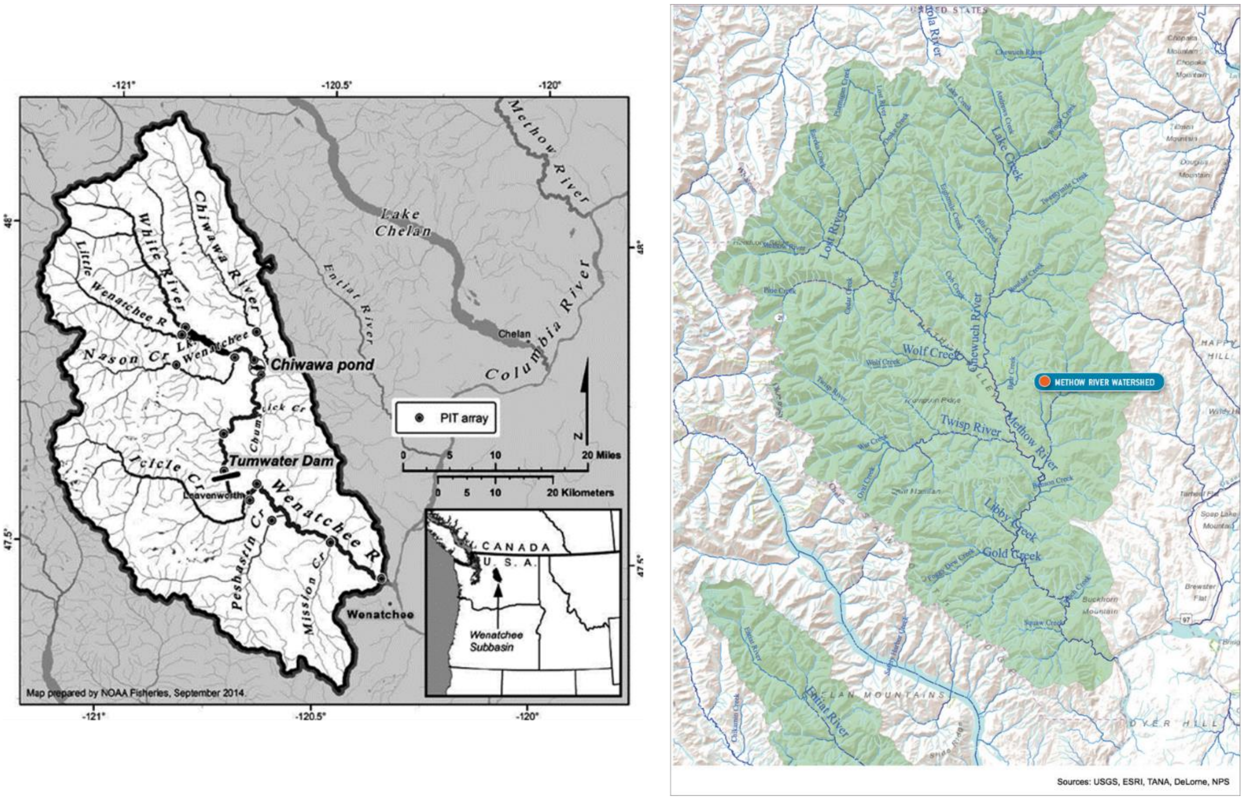

Figure 1. Maps of the Wenatchee (left) and Methow (right) basins.

The PUDs operate their hatchery programs in the upper Columbia Basin using a variety of methods considered best management practices (such as those recommended by Mobrand et al. 2005; Paquet et al. 2011). For example, broodstock were collected in places or identified using genetic methods to achieve the desired target fish; factorial mating strategies were implemented to maximize effective population size; juveniles were reared at low densities; pathogen management was implemented using best practices; and juveniles were acclimated in places where they were targeted to return as adults. Each hatchery program also had several idiosyncrasies that allow for a diversity of evaluations. For example, hatchery programs were started in different years; captive broodstock was implemented in a few programs; fish were acclimated for different lengths of time (e.g., spring vs. overwinter acclimation); fish were reared in different vessel types (e.g., raceways, circular tanks, large ponds); and fish were released in different ways (e.g., volitional vs. forced release). Some important commonalities of the hatchery programs include a primary purpose of increasing natural production while minimizing long-term reduction in productivity, generally releasing smolts at the yearling stage, and adaptive management of the programs by the hatchery committees. Brief descriptions of each of the five hatchery programs are provided below and other background can be found in Pearsons et al. (2012), and Linley et al. (2016).

Chiwawa River Program – An integrated spring Chinook Salmon hatchery program was initiated for the Chiwawa River spawning aggregate in 1989. The Chiwawa River is approximately 60 km long, drains an area of 47,397 hectares and enters the Wenatchee River at river km (RKM) 77.9. The Chiwawa River was host to the largest spawning aggregate of spring

Chinook Salmon in the Wenatchee sub-basin. The hatchery program has contributed a high percentage of hatchery-origin spawners that have spawned in the Chiwawa River, Nason Creek, White River, upper Wenatchee River, and the Little Wenatchee River since 2001 (Hillman et al. 2020; Pearsons and Miller chapter in this report). Broodstock adults were collected at a weir on the Chiwawa River and/or at Tumwater Dam. Broodstock were held and spawned at Eastbank Hatchery on the Columbia River, located 9 KM upstream of the confluence with the Wenatchee River. Fish were reared at Eastbank Hatchery on well water until they were transferred in late September or early October to the Chiwawa Acclimation Facility, located on the lower Chiwawa River, where they were reared and acclimated until the following spring. During the spring, the yearling smolts were allowed to exit the pond volitionally for a week (Johnson et al. 2015) and any remaining fish were forced out of the facility by late May.

The production goal for the Chiwawa spring Chinook Salmon supplementation program for brood years 1989 to 2009 was to release 672,000 yearling smolts into the Chiwawa River at 12 fish per pound (fpp). Brood years 2010-2011, and 2012 were transition years to a reduced program of 298,000 smolts and 205,000 smolts, respectively. Beginning with the 2013 brood, the revised production goal was to release 144,026 smolts as part of a conservation program at 18 (fpp). Targets for fork length and weight were 155 mm (CV = 9.0) and 37.8 g, respectively. Over 90% of these fish were marked with coded wire tags (CWTs). In addition, since 2006, a proportion of the juvenile spring Chinook Salmon smolts have been passive integrated transponder (PIT) tagged annually before release.

Nason Creek Program – Nason Creek is the second largest spawning aggregate in the Wenatchee subbasin, but is much smaller than the Chiwawa River spawning aggregate. Nason Creek is approximately 37 km long, drains an area of 26,547 hectares and enters the Wenatchee River below Lake Wenatchee at RKM 86.3. It enters the Wenatchee River approximately 8.4 km above the mouth of the Chiwawa River. A captive brood hatchery program was initiated by collecting eyed-eggs and alevins between 1999 and 2000 because of the precariously low abundance of adults (Hillman et al. 2020). In 2003, 36 adult captive broodstock were released into Nason Creek for natural spawning. In 2004 and 2005, 8,986 and 4,244 yearling smolts, respectively, were acclimated and released into Nason Creek. The captive broodstock program was discontinued after adult abundance increased.

A smolt supplementation program was initiated with adult collections in 2013 and the first yearling smolts were released from this program in 2015. Natural-origin adults were collected in Nason Creek for broodstock in 2013 and 2014. Since 2015, broodstock have been collected at Tumwater Dam, but most of these fish have been genetically assigned to the Chiwawa spawning aggregate (Chiwawa baseline collections from 2005 and 2006), so very few Nason natural-origin broodstock (fish that assigned to the Nason baseline collections from 2001-2006) have been used in the current supplementation program (all Nason hatchery-origin fish are marked). The first adult females from the Nason Creek hatchery program returned to Nason Creek in 2017. Fish were spawned and reared at Eastbank Hatchery, similar to the Chiwawa River hatchery program. In the fall prior to release, fish were transferred to 30-foot-diameter, dual-drain circular tanks at the Nason Creek Acclimation Facility. Fish were released as yearlings in the spring when fish migration readiness, flows, and temperatures were acceptable.

In addition to the two hatchery programs in Nason Creek, a substantial number of strays from the Chiwawa River supplementation program have spawned in Nason Creek and strays comprised over 50% of the spawners in some years (Pearsons and Miller chapter in this report). In summary, the natural-origin offspring produced in Nason Creek are likely the result of natural-origin spawners and hatchery-origin spawners from the target hatchery programs in Nason Creek and strays from the Chiwawa hatchery program (Williamson et al. 2010).

White River Program – The White River spring Chinook Salmon captive brood program was initiated in 1997 as a risk aversion measure to prevent the extinction of, to conserve, and to aid in the recovery of the naturally spawning salmon population in the White River (Ford et al. 2015a). The White River is approximately 51 km long, drains an area of 38,850 hectares, and flows directly into Lake Wenatchee. The first-generation (F1) component of the White River captive brood program was from eggs and fry collected in the White River (brood-years 1997-2009) and reared in a hatchery until spawning. The number of eggs or fry that were used for the first-generation component of the program (10,353 from 122 redds) represented at least 122 families although it was less than what would be produced from three average-sized females (average estimated fecundity/female is 4,669). The resulting progeny (F2) were then reared in a hatchery until final acclimation and released in the upper Wenatchee watershed. The first large number of juveniles was released in 2008, the last release occurred in 2015, and adults had the potential to return from juvenile releases until 2018.

The F1 and F2 rearing programs were initially located at the AquaSeed Corporation facility in Rochester, Washington. The resource managers decided to move the program to another facility because the quality of the F2 fish produced at AquaSeed was poor (e.g., poor fin quality). Transition of the programs to the Little White Salmon National Fish Hatchery (LWSNFH) near Cook, Washington began in May 2006 and was completed in February 2009.

To limit adverse domestication effects from the captive brood program, plans were to transition after two generations to a supplementation program based on broodstock captured as returning adults. Initial broodstock collections were well below program goals and disease issues limited production and release of F2 juveniles. The number of broodstock collected for the program increased dramatically in 2002 and became sufficient to meet F2 production goals. Because initial production was limited, it was decided to continue broodstock collections until 2010. As a result of this extension, broodstock collection approached or met program goals for eight consecutive years (2002-2009).

A variety of acclimation and release scenarios were conducted since 1997. Acclimation scenarios have involved naturalized features such as in-channel enclosures, stream-side tanks supplied with pass-through surface water, and net pens in Lake Wenatchee near the mouth of the White River. Release scenarios have included on-site releases from tanks, in-channel enclosures, and net pens in Lake Wenatchee. Net pens containing acclimated fish were towed to the mouth of the lake for releases during 2010, as well. Tank and net-pen acclimated fish have been loaded into transport trucks and released into the Wenatchee River (2011-2015), and direct releases of sub-yearlings and yearlings have also been conducted from a transport truck into Lake Wenatchee and the White River with no acclimation. A total of 944,591 juveniles were released between 2004 and 2015.

Methow-Chewuch Program – The Methow River is approximately 143 km long, drains an area of approximately 489,508 hectares, and enters the Columbia River at RKM 843. The Chewuch River is the largest tributary to the Methow River entering at RKM 80 at the town of Winthrop. It is approximately 80 km long and drains an area of 137,528 hectares. The hatchery program intended to supplement the Methow and Chewuch rivers was initiated with broodstock collected in 1992. The first smolts were released in 1994, and the first hatchery fish returned in 1995. The Methow Hatchery is on the right bank of the Methow River at RKM 82, and approximately 2 km upstream from the mouth of the Chewuch River. Broodstock were collected at Fulton Dam at RKM 1.8 on the Chewuch River; Foghorn Dam at RKM 82.5 on the Methow River; Wells Dam at RKM 830 on the Columbia River, 13 km downstream from the mouth of the Methow River; or at the Methow Hatchery outfall. Broodstock were assigned to the Methow-Chewuch or Twisp spawning aggregates using genetic methods. Adult brood fish were spawned, incubated, and reared at the Methow Hatchery. Final acclimation in the spring occurred primarily at the Methow Hatchery or at an acclimation pond on the Chewuch River at RKM 13.3. However, in some years, a portion of the fish from the Methow Hatchery have been spring-acclimated and released by the Yakama Nation from remote ponds on small tributaries to the Methow River upstream from the Methow Hatchery, including one on Wolf Creek (RKM 88; broods 2002, 2008, and 2009), Mid-Valley Pond (RKM 90; broods 2010, 2011, and 2012), and Goat Wall Pond (RKM 117; broods 2015-2017).

Prior to brood year 2001, resource managers attempted to maintain genetic distinction between Chewuch and Methow production, releasing progeny of presumed Chewuch-origin adults (based on capture location or CWT) only to the Chewuch River, and likewise releasing progeny of presumed Methow-origin adults only to the Methow. However, beginning with brood year 2001, resource managers composited production of Methow and Chewuch stocks into the single Methow-Chewuch stock due to chronic difficulties collecting sufficient broodstock to maintain a distinct Chewuch program. The loss of trapping facilities at Fulton Dam in 2005 ended directed broodstock collection efforts in the Chewuch River. With the historic challenges obtaining natural-origin broodstock, the proportion of natural-origin fish used in the broodstock (pNOB) has varied under pressure from fisheries managers to maintain production targets.

The production goal for the Methow-Chewuch program for brood-years 1992 through 1997 varied depending upon brood availability, with the nominal target of 500,000 yearling smolts. Releases ranged from 16,000 to 495,000 (mean, 223,000) yearling smolts, due to inconsistent broodstock-trapping efficiency at Fulton Dam on the Chewuch River and Foghorn Dam on the Methow River, and collection efforts at these locations were supplemented with collection at the Methow Hatchery outfall and Wells Dam beginning in 1996. Average pNOB during this period was 45% and ranged from zero to 79%.

For brood years 1998 through 2011, the nominal production goal was 366,000 yearling smolts. However, with consistent shortfalls in brood collection in the Twisp River, resource managers compensated for resultant shortfalls in Twisp smolt production by increasing production in the Methow-Chewuch program commensurate with the Twisp shortfall in each brood year. Smolt production for the Methow-Chewuch program averaged 357,000 (range, 196,000-498,000) yearling smolts for brood years 1998-2011. Average pNOB during this period was 19% and ranged from zero to 58%. Since brood year 2012, the production goal of 193,000 yearling smolts has been consistently achieved, and pNOB has averaged 71% (range 30% to 99%).

All spring Chinook Salmon produced for the Methow-Chewuch program were marked with CWTs, and prior to brood year 2000, were also adipose-fin clipped. For brood years 1992-2017, annual CWT mark rate ranged from 88-100 percent. A portion of the releases were also PIT tagged prior to release in 2003, 2004, and every year since 2010.

Twisp River Program – The Twisp River is a major tributary to the Methow River entering at RKM 66. It is approximately 62 km long and drains an area of about 63,714 hectares. The hatchery program intended to supplement the Twisp River spawning aggregate, was initiated with broodstock collected in 1992, and was implemented in a similar manner as the Methow-Chewuch program. Broodstock were collected at a trap in the Twisp River or at Wells Dam, with subsequent genetic identification to retain Twisp River brood fish. Adult brood fish were spawned, incubated, and reared at the Methow Hatchery. Final acclimation in the spring occurred at an acclimation pond on the Twisp River at RKM 11.5.

The nominal production goal for the Twisp River program for brood-years 1992 through 1997 was 250,000 yearling smolts (average pNOB of 65%; range zero to 100%). For brood years 1998 through 2011, the nominal production goal was 183,000 yearling smolts (average pNOB of 34%; range zero to 75%). Since brood year 2012, the production goal has been 30,000 yearling smolts (average pNOB of 74%; range 41% to 100%).

To maintain genetic distinction between the Twisp River spawning aggregate and the Methow-Chewuch composite aggregate, resource managers limited broodstock for the Twisp River program to either natural- or hatchery-origin fish from the Twisp River. Difficulty in obtaining Twisp-origin brood resulted in consistent brood limitation for the Twisp River program. Thus, annual smolt production averaged approximately 52,000 (range zero to 116,000) over the life of the program, with consistent production of approximately 30,000 smolts beginning with brood year 2012. All spring Chinook Salmon produced for the Twisp program were marked with CWTs, and prior to brood year 2000, were also adipose-fin clipped. For brood years 1992-2017, annual CWT mark rate ranged from 94-100 percent. A portion of the releases were also PIT tagged prior to release in 2003, 2004, and every year since 2010.

In 1996 and 1997, resource managers implemented a captive brood program for the Twisp spawning aggregate by vacuuming a small number of eggs from redds from naturally spawning fish in the Twisp River. Subsequent brood years through 2002 reserved 45 eggs from each crossing of Twisp broodstock for the captive brood program (goal of 30 families). Incubation and initial rearing occurred at Methow Hatchery for the 1996 and 1997 broods, but progeny from subsequent brood years were reared at the AquaSeed Corporation facility in Rochester, Washington. The captive brood program contributed little to total annual smolt production for the Twisp River program, and captive production ended with the release of F2 smolts that were progeny of F1 adults from eggs collected from adults returning to the Twisp River in 2002.

Sample collections

Baseline collections were genotyped for this project by Washington Department of Fish and Wildlife Molecular Genetics Laboratory (WDFW MGL). The target sample size was 50 samples from each of two years, both hatchery- and natural-origin (i.e., n = 200 baseline samples from each focal population). When many more samples than 50 were available for genotyping, a random subset of 50 were drawn without replacement from the full collection. Samples had been preserved in 95% ethanol or dried on chromatography paper and stored at room temperature. Baseline sample collections consisted of the oldest samples found for each population. Baseline collections had been used in previous monitoring and evaluation projects (Blankenship et al. 2007; Small et al. 2007).

Some contemporary spring Chinook Salmon samples were broodstock spawned in 2017 and 2018 from the upper Columbia spring Chinook Salmon programs (see Table 1). The White and Little Wenatchee spring Chinook Salmon in the Wenatchee basin and the Methow spring Chinook Salmon were obtained from carcasses on the spawning grounds of each sub basin. Few natural-origin carcasses are found in any one year, so to make sample-size goals, spring Chinook Salmon carcass samples from 2015 and 2016 were used to supplement the 2017 and 2018 samples (Table 1). The White, Little Wenatchee and Methow spring Chinook Salmon contemporary samples were all genotyped by WDFW MGL. All other genotypes from contemporary spring Chinook Salmon collections were genotyped by the Columbia River Inter-Tribal Fish Commission (CRITFC) (see Table 1) and were obtained from the FishGen.net online data repository.

Table 1. Samples of spring Chinook Salmon from the Wenatchee and Methow basins. Boxes surround collections that were combined to meet minimum threshold numbers for genetic analyses. Because they are combined sample there is no year associated with the sample name. Genotypes obtained from CRITFC are indicated under the WDFW code. Asterisks mark codes that had fish from two locations, Chewuch and Methow, and fish were divided according to collection data.

Category	Origin	**Wenatchee Basin**	WDFW Code	N genotyped	N analyzed	N final
Baseline	Natural	Chiwawa_River-Natural-1989	89AZ	38	37	37
	Natural	Chiwawa_River-baseline-1993	93DJ	96	93	92
	Natural	Nason_Creek-baseline-1993	93EE	51	50	49
	Natural	Nason_Creek-baseline-2000	00IQ	60	59	58
	Natural	White_River-Natural-1989	89AZ	55	52	52
	Natural	White_River-baseline	91EL	22	21	
	Natural	White_River-baseline	92DT	21	20	40
Contemporary	Hatchery	Chiwawa-contemporary-2017	CRITFC			55
	Hatchery	Chiwawa-contemporary-2018	CRITFC			55
	Hatchery	Leavenworth-Hatchery-Spring-2017	CRITFC			55
	Hatchery	Leavenworth-Hatchery-Spring-2018	CRITFC			55
	Hatchery	Nason-contemporary-2017	CRITFC			55
	Hatchery	Nason-contemporary-2018	CRITFC			55
	Natural	White-contemporary-spring	15FJ	3	3	
	Natural	White-contemporary-spring	16FW	61	61	
	Natural	White-contemporary-spring	17FM	18	18	
	Natural	White-contemporary-spring	18FJ	13	13	95
	Natural	Little_Wenatchee-contemporary-spring	15FJ	34	31	
	Natural	Little_Wenatchee-contemporary-spring	16FW	41	39	
	Natural	Little_Wenatchee-contemporary-spring	17FM	12	12	
	Natural	Little_Wenatchee-contemporary-spring	18FJ	8	8	90
		Methow Basin				
Baseline	Natural	Chewuch_River-Natural-baseline	92DO	47	3	
	Natural	Chewuch_River-Natural-baseline	93DZ	92	92	81
	Natural	Methow_River-baseline-1993	93EA	93	87	83
	Natural	Twisp_River-natural-baseline-1992	92DQ	48	46	38
	Natural	Twisp_River-baseline-1993	93EB	48	47	45
Contemporary	Hatchery	Chewuch_River-Hatchery-contemporary	15CZ	30*	16	
	Hatchery	Chewuch_River-Hatchery-contemporary	16FN	25*	4	
	Hatchery	Chewuch_River-Hatchery-contemporary	17EU	20*	10	
	Hatchery	Chewuch_River-Hatchery-contemporary	18GB	13*	6	36
	Natural	Chewuch_River-natural-contemporary	16FP	10	8	
	Natural	Chewuch_River-natural-contemporary	17EW	18	17	
	Natural	Chewuch_River-natural-contemporary	18GD	22	22	41
	Hatchery	Methow_Fish_Hatchery-Hatchery-Spring-2017	CRITFC			50
	Hatchery	Methow_Fish_Hatchery-Hatchery-Spring-2018	CRITFC			50

Category	Origin	**Wenatchee Basin**	WDFW Code	N genotyped	N analyzed	N final
	Hatchery	Methow_River-hatchery-contemporary	15CZ	30*	12	
	Hatchery	Methow_River-hatchery-contemporary	16FN	25*	18	
	Hatchery	Methow_River-hatchery-contemporary	17EU	20*	8	
	Hatchery	Methow_River-hatchery-contemporary	18GB	13*	3	41
	Natural	Methow_River-natural-contemporary	15DA	7	7	
	Natural	Methow_River-natural-contemporary	16FO	7	7	
	Natural	Methow_River-natural-contemporary	17EV	17	15	
	Natural	Methow_River-natural-contemporary	18GC	26	23	47
	Hatchery	Twisp_River-hatchery-contemporary	15DC	25	10	
	Hatchery	Twisp_River-hatchery-contemporary	16FQ	13	13	
	Hatchery	Twisp_River-hatchery-contemporary	17EX	4	4	
	Hatchery	Twisp_River-hatchery-contemporary	18GE	3	2	24
	Natural	Twisp_River-natural-contemporary	15DD	11	10	
	Natural	Twisp_River-natural-contemporary	16FR	14	14	
	Natural	Twisp_River-natural-contemporary	18GF	11	11	43
	Hatchery	Winthrop_NFH-Hatchery-Spring-2017	CRITFC			50
	Hatchery	Winthrop_NFH-Hatchery-Spring-2018	CRITFC			50

Genetic sample processing

Briefly, at WDFW MGL genomic DNA was extracted using silica membrane column extraction kits following manufacturer's protocols. We used an amplicon sequencing procedure, Genotyping in Thousands (GTseq, Campbell et al. 2015), to assay 332 Chinook Salmon single nucleotide polymorphisms (SNPs; Appendix A). Because some genotypes were obtained from CRITFC Parental Based Tagging (PBT) database and they were genotyped at some additional loci, Appendix A lists 381 loci that are in the WDFW or CRITFC panels, or both. GTseq amplifies pools of targeted SNPs in a highly multiplexed polymerase chain reaction (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 WDFW 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 R markdown scripts (G. McKinney, WDFW). All genotype data, baseline and contemporary, were evaluated for missing data and species identification (species ID; i.e., Chinook Salmon and steelhead). Species ID was determined using 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. Chinook Salmon neutral SNP marker designations were established by testing in multiple laboratories, including CRITFC and WDFW laboratories or designated as adaptive by CRITFC for markers CRITFC ascertained. Neutral loci were evaluated for missing data, deviations from Hardy-Weinberg expectations (HWE), and diversity. In summary, loci excluded from further analysis include, 1) those with more than 30% missing data across the entire dataset, 2) those invariant across the entire dataset, or 3) those with deviations from HWE in most collections.

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 subpopulation 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 individual genotypes along the first two axes and separately calculated and graphed average allelic richness among all loci within a collection. The individuals that were farthest apart on the PCA were the most genetically different from one another and those that were closest together were the most similar to one another. We statistically evaluated allele frequency similarity by performing pairwise analysis of molecular variance (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. Differences in allele frequencies among baseline and contemporary collections would be an indication that hatchery programs, among other factors, could have changed allele frequencies.

Question 2, Linkage Disequilibrium – Linkage disequilibrium (LD) is a measure that is used to assess whether a collection includes genetically discrete groups such as family or brood year groups or is from a small population, such as a hatchery with a limited broodstock, or if loci are located close together on the same chromosome. If family groups are included in a collection then parental allele combinations may be overly represented in the collection and loci appear linked. If hatchery broodstocks are small then hatchery family groups would be overly represented in the collection, with a similar result of high LD. Loci are generally screened for physical linkage (on the same chromosome) during locus development and is usually not a concern. Low LD indicate the collection is a random sample from a reasonably sized breeding population and high LDs indicate family or hatchery groups or non-random sampling. We evaluated LD two ways. First, we calculated allelic correlation coefficients for all pairwise locus comparisons within collections using PLINK (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. Differences among collections in the frequency of significant pairwise tests of LD within collection were tested using Mann-Whitney tests. Correction for multiple testing achieved a table-wide $\alpha = 0.05$ for each collection via false discovery rate (Verhoeven et al. 2005). To evaluate linkage disequilibrium, we counted the number of loci fixed for a single allele that would not be involved in a pairwise test of linkage and then summed the number of pairs of loci (out of the total number of pairs compared) that were in linkage disequilibrium at $p < 0.05$ and present this as a percentage of the total locus pairs compared (Table 2). This shows which collections had tendencies towards linkage disequilibrium before correcting for multiple tests. No minimum or maximum allowable LD target has been described. Because increased LD indicates a reduction in diversity, advice is generally to avoid increasing LD.

Table 2. Genetic statistics for Spring Chinook Salmon collections including average allelic richness (avg Rich), observed and expected heterozygosity (Het_obs, Het_exp) and the Hardy-Weinberg Equilibrium (HWE) value over all loci as expressed by F_{IS}, as well as the number of fish per collection (count). The percentage of loci out of HWE and the percentage of locus pairs in linkage disequilibrium (LD) were tallied before and after corrections for multiple tests, only uncorrected reported in this table. The effective number of breeders (N_b) was estimated using the linkage method in LDNe and the escapement values (N) were from the parent year of the spawners, average four years prior to collection.

Analysis_Unit	Count	Fixed Loci	avg Rich	Het_obs	Het_exp	F_{IS}	% loci HWE dis $p < 0.05$	% LD $p < 0.05$	N_b	95% CI for Nb Jackknife on samples		N	N_b/N
Wenatchee Basin													
Chiwawa_River-Natural-1989	37	45	1.220	0.2180	0.2187	0.0171	2.35	2.98	**NA**				
Chiwawa_River-baseline-1993	92	41	1.222	0.2227	0.2218	-0.0015	6.27	15.81	21	18	25	713	0.0295
Chiwawa-contemporary-2017	55	43	1.226	0.2260	0.2248	0.0020	4.31	4.39	128	75	328	1378	0.0927
Chiwawa-contemporary-2018	55	41	1.223	0.2190	0.2221	0.0209	0.78	4.11	187	109	535	975	0.1914
White_River-baseline	52	38	1.229	0.2296	0.2274	0.0023	2.35	3.73	248	154	581	**NA**	
White_River-Natural-1989	40	33	1.232	0.2314	0.2311	0.0082	3.14	3.89	170	84	2132	**NA**	
White-contemporary-spring	95	30	1.229	0.2254	0.2283	0.0182	2.67	4.57	347	218	760	344	1.0090
Little_Wenatchee-contemporary-spring	90	27	1.230	0.2303	0.2290	-0.0008	3.51	4.26	344	216	765	383	0.8982
Nason_Creek-baseline-1993	49	30	1.227	0.2217	0.2256	0.0274	4.31	3.80	200	126	438	288	0.6938
Nason_Creek-baseline-2000	58	40	1.225	0.2330	0.2239	-0.0322	2.75	6.30	45	32	66	83	0.5373
Nason-contemporary-2017	55	35	1.223	0.2205	0.2223	0.0170	3.92	4.21	119	68	331	409	0.2900
Nason-contemporary-2018	55	48	1.222	0.2260	0.2214	-0.0093	5.10	8.69	28	17	49	231	0.1199
Leavenworth-Hatchery-Spring-2017	55	34	1.233	0.2328	0.2320	0.0052	3.53	3.66	590	253	Infinite	212	2.7825
Leavenworth-Hatchery-Spring-2018	55	32	1.232	0.2389	0.2305	-0.0270	1.96	3.92	285	126	Infinite	407	0.7007
Methow Basin													
Twisp_River-natural-baseline-1992	38	57	1.214	0.2507	0.2118	-0.1674	5.49	4.66	34	15	277	452	0.0741
Twisp_River-baseline-1993	45	44	1.219	0.2167	0.2180	0.0166	2.35	3.46	175	109	401	414	0.4220
Twisp_River-hatchery-contemporary	24	63	1.219	0.2174	0.2162	0.0158	2.75	3.78	48	25	184	85	0.5588
Twisp_River-natural-contemporary	43	38	1.227	0.2250	0.2256	0.0140	3.14	3.63	335	143	Infinite	519	0.6445
Chewuch_River-Natural-baseline	81	23	1.221	0.2191	0.2203	0.0119	4.71	4.18	205	135	393	370	0.5546
Chewuch_River-Hatchery-contemporary	36	41	1.219	0.2174	0.2178	0.0161	2.35	3.61	118	61	613	579	0.2033
Chewuch_River-natural-contemporary	41	44	1.223	0.2232	0.2219	0.0064	3.14	3.36	431	168	Infinite	1085	0.3968
Methow_River-baseline-1993	83	25	1.232	0.2308	0.2314	0.0076	3.14	4.55	180	108	427	1202	0.1495
Methow_River-hatchery-contemporary	50	37	1.231	0.2376	0.2298	-0.0209	1.18	3.74	531	218	Infinite	1781	0.2979
Methow_River-natural-contemporary	50	40	1.224	0.2198	0.2228	0.0242	3.14	3.47	550	191	Infinite	3226	0.1706
Methow_Fish_Hatchery-Hatchery-Spring-2017	41	28	1.230	0.2280	0.2287	0.0134	1.57	3.51	266	71	Infinite	579	0.4587
Methow_Fish_Hatchery-Hatchery-Spring-2018	47	27	1.234	0.2299	0.2327	0.0221	3.53	3.40	720	186	Infinite	4566	0.1576
Winthrop_NFH-Hatchery-Spring-2017	50	37	1.230	0.2294	0.2288	0.0075	3.53	3.77	261	123	Infinite	494	0.5283
Winthrop_NFH-Hatchery-Spring-2018	50	31	1.231	0.2344	0.2298	-0.0102	0.78	4.15	161	96	417	408	0.3953

Question 3, Genetic Distance – To estimate genetic distance among collections we calculated pairwise F_{ST} and lower and upper bounds of the 95% confidence interval with the R package hierfstat using default parameters (Goudet 2005). In theory, the pairwise F_{ST} values can range from 0 to around 1 with 0 being no difference (e.g., little genetic distance and high geneflow) and 1 being large difference (e.g., different species and no geneflow). The F_{ST} value is influenced by the heterozygosity of the marker types (higher heterozygosity generally yields lower pairwise values) and thus pairwise F_{ST} values from different marker types can not be compared directly. However, in general the trends of the values parallel each other (high values with one type of marker would be similarly high with a different type of marker and *vice versa*). No minimum viable genetic distance has been identified. Increased genetic distance between a hatchery and natural collection of the same population is an indication that the hatchery broodstock represented only a subsample of the population. The goal is to avoid reducing genetic distances within and among populations that may be impacted by hatchery programs.

Question 4, Effective Population Size – 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 for the collection, rather than N_e; N_b is a better metric for monitoring (Luikart et al. 2021). The N_b is an estimate of how genetic drift affects a population and is proportional to $1/N_b$ (Waples, pers. comm.). In cases where N_b is large, drift may be difficult to calculate or to distinguish from infinity, but the point estimate is still useful for comparisons. Because subject spring Chinook Salmon 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. There is no consensus among experts on minimum viable N_e values, and as such the recommendation is generally to avoid reductions in N_e.

The N_b estimates refer to the parent generation, so to calculate N_b/N ratios, where available we obtained escapement estimates for the spawn years in the Methow River one generation prior (assuming a three-year generation) to the year the tissue samples were collected from the WDFW SCoRE database (https://fortress.wa.gov/dfw/score/score/). Escapement and broodstock numbers for the Wenatchee Basin rivers were provided by Chris Moran (WDFW, personal communication) and numbers for the Methow, Twisp and Chewuch rivers were provided by Charles Snow and Charles Frady (WDFW, personal communication).

Results

Sample collections

Genotyping went well and the majority of samples had sufficient genotypic data to include in the analyses (see Table 1). The Chewuch and Methow contemporary hatchery collections had the same WDFW collection codes and individuals were assigned to the tributary where they were collected (see Table 1 for N per collection group), based on sample data. The White and Little Wenatchee contemporary natural collections had the same WDFW collection codes and individuals were assigned to the tributary where the spawner carcass was sampled. Exploratory PCA analysis of genotypes revealed two fish collected in the Little Wenatchee River, 15FJ1961 and 15FJ2146, on October 3, 2015 and October 8, 2016, respectively, were summer-run Chinook Salmon, rather than spring-run (data not shown). Their inclusion in downstream analyses distorted results for the Little Wenatchee River collection, significantly increasing LD and HWD and decreasing N_b. Given that they were sampled late in the spawning season and because they genetically clustered with summer-run Chinook, we excluded them from final analyses.

Evaluating Loci

Of 381 SNP loci amplified, 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=12), loci with too much missing data (n=25), and loci with excess deviations from Hardy-Weinberg equilibrium (n=6).

Data analysis

Allele frequencies – Question 7.1.1 and 7.1.2 – The principal component analysis (PCA) plots show some structure among Chinook Salmon spawning in the respective basins (Figure 2). In the Wenatchee basin the White River baseline spawners plot to the right of PCA axis 1 and the Chiwawa baseline and some of the Nason contemporary spawners plot to the left of axis 1. The Chiwawa baseline collection from 1993 was composed of 14 families of 3 to 10 siblings and, the largest family groups plotted outside the main cluster. The Nason contemporary 2018 collection also was composed of family groups: there were seven families of 2 to 10 siblings and the largest family group plotted below to the left of the main cluster. Most of the White River contemporary spawners plotted towards the center near the Leavenworth hatchery samples along with the Little Wenatchee and Chiwawa rivers contemporary spawners and the Nason baseline and contemporary spawners. The inset shows that the baseline samples plotted in population clusters and that the Chiwawa families plotted in a diffuse cluster while the contemporary samples mostly plotted in a single cluster with the Nason families on the periphery. The small amount of genetic variation in the axes underscores the low differentiation among spawners. In the Methow basin, the Methow baseline spawners plotted to the left of PCA axis 1 and the Twisp spawners plotted to the right of axis 1. The center cluster was composed of the remaining Methow and Chewuch samples and the Winthrop National Fish hatchery samples. The inset shows that the baseline samples plotted in population clusters and that the contemporary samples mostly plotted in a single cluster.

Figure 2. Plot of the first two axes of a Principal Components Analysis (PCA) of Wenatchee (above) and Methow (below) spring Chinook Salmon samples. Family structure was found in some collections. Insets at right show only baseline and contemporary samples from the PCA on left.

The average allelic richness was 1.226 over all Spring Chinook Salmon collections and there was little variation between collections (Table 2). The AMOVA tests indicated that there were significant differences in allele frequencies between baseline and contemporary collections from the same tributary and different tributaries and between natural and hatchery collections from the same river (data not shown). There were two exceptions, one where the Methow river baseline 1993 was not significantly different from the Leavenworth Hatchery 2017 and where the Methow River natural 1993 was not significantly different from the Wenatchee River natural 1993. The final exception was comparisons to Nason Creek baseline 1993 where there were no significant differences when compared to the following collections from the Methow basin: Chewuch River hatchery contemporary, Chewuch River natural contemporary, Methow Fish hatchery 2017, Methow River hatchery contemporary, and Winthrop NFH 2018. Regarding observed and expected heterozygosity, results were consistent between the Wenatchee and Methow basin collections: there were no differences between the two basins in average observed and average expected heterozygosity. Within the Wenatchee basin, there were no significant differences in expected heterozygosity between baseline and contemporary collections or between baseline collections and contemporary collections from different years. In the Methow basin, there was significantly higher expected heterozygosity in the Methow baseline collection than in the natural contemporary collection. There was also significantly higher expected heterozygosity in the Methow fish hatchery 2018 collection than in the natural contemporary collection. There was significantly higher expected heterozygosity in the Twisp natural contemporary collection than in the Twisp baseline collection from 1992.

Linkage Disequilibrium – Question 7.2.1 and 7.2.2 –The highest linkage (16%) was in the Chiwawa baseline collection from 1993. Checking this collection for family structure using COLONY indicated that most of the collection was family groups, one as large as 10 siblings, and that there were few unrelated individuals. Similarly, the Nason collections from 2000 and 2018 had higher linkage than expected by chance (> 5%) and included large families. After corrections for multiple tests, no collections had more locus pairs in linkage disequilibrium than expected by chance. The Mann-Whitney tests indicated significant differences in the number of locus pairs in linkage disequilibrium in most cases, with the exceptions being the comparisons between the two Chiwawa contemporary collections and the two Leavenworth Hatchery collections in the Wenatchee basin. In the Methow basin there were no significant differences in the number of pairs of loci in linkage disequilibrium in the two Twisp baseline collections, the two Winthrop NFH collections, and the two Methow Fish Hatchery collections.

Genetic Distance – Question 7.3.1 – The pairwise F_{ST} values showed patterns of genetic relationships within and among Spring Chinook Salmon collections from the Wenatchee and Methow basins (Figures 3a, 3b, 3c). Using a lower limit of 0.001, most comparisons among collections from the same river in the same time frame (eg. Twisp 1992 and 1993) were not significantly different from zero, with the exception of Nason contemporary 2017 and 2018, and Winthrop NFH 2017 and 2018. Among the Wenatchee collections all comparisons of collections from the same river in different time frames were significantly different from zero (Figure 3b). One noteworthy pattern was that the White and Little Wenatchee contemporary collections were barely different from each other (lower confidence limit = 0.002) and shared similar relationships to other collections. Among the Methow collections (Figure 3c), all comparisons of collections from the same river in different time frames were significantly different from zero, although some values were relatively small (less than 0.007). All comparisons to the Twisp collection were high and significantly different from zero but comparisons of the Methow hatchery and natural contemporary collections to the Chewuch hatchery and natural contemporary collections were not significantly different from zero, as expected because the gene pools were combined into the MetComp gene pool. The 2017 Winthrop NFH collection was not significantly different from two Methow Fish Hatchery collections and from the Methow River hatchery contemporary collection, and the 2018 Winthrop NFH collection was not significantly different from the 2018 Methow Fish Hatchery collection and from the Methow River natural contemporary collection. In comparisons between basins, the Nason baseline 1993 collection was most similar to the Methow, Chewuch, Winthrop NFH and Leavenworth hatchery collections.

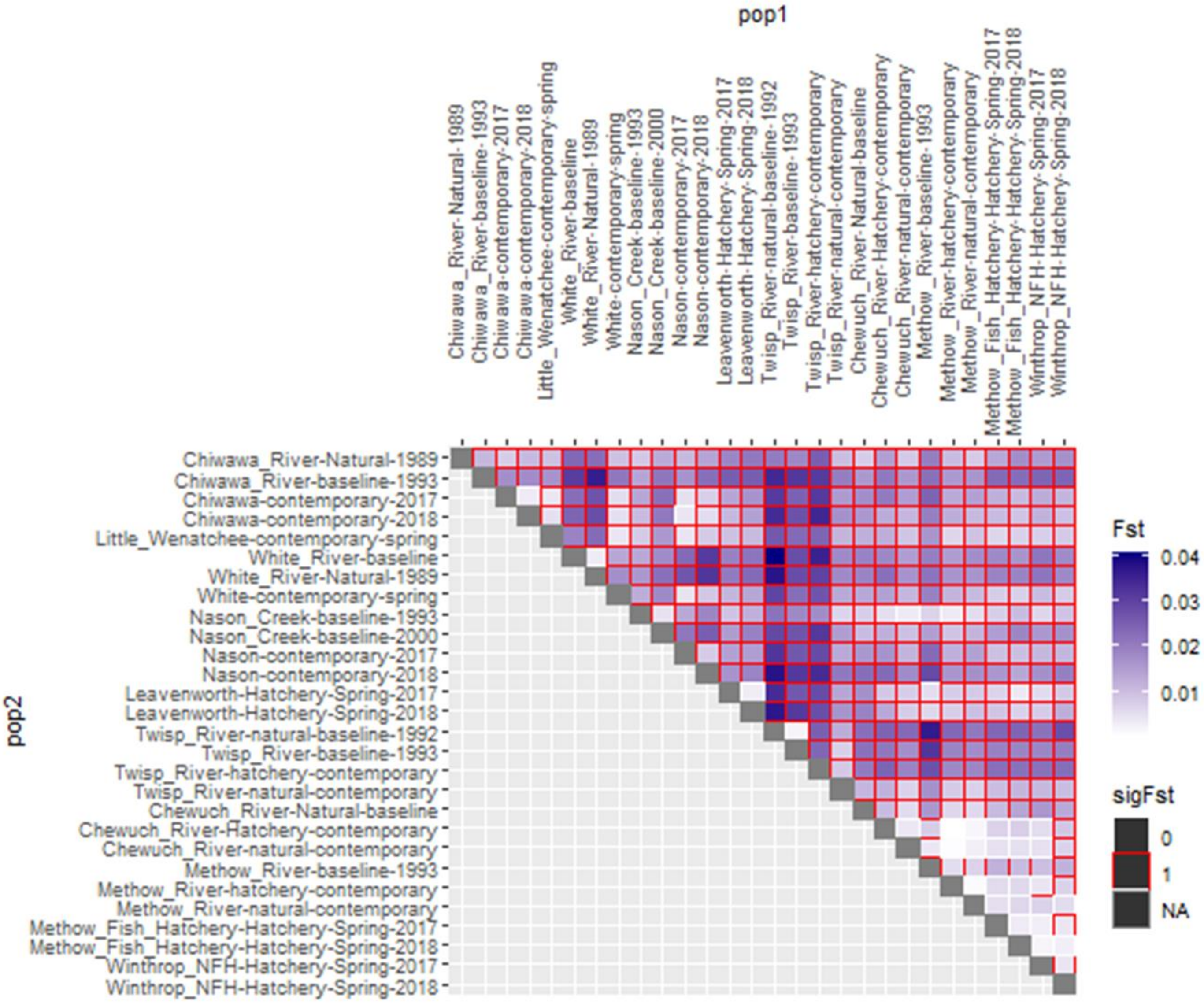

Figure 3a. Heatmap of pairwise F_{ST} values from all pairwise comparisons of collections of Upper Columbia River spring Chinook Salmon: darker color equates to larger differentiation. Values statistically greater than zero (0.001) are outlined in red – for these values the lower bound of the 95% confidence interval were greater than zero.

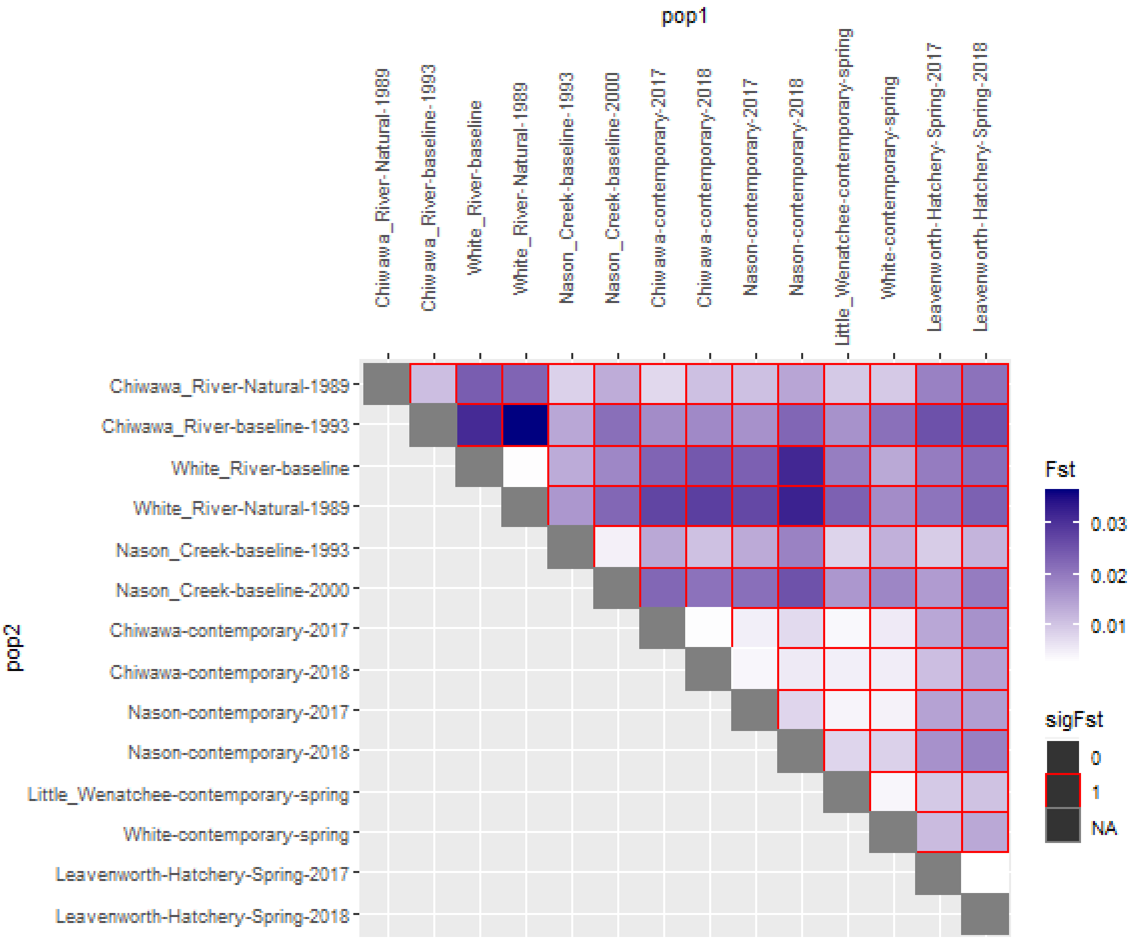

Figure 3b. Heatmap of pairwise F_{ST} values from all pairwise comparisons of collections of Wenatchee basin spring Chinook Salmon: darker color equates to larger differentiation. Values statistically greater than zero (0.001) are outlined in red – for these values the lower bound of the 95% confidence interval were greater than zero.

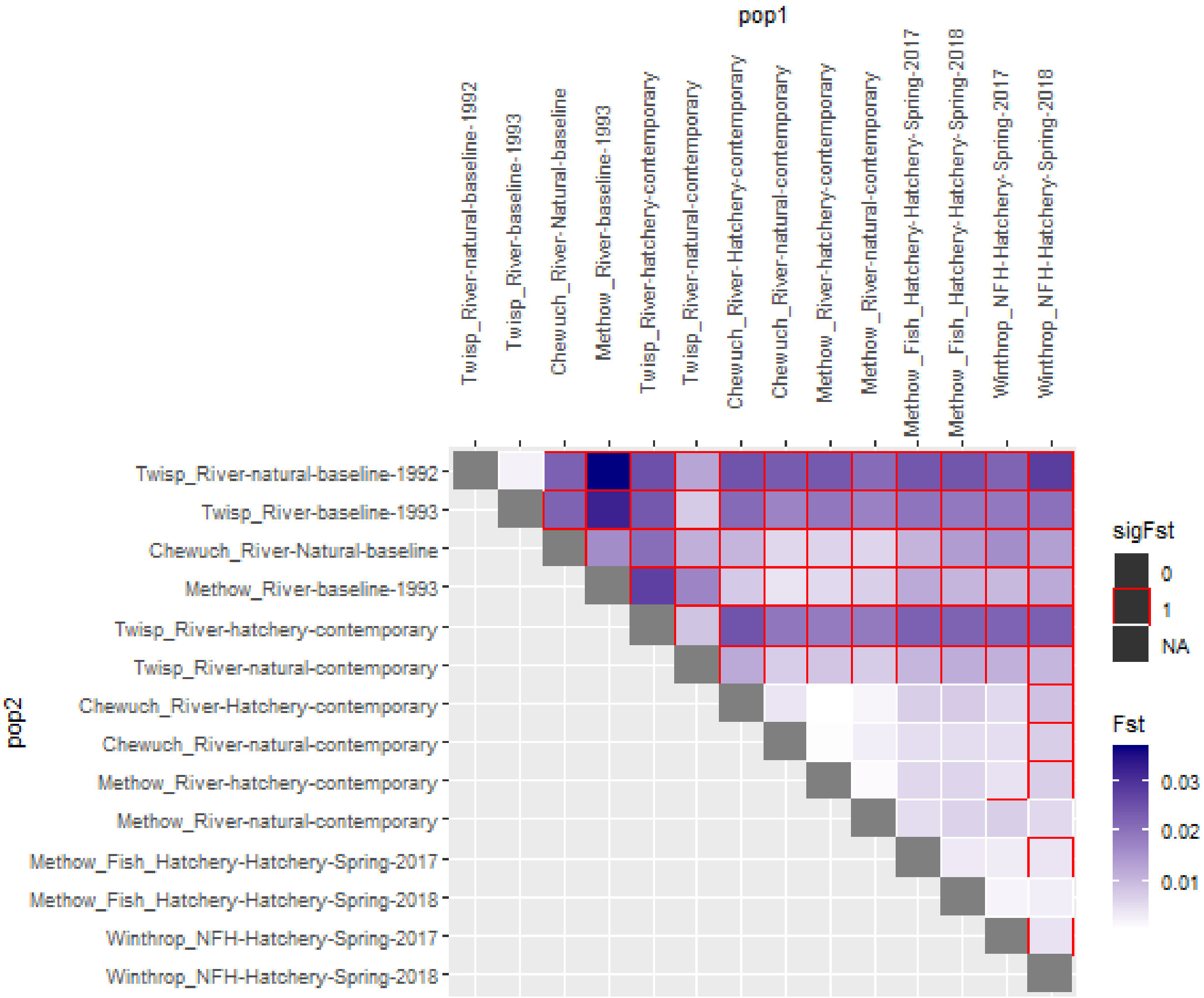

Figure 3c. Heatmap of pairwise F_{ST} values from all pairwise comparisons of collections of Methow basin spring Chinook Salmon: darker color equates to larger differentiation. Values statistically greater than zero are outlined in red – for these values the lower bound of the 95% confidence interval were greater than zero (0.001).

Effective Population Size (N_e) *– Question 7.4.1 –* The calculated effective population sizes (N_b) varied widely among collections (Figure 4). In several cases the upper confidence interval extended to infinity (Table 2). With the exception of three very small values, the upper confidence limit was infinity for N_b estimated greater than 200. In the Wenatchee basin, we were unable to obtain an estimate for the Chiwawa baseline 1989 collection. The N_b estimates for Chiwawa baseline 1993, Nason baseline 2000 and Nason contemporary 2018 were small in comparison to other calculations and their upper confidence limits fell below those of other estimates for collections from their tributaries. These collections included large family units which will bias the estimate low. For the remaining collections, although the point estimates differed, the confidence intervals overlapped suggesting that the values were not significantly different. In the Methow basin, the N_b estimates for the Twisp collections were smaller than for the Methow and Chewuch, but the confidence intervals mostly overlapped in all estimates. The upper limit for Twisp hatchery contemporary N_b estimate was the smallest among the collections and fell below the lower limits of the Methow Fish Hatchery and the Methow River natural contemporary N_b estimates.

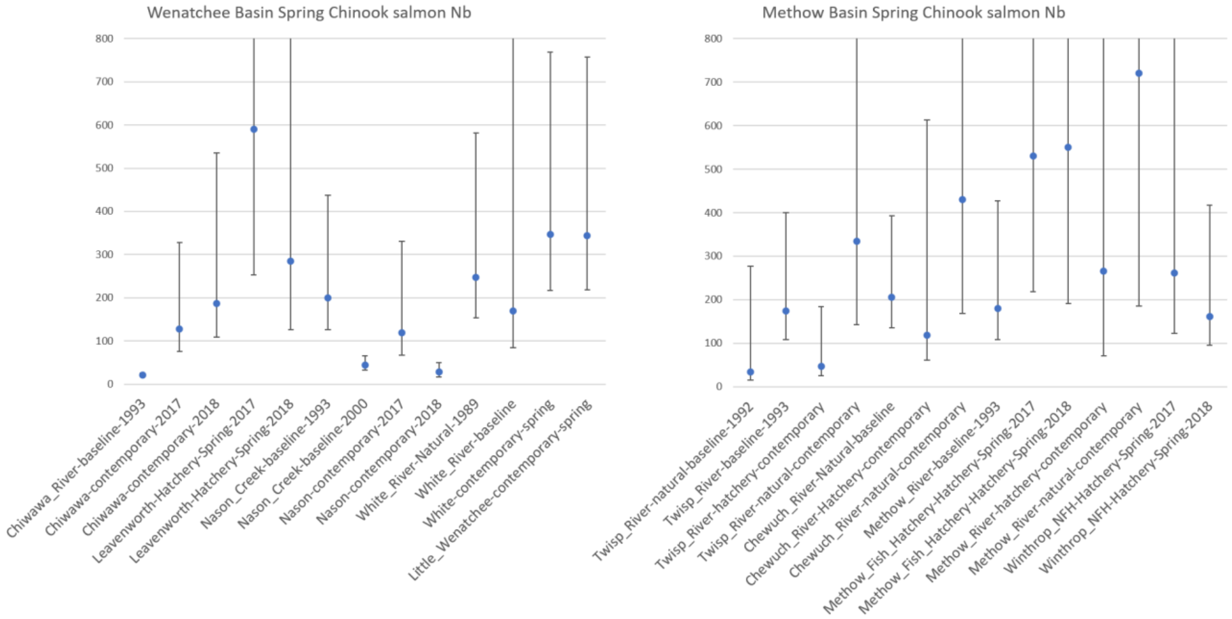

Figure 4. Estimated effective number of breeders (N_b) for Wenatchee (left) and Methow (right) spring Chinook Salmon. Bars represent 95% confidence intervals. Intervals that extend beyond the edge of the graph had no upper bound (infinity) indicating that there was insufficient linkage disequilibrium to estimate the upper bound, i.e., a large N_b estimate.

We used the average return age of four years to determine the spawner escapements (N) to use in the N_b/N calculations (Table 2). Data were unavailable before 1990. In cases where the collection was a combination of multiple years of samples, we combined the spawner escapements for those broodyears (four years prior to each of the years represented in the collection). For the Leavenworth Hatchery collections, we used the spawner escapements to the Icicle River. However, the estimated N_b for the 2017 Leavenworth Hatchery collection was higher than the spawner escapement for 2013. In the Wenatchee basin, the average N_b/N was 0.46 (excluding 2017 Leavenworth Hatchery) and ranged from 0.03 in the Chiwawa baseline 1993 collection to 1.01 in the White contemporary collection. In the Methow basin, the average N_b/N was 0.36 and ranged from 0.07 in the Twisp baseline 1992 collection to 0.64 in the Twisp natural contemporary collection.

Discussion

The monitoring plan and the current implementation of the monitoring plan have limitations, but we are unaware 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 the improvement in genetic techniques. The upper Columbia hatchery evaluations have utilized allozyme, microsatellites, and SNPs. Comparing previous findings to current ones is problematic because of differences in genetic techniques. 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 will be used in future 10 year monitoring intervals. The goal of this study was to investigate the impact of hatchery programs on naturally spawning Spring Chinook in the Wenatchee and Methow river basins. The monitoring and evaluation plan posed 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); 3) does genetic distance among subpopulation 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)?

Regarding question 1, the pairwise AMOVA tests indicated that allele frequencies varied between baseline and contemporary samples from tributaries groups in both the Wenatchee and the Methow rivers. This was corroborated by the pairwise F_{ST} analysis. These allele frequency changes suggest that genetic drift has impacted the populations, as expected for populations that declined to low abundance and required hatchery intervention. While genetic drift is a natural process, the concern is that the hatchery programs contributed to allele frequency changes through small numbers in hatchery broodstocks or over-representation of few hatchery families (Ryman-Laikre effect, Ryman and Laikre 1991). Hatchery straying is another source of allele frequency change and will be discussed below under question 3. With the exception of the Methow-Chewuch hatchery program which combined broodstock from two populations, the hatchery programs were designed to support struggling populations while retaining the genetic identity of the targeted population and met with mixed success in these efforts, mainly due to limitations in available spawners. The linkage disequilibrium calculated for question 2 provided some insight into limitations – collections with high linkage had incorporated large family groups. A high linkage signal indicated that alleles at different loci are inherited together, rather than randomly, as is the case for siblings which inherit the allele combinations of their parents. Developing broodstocks from spawners composed of families contributes to genetic drift despite meeting broodstock numerical goals – if spawners are related then they represent only their parent genetic diversity rather than a random sample of the population genetic diversity. Three baseline collections (Chiwawa, Chewuch and Methow) had higher linkage than contemporary collections and in the Nason linkage remained high in the 2018 contemporary collection. The Nason population experienced a severe bottleneck in the late 1990's and a captive brood program was temporarily employed, both of which possibly contributed to continued LD because allele combinations may take a few generations to break up. Where linkage decreased between baseline and contemporary collections, this could be a result of more random sampling in the contemporary collections where spawner numbers had increased in comparison to numbers available for the baseline collections.

Changes in genetic distance within the Wenatchee were assessed with the pairwise F_{ST} values. These distances were affected by changes in N_b and likely reflected straying as well as genetic drift. Although most values were significantly different from zero, the heat map provides a way to focus on differences and changes. Within the Wenatchee basin, between the Chiwawa baseline and 2017 and 2018 contemporary, there was roughly 2% and 1% genetic difference, respectively (numerical values illustrated by heat map in Figure 4 and available upon request). The higher difference with the 2017 collection was likely due to drift because the 2017 collection was relatively small and had a smaller calculated N_b. In the Nason, the baselines versus contemporary collections averaged roughly 2% genetic difference. The Nason 2018 collection was more differentiated from the baselines, but that collection included a large family of 10 siblings which inflated the differences in comparisons and decreased its estimated N_b. The Chiwawa and Nason contemporary collections were nearly indistinguishable, and their lower limits were barely above zero (average 0.002). In contrast, baseline collections from Chiwawa and Nason were significantly more differentiated than contemporary samples (average 0.0144_{baseline} and $0.0055_{\text{contemporary}}$, respectively, Student's T test $p = 0.01$). Pearsons and Miller (2021) reported substantial straying from the Chiwawa hatchery program into Nason Creek which likely spawned in Nason Creek and thus decreased genetic distance between spawning aggregates in the Chiwawa River and Nason Creek. Further, the Leavenworth Hatchery collections were significantly more similar to contemporary collections from the three tributaries than to their baseline collections (average $0.0139_{\text{contemporary}}$ and 0.0198_{baseline}, Student's T test $p = 0.0008$). This suggested that upper Wenatchee fish may have been incidentally collected for Leavenworth Hatchery broodstock or that Leavenworth hatchery-origin fish, which were descendants of out-of-basin Carson stock, may have interbred with upper Wenatchee populations. However, Leavenworth hatchery-origin fish were rarely collected from upper Wenatchee spawning populations (Pearsons and Miller chapter in this report). Their relatively large N_b indicates that the collections represented more genetic diversity, which also would have decreased genetic drift in the hatchery broodstock.

Strays from the Chiwawa hatchery program have also been documented in the White and Little Wenatchee Rivers (Pearsons and Miller chapter in this report). The baseline collections from the White River were significantly different from the White and Little Wenatchee rivers contemporary collections (average 0.0199). However, the baseline collections from the White and Chiwawa rivers (no baseline available for Little Wenatchee) were highly differentiated from each other (average 0.0266_{baseline}), while contemporary collections from the White and Chiwawa rivers were significantly less differentiated (average $0.0048_{\text{contemporary}}$, Student's T-test $p < 0.0001$). This suggested that over time strays from the Chiwawa hatchery program have spawned successfully in the White River, decreasing the earlier genetic distinction between the baseline gene pools. In Blankenship et al (2007), which compared Chiwawa and White rivers collections up to 2007, the populations remained distinguishable, indicating that straying from the Chiwawa gene pool into the White gene pool between 2007 and 2017 was sufficient to shift the White gene pool towards the Chiwawa gene pool. Because genetic parameters and relationships to other contemporary collections were parallel in the contemporary White and Little Wenatchee collections and the rivers both flow into the western end of Lake Wenatchee, we suspect that the Chiwawa hatchery has affected Chinook Salmon spawner aggregates similarly in the two rivers.

Within the Methow basin the pairwise F_{ST} values supported earlier observations (Small et al. 2007) that among the baseline collections the Twisp was different from the Chewuch and Methow and that the Chewuch and Methow were more similar to each other. However, the Twisp contemporary hatchery collection was significantly different from the Twisp baselines and modestly different from the Twisp contemporary natural-origin samples. The Twisp hatchery collection was the smallest in the study and the calculated N_b was also relatively small. The low but significant pairwise F_{ST} value between the contemporary Twisp hatchery and natural collections suggested that the hatchery captured a subset of the genetic diversity among the natural spawners such that the hatchery broodstock had drifted from the baseline collections. The pairwise F_{ST} values were the same in the comparison between the Twisp contemporary natural spawners and the Twisp baseline from 1993 (0.0071), and between the Twisp contemporary natural spawners and the Chewuch contemporary natural spawners (0.0070). Further, the value is only slightly larger in the comparison of the Twisp contemporary natural spawners to the Methow contemporary and natural spawners (average 0.0075). This similar level of differentiation between these contemporary collections could be the effect of straying. Recipient population stray rates were 20% in the Methow, 21% in the Chewuch, and 10% in the Twisp between 2009 and 2018 (Pearsons and Miller chapter in this report). Among the Chewuch, Methow and Winthrop NFH contemporary collections, the pairwise F_{ST} values were low and mostly insignificant. However, Chewuch and Methow baseline collections were significantly different from each other before the Met-Comp hatchery program commenced. Fisheries managers decided to treat the Methow and Chewuch as a single population since 2001 and the findings we present are consistent with that management strategy.

Genetic distances have changed over time in the Wenatchee and Methow basins and it appears that hatchery programs have facilitated the changes through intentional management decisions and through unintentional straying. However, without data predating the changes imposed by the dams and by mitigation attempts (e.g., prior to 1850), we do not know the original population structure, abundance and diversity and how current practices have altered these parameters.

One of the goals of this study was to assess changes over time in the ratio of N_b to census size (N). However, the N_b is a parameter that can be difficult to evaluate. If samples are true random representations from the population of interest, then the N_b is a reflection of the genetic diversity in the population and illustrates how genetic drift is acting on the population. However, in this study several collections had issues with small collection size and non-random sampling of family members, which makes it difficult to interpret the estimates. Census data were unavailable for some years and for other collections we combined census data for multiple years because the tissue samples were combined from multiple years. Further, we had no age data for most collections and assumed an average four-year age, although Chinook Salmon return as early as two years and as late as seven years. Keeping in mind these uncertainties, there appeared to be little pattern of N_b/N associated with time or with hatchery production in the Wenatchee basin. Although the confidence intervals overlap, the White River baseline N_b was smaller than its contemporary N_b and the contemporary N_b equaled the census size (no census size for the baseline collection). The White River contemporary N_b and census size were nearly identical to the Little Wenatchee contemporary collection, highlighting their similarity which was possibly mediated by straying from the Chiwawa Hatchery, as described above. The hatchery strays could have contributed to a higher than expected N_b/N ratio calculated in those two rivers – if hatchery strays introduced genetic diversity that elevated their estimated N_b despite moderate census sizes.

Family groups in the Nason contemporary collection in 2018 contributed to low N_b and high LD. Because there was a large 10 sibling family and four other families of three or four siblings, the genetic diversity represented essentially 35 unrelated individuals or families, rather than 55 unrelated individuals. Without biological data we are unable to identify the origins of the families, hatchery or natural, and are unable to comment on the role the hatchery program may have played in this population. We also had to assume a three year age and the 2015 brood year would have encountered drought conditions during their outmigration and poor oceanic conditions ("the blob") which negatively impacted all salmonids. However, because the Nason contemporary collection from 2017 was composed of unrelated individuals the N_b more likely better reflects the genetic diversity in the population. The Nason baseline 2000 was sampled during the bottleneck that had occurred in that population. There was an increase in genetic diversity in the 2017 contemporary collection, but the 2018 contemporary collection was similar to the 2000 baseline. As described above, this is an anomaly of the sampling rather than a biological effect. It was noteworthy that the 2017 Leavenworth Hatchery collection had an unexpectedly high N_b/N ratio indicating that the hatchery collection represented higher contributions to genetic diversity than there were spawners collected for broodstock three years prior.

Among the Methow collections, although the average N_b was higher than in the Wenatchee, the N_b/N over all collections was lower than in the Wenatchee (excluding Leavenworth Hatchery value). The census N averaged over all Methow collections was more than twice the average N for the Wenatchee, which brought down the ratio. The N_b/N was the lowest and highest in the Twisp baseline 1992 and the Twisp natural contemporary, respectively. Genetic diversity has increased in the Twisp natural spawners in the 25 years since the baselines were collected. However, the N_b/N for the Twisp hatchery contemporary is similar to the Twisp natural contemporary, but only by virtue of a low N_b for the Twisp hatchery contemporary in relation to a low N for the broodstock, rather than representing a pool of genetic diversity in the hatchery that might infuse the population (Christie et al. 2012). The relatively high N_b/N in the Twisp natural contemporary indicates that the genetic diversity in the natural spawners exceeds the genetic diversity in the hatchery spawners. However, as mentioned above, the low pairwise F_{ST} values in comparisons to the Twisp natural contemporary suggested that Chewuch and Methow strays may have contributed some genetic diversity in the Twisp natural spawners. If we averaged the N_b over all baseline, natural contemporary and hatchery collections from the three tributaries, the average N_b in the baselines (148) was less than half the average N_b of the contemporary collections (438) and the hatcheries were intermediate (300). The average N and N_b/N show a similar pattern. This indicates that genetic diversity and the number of spawners have increased in the basin since the bottlenecks experienced by baseline collections and that the hatcheries represent subsets of the genetic diversity in the river spawners.

Summary – Some patterns emerged that could illustrate effects of hatcheries on natural spawners in the Wenatchee and Methow basins. Within the Wenatchee basin the Chiwawa, Nason, White and Little Wenatchee natural spawners appear to be converging genetically, likely a result of management decisions that informed hatchery practices. Within the Methow basin the Twisp hatchery spawner collection had diverged from the Twisp baseline collections. Further, within the basin the natural spawners appear to be converging genetically, which is the expected result of combining the Chewuch and Methow broodstock in the hatchery, but also appears to extend to the Twisp natural spawners. It is likely that management decisions to create a composite Chewuch-Methow broodstock, straying within the Wenatchee and Methow, and genetic drift from low effective breeders were primary factors contributing to the patterns we observed.

With data from only two time points, baseline and contemporary, our conclusions are limited. However, in comparison to earlier work (Blankenship et al. 2007, Small et al. 2007) we comment on some of the patterns that had emerged in these systems by 2007. In the Wenatchee basin, Blankenship et al. (2007) found that the Chiwawa River natural spawners had not diverged from their baseline collections and the Chiwawa hatchery program had not affected the populations in the White River or Nason Creek. By 2017, this current study found that the Chiwawa, White and Nason populations had diverged from their respective baseline collections and were nearly indistinguishable from each other. We hypothesized that this convergence was due to common gene flow from the Chiwawa hatchery program strays documented by Pearsons and Miller (2021). In contrast, early patterns observed in the Methow basin (Small et al. 2007) continued upon their trajectories. Small et al. (2007) found that the Chewuch and Methow natural spawners collected in 2005 and 2006 had already diverged from their respective baseline collections and were then more similar to each other than to their baseline collections because of the combined hatchery broodstock. Ten years later the natural spawners collected in these rivers were indistinguishable from each other. Within the Twisp River, in 2005 the natural spawners remained similar to their baselines. The Twisp Hatchery collections were distinct from the baselines and natural spawners but were more similar to Twisp fish than to Chewuch or Methow fish. After ten years, the Twisp Hatchery broodstock had diverged further from the Twisp baseline but remained similar to the Twisp in-river spawners while the Twisp in-river spawners had diverged from the baseline and the relationship between in-river spawners in the Twisp, Chewuch and Methow suggested that fish had strayed among the rivers.

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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)

Locus Name	Purpose	Allele 1	Allele 2	Reference
Ots_101119-381	Neutral	T	C	(Janowitz-Koch et al. 2019)
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)

Locus Name	Purpose	Allele 1	Allele 2	Reference
Ots_112820-284	Neutral	C	T	(Janowitz-Koch et al. 2019)
Ots_112876-371	Neutral	C	A	(Janowitz-Koch et al. 2019)
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)

Locus Name	Purpose	Allele 1	Allele 2	Reference
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)
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)

Locus Name	Purpose	Allele 1	Allele 2	Reference
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)
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)

Locus Name	Purpose	Allele 1	Allele 2	Reference
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)
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)

Locus Name	Purpose	Allele 1	Allele 2	Reference
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)
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)

Locus Name	Purpose	Allele 1	Allele 2	Reference
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)
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)

Locus Name	Purpose	Allele 1	Allele 2	Reference
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)
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)

Locus Name	Purpose	Allele 1	Allele 2	Reference
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
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.

Campbell, N.R., Harmon, S.A., and Narum, S.R. 2015. Genotyping-in-Thousands by sequencing (GT-seq): A cost effective SNP genotyping method based on custom amplicon sequencing. Mol. Ecol. Res. 15(4): 855-867. doi:10.1111/1755-0998.12357.

The Effects of Hatchery Supplementation on Size and Age At Maturity and Fecundity of Spring and Summer Chinook Salmon in the Upper Columbia Basin

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Abstract

A common objective of conservation hatchery programs is to produce fish with phenotypic traits similar to individuals from the natural population. We evaluated the size and age at maturity, and fecundity of five spring Chinook Salmon and three summer Chinook Salmon hatchery programs. Comparisons to natural-origin fish from the targeted populations over multiple generations and during two periods of hatchery production releases (high and low number of smolts) were made for applicable programs. Generally, the hatchery-populations were composed of more, younger fish and fewer older fish, but the predominate age at maturity was similar between hatchery- and natural-origin populations. The size at maturity of returning adults was significantly affected by age and sex, and in some cases origin and period. However, when matched by age and sex, the differences in size at maturity by origin and period that were statistically significant were minor and likely of little biological relevance. For all populations, the fecundity metrics were significantly affected by fish size and weight, but fecundity differed between origins in only two populations. For all metrics, the high/low program release numbers did not substantially affect these phenotypic traits. Future analyses of these metrics should consider changes over time and consider trends between hatchery-origin and natural-origin fish. Declines in age and size at maturity are a range-wide concern for Pacific salmonids and therefore a temporal analysis of the dataset generated for the monitoring of these hatchery programs would benefit the region.

Introduction

Conservation hatchery programs should produce fish that maintain and match the phenotypic characteristics of the targeted natural population. The objective of maintaining phenotypic characteristics is to limit introgression and domestication effects while the objective of matching is intended to produce fish with any fitness benefits conferred with the phenotypic characteristics of natural-origin fish. In the Upper Columbia River Basin, conservation hatchery programs have collected data on phenotypic variables including size at maturity, age at maturity, and fecundity of natural-origin and hatchery-origin Chinook Salmon for nearly 30 years. These data provide the opportunity to evaluate how these hatchery programs have performed in matching these phenotypic traits to their targeted population over multiple generations. The question of maintaining, or not affecting, natural-origin phenotypic traits is more complex due to the non-static nature of phenotypic variables and multiple factors that can affect the size and age at maturity, and fecundity of natural-origin fish. For example, throughout the range of Pacific Salmon and in all five species there has been a well-documented decline in size and age at maturity (Ricker 1981, Jeffrey et al. 2017, Losee et al. 2019). Hatchery-origin fish introgression, as well as competition among hatchery- and natural-origin fish, are two of several theories for the observed changes. Other theories with supporting data include size-selective harvest, environmental changes such as ocean temperature and productivity, inter-species competition, and marine mammal predation (for a review of each theory see Ohlberger et al. 2018).

In this chapter, we test whether the age and size at maturity, and fecundity of returning hatchery-origin spring and summer Chinook Salmon from the Upper Columbia River Basin matches those phenotypic characteristics in their targeted natural-origin populations, and answer three programmatic monitoring questions: (1) Is the age at maturity of hatchery- and natural-origin fish similar at the time of spawning? (2) Is the size at maturity of a given age and sex of hatchery-origin fish similar to the size at maturity of the same age and sex of natural-origin fish? and, (3) Is the size versus fecundity relationship of hatchery- and natural-origin fish similar?

Methods

Data Collection and Derived Metrics

Spring and summer Chinook Salmon spawning ground surveys were used to collect data to estimate origin, age and size at maturity, and sex of carcasses within the Wenatchee and Methow subbasins. Spawning ground surveys were also used to collect data on summer Chinook Salmon in the lower Chelan River. Field methods were consistent with those described in Gallagher et al. (2007) and Murdoch et al. (2010). Surveyors walked or floated the entire distribution of spring and summer Chinook Salmon spawning habitat and sampled carcasses weekly throughout the spawning season. Chinook Salmon carcasses were counted and examined to determine sex, origin (e.g., hatchery- or natural-origin), size at maturity, distribution, and other biological characteristics. In addition, scales collected from carcasses were used to determine fish age at maturity and verify origin. The sampling goal for carcasses was at least 20% of the spawning population.

Age at maturity was estimated from scales collected from each carcass sampled. At least four scales were removed from the left side of the fish about two rows above the lateral line and on the diagonal row from the posterior insertion of the dorsal fin to the anterior insertion of the anal fin. Following methods in Quist et al. (2012), cellulose acetate impressions of each scale were made and read to determine the total age (i.e., egg-to-spawning adult) and ocean (salt) age of each fish. For spring Chinook Salmon, we evaluated differences between hatchery- and natural-origin fish using total age. For summer Chinook Salmon, we used ocean age to evaluate differences between hatchery- and natural-origin fish, because hatchery-origin summer Chinook Salmon were generally released after one year of rearing, while natural-origin summer Chinook Salmon migrate primarily as age-0 fish. In this report, we only analyzed hatchery-origin summer Chinook Salmon that were released as age-1 fish, because those releases had a natural-origin component for comparison. There were no natural-origin comparisons for the age-0 summer Chinook releases (e.g., Wells Hatchery and Turtle Rock Acclimation Facility age-0 releases).

Size at maturity was estimated by measuring the post-orbital to hypural length (POH; cm) of all carcasses sampled. Because of erosion of the caudal fin and secondary morphological changes to the head of Chinook Salmon, POH provides a more robust measure of fish size than does fork length or total length. Sex was determined by examination of gonads. For each carcass sampled, origin was determined by examining tags (e.g., CWT and PIT tags), marks (missing adipose fin), and scale analysis. Nearly all hatchery-origin fish were marked with a tag such as a CWT and/or adipose fin clipped prior to release.

Fecundity at size data for both spring and summer Chinook Salmon were collected from broodstock. To enumerate fecundity, an optical counter enumerated eyed eggs and the number of eyed eggs was added to the number of dead eggs enumerated during incubation. To determine gonadal mass, a representative sample of 50 female Chinook Salmon from across the spawning period were sampled for numbers and weight of green eggs. For each female selected, the entire gamete mass was extracted, ovarian fluid drained, and weighed to the nearest 0.1 g. A subsample of 100 green eggs were counted and weighed to within 0.01 g to estimate individual egg weight for each female. Total fecundity of each female was estimated by dividing the weight of the total egg mass by the calculated mean individual egg weight. Because each sample of the total egg mass likely contained small amounts of ovarian fluid, fecundity estimates may be overestimated slightly. Females were also measured for length (POH), weighed (post-spawning; kg), and aged following methods described earlier. Origin was determined by examining tags, marks, and scale analysis. Females were stratified by fork-length categories to obtain a representative fecundity sample for all sizes of fish. This was needed to better estimate the relationship between size and fecundity. Complete fecundity data only exist for brood years 2014 to present.

Data Analysis

We conducted separate analyses for each program. For spring Chinook Salmon, we evaluated differences between hatchery- and natural-origin age and size at maturity, and fecundity for the Chiwawa River, Nason Creek, White River, Methow/Chewuch River, and Twisp River programs. For summer Chinook Salmon, we conducted separate analyses for the Wenatchee River, Methow River, and Chelan River programs. We only analyzed fecundity data for Wells summer Chinook Salmon because there were no age at maturity or size at maturity data for natural-origin summer Chinook Salmon to compare with Wells summer Chinook Salmon. For Nason Creek spring Chinook Salmon we evaluated two different program effects. First, we examined the differences in age and size of maturity of hatchery-origin strays and natural-origin spring Chinook Salmon in Nason Creek. In this case, the “before” period (1993-2000) represented the time period when the proportion of hatchery-origin spawners (pHOS) in Nason Creek was low (mean <0.10) and the "after" period (2001-2018) represented the time period when pHOS was high (mean >0.50). Second, we evaluated the effects of the Nason Creek Spring Chinook Hatchery Program on age and size at maturity of spring Chinook Salmon in Nason Creek. In this case, the "before" period (1993-2015) represents the time period before the implementation of the Nason Creek spring Chinook Salmon program and the "after" period (2016-2018) represents the time period following the initiation of the hatchery program. For White River spring Chinook Salmon, the "before" period (1993-2007) represents the time before the influence of the spring Chinook Salmon captive brood program, while the "after" period (2008-2018) represents the time during the influence of the program.

We evaluated differences between hatchery- and natural-origin spring and summer Chinook Salmon for age and size at maturity as a complete time series (1993-2018) and an interrupted time series for four of the programs. The interrupted time series included the period "before" the reduction in hatchery production (1993-2014) and the period "after" the reduction in hatchery production (2015-2018) for most hatchery programs. For summer Chinook Salmon in the Chelan River, we used data collected from 2000 to 2018, because that is the period when intensive spawning ground surveys were conducted and there were no subyearling releases. There was no change in hatchery production of Wells summer Chinook Salmon; therefore, there was no interrupted time series to evaluate for Wells summer Chinook Salmon. The specific years for the Nason Creek and White River spring Chinook Salmon programs did not follow the same before and after dates as other programs (see below). Two-way Yates' Chi-square determined whether age at maturity of hatchery- and natural-origin Chinook Salmon differed significantly. Because of different age-at-migration characteristics, we evaluated male and female Chinook Salmon separately. For size at maturity, we evaluated the length (POH) of hatchery- and natural-origin Chinook Salmon of the same age (total age for spring Chinook Salmon and ocean age for summer Chinook Salmon). Three-way, unbalanced, general linear models, analysis of variance (GLM ANOVA) tested differences in sizes of hatchery- and natural-origin fish. This analysis included sex, origin, and age as fixed factors in the model. Where there were enough data, a four-way, unbalanced, GLM ANOVA tested differences in sizes of hatchery- and natural-origin fish before and after changes in programs. For all analyses, we interpreted a significant difference ($P \leq 0.05$) as an indication of differences between hatchery- and natural-origin fish.

For both hatchery- and natural-origin spring and summer Chinook Salmon, we used simple linear regression to describe fecundity as a function of female size (both fork length and weight), and mean egg weight and total egg weight as a function of female size. Analysis of covariance (ANCOVA) examined fecundity relationships between hatchery- and natural-origin Chinook Salmon. In this case, ANCOVA tested whether the slopes of the regression lines were the same for hatchery- and natural-origin fish. Here, we focused only on the F-test and its P-value for the origin-by-size interaction term in the analysis of variance table. Because we have fecundity data only for 2014-2018, we cannot evaluate changes in relationships before and after reduction in fish production numbers for each supplementation program. Thus, all available years were pooled together in the analysis.

Results

Spring Chinook Salmon

Chiwawa River Program

Age-at-Maturity Analysis—For the complete time series (1993-2018), age at maturity differed significantly between hatchery- and natural-origin female (Yates' Chi-square = 204.070, P = 0.000) and male spring Chinook Salmon (Yates' Chi-square = 138.640, P = 0.000) in the Chiwawa River (Figure 1). Most females and males returned at age-4; however, a larger proportion of hatchery-origin fish returned at younger ages than did natural-origin fish. For example, 94% of hatchery-origin females and 78% of the natural-origin females returned at age-4. About 22% of natural-origin females and 5% of hatchery-origin females returned at age-5. A similar pattern was observed with males: about 27% of the hatchery-origin males and 9% of natural-origin males returned at age-3. In contrast, about 21% of natural-origin males and 7% of hatchery-origin males returned at age-5.

There was little change in age at maturity before (1993-2014) and after (2014-2018) reduction in hatchery production numbers, although a larger fraction of hatchery-origin males returned as age-4 fish following the reduction in program production than before the reduction (Figure 1). During both the before and after periods, the age at maturity differed significantly between hatchery- and natural-origin female (Before: Yates' Chi-square = 167.543, P = 0.000; After: Yates' Chi-square = 34.387, P = 0.000) and male spring Chinook Salmon (Before: Yates' Chi-square = 119.657, P = 0.000; After: Yates' Chi-square = 15.282; P = 0.000) in the Chiwawa River.

Size-at-Maturity Analysis—For the complete time series (1993-2018), size at maturity differed significantly between hatchery- and natural-origin spring Chinook Salmon in the Chiwawa River (GLM ANOVA F = 6.666, P = 0.010) (Figure 2). Size at maturity was significantly affected by age, origin, and sex (GLM ANOVA F = 5.025, P = 0.007). For females, age-3 hatchery-origin fish were larger on average than age-3 natural-origin fish (mean difference = 9 cm). However, age-5 natural-origin fish were on average larger than age-5 hatchery-origin fish (mean difference = 2 cm). Likewise, for age-5 males, natural-origin fish were slightly larger than hatchery-origin fish (mean difference = 1 cm). In contrast, age-3 and age-4 hatchery-origin males were slightly larger on average than natural-origin males of the same age.

There were differences in size at maturity before and after reduction in hatchery production numbers, although sample sizes for some age groups were small (Figure 2). The significant four-way interaction term (GLM ANOVA F = 3.928, P = 0.048), which only included age-4 and 5 fish because of sample sizes, indicated that differences in sizes between hatchery- and natural-origin spring Chinook Salmon were affected by age, sex, and period. This was most apparent for males. During the before period, age-4 hatchery-origin males were slightly larger than age-4 natural-origin males, while age-5 hatchery-origin males were slightly smaller than age-5 natural-origin males. This reversed during the after period. Differences in average sizes were small (≤ 2 cm), however.

Fecundity Analysis—There were significant linear relationships between female size and fecundity, mean egg weight, and gonadal mass for both hatchery-origin and natural-origin spring Chinook Salmon in the Chiwawa River for the combined years 2014-2018 (Figure 3). Fecundity relationships between hatchery-origin and natural-origin spring Chinook Salmon differed significantly for fork length and fecundity (ANCOVA F = 4.644, P = 0.032) and fork length and mean egg weight (ANCOVA F = 4.307, P = 0.039). There were no differences in relationships between hatchery- and natural-origin females for weight and fecundity (ANCOVA F = 3.359, P = 0.068) and fork length and gonadal mass (ANCOVA F = 0.513, P = 0.474).

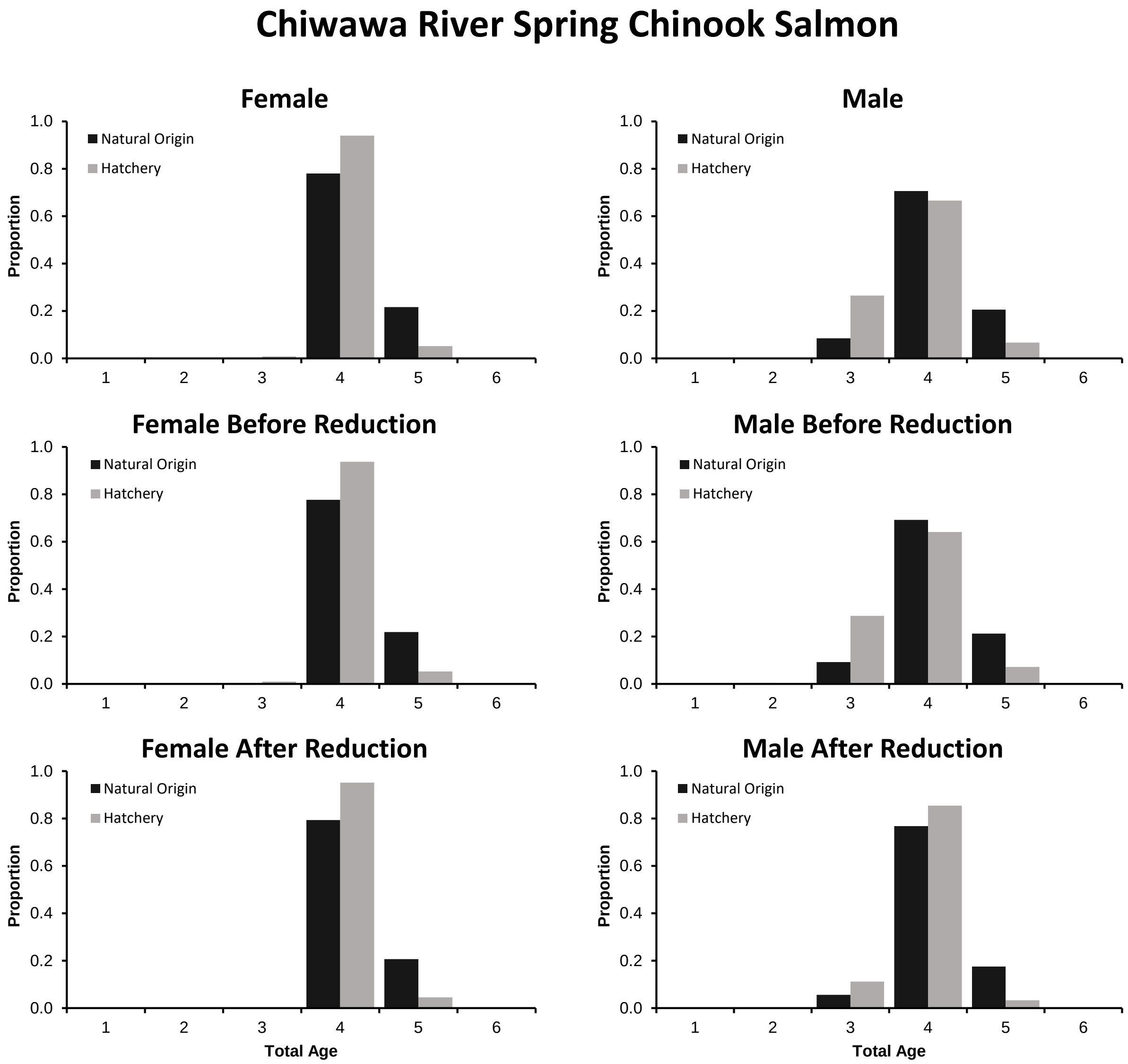


Figure 1. Proportion of hatchery- and natural-origin female and male spring Chinook Salmon spawners of different ages sampled on the spawning grounds in the Chiwawa River basin for the combined years 1993-2018 (top row), before reduction (1993-2014; middle row), and after reduction (2015-2018; bottom row) in hatchery smolt production. Sample sizes for females = 956 natural-origin and 2,322 hatchery-origin fish and for males = 647 natural-origin and 1,243 hatchery-origin fish for the combined analysis. For the before analysis, sample sizes for females = 748 natural-origin and 1,969 hatchery-origin fish and for males = 522 natural-origin and 1,091 hatchery-origin fish; and for the after analysis, sample sizes for females = 208 natural-origin and 353 hatchery-origin fish and for males = 125 natural-origin and 151 hatchery-origin fish.

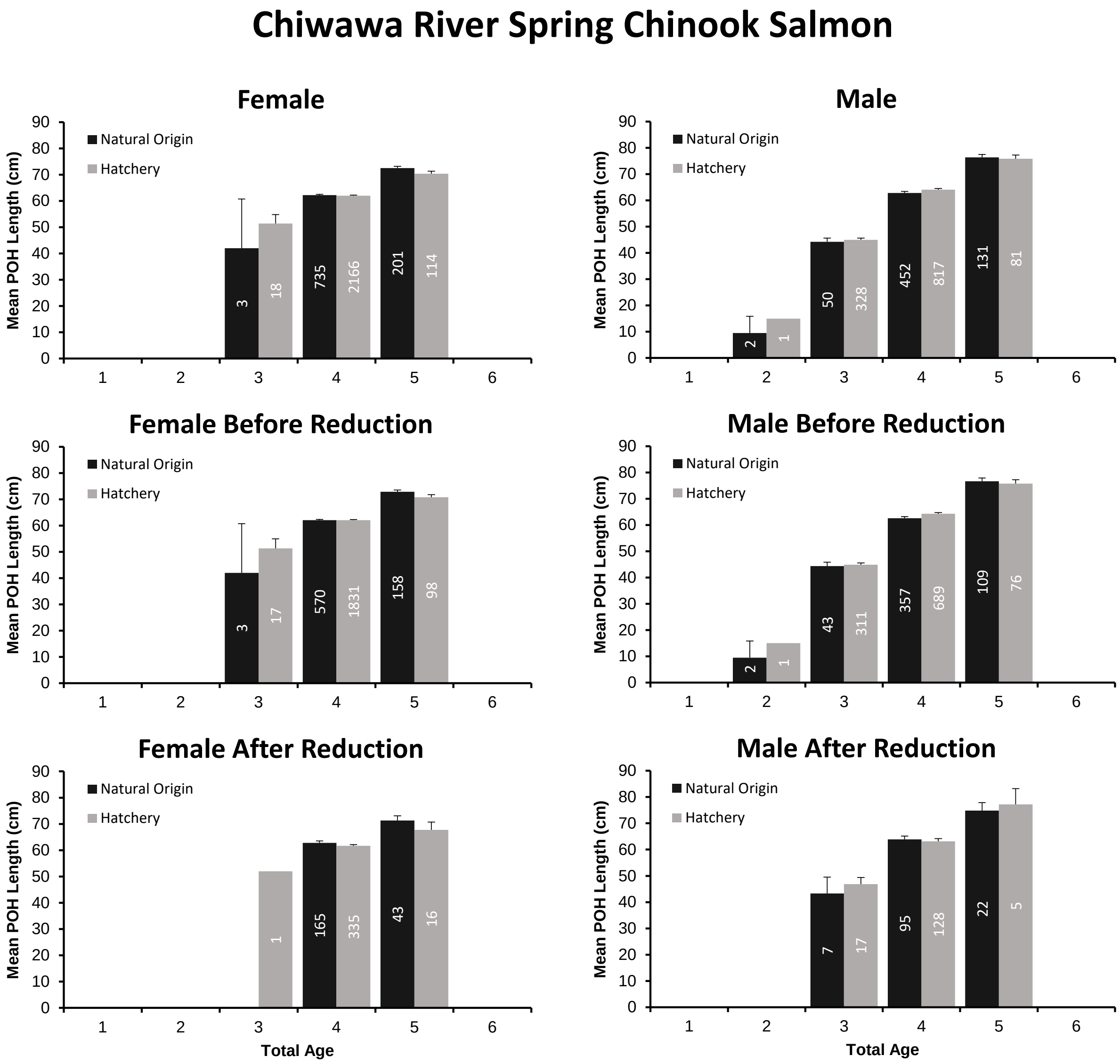


Figure 2. Mean POH length (cm) and 95% CI of hatchery- and natural-origin female and male spring Chinook Salmon spawners of different ages sampled on the spawning grounds in the Chiwawa River basin for the combined years 1993-2018 (top row), before reduction (1993-2014; middle row), and after reduction (2015-2018; bottom row) in hatchery smolt production. Sample sizes are shown within each bar.

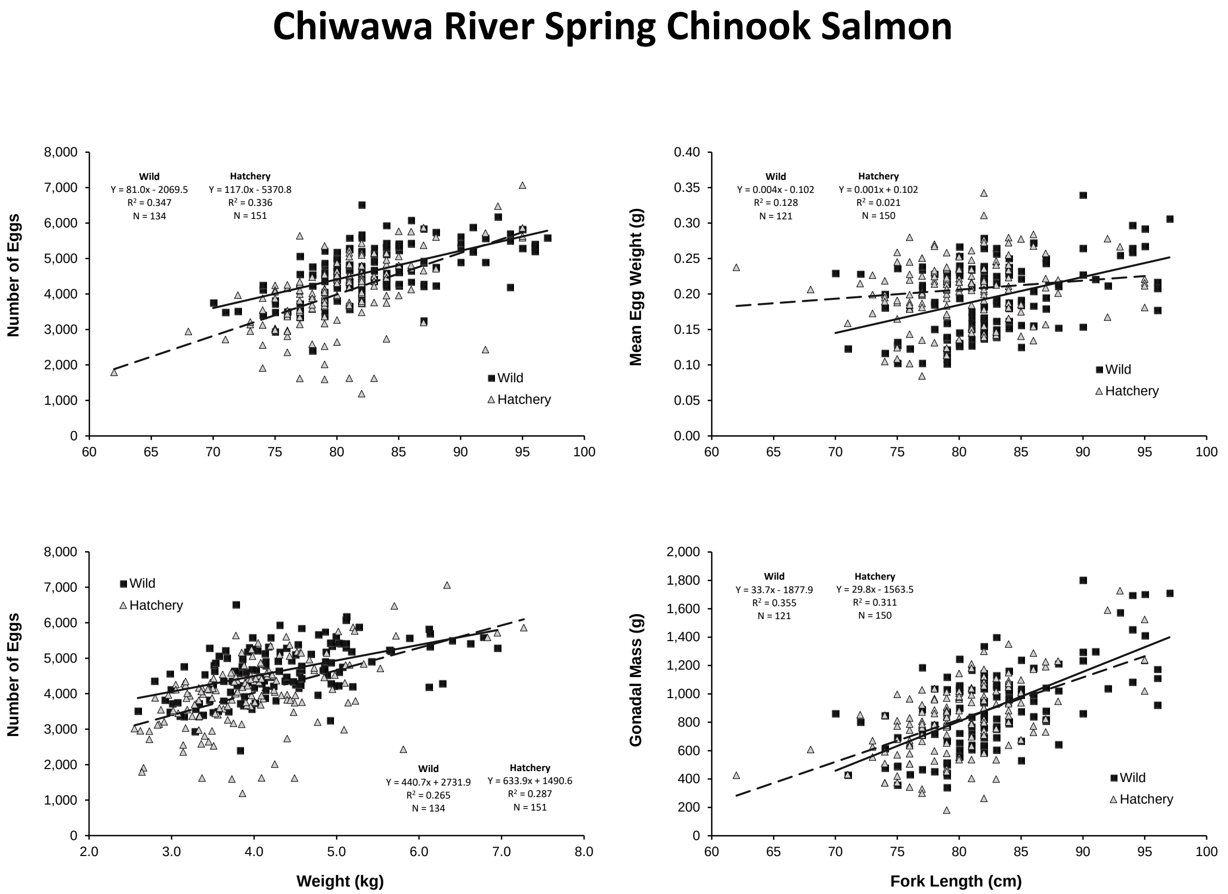


Figure 3. Relationships between fecundity (number of eggs, mean weight of eggs, and gonadal mass) and size (POH length and weight) for hatchery- (dashed line) and natural-origin (solid line) Chiwawa River spring Chinook Salmon for return years 2014-2018. Simple linear regression statistics are shown in each figure.

Effects of Hatchery-origin Strays on Natural-origin Spawners in Nason Creek

Age-at-Maturity Analysis—For the complete time series (1993-2018), age at maturity differed significantly between hatchery-origin and natural-origin female (Yates' Chi-square = 133.741, P = 0.000) and male spring Chinook Salmon (Yates' Chi-square = 232.691, P = 0.000) in Nason Creek (Figure 4). Most female and male spring Chinook Salmon returned at age-4; however, a larger proportion of hatchery-origin fish returned at younger ages than did natural-origin fish. For example, 94% of hatchery-origin females and 77% of natural-origin females returned at age-4. About 23% of natural-origin females, but only 5% of hatchery-origin females returned at age-5. A similar pattern was observed with male spring Chinook Salmon. About 44% of the hatchery-origin males, and only 7% of natural-origin males returned at age-3. In contrast, about 19% of natural-origin males, and only 4% of hatchery-origin males returned at age-5.

There were changes in age at maturity before (1993-2000) and after (2001-2018) the increase in pHOS in Nason Creek and this was most apparent in males (Figure 4). For males, the proportion of age-3 returns decreased from the before to after period, while age-4 males increased from the before to after period. During both the before and after periods, age at maturity differed significantly between hatchery- and natural-origin female (Before: Yates' Chi-square = 5.061, P = 0.024; After: Yates' Chi-square = 119.625, P = 0.000) and male spring Chinook Salmon (Before: Yates' Chi-square = 28.501, P = 0.000; After: Yates' Chi-square = 204.031; P = 0.000) in Nason Creek.

Size-at-Maturity Analysis—For the complete time series (1993-2018), size at maturity did not differ significantly between hatchery- and natural-origin female or male spring Chinook Salmon in Nason Creek (GLM ANOVA F = 2.384, P = 0.123) (Figure 5). There were, however, significant differences in size at maturity among age classes (GLM ANOVA F = 677.8, P = 0.000) and sex (GLM ANOVA F = 7.956, P = 0.005). Regardless of origin, older fish were larger than younger fish and older males were larger than older females.

Size at maturity did not differ significantly between hatchery- and natural-origin female or male spring Chinook Salmon from before (1993-2000) to after (2001-2018) the increase in pHOS in Nason Creek (GLM ANOVA F = 1.737, P = 0.188) (Figure 5). There were significant differences in size at maturity between male and female fish (GLM ANOVA F = 4.064, P = 0.044) and among ages (GLM ANOVA F = 120.678, P = 0.000), but those differences did not change from the before to after period (GLM ANOVA F = 1.478, P = 0.224).

Fecundity Analysis—There were significant linear relationships between female size and fecundity, mean egg weight, and gonadal mass for both hatchery- and natural-origin spring Chinook Salmon in Nason Creek for the combined years 2014-2018 (Figure 6). There were no differences in relationships between hatchery- and natural-origin fish for fork length and fecundity (ANCOVA F = 1.959, P = 0.163), female weight and fecundity (ANCOVA F = 3.273, P = 0.072), fork length and mean egg weight (ANCOVA F = 0.135, P = 0.714) or fork length and gonadal mass (ANCOVA F = 2.219, P = 0.138).

Nason Creek Spring Chinook Hatchery Program

Age-at-Maturity Analysis—Results for the complete time series (1993-2018) in Nason Creek were described above under the Effects of Hatchery-origin Strays on Natural-origin Spawners in Nason Creek section.

There was little change in age at maturity of spring Chinook Salmon before (1993-2015) and during (2016-2018) the implementation of the Nason Creek Supplementation Program (Figure 7). For both the before and during supplementation periods, the age at maturity differed significantly between hatchery- and natural-origin female (Before: Yates' Chi-square = 124.694, P = 0.000; After: Yates' Chi-square = 7.788, P = 0.005) and male spring Chinook Salmon (Before: Yates' Chi-square = 213.035, P = 0.000; After: Yates' Chi-square = 15.032; P = 0.000) in Nason Creek.

Size-at-Maturity Analysis—Results for the complete time series (1993-2018) in Nason Creek were described above under the Effects of Hatchery-origin Strays on Natural-origin Spawners in Nason Creek section.

Because of a lack of data for the during supplementation period, we could not evaluate statistically the effects of period, age, sex, and origin on size at maturity in Nason Creek. However, there was a difference in size among age classes, with older fish being larger than younger fish (Figure 8). In addition, there were differences in sizes between males and females, with older males generally larger than older females.

Fecundity Analysis—These results were described above under the Straying Effects on Nason Creek section.

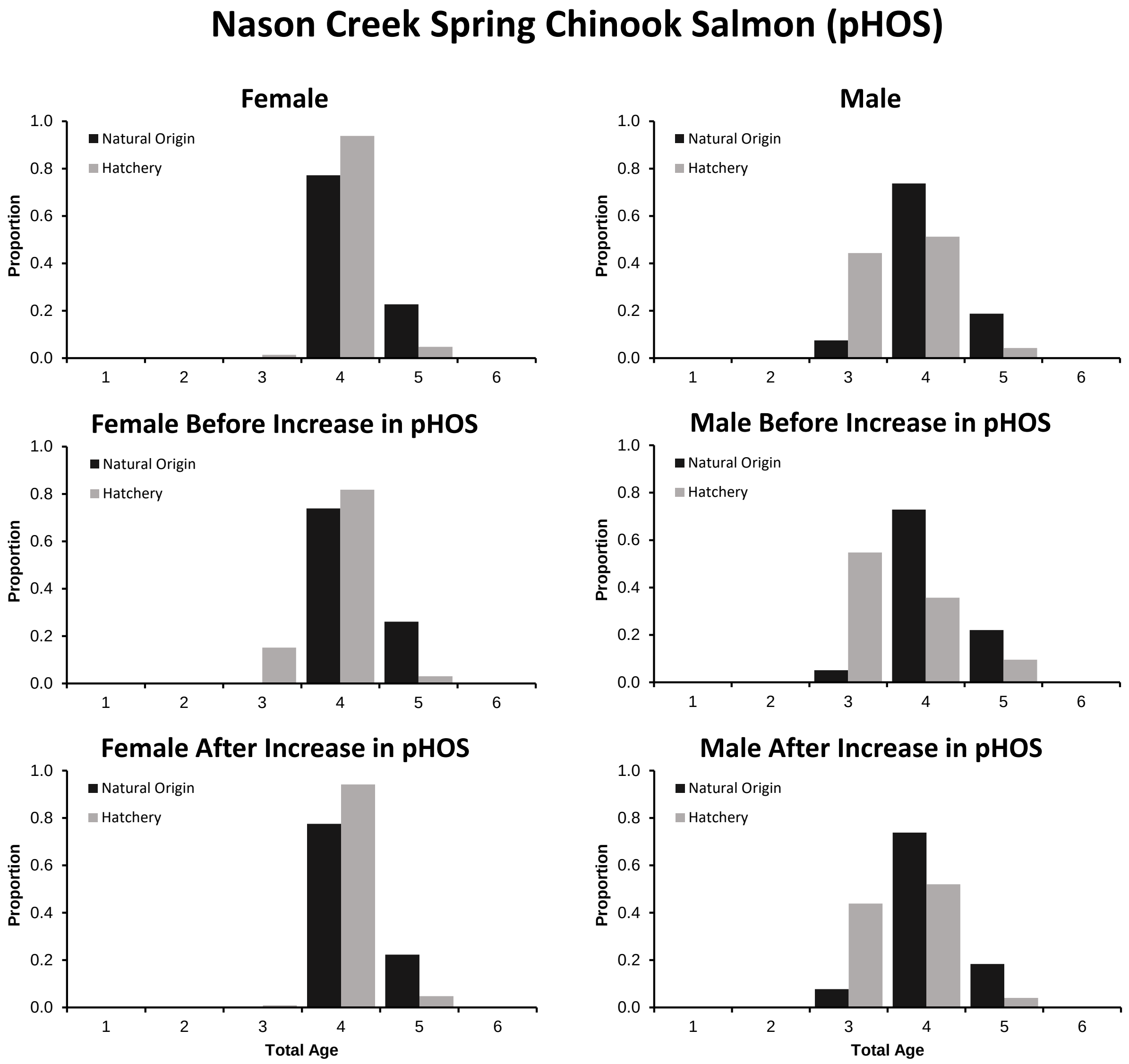


Figure 4. Proportion of hatchery- and natural-origin female and male spring Chinook Salmon spawners of different ages sampled on the spawning grounds in Nason Creek for the combined years 1993-2018 (top row), before increase in pHOS (1993-2000; middle row), and after increase in pHOS (2001-2018; bottom row). Sample sizes for females = 705 natural-origin and 1,086 hatchery-origin fish and for males = 495 natural-origin and 883 hatchery-origin fish for the combined analysis. For the before analysis, sample sizes for females = 69 natural-origin and 33 hatchery-origin fish and for males = 59 natural-origin and 42 hatchery-origin fish; and for the after analysis, sample sizes for females = 636 natural-origin and 1,053 hatchery-origin fish and for males = 436 natural-origin and 841 hatchery-origin fish.

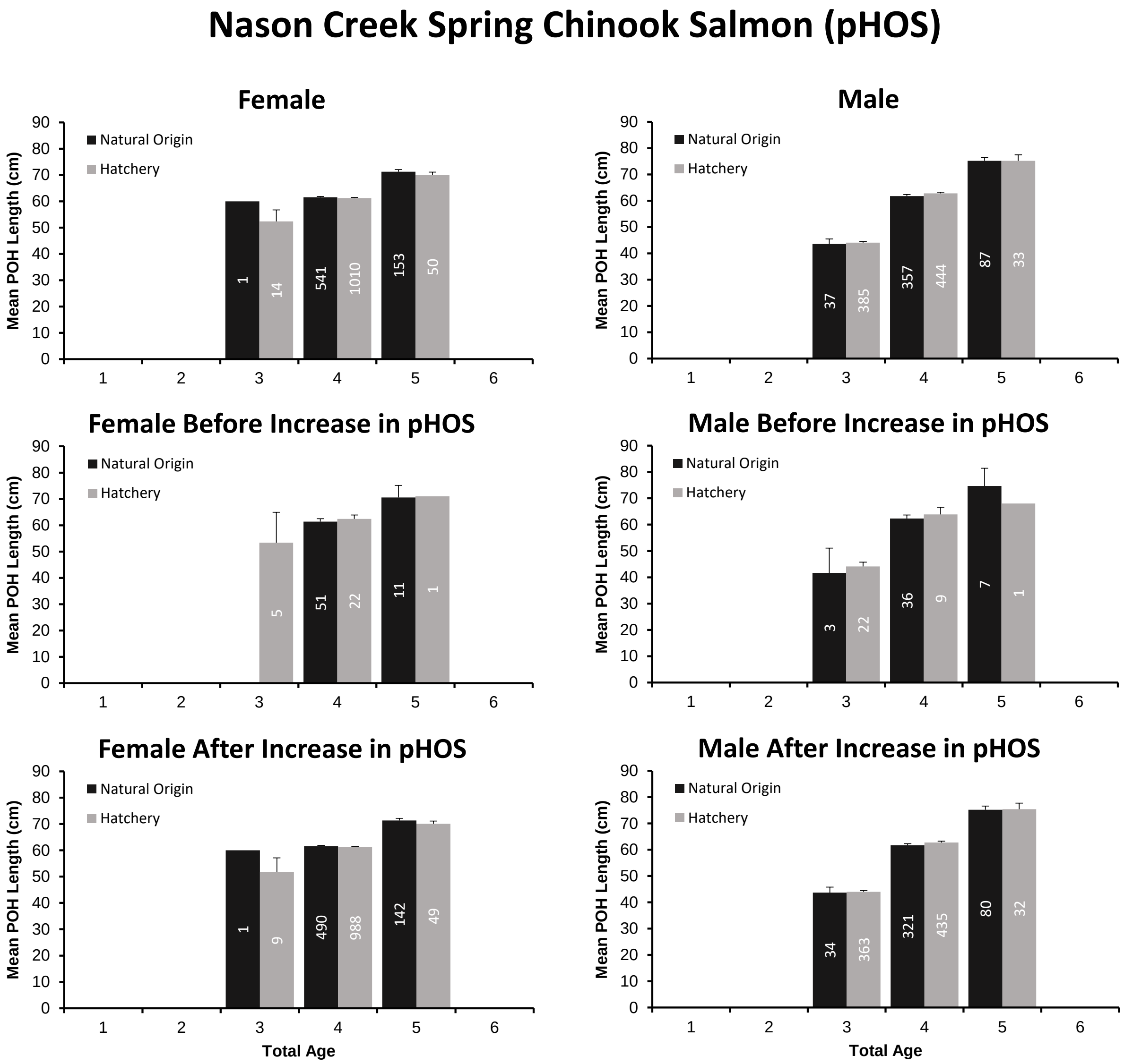


Figure 5. Mean POH length (cm) and 95% CI of hatchery- and natural-origin female and male spring Chinook Salmon spawners of different ages sampled on the spawning grounds in Nason Creek for the combined years 1993-2018 (top row), before increase in pHOS (1993-2000; middle row), and after increase in pHOS (2001-2018; bottom row). Sample sizes are shown within each bar.

Nason Creek Spring Chinook Salmon

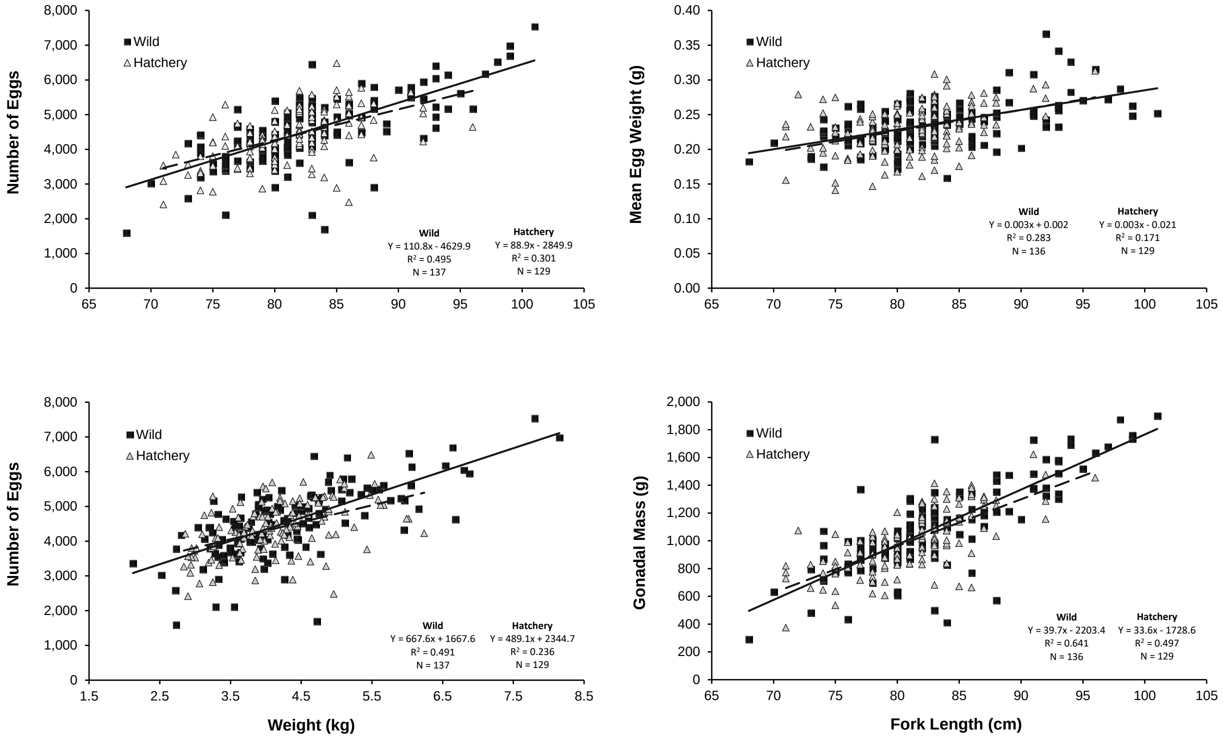


Figure 6. Relationships between fecundity (number of eggs, mean weight of eggs, and gonadal mass) and size (POH length and weight) for hatchery- (dashed line) and natural-origin (solid line) Nason Creek spring Chinook Salmon for return years 2014-2018. Simple linear regression statistics are shown in each figure.

Nason Creek Spring Chinook Salmon (Supplementation)

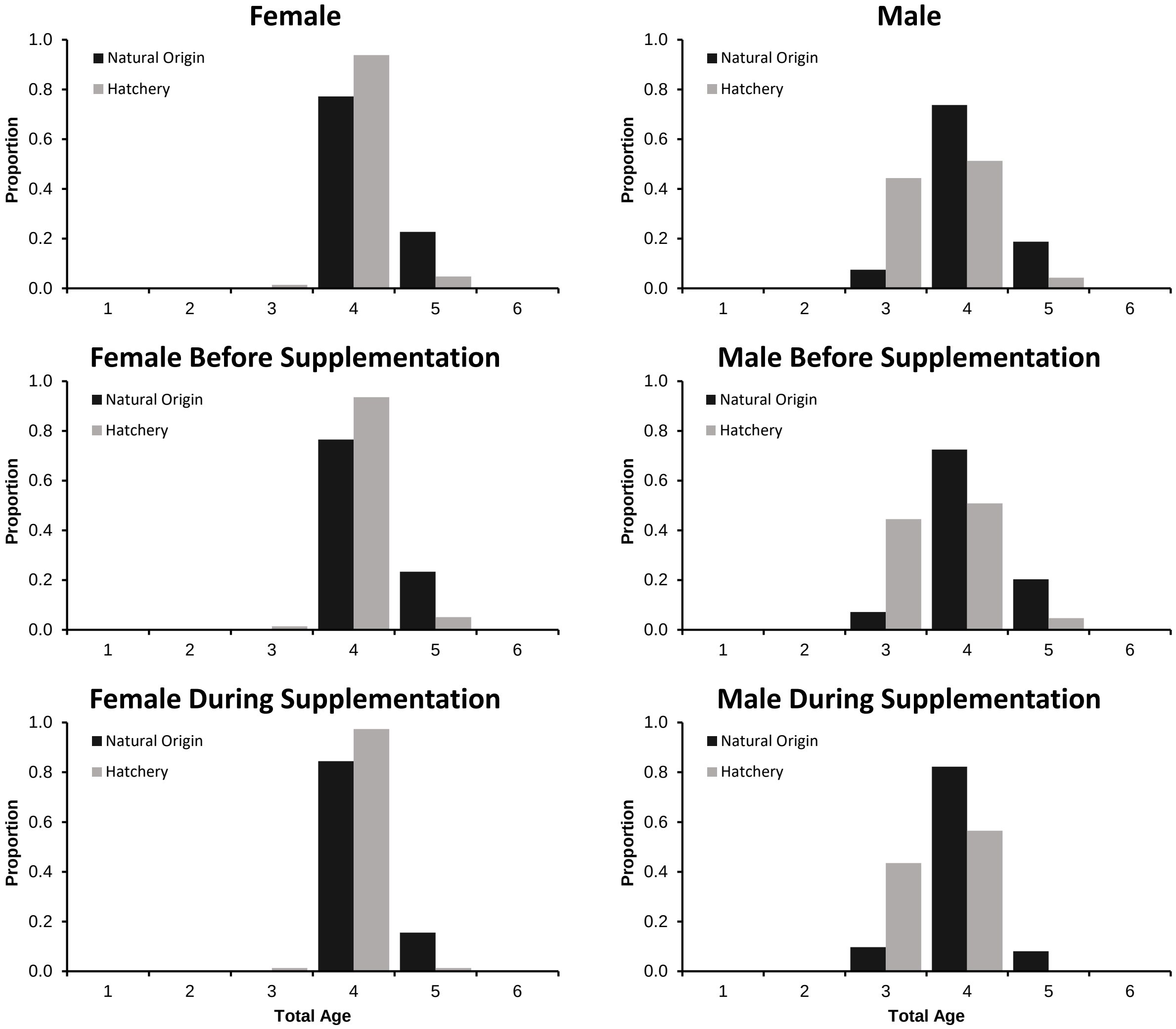


Figure 7. Proportion of hatchery- and natural-origin female and male spring Chinook Salmon spawners of different ages sampled on the spawning grounds in Nason Creek for the combined years 1993-2018 (top row), before supplementation (1993-2015; middle row), and during supplementation (2016-2018; bottom row). Sample sizes for females = 705 natural-origin and 1,086 hatchery-origin fish and for males = 495 natural-origin and 883 hatchery-origin fish for the combined analysis. For the before analysis, sample sizes for females = 647 natural-origin and 1,008 hatchery-origin fish and for males = 433 natural-origin and 814 hatchery-origin fish; and for the during analysis, sample sizes for females = 58 natural-origin and 78 hatchery-origin fish and for males = 62 natural-origin and 69 hatchery-origin fish.

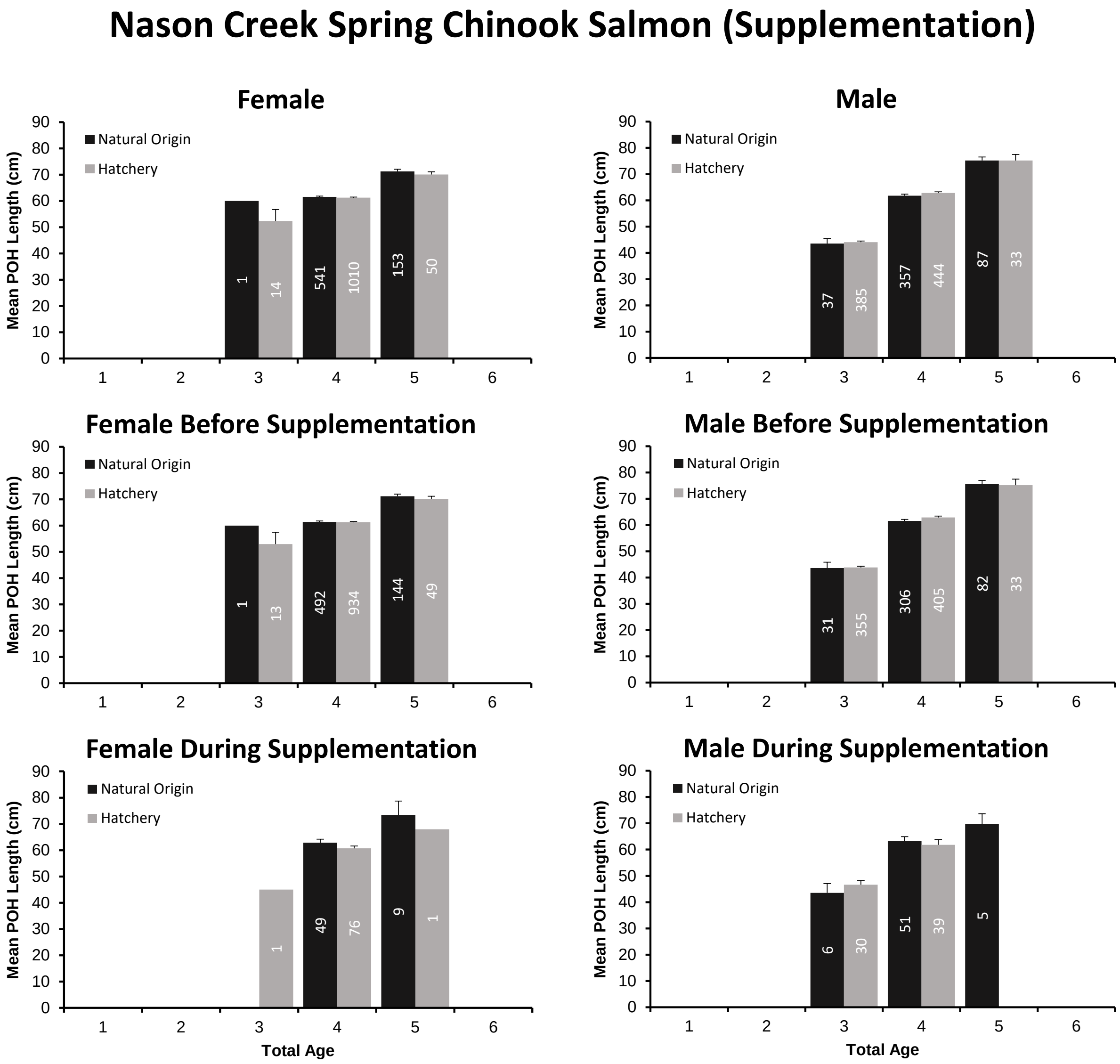


Figure 8. Mean POH length (cm) and 95% CI of hatchery- and natural-origin female and male spring Chinook Salmon spawners of different ages sampled on the spawning grounds in Nason Creek for the combined years 1993-2018 (top row), before supplementation (1993-2015; middle row), and during supplementation (2016-2018; bottom row). Sample sizes are shown within each bar.

White River Program

Age-at-Maturity Analysis—For the complete time series (1993-2018), age at maturity differed significantly between hatchery- and natural-origin females (Yates' Chi-square = 24.659, P = 0.000) but not between hatchery- and natural-origin male spring Chinook Salmon (Yates' Chi-square = 5.119, P = 0.077) in the White River (Figure 9). Most females and males returned at age-4; however, a larger proportion of hatchery-origin fish returned at younger ages than did natural-origin fish. For example, 95% of hatchery-origin females and 72% of natural-origin females returned at age-4. About 28% of natural-origin females and 5% of hatchery females returned at age-5. A similar pattern was observed with males: about 22% of natural-origin males returned at age-5, while no hatchery males returned at age-5.

There was little change in age at maturity before (1993-2007) and during (2008-2018) the implementation of the captive-brood program in the White River (Figure 9). For both the before and during periods, the age at maturity differed significantly between hatchery- and natural-origin females (Before: Yates' Chi-square = 12.891, P = 0.000; After: Yates' Chi-square = 10.315, P = 0.001) but not for male spring Chinook Salmon (Before: Yates' Chi-square = 5.584, P = 0.061; After: Yates' Chi-square = 0.359; P = 0.359).

Size-at-Maturity Analysis—Sample sizes were too small to evaluate statistically the effects of origin, sex, and age on size at maturity of spring Chinook Salmon in the White River. Over the complete time series (1993-2018), however, there were small differences in sizes between hatchery- and natural-origin fish within each age class (Figure 10). There were clear differences in sizes among ages with older fish larger than younger fish.

Because of a lack of data, we could not evaluate statistically the effects of period, age, sex, and origin on size at maturity in the White River. Differences in sizes among age classes were consistent during the before and during supplementation periods and differences in sizes between hatchery- and natural-origin fish were small during both periods (Figure 10).

Fecundity Analysis—No comparative fecundity data similar to what was done for other programs were collected for the White River program. This was because broodstock were collected as eyed eggs or fry from the White River (Ford et al. 2015).

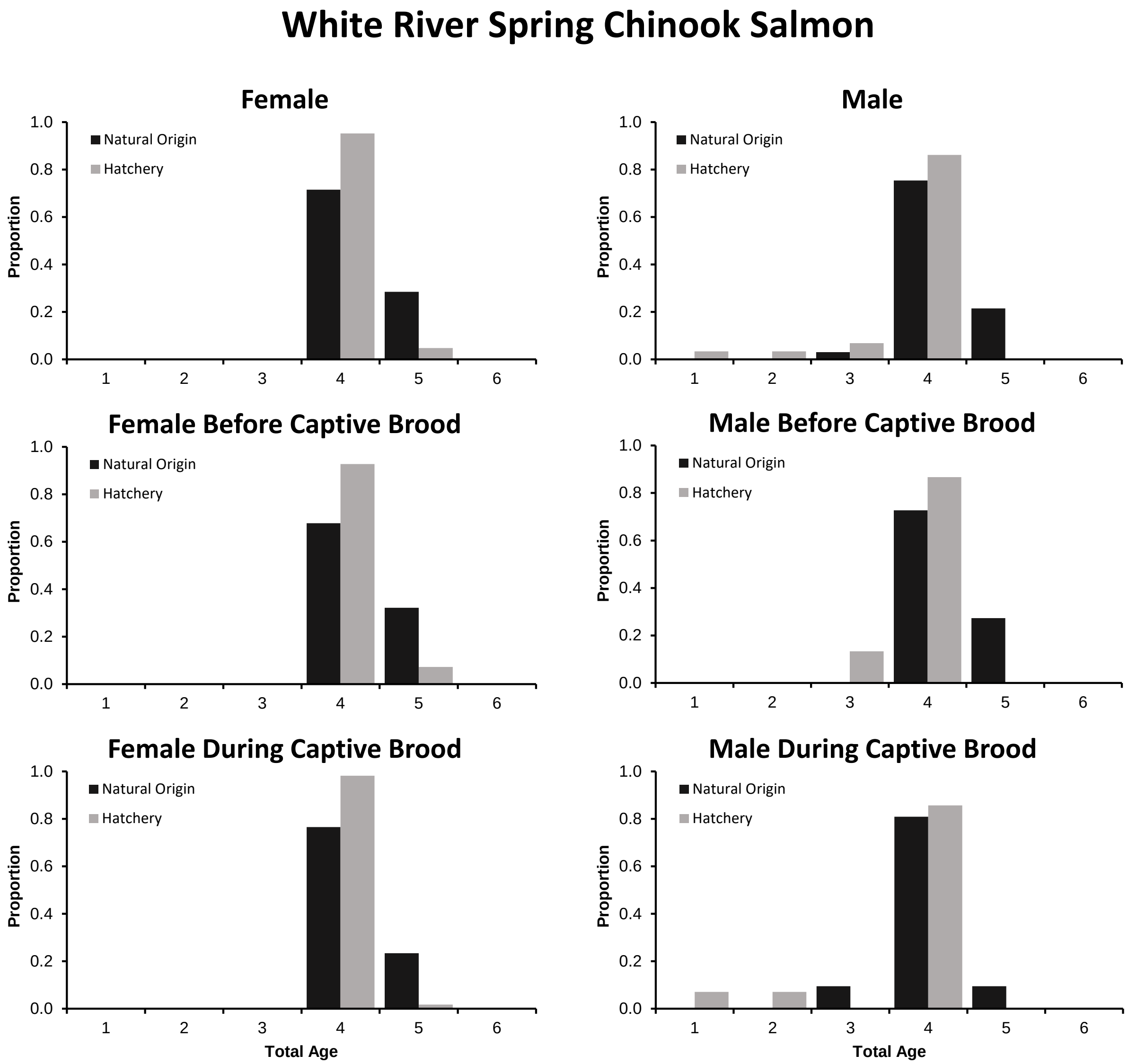


Figure 9. Proportion of hatchery- and natural-origin female and male spring Chinook Salmon spawners of different ages sampled on the spawning grounds in the White River basin for the combined years 1993-2018 (top row), before the captive brood program (1993-2007; middle row), and during the captive brood program (2008-2018; bottom row). Sample sizes for females = 151 natural-origin and 125 hatchery-origin fish and for males = 65 natural-origin and 29 hatchery-origin fish for the combined analysis. For the before analysis, sample sizes for females = 87 natural-origin and 69 hatchery-origin fish and for males = 44 natural-origin and 15 hatchery-origin fish; and for the during analysis, sample sizes for females = 64 natural-origin and 56 hatchery-origin fish and for males = 21 natural-origin and 14 hatchery-origin fish.

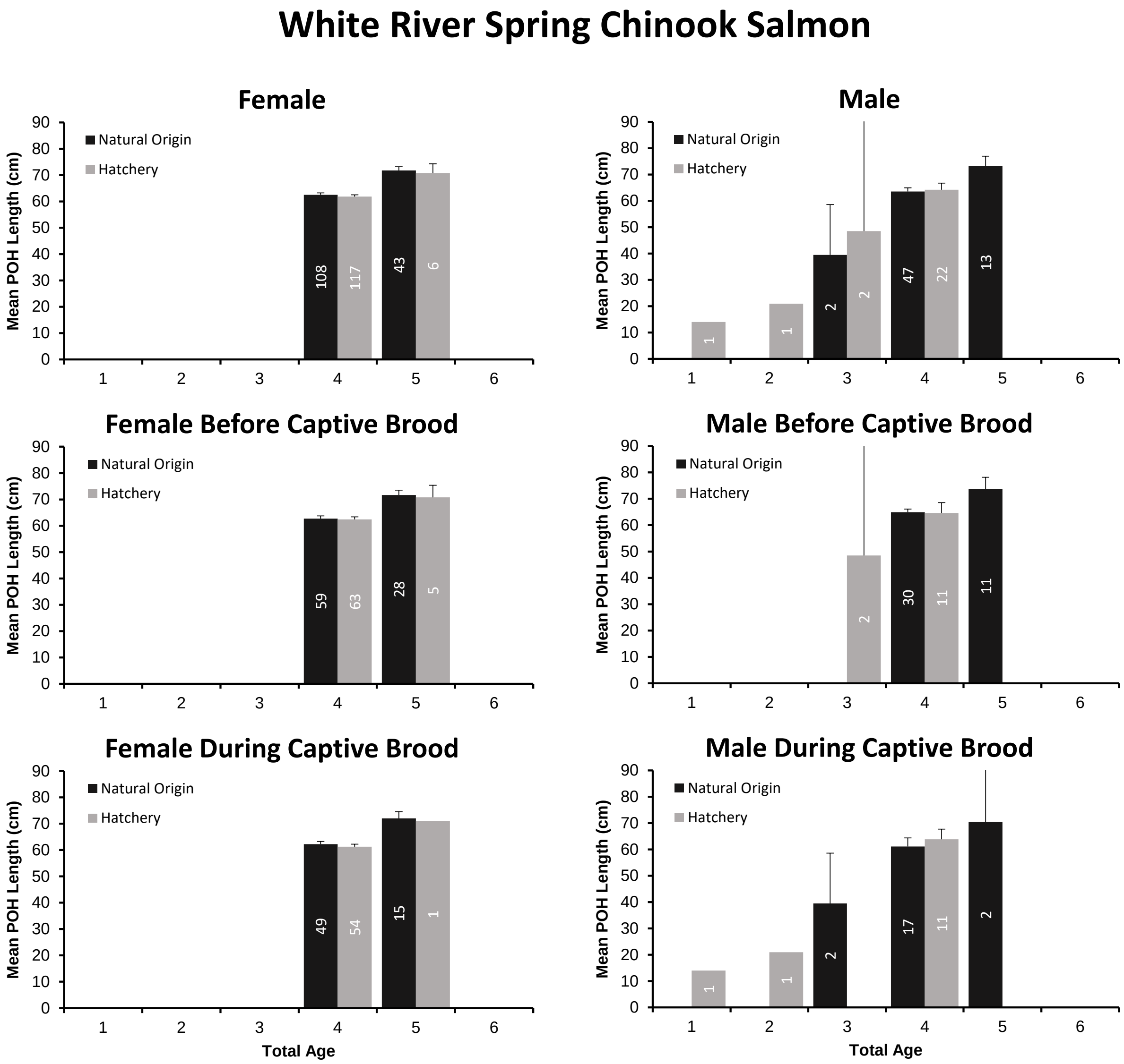


Figure 10. Mean POH length (cm) and 95% CI of hatchery- and natural-origin female and male spring Chinook Salmon spawners of different ages sampled on the spawning grounds in the White River basin for the combined years 1993-2018 (top row), before the captive brood program (1993-2007; middle row), and during the captive brood program (2008-2018; bottom row). Sample sizes are shown within each bar.

Methow-Chewuch Program

Age-at-Maturity Analysis—For the complete time series (1993-2018), age at maturity differed significantly between hatchery- and natural-origin female (Yates' Chi-square = 143.960, P = 0.000) and male spring Chinook Salmon (Yates' Chi-square = 263.369, P = 0.000) in the Methow and Chewuch rivers (Figure 11). Most females and males returned at age-4; however, a larger proportion of hatchery-origin fish returned at younger ages than did natural-origin fish. For example, 90% of hatchery-origin females and 77% of the natural-origin females returned at age-4. About 23% of natural-origin females and 10% of hatchery-origin females returned at age-5. A similar pattern was observed with males. About 33% of the hatchery-origin males and 7% of natural-origin males returned at age-3. In contrast, about 20% of natural-origin males and 9% of hatchery-origin males returned at age-5.

There was little change in age at maturity before (1993-2014) and after (2014-2018) reduction in hatchery production numbers, although a larger fraction of hatchery- and natural-origin males returned as age-4 fish following the reduction in program production (Figure 11). During both the before and after periods, age at maturity differed significantly between hatchery- and natural-origin females (Before: Yates' Chi-square = 142.913, P = 0.000; After: Yates' Chi-square = 10.169, P = 0.001). Age at maturity differed significantly between hatchery- and natural-origin males before reduction (Yates' Chi-square = 250.188, P = 0.000) but not after reduction in hatchery production (Yates' Chi-square = 3.773; P = 0.152).

Size-at-Maturity Analysis—For the complete time series (1993-2018), size at maturity was significantly affected by sex and age (GLM ANOVA F = 82.040, P = 0.000) but not by origin (GLM ANOVA F = 3.807, P = 0.051) (Figure 12). Older fish of both sexes were larger than younger fish and older males were generally larger than older females. Except for age-3 females, size differences between hatchery- and natural-origin fish within each age group were small, generally less than 0.5 cm on average.

There were significant differences in the size at maturity before and after reduction in hatchery production (GLM ANOVA F = 7.129, P = 0.008) (Figure 12). For most age groups, both hatchery- and natural-origin fish were smaller following the reduction in hatchery production; however, the change in size was only about 1 cm on average. During both time periods for both hatchery- and natural-origin fish, older males were larger on average than females of the same age (GLM ANOVA F = 22.459, P = 0.000).

Fecundity Analysis—There were significant linear relationships between female size and fecundity, mean egg weight, and gonadal mass for both hatchery- and natural-origin spring Chinook Salmon in the Methow and Chewuch rivers for the combined years 2014-2018 (Figure 13). There were no differences in relationships between hatchery- and natural-origin fish for fork length and fecundity (ANCOVA F = 0.418, P = 0.518), female weight and fecundity (ANCOVA F = 0.261, P = 0.610), fork length and mean egg weight (ANCOVA F = 0.316, P = 0.574) and fork length and gonadal mass (ANCOVA F = 2.123, P = 0.146).

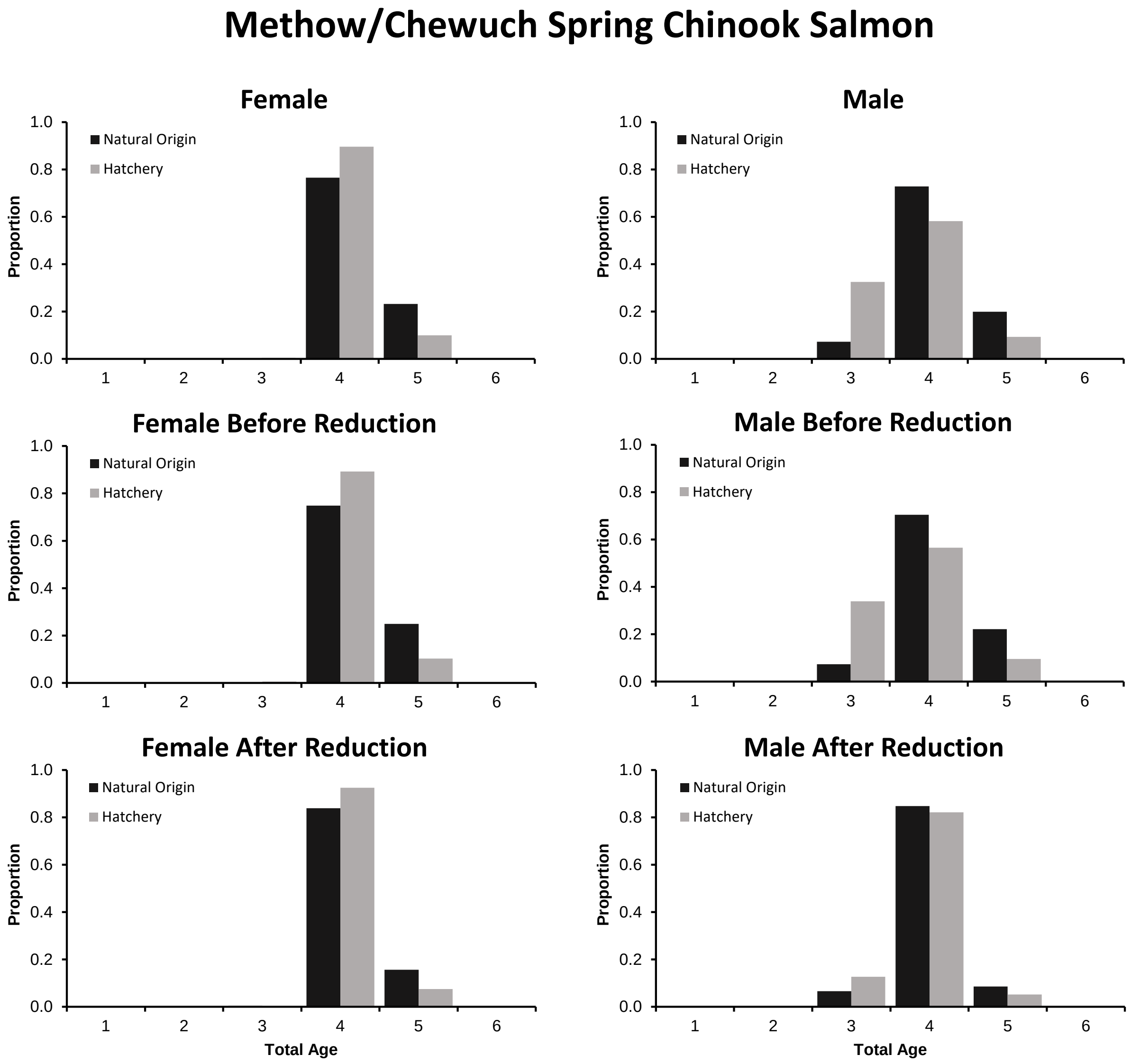


Figure 11. Proportion of hatchery- and natural-origin female and male spring Chinook Salmon spawners of different ages sampled on the spawning grounds in the Methow and Chewuch rivers for the combined years 1993-2018 (top row), before reduction (1993-2014; middle row), and after reduction (2015-2018; bottom row) in hatchery smolt production. Sample sizes for females = 1,163 natural-origin and 4,351 hatchery-origin fish and for males = 923 natural-origin and 3,263 hatchery-origin fish for the combined analysis. For the before analysis, sample sizes for females = 946 natural-origin and 3,873 hatchery-origin fish and for males = 772 natural-origin and 3,050 hatchery-origin fish; and for the after analysis, sample sizes for females = 217 natural-origin and 478 hatchery-origin fish and for males = 151 natural-origin and 213 hatchery-origin fish.

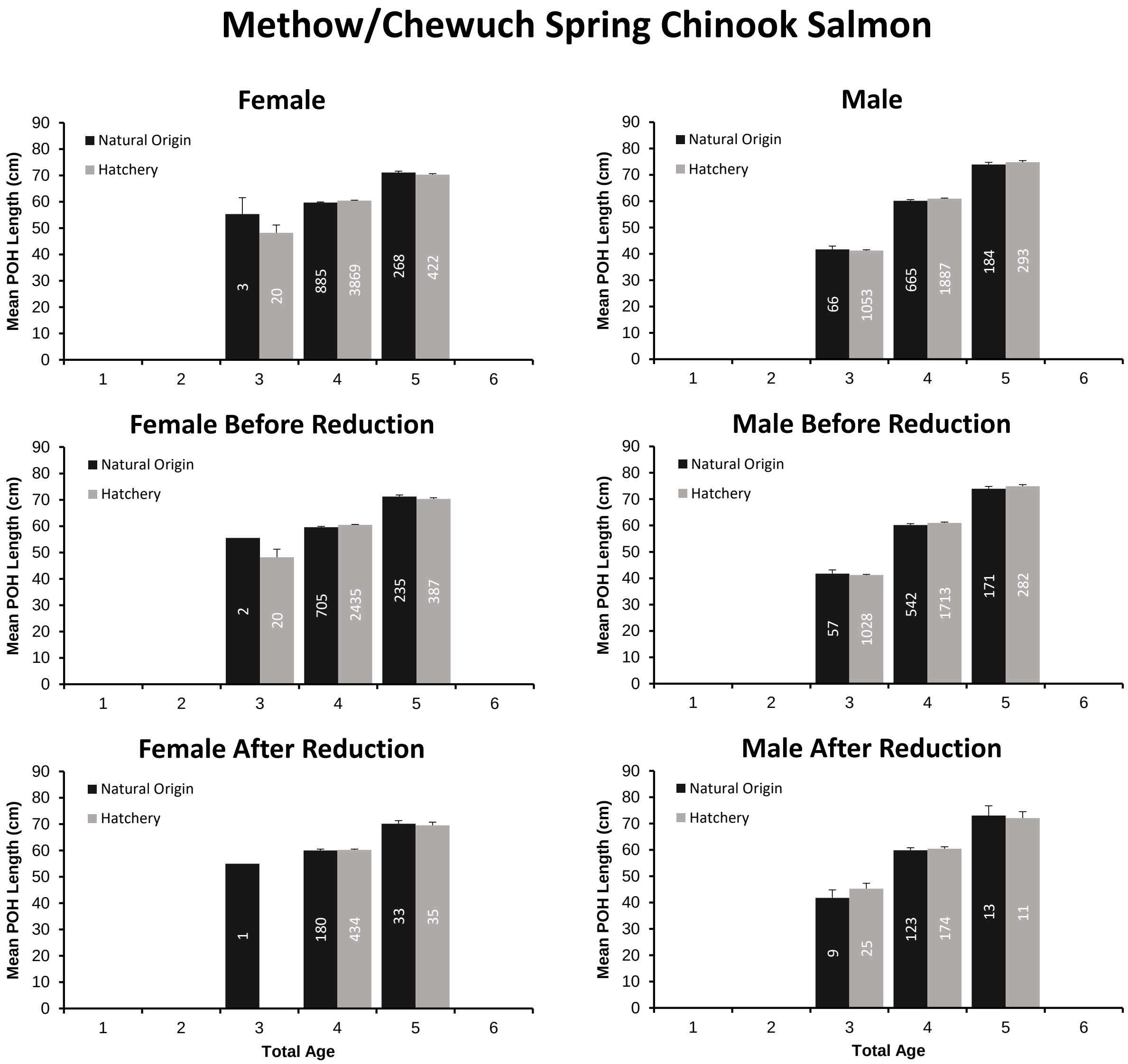


Figure 12. Mean POH length (cm) and 95% CI of hatchery- and natural-origin female and male spring Chinook Salmon spawners of different ages sampled on the spawning grounds in the Methow and Chewuch rivers for the combined years 1993-2018 (top row), before reduction (1993-2014; middle row), and after reduction (2015-2018; bottom row) in hatchery smolt production. Sample sizes are shown within each bar.

Methow/Chewuch Spring Chinook Salmon

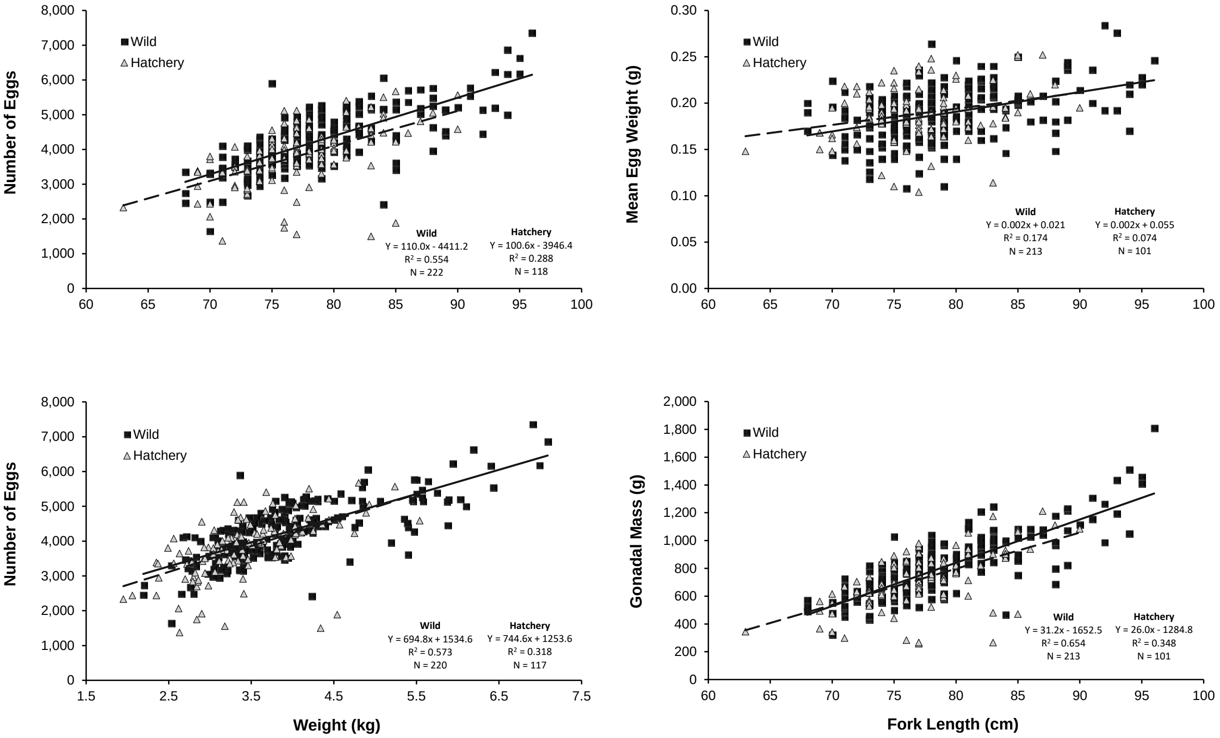


Figure 13. Relationships between fecundity (number of eggs, mean weight of eggs, and gonadal mass) and size (POH length and weight) for hatchery- (dashed line) and natural-origin (solid line) Methow/Chewuch spring Chinook Salmon for return years 2014-2018. Simple linear regression statistics are shown in each figure.

Twisp River Program

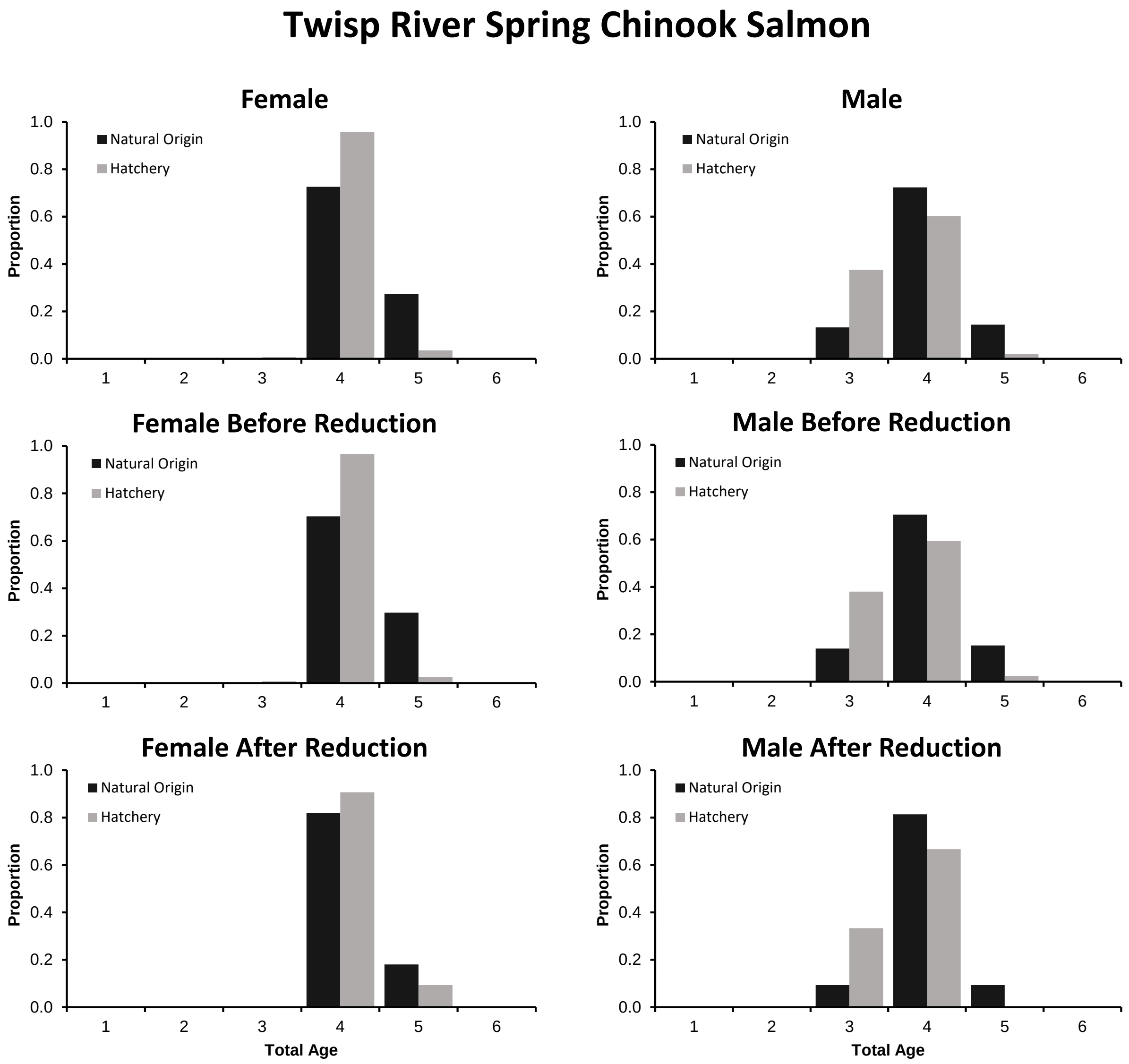
Age-at-Maturity Analysis—For the complete time series (1993-2018), age at maturity differed significantly between hatchery- and natural-origin female (Yates' Chi-square = 64.722, P = 0.000) and male spring Chinook Salmon (Yates' Chi-square = 45.211, P = 0.000) in the Twisp River (Figure 14). Most females and males returned at age-4; however, a larger proportion of hatchery-origin fish returned at younger ages than did natural-origin fish. For example, 96% of hatchery-origin females and 73% of the natural-origin females returned at age-4. About 27% of natural-origin females and 4% of hatchery-origin females returned at age-5. A similar pattern was observed with males: about 38% of the hatchery-origin males and 13% of natural-origin males returned at age-3. In contrast, about 14% of natural-origin males and 2% of hatchery males returned at age-5.

There was little change in age at maturity before (1993-2014) and after (2014-2018) reduction in hatchery production numbers, although a larger proportion of hatchery- and natural-origin males returned as age 4 fish following the reduction in program production (Figure 14). During the before period, age at maturity differed significantly between hatchery- and natural-origin females (Yates' Chi-square = 68.527, P = 0.000) and males (Yates' Chi-square = 40.255, P = 0.000). During the after period, however, age-at maturity did not differ significantly between hatchery- and natural-origin females (Yates' Chi-square = 0.820, P = 0.365) and males (Yates' Chi-square = 0.962, P = 0.327).

Size-at-Maturity Analysis—For the complete time series (1993-2018), size at maturity was significantly affected by sex and age (GLM ANOVA F = 13.922, P = 0.000) but not by origin (GLM ANOVA F = 1.424, P = 0.233) (Figure 15). Older fish of both sexes were larger than younger fish and older males were generally larger than older females. Size differences between hatchery- and natural-origin fish within each age group were small, generally less than 1.5 cm on average.

Because of a lack of data, we could not evaluate statistically the effects of period, age, sex, and origin on size at maturity in the Twisp River. Differences in sizes among age classes were consistent during the before and after reduction periods and differences in sizes between hatchery- and natural-origin fish were small during both periods (Figure 15).

Fecundity Analysis—Except for the relationship between fork length and mean egg weight for natural-origin spring Chinook Salmon, all the other fecundity relationships for both hatchery- and natural-origin spring Chinook Salmon in the Twisp River were significant for the combined years 2014-2018 (Figure 16). Fecundity relationships between hatchery- and natural-origin fish differed significantly for fork length and fecundity (ANCOVA F = 5.362, P = 0.025) and fork length and mean egg weight (ANCOVA F = 5.252, P = 0.027). There were no differences in relationships between hatchery- and natural-origin fish for female weight and fecundity (ANCOVA F = 3.895, P = 0.055) and fork length and total egg weight (ANCOVA F = 0.001, P = 0.982).



Twisp River Spring Chinook Salmon

Female

Male

Female Before Reduction

Male Before Reduction

Female After Reduction

Male After Reduction

Figure 14. Proportion of hatchery- and natural-origin female and male spring Chinook Salmon spawners of different ages sampled on the spawning grounds in the Twisp River for the combined years 1993-2018 (top row), before reduction (1993-2014; middle row), and after reduction (2015-2018; bottom row) in hatchery smolt production. Sample sizes for females = 314 natural-origin and 311 hatchery-origin fish and for males = 264 natural-origin and 229 hatchery-origin fish for the combined analysis. For the before analysis, sample sizes for females = 253 natural-origin and 268 hatchery-origin fish and for males = 221 natural-origin and 205 hatchery-origin fish; and for the after analysis, sample sizes for females = 61 natural-origin and 43 hatchery-origin fish and for males = 43 natural-origin and 24 hatchery-origin fish.

Twisp River Spring Chinook Salmon

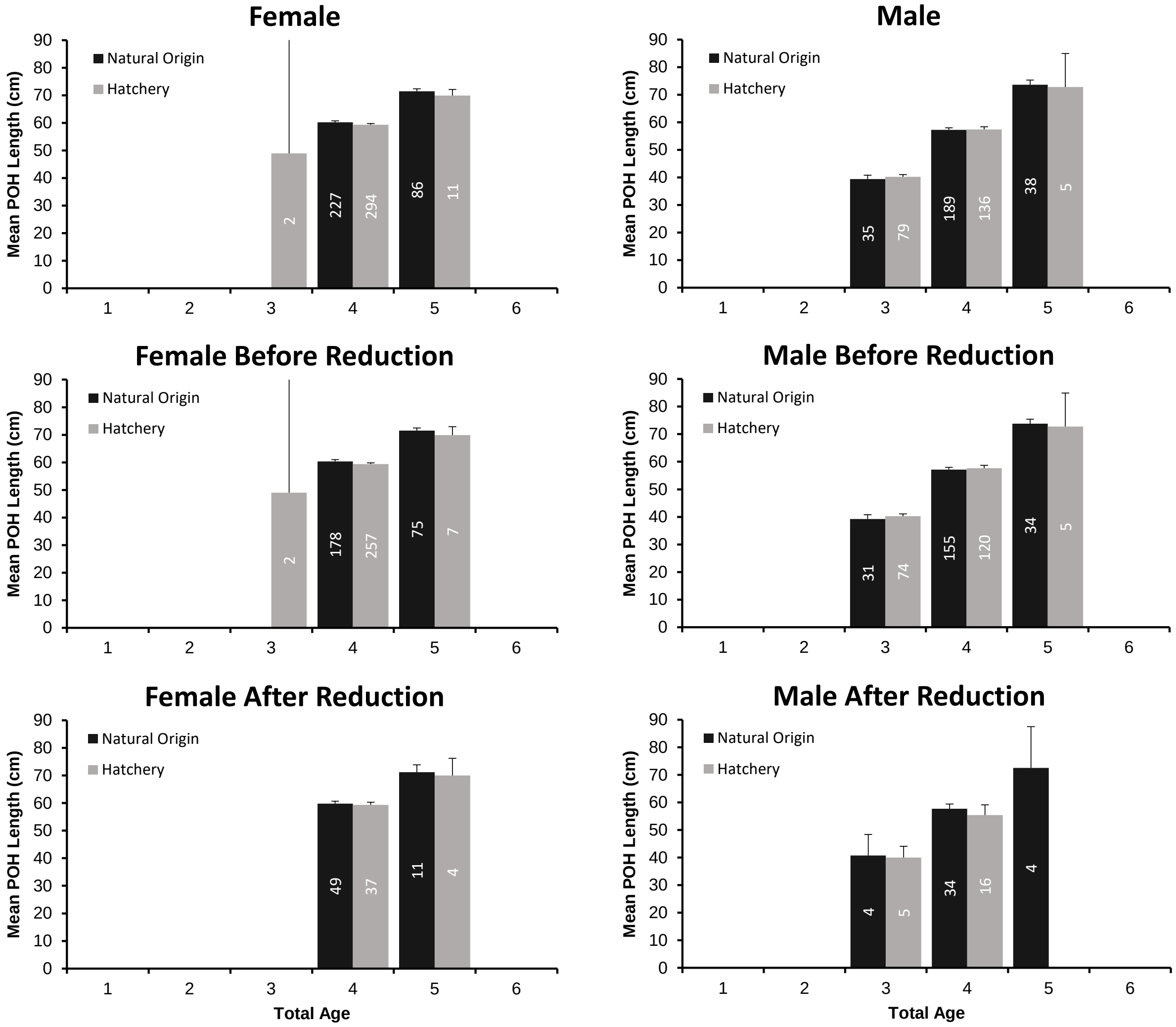


Figure 15. Mean POH length (cm) and 95% CI of hatchery- and natural-origin female and male spring Chinook Salmon spawners of different ages sampled on the spawning grounds in the Twisp River for the combined years 1993-2018 (top row), before reduction (1993-2014; middle row), and after reduction (2015-2018; bottom row) in hatchery smolt production. Sample sizes are shown within each bar.

Twisp River Spring Chinook Salmon

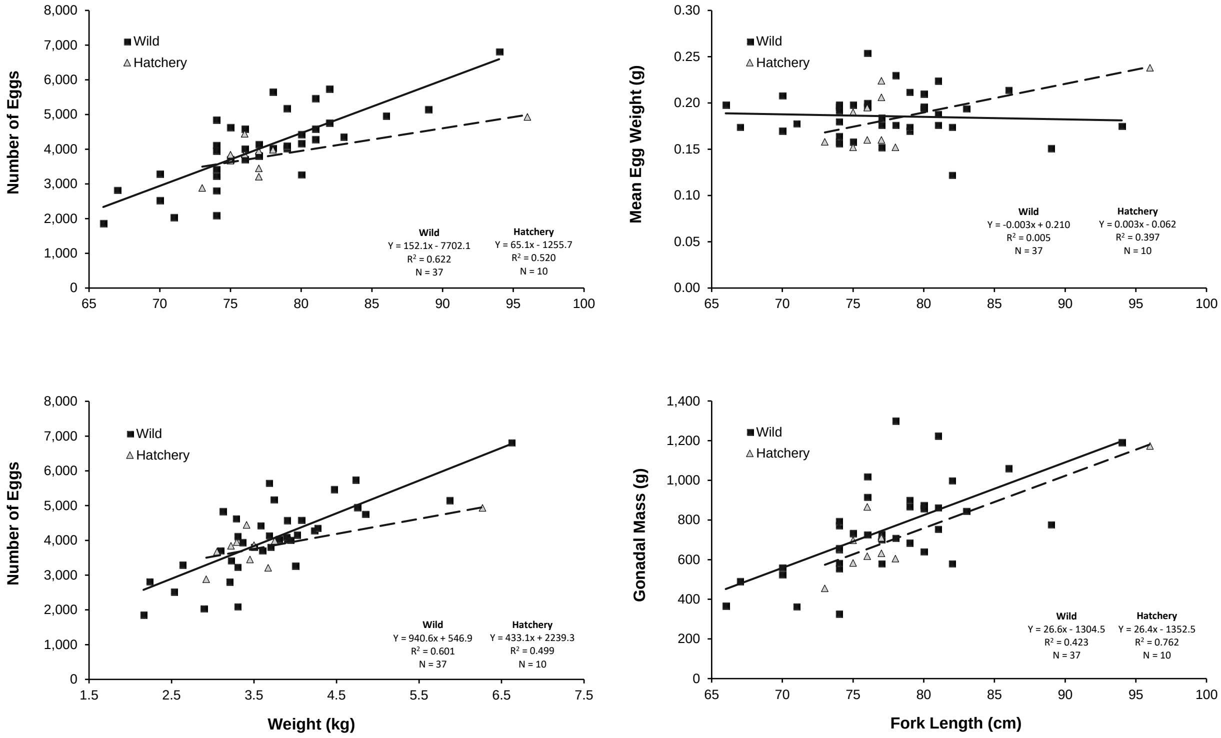


Figure 16. Relationships between fecundity (number of eggs, mean weight of eggs, and gonadal mass) and size (POH length and weight) for hatchery- (dashed line) and natural-origin (solid line) Twisp River spring Chinook Salmon for return years 2014-2018. Simple linear regression statistics are shown in each figure.

Summer Chinook Salmon

Wenatchee River Program

Age-at-Maturity Analysis—For the complete time series (1993-2018), age at maturity differed significantly between hatchery- and natural-origin female (Yates' Chi-square = 1,050.133, P = 0.000) and male summer Chinook Salmon (Yates' Chi-square = 976.779, P = 0.000) in the Wenatchee River (Figure 17). Most female and male summer Chinook Salmon returned at ocean-age-3; however, a larger proportion of hatchery-origin fish returned at younger ocean ages than did natural-origin fish. Specifically, a higher proportion of hatchery-origin females returned as ocean-age-2 and 3 fish than did natural-origin females. In contrast, a higher proportion of natural-origin females returned as ocean-age-4 fish than did hatchery-origin females. Similarly, a higher proportion of hatchery-origin males returned as ocean-age-1 and 2 fish than did natural-origin males, while a higher proportion of natural-origin males returned as ocean-age-3 and 4 fish than did hatchery-origin males.

There was a change in age at maturity before (1993-2014) and after (2014-2018) reduction in hatchery production numbers, although comparisons are affected by the small number of hatchery-origin fish sampled during the after period (Figure 17). During the before period, age at maturity differed significantly between hatchery and natural-origin female (Yates' Chi-square = 889.751, P = 0.000) and male (Yates' Chi-square = 889.751, P = 0.000) summer Chinook Salmon. During the after period, hatchery-origin females returned at a younger ocean age compared to the before period (Figure 17). There was less of a change in the age at maturity of natural-origin females between the before and after periods. In addition, there was little change in the age at maturity for hatchery- and natural-origin males between the before to after periods. Because of small sample sizes, statistical analyses could not be conducted on data collected during the after period.

Size-at-Maturity Analysis—For the complete time series (1993-2018), size at maturity differed significantly between hatchery- and natural-origin summer Chinook Salmon in the Wenatchee River (GLM ANOVA F = 4.346, P = 0.037) (Figure 18). Size at maturity was significantly affected by age, origin, and sex (GLM ANOVA F = 4.225, P = 0.002). For females, ocean-age-2 and 5 natural-origin fish were larger on average than ocean-age-2 and 5 hatchery-origin fish, respectively (mean differences = 4 and 3 cm, respectively). For males, ocean-age-1, 2, and 5 natural-origin fish were larger on average than ocean-age-1, 2, and 5 hatchery-origin fish, respectively (mean differences = 2, 2, and 4 cm, respectively). For both sexes, samples sizes are low for ocean-age-5 fish.

Because of a lack of data, we could not evaluate statistically the effects of period, age, sex, and origin on size at maturity of summer Chinook Salmon in the Wenatchee River. Differences in sizes among ocean-age classes were consistent during the before and after reduction periods and differences in sizes between hatchery- and natural-origin fish were relatively small during both periods (Figure 18). A notable difference was observed with size at maturity for ocean-age-2 females. During the before period, ocean-age-2 natural-origin females were on average 4 cm larger than ocean-age-2 hatchery-origin females. During the after period, ocean-age-2 natural-origin females were on average 4 cm smaller than ocean-age-2 hatchery-origin females.

Fecundity Analysis—Because only natural-origin summer Chinook Salmon are collected for broodstock for the Wenatchee program, there are no comparisons of fecundity relationships between hatchery- and natural-origin summer Chinook Salmon in the Wenatchee River. Based on examination of natural-origin summer Chinook Salmon, there were significant linear relationships between female size and fecundity, mean egg weight, and gonadal mass for the combined years 2014-2018 (Figure 19).

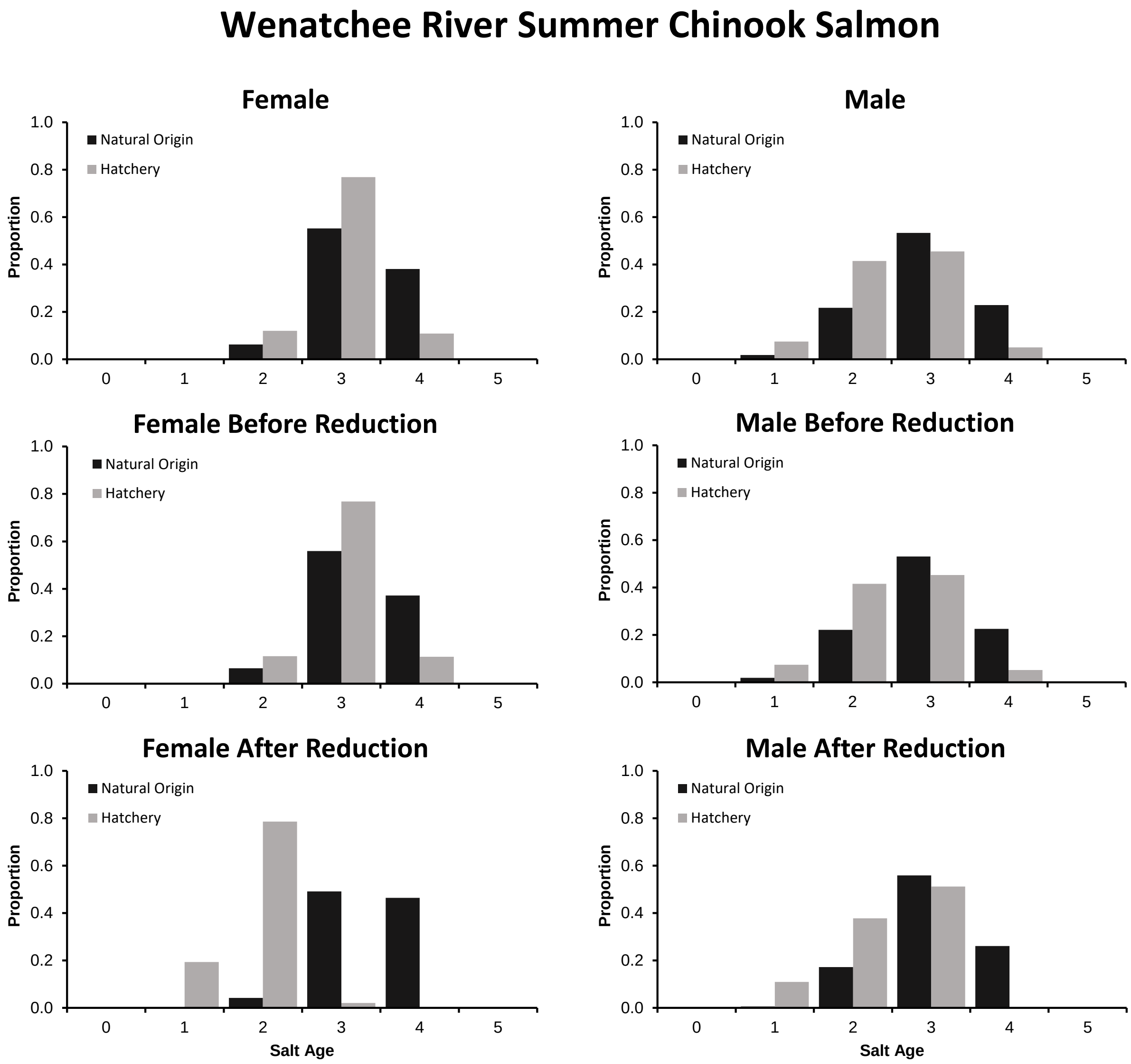


Figure 17. Proportion of hatchery- and natural-origin female and male summer Chinook Salmon spawners of different ocean (salt) ages sampled on the spawning grounds in the Wenatchee River basin for the combined years 1993-2018 (top row), before reduction (1993-2014; middle row), and after reduction (2015-2018; bottom row) in hatchery smolt production. Sample sizes for females = 15,026 natural-origin and 3,725 hatchery-origin fish and for males = 11,960 natural-origin and 2,664 hatchery-origin fish for the combined analysis. For the before analysis, sample sizes for females = 13,525 natural-origin and 3,529 hatchery-origin fish and for males = 11,060 natural-origin and 2,582 hatchery-origin fish; and for the after analysis, sample sizes for females = 1,501 natural-origin and 196 hatchery-origin fish and for males = 900 natural-origin and 82 hatchery-origin fish.

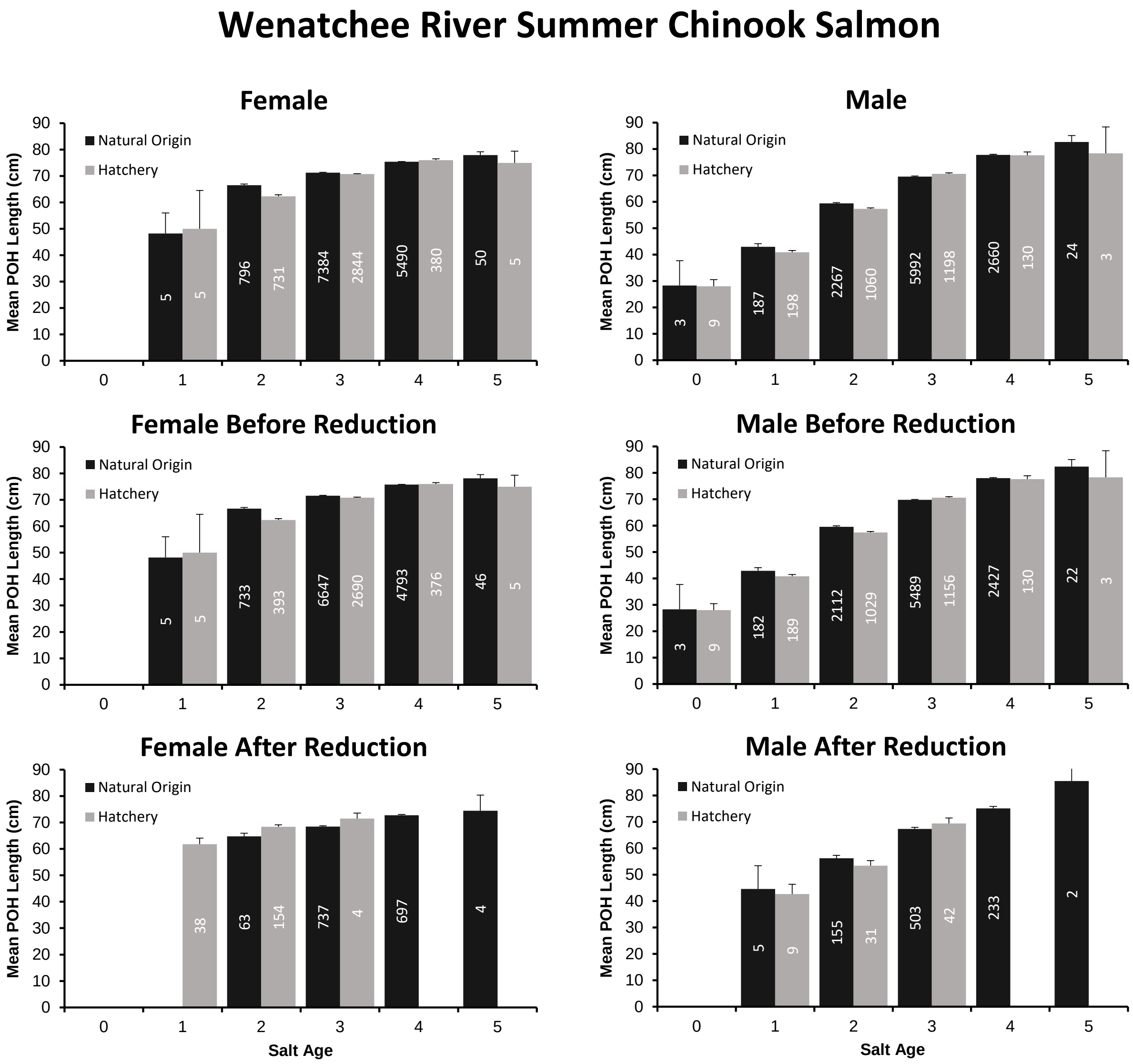


Figure 18. Mean POH length (cm) and 95% CI of hatchery- and natural-origin female and male summer Chinook Salmon spawners of different ocean (salt) ages sampled on the spawning grounds in the Wenatchee River basin for the combined years 1993-2018 (top row), before reduction (1993-2014; middle row), and after reduction (2015-2018; bottom row) in hatchery smolt production. Sample sizes are shown within each bar.

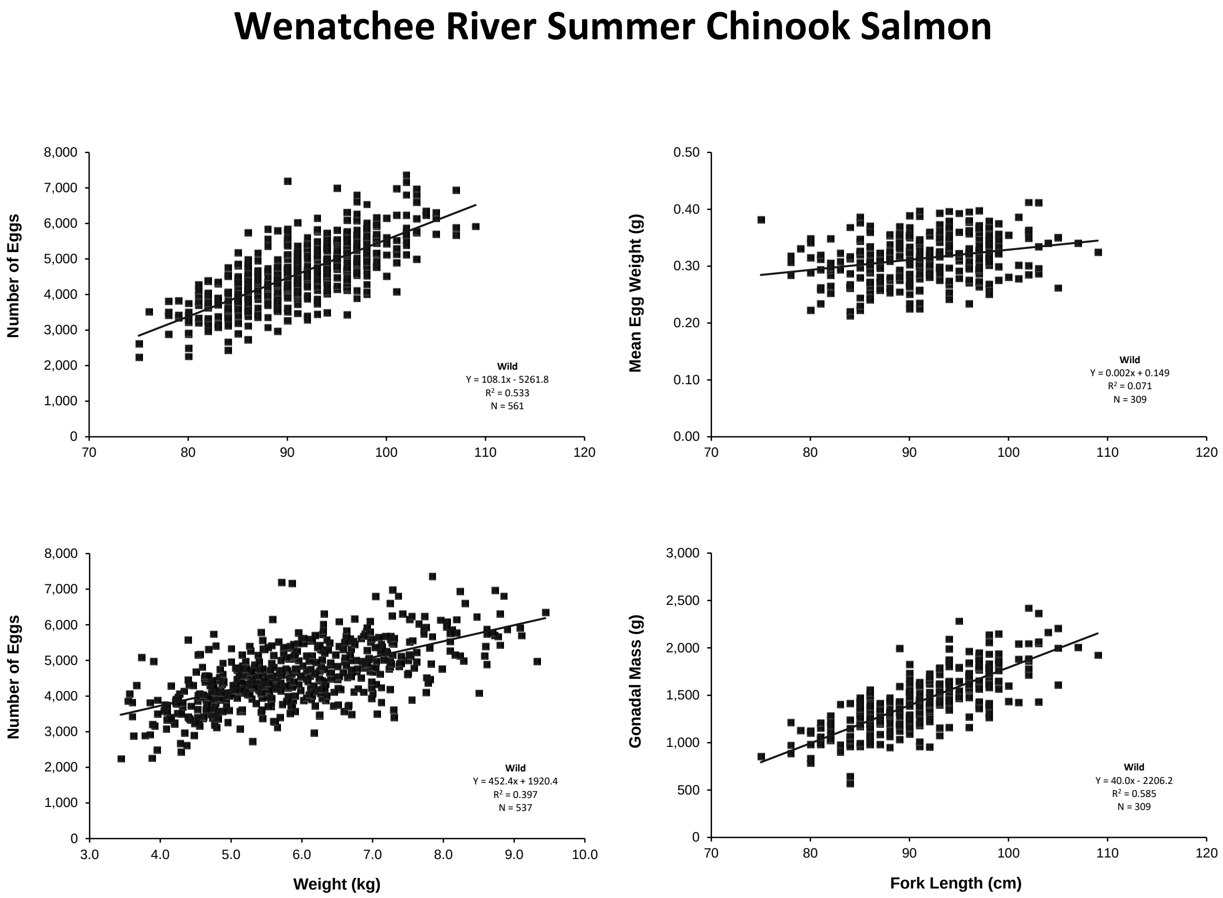


Figure 19. Relationships between fecundity (number of eggs, mean weight of eggs, and gonadal mass) and size (POH length and weight) for natural-origin Wenatchee River summer Chinook Salmon for return years 2014-2018. No hatchery-origin fish are collected for the Wenatchee Summer Chinook Salmon program. Simple linear regression statistics are shown in each figure.

Methow River Program

Age-at-Maturity Analysis—For the complete time series (1993-2018), age at maturity differed significantly between hatchery- and natural-origin female (Yates' Chi-square = 805.448, P = 0.000) and male summer Chinook Salmon (Yates' Chi-square = 897.500, P = 0.000) in the Methow River (Figure 20). Most females returned at ocean-age-3; however, a larger proportion of hatchery-origin fish returned at younger ocean ages than did natural-origin fish. Specifically, a higher proportion of natural-origin females returned as ocean-age-4 fish than did hatchery-origin females. A higher proportion of hatchery-origin males returned as ocean-age-2 fish, while a higher proportion of natural-origin males returned as ocean-age-3 fish. As with female summer Chinook, hatchery-origin males returned at a younger ocean age than did natural-origin males.

There was a change in age at maturity before (1993-2014) and after (2014-2018) reduction in hatchery production numbers (Figure 20). During both the before and after periods, age at maturity differed significantly between hatchery and natural-origin female (Before: Yates' Chi-square = 578.136, P = 0.000; After: Yates' Chi-square = 222.104, P = 0.000) and male

(Before: Yates' Chi-square = 708.532, P = 0.000; After: Yates' Chi-square = 177.916, P = 0.000) summer Chinook Salmon. Compared to the before period, nearly equal proportions of natural-origin females returned as ocean-age-3 and 4 fish during the after period, while there was little change in age at maturity for hatchery-origin females between the before and after periods. A larger proportion of hatchery-origin males returned as ocean-age-2 fish during the after period, while a larger proportion of natural-origin males returned as ocean-age-4 fish during the after period compared to the before period.

Size-at-Maturity Analysis—For the complete time series (1993-2018), size at maturity differed significantly between hatchery- and natural-origin summer Chinook Salmon in the Methow River (GLM ANOVA F = 6.796, P = 0.009) (Figure 21). Size at maturity was significantly affected by age, origin, and sex (GLM ANOVA F = 10.503, P = 0.000). For females, ocean-age-2 natural-origin fish were larger on average than ocean-age-2 hatchery-origin fish (mean differences = 3 cm). For males, ocean-age-0 and 1 natural-origin fish were larger on average than ocean-age-0, and 1 hatchery-origin fish, respectively (mean differences = 6 and 3 cm, respectively). Sample sizes for ocean-age-5 fish for both sexes are too small to evaluate origin differences adequately.

There were significant differences in the size at maturity before and after reduction in hatchery production numbers (GLM ANOVA F = 123.000, P = 0.000) (Figure 21). For most age groups, both hatchery- and natural-origin fish were smaller following the reduction in hatchery production, with the change in size ranging from 2-5 cm on average. During both time periods for both hatchery- and natural-origin fish, older males were larger on average than females of the same age (GLM ANOVA F = 4.363, P = 0.013).

Fecundity Analysis—Because only natural-origin summer Chinook Salmon are collected for broodstock for the Methow program, there are no comparisons of fecundity relationships between hatchery and natural-origin summer Chinook Salmon in the Methow River. Based on examination of natural-origin fish, there were significant linear relationships between female size and fecundity, mean egg weight, and gonadal mass for the combined years 2014-2018 (Figure 22).

In contrast, both hatchery and natural-origin summer Chinook Salmon fecundity data are available for the Wells summer Chinook Salmon program, although sample sizes of natural-origin fish are small. Analyses of these fish indicated significant linear relationships between female size and fecundity, mean egg weight, and gonadal mass for both hatchery and natural-origin summer Chinook Salmon for the combined years 2014-2018 (Figure 23). There were no differences in relationships between hatchery and natural-origin fish for fork length and fecundity (ANCOVA F = 0.725, P = 0.395), female weight and fecundity (ANCOVA F = 0.617, P = 0.433), fork length and mean egg weight (ANCOVA F = 0.308, P = 0.579), and fork length and gonadal mass (ANCOVA F = 0.006, P = 0.940).

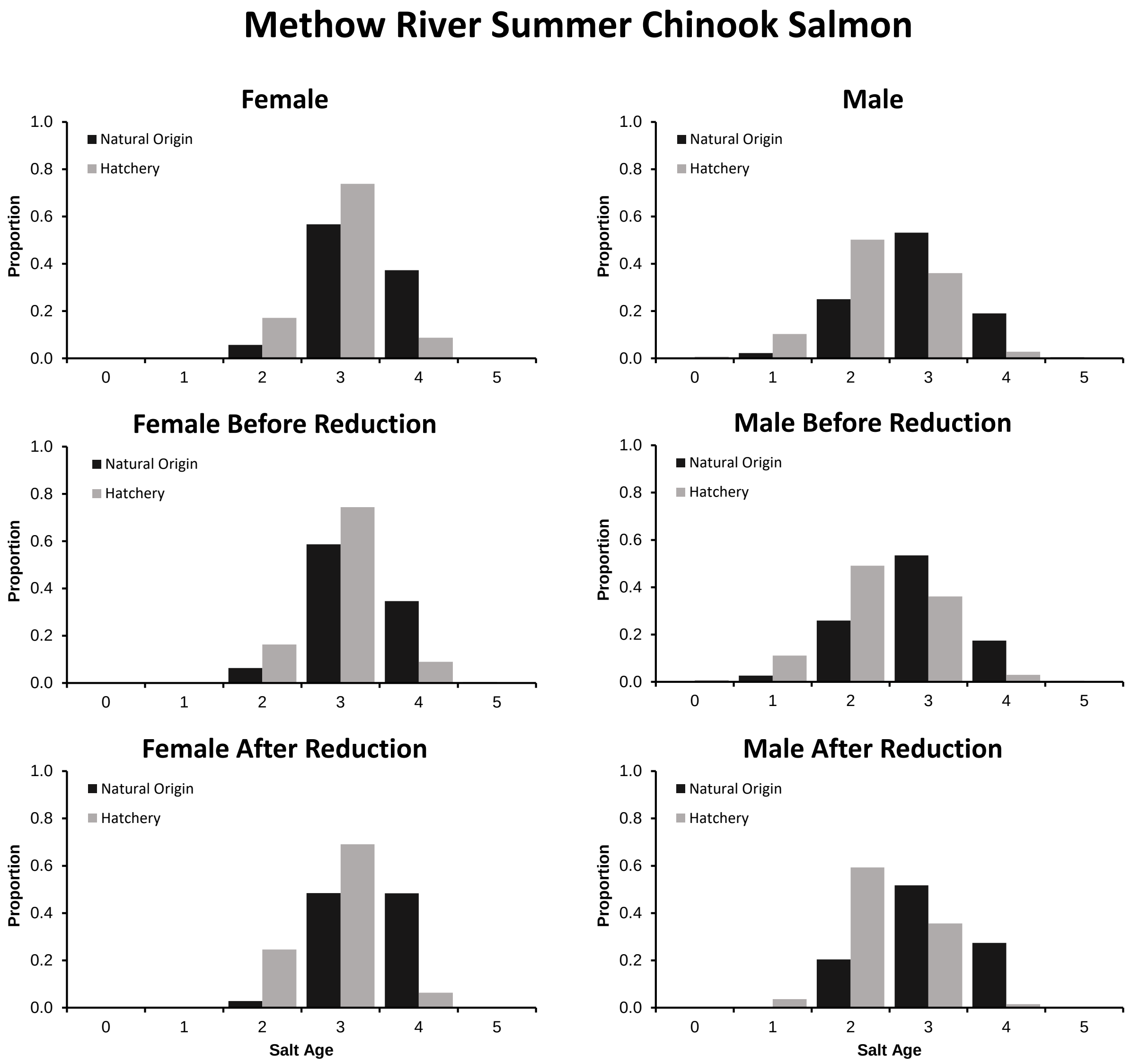


Figure 20. Proportion of hatchery- and natural-origin female and male summer Chinook Salmon spawners of different ocean (salt) ages sampled on the spawning grounds in the Methow River basin for the combined years 1993-2018 (top row), before reduction (1993-2014; middle row), and after reduction (2015-2018; bottom row) in hatchery smolt production. Sample sizes for females = 3,935 natural-origin and 2,774 hatchery-origin fish and for males = 3,927 natural-origin and 2,537 hatchery-origin fish for the combined analysis. For the before analysis, sample sizes for females = 3,186 natural-origin and 2,489 hatchery-origin fish and for males = 3,310 natural-origin and 2,262 hatchery-origin fish; and for the after analysis, sample sizes for females = 749 natural-origin and 285 hatchery-origin fish and for males = 617 natural-origin and 275 hatchery-origin fish.

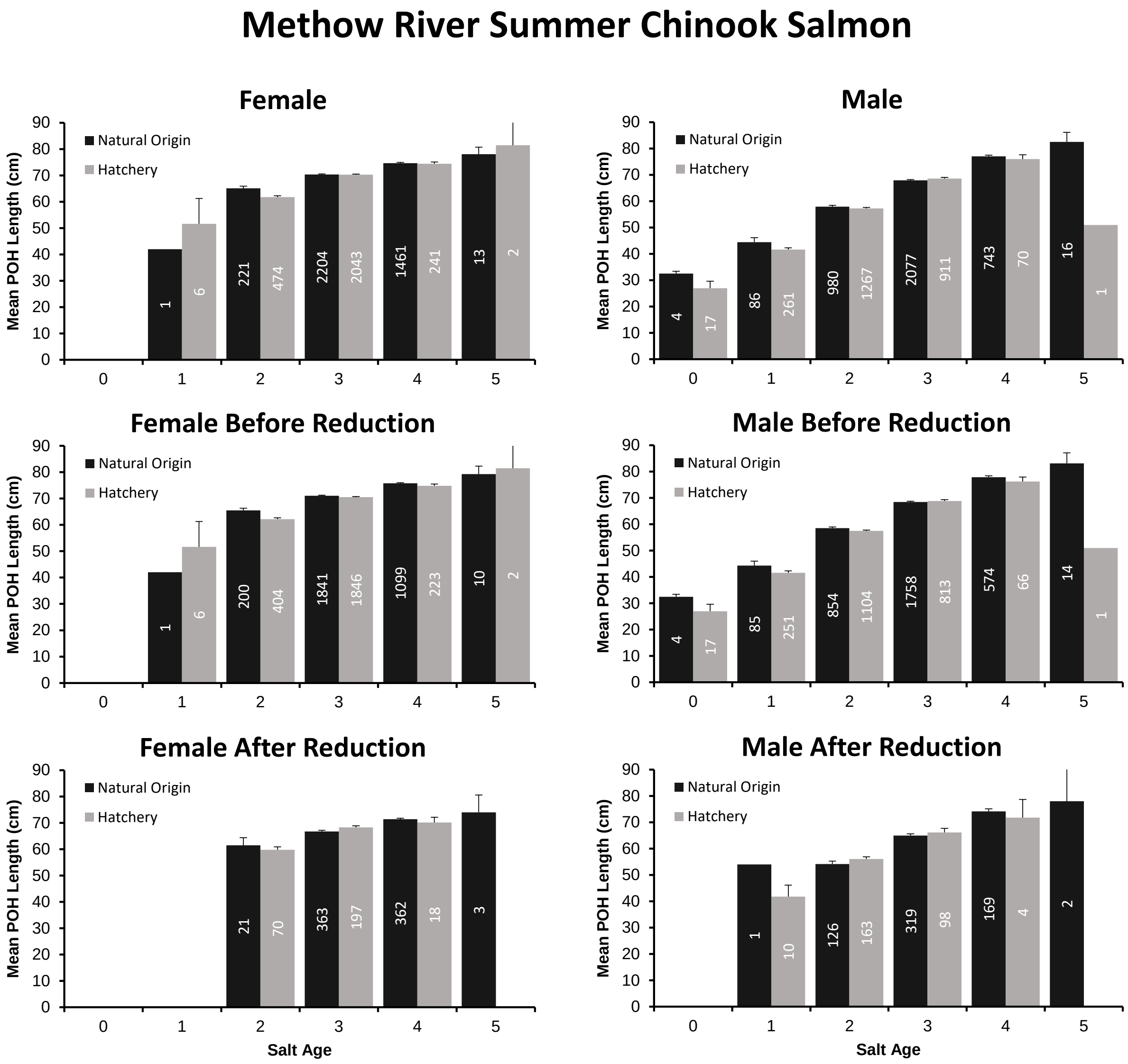


Figure 21. Mean POH length (cm) and 95% CI of hatchery- and natural-origin female and male summer Chinook Salmon spawners of different ocean (salt) ages sampled on the spawning grounds in the Methow River basin for the combined years 1993-2018 (top row), before reduction (1993-2014; middle row), and after reduction (2015-2018; bottom row) in hatchery smolt production. Sample sizes are shown within each bar.

Methow River Summer Chinook Salmon

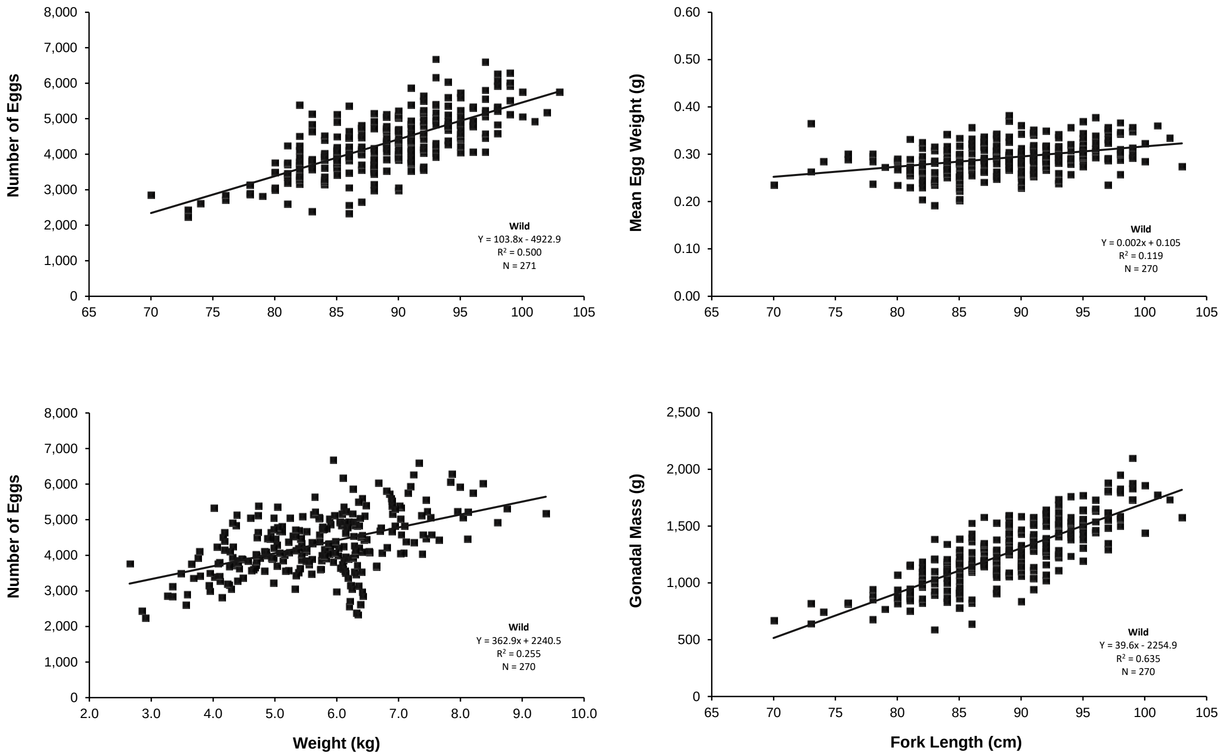


Figure 22. Relationships between fecundity (number of eggs, mean weight of eggs, and gonadal mass) and size (POH length and weight) for natural-origin Methow River summer Chinook Salmon for return years 2014-2018. No hatchery-origin fish are collected for the Methow Summer Chinook Salmon program. Simple linear regression statistics are shown in each figure.

Wells Summer Chinook Salmon

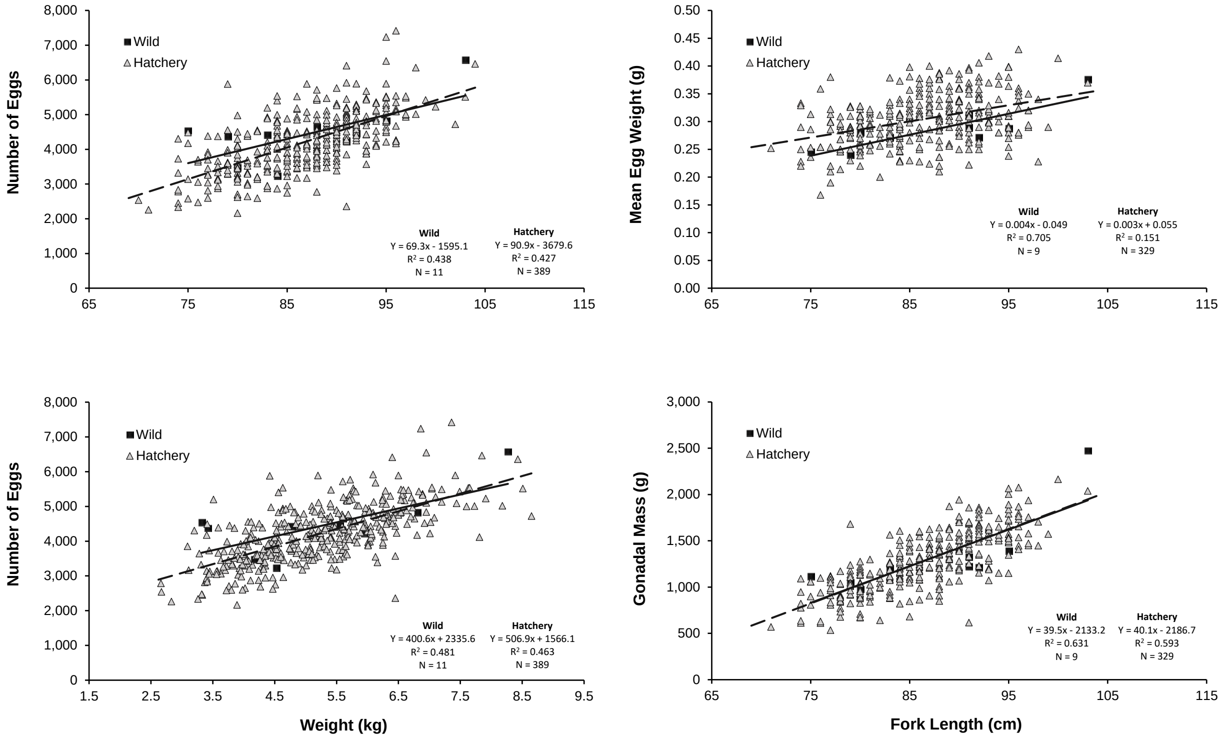


Figure 23. Relationships between fecundity (number of eggs, mean weight of eggs, and gonadal mass) and size (POH length and weight) for hatchery- (dashed line) and natural-origin (solid line) Wells summer Chinook Salmon for return years 2014-2018. Simple linear regression statistics are shown in each figure.

Chelan River Program

Age-at-Maturity Analysis—For the complete time series (2000-2018), age at maturity differed significantly between hatchery- and natural-origin female (Yates' Chi-square = 432.131, P = 0.000) and male summer Chinook Salmon (Yates' Chi-square = 98.590, P = 0.000) in the Chelan River (Figure 24). A larger proportion of hatchery-origin fish returned at younger ocean ages than did natural-origin fish. Most hatchery-origin females returned at ocean-age-3, and nearly all natural-origin females returned at ocean-ages 3 or 4, in nearly equal proportions. A higher proportion of hatchery-origin males returned as ocean-age-1 and 2 fish, while a higher proportion of natural-origin males returned as ocean-age-3 and 4 fish.

Because hatchery-origin summer Chinook Salmon from several different hatchery programs have spawned in the Chelan River since before the 1990s, there is no comparison of before and after periods for Chelan River summer Chinook Salmon.

Size-at-Maturity Analysis—For the complete time series (2000-2018), size at maturity differed significantly between hatchery and natural-origin summer Chinook Salmon in the

Chelan River (GLM ANOVA F = 55.285, P = 0.000) (Figure 25). Size at maturity was significantly affected by age, origin, and sex (GLM ANOVA F = 4.055, P = 0.017). For both females and males, hatchery-origin fish were generally larger than natural-origin fish across most age groups. Those differences in sizes were on average 2-5 cm depending on age group.

Because hatchery-origin summer Chinook Salmon from several different hatchery programs have spawned in the Chelan River since before the 1990s, there is no comparison of before and after periods for Chelan River summer Chinook Salmon.

Fecundity Analysis—Because only hatchery-origin summer Chinook Salmon are collected for broodstock for the Chelan River summer Chinook Salmon program, there are no comparisons of fecundity relationships between hatchery- and natural-origin summer Chinook Salmon in the Chelan River. Based on examination of hatchery-origin summer Chinook Salmon, there were significant linear relationships between female size and fecundity, mean egg weight, and gonadal mass for the combined years 2014-2018 (Figure 26).

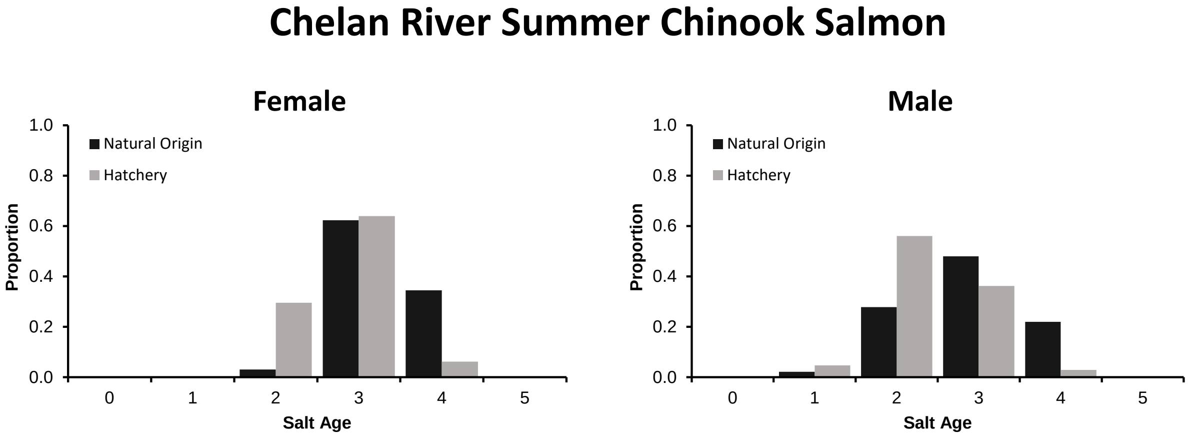


Figure 24. Proportion of hatchery- and natural-origin female and male summer Chinook Salmon spawners of different ocean (salt) ages sampled on the spawning grounds in the Chelan River for the combined years 2000-2018. Sample sizes for females = 891 natural-origin and 1,262 hatchery-origin fish and for males = 273 natural-origin and 444 hatchery-origin fish for the combined analysis.

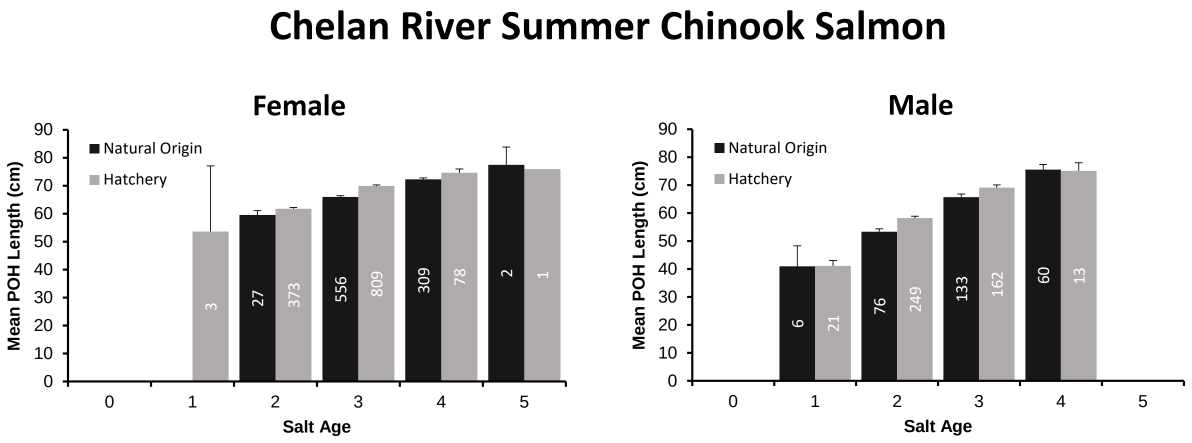


Figure 25. Mean POH length (cm) and 95% CI of hatchery- and natural-origin female and male summer Chinook Salmon spawners of different ocean (salt) ages sampled on the spawning grounds in the Chelan River for the combined years 2000-2018. Sample sizes are shown within each bar.

Chelan River Summer Chinook Salmon

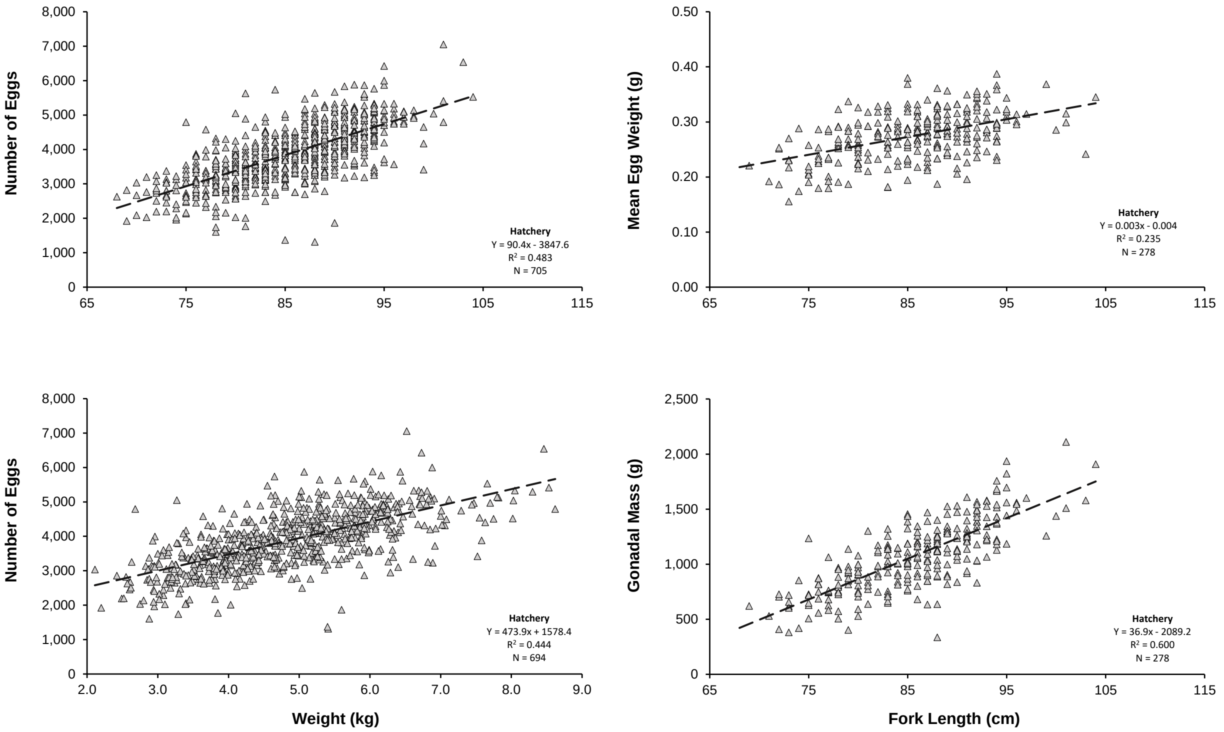


Figure 26. Relationships between fecundity (number of eggs, mean weight of eggs, and gonadal mass) and size (POH length and weight) for hatchery-origin Chelan River summer Chinook Salmon for return years 2014-2018. No natural-origin fish are collected for the Chelan Summer Chinook Salmon program. Simple linear regression statistics are shown in each figure.

Discussion

We observed similar patterns for most hatchery- and natural-origin adult Spring Chinook and Summer Chinook Salmon for all hatchery programs and these patterns were generally consistent with published studies from other locations inside and outside the Columbia River Basin (Knudsen et al. 2006; 2008). As such, similar mechanisms are likely influencing hatchery programs at a broad scale. For age at maturity, hatchery-origin fish universally returned at a younger age than natural-origin fish, and with a few exceptions, there were no changes in programs with a before and after period. While the difference in age structure between hatchery- and natural-origin populations were statistically significant, in all cases the predominate age at maturity was the same. For example, in Spring Chinook the large majority of male and female hatchery- and natural-origin fish returned at age-4. For Summer Chinook, the majority of hatchery- and natural-origin females returned at salt age-3, with the majority of males distributed between salt age-2 and age-3. All of the Spring Chinook hatchery programs produced few age-5 returns relative to the proportions of natural-origin age-5 returns in the respective populations and likewise for the age-4 returns in the summer Chinook programs. A notable change from the before to after periods was the reduction in age-3 fish returning to Nason Creek. All hatchery-origin fish in Nason Creek in the before period were strays. With the reduction in release number in the after period from nearby hatchery programs, there were likely fewer strays, which are often age-3 fish, returning to Nason Creek.

The size at maturity of returning adult fish was significantly affected by age and sex and in some cases origin and period. However, when matched by age and sex, the differences in size by origin and period that were statistically significant were minor and likely of little biological relevance. For example, the largest difference of all the age and sex matched comparisons was for age-3 females in the Chiwawa River, where hatchery-origin fish were on average 9 cm larger than natural-origin fish, and where the sample size for natural-origin fish was n = 3. In most cases, the differences in size by origin were on the order of 2-3 cm for significant and non-significant tests.

For all populations the fecundity metrics were significantly affected by fish size and weight. In the Chiwawa River and Twisp River, differences in fecundity between hatchery- and natural-origin fish were significant for length vs. fecundity and egg weight. A visual examination of the relationships suggests that in the Chiwawa River the differences between the hatchery- and natural-origin fork length-fecundity relationship was driven by a larger number of smaller hatchery-origin females with low fecundity. The difference in the length to egg-weight relationship, however, was explained by higher egg weight of smaller hatchery-origin females. In the Twisp, conclusions were more tenuous due to the small sample size (e.g., n = 10). As with size at maturity, the few differences in the fecundity metrics between hatchery- and natural-origin fish were small and may have little biological relevance.

Generally, and beyond the Upper Columbia Basin, hatchery-origin fish return at an early age (Tillotson et al. 2021). This is likely explained by the relatively large size of smolts at release, which leads to earlier maturation and thus an early return to fresh water (Vøllestad et al. 2004). Managers of hatchery programs in the upper Columbia River and in most other areas have chosen to produce bigger smolts than their natural-origin counterparts in order to achieve high post-release survival of these fish (Feldhaus et al. 2016). Improvements in hatchery management techniques have been implemented at the hatchery programs analyzed here to reduce early maturation, specifically aimed at reducing mini-jacks (Harstad et al. 2018). These efforts will likely have cascading effects through the age classes and future evaluations may show improvements to the overall age-at-return structure. However, trade-offs associated with post-release survival and age at maturation will occur. One of the main consequences of deviating from the natural-origin fish growth and size template is the deviation of some phenotypic characteristics of returning fish. Larger smolts typically have higher post-release survival (Gosselin et al. 2019; Vøllestad et al. 2004; but see Feldhaus et al. 2016) but also mature at younger ages and smaller sizes, which are traits associated with lower fecundity (Claiborne et al. 2011; Tattam et al. 2015). Yet, hatchery fish typically have higher adult-to-adult survival rates than natural-origin fish (Pearsons et al., Chapter 1 of this report), which on a broodyear-basis could result in a larger hatchery-origin egg escapement despite lower fecundities on a per-fish basis.

Managers are in the position of considering the many complicated, and often mutually exclusive trade-offs between hatchery-origin fish survival and matching the phenotypic traits of natural-origin fish (Larsen et al. 2019). For example, they must consider the potential influences of parental effects in the broodstock on age and size at return (Church et al. 2021; Forest et al.

2017), phenotypic and phenologic consequences of synergistic interactions between rearing practices and parental phenotype (Winsor et al. 2021), and local adaptations potentially mediating age and size at return (McKinney et al. 2020). Additionally, managers must also weigh the risks to population fitness posed by program objectives (Waters et al. 2018).

Future analyses of these metrics should consider changes over time and consider trends between hatchery-origin and natural-origin fish. Declines in age at maturity and size at maturity are a Pacific-wide concern (Oke et al. 2020; Ohlberger et al. 2018) and therefore a temporal analysis of the dataset generated for the monitoring of these hatchery programs would benefit the region. Finally, data used in these analyses did not accurately account for the contribution of minijacks to cohort age structure, when minijacks have been found to comprise a substantial component of total "returns" from local programs, influencing apparent HRRs and SARs (Harstad et al. 2018).

Acknowledgments

We thank the many people who produced fish and collected data presented in this manuscript. Those that helped produce the fish were personnel from the Washington Department of Fish and Wildlife, Aquaseed Corporation, and the United States Fish and Wildlife Service. Those that helped collect data included personnel from the aforementioned agencies as well as Chelan Public Utility District and Douglas Public Utility District. We also thank the hatchery committees and co-managers who originally envisioned these programs and that adaptively managed the programs. We thank Grant, Chelan, and Douglas County Public Utility Districts for funding this work.

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Numbers and Sizes of Fish Released from Hatcheries in the Upper Columbia Basin

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Abstract

Chelan, Douglas, and Grant PUDs produce salmon and steelhead for mitigation under various agreements including the Rock Island Habitat Conservation Plan (HCP), the Rocky Reach HCP, the Wells HCP, and the Priest Rapids Settlement Agreement and associated Biological Opinion. The various hatchery programs are monitored for the number of fish released, as well as metrics for fish size at release and condition. The programs include Summer Chinook Salmon, Spring Chinook Salmon, and summer steelhead produced and released at a variety of facilitates in the Wenatchee River Subbasin, Methow River Subbasin, and Columbia River. Programs generally met or exceeded the release-number targets. Specific programs did not meet the release-number targets in all years, but all programs met or exceeded targets in the majority of years, with the exception of the White River spring Chinook Salmon captive broodstock program. This program was in development for all of its history and tested numerous fish culture and release strategies. Therefore, the program was not able to meet targets that remained consistent across years. Most programs met or were close to meeting the CV target on average. Meeting the CV targets for steelhead programs was more difficult than for the Chinook Salmon programs. Meeting fish-per-pound (fpp) targets was more difficult in Spring Chinook Salmon and conservation steelhead programs, potentially because these programs use natural-origin broodstock. Spring Chinook Salmon exhibited near-isometric growth. Steelhead exhibited negative allometric growth, as did Wells and Methow summer Chinook Salmon. However, Wenatchee and Chelan Falls summer Chinook Salmon exhibited isometric or positive allometric growth. Condition factors across all programs were very close to or exceeded 1. Trade-offs between post-release survival and age at maturation influence hatchery rearing strategies. Large Chinook Salmon generally survive better than small fish, but they also are more prone to mature at younger ages. Hatchery programs that use natural-origin fish for broodstock may experience higher levels of precocial maturation than those that use hatchery-origin fish for broodstock. In addition, larger fish also pose ecological risks to other fish through mechanisms such as competition or predation. In general, the length targets, and some of the metrics that used a single value (e.g., length and weight) associated with a range of fpp targets, were not useful. Adaptation of targets may occur to achieve a better suite of benefits among the many trade-offs involved in growing fish to a target size or weight.

Introduction

Chelan, Douglas, and Grant PUDs produce salmon and steelhead for mitigation under various agreements including the Rock Island Habitat Conservation Plan (HCP), the Rocky Reach HCP, the Wells HCP, and the Priest Rapids Settlement Agreement. The targets for number of fish to be produced and fish per pound were established in the Habitat Conservation Plans, Hatchery and Genetic Management plans, hatchery recalculation implementation plans, Hatchery Monitoring and Evaluation Plan, or were subsequently adjusted by the HCP Hatchery Committees or Priest Rapids Hatchery Sub-Committee through formal processes. The various hatchery programs are monitored for the number of fish released, as well as metrics for fish size at release and condition. The programs include Summer Chinook Salmon, Spring Chinook Salmon, and summer steelhead, produced and released at a variety of facilitates in the Wenatchee River Subbasin, Methow River Subbasin, and Columbia River.

Methods

Study Area

The study area encompasses the Wenatchee River Subbasin, the Methow River Subbasin, and the Columbia River. The hatchery programs, fish production facilities, and release locations are provided in Table 1.

Table 1. Fish production facilities and release locations.

Program	Type	Facility	Release Location
Chiwawa River Spring Chinook	Conservation	Eastbank Hatchery and Chiwawa Acclimation Facility	Chiwawa River
Nason Creek Spring Chinook	Conservation and Safety-Net	Eastbank Hatchery and Nason Creek Acclimation Facility	Nason Creek
White River Spring Chinook	Conservation	Aquaseed; Little White Salmon National Fish Hatchery; various acclimation sites	White River; Lake Wenatchee; Wenatchee River
Methow River Spring Chinook	Conservation	Methow Hatchery and Goat Wall Acclimation Pond	Methow River
Chewuch River Spring Chinook	Conservation	Methow Hatchery and Chewuch Acclimation Pond	Chewuch River
Twisp River Spring Chinook	Conservation	Methow Hatchery and Twisp Acclimation Pond	Twisp River
Wenatchee River Summer Steelhead	Conservation and Safety-Net	Eastbank Hatchery	Wenatchee River
Twisp River Summer Steelhead	Conservation	Winthrop National Fish Hatchery and Wells Hatchery	Twisp River, Methow River
Methow River Summer Steelhead	Safety-Net	Wells Hatchery	Methow River
Columbia River Summer Steelhead	Safety-Net	Wells Hatchery	Columbia River
Wenatchee River Summer Chinook	Conservation/Harvest	Eastbank Hatchery and Dryden Acclimation Facility	Wenatchee River
Chelan Falls Summer Chinook	Harvest	Chelan Falls Hatchery	Chelan River
Wells Yearling Summer Chinook	Harvest	Wells Hatchery	Columbia River
Wells Subyearling Summer Chinook	Harvest	Wells Hatchery	Columbia River
Methow River Summer Chinook	Conservation/Harvest	Eastbank Hatchery and Carlton Acclimation Facility	Methow River

Hatchery Production Targets

The targets for number of fish to be produced and fish per pound were established in the Habitat Conservation Plans and Hatchery and Genetic Management plans, hatchery recalculation implementation plans, Hatchery Monitoring and Evaluation Plan, or formally adjusted by the

Hatchery Committees or Priest Rapids Coordination Committee's Hatchery Sub-Committee. The Committees also adopted targets for coefficient of variation. Fish weight is described by the fish-per-pound (fpp) targets. The Committees adopted the concept of using Condition Factor targets, but such targets have not yet been identified. Targets for mean fish length have not been formally adopted in the Monitoring and Evaluation (M&E) Plan but are reported in the M&E Annual Reports. Previous fish length and weight targets obtained from Piper (1952) were not appropriate based on empirical data for Upper Columbia populations and were abandoned. Length targets in the M&E Reports are either the same as, or similar to, the Piper targets and are not compatible with the fpp targets. Meeting these fpp targets is typically mutually exclusive of meeting the length target. All the rearing targets and metrics are presented in Table 2. Metrics that do not have quantitative targets are presented in summary statistics.

Table 2. Hatchery program production and fish size targets.

Program	Production Target	Length Target (mm)	CV	Weight (g)	Fish/Pound
Chiwawa River Spring Chinook	144,026	155	9	37.8	18
Nason Creek Spring Chinook	223,670	155	9	37.8	18-24
White River Spring Chinook	150,000	NA	9	NA	18-24
Methow River Spring Chinook	133,249	137	9	30.2	15
Chewuch River Spring Chinook	60,516	136	9	30.2	15
Twisp River Spring Chinook	30,000	135	9	30.2	15
Wenatchee River Summer Steelhead	247,300	191	9	75.6	6
Twisp River Summer Steelhead	48,000	191	9	75.6	6
Methow River Summer Steelhead	100,000	191	9	75.6	6
Columbia River Summer Steelhead	160,000	191	9	75.6	6
Wenatchee River Summer Chinook	500,001	163	9	30.0-45.4	10-18
Chelan River Summer Chinook	576,000	161	9	20.0-45.4	10-22
Wells Yearling Summer Chinook	320,000	168	7	45.4	10
Wells Subyearling Summer Chinook	484,000	NA	7	9.1	50
Methow River Summer Chinook	200,000	163	9	45.4	13-18

Data Collection and Derived Metrics

For each program, fish were enumerated during coded wire tagging and/or marking. Because marking and tagging often occurred weeks to several months before fish were released, hatchery managers kept track of fish that died before release and subtracted those fish from the number marked. Thus, the total number of fish released from a specific program was the number of fish marked minus the number of marked fish that died before release (and any live fish retained for early maturation studies or other studies).

To estimate fish size, a sample of about 200 fish was randomly collected from each stock using cast nets or dip nets when fish were crowded. Each fish was measured for fork length (mm) and weighed to the nearest 0.1 g. Arithmetic means were calculated for both length (L) and weight (W), and weight was also converted to fish per pound (fpp). The coefficient of variation (CV) for length was calculated as the ratio of the sample standard deviation to the sample mean. Because this estimate is generally biased low, the ratio was corrected by multiplying it by (1 + 1/4n), where n = sample size. For each fish we also calculated Fulton Condition Factors using the equation, $K_{FL} = (W/L^3) \times 100{,}000$, where K_{FL} is the condition factor based on fork length (Neumann et al. 2012).

Data Analysis

No statistical analyses were needed to evaluate numbers and sizes (lengths and weights) of fish released from each hatchery program. Here, we simply compared the numbers and sizes of fish released to established management targets. In contrast, we used simple linear regression to evaluate the relationship between fish length and weight for each program. We used common logarithms (log with base 10) to transform both length and weight data for analysis. We examined the *b* parameter (slope of the length-weight relationship) to determine the allometric growth of fish (Neumann et al. 2012). Values of *b* less than 3 indicated that fish body form became slimmer with increasing length (negative allometric growth), values greater than 3 indicated that fish body form became deeper and/or wider with increasing length (positive allometric growth), and values equal to 3 indicated isometric growth.

Results

Wenatchee River Conservation and Safety-Net Summer Steelhead

Number Released—The recent goal of the supplementation program is to release 247,300 (±10%) juvenile Steelhead into the Wenatchee River Subbasin annually. During the six-year period (2012-2017) under the recent goal of the program, the program achieved that goal for five brood years (Figure 1). Numbers released ranged from 195,344-264,758 (average = 241,351) juveniles.

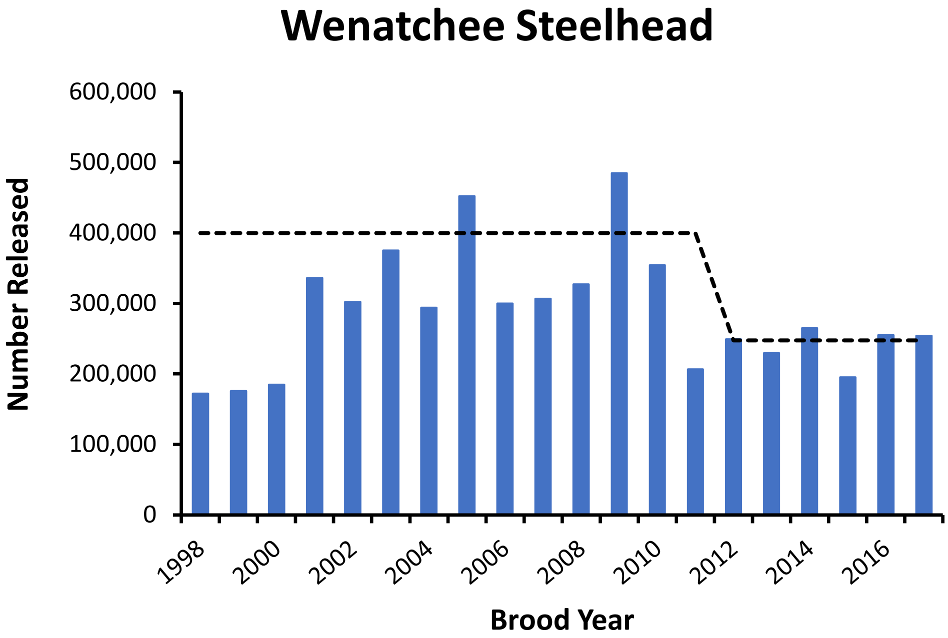

Figure 1. Number of juvenile Steelhead released in the Wenatchee River Subbasin for brood years 1998-2017. The dashed horizontal line represents the target release number (400,000 from 1998-2011 and 247,300 from 2012-2017).

Size at Release—The current goal of the supplementation program (since brood year 2012) is to release juvenile Steelhead in the Wenatchee River Subbasin that average 191-mm long (fork length) with a CV of 9.0, and 75.6 g (6 fish/pound). During the six-year period under the recent goal of the program, the length target has not been reached and the CV target was exceeded in all those years (Figure 2). Mean lengths of fish released ranged from 127-180 mm (average = 154 mm), while CVs ranged from 9-22 (average = 16). In addition, the mean weight target and the fish per pound target was not achieved during the recent six-year period a (Figure 2). Throughout the recent six years, mean weights ranged from 27-71 g (average = 45 g) and fish per pound ranged from 6-17 (average = 11 fish/pound).

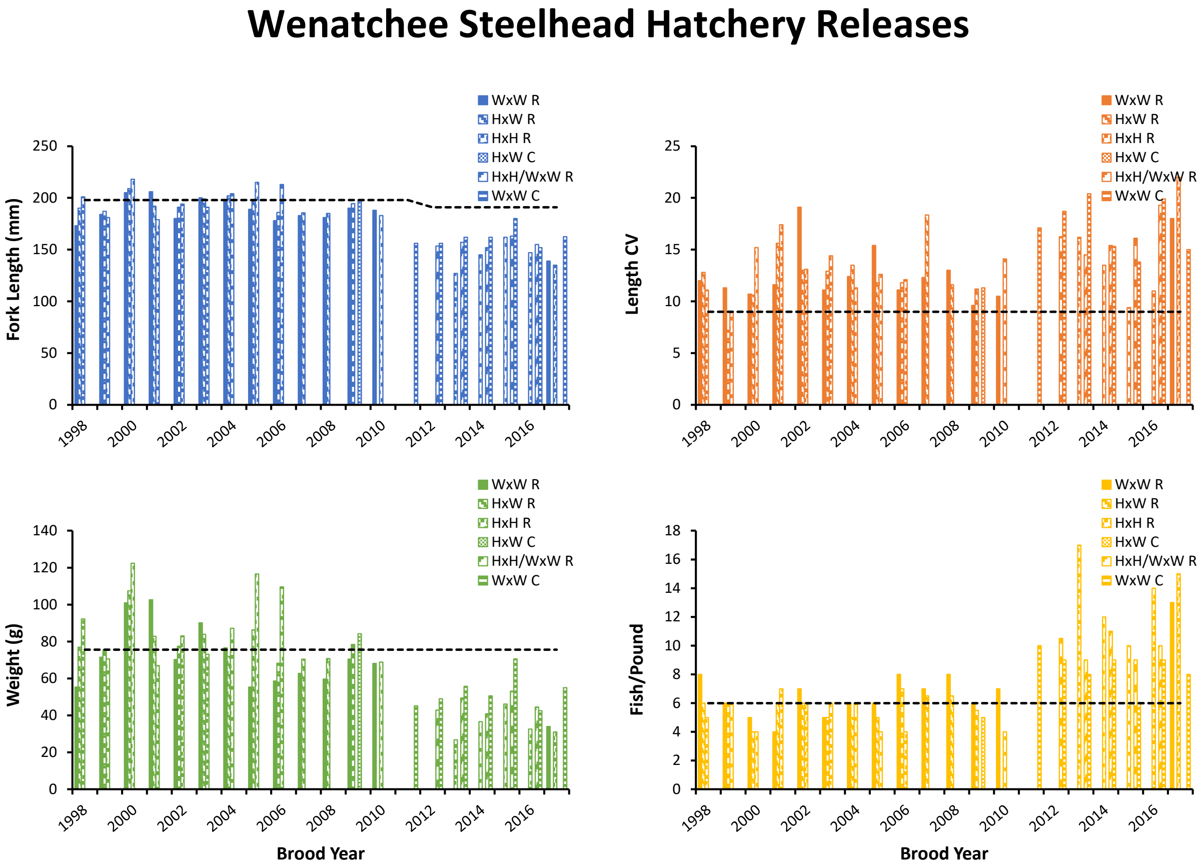

Figure 2. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of juvenile Steelhead released in the Wenatchee River Subbasin for brood years 1998-2017. The dashed horizontal lines represent the target length (198 mm from 1998-2011 and 191 mm from 2012-2017), length CV (9), weight (75.6 g), and fish per pound (6 fish per pound). W = wild (natural-origin fish), H = hatchery-origin fish, R = raceway, and C = recirculating aquatic system.

Length-Weight Relationship—There was a significant relationship between the length and weight of juvenile hatchery Steelhead (Figure 3). Length explained 97% of the variation in weight of juvenile fish. In addition, the relationship indicated a mean condition 2.83 for juvenile hatchery steelhead, suggesting negative allometric growth. The Fulton condition factor averaged 1.12 (range, 0.36-3.55).

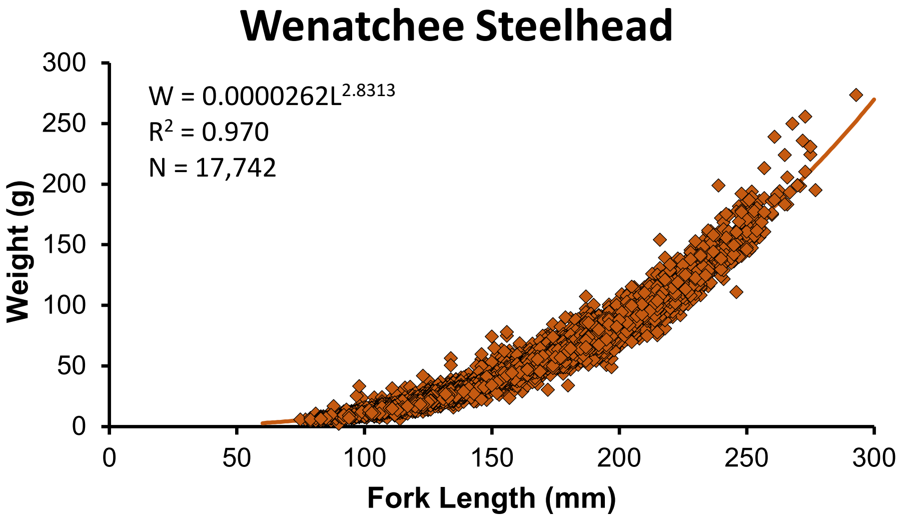

Figure 3. Relationship between fork length (mm) and weight (g) of juvenile Wenatchee River Steelhead sampled before release during 2003-2018.

Methow River Safety-Net Summer Steelhead

Number Released—The recent goal of the supplementation program is to release 100,000 (±10%) juvenile Steelhead into the Methow River annually. During the six-year period under the recent goal of the program, the program achieved that goal in five brood years, and did not achieve it in one brood year (Figure 4). Numbers released ranged from 72,768-106,716 (average = 96,823) juveniles.

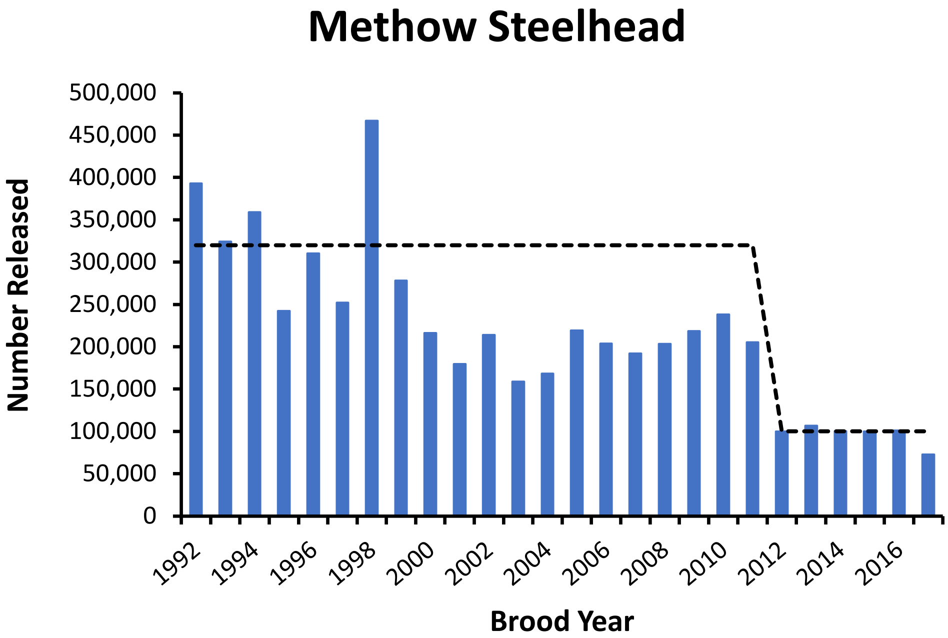

Figure 4. Number of juvenile steelhead released in the Methow River for brood years 1992-2017. The dashed horizontal line represents the target release number (320,000 from 1992-2011 and 100,000 from 2012-2017).

Size at Release—The current goal of the safety-net program (since brood year 2012) is to release juvenile Steelhead in the Methow River that average 191-mm long (fork length) with a CV of 9.0, and 75.6 g (6 fish/pound). During the six-year period under the recent goal of the program, the length target has been reached in nearly all years (Figure 5). The CV target, however, was exceeded in all those years. Mean lengths of fish released ranged from 181-202 mm (average = 190 mm), while CVs ranged from 10-14 (average = 12). In addition, the mean weight and fish-per-pound targets were achieved in most years (Figure 5). Throughout the recent six years, mean weights ranged from 61-81 g (average = 73 g) and fish per pound ranged from 6-8 (average = 6 fish/pound).

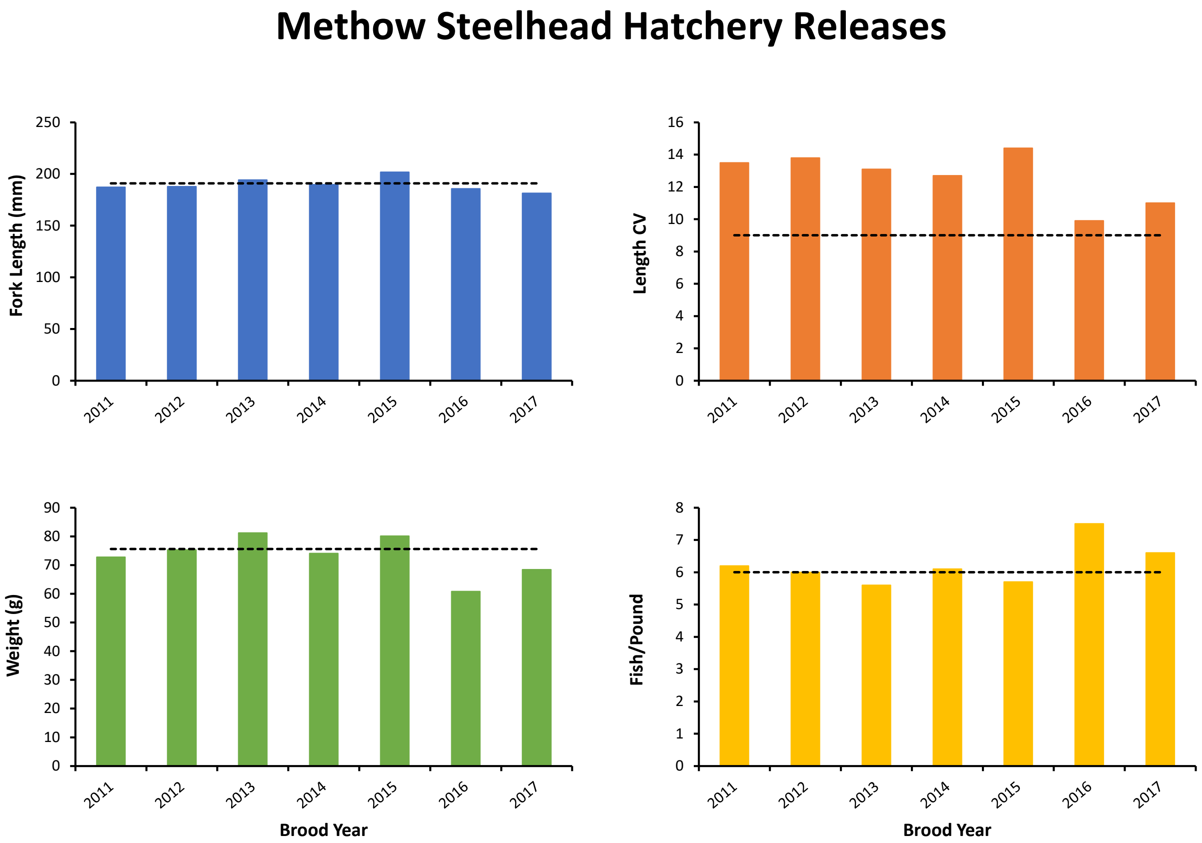

Figure 5. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of juvenile steelhead released in the Methow River for brood years 2011-2017. The dashed horizontal lines represent the target length (191 mm), length CV (9), weight (75.6 g), and fish per pound (6 fish per pound).

Length-Weight Relationship—There was a significant relationship between the length and weight of juvenile hatchery steelhead (Figure 6). Length explained 94% of the variation in weight of juvenile fish. In addition, the relationship indicated a mean condition 2.94 for juvenile hatchery steelhead, suggesting negative allometric growth. The Fulton condition factor averaged 0.99 (range, 0.66-1.56).

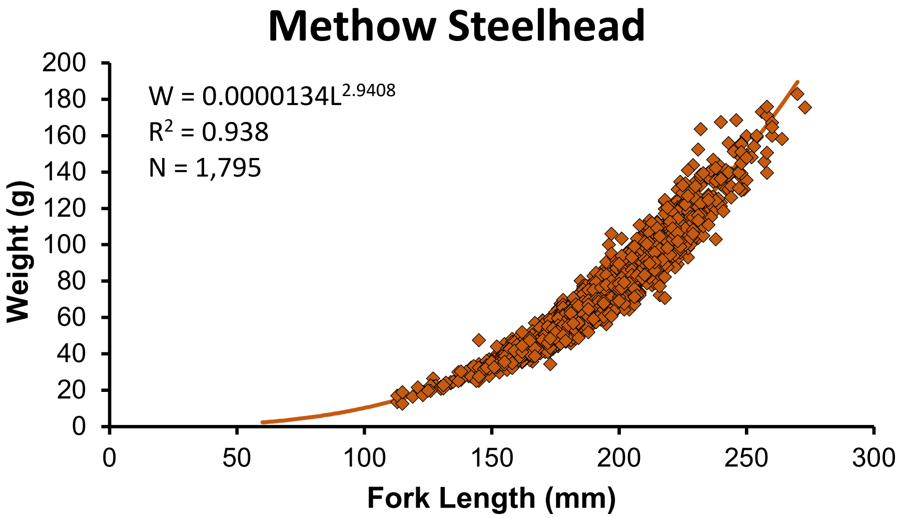

Figure 6. Relationship between fork length (mm) and weight (g) of juvenile Methow River steelhead sampled before release during 2013-2018.

Twisp River Conservation Summer Steelhead

Number Released—The recent goal of the conservation program is to release 48,000 (±10%) juvenile steelhead into the Twisp River annually. During the six-year period under the recent goal of the program, the program achieved that goal in four brood years and exceeded it in two brood years (Figure 7). Numbers released ranged from 50,787-59,226 (average = 54,280) juveniles.

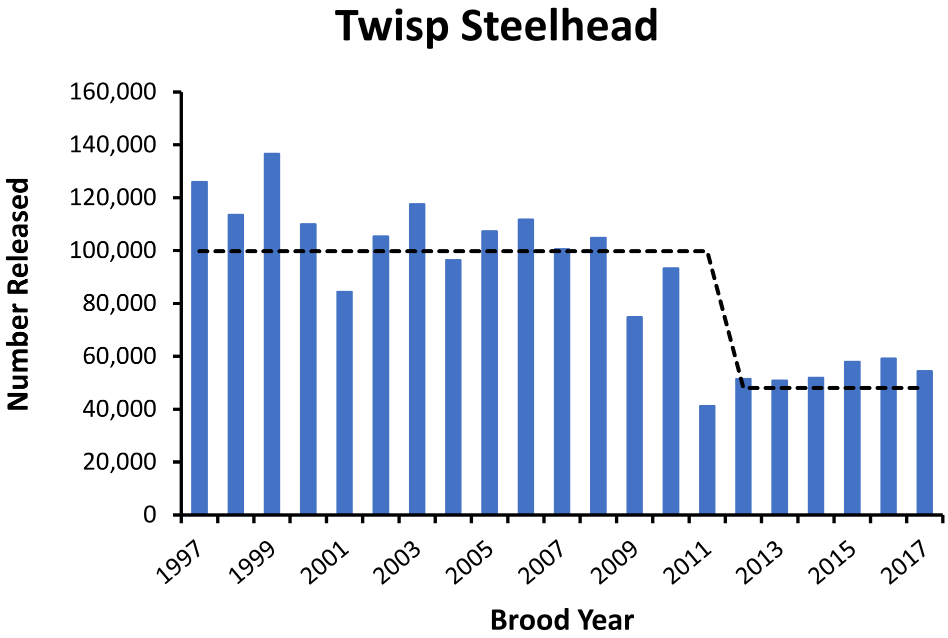

Figure 7. Number of juvenile Steelhead released in the Twisp River for brood years 1997-2017. The dashed horizontal line represents the target release number (99,666 from 1997-2011 and 48,000 from 2012-2017).

Size at Release—The current goal of the supplementation program (since brood year 2012) is to release juvenile Steelhead in the Methow River that average 191-mm long (fork length) with a CV of 9.0, and 75.6 g (6 fish/pound). During the six-year period under the recent goal of the program, lengths were generally below the target while CV exceeded the target (Figure 8). Mean lengths of fish released ranged from 155-182 mm (average = 167 mm), while CVs ranged from 10-15 (average = 13). In addition, the mean weight fell below the target and fish per pound exceeded the target in all years (Figure 8). Throughout the recent six years, mean weights ranged from 44-68 g (average = 54 g) and fish per pound ranged from 7-11 (average = 9 fish/pound).

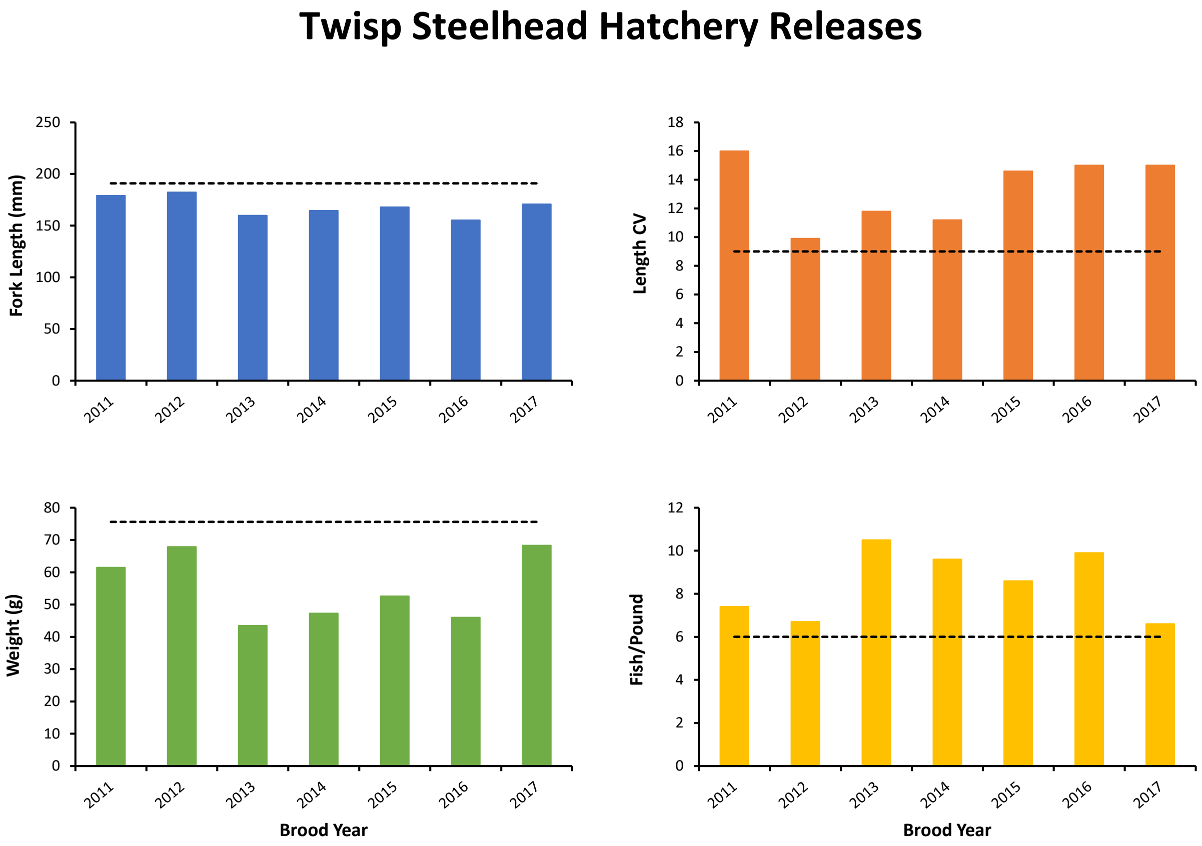
Twisp Steelhead Hatchery Releases

Figure 8. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of juvenile steelhead released in the Twisp River for brood years 2011-2017. The dashed horizontal lines represent the target length (191 mm), length CV (9), weight (75.6 g), and fish per pound (6 fish per pound).

Length-Weight Relationship—There was a significant relationship between the length and weight of juvenile hatchery steelhead (Figure 9). Length explained 94% of the variation in weight of juvenile fish. In addition, the relationship indicated a mean condition 2.94 for juvenile hatchery Steelhead, suggesting negative allometric growth. The Fulton condition factor averaged 1.12 (range, 0.77-1.74).

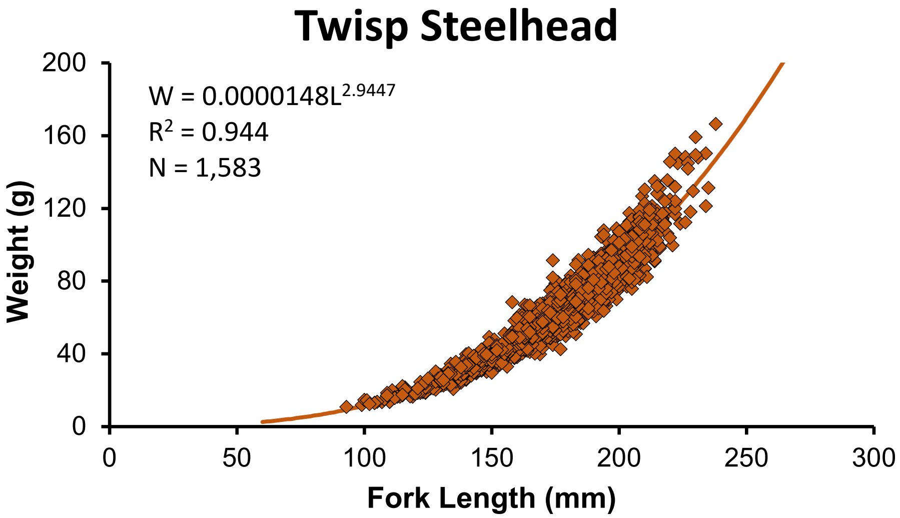

Figure 9. Relationship between fork length (mm) and weight (g) of juvenile Twisp River steelhead sampled before release during 2011-2018.

Columbia River (Wells) Safety-Net Summer Steelhead

Number Released—The recent goal of the safety-net program is to release 160,000 (±10%) juvenile steelhead in the Columbia River from the Wells Hatchery annually. During the five-year period when the Columbia Safety-Net Program began implementation (2013-2017), the release goal of the program was not achieved in one brood year, was achieved in two brood years, and exceeded in two brood years (Figure 10). Numbers released (2011-2017) ranged from 55,541-210,328 (average = 152,535) juveniles.

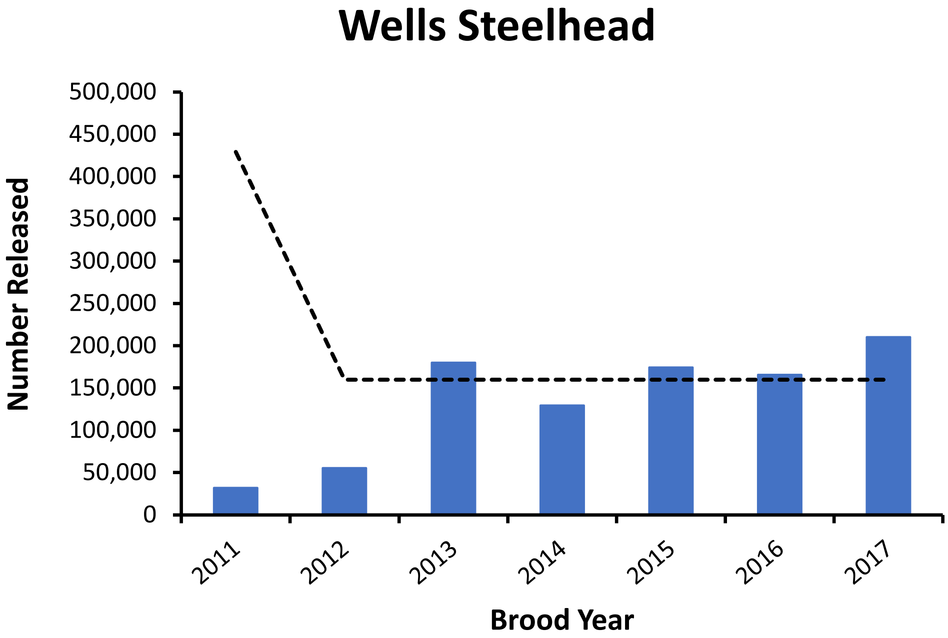

Figure 10. Number of juvenile steelhead released from the Wells Hatchery to the Columbia River for brood years 2011-2017. Note that the current Columbia Safety-Net program (160,000) began releases with brood year 2013. The dashed horizontal line represents the target release number (429,000 before 2012 and 160,000 from 2012-2017).

Size at Release—Information on size at release are presented under the Methow River steelhead section.

Length-Weight Relationship—Information on length-weight relationship is presented under the Methow River steelhead section.

Chiwawa River Spring Chinook Salmon

Number Released—The recent goal of the supplementation program is to release 144,026 (±10%) juvenile spring Chinook Salmon into the Chiwawa River annually. During the five-year period under the recent goal of the program, the program achieved that goal for five brood years (Figure 11). Numbers released ranged from 144,360-163,411 (average = 152,661) juveniles.

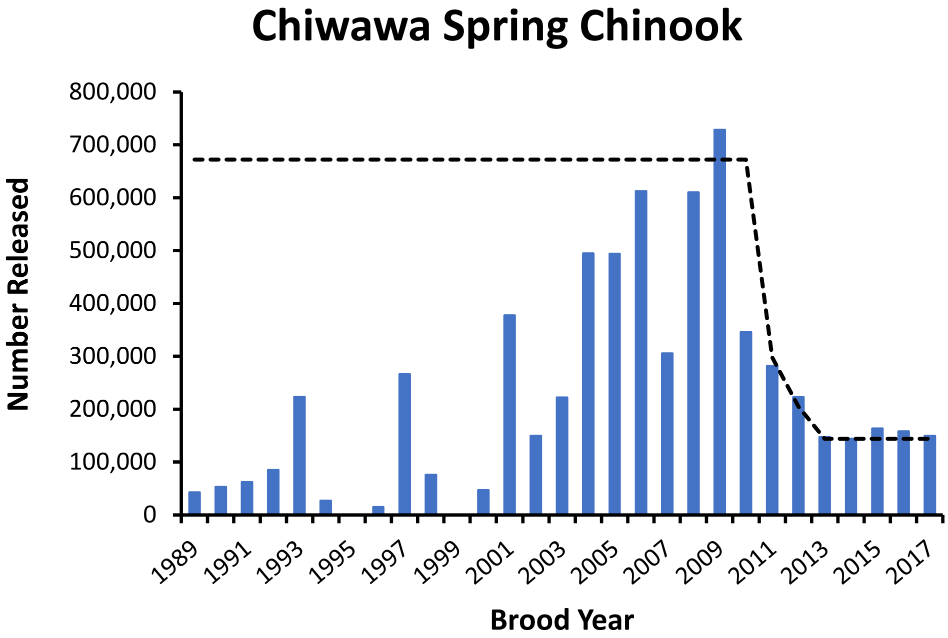

Figure 11. Number of juvenile spring Chinook Salmon released in the Chiwawa River for brood years 1989-2017. The dashed horizontal line represents the target release number (672,000 from 1989-2010, 298,000 in 2011, 205,000 in 2012, and 144,026 from 2013-2017).

Size at Release—The current goal of the supplementation program (since brood year 2012) is to release juvenile spring Chinook Salmon in the Chiwawa River that average 155-mm long (fork length) with a CV of 9.0, and 37.8 g (18 fish/pound). During the six-year period under the recent goal of the program, lengths were below the target while CV generally exceeded the target (Figure 12). Mean lengths of fish released ranged from 127-141 mm (average = 132 mm), while CVs ranged from 7-16 (average = 10). In addition, the mean weight fell below the target and fish per pound met or fell below the target during the six-year period (Figure 12). Throughout the recent six years, mean weights ranged from 25-35 g (average = 28 g) and fish per pound ranged from 13-18 (average = 17 fish/pound).

Chiwawa Spring Chinook Salmon Hatchery Releases

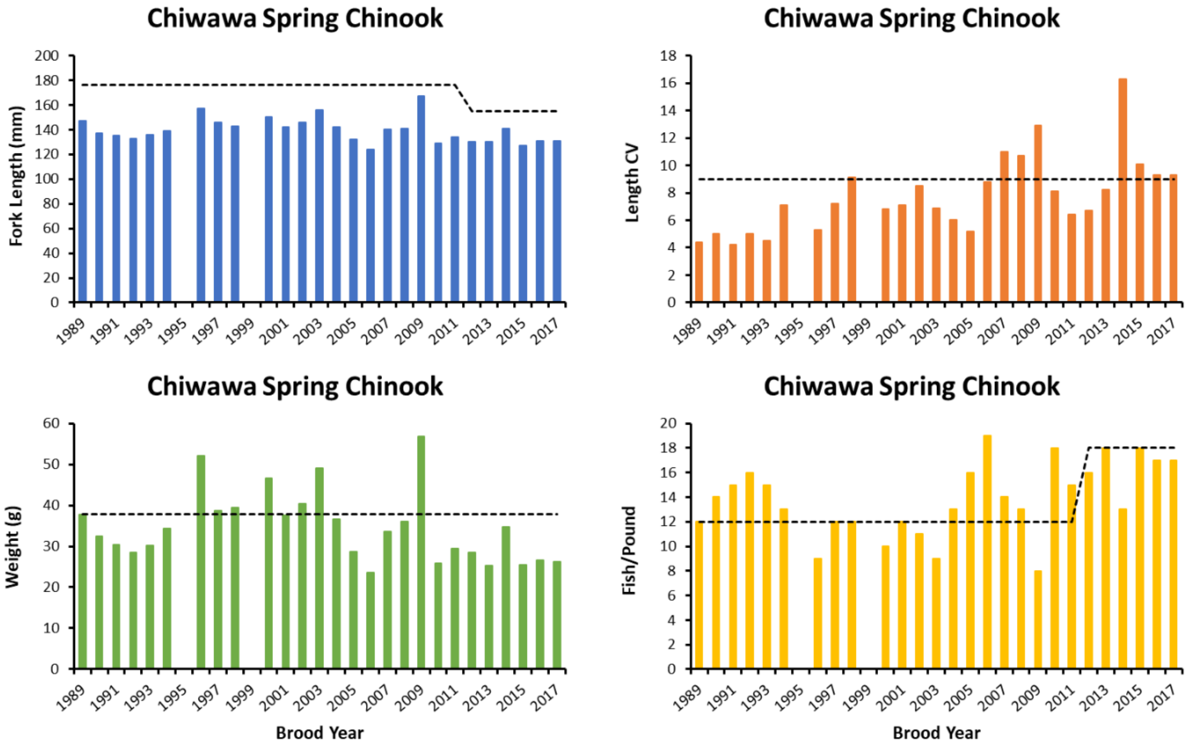

Figure 12. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of juvenile spring Chinook Salmon released in the Chiwawa River for brood years 1989-2017. The dashed horizontal lines represent the target length (176 mm from 1989-2011 and 155 mm from 2012-2017), length CV (9), weight (37.8 g), and fish per pound (12 fish per pound from 1989-2011 and 18 fish per pound from 2012-2017).

Length-Weight Relationship—There was a significant relationship between the length and weight of juvenile hatchery spring Chinook Salmon (Figure 13). Length explained 95% of the variation in weight of juvenile fish. In addition, the relationship indicated a mean condition 3.01 for juvenile hatchery spring Chinook Salmon, suggesting near isometric growth. The Fulton condition factor averaged 0.99 (range, 0.66-1.56).

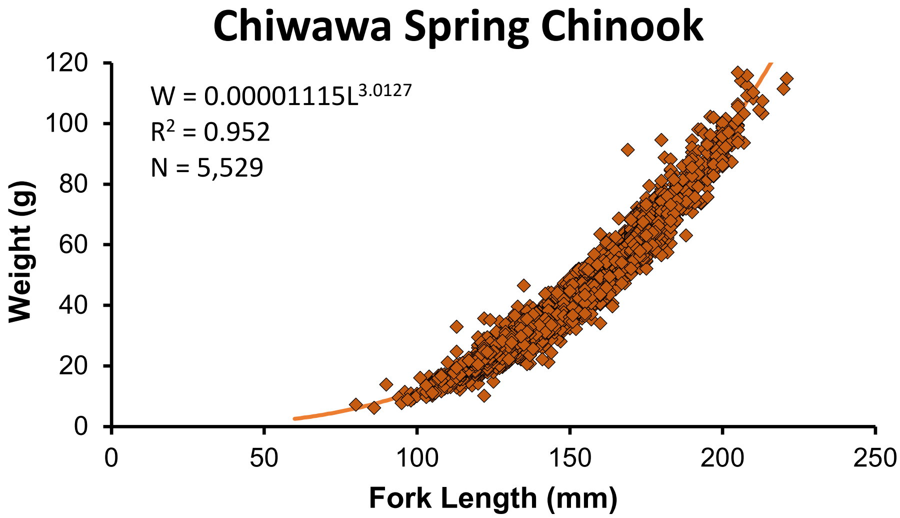

Figure 13. Relationship between fork length (mm) and weight (g) of juvenile Chiwawa River spring Chinook Salmon sampled before release during 2003-2018.

Nason Creek Spring Chinook Salmon

Number Released—The goal of the supplementation program is to release 223,670 (±10%) juvenile spring Chinook Salmon into Nason Creek annually (combined conservation and safety-net programs). During the five-year period of the program, the program reached that goal in Nason Creek for three of those brood years or four of the five years if the fish released into the Chiwawa River as part of Grant PUDs production in 2016 were included (Figure 14). Numbers released into Nason Creek ranged from 32,215-243,127 (average = 156,751) juveniles. For brood year 2014, most of the Nason Creek program was transferred to the Chiwawa Acclimation Facility and 196,866 of these fish were released in the Chiwawa River because of a water intake problem at the Nason Creek Acclimation Facility. The Nason Creek release was 32,215 in brood year 2014 but totaled 229,081 with the fish that were released into the Chiwawa River.

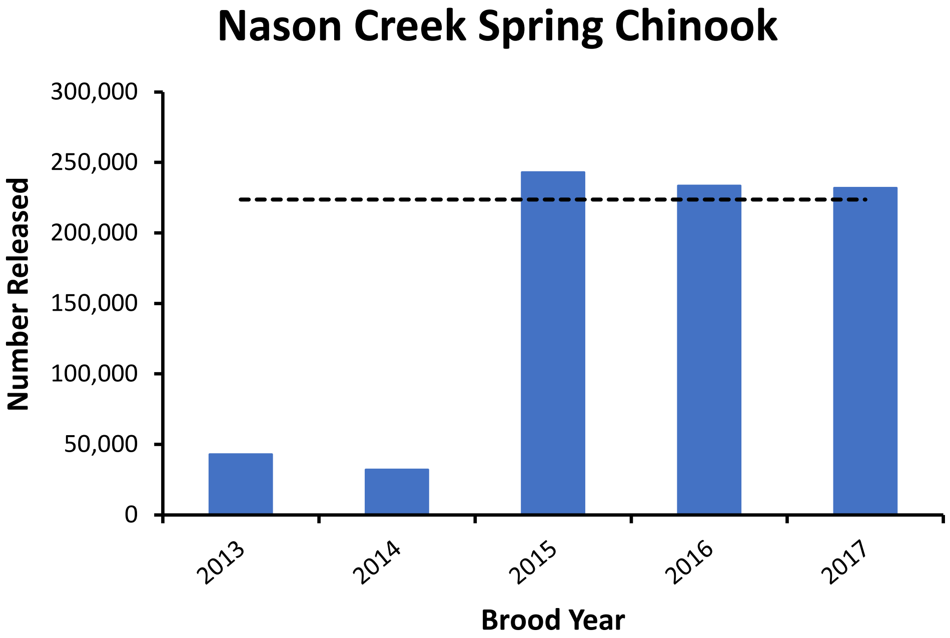

Figure 14. Number of juvenile spring Chinook Salmon released in Nason Creek for brood years 2013-2017. The dashed horizontal line represents the target release number (223,670). For brood year 2014, most of the Nason Creek program was transferred to the Chiwawa Acclimation Facility and 196,866 of these fish were released in the Chiwawa River because of a water intake problem at the Nason Creek Acclimation Facility. The total released for brood year 2014 was 229,081.

Size at Release—The goal of both the conservation (WxW) and safety net (HxH) programs is to release juvenile spring Chinook Salmon in Nason Creek that average 155-mm long (fork length) with a CV of 9.0, and 37.8 g (18-24 fish/pound). During the five-year period of the program, both lengths and CVs were generally below their respective targets (Figure 15). Mean lengths of fish released ranged from 119-129 mm (average = 122 mm) for the conservation program and 115-134 mm (average = 122) for the safety-net program. CVs ranged from 7-8 (average = 7) for the conservation program and 6-13 (average = 9) for the safety-net program. The mean weight for both programs fell below the target and fish per pound generally exceeded the target (Figure 15). Mean weights ranged from 21-28 g (average = 23) for the conservation program and 19-29 g (average = 22 g) for the safety-net program. Fish per pound ranged from 16-22 (average = 20 fish/pound) for the conservation program and 16-24 (average = 21 fish/pound) for the safety-net program.

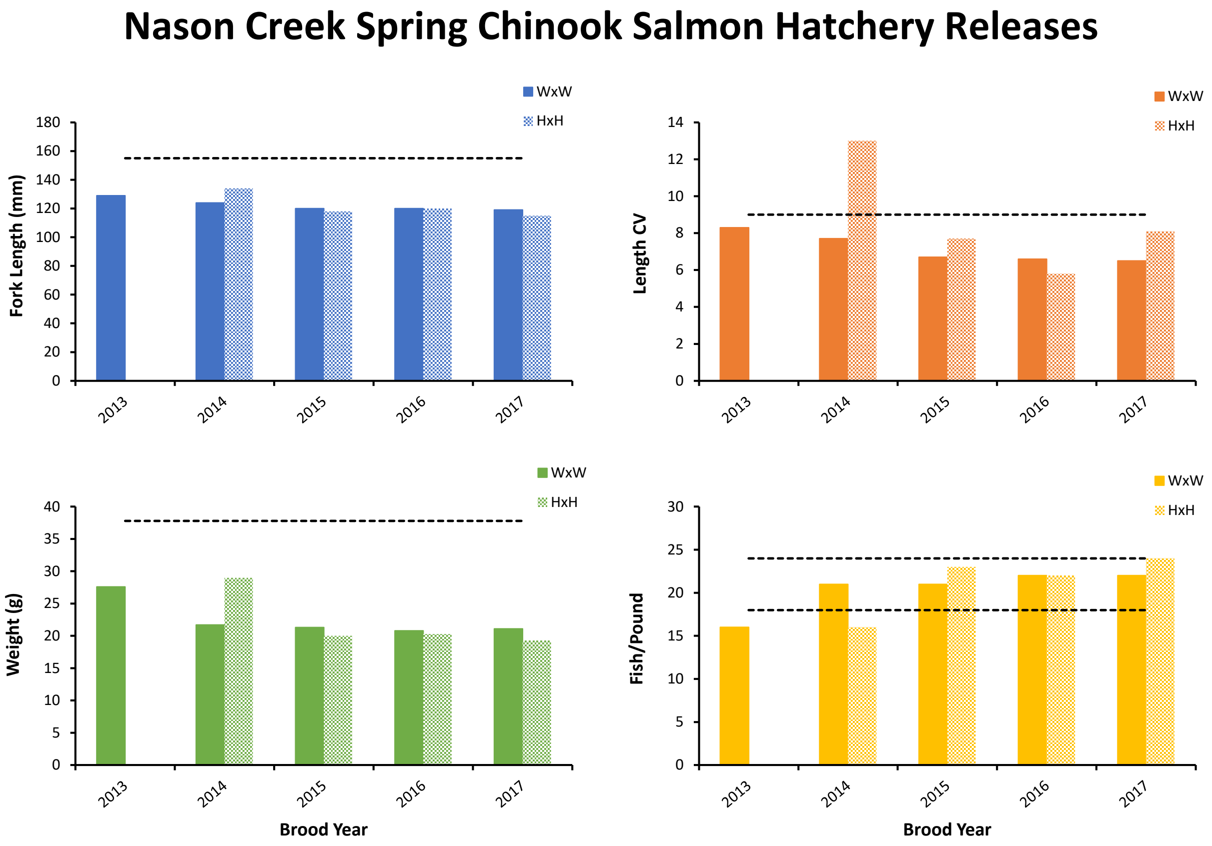

Figure 15. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of juvenile spring Chinook Salmon released in Nason Creek for brood years 2013-2017. The dashed horizontal lines represent the target length (155 mm), length CV (9), weight (37.8 g), and fish per pound (18-24 fish per pound). WxW represents the conservation program while HxH represents the safety-net program.

Length-Weight Relationship—There was a significant relationship between the length and weight of juvenile hatchery spring Chinook Salmon (Figure 16). Length explained 95% of the variation in weight of juvenile fish. In addition, the relationship indicated a mean condition 2.99 for juvenile hatchery spring Chinook Salmon, suggesting near isometric growth. The Fulton condition factor averaged 1.19 (range, 0.61-2.23).

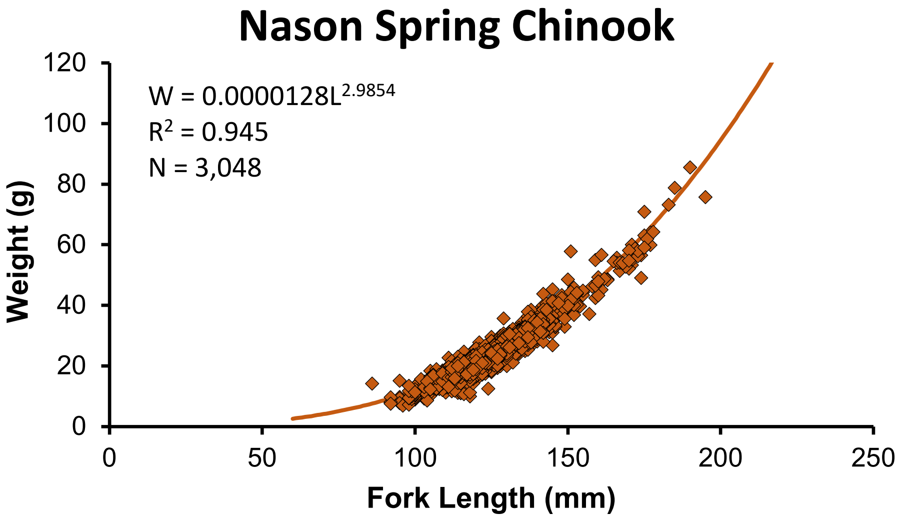

Figure 16. Relationship between fork length (mm) and weight (g) of juvenile Nason Creek spring Chinook Salmon sampled before release during 2013-2018.

White River Spring Chinook Salmon

Number Released—The goal of the supplementation program was to release 150,000 (±10%) juvenile spring Chinook Salmon into various release locations annually, including the White River, Lake Wenatchee, and the Wenatchee River. The release strategies were highly variable across years (Table 3). During the twelve-year period of the program, the program reached that goal for two of those brood years (Figure 17). Numbers released ranged from 1,639 to 281,677 (average = 78,716) juveniles.

Table 3. White River Spring Chinook Salmon releases from Brood Years 2002-2013.

Brood Year	Release Year	Number Released	Acclimation Site	Acclimation Vessel	Release Scenario
2002	2004	2,589	WR RM 11.5	Tanks	White River
2003	2005	2,096	WR RM 11.5	Tanks	White River
2004	2006	1,639	WR RM 11.5	Tanks	White River
2005	2007	69,032	Lake Wenatchee	Net Pens	Lake Wenatchee
2006	2008	139,644	NA	NA	White River
2006	2008	142,033	NA	NA	White River
2007	2009	87,671	Lake Wenatchee	Net Pens	Lake Wenatchee
2007	2009	44,172	None	None	Lake Wenatchee
2008	2010	10,156	WR Bridge	Eddy Pen	Escape
2008	2010	38,400	Lake Wenatchee	Net Pens	Mouth of Lake
2009	2011	12,000	WR RM 11.5	Side Channel	Escape
2009	2011	10,000	WR RM 11.5	Tanks	White River
2009	2011	28,000	WR Bridge	Tanks	White River Wenatchee River
2009	2011	14,596	WR Bridge	Eddy Pen	Escape
2009	2011	48,000	Lake Wenatchee	Net Pens	Wenatchee River
2010	2012	18,850	WR Bridge	Tanks	Wenatchee River
2011	2013	42,000	WR Bridge	Tanks	Wenatchee and White Rivers
2011	2013	105,000	Lake Wenatchee	Net Pens	Wenatchee River
2012	2014	42,000	WR Bridge	Tanks	Wenatchee River
2012	2014	55,713	Lake Wenatchee	Net Pens	Wenatchee River
2013	2015	31,000	WR Bridge	Tanks	Wenatchee River

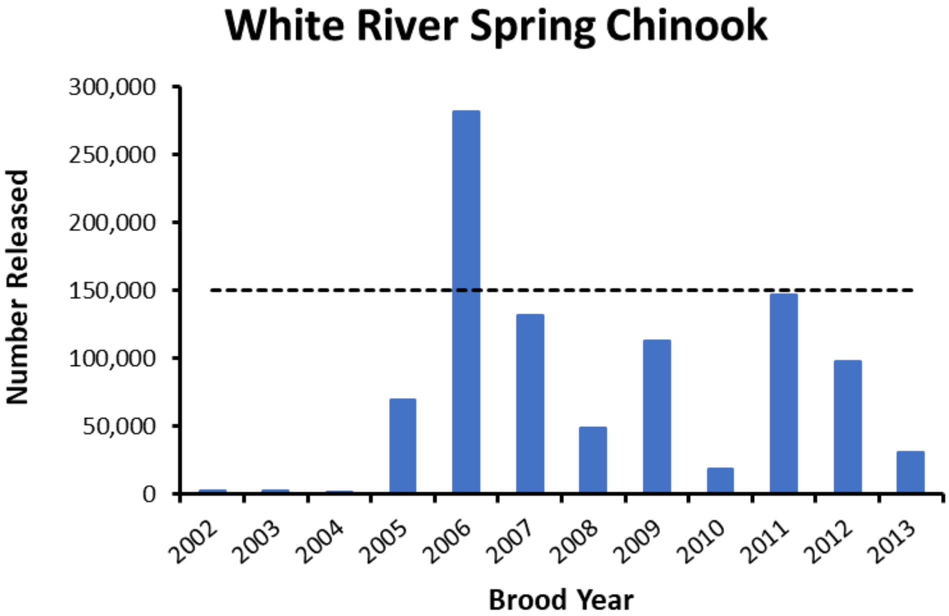

Figure 17. Number of juvenile spring Chinook Salmon released in White River, Lake Wenatchee, and Wenatchee River for brood years 2002-2013. The dashed horizontal line represents the target release number (150,000).

Size at Release—The goal of the captive broodstock program was to release juvenile spring Chinook Salmon that average 18-24 fish/pound (see Figure 18). Mean lengths of fish released ranged from 125-207 mm (average = 145 mm). CVs ranged from 8-12 (average = 9). Mean weights ranged from 23-118 g (average = 40 g). Fish per pound ranged from 4-31 (average = 18 fish/pound).

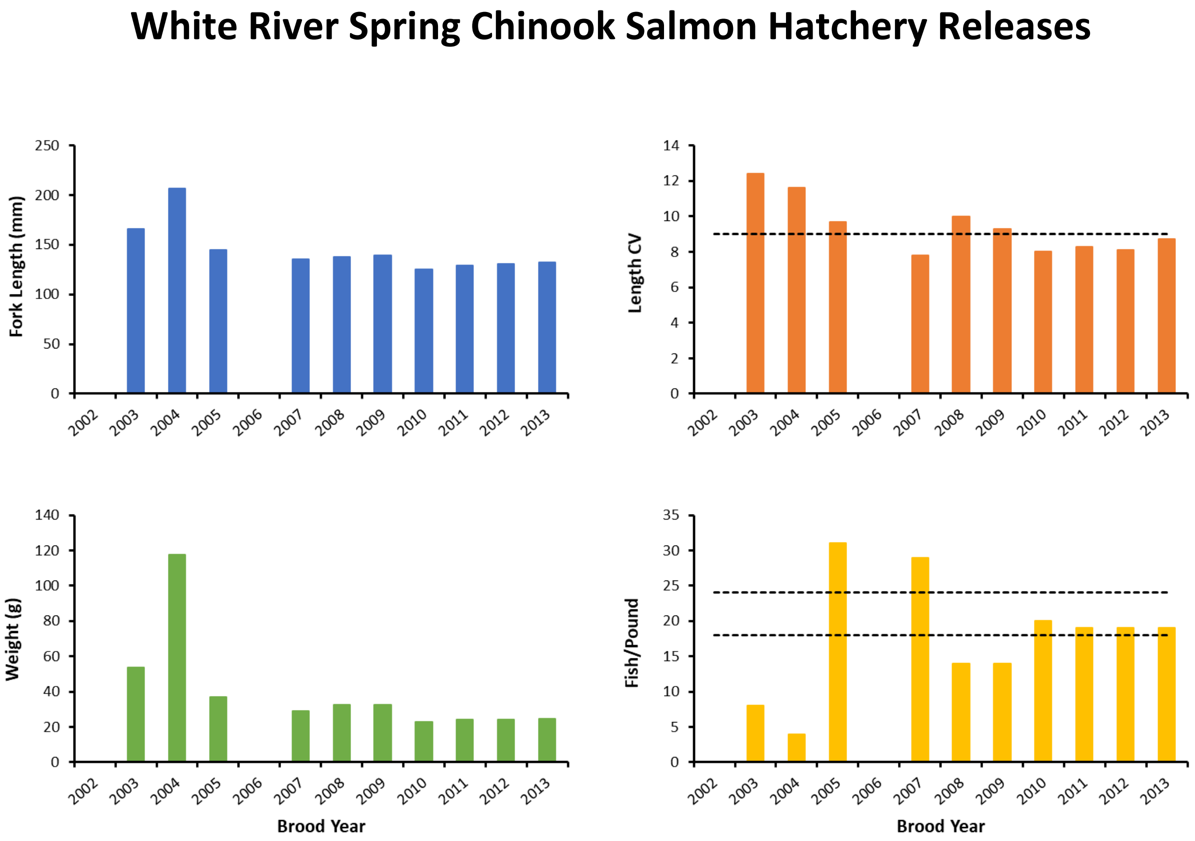

Figure 18. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of juvenile spring Chinook Salmon released in White River for brood years 2002-2013. The dashed horizontal lines represent the target length CV (9; provided for reference – no CV target was formally identified for this program) and fish per pound (18-24 fish per pound range shown on graph).

Methow River Spring Chinook Salmon

Number Released—The recent goal of the conservation program is to release 133,249 (±10%) juvenile spring Chinook Salmon into the Methow River annually. During the six-year period under the recent goal of the program, the program exceeded that goal in five brood years and did not achieve it in one brood year (Figure 19). Numbers released ranged from 59,260-196,711 (average = 146,810) juveniles.

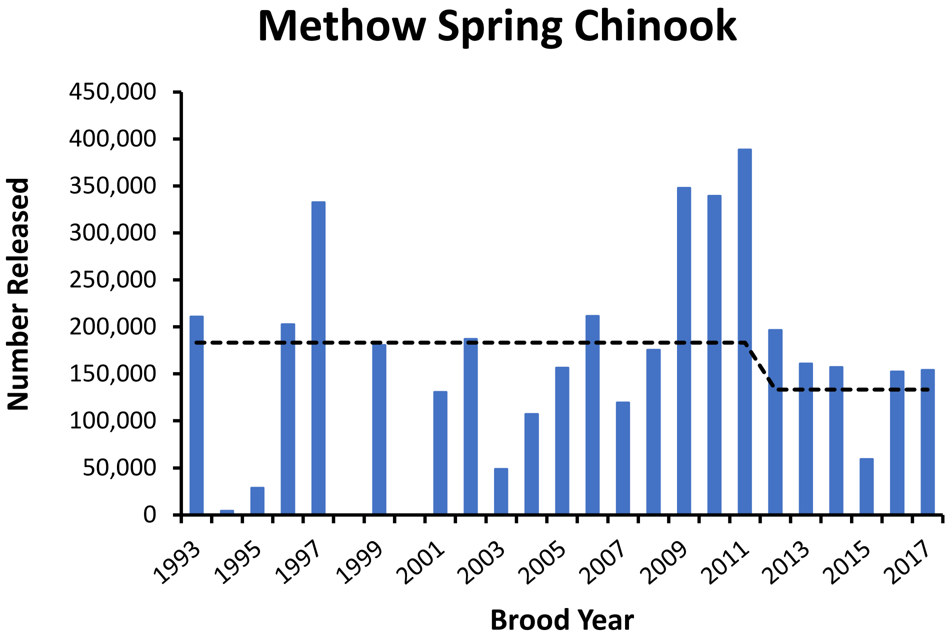

Figure 19. Number of juvenile spring Chinook Salmon released in the Methow River for brood years 1993-2017. The dashed horizontal line represents the target release number (183,334 from 1993-2011 and 133,249 from 2012-2017).

Size at Release—The current goal of the conservation program (since brood year 2012) is to release juvenile spring Chinook Salmon in the Methow River that average 137-mm long (fork length) with a CV of 9.0, and 30.2 g (15 fish/pound). During the six-year period under the recent goal of the program, lengths were near the target while CVs were at or below the target (Figure 20). Mean lengths of fish released ranged from 131-141 mm (average = 134 mm), while CVs ranged from 7-9 (average = 8). Both mean weights and fish per pound fluctuated above and below their respective targets during the six-year period (Figure 20). Throughout the recent six years, mean weights ranged from 27-34 g (average = 29 g) and fish per pound ranged from 14-17 (average = 16 fish/pound).

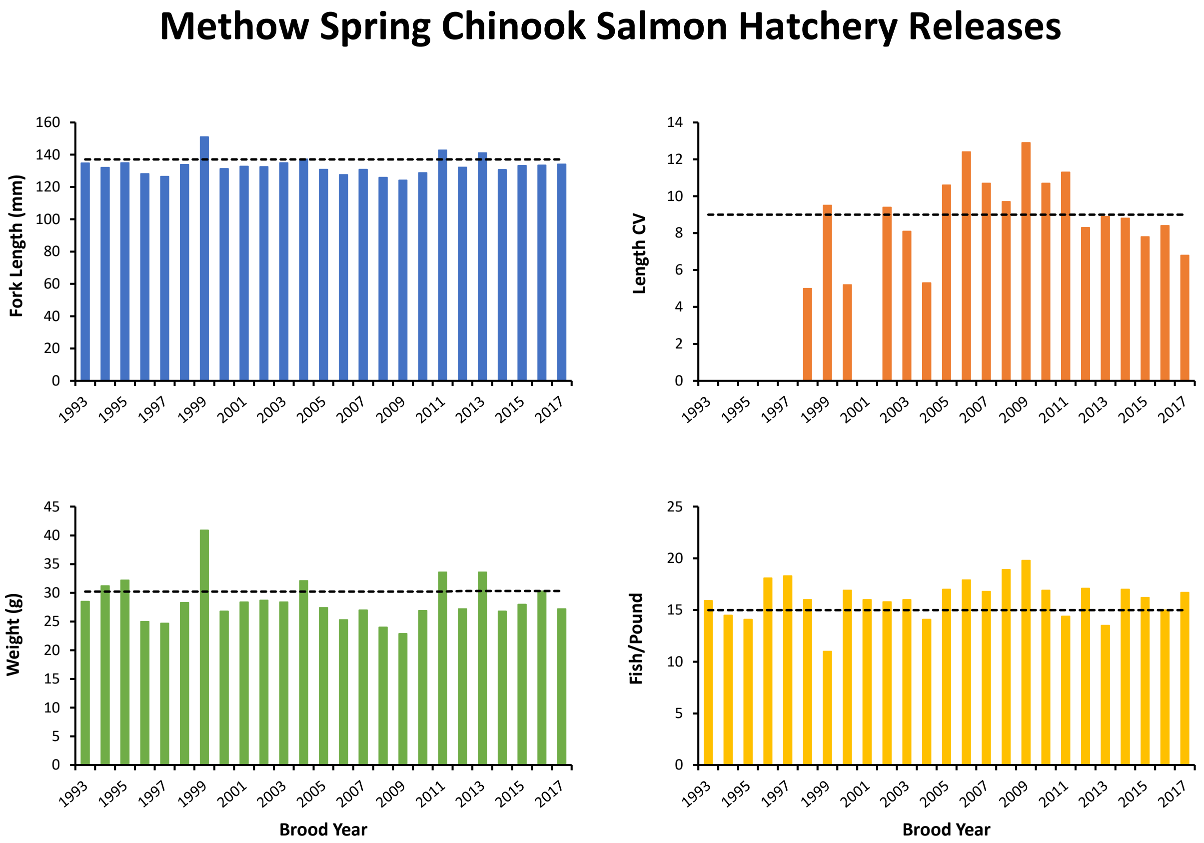

Figure 20. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of juvenile spring Chinook Salmon released in the Methow River for brood years 1993-2017. The dashed horizontal lines represent the target length (137 mm), length CV (9.0), weight (30.2 g), and fish per pound (15 fish per pound).

Length-Weight Relationship—There was a significant relationship between the length and weight of juvenile hatchery spring Chinook Salmon (Figure 21). Length explained 94% of the variation in weight of juvenile fish. In addition, the relationship indicated a mean condition 3.02 for juvenile hatchery spring Chinook Salmon, suggesting near isometric growth. The Fulton condition factor averaged 1.16 (range, 0.64-1.91).

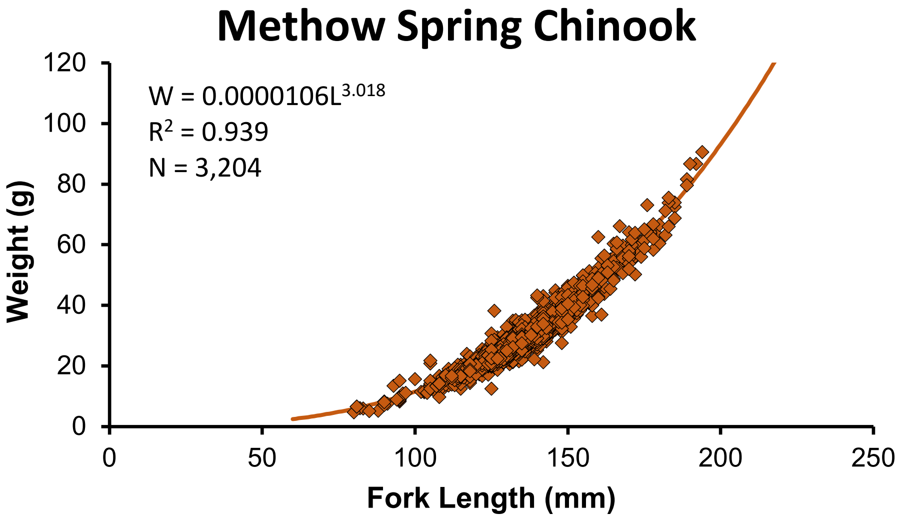

Figure 21. Relationship between fork length (mm) and weight (g) of juvenile Methow River spring Chinook Salmon sampled before release during 2003-2018.

Chewuch River Spring Chinook Salmon

Number Released—The recent goal of the conservation program is to release 60,516 (±10%) juvenile spring Chinook Salmon into the Chewuch River annually. During the six-year period under the recent goal of the program, the program achieved that goal for three and exceed the goal for two of the five brood years with program releases (Figure 22). There was no Chewuch program for brood year 2012. Numbers released ranged from 60,860-72,000 (average = 67,131) juveniles.

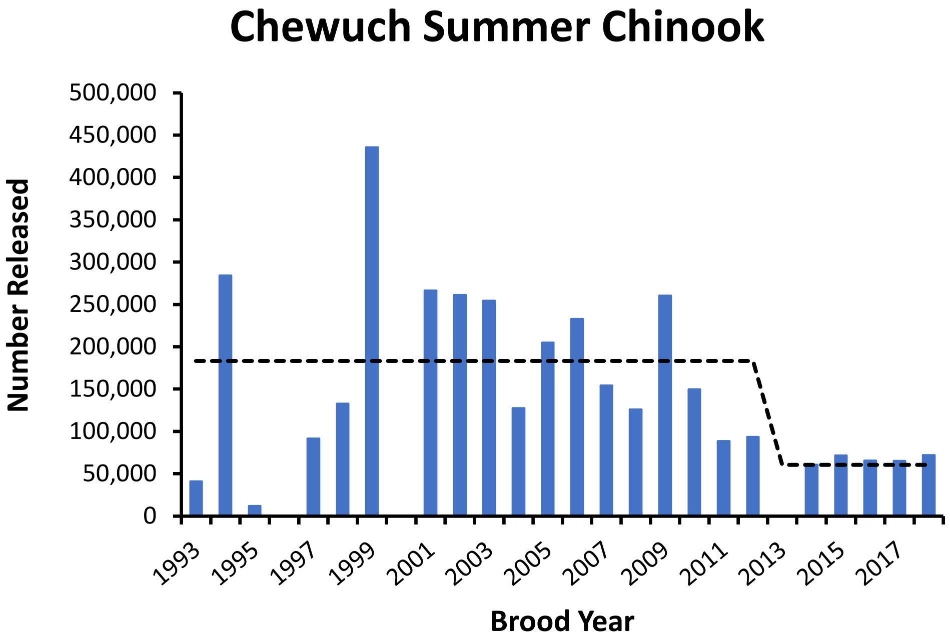

Figure 22. Number of juvenile spring Chinook Salmon released in the Chewuch River for brood years 1994-2017. The dashed horizontal line represents the target release number (183,333 from 1994-2011 and 60,516 from 2012-2017).

Size at Release—The current goal of the conservation program (since brood year 2012) is to release juvenile spring Chinook Salmon in the Chewuch River that average 136-mm long (fork length) with a CV of 9.0, and 30.2 g (15 fish/pound). During the six-year period under the recent goal of the program, lengths were near the target while CVs were both above and below the target (Figure 23). Mean lengths of fish released ranged from 126-134 mm (average = 132 mm), while CVs ranged from 6-13 (average = 10). Both mean weights and fish per pound fluctuated above and below their respective targets during the six-year period (Figure 23). Throughout the recent six years, mean weights ranged from 24-32 g (average = 28 g) and fish per pound ranged from 14-19 (average = 16 fish/pound).

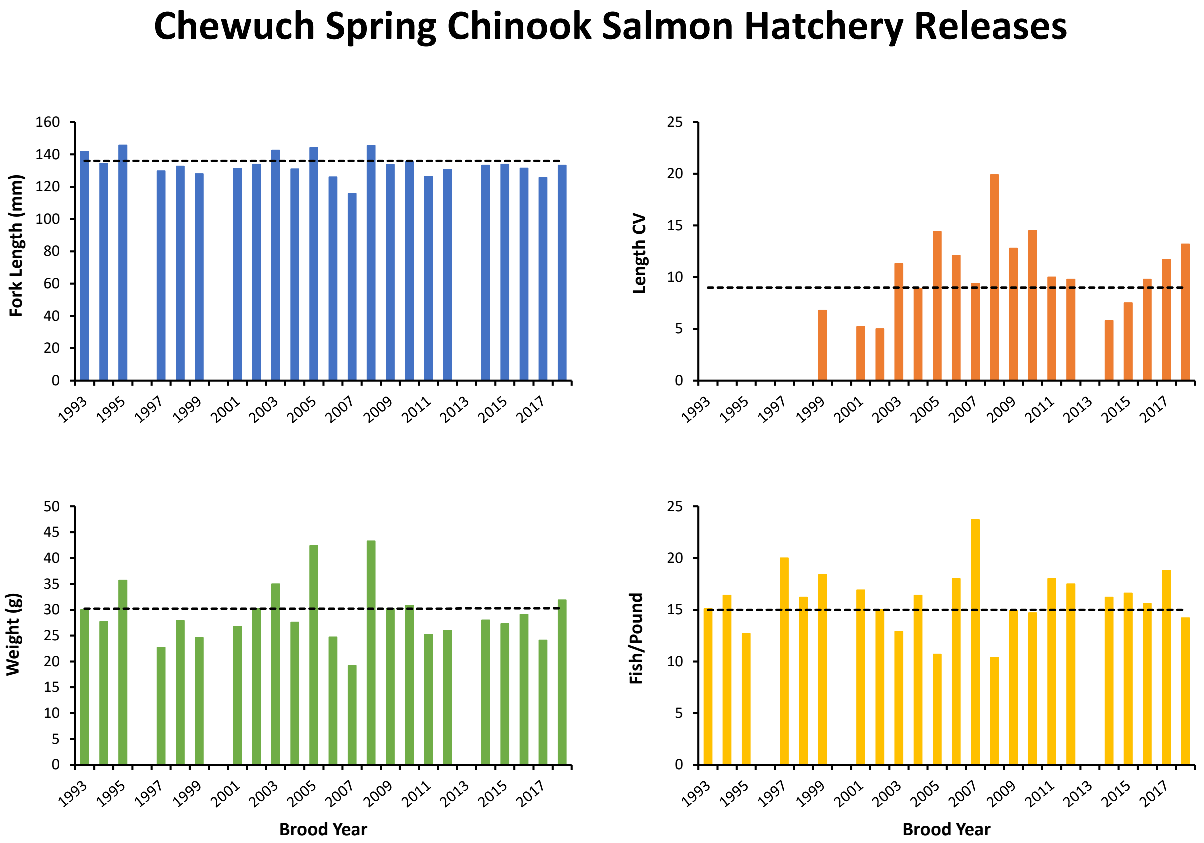

Figure 23. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of juvenile spring Chinook Salmon released in the Chewuch River for brood years 1992-2017. The dashed horizontal lines represent the target length (137 mm), length CV (9.0), weight (30.2 g), and fish per pound (15 fish per pound).

Length-Weight Relationship—There was a significant relationship between the length and weight of juvenile hatchery spring Chinook Salmon (Figure 24). Length explained 95% of the variation in weight of juvenile fish. In addition, the relationship indicated a mean condition 3.13 for juvenile hatchery spring Chinook Salmon, suggesting positive allometric growth. The Fulton condition factor averaged 1.19 (range, 0.75-2.09).

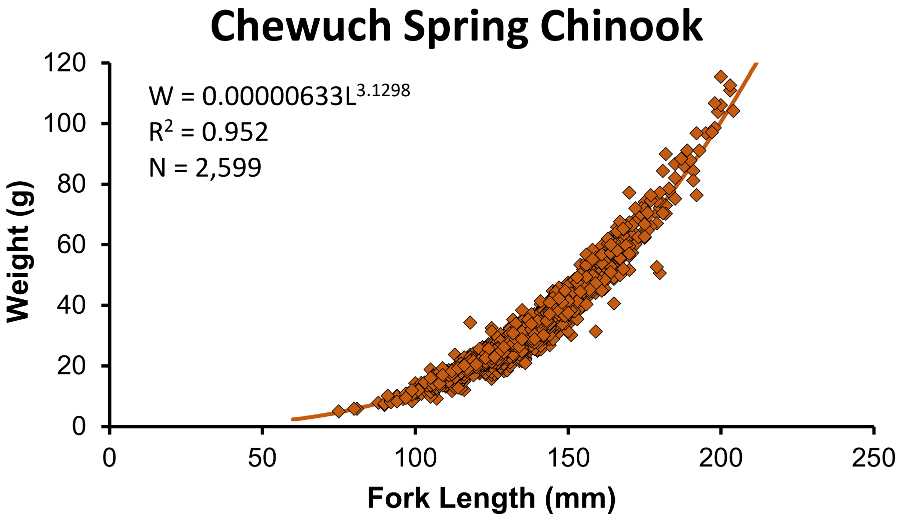

Figure 24. Relationship between fork length (mm) and weight (g) of juvenile Chewuch River spring Chinook Salmon sampled before release during 2003-2018.

Twisp River Spring Chinook Salmon

Number Released—The recent goal of the conservation program is to release 30,000 (±10%) juvenile spring Chinook Salmon into the Twisp River annually. During the six-year period under the recent goal of the program, the program achieved the goal for four brood years and exceeded the goal for two brood years (Figure 25). Numbers released ranged from 29,333-48,924 (average = 36,137) juveniles.

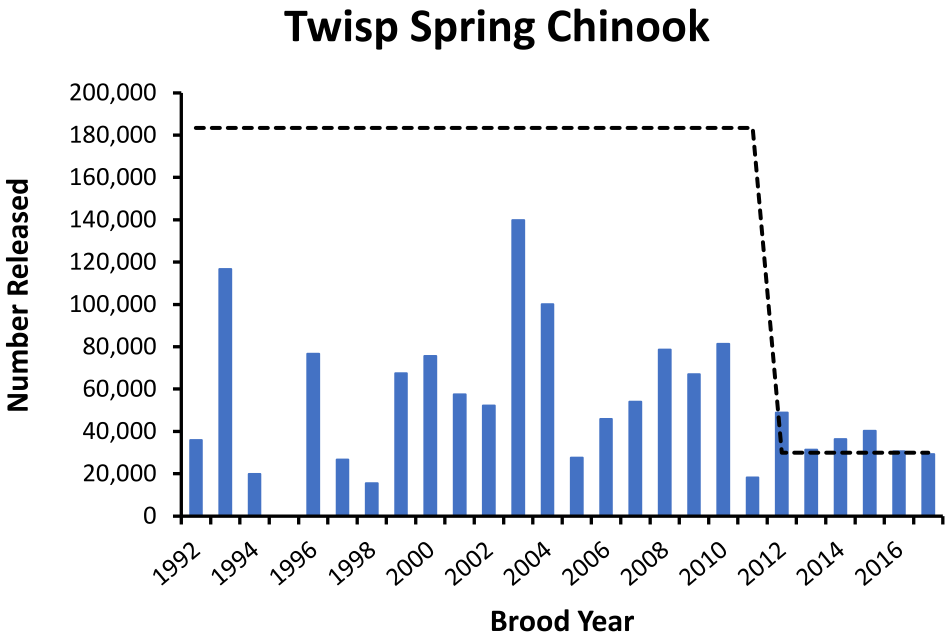

Figure 25. Number of juvenile spring Chinook Salmon released in the Twisp River for brood years 1992-2017. The dashed horizontal line represents the target release number (183,333 from 1992-2011 and 30,000 from 2012-2017).

Size at Release—The current goal of the conservation program (since brood year 2012) is to release juvenile spring Chinook Salmon in the Twisp River that average 135-mm long (fork length) with a CV of 9.0, and 30.2 g (15 fish/pound). During the six-year period under the recent goal of the program, lengths were near the target while CVs were both above and below the target (Figure 26). Mean lengths of fish released ranged from 125-138 mm (average = 132 mm), while CVs ranged from 6-11 (average = 9). Mean weights were generally at or below the target while fish per pound fluctuated above and below the target during the six-year period (Figure 26). Throughout the recent six years, mean weights ranged from 25-31 g (average = 28 g) and fish per pound ranged from 15-18 (average = 16 fish/pound).

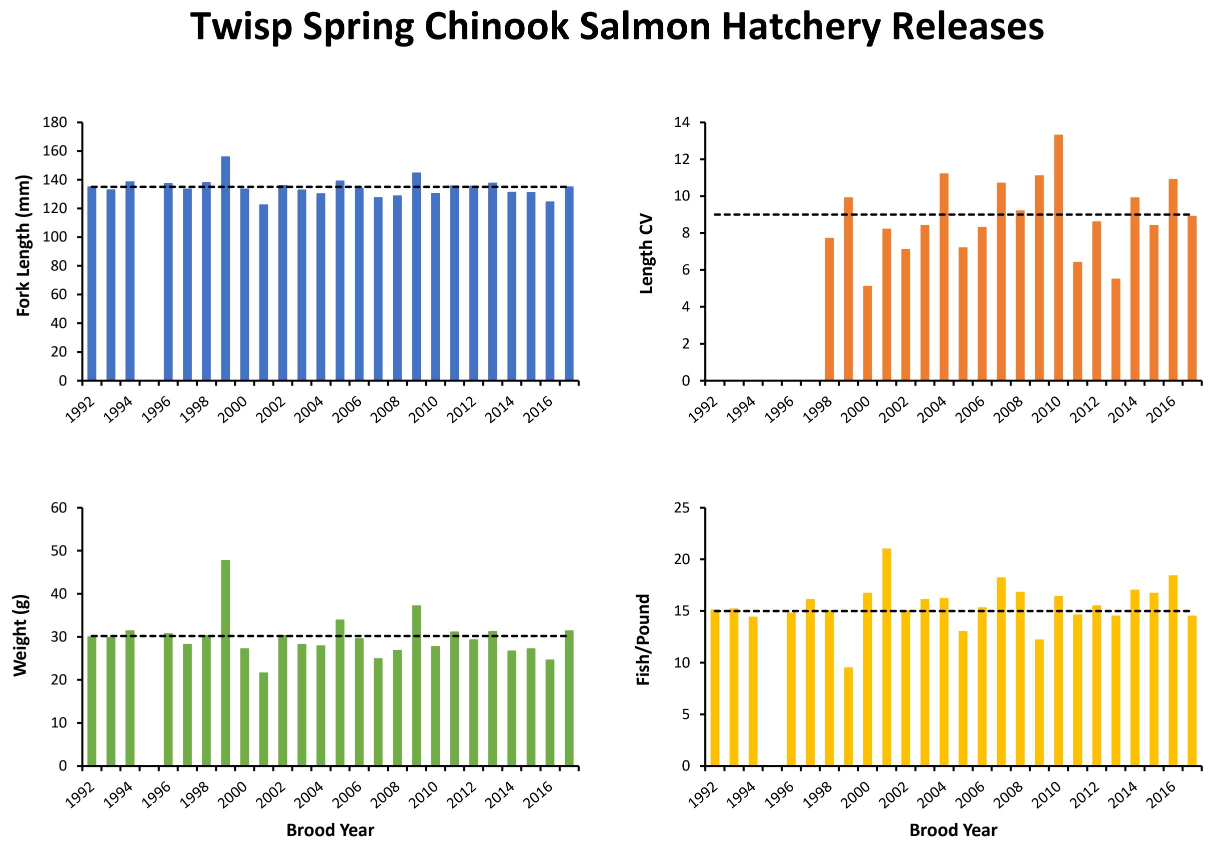

Figure 26. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of juvenile spring Chinook Salmon released in the Twisp River for brood years 1992-2017. The dashed horizontal lines represent the target length (135 mm), length CV (9.0), weight (30.2 g), and fish per pound (15 fish per pound).

Length-Weight Relationship—There was a significant relationship between the length and weight of juvenile hatchery spring Chinook Salmon (Figure 27). Length explained 97% of the variation in weight of juvenile fish. In addition, the relationship indicated a mean condition 2.97 for juvenile hatchery spring Chinook Salmon, suggesting near isometric growth. The Fulton condition factor averaged 1.19 (range, 0.45-2.92).

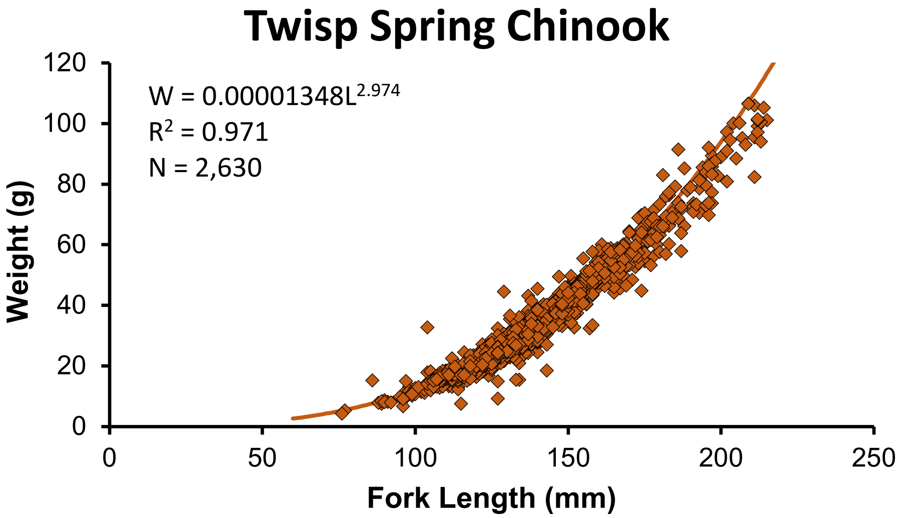

Figure 27. Relationship between fork length (mm) and weight (g) of juvenile Twisp River spring Chinook Salmon sampled before release during 2003-2018.

Wenatchee River Summer Chinook Salmon

Number Released—The recent goal of the supplementation program is to release 500,001 (±10%) juvenile summer Chinook Salmon into the Wenatchee River annually. During the six-year period under the recent goal of the program, the program achieved that goal for each of the six brood years (Figure 28). Numbers released ranged from 470,570-550,877 (average = 509,522) juveniles.

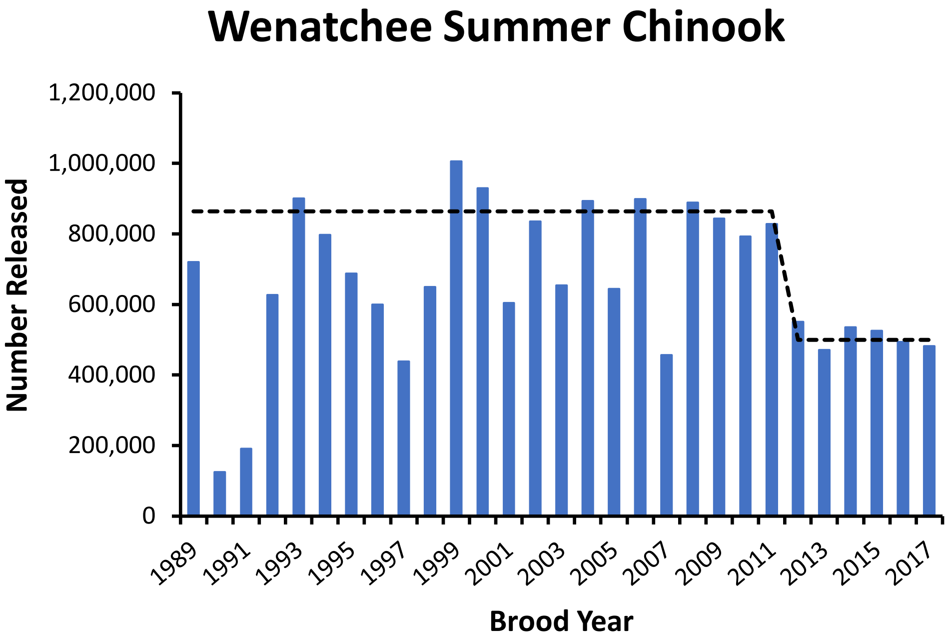

Figure 28. Number of juvenile summer Chinook Salmon released in the Wenatchee River for brood years 1989-2017. The dashed horizontal line represents the target release number (864,000 from 1989-2011 and 500,001 from 2012-2017).

Size at Release—The current goal of the supplementation program (since brood year 2012) is to release juvenile summer Chinook Salmon in the Wenatchee River that average 163-mm long (fork length) with a CV of 9.0, and 30.0-45.4 g (10-18 fish/pound). During the six-year period under the recent goal of the program, lengths were below the target while CVs were generally above the target (Figure 29). Mean lengths of fish released ranged from 139-158 mm (average = 148 mm), while CVs ranged from 7-13 (average = 10). Mean weights were within the target range (brood years 2012-2014) or below the target (brood years 2015-2017). Likewise, fish per pound was within the target range (brood years 2012-2014) or below the target (brood years 2015-2017) (Figure 29). Throughout the recent six years, mean weights ranged from 29-41 g (average = 34 g) and fish per pound ranged from 11-16 (average = 14 fish/pound).

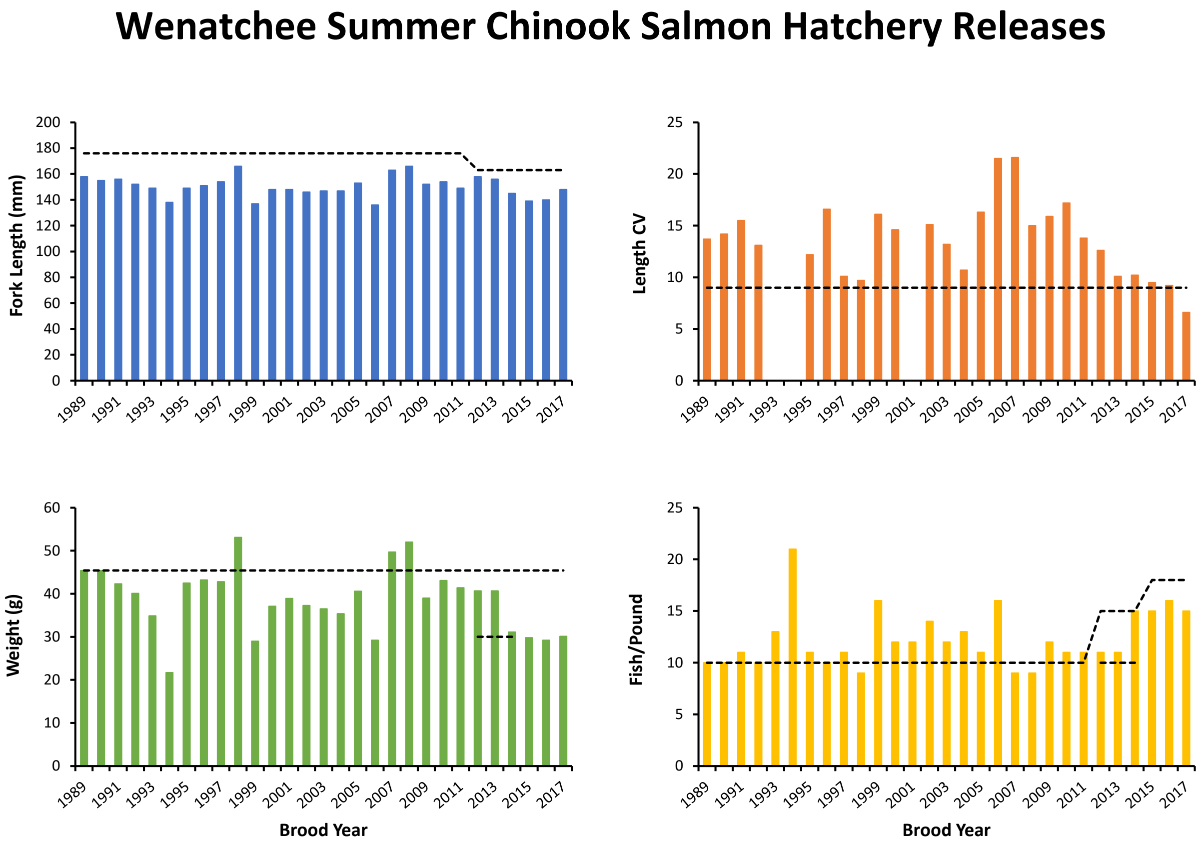

Figure 29. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of juvenile summer Chinook Salmon released in the Wenatchee River for brood years 1989-2017. The dashed horizontal lines represent the target length (135 mm from 1989-2011 and 163 from 2012-2017), length CV (9.0), weight (45.4 g with a range of 30.0-45.4 g for brood years 2012-2014), and fish per pound (10 fish per pound for brood years 1989-2011, a range of 10-15 fish per pound for brood years 2012-2014, and 18 fish per pound for brood years 2015-2017).

Length-Weight Relationship—There was a significant relationship between the length and weight of juvenile hatchery summer Chinook Salmon (Figure 30). Length explained 94% of the variation in weight of juvenile fish. In addition, the relationship indicated a mean condition 2.99 for juvenile hatchery summer Chinook Salmon, suggesting near isometric growth. The Fulton condition factor averaged 1.04 (range, 0.37-2.90).

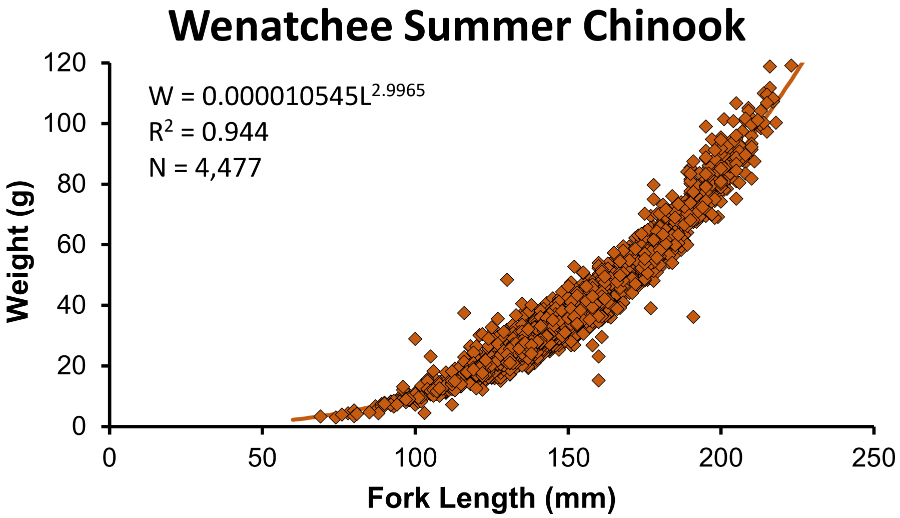

Figure 30. Relationship between fork length (mm) and weight (g) of juvenile Wenatchee River summer Chinook Salmon sampled before release during 2003-2018.

Chelan Falls Summer Chinook Salmon

Number Released—The goal of the supplementation program is to release 576,000 (±10%) juvenile summer Chinook Salmon into the Chelan River annually. During the eight-year period of the program, the program achieved the goal for six brood years, and was below the goal for two brood years (Figure 31). Numbers released ranged from 442,063-600,894 (average = 543,629) juveniles.

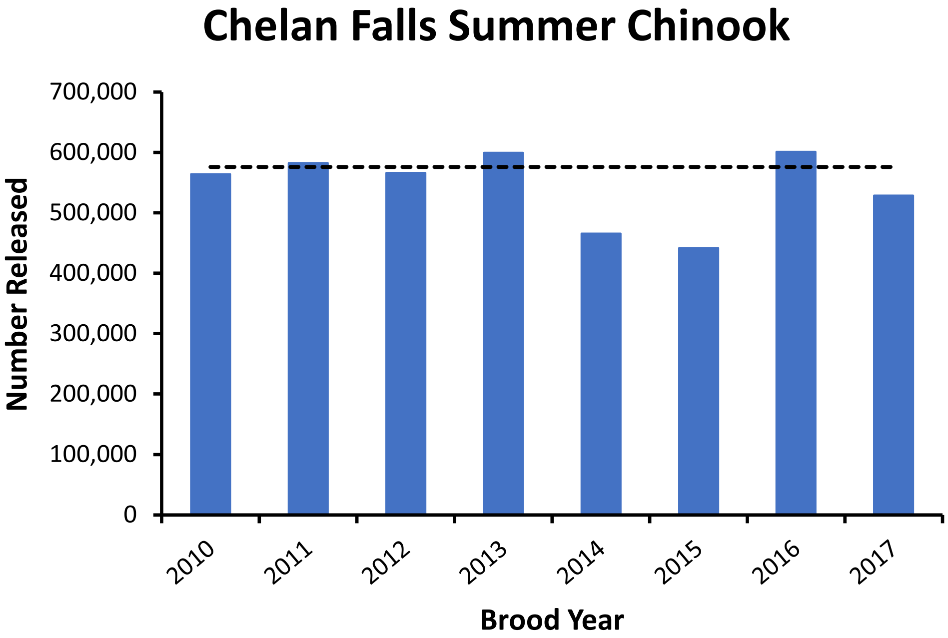

Figure 31. Number of juvenile summer Chinook Salmon released in the Chelan River for brood years 2010-2017. The dashed horizontal line represents the target release number (576,000).

Size at Release—The goal of the supplementation program is to release juvenile summer Chinook Salmon in the Chelan River that average 161-mm long (fork length) with a CV of 9.0, and 20.0-45.4 g (10-22 fish/pound) depending on brood year. During the eight-year period of the program, lengths were below the target while CVs were above the target (Figure 32). Mean lengths of fish released ranged from 129-148 mm (average = 140 mm), while CVs ranged from 10-27 (average = 16). Mean weights were within the target range (brood years 2012-2014) or below the target (brood years 2010-2011 and 2015-2017). Fish per pound was within the target range (brood years 2012-2014) or near the target (brood years 2010-2011 and 2015-2017) (Figure 32). Throughout the recent eight years, mean weights ranged from 25-43 g (average = 34 g) and fish per pound ranged from 11-19 (average = 14 fish/pound).

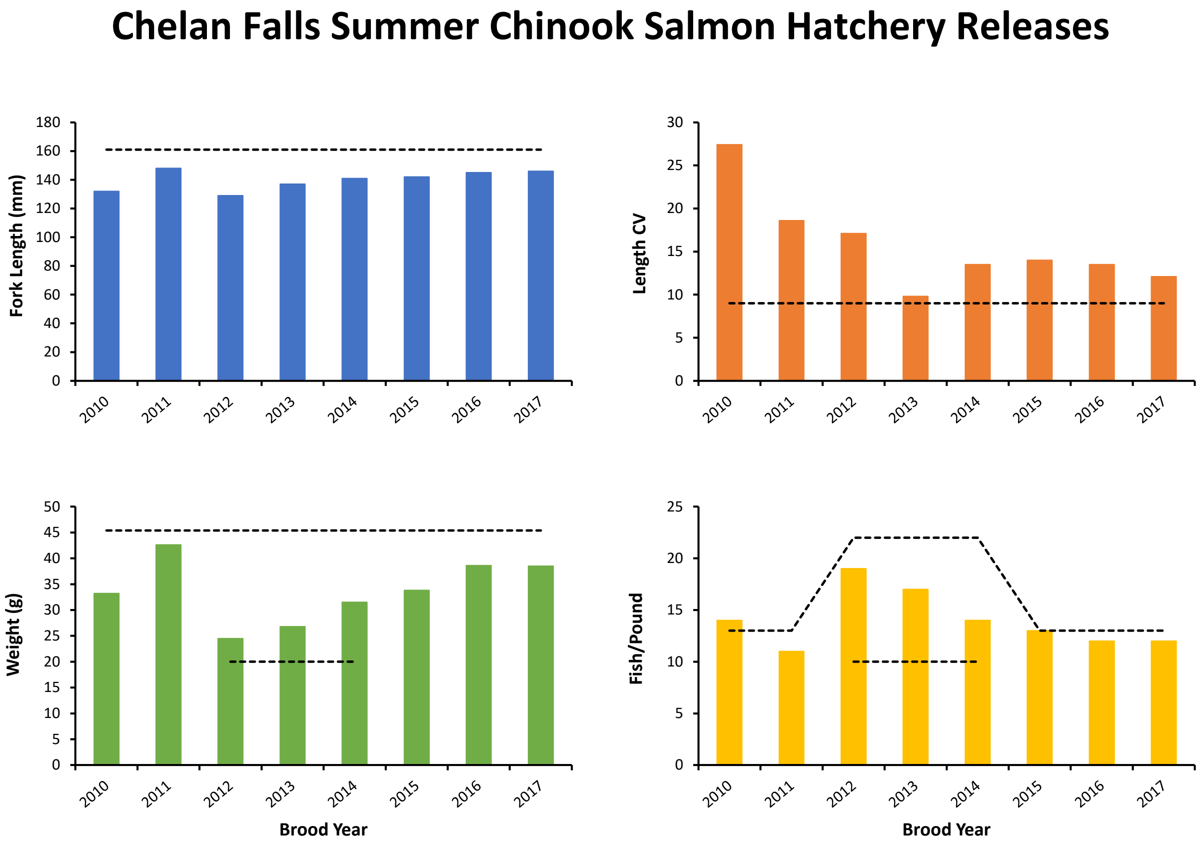

Figure 32. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of juvenile summer Chinook Salmon released in the Chelan River for brood years 2010-2017. The dashed horizontal lines represent the target length (161 mm), length CV (9.0), weight (45.4 g with a range of 20.0-45.4 g for brood years 2012-2014), and fish per pound (13 fish per pound for brood years 2010-2011, a range of 10-22 fish per pound for brood years 2012-2014, and 13 fish per pound for brood years 2015-2017).

Length-Weight Relationship—There was a significant relationship between the length and weight of juvenile hatchery summer Chinook Salmon (Figure 33). Length explained 95% of the variation in weight of juvenile fish. In addition, the relationship indicated a mean condition 3.12 for juvenile hatchery summer Chinook Salmon, suggesting positive allometric growth. The Fulton condition factor averaged 1.09 (range, 0.44-1.99).

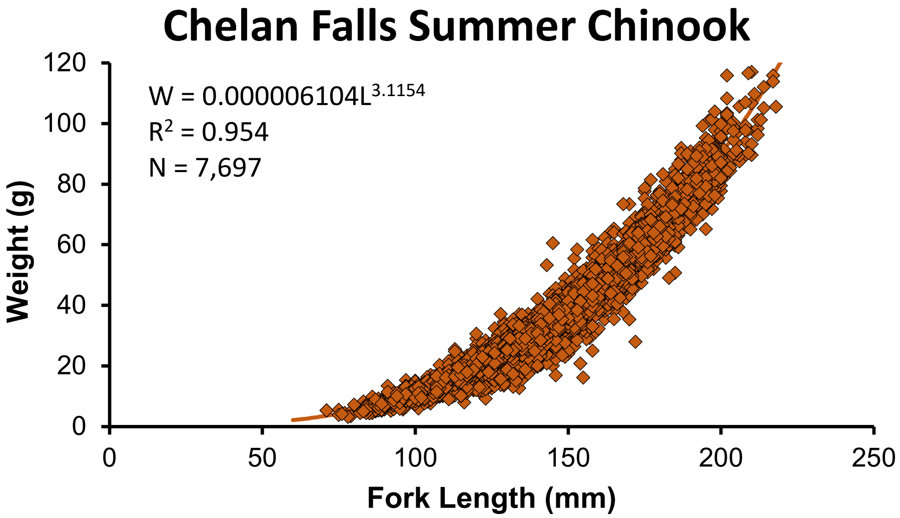

Figure 33. Relationship between fork length (mm) and weight (g) of juvenile Chelan Falls summer Chinook Salmon sampled before release during 2010-2018.

Methow River Summer Chinook Salmon

Number Released—The recent goal of the supplementation program is to release 200,000 (±10%) juvenile summer Chinook Salmon into the Methow River annually. During the six-year period under the recent goal of the program, the program achieved that goal for three brood years and was below the goal for three brood years (Figure 34). Numbers released ranged from 143,594-209,490 (average = 180,781) juveniles.

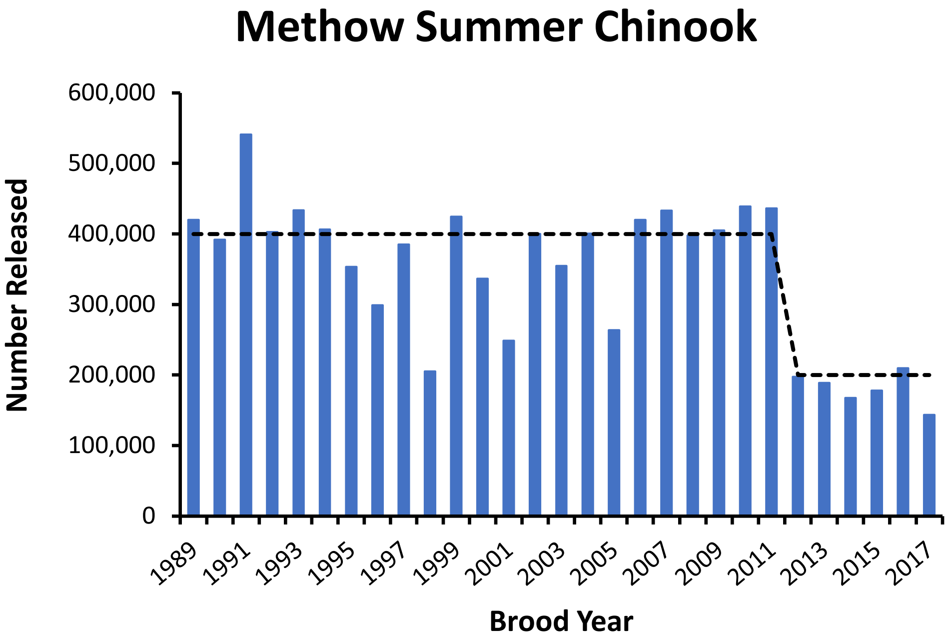

Figure 34. Number of juvenile summer Chinook Salmon released in the Methow River for brood years 1989-2017. The dashed horizontal line represents the target release number (400,000 from 1989-2011 and 200,000 from 2012-2017).

Size at Release—The current goal of the supplementation program (since brood year 2012) is to release juvenile summer Chinook Salmon in the Methow River that average 163-mm long (fork length) with a CV of 9.0, and 45.4 g (13-18 fish/pound). During the six-year period under the recent goal of the program, lengths were below the target while CVs fluctuated above and below the target (Figure 35). Mean lengths of fish released ranged from 125-158 mm (average = 136 mm), while CVs ranged from 8-13 (average = 10). Mean weights were below the target while fish per pound was within the target range (Figure 35). Throughout the recent six years, mean weights ranged from 23-42 g (average = 29 g) and fish per pound ranged from 11-20 (average = 16 fish/pound).

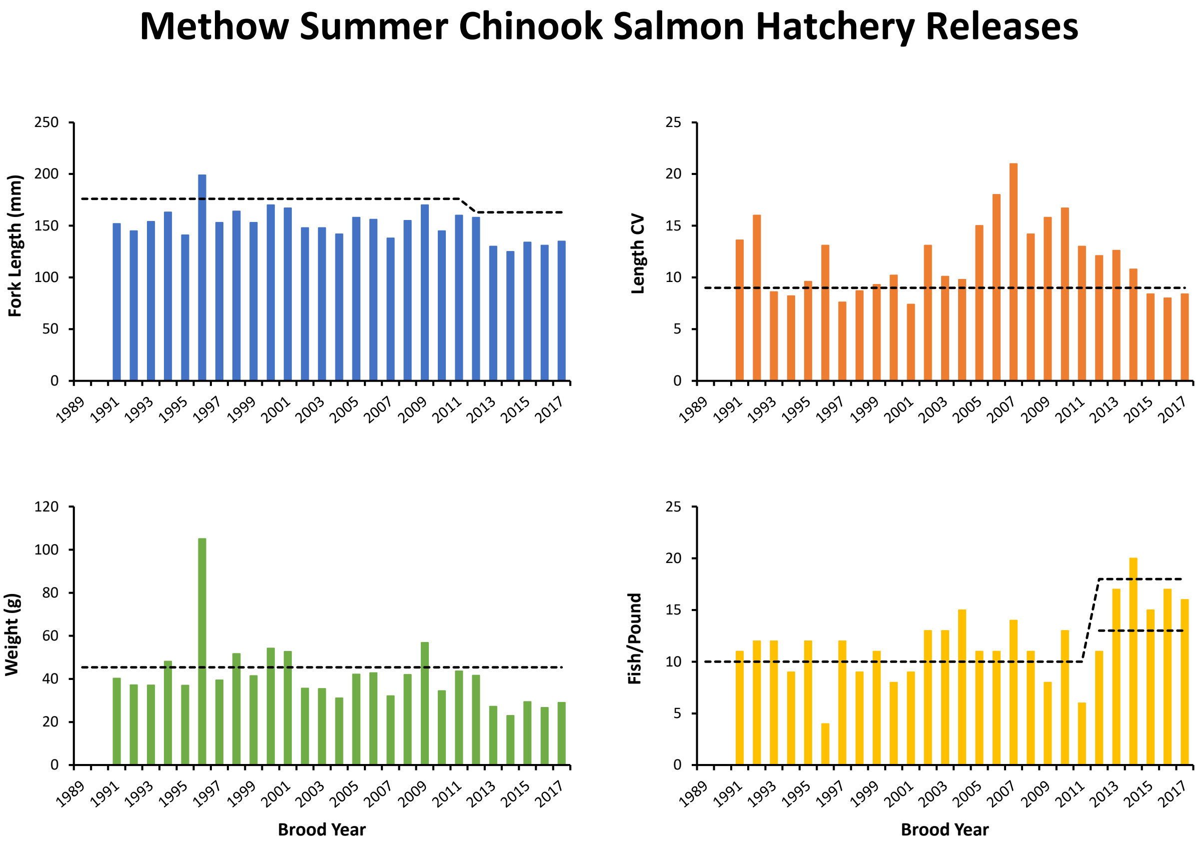

Figure 35. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of juvenile summer Chinook Salmon released in the Methow River for brood years 1989-2017. The dashed horizontal lines represent the target length (176 mm from 1989-2011 and 163 from 2012-2017), length CV (9.0), weight (45.4 g), and fish per pound (10 fish per pound for brood years 1989-2011 and a range of 13-18 fish per pound for brood years 2012-2017).

Length-Weight Relationship—There was a significant relationship between the length and weight of juvenile hatchery summer Chinook Salmon (Figure 36). Length explained 95% of the variation in weight of juvenile fish. In addition, the relationship indicated a mean condition 2.83 for juvenile hatchery summer Chinook Salmon, suggesting negative allometric growth. The Fulton condition factor averaged 1.12 (range, 0.54-2.82).

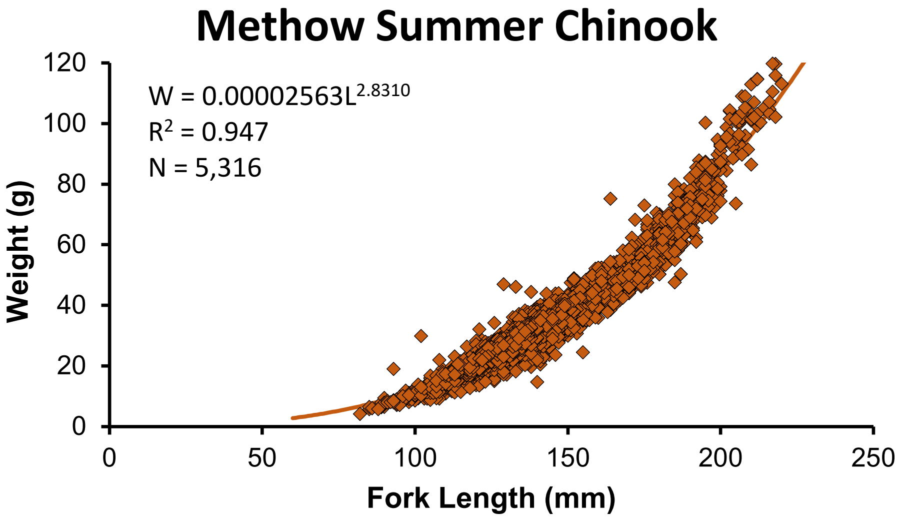

Figure 36. Relationship between fork length (mm) and weight (g) of juvenile Methow River summer Chinook Salmon sampled before release during 2003-2018.

Wells Subyearling Summer Chinook Salmon

Number Released—The goal of the supplementation program is to release 484,000 (±10%) subyearling summer Chinook Salmon from the Wells Fish Hatchery annually. During the 25-year period of the program, the program did not achieve that goal in 10 brood years, it achieved that goal in 14 brood years, and exceeded the goal in 1 brood year (Figure 37). Numbers released ranged from 187,382-541,923 (average = 433,474) juveniles.

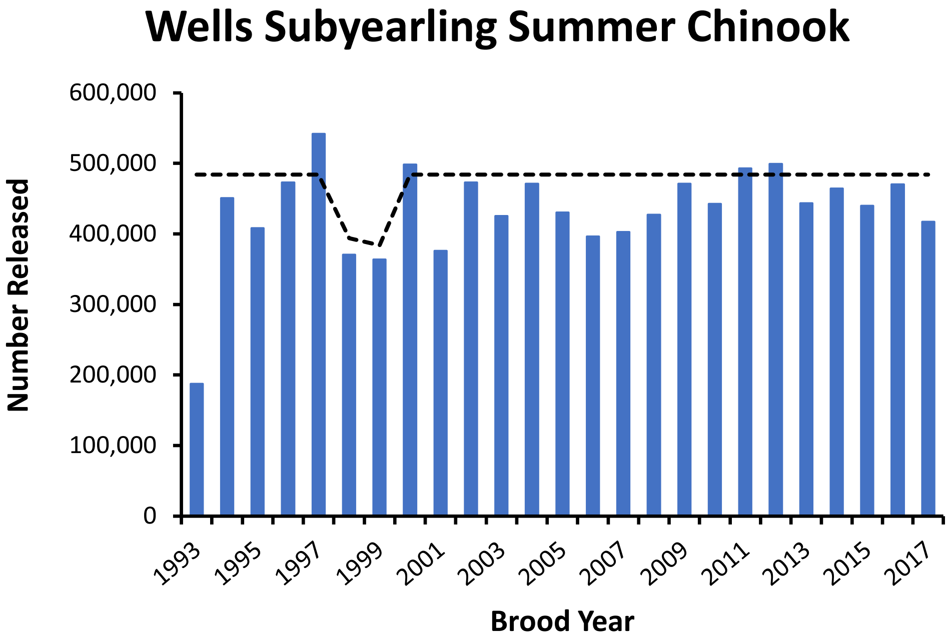

Figure 37. Number of subyearling summer Chinook Salmon released from the Wells Fish Hatchery for brood years 1993-2017. The dashed horizontal line represents the target release number (484,000 except for 1998-1999).

Size at Release—The current goal of the supplementation program (since brood year 2012) is to release subyearling summer Chinook Salmon from the Wells Fish Hatchery that average 9.1 g (50 fish/pound) and have a fork length CV of 7.0 (there was not fork length goal from 2012-2017). The Wells subyearling program is reared to achieve release by a certain date and not to achieve a specific size. During the six-year period under the recent goal of the program, CVs fluctuated above and below the target (Figure 38). CVs ranged from 6-11 (average = 7). Mean weights were below the target while fish per pound was above the target (Figure 38). Throughout the recent six years, mean weights ranged from 6-8 g (average = 7 g) and fish per pound ranged from 55-78 (average = 65 fish/pound).

Wells Subyearling Summer Chinook Salmon Hatchery Releases

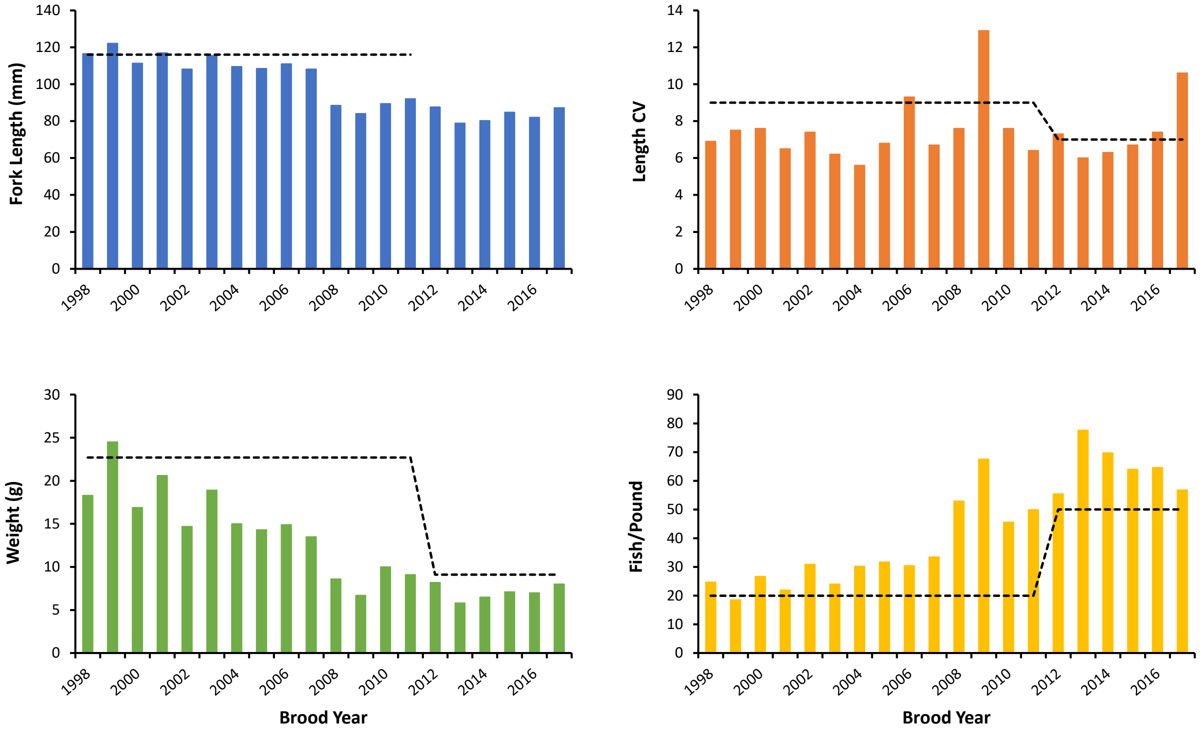

Figure 38. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of subyearling summer Chinook Salmon released from the Wells Fish Hatchery for brood years 1998-2017. The dashed horizontal lines represent the target length (116 mm from 1998-2011; there was no target from 2012-2017), length CV (9.0 from 1998-2011 and 7.0 from 2012-2017), weight (22.7 g from 1998-2011 and 9.1 from 2012-2017), and fish per pound (20 fish per pound for brood years 1998-2011 and 50 fish per pound for brood years 2012-2017).

Length-Weight Relationship—There was a significant relationship between the length and weight of juvenile hatchery summer Chinook Salmon (Figure 39). Length explained 99% of the variation in weight of juvenile fish. In addition, the relationship indicated a mean condition 2.84 for juvenile hatchery summer Chinook Salmon, suggesting negative allometric growth. The Fulton condition factor averaged 1.12 (range, 0.62-2.91).

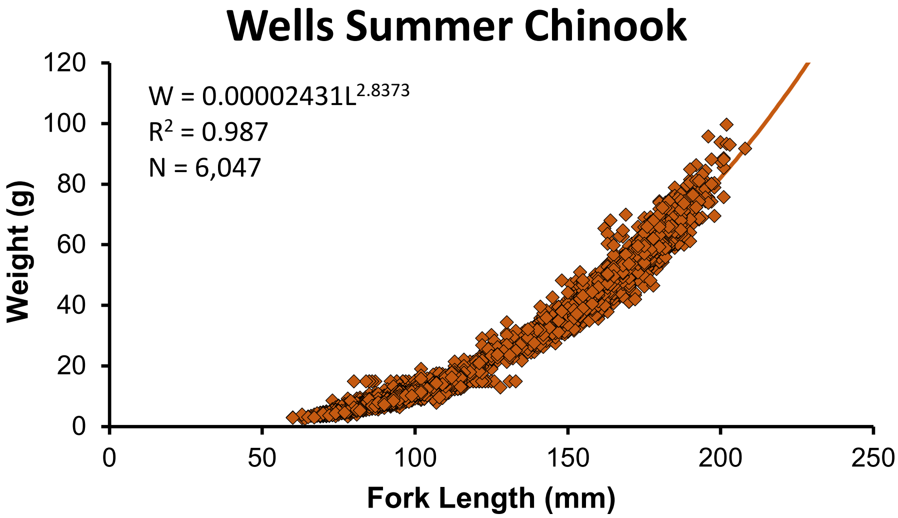

Figure 39. Relationship between fork length (mm) and weight (g) of juvenile Wells summer Chinook Salmon sampled before release during 2003-2018.

Wells Yearling Summer Chinook Salmon

Number Released—The goal of the supplementation program is to release 320,000 (±10%) yearling summer Chinook Salmon from the Wells Fish Hatchery annually. During the 26-year period of the program, the program achieved that goal in 18 brood years, exceeded it in 7 brood years, and did not achieve it in 1 brood year (Figure 40). Numbers released ranged from 185,200-457,770 (average = 330,558) juveniles.

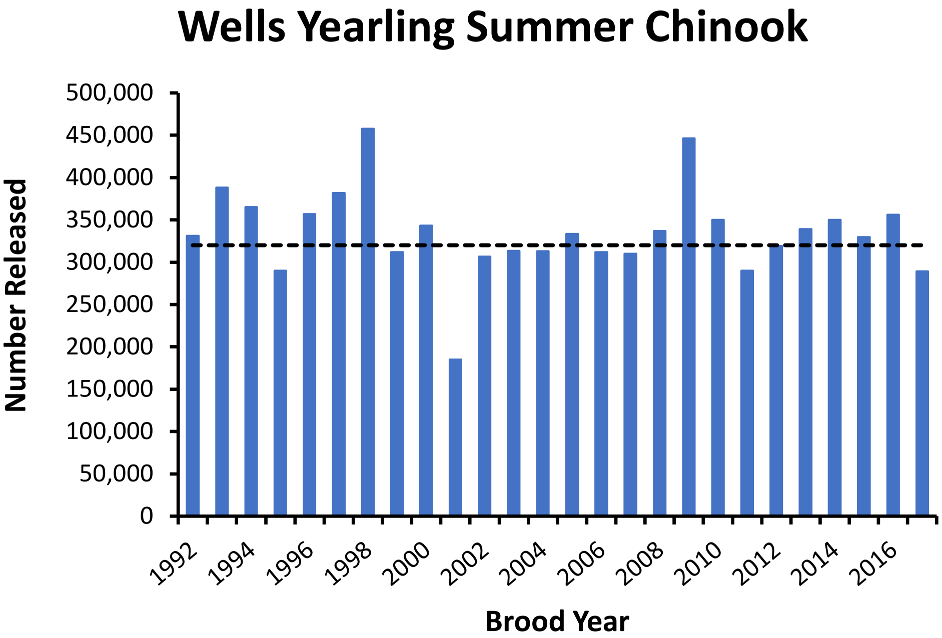

Figure 40. Number of yearling summer Chinook Salmon released from the Wells Fish Hatchery for brood years 1992-2017. The dashed horizontal line represents the target release number (320,000).

Size at Release—The current goal of the supplementation program (since brood year 2012) is to release yearling summer Chinook Salmon from the Wells Fish Hatchery that average 168-mm long (fork length with a CV of 7.0), and 45.4 g (10 fish/pound). During the six-year period under the recent goal of the program, lengths were near the target while CVs fluctuated above and below the target (Figure 41). Mean lengths of fish released ranged from 153-168 mm (average = 163 mm), while CVs ranged from 6-9 (average = 8). Mean weights were generally above the target while fish per pound was generally below the target during the six-year period (Figure 41). Throughout the recent six years, mean weights ranged from 38-50 g (average = 46 g) and fish per pound ranged from 9-12 (average = 10 fish/pound).

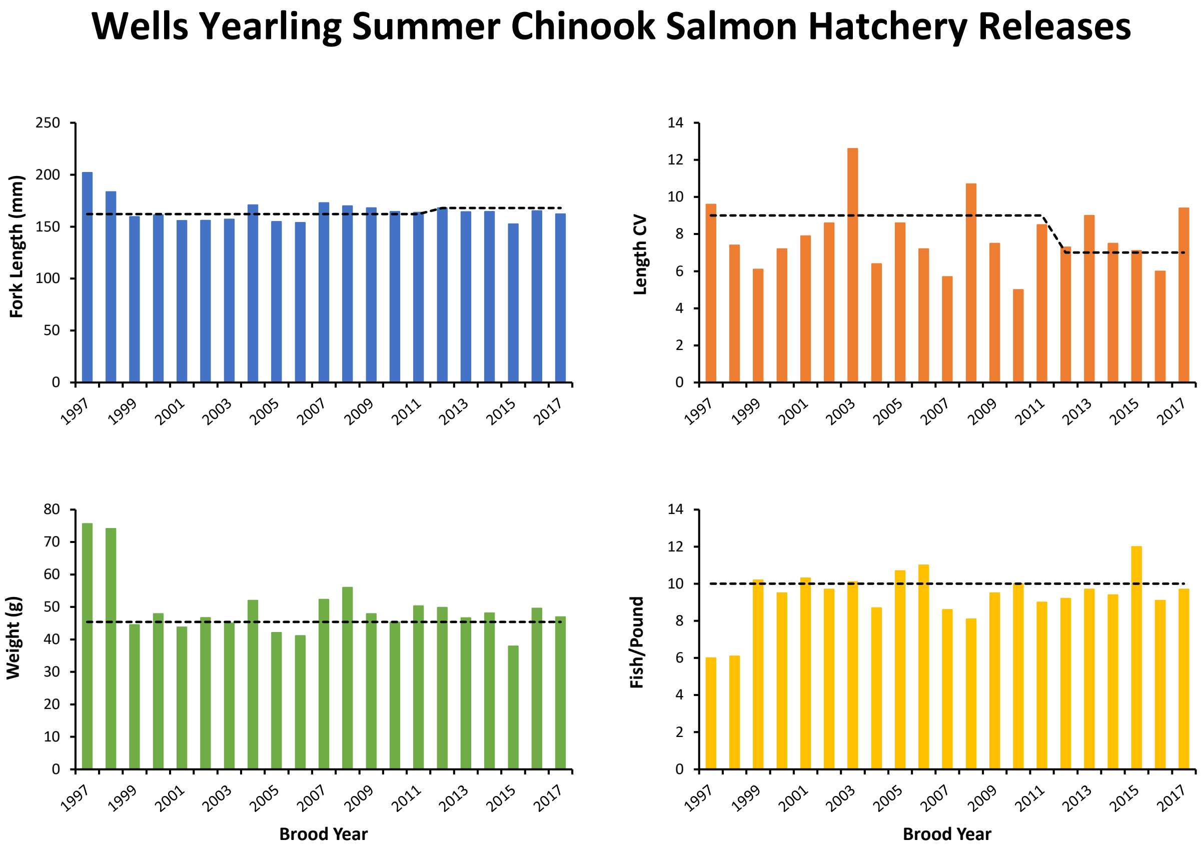

Figure 41. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of yearling summer Chinook Salmon released from the Wells Fish Hatchery for brood years 1997-2017. The dashed horizontal lines represent the target length (162 mm from 1997-2011 and 168 mm from 2012-2017), length CV (9.0 from 1997-2011 and 7.0 from 2012-2017), weight (45.4 g), and fish per pound (10).

Length-Weight Relationship—The length-weight results for Wells Fish Hatchery summer Chinook Salmon are shown under the Wells Subyearling Summer Chinook Salmon section.

Discussion

Programs generally met or exceeded the program release number targets. Specific programs did not meet the release number targets in all years, but all programs met or exceeded targets in the majority of years, with the exception of the White River spring Chinook Salmon program. This program was in development for all of its history and tested numerous fish culture and release strategies. Therefore, the program was not able to meet targets that remained consistent across years. There are a variety of reasons why release targets were not met in some years. The Hatchery Committees developed and approved hatchery implementation plans that specify the number of broodstock to collect to meet target production goals. These plans attempted to predict the number of eggs produced per female based upon mean fecundities during the previous 5 years. In addition, the mean hatchery survival was used to determine how many eggs are needed to produce the desired number of smolts to release. Lower than average fecundities or hatchery survivals was the main reason for failing to meet hatchery release targets.

In general, the length targets, and some of the metrics that used a single value (e.g., length and weight) associated with a range of fpp targets, were not useful. When programs meet the fish per pound metric the length metric cannot be met. This metric should be discarded or realistic length targets need to be developed. Most programs met or were close to meeting the CV target on average. Meeting the CV targets in steelhead programs is more difficult than in the Chinook Salmon programs. Meeting fish-per-pound targets was more difficult in spring Chinook Salmon and conservation steelhead programs. This may be because these programs use natural-origin broodstock and also because attempts are made to reduce precocious maturation by slowing growth or producing fish that do not exceed a size threshold. Spring Chinook Salmon tended to be slightly smaller than the target. Fish were reared to balance achieving threshold size for release while hedging against larger fish that may exhibit higher rates of precocity. In addition, meeting the 6 fpp target for conservation steelhead was difficult, and likely not desirable, due to the short rearing time with spring-spawned steelhead programs. Those Chinook Salmon programs that target a range of fpp at release were sometimes paired with single values for length and weight (e.g., Nason and White spring Chinook, Methow summer Chinook). This was likely a legacy of past targets that were not updated when the fpp ranges were updated to reduce unnaturally high proportions of precocious maturation. The programs that have an updated range for target fpp have been managed primarily to hit the fpp target rather than individual length or weight targets. Targets for programs with a range of target fpps are good candidates for revision.

Spring Chinook Salmon exhibited near-isometric growth. Steelhead exhibited negative allometric growth, as did Wells and Methow summer Chinook Salmon. However, Wenatchee and Chelan Falls summer Chinook Salmon exhibited isometric or positive allometric growth. Condition factors across all programs were very close to or exceeded 1.

Trade-offs between post release survival and age at maturation influence the hatchery rearing strategies. Large Chinook Salmon generally survive better than small fish, but they also are more prone to maturation at younger ages. Hatchery programs that use natural-origin fish for broodstock may also experience higher levels of precocious maturation than if hatchery-origin fish were used for broodstock (Larsen et al. 2020). Attempts to reduce precocious maturation of Chinook Salmon released into Nason Creek has also resulted in smaller fish that don’t meet some of the size targets. In addition, larger fish also pose ecological risks to other fish through mechanisms such as competition or predation. Fish that are released from hatcheries continue to be substantially larger than natural-origin fish, even when they fail to meet the size targets. Evaluations of survival and age at maturation that are contained in other portions of the monitoring plan will inform whether current size at release targets are achieving the acceptable trade-offs desired by fishery managers. Adaptation of targets may occur to achieve a better suite of benefits among the many trade-offs involved in growing fish to a target size or weight.

Acknowledgments

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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.

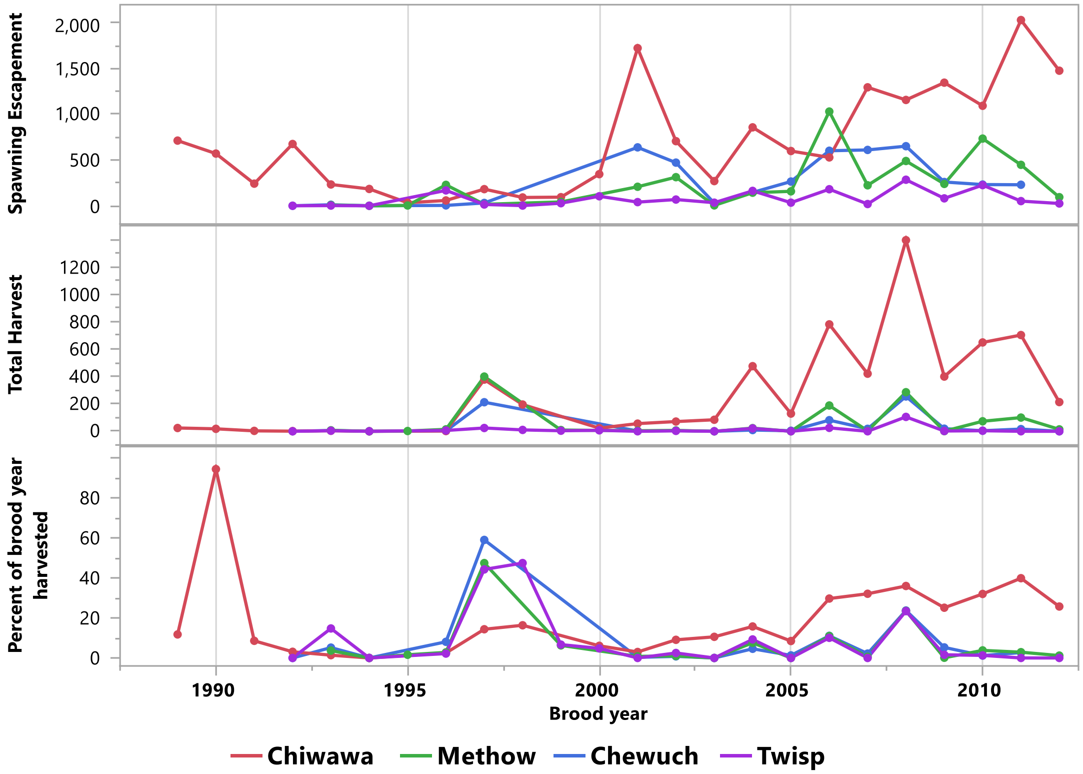
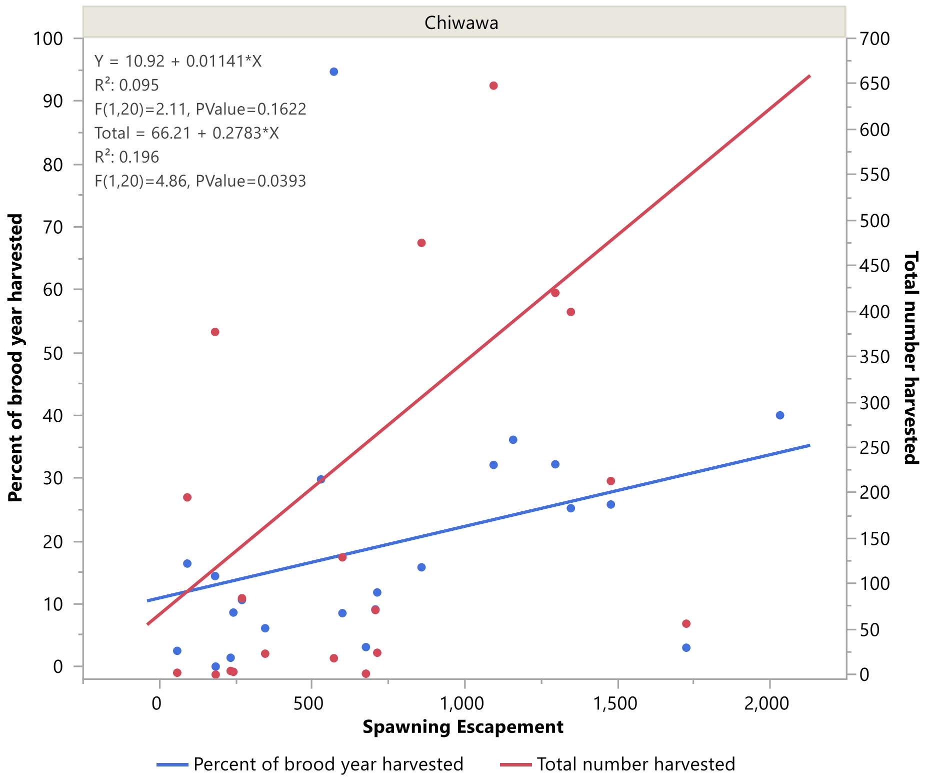
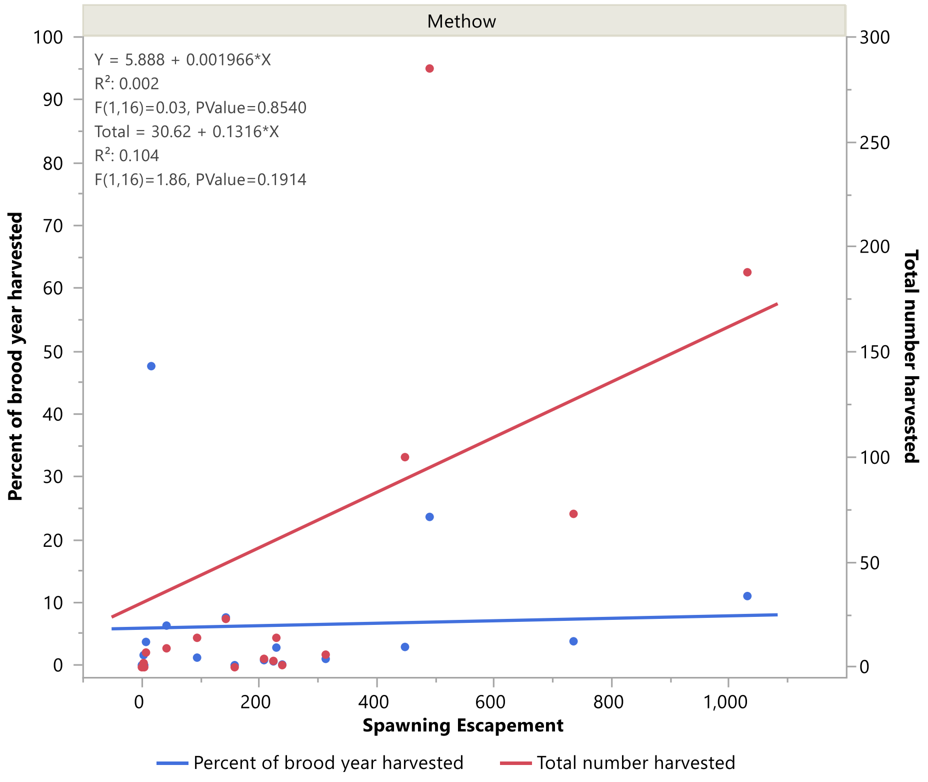
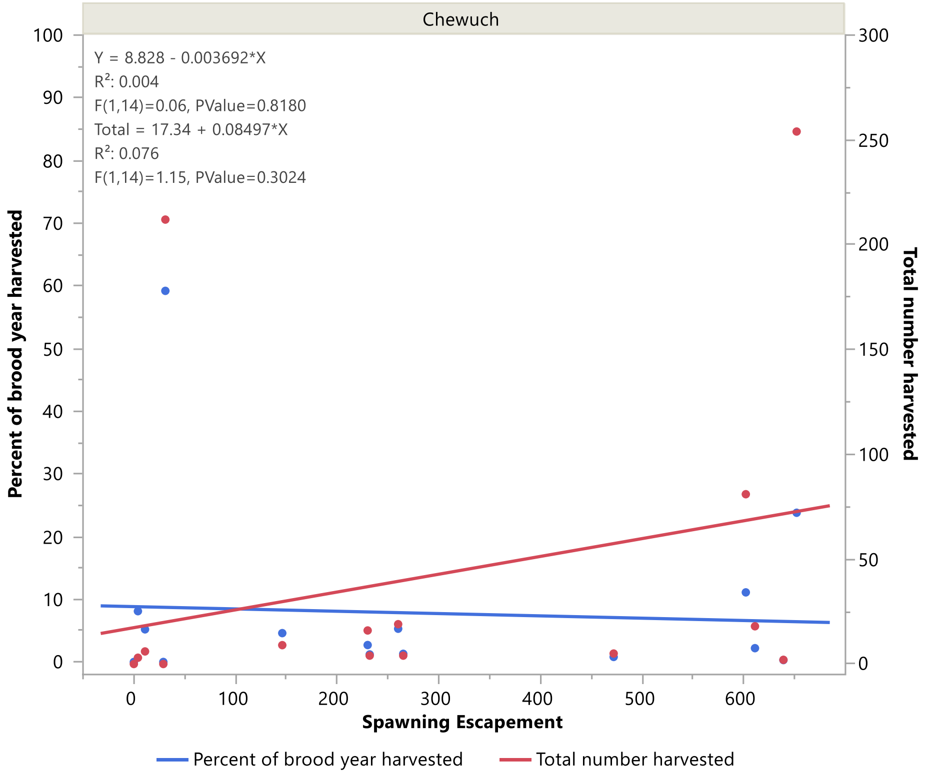


Figure 1. Spawning escapement, total harvest, and percent of brood year harvested for hatchery spring Chinook Salmon from the Chiwawa ($\bar{x}$ = 25.6%), Methow ($\bar{x}$ = 5.1%), Chewuch ($\bar{x}$ = 5.8%), and Twisp ($\bar{x}$ = 4.6%) rivers (averages represent percent of brood year harvested over 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
0
10
20
30
40
50
60
70
80
90
100
0
50
100
150
200
250
300
350
400
450
500
550
600
650
700
0
500
1,000
1,500
2,000
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
0
10
20
30
40
50
60
70
80
90
100
0
50
100
150
200
250
300
0
200
400
600
800
1,000
Percent of brood year harvested
Total number harvested



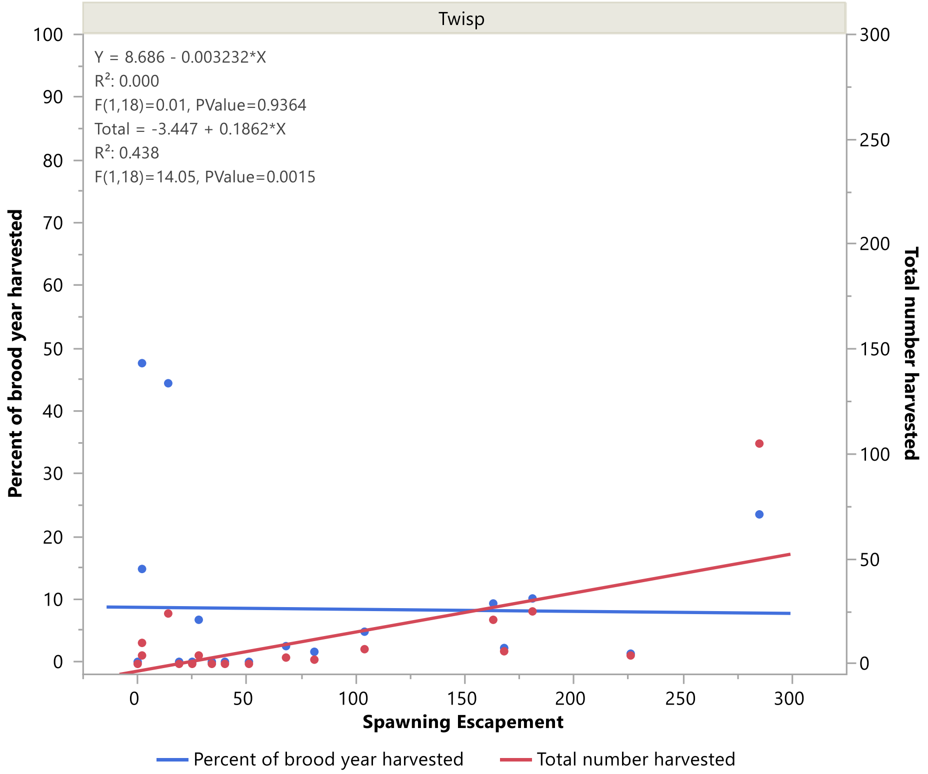


Figure 2. Spawning escapement versus percent of brood year harvested and total number of hatchery fish harvested for spring Chinook Salmon from the Chiwawa, Methow, Chewuch, and Twisp rivers.

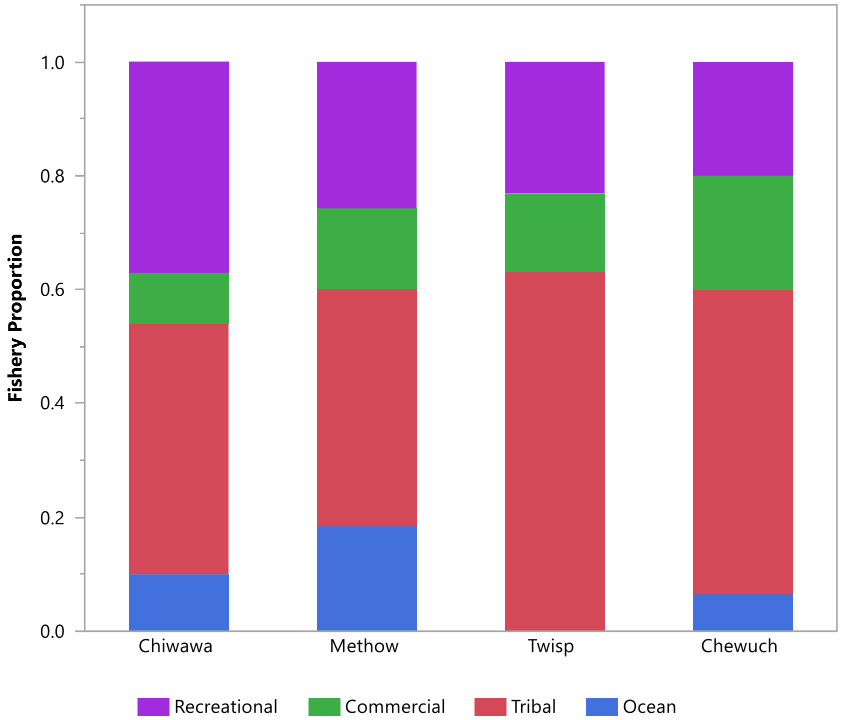


Figure 3. Fishery proportions (mean values) for spring Chinook Salmon harvested from the Chiwawa, Methow, Twisp, and Chewuch rivers.

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.

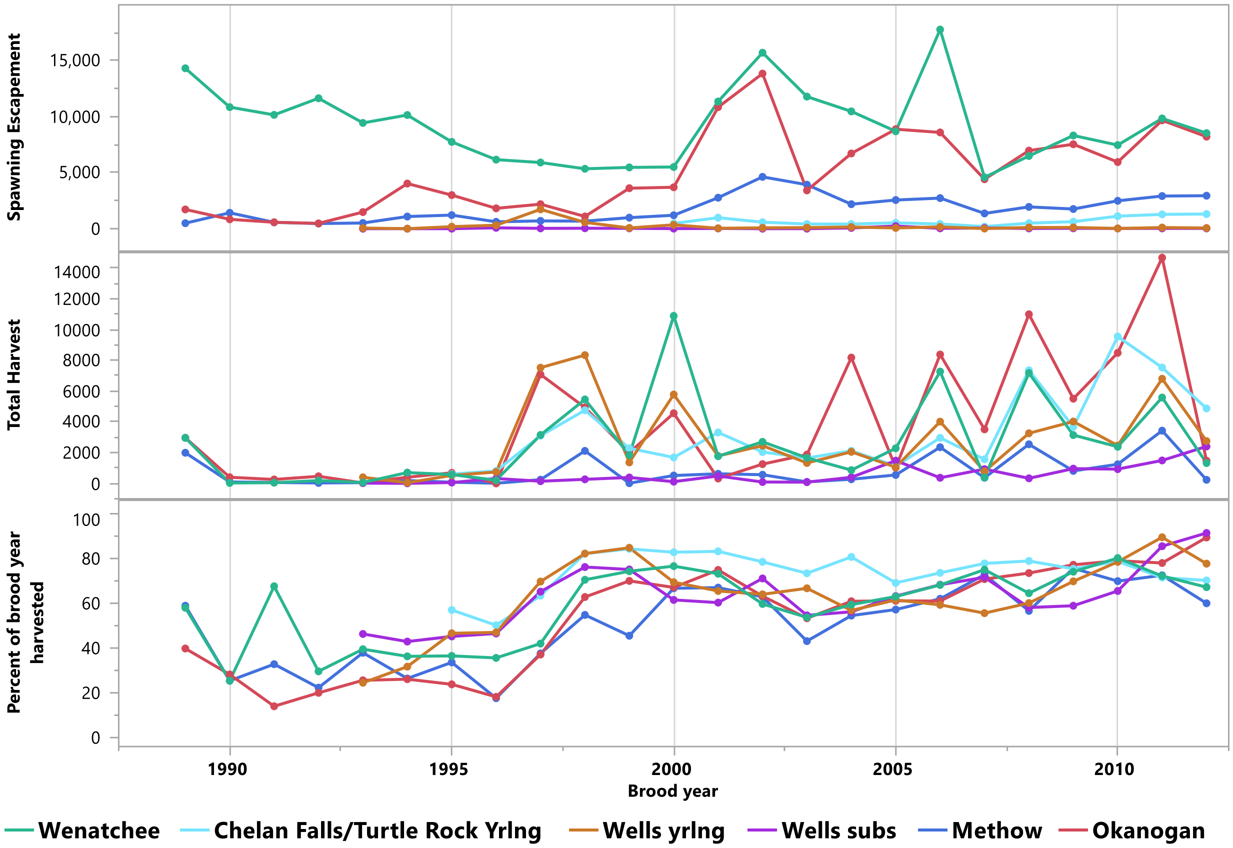


Figure 4. Spawning escapement, total harvest, and percent of brood year harvested for hatchery-origin summer Chinook Salmon from the Wenatchee River ($\bar{x}$ = 67.8%), Chelan Falls/Turtle Rock yearling program ($\bar{x}$ = 74.6%), Wells Hatchery yearling program ($\bar{x}$ = 67.6%), Wells Hatchery 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).

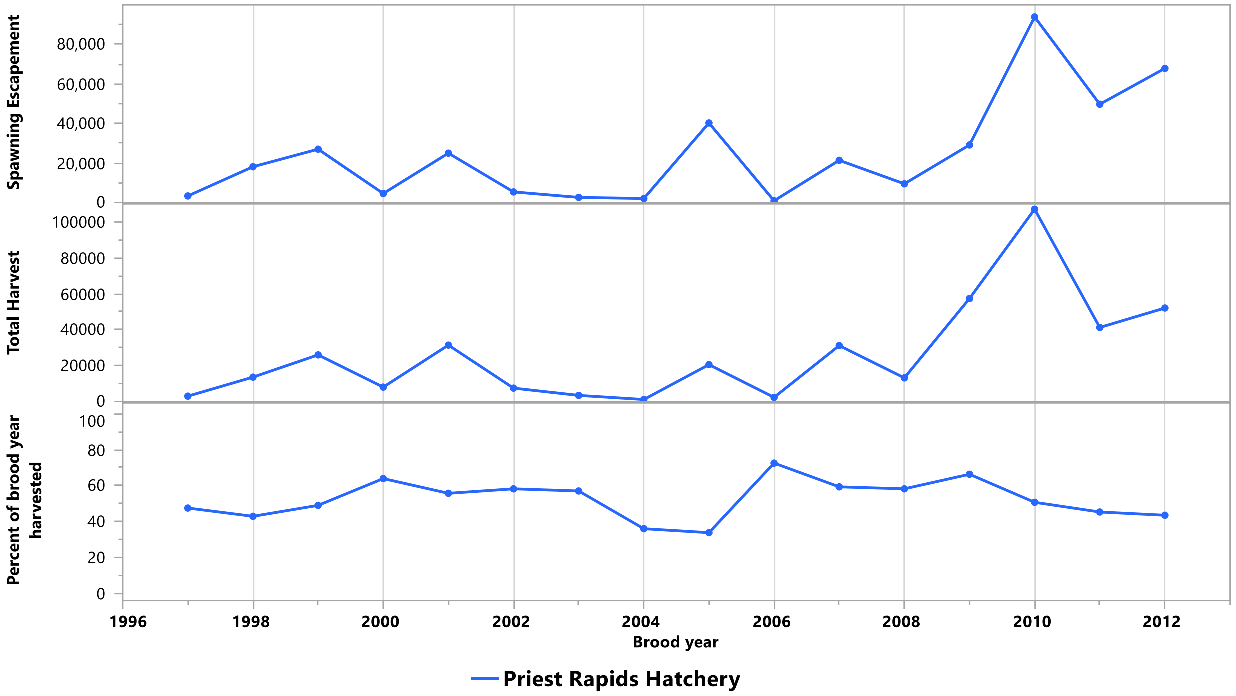
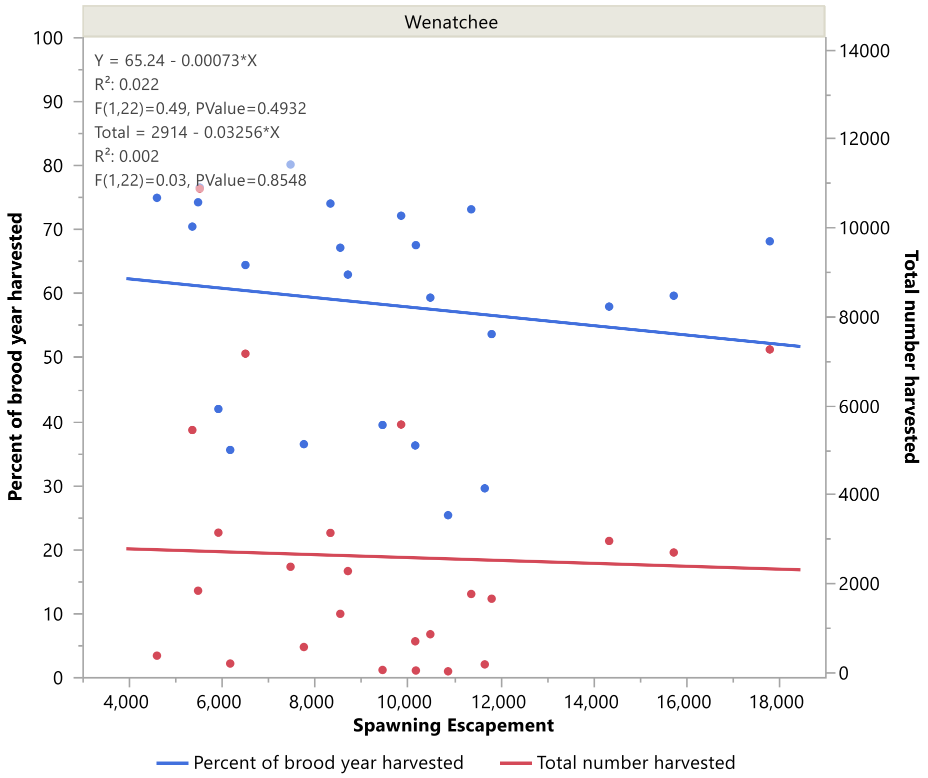
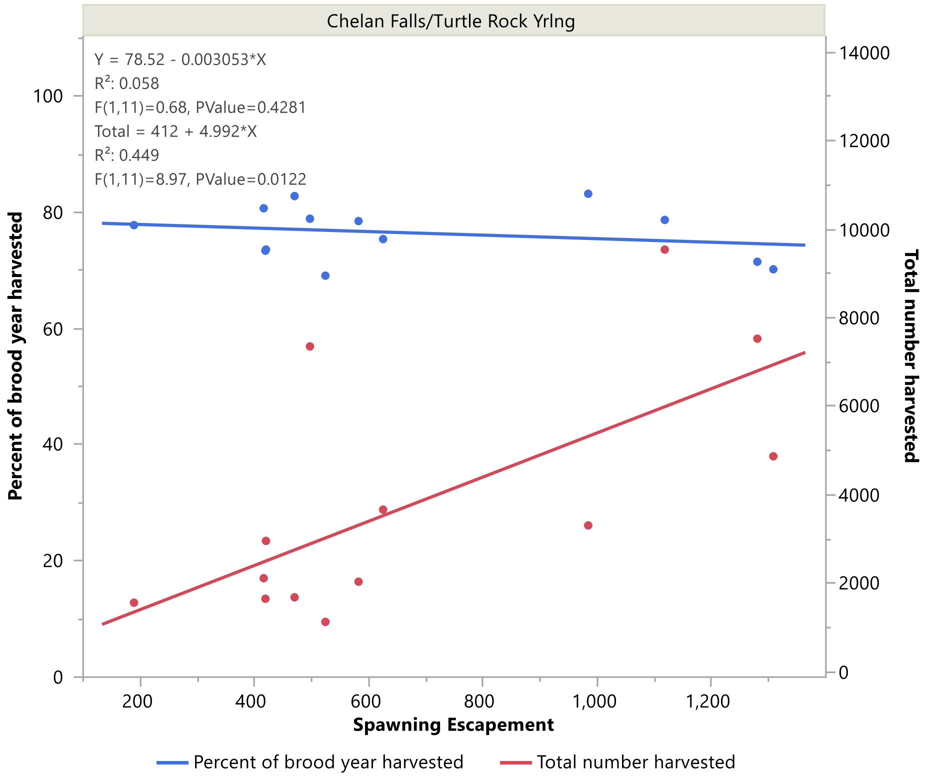
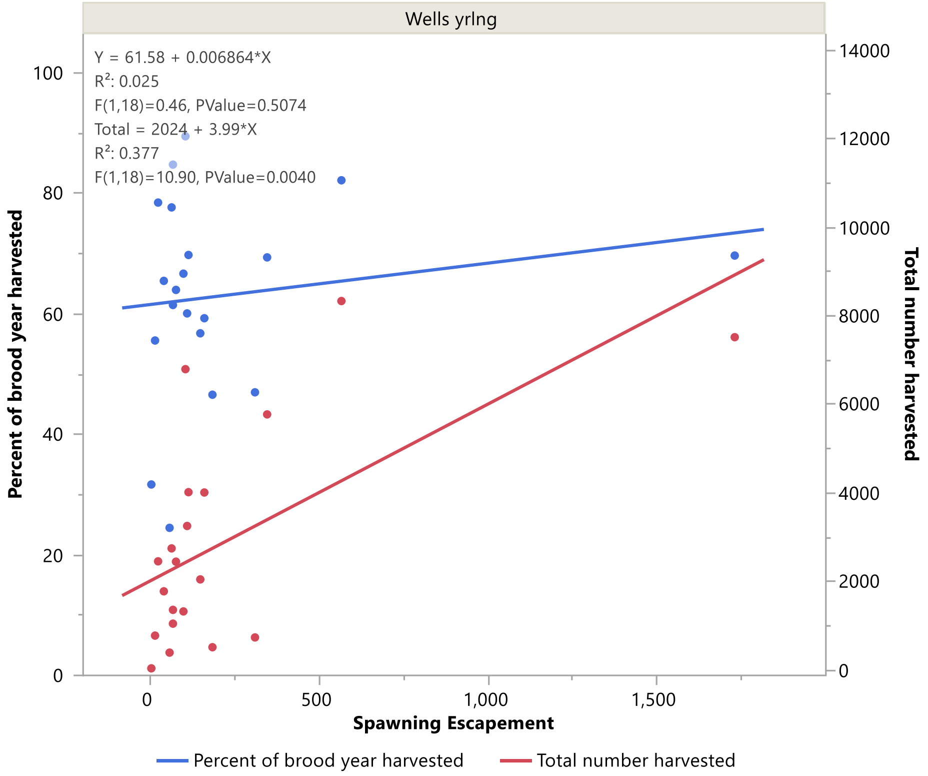
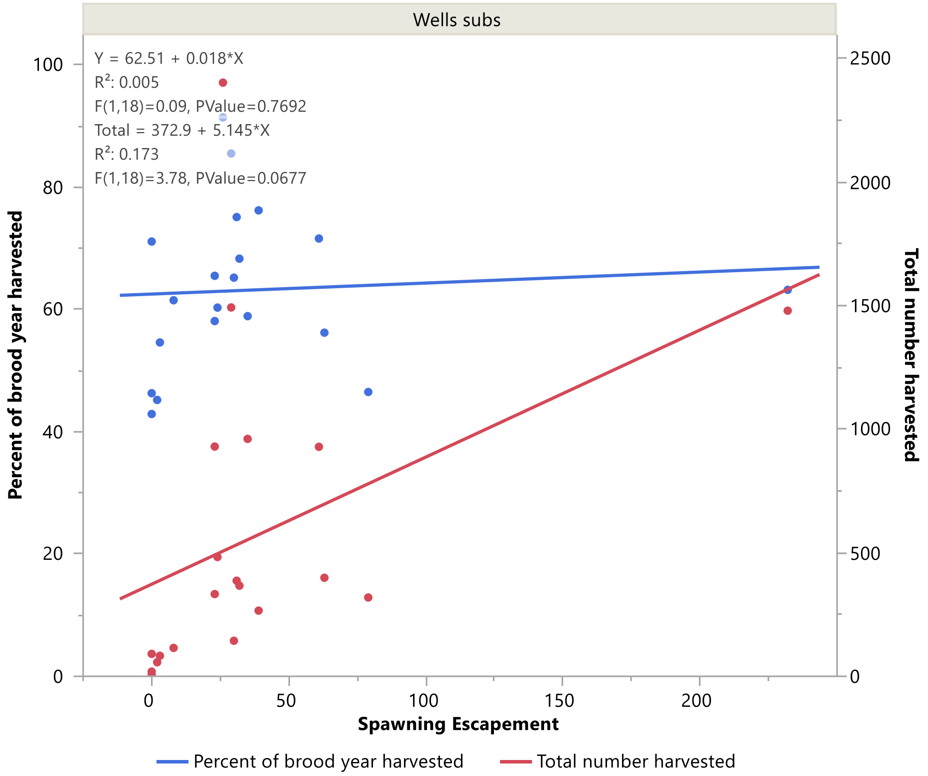


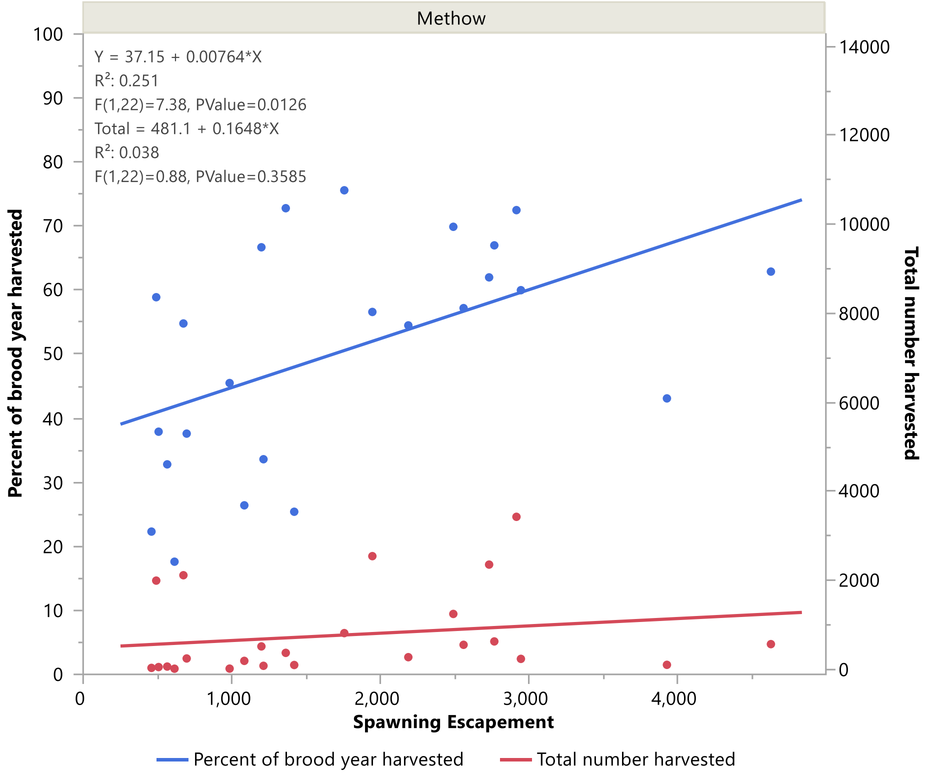
Figure 5. Spawning escapement, total harvest, and percent of brood year harvested for hatchery fall Chinook Salmon from Priest Rapids Hatchery ($\bar{x}$ = 52.5%) program (average represent percent of brood year harvested over brood years 2004-2012).




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
0
20
40
60
80
100
0
2000
4000
6000
8000
10000
12000
14000
200
400
600
800
1,000
1,200
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
0
20
40
60
80
100
0
2000
4000
6000
8000
10000
12000
14000
0
500
1,000
1,500
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
0
20
40
60
80
100
0
500
1000
1500
2000
2500
0
50
100
150
200
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
0
10
20
30
40
50
60
70
80
90
100
0
2000
4000
6000
8000
10000
12000
14000
0
1,000
2,000
3,000
4,000
Percent of brood year harvested
Total number harvested

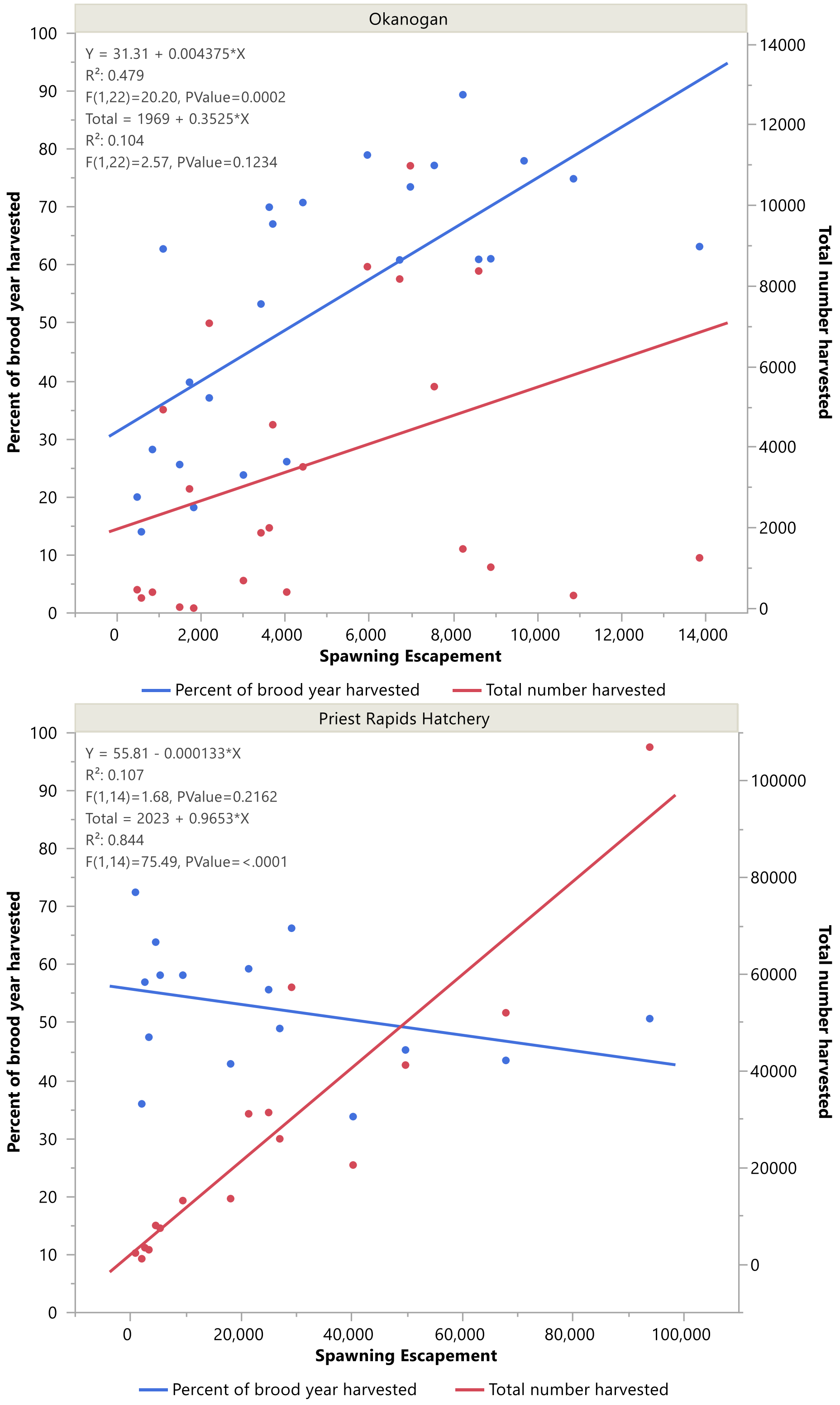


Figure 6. Spawning escapement versus percent of brood year harvested and number harvested for hatchery-origin summer Chinook Salmon from the Wenatchee River, Chelan Falls/Turtle Rock yearling program, Wells Hatchery yearling program, Wells Hatchery subyearling program, Methow River, Okanogan River, and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

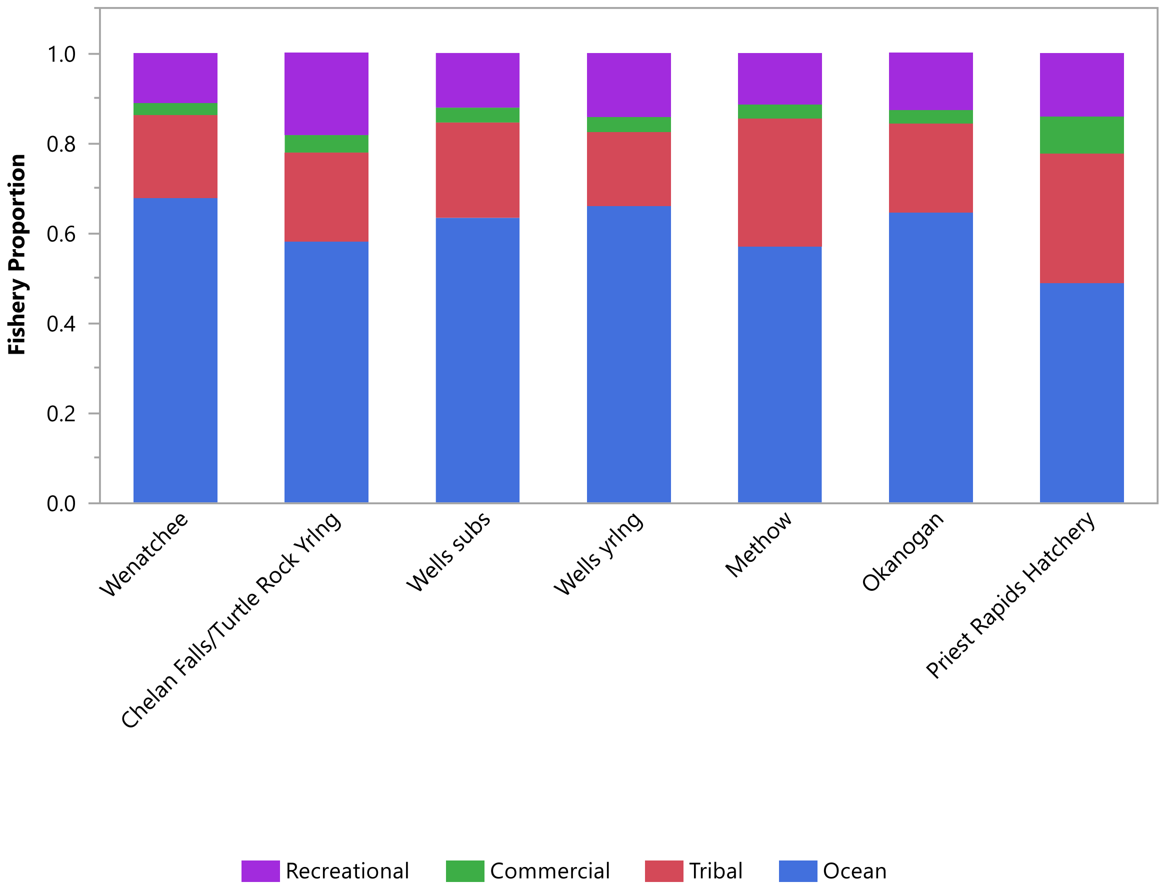


Figure 7. Fishery proportions (mean values) for summer Chinook Salmon harvested from the Wenatchee River, Chelan Falls/Turtle Rock yearling program, Wells Hatchery subyearling program, Wells Hatchery yearling program, Methow River, Okanogan River, and fall Chinook Salmon from Priest Rapids Hatchery.

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.

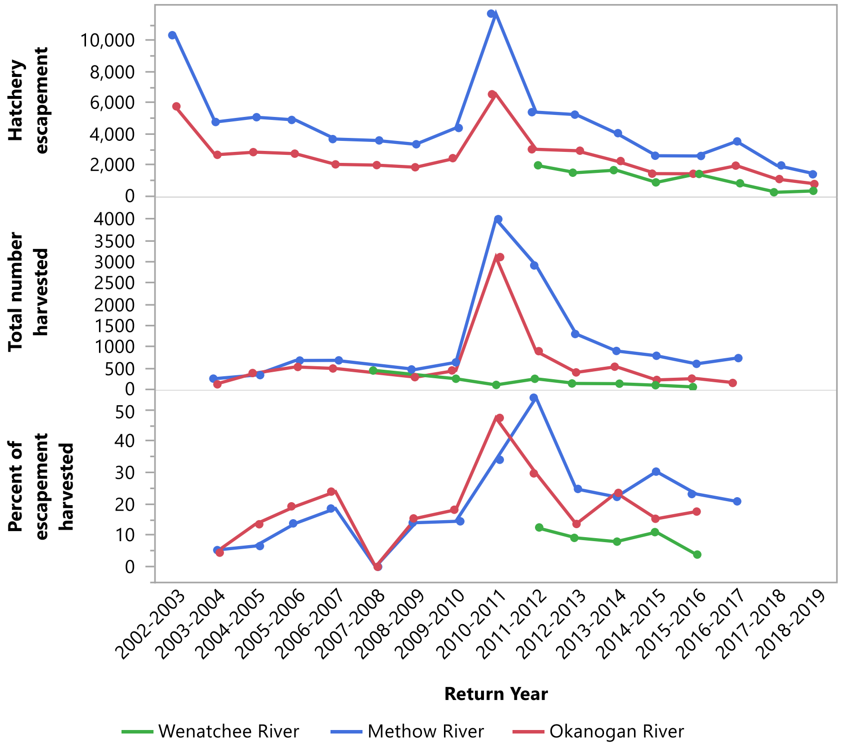
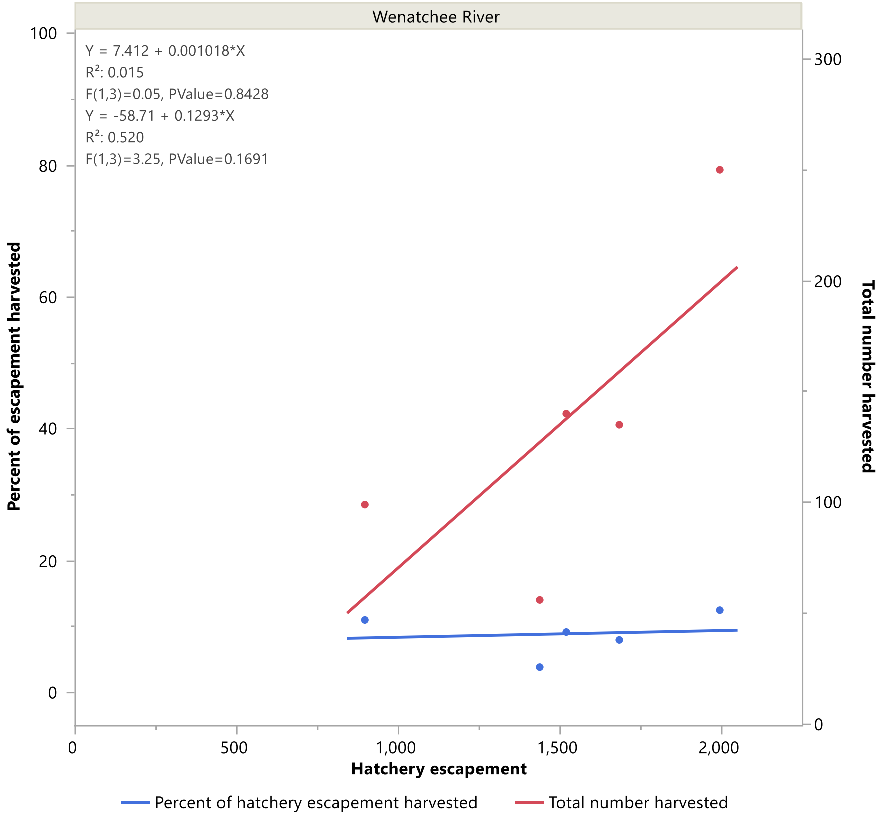
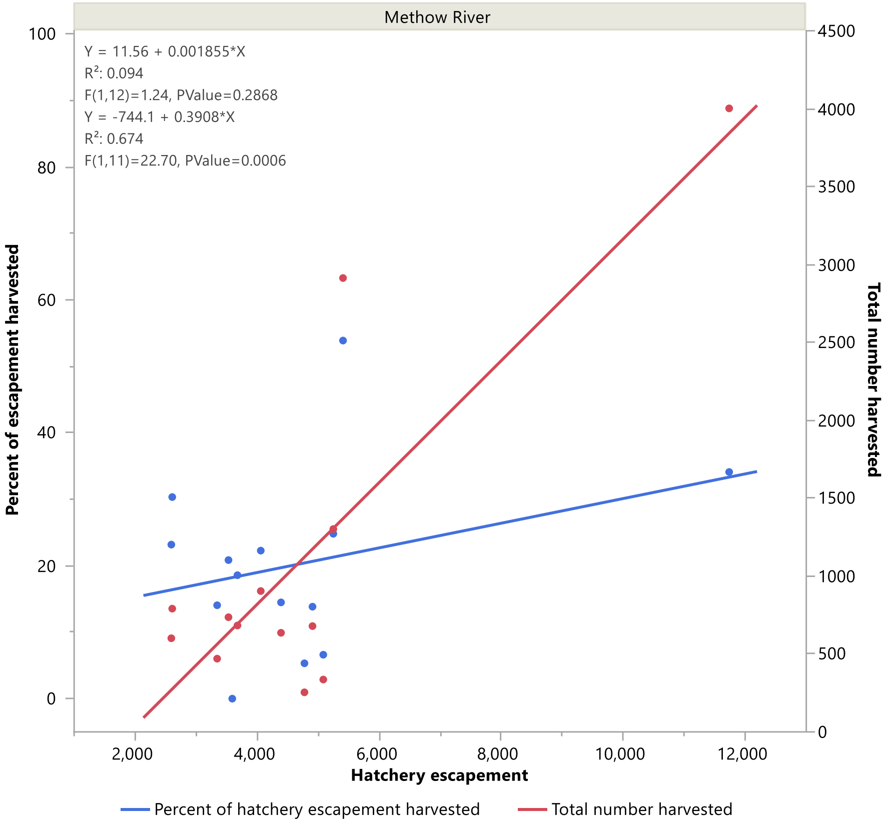


Figure 8. Escapement, total number harvested, and percent harvest of hatchery-origin steelhead escapement to the Wenatchee ($\bar{x}$ = 8.7%), Methow ($\bar{x}$ = 20.2%), Okanogan ($\bar{x}$ = 18.6%) rivers (averages represent return years 2003-2017 for the Methow and Okanogan rivers and 2011-2016 for 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
0
20
40
60
80
100
Total number harvested
0
100
200
300
Hatchery escapement
0
500
1,000
1,500
2,000
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
0
20
40
60
80
100
Total number harvested
0
500
1000
1500
2000
2500
3000
3500
4000
4500
Hatchery escapement
2,000
4,000
6,000
8,000
10,000
12,000
Percent of hatchery escapement harvested
Total number harvested

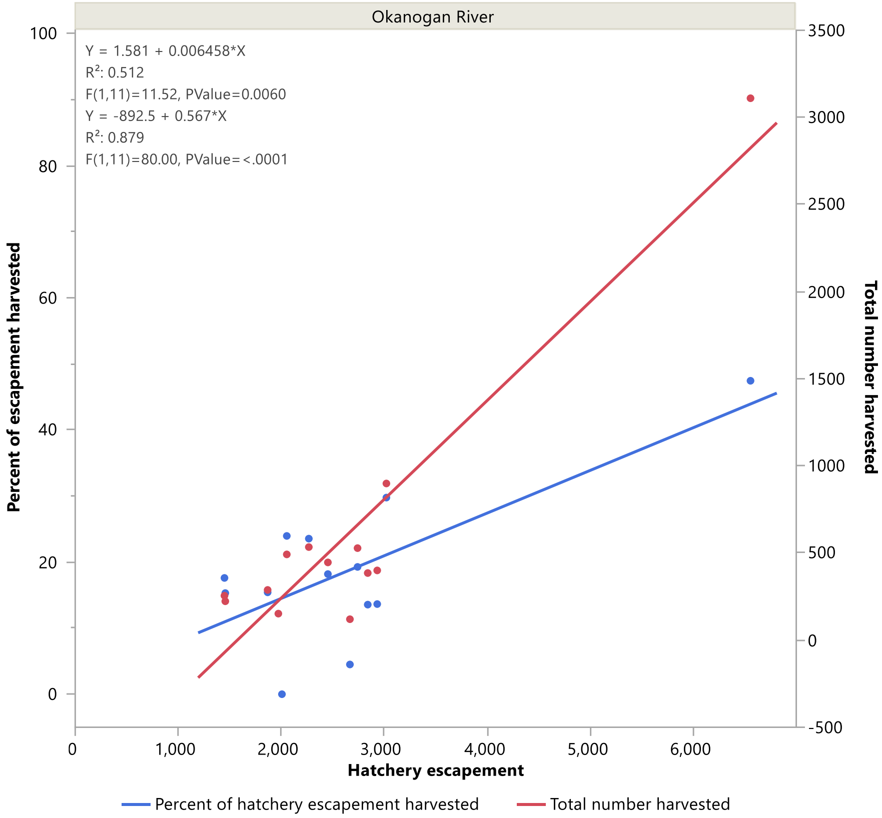


Figure 9. Escapement versus percent of escapement harvested and number harvested of hatchery-origin steelhead from the Wenatchee, Methow, and Okanogan rivers.

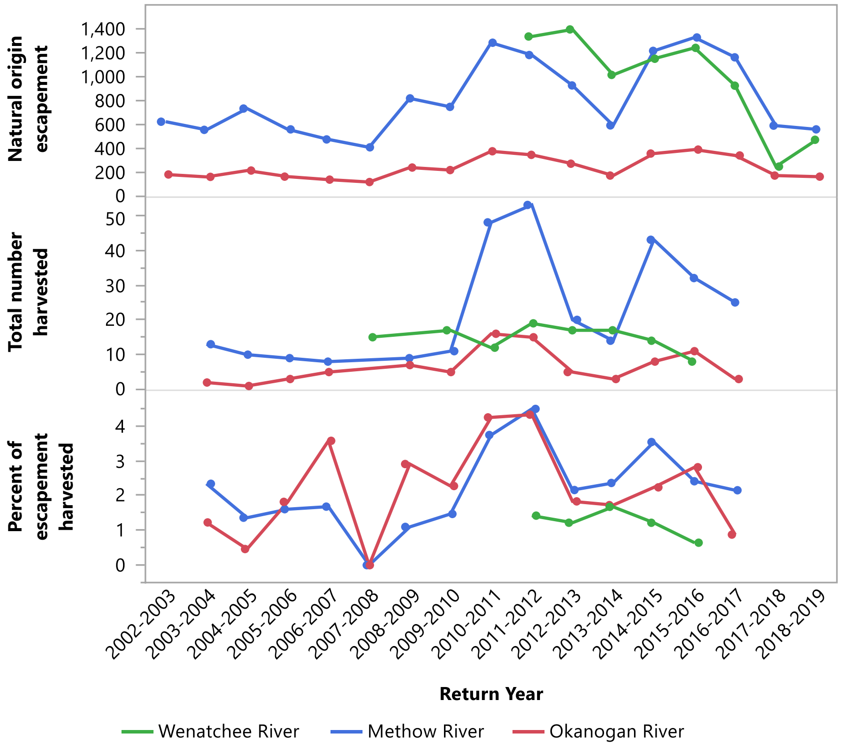
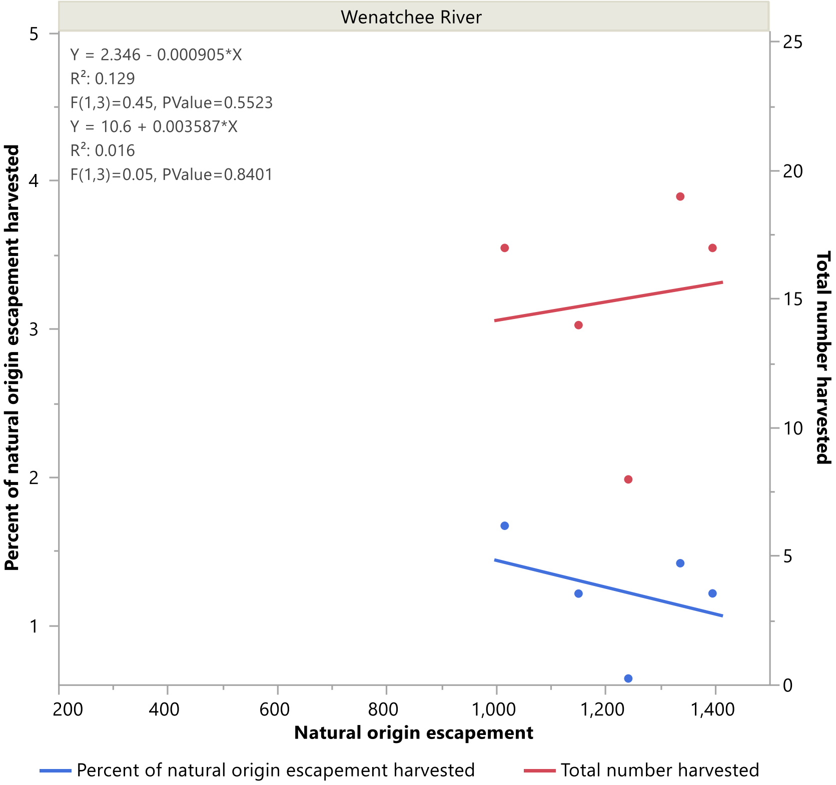
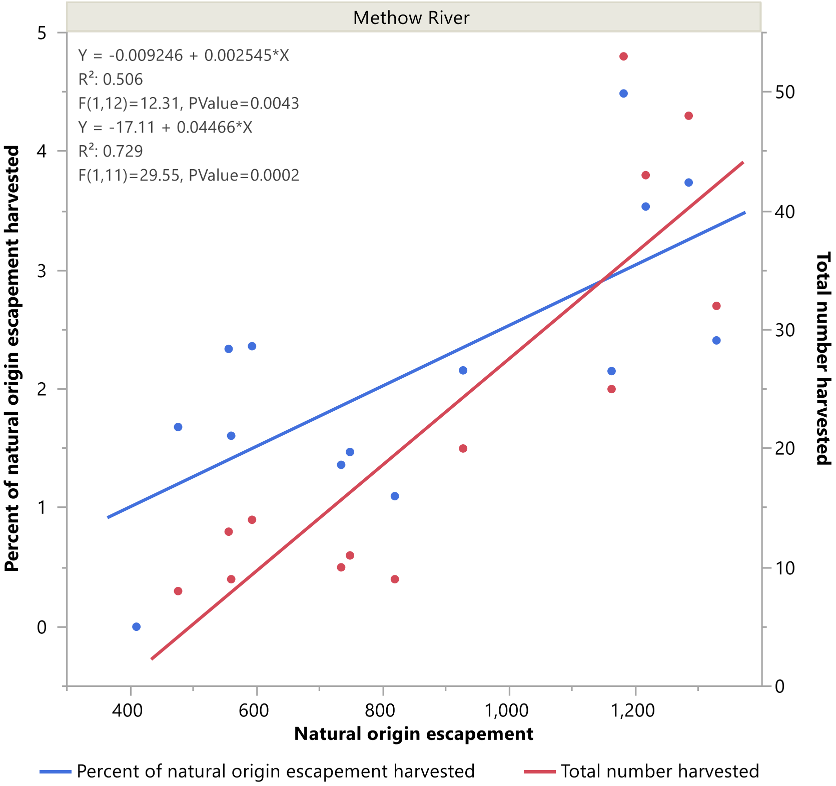


Figure 10. Escapement, total number harvested, and percent of escapement harvested of natural-origin steelhead for the Wenatchee ($\bar{x}$ = 1.36%), Methow ($\bar{x}$ = 2.17%), and Okanogan ($\bar{x}$ = 2.16%), rivers (averages represent returns years 2003-2017 for the Methow and Okanogan rivers and 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
1
2
3
4
5
Total number harvested
0
5
10
15
20
25
200
400
600
800
1,000
1,200
1,400
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
0
1
2
3
4
5
Total number harvested
0
10
20
30
40
50
400
600
800
1,000
1,200
Natural origin escapement
Percent of natural origin escapement harvested
Total number harvested

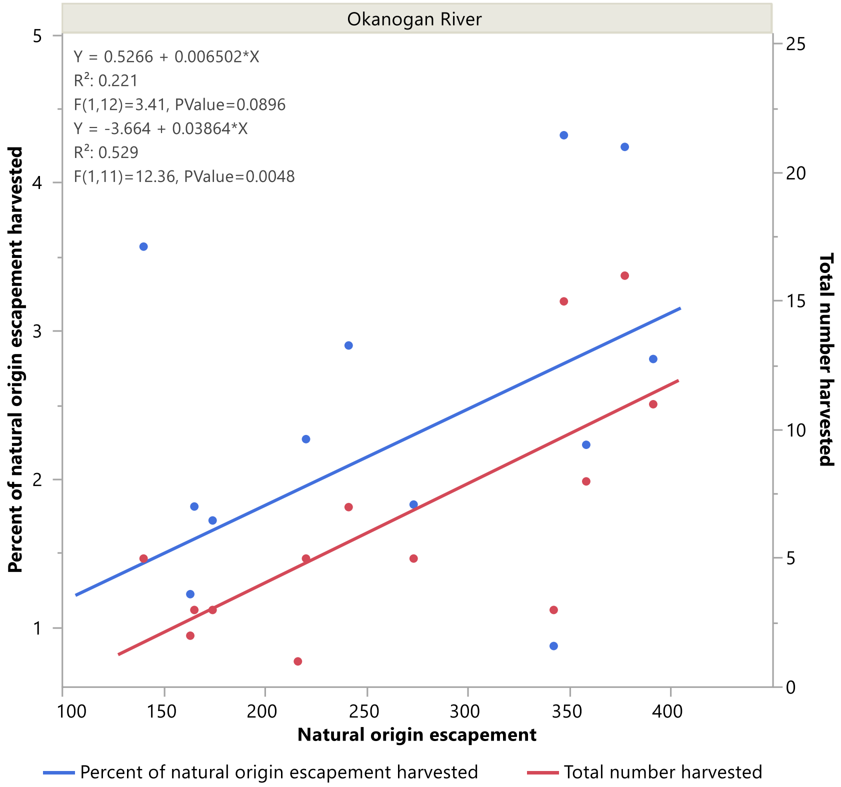


Figure 11. Escapement versus percent of escapement harvested and total number harvested of natural-origin steelhead from the Wenatchee, Methow, and Okanogan rivers.

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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