

Comprehensive Evaluation of Middle Columbia River Public Utility District's Steelhead Hatchery Programs

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Executive Summary

The three Public Utility Districts (PUD) of the middle Columbia River are charged with achieving and maintaining no net impact on Salmon and steelhead from 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 when passing the hydroelectric projects. The PUDs implement a comprehensive monitoring and evaluation plan to determine whether the performance of the hatchery programs achieves the goals described in the plan (Hillman et al. 2019). This report compiles the results of multiple analyses of monitoring and evaluation data collected for Grant, Chelan, and Douglas County PUD's summer steelhead hatchery programs through 2018. Other covered species (e.g., spring, summer, and fall Chinook Salmon, Sockeye Salmon, and steelhead) are presented in other reports. Authorship, titles, and abstracts of each of the report chapters are presented below.

1) Mackey, G., and T. W. Hillman. Wenatchee and Methow summer steelhead status of natural replacement rate and stock-recruit assessment.

The Wenatchee and Methow summer steelhead (*Oncorhynchus mykiss*) populations are the focus of conservation hatchery programs. These populations are part of the Upper Columbia Distinct Population Segment, listed as threatened under the Endangered Species Act. Conservation hatchery programs are intended to increase the number of spawning adults to affect a subsequent increase in the number of natural-origin recruits (NOR). For the natural population to remain stable or to increase, the Natural Replacement Rate (NRR), the ratio of NORs to the parent spawning population, must be greater than or equal to one, a level where parents are replaced by their offspring as spawners in the next generation. We evaluated the population dynamics and NRR of the Wenatchee and Methow steelhead populations using stock-recruit models and assessed the magnitude and trends of NRR in these populations. The hypotheses explored were 1) there was no difference in the number of natural-origin spawners over time (or conversely it increased/decreased over time), and 2) the natural replacement rate remained constant or increased/decreased over time. Natural-origin spawners increased in the Wenatchee, but remained static at very low abundance in the Methow. Both the Wenatchee and Methow populations had NRR median values well below replacement. The Wenatchee NRR would need to double to achieve replacement and the Methow would need to increase five-fold. The Wenatchee NRR declined over time while the Methow NRR remained static at very low levels. The Hatchery Replacement Rate (HRR) exceeded NRR in all years for both populations. Stock-recruit modeling was used to further explore the dynamics of these populations. In the Wenatchee, replacement, as estimated by the Smooth Hockey Stick model, would occur up to approximately 573 spawners. Replacement of the Methow population is estimated to occur up to approximately 322 spawners. The 90th quantile estimates of carrying capacity suggest that at equilibrium carrying capacity the Wenatchee population is at 37% of and the Methow population at 41% of habitat carrying capacity. Both populations fall below replacement at or below the minimum conservation number of spawners (~500) and abundance of the populations is low. Hatchery fish spawning in nature appear to be producing few returning adult offspring. The proportion of hatchery-origin spawners on the spawning grounds was negatively related to returning adult abundance in the Methow population, but there was no relationship in the

Wenatchee population. However, the pHOS data lacks contrast, with a lack of observations in the lower two-thirds of the pHOS range. More robust assessment of these programs could be achieved by employing management designed to test hypotheses by using reference streams with the Upper Columbia subbasins and imparting intentional levels of contrast into the management strategies. These populations face low replacement rates and demographic risks. It is imperative to design management to identify the factors negatively affecting these populations so that future management can address those factors.

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) Shelby, K. K., T. W. Hillman, and C. C. Willard. Adult migration and spawn timing of summer steelhead in the Wenatchee and Methow River subbasins.

Success of integrated hatchery programs relies, in part, on similar migration and spawn timing of hatchery- and natural-origin conspecifics. Synchronous migration timing between hatchery- and natural-origin steelhead ensures that hatchery- and natural-origin fish experience comparable migration conditions to allow for similar arrival timing at the spawning grounds. An overlap in spawn timing ensures that hatchery- and natural-origin fish are, at minimum, present on the spawning grounds at similar times to allow interbreeding among these groups. This study uses Passive Integrated Transponders (PIT) tag data to evaluate adult migration and spawn timing between hatchery-origin and natural-origin summer steelhead originating from the Wenatchee and Methow sub-basins in Washington State. Migration timing was evaluated at PIT-tag interrogation systems located within adult fishways at dams. Paired t-tests, comparing the mean day of year (DOY) that 10%, 50%, and 90% of hatchery- and natural-origin steelhead passed interrogation sites, indicated that natural-origin steelhead tended to arrive slightly earlier than hatchery-origin adults in their migration through Bonneville and Priest Rapids Dams located on the Columbia River, although these differences were not significant, generally indicating similar

migration timing. However, as these populations moved farther up the Columbia River approaching their spawning grounds, migration timing between hatchery- and natural-origin steelhead began to differentiate. Wenatchee hatchery-origin steelhead arrived earlier at Rock Island Dam for the latter (90%) portion of the run. Migration through Tumwater Dam showed a bimodal distribution where, at 50% of the run, natural-origin steelhead arrived 12 days earlier than their hatchery conspecifics. Methow natural-origin steelhead arrived earlier than their hatchery-origin counterparts at Priest Rapids Dam (50% of the run) and at Wells Dam (10% and 50% of run). Spawn timing, evaluated at instream PIT-tag interrogation array systems located within spawning tributaries, indicated similar arrival timing to spawning grounds between hatchery- and natural-origin steelhead for both the Wenatchee and Methow populations. Further analysis is needed to evaluate year-specific patterns and mechanisms causing observed differences, especially given the large variation observed in the pooled analysis.

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) Seamons, T. R., S. Brown, A. Louden, G. McKinney, M. P. Small, T. N. Pearsons, T. H. Kahler, and C. C. Willard. Evaluation of genetic metrics of adult hatchery- and natural-origin steelhead in the Upper Columbia Basin.

In 1997, the upper Columbia River summer steelhead evolutionarily significant unit (ESU), was listed as threatened under the Endangered Species Act (ESA). Hatchery programs already underway were used to supplement wild steelhead populations in the Wenatchee, Methow, and Okanogan rivers for conservation and fishery benefits. Hatchery propagation comes with genetic risks to wild populations of reduced within- and among-population diversity and domestication. 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 steelhead. Current hatchery programs are integrated and broodstock are collected locally within each population. Hatchery collections (baseline or contemporary) had higher levels of linkage disequilibrium and lower estimates of effective number of breeders (N_b) than collections from natural-origin fish due to strong family structure and small number of parents spawned. In addition, contemporary hatchery collections were genetically distant from natural baseline and contemporary collections. This indicates genetic drift is occurring in the hatchery collections to a higher degree than in the naturally spawning population. This pattern is likely mostly due to the low number of steelhead used as broodstock in upper Columbia River steelhead hatchery programs. Contemporary hatchery collections from 2018 tended to be quite different from all other collections likely due to low number of broodstock and decreased survival of the 2014 cohort due to poor ocean conditions. These results run counter to long-term conservation goals and may impact the long-term viability of these populations. Management for increased abundance and Proportionate Natural Influence (PNI) goals may exacerbate these shifts by removing natural-origin adults from the spawning grounds for use as broodstock, releasing numbers of juvenile fish that annually exceed pHOS targets upon returning as adults, and use of already small broodstock populations.

9) 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 facilities 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.

10) 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.

11). The effects of hatchery supplementation on size and age at maturity, and fecundity of summer steelhead in the upper Columbia Basin (*in prep.*)

This chapter is forthcoming, with several review steps remaining. Upon completion of the necessary review steps, it will be finalized as a supplement to this report.

Please read the full chapters (below) 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 of the middle Columbia River are charged with achieving and maintaining no net impact on Salmon and steelhead from construction and operation of five Columbia River dams. One of the main components of the PUDs attainment of no net impact is the production of hatchery fish to replace juveniles lost passing through the hydroelectric projects. The PUDs implement a comprehensive monitoring plan to determine the performance of the hatchery programs in achieving their goals (Hillman et al. 2019). This report compiles the results of multiple analyses of monitoring and evaluation data collected for Grant, Chelan, and Douglas PUD's summer steelhead hatchery programs through 2018. Other species (e.g., spring Chinook Salmon, summer Chinook Salmon, fall Chinook Salmon, and Sockeye Salmon) covered by the monitoring and evaluation efforts are presented in other reports, and some of the chapters included in this report analyzed more than one species and are thus included in multiple 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 statistics 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 whether 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 on 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 requirements of 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 whether the hatchery programs are operating consistent with the goals as outlined in the relevant M&E Plan. The review will determine whether 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 whether 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.	11
9	Determine if hatchery fish were released at the programmed size and number.	9
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.	10

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, and edits in response to those comments are incorporated into the final chapters as indicated 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 respective hatchery committees.

Acknowledgments

Thanks are due to the many people who 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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Wenatchee and Methow Summer Steelhead Status of Natural Replacement Rate and Stock-Recruit Assessment

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Abstract

The Wenatchee and Methow summer steelhead (*Oncorhynchus mykiss*) populations are the focus of conservation hatchery programs. These populations are part of the Upper Columbia Distinct Population Segment, listed as threatened under the Endangered Species Act. Conservation hatchery programs are intended to increase the number of spawning adults to affect a subsequent increase in the number of natural-origin recruits (NOR). For the natural population to remain stable or to increase, the Natural Replacement Rate (NRR), the ratio of NORs to the parent spawning population, must be greater than or equal to one, a level where parents are replaced by their offspring as spawners in the next generation. We evaluated the population dynamics and NRR of the Wenatchee and Methow steelhead populations using stock-recruit models and assessed the magnitude and trends of NRR in these populations. The hypotheses explored were 1) there was no difference in the number of natural-origin spawners over time (or conversely it increased/decreased over time), and 2) the natural replacement rate remained constant or increased/decreased over time. Natural-origin spawners increased in the Wenatchee, but remained static at very low abundance in the Methow. Both the Wenatchee and Methow populations had NRR median values well below replacement. The Wenatchee NRR would need to double to achieve replacement and the Methow would need to increase five-fold. The Wenatchee NRR declined over time while the Methow NRR remained static at very low levels. The Hatchery Replacement Rate (HRR) exceeded NRR in all years for both populations. Stock-recruit modeling was used to further explore the dynamics of these populations. In the Wenatchee, replacement, as estimated by the Smooth Hockey Stick model, would occur up to approximately 573 spawners. Replacement of the Methow population is estimated to occur up to approximately 322 spawners. The 90th quantile estimates of carrying capacity suggest that at equilibrium carrying capacity the Wenatchee population is at 37% of and the Methow population at 41% of habitat carrying capacity. Both populations fall below replacement at or below the minimum conservation number of spawners (~500) and abundance of the populations is low. Hatchery fish spawning in nature appear to be producing few returning adult offspring. The proportion of hatchery-origin spawners on the spawning grounds was negatively related to returning adult abundance in the Methow population, but there was no relationship in the Wenatchee population. However, the pHOS data lacks contrast, with a lack of observations in the lower two-thirds of the pHOS range. More robust assessment of these programs could be achieved by employing management designed to test hypotheses by using reference streams with the Upper Columbia subbasins and imparting intentional levels of contrast into the management strategies. These populations face low replacement rates and demographic risks. It is imperative to design management to identify the factors negatively affecting these populations so that future management can address those factors.

Introduction

The Wenatchee and Methow summer steelhead (*Oncorhynchus mykiss*) populations are the focus of conservation hatchery programs. These populations are part of the Upper Columbia Distinct Population Segment (DPS), listed as threatened under the Endangered Species Act (ESA). Conservation hatchery programs are intended to increase the number of spawning adults (i.e., the combined number of naturally produced and hatchery fish spawning in nature) to affect a subsequent increase in the number of natural-origin recruits (NOR). For the natural population to remain stable or to increase, the Natural Replacement Rate (NRR), the ratio of NORs to the parent spawning population, must be greater than or equal to one, a level where parents are replaced by their offspring as spawners in the next generation.

We evaluated the population dynamics and NRR of the Wenatchee and Methow steelhead populations using stock-recruit models and assessed the magnitude and trends of NRR in these populations. The hypotheses explored were 1) there was no difference in the number of natural-origin spawners over time (or conversely it increased/decreased over time), and 2) the natural replacement rate remained constant or increased/decreased over time.

Methods

Study Area

The Wenatchee and Methow rivers are tributaries to the Columbia River in Washington. The National Marine Fisheries Service described the DPS as at high risk of extinction, with three of the four populations at “high risk,” including the Methow population. The Wenatchee population was classified as “maintained” (NMFS 2015).

The populations have been supplemented with releases of hatchery yearlings (smolts) for many years (Wenatchee since 1999 and Methow since 1993; Table 1). Suitable reference populations to conduct before-after control impact (BACI) analyses have not been identified, and such analyses are further precluded because there is not an identifiable “before” treatment period with suitable data available.

Table 1. Hatchery steelhead smolt releases to the Methow and Wenatchee subbasins.

Release Year	Methow Subbasin Releases			Total	Wenatchee Subbasin Releases
	Wells Hatchery	WNFH S1	WNFH S2		
1993	392,815	0	0	392,815	--
1994	324,200	0	0	324,200	--
1995	359,170	0	0	359,170	--
1996	242,400	141,798	0	384,198	--
1997	310,480	104,798	0	415,278	--
1998	378,320	0	0	378,320	--
1999	580,417	112,908	0	693,325	172,078
2000	414,880	105,510	0	520,390	175,701
2001	326,270	98,834	0	425,104	184,639
2002	264,110	150,488	0	414,598	335,933
2003	319,238	119,370	0	438,608	302,060
2004	276,330	113,603	0	389,933	374,867
2005	264,726	110,368	0	375,094	294,114
2006	326,565	102,600	0	429,165	452,184
2007	315,534	122,515	0	438,049	299,937
2008	292,580	116,897	0	409,477	306,690
2009	308,512	102,418	0	410,930	327,143
2010	293,327	71,208	29,170	393,705	484,772
2011	331,455	63,936	43,205	438,596	354,314
2012	246,500	57,858	59,352	363,710	206,397
2013	151,406	53,827	57,894	263,127	249,004
2014	157,503	49,799	90,599	297,901	229,836
2015	152,318	19,405	76,078	247,801	264,758
2016	157,825	0	128,585	286,410	195,344
2017	160,502	0	219,220	379,722	255,168
2018	127,065	0	150,392	277,457	253,994
2019	162,805	13,780	199,427	376,012	216,666

Data Used in the Analyses

Data have been collected on abundance of natural-origin and hatchery-origin adult returns and spawners for many years in the Wenatchee and Methow subbasins. The steelhead stock-recruit data are complicated due to the numerous datasets in circulation. We chose to rely primarily on data provided by the Washington Department of Fish and Wildlife (WDFW; M. Hughes, B. Truscott, and C. Snow, personal communication, Oct. 2020) and within Hillman et al. (2020) and Snow et al. (2020). Although data for the Wenatchee and Methow populations date back to brood years 1978 and 1977, respectively, only data after brood years 1994 and 1992 were considered to be reliable (WDFW; Ben Truscott and Charlie Snow, personal communication, Oct. 2020). A

second stock-recruit dataset for the Methow population based on redd-count expansions was also analyzed.

A Bayesian nested patch occupancy (POM) steelhead abundance model (Waterhouse, et al., 2020) was developed to estimate steelhead spawning escapement in the Wenatchee and Methow subbasins. Returning steelhead adults were trapped at the Priest Rapids Dam Off Ladder Adult Fish Trap, PIT tagged, and sampled for biological data, annually. These PIT tagged fish were then tracked as they ascended the Columbia River and its tributaries. The sampling data and detection histories of the tagged fish were subsequently used in the POM to estimate escapement to the tributaries and combined with redd count surveys in the mainstem Wenatchee and Methow Rivers. All steelhead that escaped to the various tributaries were assumed to be spawners (i.e., pre-spawn mortality mainly occurs only in the mainstem where redd counts are conducted (See 2021). This is currently the preferred method for estimating spawning escapement for the Wenatchee and Methow steelhead populations, but has only been in use since 2014 for the Wenatchee population and 2015 for the Methow population. This change in methodology to estimate spawner escapement necessitated a conversion of the older Wenatchee and Methow data to this newer, more robust estimation method. The older method was based on run reconstruction; dam counts were apportioned to Upper Columbia subbasins (i.e., Wenatchee, Entiat, Methow and Okanogan) based on previously conducted radio-telemetry. For the data conversion, we used the results of the POM (Wenatchee brood years 2014-2019; Methow brood years 2015-2019) to develop linear regression models (natural-origin spawners as the independent variable and the POM spawner estimates as the dependent variable) to adjust steelhead spawner and recruit abundance in the entire datasets to be consistent with abundances that would have been predicted by the POM for years pre-dating the implementation of the model. The Wenatchee regression model used the calculated intercept and the Methow regression model was forced through the origin to avoid negative population estimates (Figures 1a and 1b). Spawning escapement (hatchery-origin and natural-origin) was adjusted by predicting spawning escapement using the POM regression models (Figures 2a and 2b). The adjusted escapement values closely tracked the previous escapement estimates with the POM estimates consistently lower than the previous estimates.

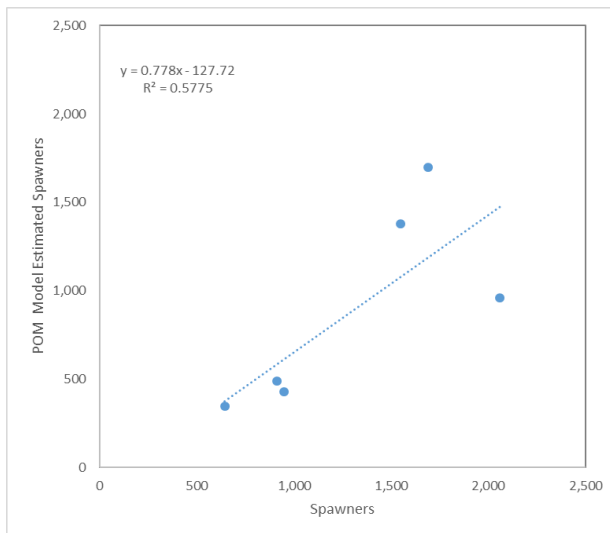


Figure 1a. Wenatchee spawners vs. POM regression

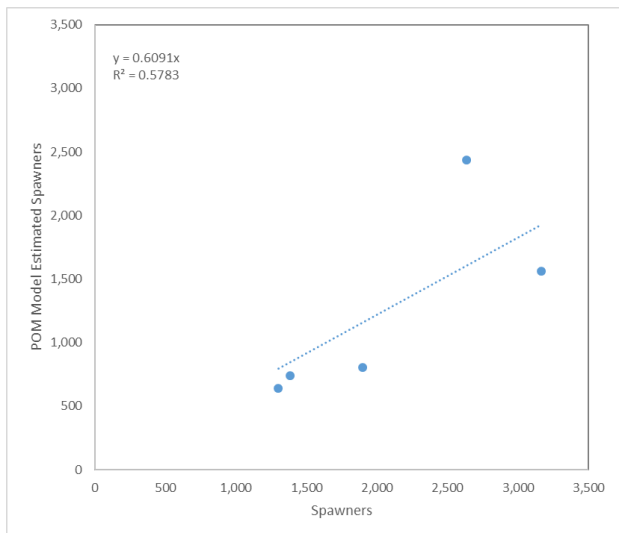


Figure 1b. Methow spawners vs. POM regression

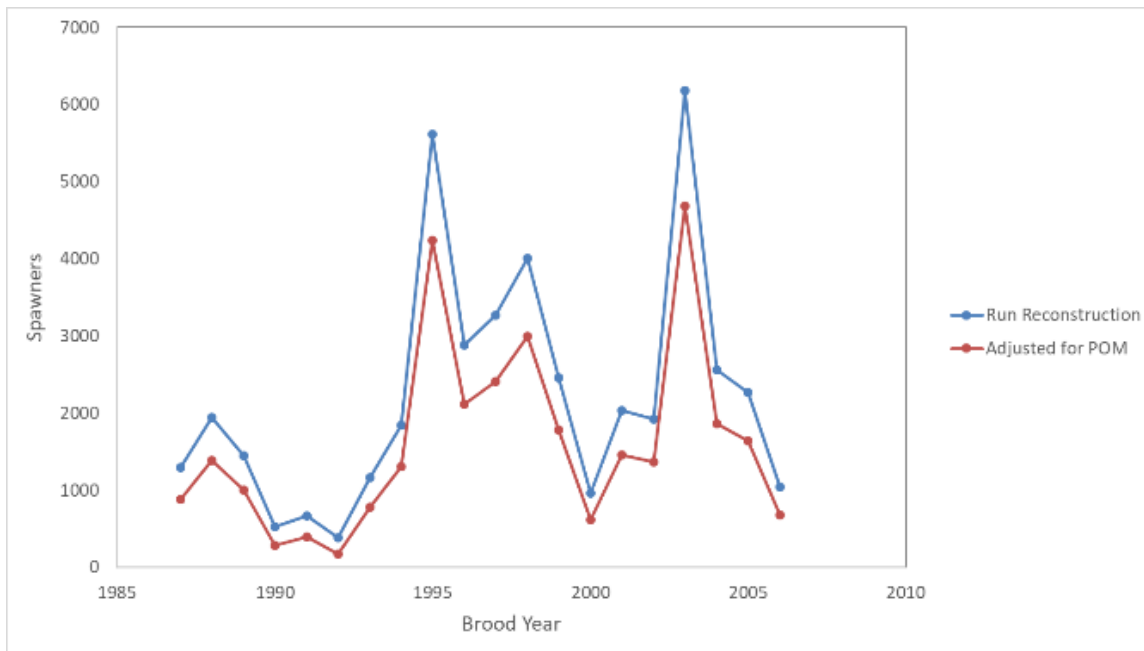


Figure 2a. Wenatchee spawners and POM adjusted spawners by brood year.

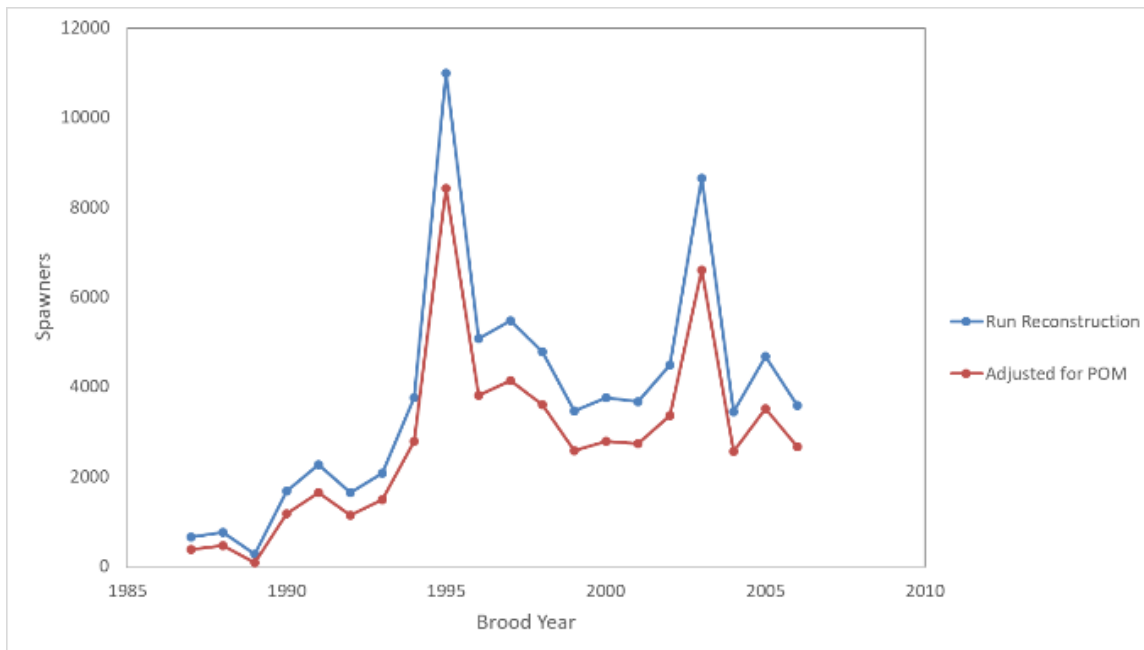


Figure 2b. Methow spawners and POM adjusted spawners by brood year.

Annual removals of natural-origin fish for broodstock and harvest were added to the POM regression model adjusted returns to obtain the total returns. The return estimates were then parsed into age class cohorts, based on estimates of age class proportions obtained from ages determined by annual scale reading and summed across years to obtain total returns per cohort. Spawning

escapement estimates consisted of annual hatchery-origin and natural-origin population estimates adjusted with the POM regression model (Table 2). The age structure data for the Methow contained a category of fish of unknown age. In these cases the known age class proportions were normalized to sum to one and subsequently applied to the unknown age class category. This approach assigned presumed age classes to ensure conversion of all annual returns to cohort age classes. Age structure data for the Wenatchee population did not require this adjustment.

Table 2. Wenatchee and Methow stock-recruit data

Brood Year	Wenatchee POM-Adjusted		Methow POM-Adjusted		Methow Redd-Expansion	
	Spawners	Recruits	Spawners	Recruits	Spawners	Recruits
1992	--	--	1,728	665	--	--
1993	--	--	1,270	76	--	--
1994	881	105	383	76	--	--
1995	1,384	195	457	109	--	--
1996	1,002	661	77	293	--	--
1997	280	1,230	1,170	420	--	--
1998	394	980	1,637	81	--	--
1999	170	371	1,146	527	--	--
2000	779	789	1,480	434	--	--
2001	1,304	800	2,789	241	--	--
2002	4,238	323	8,416	221	1,760	395
2003	2,118	398	3,815	403	3,492	450
2004	2,413	581	4,133	537	2,196	1,047
2005	2,991	1,181	3,593	712	3,183	1,171
2006	1,785	2,391	2,569	936	1,356	1,545
2007	623	1,106	2,790	541	1,288	1,523
2008	1,456	947	2,730	503	1,847	842
2009	1,371	888	3,357	790	1,837	1,200
2010	4,683	1533	6,599	626	3,680	1,976
2011	1,864	674	2,554	1,076	1,325	970
2012	1,635	234	3,507	267	1,105	1,371
2013	681	71	2,660	489	1,297	288

For the Methow population, an estimate of spawners was derived from redd counts expanded to the number of spawners by an assumption of the female:red ratio and the ratio of males to females based on Wells Dam stock assessment (Tables 5.13 and 5.23 in Snow et al. 2019). These spawner data incorporate pre-spawn mortality, resulting in roughly 40% fewer spawners than predicted by the estimates derived from the Wells Dam counts (C. Snow, personal communication, April 2021). For the Wenatchee population, using results from the PIT-tag based escapement estimates in the tributaries to the Wenatchee Subbasin, a fish-per-red estimate was calculated for the mainstem Wenatchee River above and below Tumwater dam, based on the sex ratio of PIT tagged fish (tagged at Priest Rapids OLAF) last observed in those areas. The

estimates of redds from the steelhead redd surveys were translated to estimates of natural- and hatchery-origin spawners for the mainstem Wenatchee River and tributaries. Finally, estimates of escapement were compared to estimates of spawners, and an estimate of pre-spawn mortality was calculated. However, steelhead redd surveys are conducted during increasing spring runoff making detection of redds difficult due to high water and turbidity. Therefore, redd counts are likely a minimum estimate and rely on assumptions regarding the number of redds constructed by individual females and the sex ratio of the spawning escapement.

In summary, the POM-adjusted approach likely overestimates the number of fish that actually spawned because it cannot fully account for pre-spawn mortality after the fish pass their last detection site, while the redd-based estimate likely underestimates the number of fish that spawned because not all redds can be detected. Both data sets were modeled and presented. We chose to focus on the data that were adjusted by the POM for the following reasons: 1) both spawners and recruits were adjusted using the regression model, 2) the POM-adjusted data does account for pre-spawn mortality (but not to the same degree that redd counts do), 3) both spawners and recruits were estimated using the same baseline methodologies (dam counts) and point in their life histories (returning adults), making interpretation of replacement rate more intuitive, 4) although both methods require assumptions and adjustments, the dam counts are likely more reliable than redd counts; therefore, the basis of the data is likely more robust and consistent year to year, 5) both the Wenatchee and Methow steelhead populations have data sets based on dam counts and adjustable by the POM regression method, and 6) the data set for the POM-adjusted data is ten years longer than the redd-based data for the Methow, nearly doubling the length of the time series.

Stock-Recruit Modeling

All stock recruit modeling was performed in R (R Core Team, 2021). Data manipulation was performed using the packages `openxlsx` (Schauberger and Walker 2020) and `dplyr` (Wickham et al., 2021). Estimation of non-linear regression starting parameters used to fit the density-independent, Beverton-Holt, and Ricker models was performed using the package `FSA` (Ogle et al., 2021). Starting values for the Smooth Hockey Stick model were estimated empirically. Functions for the density-independent, Beverton-Holt (Hilborn and Walters, 1992), Ricker (Hilborn and Walters, 1992), and Smooth Hockey Stick (Froese 2008) models were written in R and parameters were estimated using nonlinear regression with the `nls` function (R Core Team, 2021). The models were natural-log transformed for parameter estimation. The models used for parameterization are provided below:

$$\text{Density-Independent: } \log(\text{Recruits}) \sim \log(\alpha * \text{Spawners})$$

$$\text{Beverton-Holt: } \log(\text{Recruits}) \sim \log(\alpha * \text{Spawners} / (\beta + \text{Spawners}))$$

$$\text{Ricker: } \log(\text{Recruits}) \sim \log(\alpha * \text{Spawners} * e^{-\beta * \text{Spawners}})$$

$$\text{Smooth Hockey Stick: } \log(\text{Recruits}) \sim A + \log(1 - e^{-\alpha * \text{Spawners} / e^A})$$

$$\text{where } A = \log(R_{\infty})$$

Analyses and graphing of the parameters and residuals were performed with the package `nlstools` (Baty et. al., 2015). Residuals were bootstrapped (1,000 iterations) to estimate parameter confidence intervals, distribution, correlation, and potential for negative parameter estimates. However, the Smooth Hockey Stick model failed to converge; therefore, parameter confidence intervals reported are from parametric estimation using the `nlm` function. Bootstrap results for the other models are provided in graphical representation (Appendix A). Residuals were analyzed for autocorrelation (`runs` test) and normality (Shapiro-Wilk normality test).

The 90th quantile of the Beverton-Holt, Ricker, and Smooth Hockey Stick models were fit using nonlinear quantile regression with the `quantreg` package (Koenker 2021). The 90th quantile was chosen to avoid fitting the models near the extremes of the data distributions. The 90th quantile modeling describes the greatest stock-recruit response that is likely given the observed data.

Predicted results of each model were created using the package `dplyr` (Wickham et. al., 2021). All stock-recruit model graphing was done using the package `ggplot2` (Wickham 2016).

Analysis of variance (ANOVA) was performed on each pairwise comparison of the density-independent model versus each density-dependent stock-recruit model to evaluate whether the data followed a structure dependent or independent of density. No corrections were made to critical values for multiple comparisons. The `AICmodavg` package (Mazerolle 2020) was used for Akaike Information Criterion analysis for small sample sizes (AICc) to evaluate the quality of the models. Descriptive statistics were estimated using the package `pastecs` (Grosjean and Ibanez 2018) and graphed using `ggplot`. The package `knitr` (Xie 2019) was used to format results tables.

Carrying capacity was estimated using the Smooth Hockey Stick models and the 90th quantile Smooth Hockey Stick models. The maximum recruitment (K_r) was estimated by using the model to predict recruitment across a range of spawners until maximum recruitment was achieved. The number of spawners required to produce K_r (K_{sp}) was estimated using graphical interpretation and tabular data. This approach avoided grossly overestimating K_{sp} due to the extremely long asymptote behavior of the model.

Analysis of Proportion of Hatchery-Origin Spawners

The effect of proportion of hatchery-origin spawners (pHOS) on recruitment was evaluated by performing linear regression on the residuals from the best stock-recruit model for each population (dependent variable) by the brood year pHOS for that population (independent variable).

Natural Replacement Rate and Hatchery Replacement Rate

The natural replacement rate (NRR) of wild summer steelhead in the Wenatchee and Methow river subbasins was calculated as the number of natural-origin recruits divided by the overall spawning population of hatchery-origin and natural-origin adults of the parent brood (*sensu* Table 5.23 Snow et al. 2020; Table 3.40 Hillman et al. 2020).

Comparison of Hatchery Replacement Rate (HRR) to Natural Replacement Rate (NRR) was conducted by paired t-test on brood years 1998-2012. In addition, HRR was compared to the program targets and the frequency of meeting or not meeting the target was reported.

Carrying Capacity

Habitat and population carrying capacities were assessed. Habitat carrying capacity was estimated and results of other studies compiled by T. Hillman (personal communication). Hillman compiled various studies that estimated steelhead smolt production in the Wenatchee and Methow subbasins using per unit subbasin area, per unit effective subbasin area, per unit subbasin intrinsic potential area, and HQI, SPM, and GAFM models.

Carrying capacity was estimated at the mean response (i.e., equilibrium carrying capacity) and 90th quantile levels (proxy estimate of habitat carrying capacity) from the stock-recruit modeling using R_{∞} from the Smooth Hockey Stick model to estimate carrying capacity of adult recruits (K_r). Smolt to adult return (SAR) estimates derived from natural-origin emigrant PIT tags (Snow et al., 2020; Hillman et al., 2020) were used to back-calculate the number of smolts required to produce the adult K_r , providing an estimate of K_r for smolts. The SAR tagging locations were the Lower Methow River rotary screw trap in the Methow Subbasin (2006-2017), and the Nason Creek, Chiwawa River, and Lower Wenatchee River rotary screw traps in the Wenatchee Subbasin (2006-2016; Wenatchee estimates were averaged to obtain one estimate). The terminus of the SAR data for the Methow population was Wells Dam and for the Wenatchee population was Bonneville Dam.

Results

Wenatchee Summer Steelhead

Adult spawner abundance ranged from 170 to 4,683 with a median of 1,378. Adult recruit abundance ranged from 71 to 2,391 with a median of 732 (Figure 3).

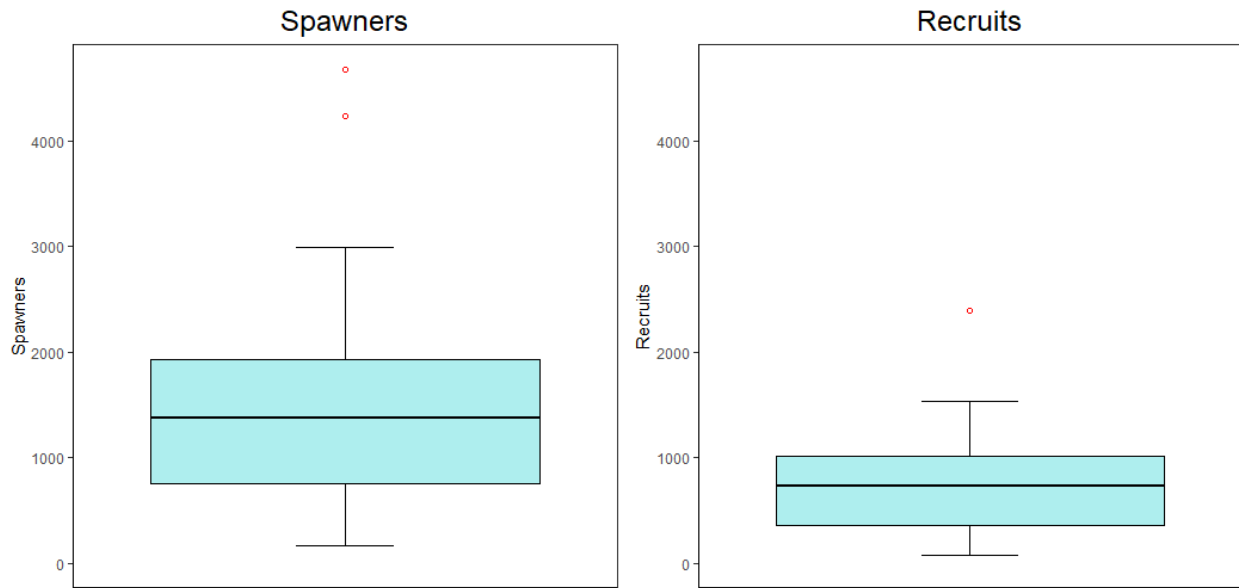


Figure 3. Wenatchee summer steelhead boxplots for spawner abundance and adult recruit abundance. Box hinges indicate the first and third quartiles (25th and 75th percentiles) with the median (thick bar). Whiskers represent 1.5 times the interquartile range (range between the 25th and 75th percentiles). Outliers are shown in red.

The total spawners (hatchery-origin + natural-origin) in the Wenatchee Subbasin exhibited a highly variable but positive trend from brood years 1994-2013 (Figure 4). Recruits also exhibited a positive trend, presumably related to the increase in abundance of spawners (Figure 4). However, recruits per spawner (i.e., Natural Replacement Rate [NRR]) declined from brood years 2007 through 2013 and was below replacement in 14 of 20 years (70%) (Figure 4). Median NRR was 0.504 (range 0.076-4.393).

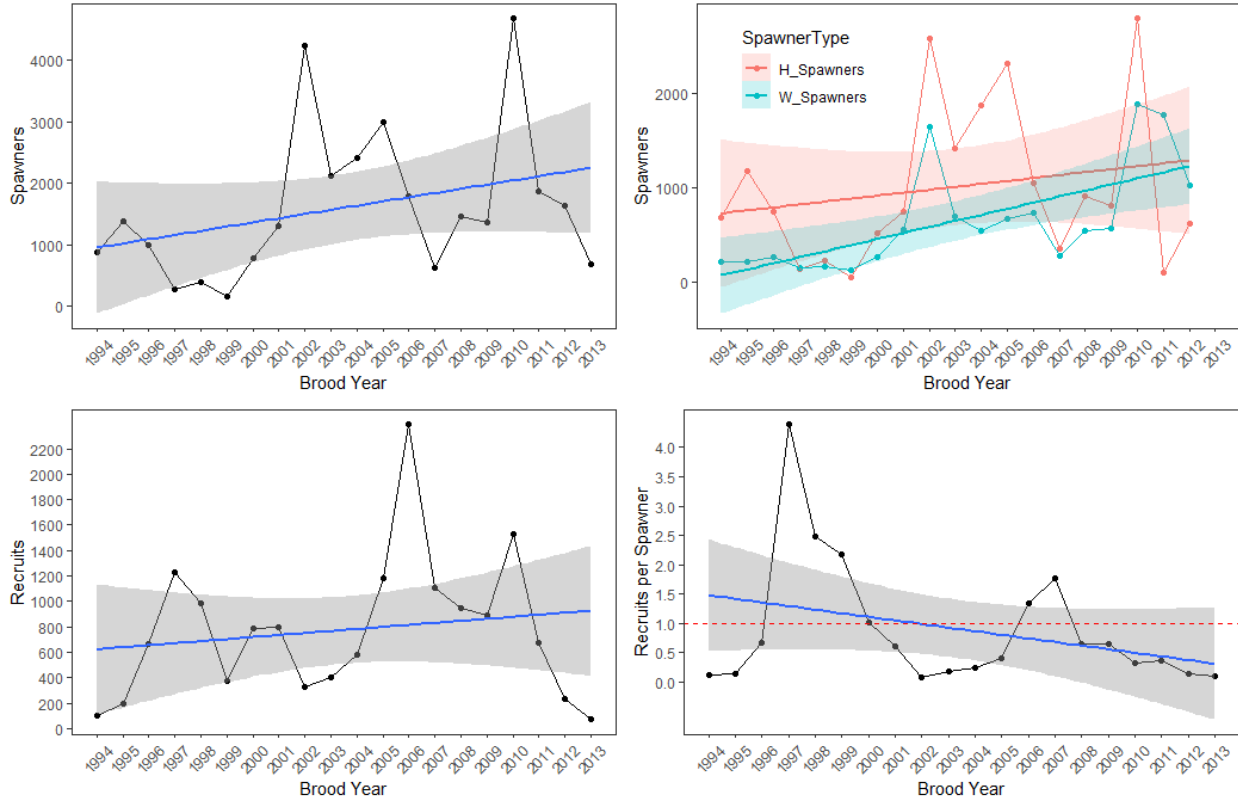


Figure 4. Upper left: total spawners by brood year – Wenatchee Subbasin. Upper right: hatchery- and natural-origin spawners by brood year – Wenatchee Subbasin. Lower left: recruits by brood year – Wenatchee Subbasin. Lower Right: recruits per spawner (hatchery-origin + natural-origin) by brood year – Wenatchee Subbasin. Red dashed line is replacement. Trend lines are linear models with 95% confidence intervals (shaded).

Stock-recruit models were fit to the Wenatchee data and a density-independent model was fit to test the hypothesis that the stock-recruit relationship in the Wenatchee was density-dependent. Analysis of variance of each density-independent versus density-dependent model comparison confirmed that the density-dependent models were significantly different from the density-independent model for the Wenatchee data (Table 3). Akaike Information Criteria (AICc) indicated that the Smooth Hockey Stick was the most informative model, but virtually indistinguishable from the Beverton-Holt model, and the density-independent model was least informative (Table 4). Therefore, the density-independent model was excluded from further analysis.

Table 3. Wenatchee ANOVA density-independent model vs. density-dependent models.

Model 1	Model 2	F-value	p-value
Density-Independent	Beverton-Holt	12.2440	0.0026
Density-Independent	Ricker	6.5567	0.0197
Density-Independent	Smooth Hockey Stick	12.2570	0.0026

The AICc results, model parameters, parameter confidence intervals, and parameter correlations are presented in Table 4.

Table 4. Wenatchee stock-recruit modelling parameters and fit.

Model	AICc	Δ AICc	Parameter	Parameter Estimates	95% CI	Correlation
Smooth Hockey Stick	58.97	0.00	α	7.67	-47.72 – 63.06	α, R_∞ : -0.25
			R_∞	573.41	311.90 – 834.93	
Beverton-Holt	58.98	0.01	α	592.76	380.83 – 1,238.00	α, β : 0.71
			β	33.76	-97.26 – 1,039.00	
Ricker	63.15	4.17	α	1.06	0.54 – 2.09	α, β : 0.80
			β	0.0005	0.0002 – 0.0009	
Density-Independent	66.57	7.59	α	0.48	0.22 – 0.74	

Analysis of Density-Dependent Model Parameters

The confidence intervals for the Smooth Hockey Stick α and Beverton Holt β parameters both captured zero (Table 4), suggesting that the model fits were not robust, but also suggesting that the relatively short data sets with large variance make fitting models difficult. The Ricker model was not as good a fit as the other models but had more stable parameter estimates.

Bootstrap analysis of the density-dependent models residuals indicated that residuals were not different from a normal distribution (Shapiro-Wilk Normality Test; Table 5) and were not autocorrelated (i.e., did not differ from random; Runs Test) except for the Smooth Hockey Stick residuals ($p=0.0477$).

Table 5. Wenatchee stock-recruit residuals analysis.

Model	Shapiro-Wilk Normality Test		Runs Test	
	W	p-value	Standard Normal	p-value
Smooth Hockey Stick	0.9378	0.2175	1.9801	0.0477
Beverton Holt	0.9387	0.2264	1.6311	0.1029
Ricker	0.9584	0.5118	1.1513	0.2496

All three stock-recruit models and the 90th quantile models were successfully fit to the Wenatchee data (Figure 5). The Smooth Hockey Stick and Beverton-Holt models fit the data very similarly (Figures 5 and 6). The Smooth Hockey Stick model was used for estimation of carrying capacity of recruits (K_r) and the number of spawners necessary to produce K_r (K_{sp}). The Smooth Hockey Stick model estimated K_r of 573 with a K_{sp} of 542 spawners. The 90th quantile Smooth Hockey Stick model estimated K_r of 1,533 with a K_{sp} of 1,387 spawners (Figure 6). The population is above replacement at these K_{sp} levels.

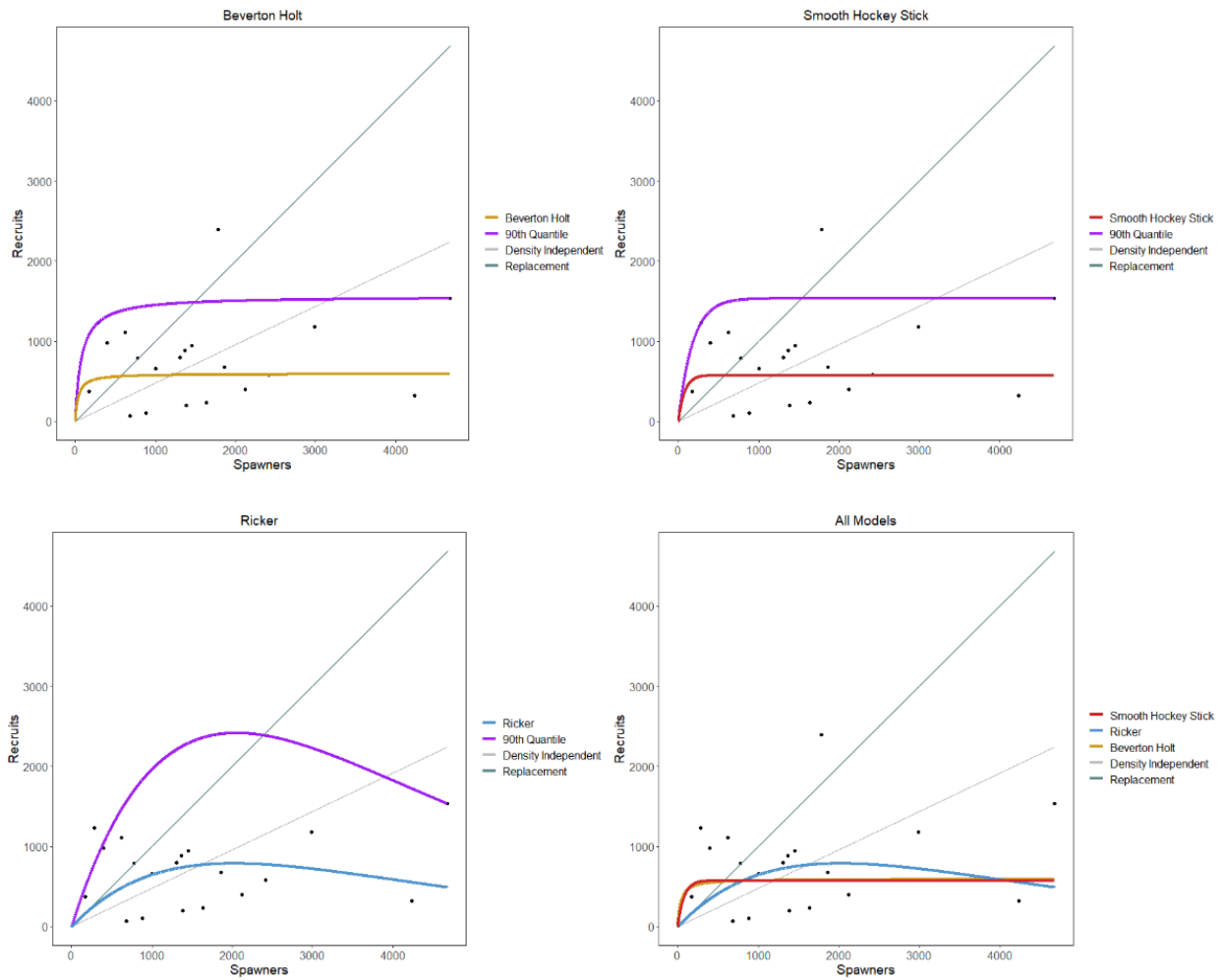


Figure 5. Upper left: Beverton-Holt model and 90th quantile – Wenatchee Subbasin. Upper right: Smooth Hockey Stick model and 90th quantile – Wenatchee Subbasin. Lower left: Ricker model and 90th quantile – Wenatchee Subbasin. Lower right: All three stock-recruit models – Wenatchee Subbasin (note the Smooth Hockey Stick curve overlays the Beverton-Holt curve).

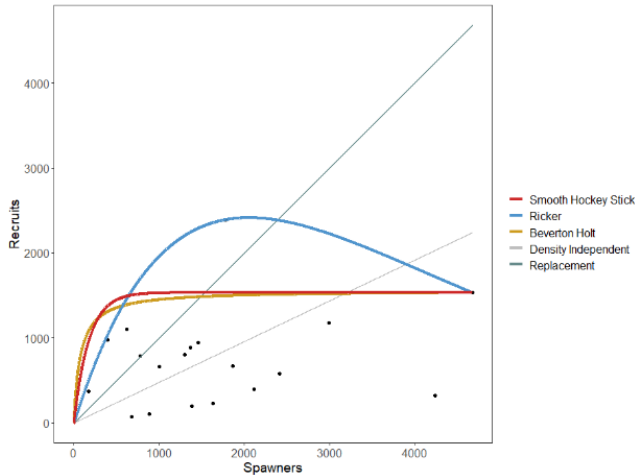


Figure 6. 90th quantile fits of Beverton-Holt, Smooth Hockey Stick, and Ricker models – Wenatchee Subbasin.

Methow Summer Steelhead

The following analyses were performed on the Methow POM-adjusted dataset. Adult spawner abundance ranged from 77 to 8,416 with a median of 2,614. Adult recruit abundance ranged from 65 to 1,076 with a median of 427 (Figure 7).

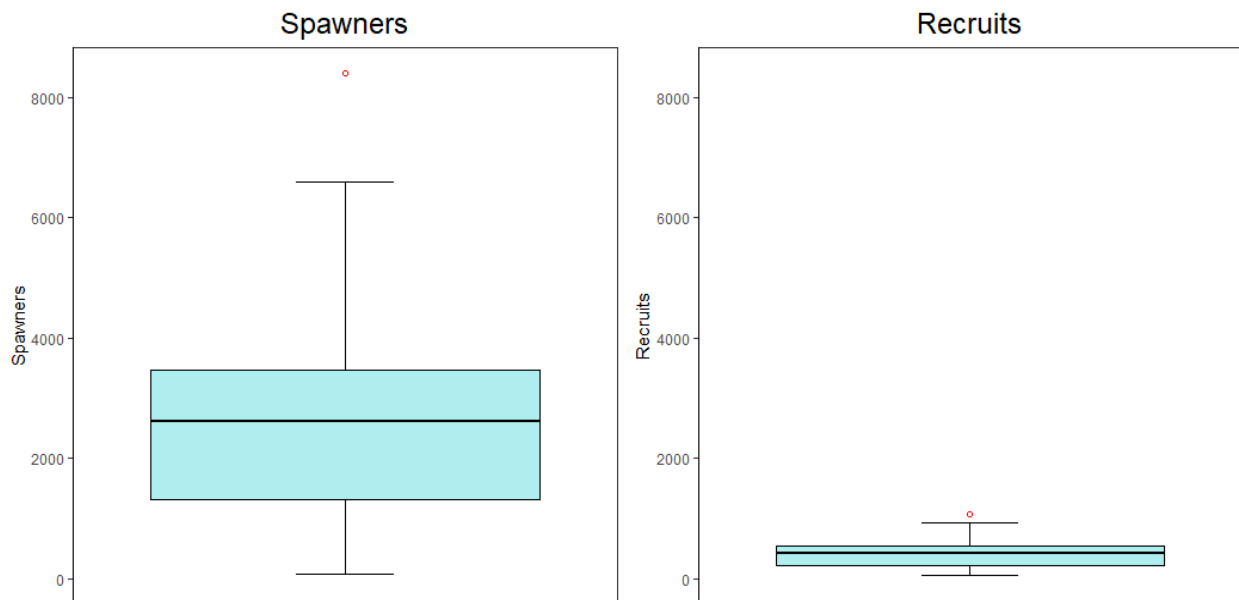


Figure 7. Methow summer steelhead boxplots for spawner abundance and adult recruit abundance. Box hinges indicate the first and third quartiles (25th and 75th percentiles) with the median (thick bar). Whiskers represent 1.5 times the interquartile range (range between the 25th and 75th percentiles). Outliers are shown in red.

The total spawners (hatchery-origin + natural-origin) in the Methow Subbasin exhibited a highly variable but positive trend from brood years 1992-2013 driven almost entirely by increasing hatchery-origin spawners (Figure 8). Recruits also exhibited a positive trend with a heteroscedastic distribution, presumably related to the increase in abundance of spawners (Figure 8), mostly influenced by hatchery-origin spawners (Figure 8). However, with the exception of brood year 1996, recruits per spawner (i.e., Natural Return rate [NRR]) remained static or declined slightly from brood years 1992 through 2013 and was far below replacement (>95% of years were below replacement) (Figure 8). Median NRR was 0.189 (range 0.026-3.805).

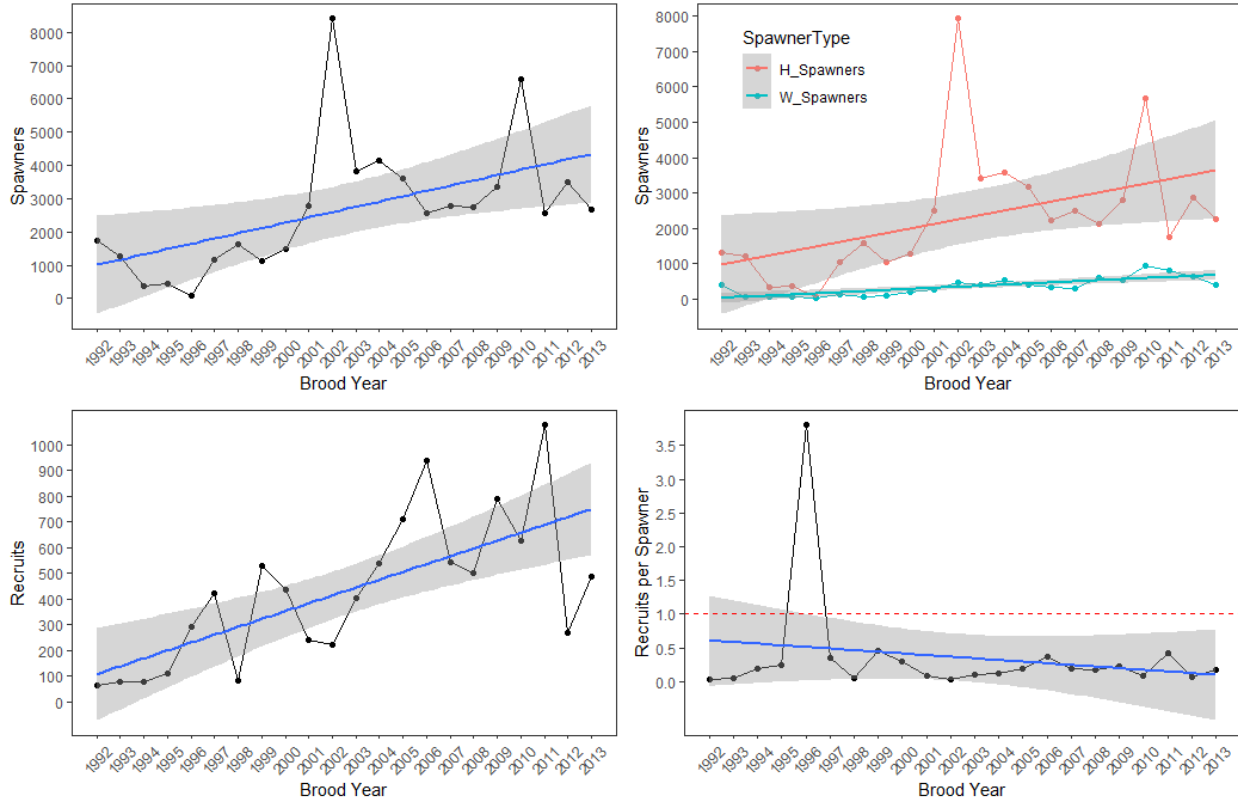


Figure 8. Upper left: total spawners by brood year – Methow Subbasin. Upper right: hatchery- and natural-origin spawners by brood year – Methow Subbasin. Lower left: recruits by brood year – Methow Subbasin. Lower right: recruits per spawner (hatchery-origin + natural-origin) by brood year – Methow Subbasin. Red dashed line is replacement. Trend lines are linear models with 95% confidence intervals (gray shaded).

Stock-recruit models were fit to the Methow POM-adjusted data and a density-independent model was fit to test the hypothesis that the stock-recruit relationship in the Methow was density-dependent. Analysis of variance of each density-independent versus density-dependent model comparison confirmed that the density-dependent models were significantly different from the density-independent model for the Methow data (Table 6). Akaike Information Criteria (AICc) indicated that the Beverton-Holt model was the most informative model and the density-

independent model was least informative (Table 7). Therefore, the density-independent model was excluded from further analysis.

Table 6. Methow ANOVA Density Independent Model vs. Density Dependent Models.

Model 1	Model 2	F-value	p-value
Density-Independent	Beverton-Holt	10.7200	0.0038
Density-Independent	Ricker	7.6275	0.0120
Density-Independent	Smooth Hockey Stick	9.3504	0.0062

The AICc results, model parameters, parameter confidence intervals, and parameter correlations are presented in Table 7. Akaike Information Criteria (AICc) indicated that the Beverton-Holt was the most informative model.

Table 7. Methow stock-recruit modelling parameters and fit.

Model	AICc	Δ AICc	Parameter	Parameter Estimates	95% CI	Correlation
Beverton-Holt	61.61	0.00	α	383.42	262.39– 717.80	α, R_∞ : 0.67
			β	221.59	34.25– 1,752.70	
Smooth Hockey Stick	62.62	1.00	α	10.04	-69.12– 89.21	α, β : -0.16
			R_∞	322.01	214.65– 482.99	
Ricker	63.95	2.33	α	0.36	0.20– 0.67	α, β : 0.81
			β	0.0003	0.0001– 0.0005	
Density-Independent	68.36	6.74	α	0.17	0.09–0.25	

Analysis of Density-Dependent Model Parameters

The confidence interval for the Smooth Hockey Stick parameter α captured zero (Table 7), suggesting that the model fit was not robust, but also suggesting that the relatively short data sets with large variance make fitting models difficult.

Bootstrap analysis of the density-dependent models residuals indicated that residuals of the Beverton-Holt and Smooth Hockey Stick models were significantly different from a normal distribution (Shapiro-Wilk Normality Test; Table 8). None of the models produced autocorrelated residuals (i.e., did not differ from random; Runs Test).

Table 8. Methow stock-recruit residuals analysis.

Model	Shapiro-Wilk Normality Test		Runs Test	
	W	p-value	Standard Normal	p-value
Beverton-Holt	0.9087	0.0445	0.3878	0.6982
Smooth Hockey Stick	0.8934	0.0220	0.3878	0.6982
Ricker	0.9358	0.1616	1.0700	0.2847

All three stock-recruit models and the 90th quantile models were successfully fit to the Methow POM-adjusted data (Figures 9). The Smooth Hockey Stick and Beverton-Holt models fit the data very similarly (Figure 9). The Smooth Hockey Stick model was used for estimation of carrying capacity of recruits (K_r) and the number of spawners necessary to produce K_r (K_{sp}) due to the similarity in fit to the Beverton Holt model and convenience of estimating these data. The Smooth Hockey Stick model estimated K_r of 322 with a K_{sp} of 332 spawners. The 90th quantile Smooth Hockey Stick model estimated K_r of 790 with a K_{sp} of 1,340 spawners (Figure 10). The population is below replacement at these K_{sp} levels.

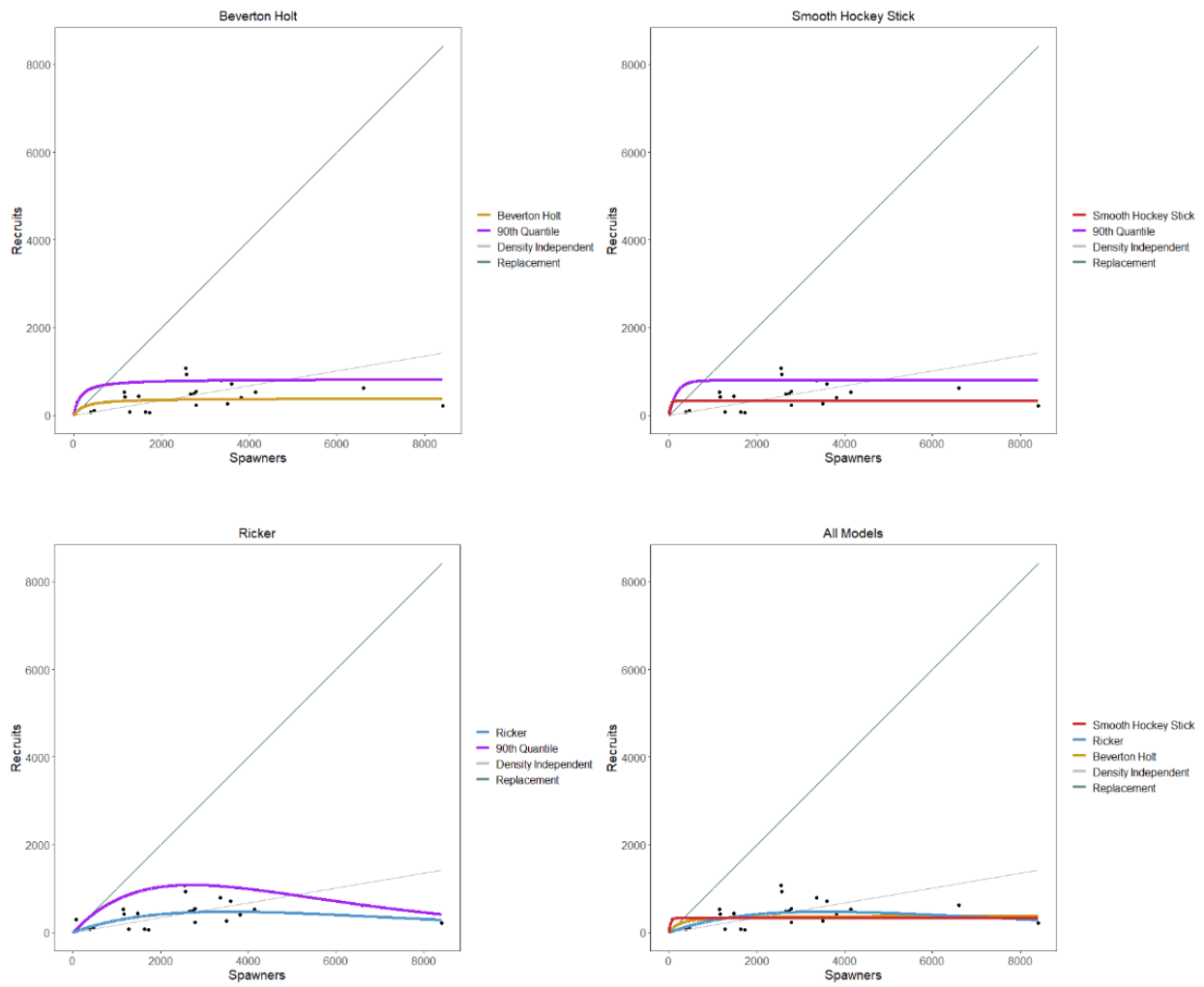


Figure 9. Upper left: Beverton-Holt model and 90th quantile – Methow Subbasin.
 Upper right: Smooth Hockey Stick model and 90th quantile – Methow Subbasin.
 Lower left: Ricker model and 90th quantile – Methow Subbasin.
 Lower right: all three stock-recruit models – Methow Subbasin.

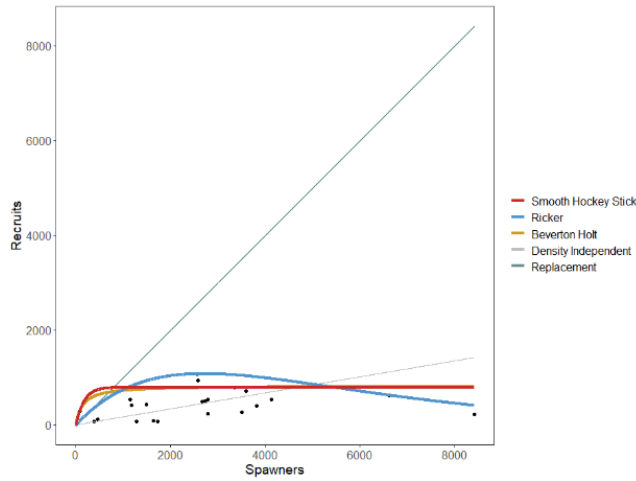


Figure 10. 90th Quantile Fits of Beverton-Holt, Smooth Hockey Stick, and Ricker Models – Methow Subbasin.

Beverton-Holt and Ricker models fitted to the redd-expansion data reveal a similar pattern of the population being below replacement. The data do not contain sufficient range in the number of spawners to estimate the point at which the population falls below replacement, but it appears to never achieve replacement according to the Ricker model and falls below replacement upon reaching 920 spawners according to Beverton-Holt model. The Beverton-Holt 90th quantile model estimated that the population falls below replacement when spawners exceed 1,652 (Figure 11).

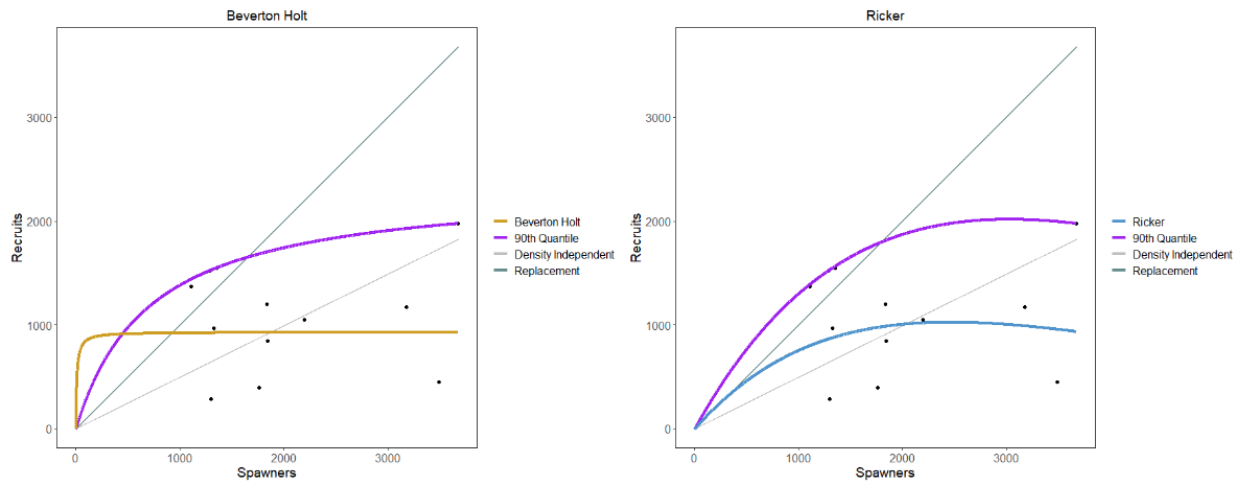


Figure 11. Stock-recruit models fitted to the redd-expansion data. Left: Beverton-Holt model and 90th quantile – Methow Subbasin. Right: Ricker model and 90th quantile – Methow Subbasin.

Analysis of Proportion of Hatchery-Origin Spawners

The Wenatchee population residuals of the Smooth Hockey Stick model residuals were not significantly related to pHOS ($P > 0.881$; Figure 12a). In contrast, the Methow population Beverton-Holt model residuals were negatively related to pHOS ($P = 0.041$); Figure 12b). However, the range of the Methow pHOS data is very limited, with all observations greater than 0.68. The Wenatchee pHOS data are predominantly greater than 0.50.

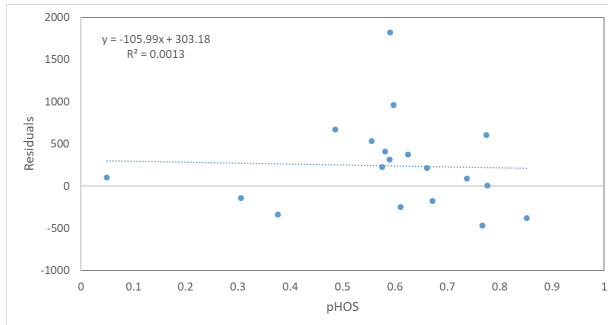


Figure 12a. Wenatchee pHOS versus Smooth Hockey Stick model residuals.

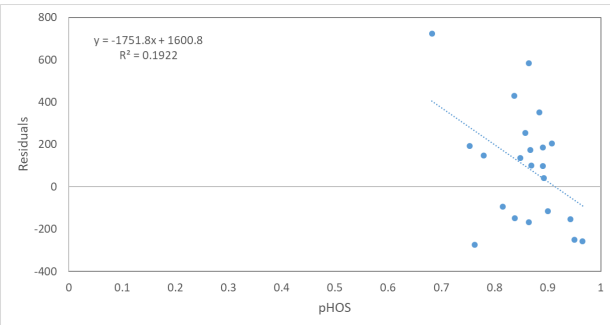


Figure 12b. Methow pHOS versus Beverton-Holt model residuals.

Hatchery Replacement Rate

The HRRs of the Wenatchee and Methow subbasin hatchery programs (Figures 13a and 13b) were significantly greater than the NRR of the respective subbasins (Table 9). The HRR for both subbasins exceeded NRR in every year (paired sample t-test and paired-sample sign test, Table 9). The Wenatchee subbasin did not meet or exceed the program target in 3 of 15 years. The Methow subbasin did not meet or exceed the program target in 4 of 15 years (Table 9).

Table 9. Comparison of hatchery replacement rate (HRR) to program target HRR and natural replacement rate (NRR) for the Wenatchee and Methow subbasins, brood years 1998-2012.

Program/Stock	HRR Target Analyses					Paired-Sample T-Test			Paired-Sample Sign Test
	HRR Target	No. Years	No. Yrs HRR ≥ Target	No. Yrs HRR < Target in last 5 Yrs*	No. Yrs HRR ≥ NRR	t-value	P-value	Power	P-value
Wenatchee	6.9	15	7	3	15	4.330	0.001	0.979	0.000
Methow	26.5	15	8	4	15	5.789	0.000	0.999	0.000

* Colors indicate varying degrees of management action: Green = no action necessary; Red = action may be necessary (See Appendix 2 in Hillman et al. 2017).

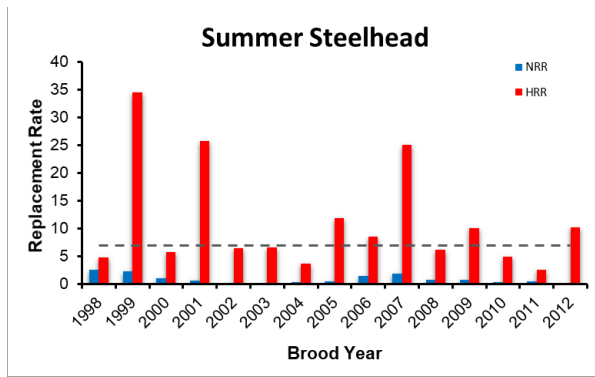


Figure 13a. Wenatchee HRR and NRR, with HRR target (dashed line).

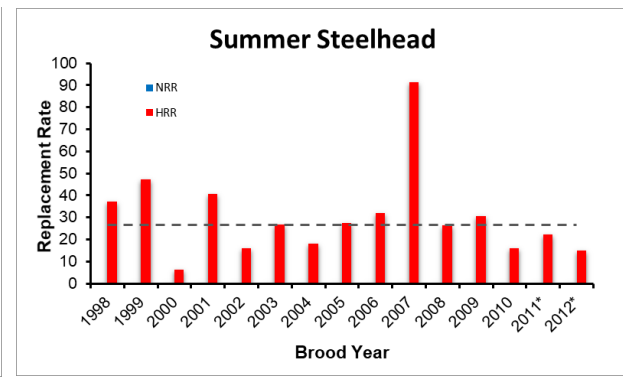


Figure 13b. Methow HRR and NRR, with HRR target (dashed line).

Carrying Capacity

T. Hillman (personal communication) compiled and estimated steelhead carrying capacities for emigrating juveniles in the Wenatchee and Methow using a variety of sources and methods (Table 10). The median estimate for the Wenatchee was 105,590 smolts (range 10,875-129,726). The median estimate for the Methow was 130,357 smolts (range 10,037-449,723). Estimates of the 90th quantile carrying capacity for the Wenatchee was 169,781 smolts (Table 11), similar to, but slightly higher than the median of the estimates in Table 10. Estimates of the 90th quantile carrying capacity for the Methow was 111,846 smolts (Table 11), similar to, but slightly lower than the median of the estimates in Table 10.

Table 10. Compilation of summer steelhead smolt habitat carrying capacity estimates with minimum, median, and maximum values reports. Compiled by T. Hillman, 2011.

Subbasin	Subbasin Area Method	Effective Subbasin Area				Intrinsic Potential			HQI	SPM
		Raymond ¹	Buckman ²	DeShazo ³	Miller/Walter ⁴	Mullan ⁵	WDFW ⁶	Thurrow ⁷	Mullan ⁵	NPPC ⁸
Wenatchee	103,578	117,024	128,361	122,875	10,875	97,779	62,169	129,726	107,601	100,000
Methow	449,723	140,992	154,651	148,042	10,037	90,238	57,374	119,721	104,586	169,610

Citations in table: ¹Raymond (1979); ²Buckman (1990); ³DeShazo et al. (1987); ⁴Miller and Walter (2011); ⁵Mullan et al. (1992); ⁶WDFW (1999); ⁷Thurrow (1987); ⁸NPPC (1989)

Carrying capacities of adult recruits and juvenile emigrants were estimated at both the equilibrium (mean) and 90th quantile levels (Table 11). The equilibrium carrying capacity of emigrants for the Wenatchee was 63,502 and the 90th quantile estimate was 169,781. The equilibrium carrying capacity in the Wenatchee was 0.37 of the 90th quantile estimate. The equilibrium carrying capacity of emigrants for the Methow was 45,588 and the 90th quantile estimate was 111,846 (Table 11). The equilibrium carrying capacity in the Methow was 0.41 of the 90th quantile estimate.

Table 11. Comparisons of Smooth Hockey Stick-derived carrying capacities and carrying capacities estimated by various areal and habitat based method.

Population	SAR	SAR Terminus	Kr _{adults} 90 th Quantile	Kr _{emigrants} 90 th Quantile	Kr _{adults} equilibrium	Kr _{emigrants} equilibrium
Wenatchee	0.009	Bonneville Dam	1,532	169,781	573	63,502
Methow	0.007	Wells Dam	790	111,846	322	45,588

Discussion

Both the Wenatchee and Methow populations have NRR median values well below replacement, and these estimated NRRs comport with those published in annual reports. The Wenatchee median NRR (0.504) would need to double to achieve replacement and the Methow median NRR (0.189) would need to increase five-fold. However, the NRR metric is very broad and provides little insight into the dynamics of the population. In the Wenatchee population, replacement, as estimated by the Smooth Hockey Stick model, would occur up to approximately 573 spawners. Commonly, 500 spawners is used as a demographic and genetic threshold in conservation biology to avoid deleterious genetic effects and provide a minimum measure of demographic resilience (McClure et al. 2003, McElhany et al. 2000). It appears the Wenatchee population is at this threshold with the ability to replace itself, but there is no scope for loss of fitness or productivity. Replacement of the Methow population is estimated to occur up to approximately 322 spawners. The NRR in the Methow is extremely low, but notably, appears to be heavily affected by the number of hatchery-origin fish. The natural-origin population of spawners fluctuates very little across years while the hatchery-origin spawners have increased across the years, concurrent with a decline in NRR. In contrast, the Wenatchee hatchery-origin and natural-origin spawner numbers tend to track each other across years. However, the proportion of hatchery-origin spawners on the spawning grounds is confounded by abundance.

There are three hypotheses that may explain the observed patterns of population dynamics in the Methow and Wenatchee steelhead populations in regard to the conservation hatchery programs:

1. The hatchery programs are having little to no effect on natural production. Most or all natural production is by natural-origin spawners that are maintaining the populations at low levels.
2. Without the conservation hatchery programs, the abundance of the natural-origin populations would be even lower than they are now because the hatchery programs are supporting the natural-origin populations and helping to maintain them at a low levels.
3. The abundance of the natural populations would be higher than it is now, but the influx of hatchery-origin fish is reducing the productivity of the natural-origin fish, putting the natural population at risk of extirpation.

There is a commonality in all three of these hypotheses: the hatchery-origin spawners are producing remarkably few natural-origin offspring to the returning adult stage. Although HRR

exceeded NRR every year in the Wenatchee and Methow subbasins and exceeded the HRR target in most years, this increase in production of progeny via the hatcheries may not result in an increase in abundance of the natural population. The interaction of hatchery programs and natural populations requires multifaceted assessment. Given the number of hatchery-origin fish on the spawning grounds, even if they had low fitness compared to natural-origin fish, an increase in natural-origin recruits would be expected. The juvenile equilibrium carrying capacities (K_r mean response) estimated by the Smooth Hockey Stick models in the Wenatchee and Methow populations are likely not reflective of the available habitat. The 90th quantile and habitat-based estimates of carrying capacity suggest that the Wenatchee population is at 37% of carrying capacity and the Methow population at 41%. However, that may indicate a reduced aggregate fitness among hatchery-origin and natural-origin spawners that is exacerbated as the number of spawners increases, even at very small numbers of spawners. The relationship between pHOS and productivity in the Methow Subbasin suggests that pHOS may be negatively related to adult recruitment. However, in both the Methow and Wenatchee subbasins, the range of pHOS within the data is too limited to draw strong conclusions about the effect of pHOS on natural productivity.

All three hypotheses listed above indicate that maintaining the current management strategy will not recover steelhead and may further exacerbate their decline. Unfortunately, we have no way to evaluate any of these hypotheses at this time. All three are directly related to management actions that can be modified, but there is no information specific to these populations on which to act. Hypotheses 1 and 3 are not mutually exclusive. These two hypotheses may interact where natural-origin fish are able to maintain themselves at a low level, but the presence of hatchery-origin fish is preventing the populations from achieving greater productivity. Hypotheses 1 and 2, and 2 and 3 are mutually exclusive. Clearly the populations are not responding to hatchery supplementation as hoped. The observed increase in spawner abundance has not resulted in an increase in natural-origin recruits, and productivity of natural spawning is at such low levels, particularly for the Methow population, that the populations are at high risk of extinction.

Analyses of these populations are hampered by limitations in the data comprising available datasets, including high variability, lack of contrast, and fairly short time series. Although longer datasets exist, the methodologies used to collect the older data are uncertain. The process of assembling the data used in these analyses relied upon a number of assumptions and required numerous adjustments to arrive at a final dataset. It is unclear how much of the variation in these data is due to artifacts or bias. Looking forward, continued application of the recently employed POM methodology will take many years to amass a large enough dataset necessary for these types of analyses. Additionally, in 2012, managers made changes to the supplementation programs that included large reductions in the production of hatchery-origin smolts (particularly in the Wenatchee Subbasin). We did not have enough years of data following the changes in smolt production to adequately evaluate the effects of the changes.

Stock-recruit analyses were primarily developed to manage fisheries. Under a conservation scenario, these types of models describe the relationship of stock to recruits but do not explain why the relationship exists, nor what factors contribute to the productivity and carrying capacity of the population. Under such circumstances, analysis becomes more descriptive than explanatory, and even when a result has been clearly delineated, it will still leave scientists and managers without the means to understand why a result occurred. Explaining results will require years more of

experimental investigations. More robust assessment of these programs could be achieved by employing management designed to test management-based hypotheses by imparting contrast into the management strategies. Furthermore, reliance on reference streams that are outside of the Upper Columbia region confounds analyses because factors affecting other regions where reference streams may be located cannot be accounted for the analyses. Development of management strategies that include intentional levels of contrast, including reference streams within the Wenatchee and Methow subbasins, would provide an opportunity to assess the hatchery program effects on the populations while minimizing confounding factors. This would serve two important purposes: 1) it would allow managers to test different management strategies simultaneously, and 2) it would provide empirical data for assessment of the different management strategies and allow managers to choose the most effective one(s) to improve the chances of recovering these populations that face low replacement rates and demographic risks. Analysis of such management strategies requires many years of observation to detect effects. It is imperative to design management strategies to identify the factors that positively and negatively affect these populations so that future management can address those factors.

Acknowledgements

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Appendix A

Supporting Figures from Stock-Recruit Modeling by Subbasin and Model

Wenatchee Population Beverton-Holt Analyses of Model Parameters and Residuals

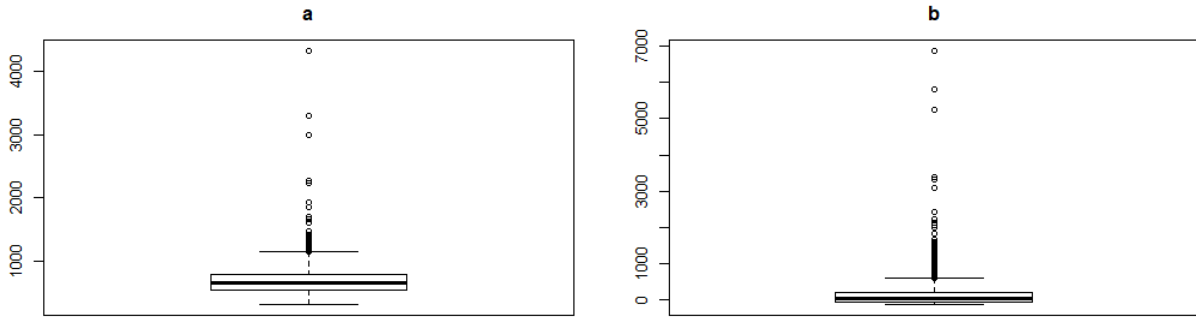


Figure 14. Beverton-Holt Model parameter box plots – Wenatchee.

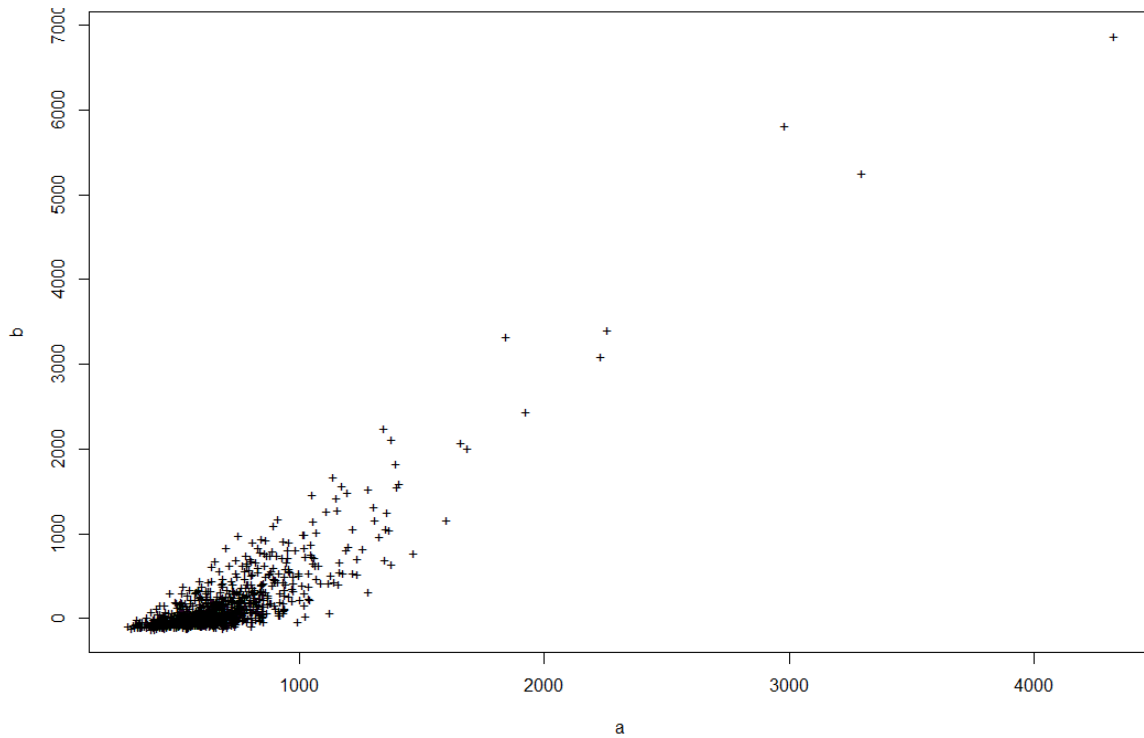


Figure 15. Beverton-Holt Model parameter correlation – Wenatchee.

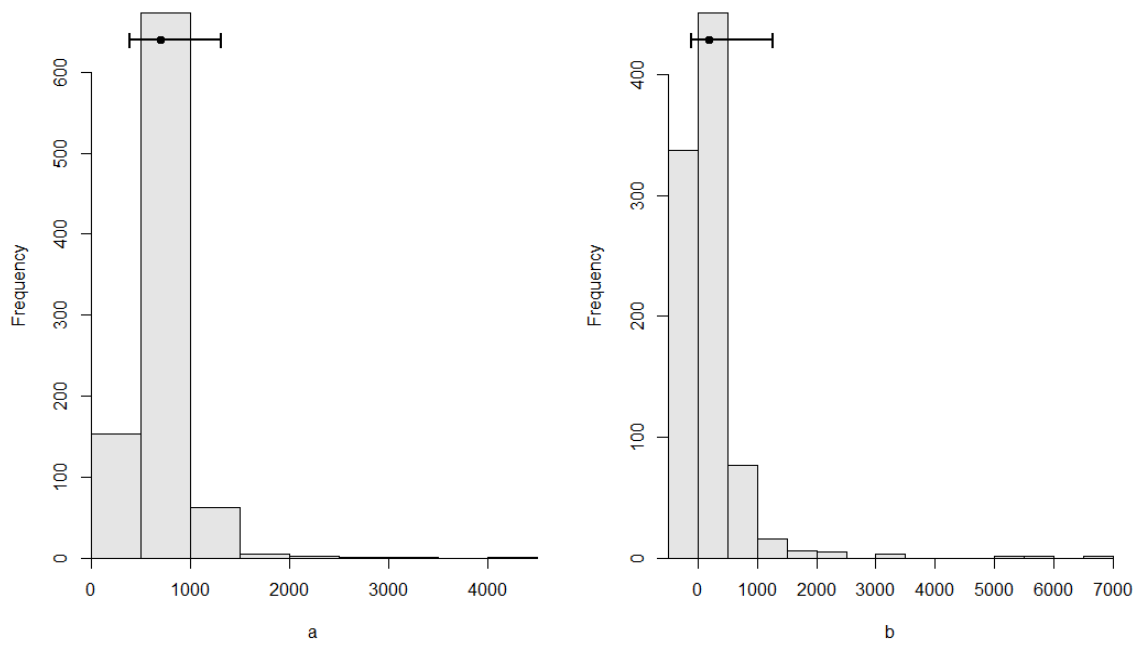


Figure 16. Beverton-Holt Model parameter histograms – Wenatchee.

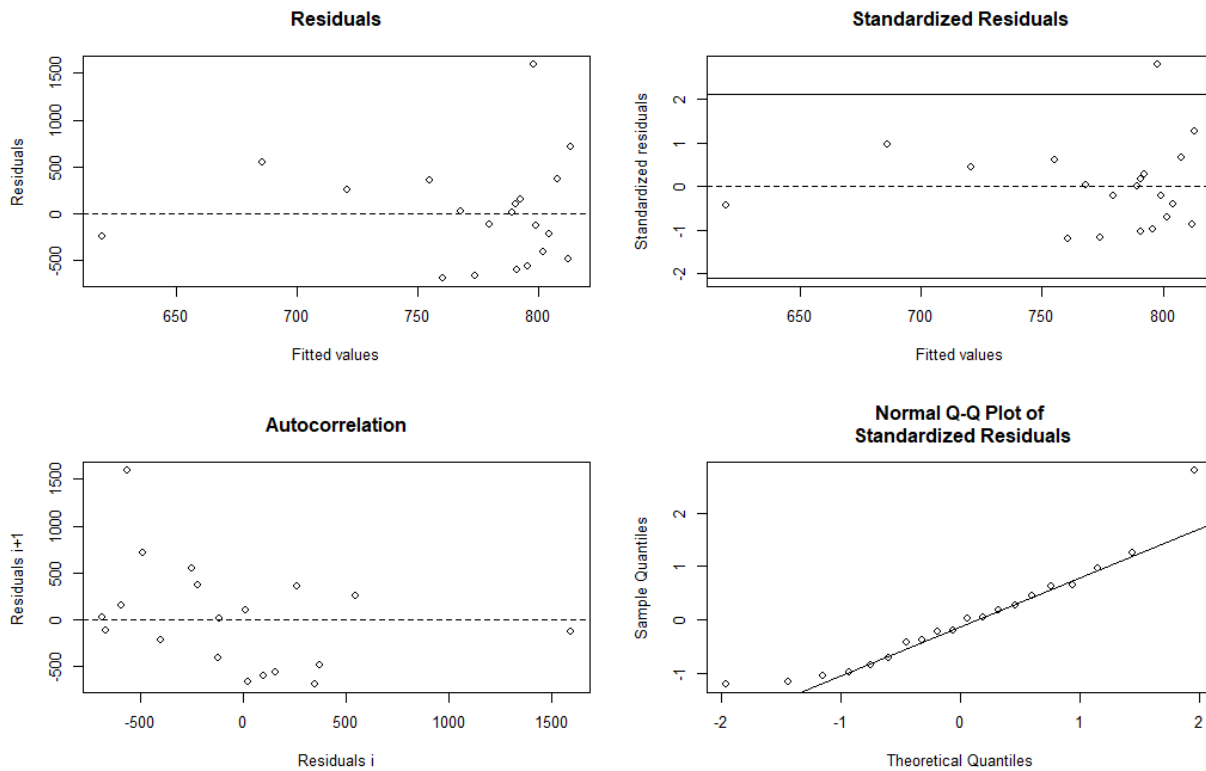


Figure 17. Beverton-Holt Model residuals analysis plots – Wenatchee.

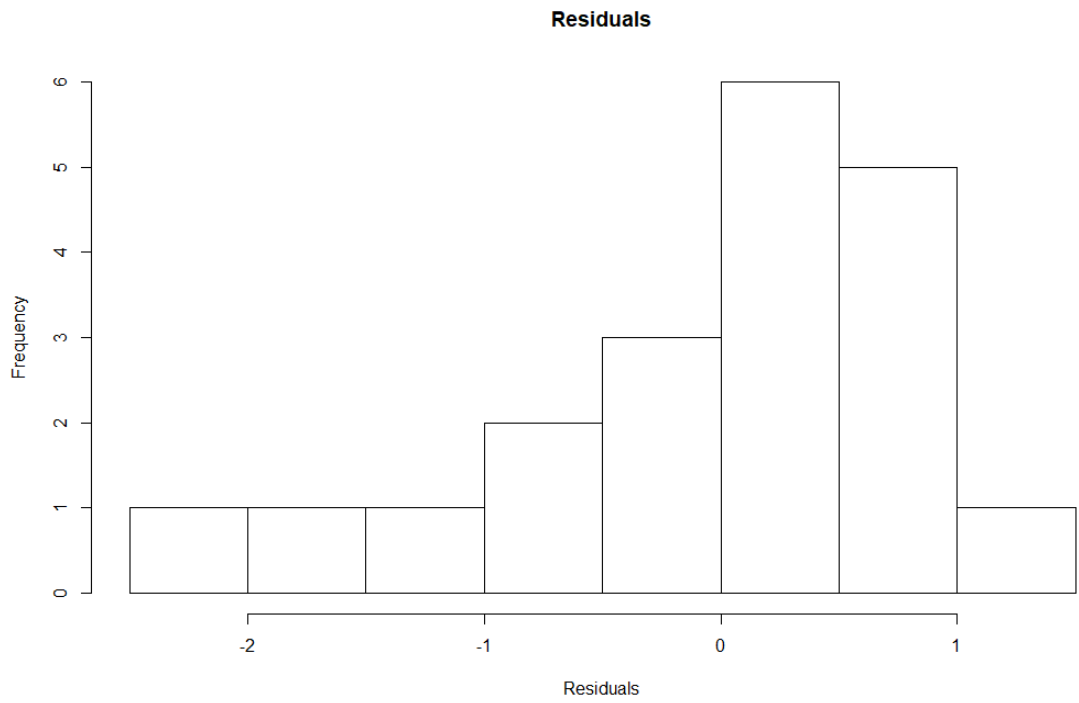


Figure 18. Beverton-Holt Model residuals histogram – Wenatchee.

Wenatchee Population Ricker Analyses of Model Parameters and Residuals

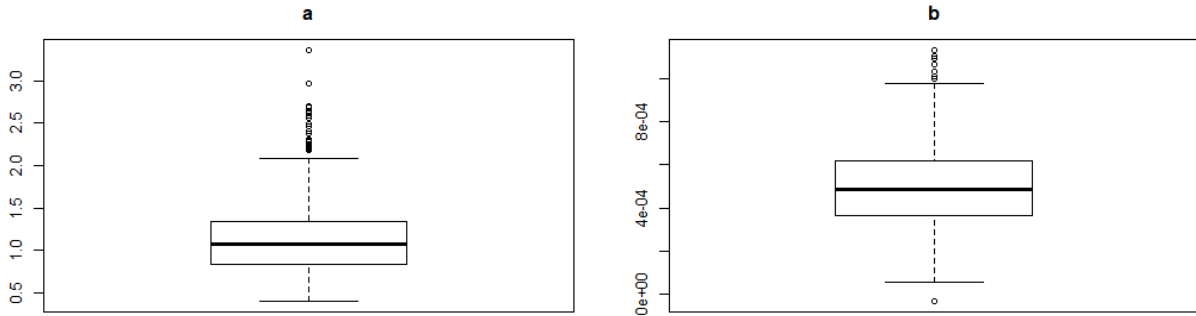


Figure 19. Ricker Model parameter box plots – Wenatchee.

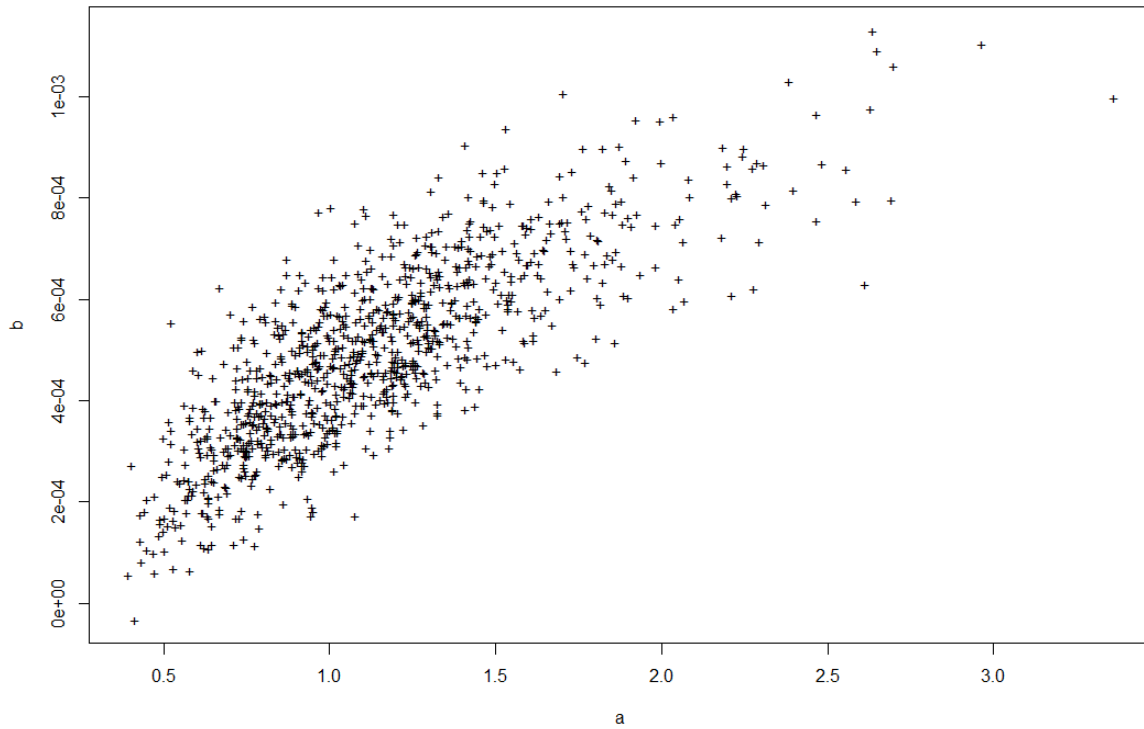


Figure 20. Ricker Model parameter correlation – Wenatchee.

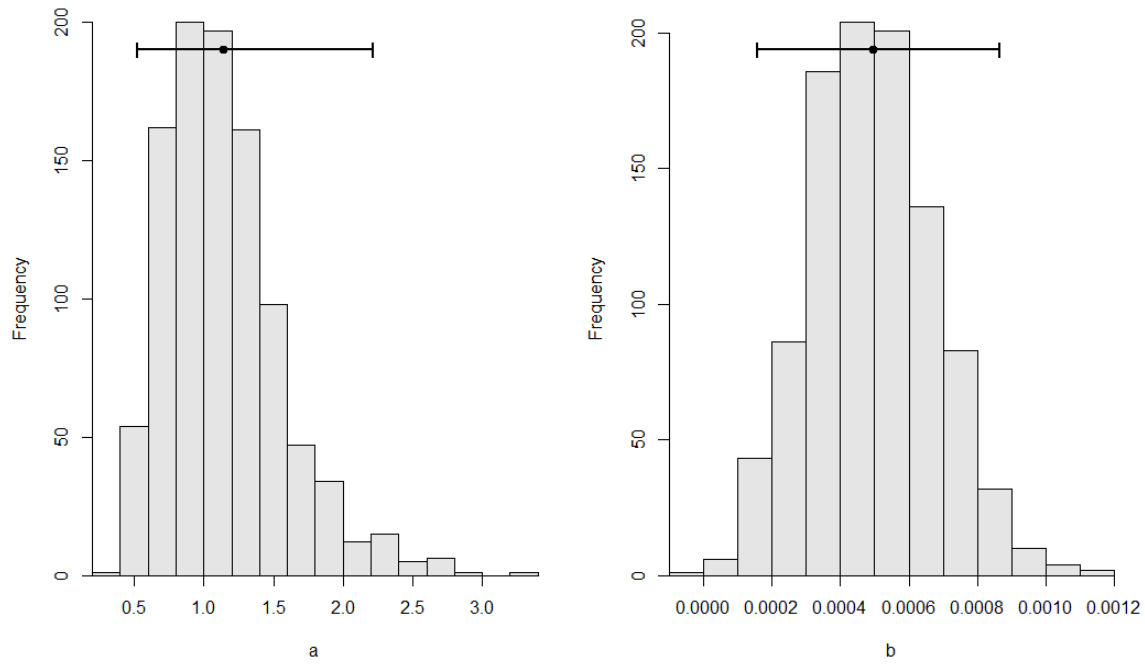


Figure 21. Ricker Model parameter histograms – Wenatchee.

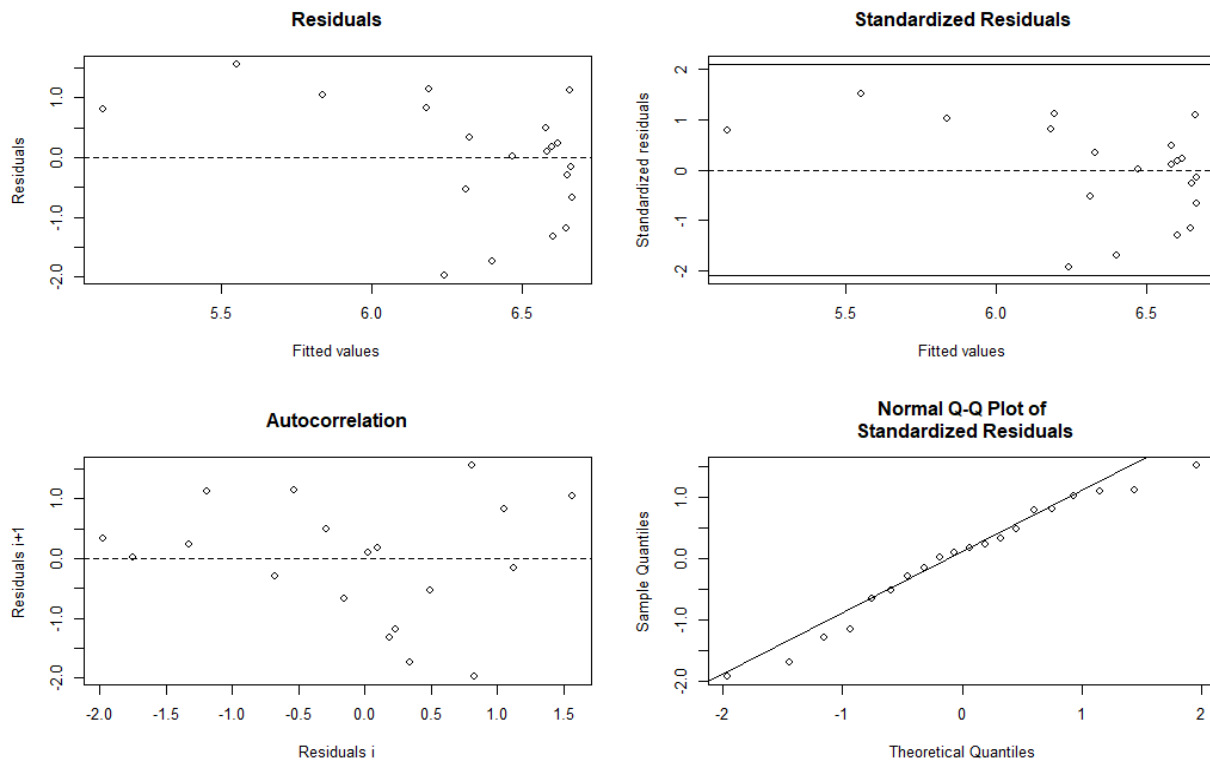


Figure 22. Ricker Model residuals analysis plots – Wenatchee.

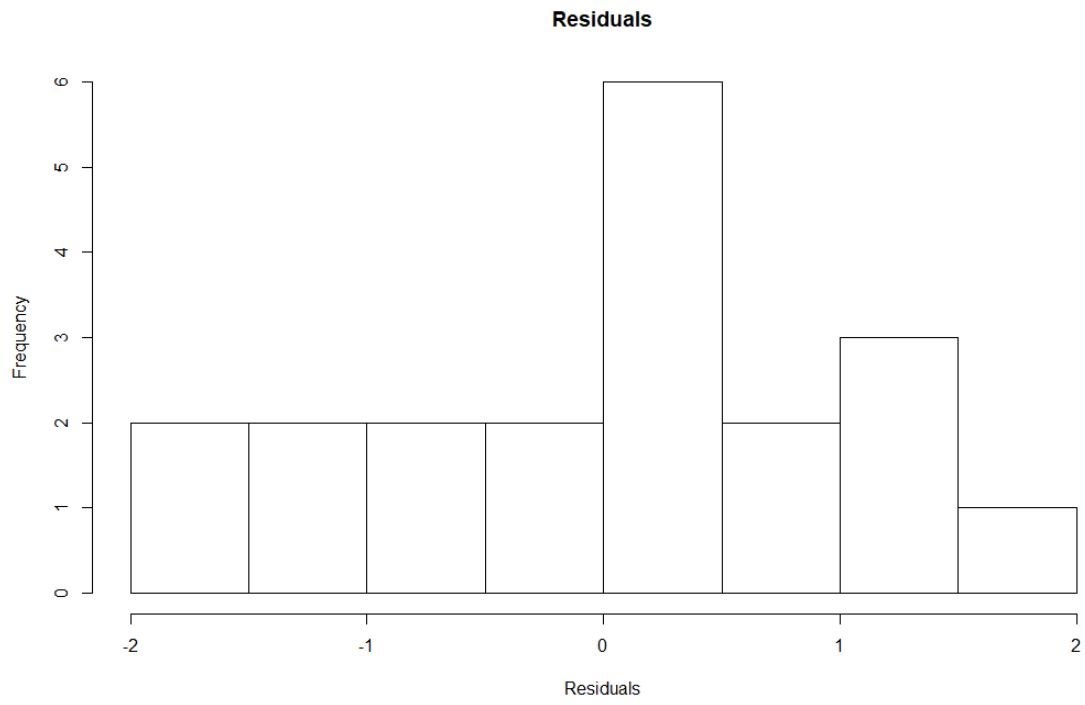


Figure 23. Ricker Model residuals histogram – Wenatchee.

Wenatchee Population Smooth Hockey Stick Analyses of Residuals

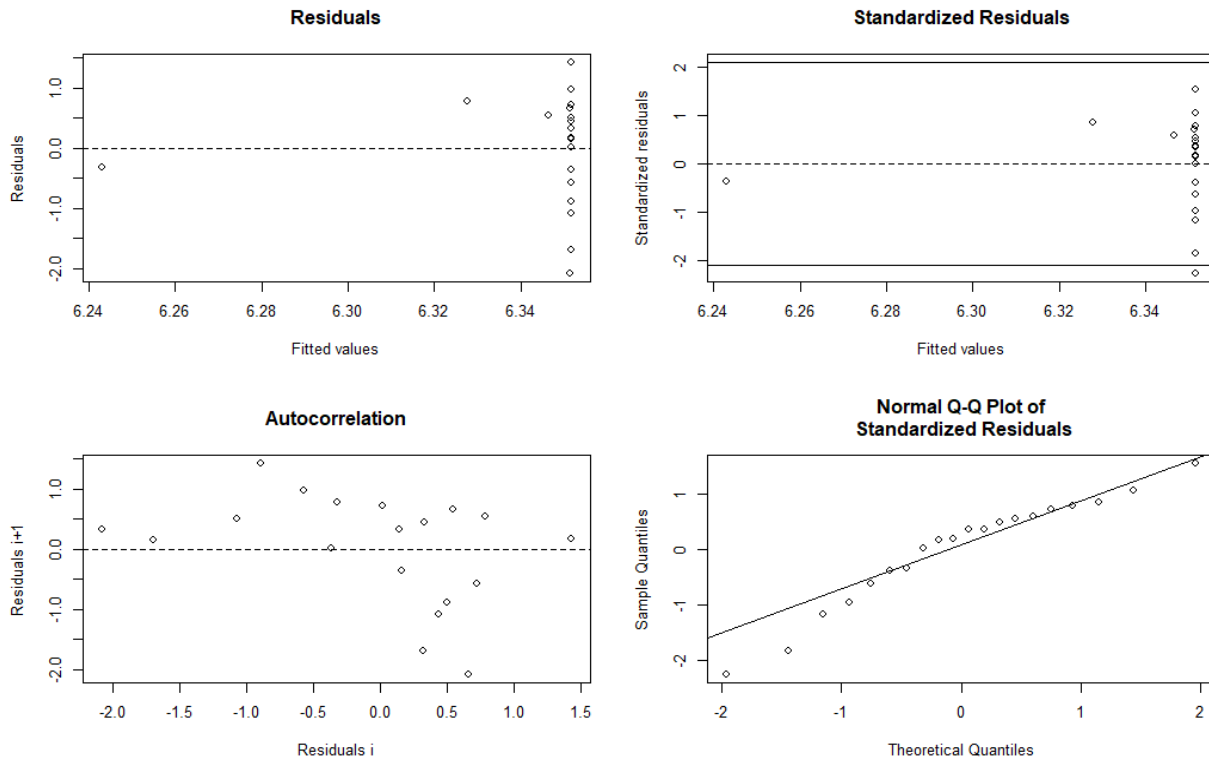


Figure 24. Smooth Hockey Stick Model residuals analysis plots – Wenatchee.

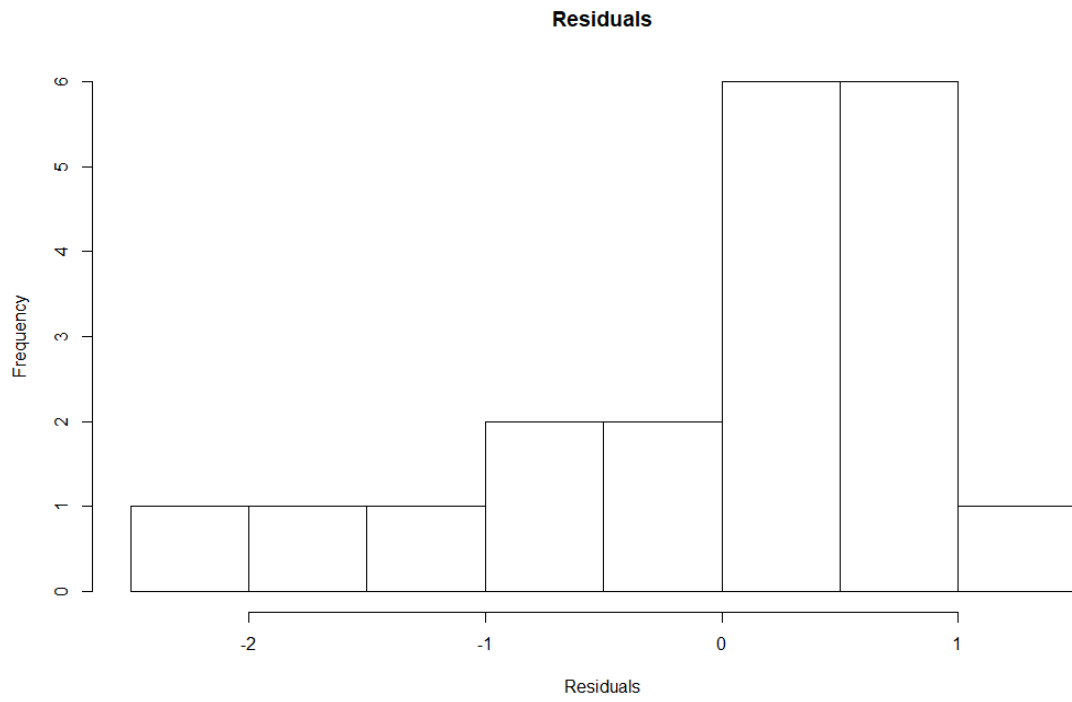


Figure 25. Smooth Hockey Stick Model residuals histogram – Wenatchee.

Methow Population Beverton-Holt Analyses of Model Parameters and Residuals – POM-Adjusted Data

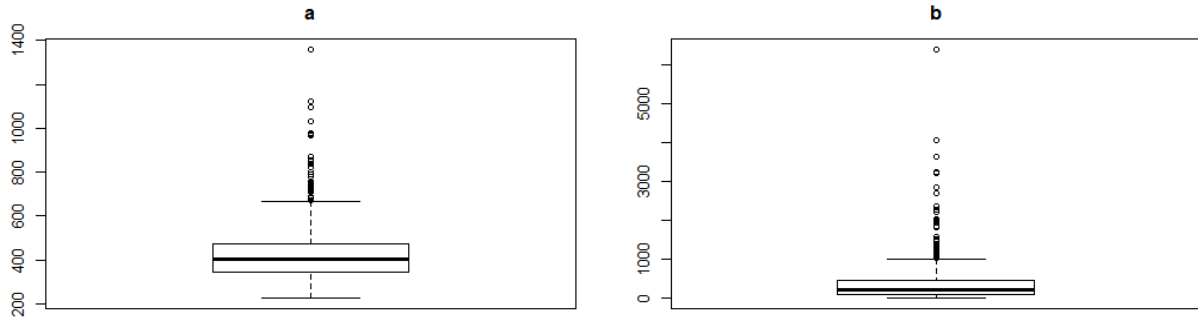


Figure 26. Beverton-Holt Model parameter box plots – Methow POM-Adjusted Data.

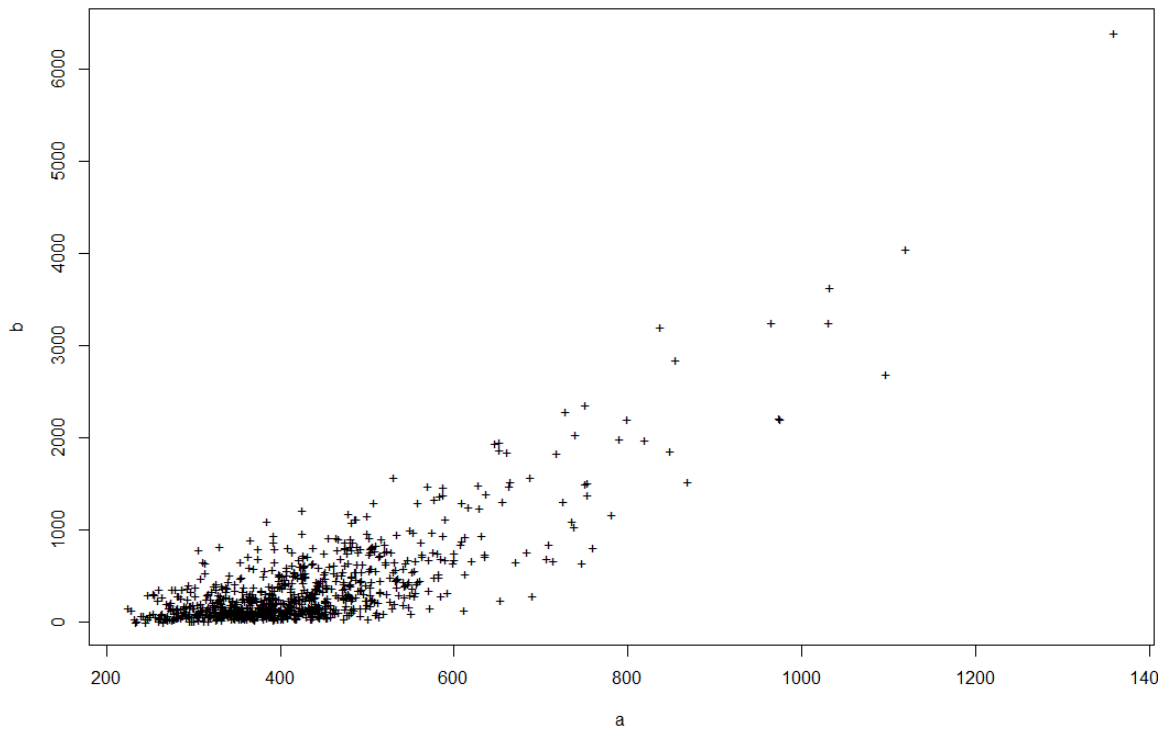


Figure 27. Beverton-Holt Model parameter correlation - Methow POM-Adjusted Data.

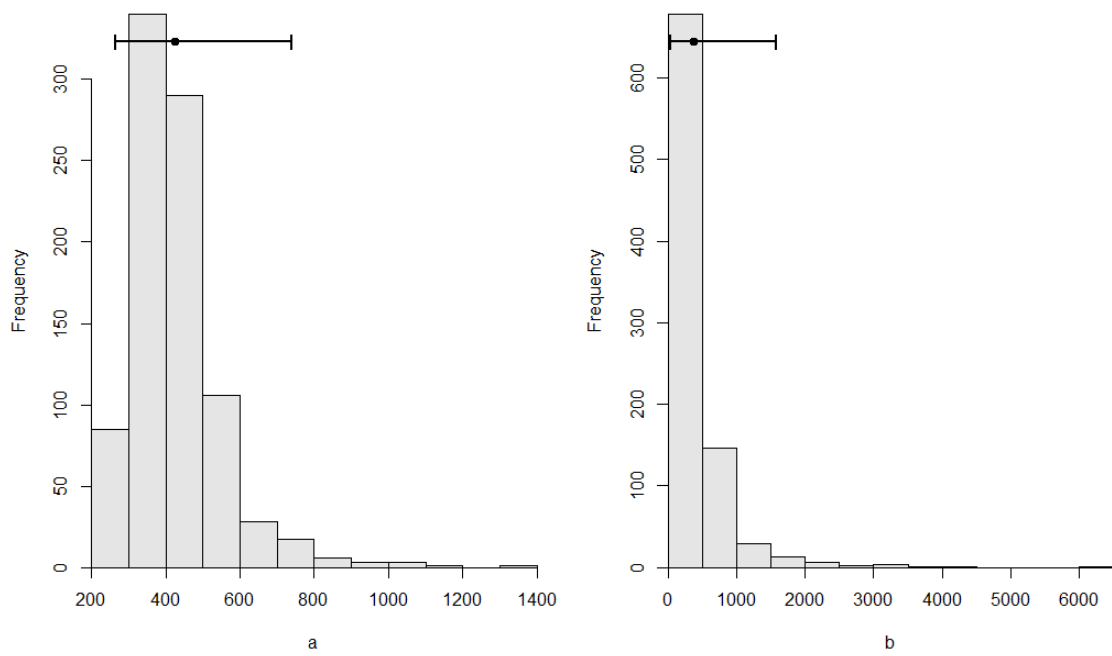


Figure 28. Beverton-Holt Model parameter histograms – Methow POM-Adjusted Data.

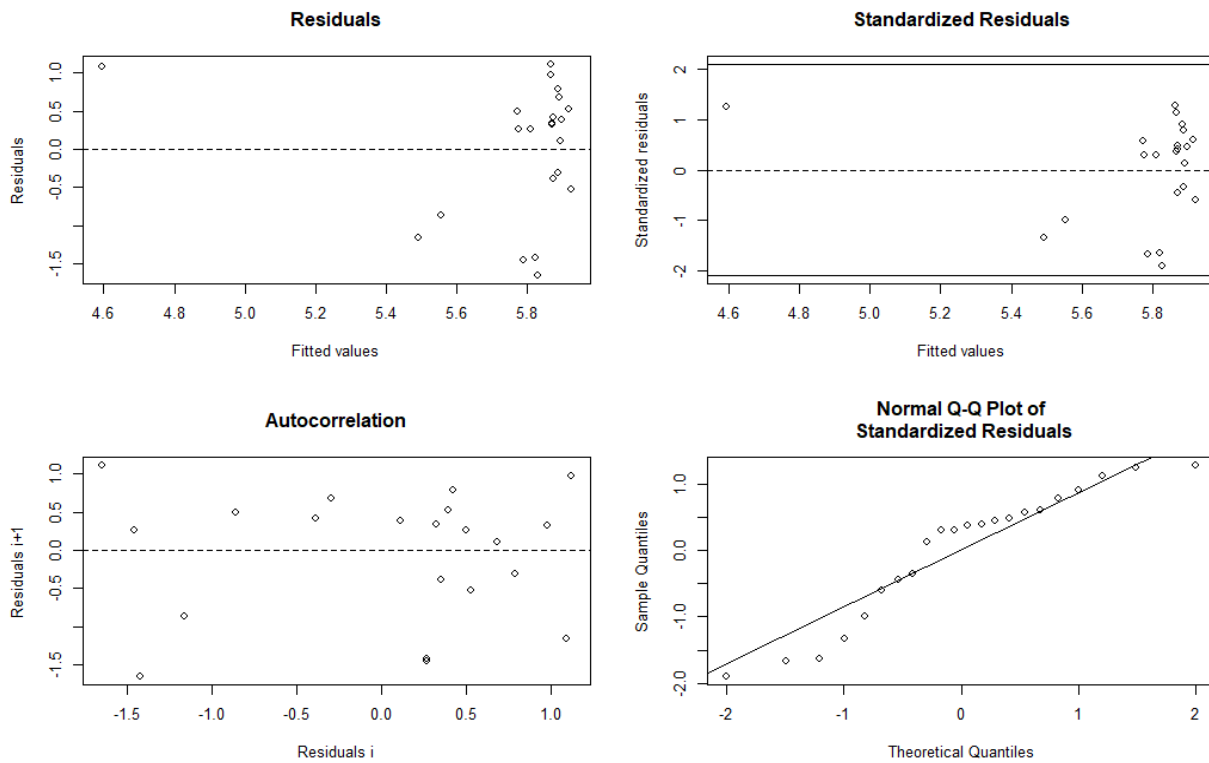


Figure 29. Beverton-Holt Model residuals analysis plots – Methow POM-Adjusted Data.

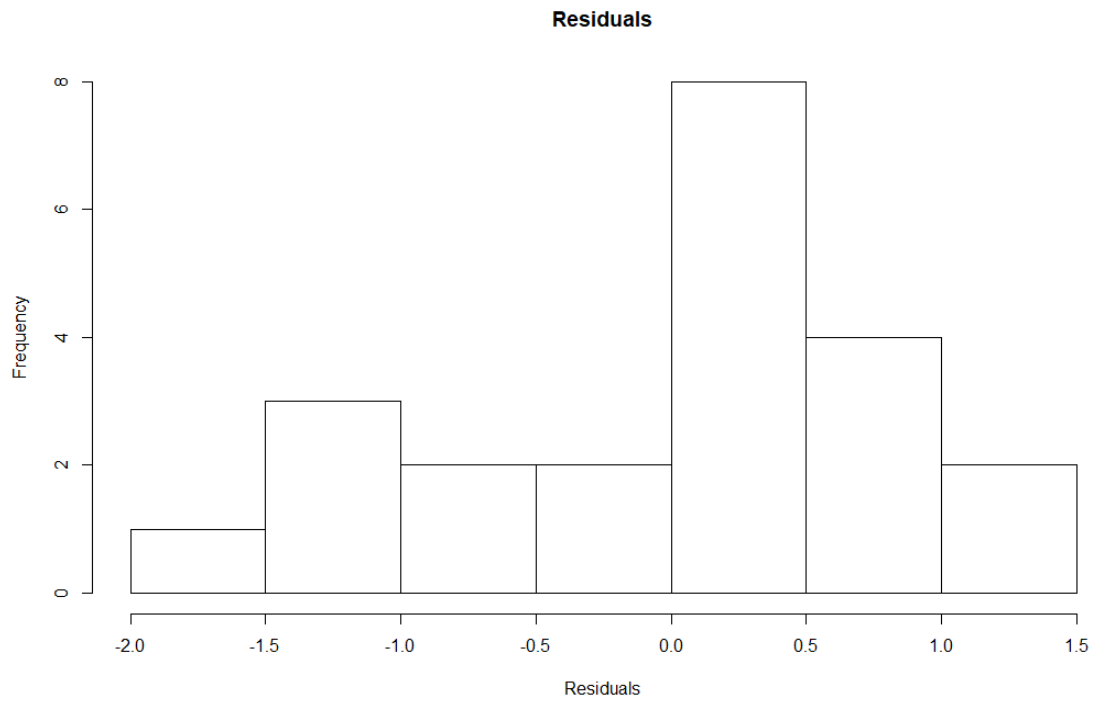


Figure 30. Beverton-Holt Model residuals histogram – Methow POM-Adjusted Data.

Methow Population Ricker Analyses of Model Parameters and Residuals – POM-Adjusted Data

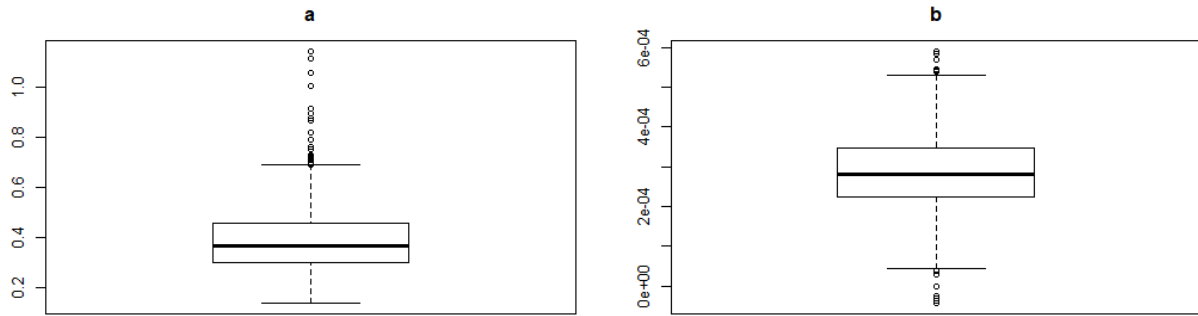


Figure 31. Ricker Model parameter box plots – Methow POM-Adjusted Data.

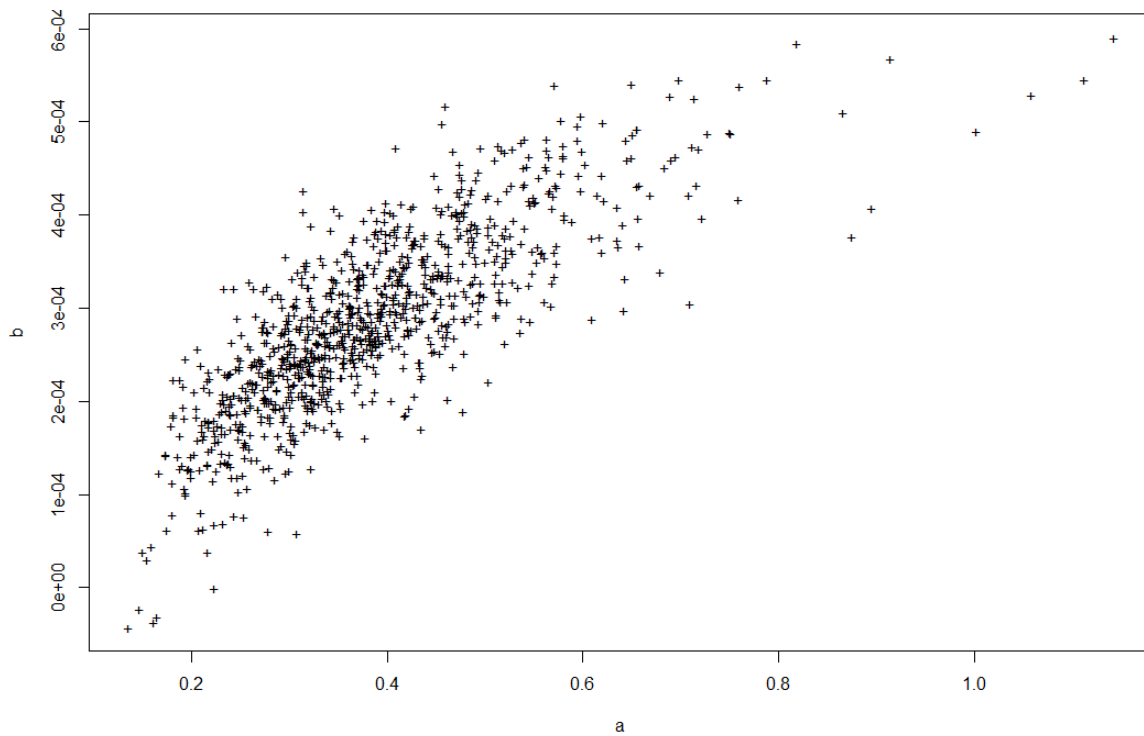


Figure 32. Ricker Model parameter correlation - Methow POM-Adjusted Data.

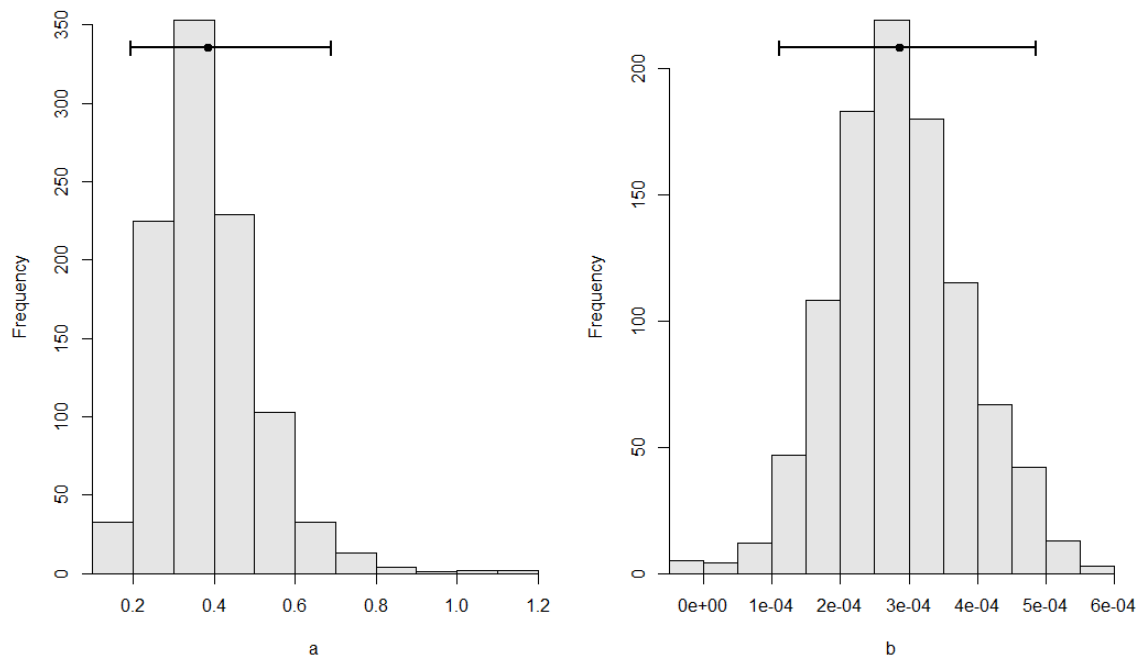


Figure 33. Ricker Model parameter histograms – Methow POM-Adjusted Data.

Methow Population Ricker Analyses of Model Residuals – POM-Adjusted Data

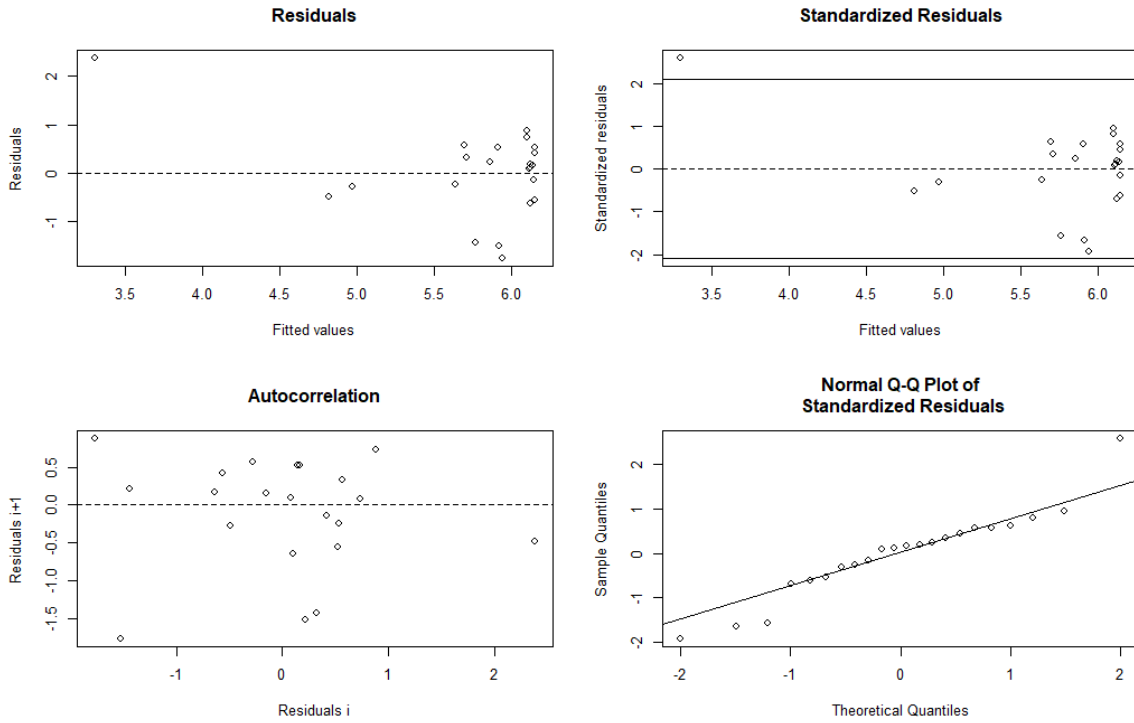


Figure 34. Ricker Model residuals analysis plots – Methow POM-Adjusted Data.

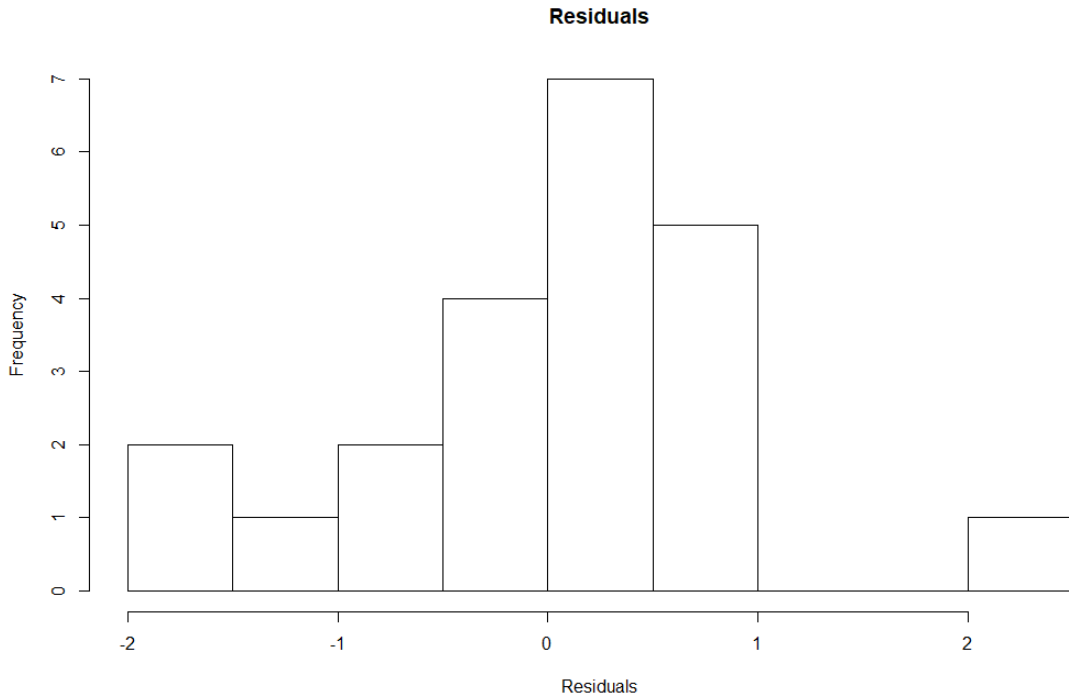


Figure 35. Ricker Model residuals histogram – Methow POM-Adjusted Data.

Methow Population Beverton-Holt Analyses of Model Residuals – Redd Expanded Data

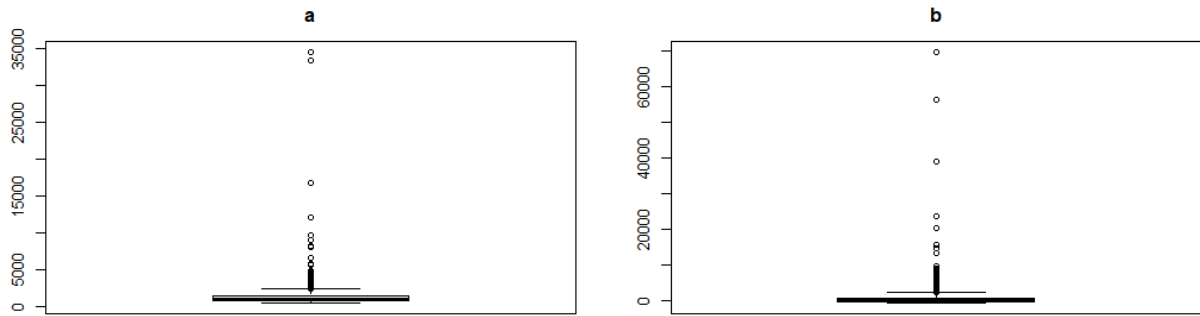


Figure 36. Beverton Holt-Model parameter box plots – Methow Redd Expanded Data.

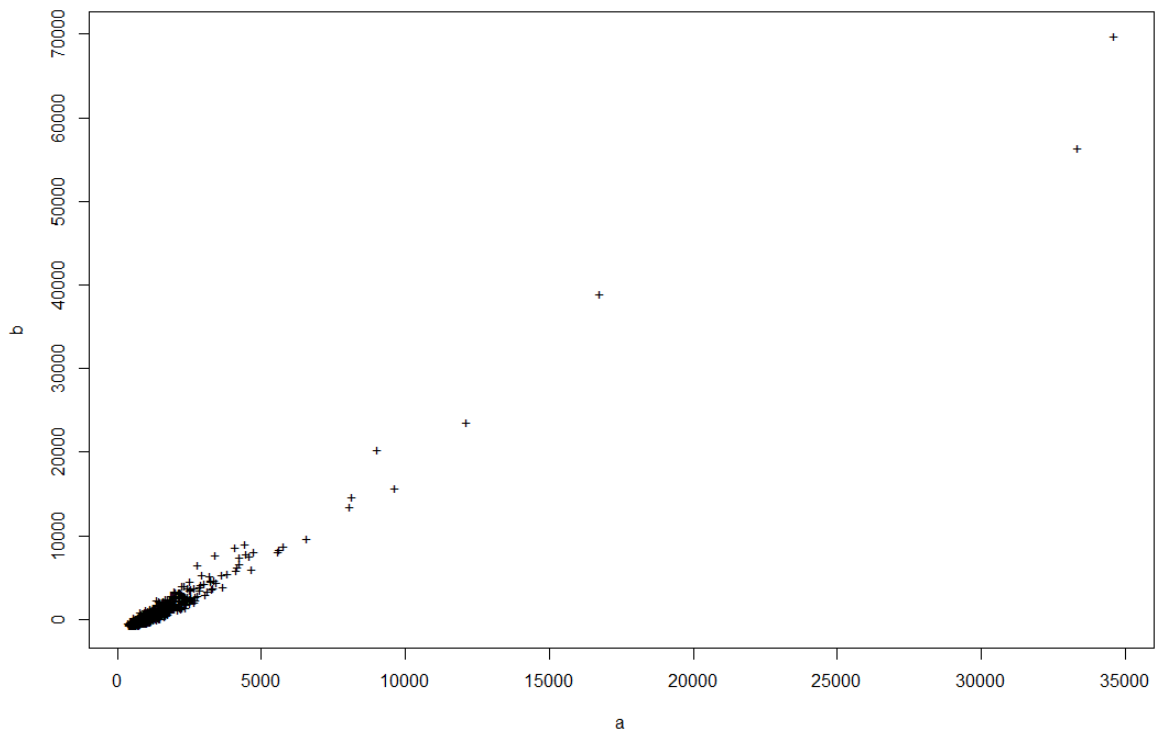


Figure 37. Beverton-Holt Model parameter correlation - Methow Redd Expanded Data.

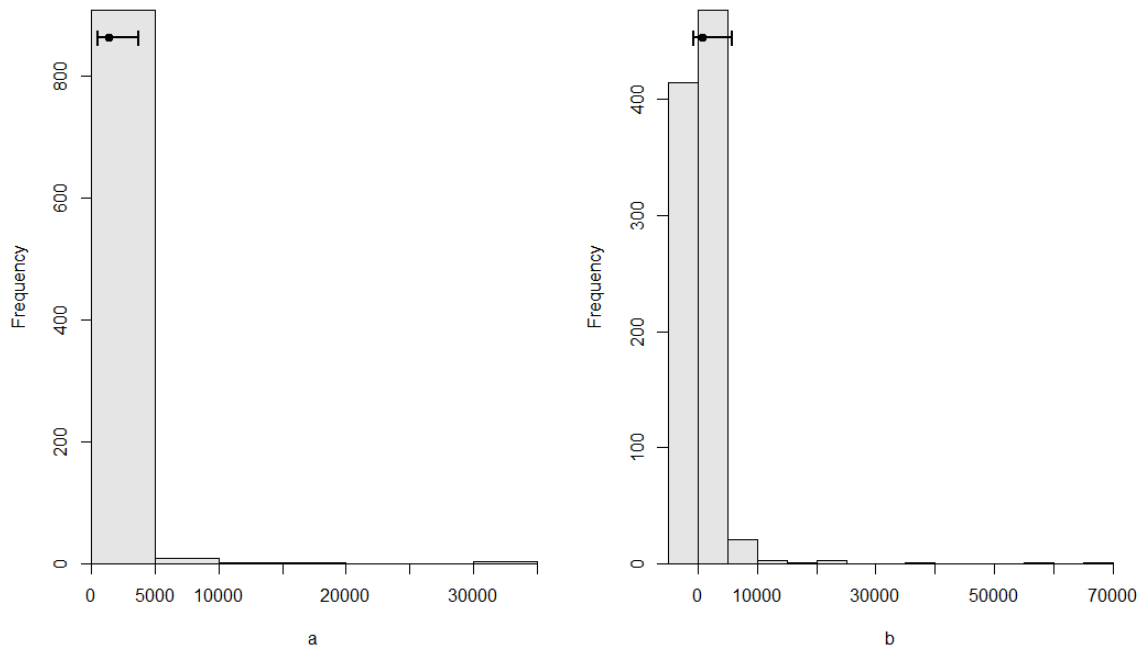


Figure 38. Beverton-Holt Model parameter histograms – Methow Redd Expanded Data.

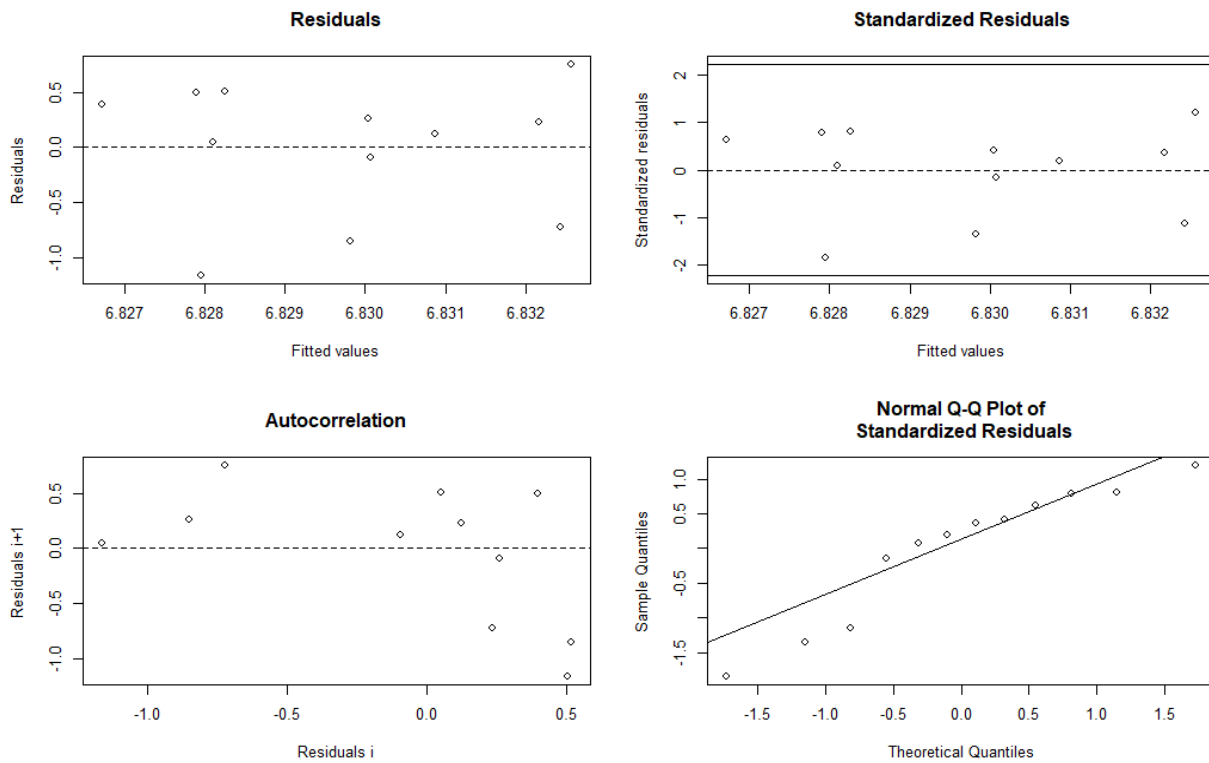


Figure 39. Beverton-Holt Model residuals analysis plots – Methow Redd Expanded Data.

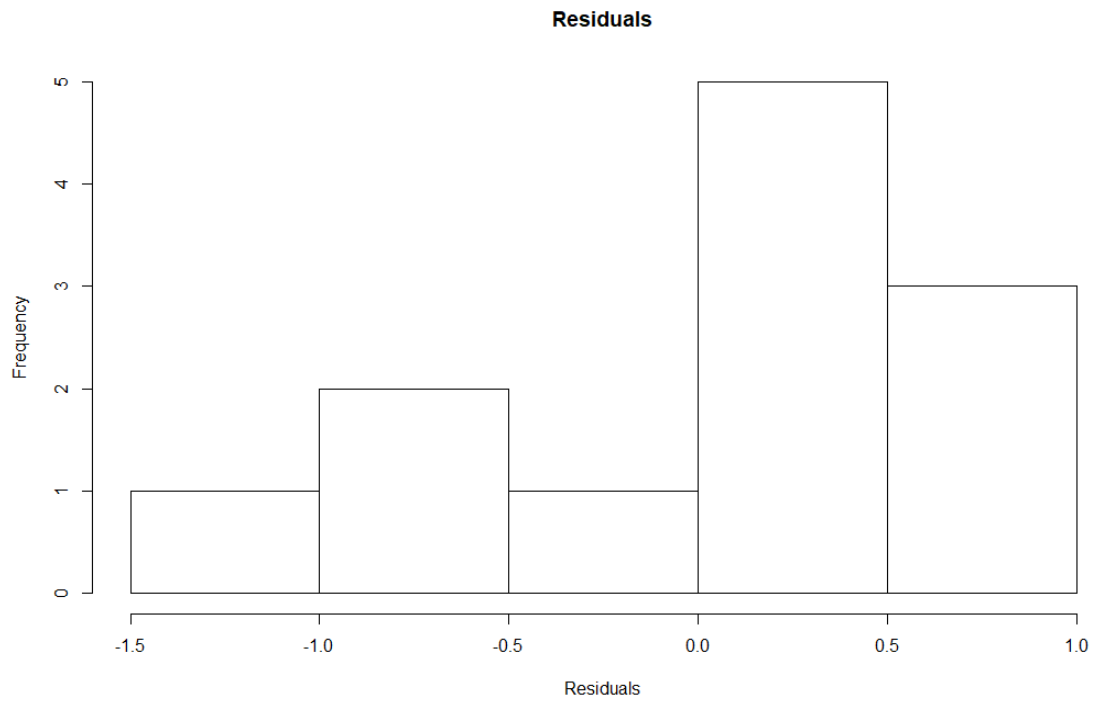


Figure 40. Beverton-Holt Model residuals histogram – Methow Redd Expanded Data.

Methow Population Ricker Analyses of Model Residuals – Redd Expanded Data

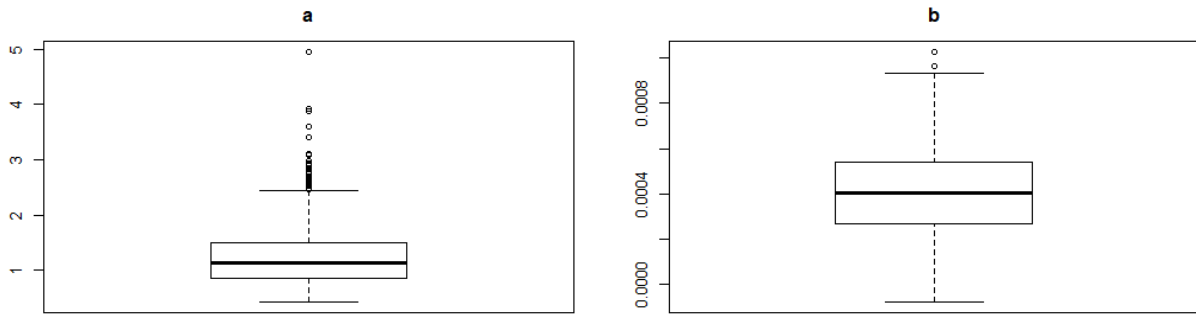


Figure 41. Ricker Model parameter box plots – Methow Redd Expanded Data.

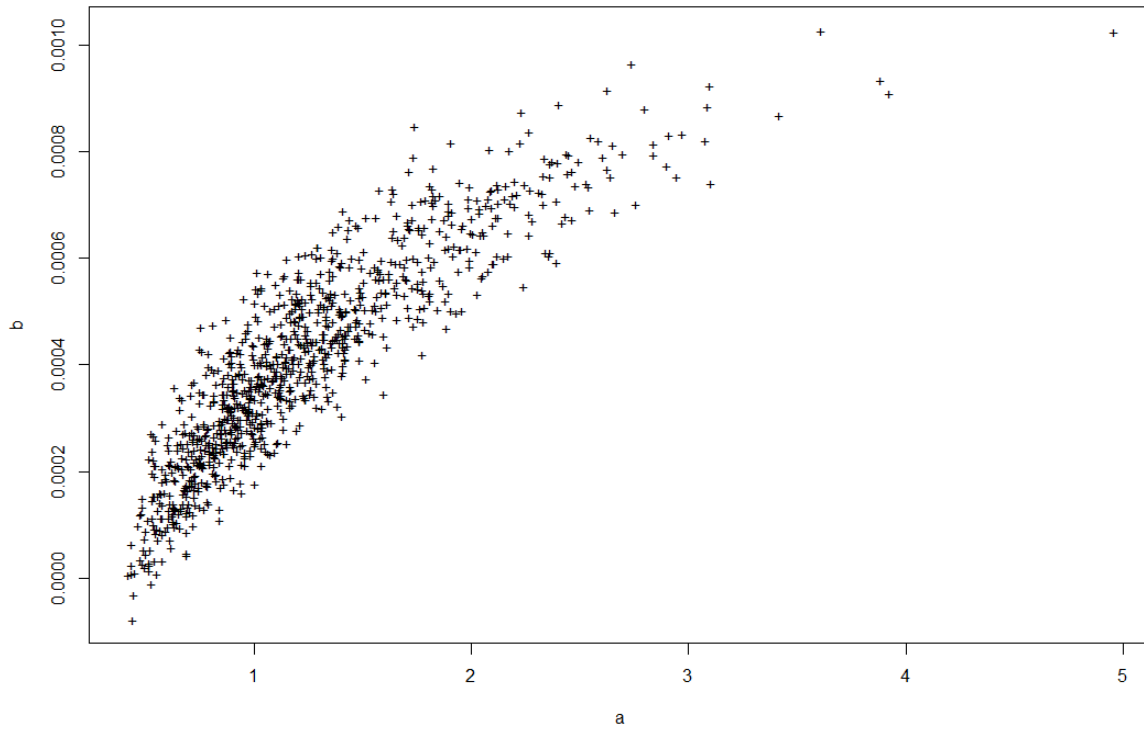


Figure 42. Ricker Model parameter correlation - Methow Redd Expanded Data.

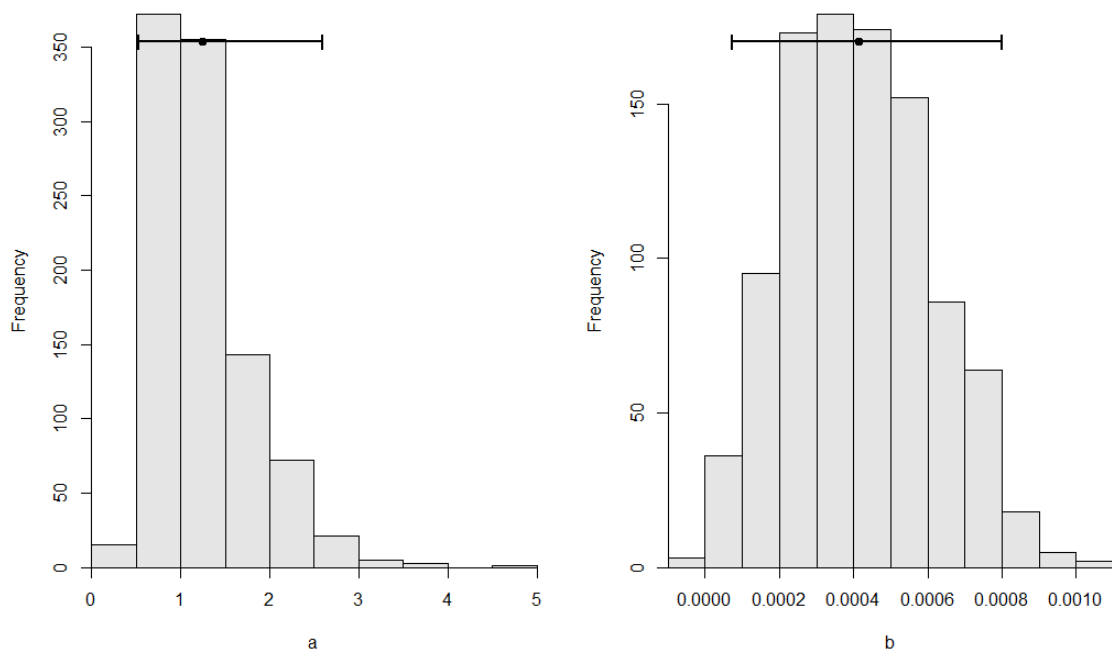


Figure 43. Ricker Model parameter histograms – Methow Redd Expanded Data.

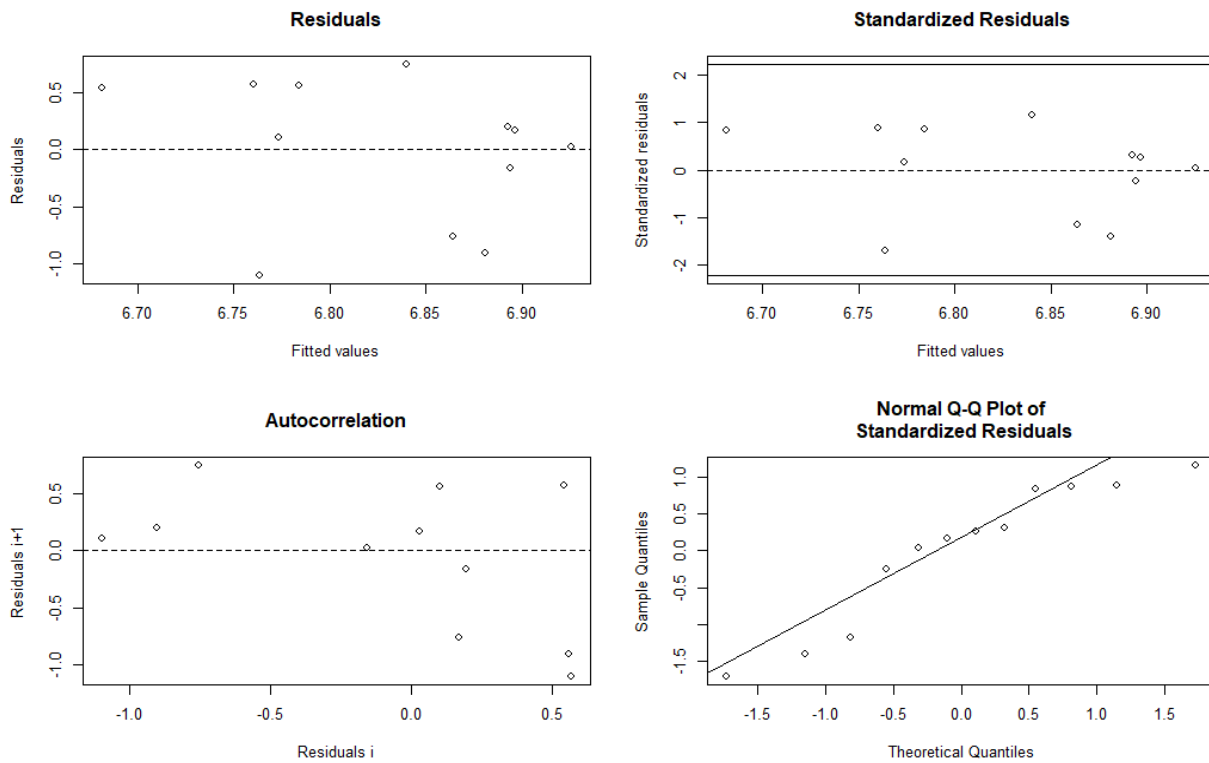


Figure 44. Ricker Model residuals analysis plots – Methow Redd Expanded Data.

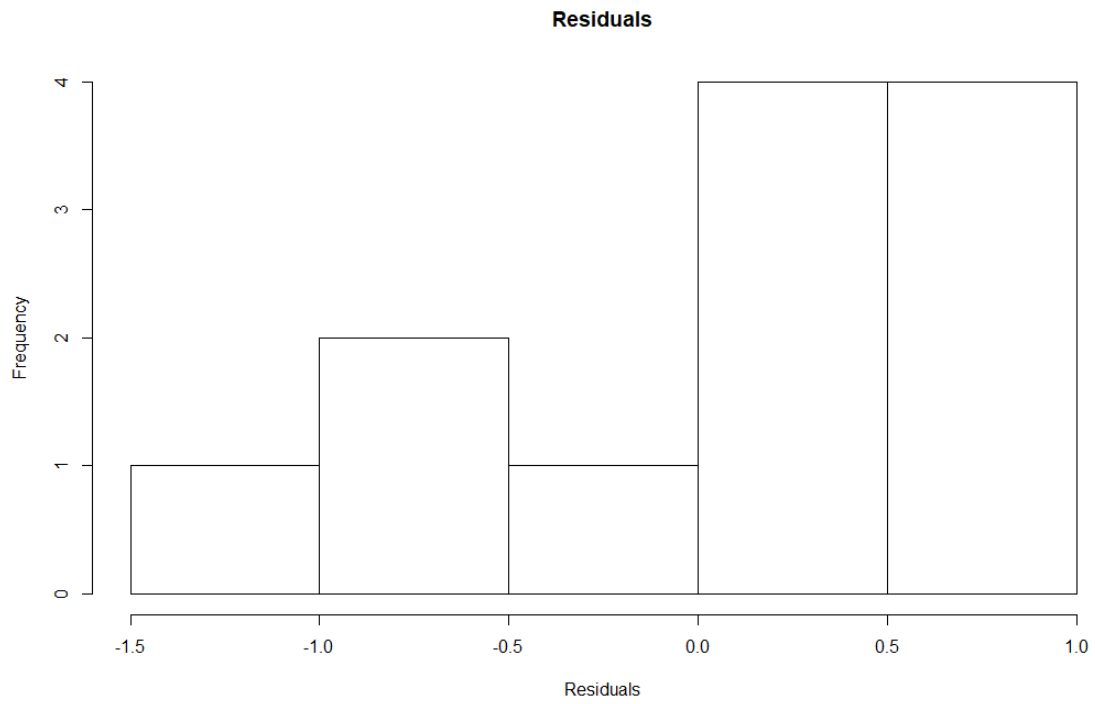


Figure 45. Ricker Model residuals histogram – Methow Redd Expanded Data.

Appendix B

R Code Used in the Analyses

```
library(openxlsx)
library(ggplot2)
library(nlstools)
library(AICcmodavg)
library(bbmle)
library(FSA)
library(quantreg)
library(dplyr)
library(FSAdata)
library(tidyr)
library(pastecs)
library(knitr)
library(gridExtra)
library(WriteXLS)

par(pty="s") #forces graphs to have a size ration of 1 (square)

#Set working directory and list files
setwd("S:\\GregM\\Monitoring and Evaluation\\10 Year Report\\2020\\Data\\Steelhead Stock Recruit")
#setwd("K:\\10 Year Report\\2020\\Data\\Steelhead Stock Recruit")

list.files()

#Get data
SRDataXLSX<-read.xlsx("Steelhead_SR_Oct_2020.xlsx", sheet="Methow")

SRData<-SRDataXLSX[order(SRDataXLSX$Spawners),]

SRData
```

```

# Define Variables

stock<-SRData$Spawners

recruits<-SRData$Recruits

logR<-SRData$ln_Recruits

#Create x and y axis limits based on the data

xmin=0

xmax=max(c(recruits,stock))

xmin

xmax

ymin=0

ymax=max(c(recruits,stock))

ymin

ymax

##### Descriptive Stats
#####

#Get descriptive stats using the pastecs package

options(scipen=100)

options(digits=2)

SummaryStats<-stat.desc(SRData)

SummaryStats

#####RMarkdown Table of Descriptive Stats#####

---

title: "Example for tables"

author: "Gregory Mackey"

output: word_document

---

#Create R MarkDown table of SummaryStats output - paste into Word with Courier 6-point font

```

```

library(knitr)

#Data
data("SummaryStats")

#`` {r,echo=FALSE,message=FALSE,warning=FALSE}
kable(SummaryStats,caption = "Table 1: Summary Statistics",align = rep('c',5))
#``

####Add a boxplot of the Spawners Data####
SpawnerBoxPlot<-ggplot(SRData, aes(y=Spawners, ymin=ymin, ymax=ymax))+
  stat_boxplot(geom ='errorbar') +
  geom_boxplot(fill = "paleturquoise2", color="black", outlier.color="red", outlier.shape=1,width=3)+
  scale_x_discrete()+
  scale_y_continuous(name = "Spawners",
    #breaks = seq(0, 175, 25),
    limits=c(ymin, ymax))+
  labs(title="Spawners")
SpawnerBoxPlot<-SpawnerBoxPlot+theme_bw()+ theme(axis.line = element_line(colour = "black"),
  panel.grid.major = element_blank(),
  panel.grid.minor = element_blank(),
  panel.background = element_blank(),
  plot.title=element_text(hjust=0.5, size=18),
  aspect.ratio=1)

####Add a boxplot of the Recruits Data####
RecruitBoxPlot<-ggplot(SRData, aes(y=Recruits, ymin=ymin, ymax=ymax))+
  stat_boxplot(geom ='errorbar') +
  geom_boxplot(fill = "paleturquoise2", color="black", outlier.color="red", outlier.shape=1,width=3)+
  scale_x_discrete()+
  scale_y_continuous(name = "Recruits",

```

```

#breaks = seq(0, 175, 25),
limits=c(ymin, ymax))+
labs(title="Recruits")
RecruitBoxPlot<-RecruitBoxPlot+theme_bw()+ theme(axis.line = element_line(colour = "black"),
panel.grid.major = element_blank(),
panel.grid.minor = element_blank(),
panel.background = element_blank(),
plot.title=element_text(hjust=0.5, size=18),
aspect.ratio=1)

#Arrange the boxplots on one page
grid.arrange(SpawnerBoxPlot, RecruitBoxPlot, nrow=1)

#####Set Decimal Places Options for the Rest of the
Analyses#####
options(scipen=999)
options(digits=4)

##### Stock Recruit Models
#####

bh1s<-srStarts(Recruits~Spawners, data=SRData, type="BevertonHolt", param=1) #estimates starting parameter for BH model
unlist(bh1s)

alpha_start=bh1s[1]
alpha_start
beta_start=bh1s[2]
beta_start

```

```
##### Density Independent
```

```
#####
```

```
DIa=0.17 #density independent starting parameter; Methow = 0.17, Wenatchee = 0.48
```

```
bh0<-ln_Recruits~log(a*Spawners)
```

```
bh0s<-bh1s[1]
```

```
bh0nls<-nls(bh0, data=SRData, start=list(a=DIa))
```

```
overview(bh0nls)
```

```
coef(bh0nls)[1]
```

```
##### Beverton Holt
```

```
#####
```

```
#bh1<-ln_Recruits~log((a*Spawners)/(1+b*Spawners))
```

```
bh1<-ln_Recruits~log(a*Spawners/(b+Spawners))
```

```
bh1nls<-nls(bh1,data=SRData, start=bh1s)
```

```
overview(bh1nls)
```

```
##### BH Quantile Regression
```

```
#####
```

```
#Quantile Regression - fit the 90th quantile
```

```
taus<-c(0.90)
```

```
Qalpha_start=bh1s[1] #provide starting parameter estimate for quantile regression
```

```
Qalpha_start
```

```
Qbeta_start=bh1s[2] #provide starting parameter estimate for quantile regression
```

```
Qbeta_start
```

```
QRBH1<-nlrq(ln_Recruits~log(a*Spawners/(b+Spawners)),start=list(a=Qalpha_start,b=Qbeta_start), tau=taus, data=SRData)
```

```
QRBH1
```

```
summary(QRBH1)
```

```
##### Plot
```

```
#####
```

```
plot(Recruits~Spawners,data=SRData, xlim=c(xmin, xmax), ylim=c(ymin, ymax))
```

```
curve(coef(bh1nls)[1]*x/(coef(bh1nls)[2]+x),from=0,to=xmax,col="red",lwd=2,add=TRUE)
```

```
curve(coef(QRBH1)[1]*x/(coef(QRBH1)[2]+x),from=0,to=xmax,col="purple",lwd=2,add=TRUE)
```

```
curve(coef(bh0nls)[1]*x,from=0,to=xmax,col="blue",lwd=2,add=TRUE)
```

```
abline(0,1, col="gray")
```

```
legend("topleft",legend=c("density independent","density dependent", "replacement", "95th Quantile"),
```

```
col=c("blue","red","gray", "purple"),lwd=2,cex=0.6)
```

```
##### BH Residuals Analysis
```

```
#####
```

```
bootbh1<-nlsBoot(bh1nls, niter=1000)
```

```
confint(bootbh1, plot=TRUE)
```

```
#Plot Bootstrapped Residuals
```

```
plot(bootbh1)
```

```
plot(bootbh1, type = "boxplot", ask = FALSE)
```

```
plot(nlsResiduals(bh1nls))
```

```
test.nlsResiduals(nlsResiduals(bh1nls))
```

```
bh1nlsResiduals<-nlsResiduals(bh1nls)
```

```
bh1nlsResiduals
```

```
plot(bh1nlsResiduals, which=0)
```

```
plot(bh1nlsResiduals, which=5)
```

```
residuals(bh1nls)
```

```
#####
```

```
#####
```

```
##### Ricker
```

```
#####
```

```
##Ricker Function - see Hilborn and Walters: Quantitative Fisheries Stock Assessment. 1992. Chapman and Hall.
```

```
#R=a*S*Ine^(-b*S) #where R=recruits; S=Spawners (stock);
```

```
# alpha=slope at the origin; e=natural log base
```

```
#Define Parameters
```

```
alpha_start=0.36 #provide starting parameter estimate: Wenatchee = 2; Methow= 0.36
```

```
R_start=0.0003 #provide starting parameter estimate: Wenatchee = 0.0005; Methow= 0.0003
```

```
Ine=exp(1) #natural log base
```

```
Ine
```

```
#Ricker model - uses non linear regression to estimate parameters
```

```
RSRFormula<- as.formula(In_Recruits~log(a*Spawners*Ine^(-b*Spawners)))
```

```
RSR<-nls(RSRFormula,start=list(a=alpha_start,b=R_start), data=SRData)
```

```
overview(RSR)
```



```
##### Ricker Quantile Regression
#####

#Quantile Regression - fit the 90th quantile
taus<-c(0.90)

Qalpha_start=2 #provide starting parameter estimate for quantile regression: Wenatchee = 2; Methow= 0.36
QR_start=0.0005 #provide starting parameter estimate for quantile regression: Wenatchee = 0.0005; Methow= 0.0003

QRSR<-nlrq(ln_Recruits~log(a*Spawners*ln^(-b*Spawners)),start=list(a=Qalpha_start,b=QR_start), tau=taus, data=SRData)
QRSR
summary(QRSR)

##### Plot
#####

plot(Recruits~Spawners,data=SRData, xlim=c(xmin, xmax), ylim=c(ymin, ymax))
curve(coef(RSR)[1]*x*ln^(-coef(RSR)[2]*x),from=0,to=xmax,col="red",lwd=2,add=TRUE)
curve(coef(QRSR)[1]*x*ln^(-coef(QRSR)[2]*x),from=0,to=xmax,col="purple",lwd=2,add=TRUE)
curve(coef(bh0nls)[1]*x,from=0,to=xmax,col="blue",lwd=1,add=TRUE)
abline(0,1, col="gray", lwd=1)
legend("topleft",legend=c("density independent","density dependent", "replacement", "95th Quantile"),
      col=c("blue","red","gray", "purple"),lwd=2,cex=0.6)

##### Ricker Residuals Analysis
#####

bootRSR<-nlsBoot(RSR, niter=1000)
confint(bootRSR, plot=TRUE)
```

```

#Plot Bootstrapped Residuals

plot(bootRSR)

plot(bootRSR, type = "boxplot", ask = FALSE)

plot(nlsResiduals(RSR))

test.nlsResiduals(nlsResiduals(RSR))

RSRResiduals<-nlsResiduals(RSR)

RSRResiduals

plot(RSRResiduals, which=0)

plot(RSRResiduals, which=5)

residuals(RSR)

#####

#####

##### Smooth Hockey Stick

#####

#####

##Smooth Hockey Stick Function - see Froese 2008. J. Appl. Ichthyol. 24. 704-704

#R=Rinf(1-e^((-alpha/Rinf)S) #where R=recruits; Rinf=carrying capacity of recruits;
# alpha=slope at the origin; e=natural log base

#help estimate starting parameters using nlstools. Make sure to run the formula code, below, first!!

```

```

#preview(SHSFormula,data= SRData, start=list(a=900, b=900, lnc=exp(1)), variable=2)

#Define Parameters
#alpha_start=9 #provide starting parameter estimate: Wenatchee = 7; Methow = 10
#Rinf_start=300 #provide starting parameter estimate: Wenatchee = 575; Methow = 322
#lnc=exp(1)    #natural log base
#lnc

#Smooth Hockey Stick model - uses non linear regression to estimate parameters
#SHSFormula<- as.formula(ln_Recruits~log(b*(1-lnc^((-1*a/b)*Spawners))))
#SHS<-nls(SHSFormula,start=list(a=alpha_start,b=Rinf_start), data=SRData)
#SHS
#overview(SHS)

#####

alpha_start=10
Rinf=322
A=log(Rinf)
lnc=exp(1)

# Smooth Hockey Stick Parameter Estimation Formula -- This is the recommended parameter estimation formula.
#The estimated parameter A must be transformed in order to use the model for prediction
SHSFormula<- as.formula(ln_Recruits~A+log(1-lnc^((-a*Spawners/(lnc^A))))

#help estimate starting parameters using nlstools. Make sure to run the formula code, below, first!!
preview(SHSFormula,data= SRData, start=list(a=alpha_start, A=A, lnc=exp(1)), variable=2)

#Smooth Hockey Stick model - uses non linear regression to estimate parameters
SHS<-nls(SHSFormula,start=list(a=alpha_start,A=A), data=SRData)
SHS
overview(SHS)

```

```

Parameter_A<-exp(1)^coef(SHS)[2]
Parameter_A #transformed from natural log value to real number

##### SHS Quantile Regression
#####

#Quantile Regression - fit the 90th quantile Methow a=5, b=800; Wenatchee a=6, b=2416
taus<-c(0.90)

Qalpha_start=6 #provide starting parameter estimate for quantile regression:
QR_start=2416 #provide starting parameter estimate for quantile regression:
QA<-log(QR_start)

#QSHS<-nlrq(ln_Recruits~log(b*(1-lne^((-1*a/b)*Spawners))),start=list(a=Qalpha_start,b=QR_start), tau=taus, data=SRData)
#summary(QSHS)

QSHS<-nlrq(ln_Recruits~A+log(1-lne^(-a*Spawners/(lne^A))),start=list(a=Qalpha_start,A=QA), tau=taus, data=SRData)
summary(QSHS)

Rinf_Estimate<-exp(1)^coef(QSHS)[2]
Rinf_Estimate #transformed from natural log value to real number

##### Plot
#####

plot(Recruits~Spawners,data=SRData, xlim=c(xmin, xmax), ylim=c(ymin, ymax))
curve(coef(SHS)[2]*(1-lne^((-1*coef(SHS)[1]/coef(SHS)[2])*x)),from=0,to=xmax,col="red",lwd=2,add=TRUE)

curve(coef(SHS)[2]+log(1-lne^(-coef(SHS)[1]*x/(lne^coef(SHS)[2]))),from=0,to=xmax,col="red",lwd=2,add=TRUE)

curve(coef(QSHS)[2]*(1-lne^((-1*coef(QSHS)[1]/coef(QSHS)[2])*x)),from=0,to=xmax,col="purple",lwd=2,add=TRUE)
curve(coef(bh0nls)[1]*x,from=0,to=xmax,col="blue",lwd=1,add=TRUE)

```

```

abline(0,1, col="gray", lwd=1)
legend("topleft",legend=c("density independent","density dependent", "replacement", "95th Quantile"),
      col=c("blue","red","gray", "purple"),lwd=2,cex=0.6)

##### SHS Residuals Analysis
#####

bootSHS<-nlsBoot(SHS, niter=1000)
confint(bootSHS, plot=TRUE)

#Plot Bootstrapped Residuals
plot(bootSHS)
plot(bootSHS, type = "boxplot", ask = FALSE)

plot(nlsResiduals(SHS))
test.nlsResiduals(nlsResiduals(SHS))

SHSResiduals<-nlsResiduals(SHS)
SHSResiduals

plot(SHSResiduals, which=0)
plot(SHSResiduals, which=5)

SHSResiduals<-data.frame(residuals(SHS))
SHSResiduals

#####
#####

```

```
##### ANOVA
```

```
#####
```

```
anova(bh0nls, bh1nls) # test models to see if there is a significant difference among the models
```

```
anova(bh0nls, RSR)
```

```
anova(bh0nls, SHS)
```

```
anova(bh1nls, RSR)
```

```
anova(bh1nls, SHS)
```

```
anova(RSR, SHS)
```

```
##### AIC
```

```
#####
```

```
#####
```

```
##AIC
```

```
## Use aiccmodavg package to calculate AICc for each model
```

```
##Create candidate model list
```

```
Cand.models<-list("Smooth Hockey Stick" = SHS, "Ricker" = RSR, "Beverton Holt" = bh1nls, "Density Independent"=bh0nls)
```

```
## AICc method for class 'AICnls'; second.ord=TRUE means AICc is returned in the results
```

```
aictab(cand.set = Cand.models, modnames = NULL,
```

```
second.ord = TRUE, nobs = NULL, sort = TRUE)
```

```
##Create candidate model list
```

```
Cand.models<-list("Ricker" = RSR, "Beverton Holt" = bh1nls, "Density Independent"=bh0nls)
```

```

## AICc method for class 'AICnls'; second.ord=TRUE means AICc is returned in the results
aictab(cand.set = Cand.models, modnames = NULL,
      second.ord = TRUE, nobs = NULL, sort = TRUE)

##### Plot All Models
#####

plot(Recruits~Spawners,data=SRData, xlim=c(xmin, xmax), ylim=c(ymin, ymax))
curve(coef(SHS)[2]*(1-lne^((-1*coef(SHS)[1]/coef(SHS)[2])*x)),from=0,to=xmax,col="red",lwd=2,add=TRUE) #Smooth
Hockey Stick Model
curve(coef(RSR)[1]*x*lne^(-coef(RSR)[2]*x),from=0,to=xmax,col="blue",lwd=2,add=TRUE) #Ricker Model
curve(coef(bh1nls)[1]*x/(coef(bh1nls)[2]+x),from=0,to=xmax,col="purple",lwd=2,add=TRUE) #Beverton Holt Model
abline(0,1, col="gray", lwd=1) #Replacement Line
legend("topleft",legend=c("Smooth Hockey Stick", "Ricker", "Beverton Holt", "Replacement"),
      col=c("red","blue","purple", "gray"),lwd=2,cex=0.6)

```

```

##### Plot All 95th Quantiles
#####

plot(Recruits~Spawners,data=SRData, xlim=c(xmin, xmax), ylim=c(ymin, ymax))
curve(coef(QSHS)[2]*(1-lne^((-1*coef(QSHS)[1]/coef(QSHS)[2])*x)),from=0,to=xmax,col="red",lwd=2,add=TRUE) #Smooth
Hockey Stick Model
curve(coef(QRSR)[1]*x*lne^(-coef(QRSR)[2]*x),from=0,to=xmax,col="blue",lwd=2,add=TRUE) #Ricker Model
curve(coef(QRBH1)[1]*x/(coef(QRBH1)[2]+x),from=0,to=xmax,col="purple",lwd=2,add=TRUE) #Beverton Holt Model
abline(0,1, col="gray", lwd=1) #Replacement Line
legend("topleft",legend=c("Smooth Hockey Stick", "Ricker", "Beverton Holt", "Replacement"),
      col=c("red","blue","purple", "gray"),lwd=2,cex=0.6)

```

```
#####
##### Plot in GGPlot
#####

#create predicted dataframe for SHS and Density Independent Fit

predSR<-data.frame(S=seq(0,max(SRData$Spawners), by=1))
predSR$BHM<-coef(bh1nls)[1]*predSR$$/(coef(bh1nls)[2]+predSR$$)
predSR$RSR<-coef(RSR)[1]*predSR$$*ln^(-coef(RSR)[2]*predSR$$)
predSR$SHS<-exp(1)^coef(SHS)[2]*(1-ln^((-1*coef(SHS)[1]/exp(1)^coef(SHS)[2])*predSR$$))
predSR$DIM<-coef(bh0nls)[1]*predSR$$
predSR$OneToOne<-predSR$$

predSR$BHM90<-coef(QRBH1)[1]*predSR$$/(coef(QRBH1)[2]+predSR$$)
predSR$RSR90<-coef(QRSR)[1]*predSR$$*ln^(-coef(QRSR)[2]*predSR$$)
#predSR$SHS90<-coef(QSHS)[2]*(1-ln^((-1*coef(QSHS)[1]/coef(QSHS)[2])*predSR$$))
predSR$SHS90<-Rinf_Estimate*(1-ln^((-1*coef(QSHS)[1]/Rinf_Estimate)*predSR$$))

predSR
write.csv(predSR, "C:\\Users\\GregM\\Desktop\\SR_Prediction.csv") #export csv of the predSR dataframe to the desktop

#Add Residuals to SRData
SRData<-cbind(SRData, SHSResiduals)
SRData$pHOS<-(SRData$H_Spawners/SRData$Spawners)
SRData

#Plot Residuals from SR Model SHS verses pHOS
SHSPlot<-ggplot(data=SRData, aes(x=pHOS,y=residuals.SHS.))+geom_point()
```



```
SHSPlot+theme_bw()
```

```
#Plot the Beverton Holt Relationship with the fitted model results and Density Independent Model
```

```
SHSPlot1<-ggplot(data=SRData, aes(x=Spawners,y=Recruits))+geom_point()+  
  geom_line(data=predSR, aes(x=S, y=DIM,colour="Density Independent"),lwd=0.5)+  
  geom_line(data=predSR, aes(x=S, y=OneToOne,colour="Replacement"),lwd=0.5)+  
  geom_line(data=predSR, aes(x=S, y=BHM90,colour="90th Quantile"),lwd=1.5)+  
  geom_line(data=predSR, aes(x=S, y=BHM,colour="Beverton Holt"),lwd=1.5)+  
  #geom_line(data=predSR, aes(x=S, y=RSR,colour="Ricker"),lwd=1.5)+  
  #geom_line(data=predSR, aes(x=S, y=SHS,colour="Smooth Hockey Stick"),lwd=1.5)+  
  expand_limits(x=c(0,xmax))+  
  expand_limits(y=c(0,ymax))+  
  scale_colour_manual("",  
    breaks=c("Beverton Holt", "90th Quantile", "Density Independent", "Replacement"),  
    values=c("Beverton Holt"="goldenrod3", "90th Quantile"="purple", "Density Independent"="gray",  
"Replacement"="paleturquoise4"))+  
  xlab("Spawners")+  
  ylab("Recruits")+  
  labs(title="Beverton Holt")  
BHPPlot<-SHSPlot1+theme_bw()+theme(  
  panel.grid.major = element_blank(),  
  panel.grid.minor = element_blank(),  
  panel.background = element_blank(),  
  plot.title=element_text(hjust=0.5, size=14),  
  axis.text=element_text(size=12),  
  axis.title=element_text(size=14),  
  legend.text=element_text(size=12),  
  aspect.ratio=1)
```

BHPlot

#Plot the Ricker Relationship with the fitted model results and Density Independent Model

```
SHSPlot2<-ggplot(data=SRData, aes(x=Spawners,y=Recruits))+geom_point()+
  geom_line(data=predSR, aes(x=S, y=DIM,colour="Density Independent"),lwd=0.5)+
  geom_line(data=predSR, aes(x=S, y=OneToOne,colour="Replacement"),lwd=0.5)+
  #geom_line(data=predSR, aes(x=S, y=BHM,colour="Beverton Holt"),lwd=1.5)+
  geom_line(data=predSR, aes(x=S, y=RSR90,colour="90th Quantile"),lwd=1.5)+
  geom_line(data=predSR, aes(x=S, y=RSR,colour="Ricker"),lwd=1.5)+
  #geom_line(data=predSR, aes(x=S, y=SHS,colour="Smooth Hockey Stick"),lwd=1.5)+
  expand_limits(x=c(0,xmax))+
  expand_limits(y=c(0,ymax))+
  scale_colour_manual("",
    breaks=c("Ricker", "90th Quantile", "Density Independent", "Replacement"),
    values=c("Ricker"="steelblue3", "90th Quantile"="purple","Density Independent"="gray",
"Replacement"="paleturquoise4"))+
  xlab("Spawners")+
  ylab("Recruits")+
  labs(title="Ricker")
RickerPlot<-SHSPlot2+theme_bw()+theme(
  panel.grid.major = element_blank(),
  panel.grid.minor = element_blank(),
  panel.background = element_blank(),
  plot.title=element_text(hjust=0.5, size=14),
  axis.text=element_text(size=12),
  axis.title=element_text(size=14),
  legend.text=element_text(size=12),
  aspect.ratio=1)
```

RickerPlot

```
#Plot the Smooth Hockey Stick Relationship with the fitted model results and Density Independent Model
```

```
SHSPlot3<-ggplot(data=SRData, aes(x=Spawners,y=Recruits))+geom_point()+  
  geom_line(data=predSR, aes(x=S, y=DIM,colour="Density Independent"),lwd=0.5)+  
  geom_line(data=predSR, aes(x=S, y=OneToOne,colour="Replacement"),lwd=0.5)+  
  #geom_line(data=predSR, aes(x=S, y=BHM,colour="Beverton Holt"),lwd=1.5)+  
  #geom_line(data=predSR, aes(x=S, y=RSR,colour="Ricker"),lwd=1.5)+  
  geom_line(data=predSR, aes(x=S, y=SHS90,colour="90th Quantile"),lwd=1.5)+  
  geom_line(data=predSR, aes(x=S, y=SHS,colour="Smooth Hockey Stick"),lwd=1.5)+  
  expand_limits(x=c(0,xmax))+  
  expand_limits(y=c(0,ymax))+  
  scale_colour_manual("",  
    breaks=c("Smooth Hockey Stick", "90th Quantile", "Density Independent", "Replacement"),  
    values=c("Smooth Hockey Stick"="firebrick3", "90th Quantile"="purple", "Density Independent"="gray",  
"Replacement"="paleturquoise4"))+  
  xlab("Spawners")+  
  ylab("Recruits")+  
  labs(title="Smooth Hockey Stick")  
SmoothHockeyPlot<-SHSPlot3+theme_bw()+theme(  
  panel.grid.major = element_blank(),  
  panel.grid.minor = element_blank(),  
  panel.background = element_blank(),  
  plot.title=element_text(hjust=0.5, size=14),  
  axis.text=element_text(size=12),  
  axis.title=element_text(size=14),  
  legend.text=element_text(size=12),  
  aspect.ratio=1)  
SmoothHockeyPlot
```

```
#Plot all the SR Models on one graph
```

```

SHSPlot4<-ggplot(data=SRData, aes(x=Spawners,y=Recruits))+geom_point()+
  geom_line(data=predSR, aes(x=S, y=DIM,colour="Density Independent"),lwd=0.5)+
  geom_line(data=predSR, aes(x=S, y=OneToOne,colour="Replacement"),lwd=0.5)+
  geom_line(data=predSR, aes(x=S, y=BHM,colour="Beverton Holt"),lwd=1.5)+
  geom_line(data=predSR, aes(x=S, y=RSR,colour="Ricker"),lwd=1.5)+
  geom_line(data=predSR, aes(x=S, y=SHS,colour="Smooth Hockey Stick"),lwd=1.5)+
  expand_limits(x=c(0,xmax))+
  expand_limits(y=c(0,ymax))+
  scale_colour_manual("",
    breaks=c("Smooth Hockey Stick", "Ricker", "Beverton Holt", "Density Independent", "Replacement"),
    values=c("Smooth Hockey Stick"="firebrick3", "Ricker"="steelblue3", "Beverton Holt"="goldenrod3",
"Density Independent"="gray", "Replacement"="paleturquoise4"))+
  xlab("Spawners")+
  ylab("Recruits")+
  labs(title="All Models")
AllModelsPlot<-SHSPlot4+theme_bw()+theme(
  panel.grid.major = element_blank(),
  panel.grid.minor = element_blank(),
  panel.background = element_blank(),
  plot.title=element_text(hjust=0.5, size=14),
  axis.text=element_text(size=12),
  axis.title=element_text(size=14),
  legend.text=element_text(size=12),
  aspect.ratio=1)
AllModelsPlot
#####Arrange SR Graph on one page#####
grid.arrange(BHPlot, SmoothHockeyPlot, RickerPlot, AllModelsPlot, nrow=2)

#Plot all the Quantile SR Models on one graph

```

```

SHSPlot5<-ggplot(data=SRData, aes(x=Spawners,y=Recruits))+geom_point()+
  geom_line(data=predSR, aes(x=S, y=DIM,colour="Density Independent"),lwd=0.5)+
  geom_line(data=predSR, aes(x=S, y=OneToOne,colour="Replacement"),lwd=0.5)+
  geom_line(data=predSR, aes(x=S, y=BHM90,colour="Beverton Holt"),lwd=1.5)+
  geom_line(data=predSR, aes(x=S, y=RSR90,colour="Ricker"),lwd=1.5)+
  geom_line(data=predSR, aes(x=S, y=SHS90,colour="Smooth Hockey Stick"),lwd=1.5)+
  expand_limits(x=c(0,xmax))+
  expand_limits(y=c(0,ymax))+
  scale_colour_manual("",
    breaks=c("Smooth Hockey Stick", "Ricker", "Beverton Holt", "Density Independent", "Replacement"),
    values=c("Smooth Hockey Stick"="firebrick3", "Ricker"="steelblue3", "Beverton Holt"="goldenrod3",
"Density Independent"="gray", "Replacement"="paleturquoise4"))+
  xlab("Spawners")+
  ylab("Recruits")
Q90Plot<-SHSPlot5+theme_bw()+theme(
  panel.grid.major = element_blank(),
  panel.grid.minor = element_blank(),
  #plot.title=element_text(hjust=0.5, size=14),
  axis.text=element_text(size=12),
  axis.title=element_text(size=14),
  legend.text=element_text(size=12),
  panel.background = element_blank(),
  aspect.ratio=1)

```

Q90Plot

#Plot the Annual Stock Recruit Data (Spawners by Year)

#Add a Recruits/Spawner Field to SRData

```
SRData$RecruitsPerSpawner<-SRData$Recruits/SRData$Spawners
```

SRData

```

#Make SRData long form at to graph hatchery and wild spawners on the same graph
SRData_Long<-SRData%>%pivot_longer(H_Spawners:W_Spawners, names_to = "SpawnerType", values_to="Count")
SRData_Long

#Graph of Hatchery and Wild Spawners by Brood Year
SHSPlong<-ggplot(data=SRData_Long, aes(x=BroodYear,y=Count, colour=SpawnerType, fill=SpawnerType))+
  geom_point()+
  geom_line()+
  #geom_smooth(method="lm", formula=y~x)+
  stat_smooth(method = "lm", formula=y~x, se=TRUE, alpha=0.2)+
  scale_x_continuous(breaks = round(seq(min(SRData_Long$BroodYear), max(SRData_Long$BroodYear), by = 1),1)) +
  scale_y_continuous(breaks = round(seq(min(0), max(SRData$Spawners), by = 1000),1)) +
  xlab("Brood Year")+
  ylab("Spawners")
HWbyBY<-SHSPlong+theme_bw()+theme(legend.position=c(0.2,0.8))+
  theme(axis.text.x=element_text(angle = 45, vjust = 0.5),
  panel.grid.major = element_blank(),
  panel.grid.minor = element_blank(),
  panel.background = element_blank())
HWbyBY

#Graph of Total Spawners by Brood Year
SHSPlot<-ggplot(data=SRData, aes(x=BroodYear,y=Spawners))+geom_point()+ geom_line()+ geom_smooth(method="lm",
formula=y~x)+
  scale_x_continuous(breaks = round(seq(min(SRData$BroodYear), max(SRData$BroodYear), by = 1),1)) +
  scale_y_continuous(breaks = round(seq(min(0), max(SRData$Spawners), by = 1000),1)) +
  xlab("Brood Year")+
  ylab("Spawners")

```

```

TSbyBY<-SHSPlot+theme_bw()+theme(axis.text.x=element_text(angle = 45, vjust = 0.5),
    panel.grid.major = element_blank(),
    panel.grid.minor = element_blank(),
    panel.background = element_blank())

TSbyBY

#Graph of Recruits by Brood Year
SHSPlot<-ggplot(data=SRData, aes(x=BroodYear,y=Recruits))+geom_point()+ geom_line()+ geom_smooth(method="lm",
formula=y~x)+
    scale_x_continuous(breaks = round(seq(min(SRData$BroodYear), max(SRData$BroodYear), by = 1),1)) +
    scale_y_continuous(breaks = round(seq(min(0), max(SRData$Recruits), by = 200),1)) +
    xlab("Brood Year")+
    ylab("Recruits")

RbyBY<-SHSPlot+theme_bw()+theme(axis.text.x=element_text(angle = 45, vjust = 0.5),
    panel.grid.major = element_blank(),
    panel.grid.minor = element_blank(),
    panel.background = element_blank())

RbyBY

#Graph of Recruits per Spawner by Brood Year
SHSPlot<-ggplot(data=SRData, aes(x=BroodYear,y=RecruitsPerSpawner))+geom_point()+ geom_line()+
geom_smooth(method="lm", formula=y~x)+
    scale_x_continuous(breaks = round(seq(min(SRData$BroodYear), max(SRData$BroodYear), by = 1),1)) +
    scale_y_continuous(breaks = round(seq(min(0), max(SRData$RecruitsPerSpawner), by = 0.5),1)) +
    xlab("Brood Year")+
    ylab("Recruits per Spawner")+
    geom_hline(yintercept = 1, color="red", linetype = "dashed")

RpSbyBY<-SHSPlot+theme_bw()+theme(axis.text.x=element_text(angle = 45, vjust = 0.5),
    panel.grid.major = element_blank(),
    panel.grid.minor = element_blank(),
    panel.background = element_blank(),

```

```

        legend.position="none")

RpSbyBY

#Arrange Graphs of variables vs Brood Year on one page
grid.arrange(TSbyBY, HWbyBY, RbyBY, RpSbyBY, nrow=2)

#NRR Graphs

#Graph of NRR by Brood Year
NRRPlot<-ggplot(data=SRData, aes(x=BroodYear,y=NRR))+geom_point()+ geom_line()+ geom_smooth(method="lm",
formula=y~x)+
  scale_x_continuous(breaks = round(seq(min(SRData$BroodYear), max(SRData$BroodYear), by = 1),1)) +
  scale_y_continuous(breaks = round(seq(min(0), max(SRData$NRR), by = 0.5),1)) +
  xlab("Brood Year")+
  ylab("NRR")+
  geom_hline(yintercept = 1, color="red", linetype = "dashed")
NRRGraph<-NRRPlot+theme_bw()+theme(axis.text.x=element_text(angle = 45, vjust = 0.5),
  panel.grid.major = element_blank(),
  panel.grid.minor = element_blank(),
  panel.background = element_blank(),
  legend.position="none")

NRRGraph

##### R Citation #####
citation()
citation("openxlsx")
citation("ggplot2")
citation("nlstools")
citation("AICcmodavg")
citation("FSA")

```


`citation("quantreg")`

`citation("dplyr")`

`citation("pastecs")`

`citation("knitr")`

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:

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

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:

$$R = \frac{\alpha S}{\beta + S} \quad (2)$$

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:

$$R = \alpha S e^{-\beta S} \quad (3)$$

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:

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

or equivalently

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

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:

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

or equivalently

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

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:

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

or equivalently

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

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 $\Delta AICc \leq 2$ 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

$$r_i = R_i - \hat{R}_i, \quad (10)$$

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

$$r_i = \beta_0 + \beta_1 \text{pHOS}_i + \epsilon_i, \quad (11)$$

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 H02.2.1.2 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:

$$\frac{R_i}{S_i} = \beta_0 + \beta_1 \text{pHOS}_i + \epsilon_i, \quad (12)$$

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).

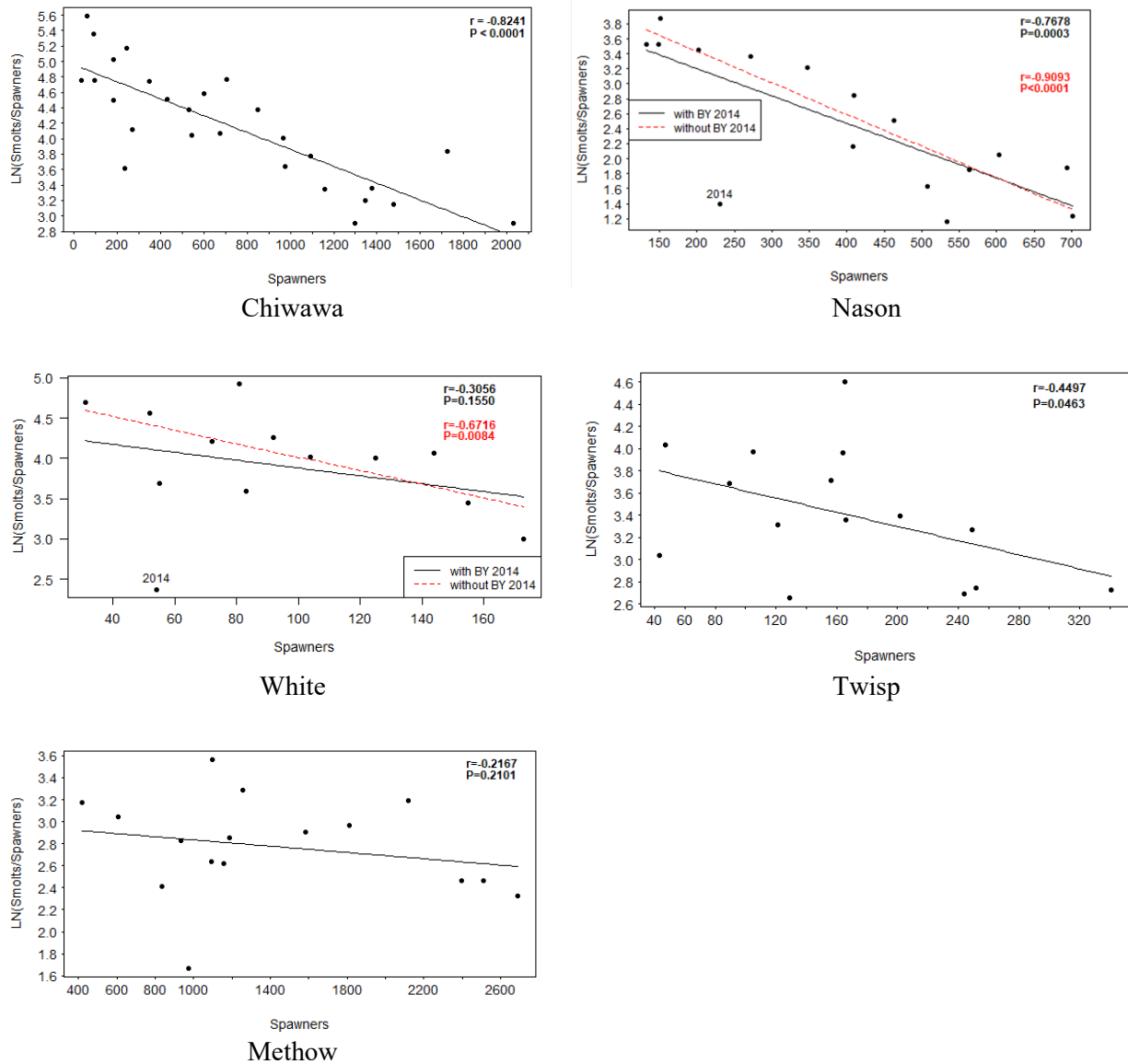


Figure 1. Smolts per spawner (log scale) versus spawner abundance for each population, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. Plots with and without the 2014 brood year (possible outlier) are shown for Nason and White.

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.

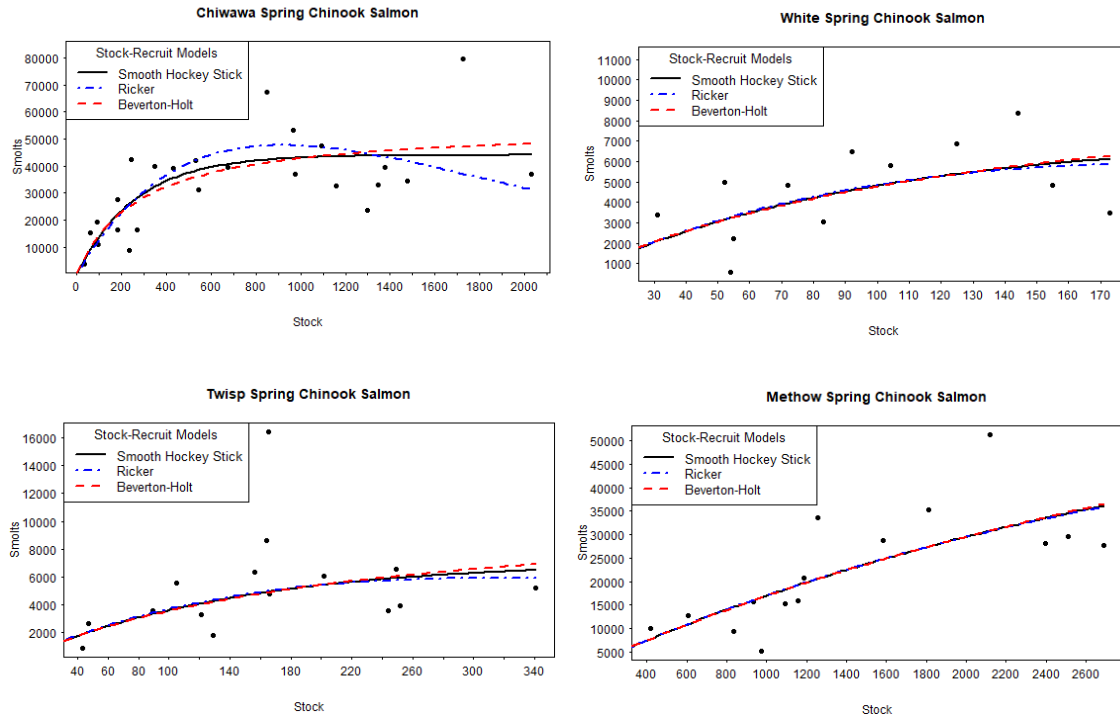


Figure 2. Stock-recruitment models fit to smolt and spawner data for Spring Chinook salmon populations (plot for White population includes 2014 brood year).

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). $\Delta AICc$ 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*	$\Delta AICc$	Parameter ^a	Parameter Estimates	95% CI	Correlation
Chiwawa	Smooth Hockey Stick	0.00	α	168	118.2 – 248.7	$\alpha, R_{\infty}: -0.39$
			R_{∞}	44,090	35,095 – 56,732	
	Beverton-Holt	0.75	α	54,825	40,678 – 77,093	$\alpha, \beta: 0.87$
			β	278	134.5 – 559.0	
	Ricker	0.71	α	141	109.2 – 184.3	$\alpha, \beta: 0.80$
			β	0.0011	0.0008 – 0.0014	

Population	Model*	ΔAIC_c	Parameter ^a	Parameter Estimates	95% CI	Correlation	
Nason	Smooth Hockey Stick	NA	K	47,760	40,825 – 56,520	α , R_∞ : NA	
			α	NA	NA		
			R_∞	NA	NA		
	Beverton-Holt	NA	α	NA	NA	α , β : NA	
			β	NA	NA		
	Ricker	NA	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	NA	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	NA	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	NA	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 $R_\infty = 0.6241$.

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

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

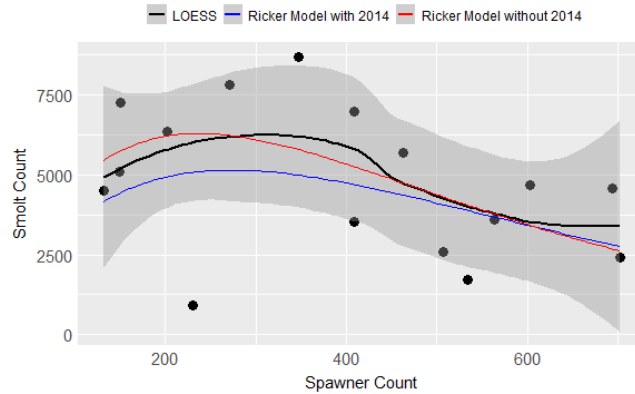


Figure 3. Stock and smolt data with fitted LOESS curve and Ricker Model (with and without data from 2014) for Nason Creek Spring Chinook Salmon, 2002–2017.

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 , $P\geq 0.8533$ 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.

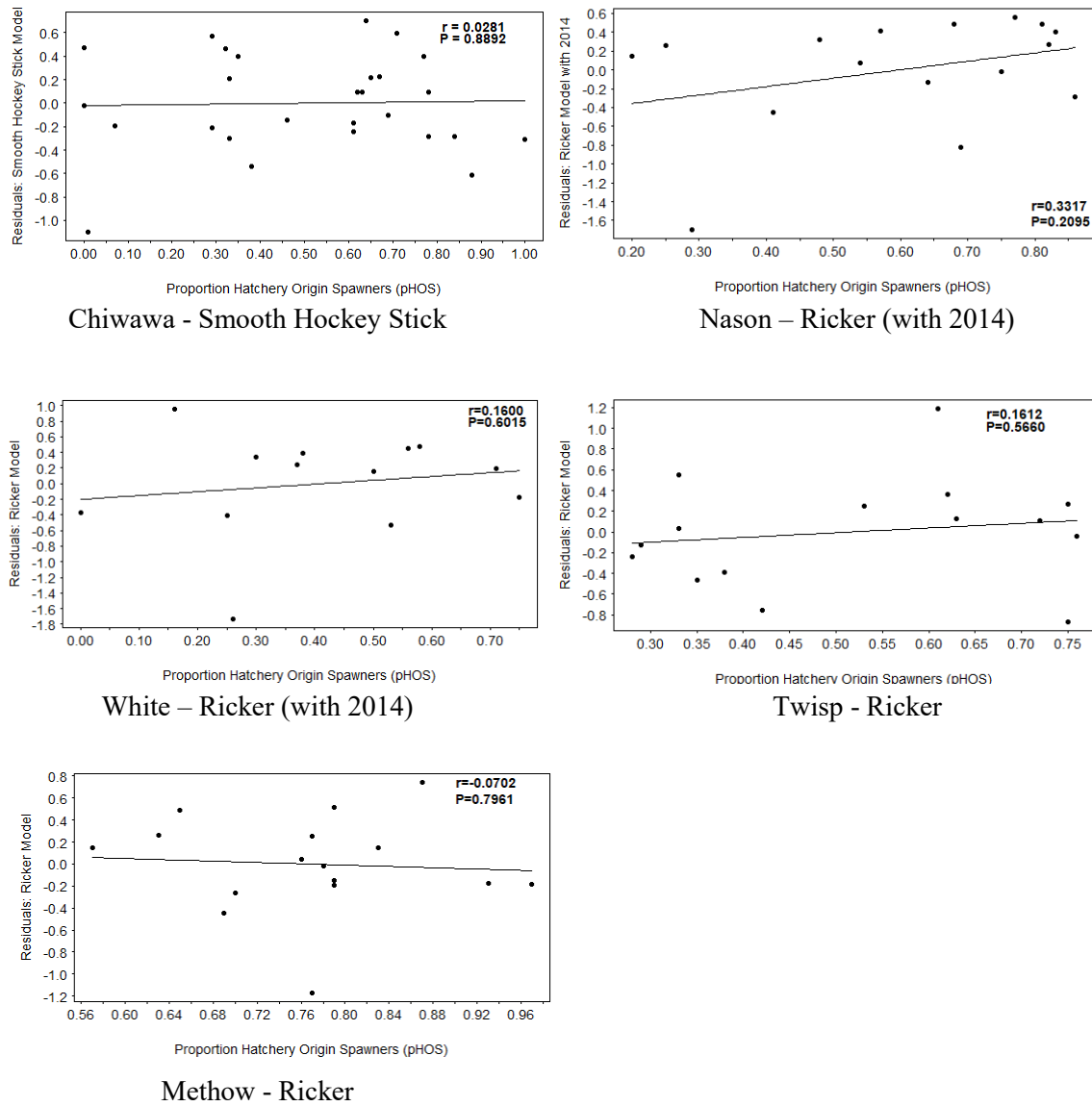


Figure 4. Proportion Hatchery Origin Spawners versus Residuals from stock recruit model. P-value from two-sided t-test and Pearson correlation coefficient (r) are provided in the figure. The stock-recruitment model with the lowest AICc value for each population was chosen for this figure. Plots with 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 ($\Delta AICc = 5.81$ compared to Ricker model) and examination of model residuals (not shown). The fitted Beverton-Holt model for smolts per redd was (Table 4):

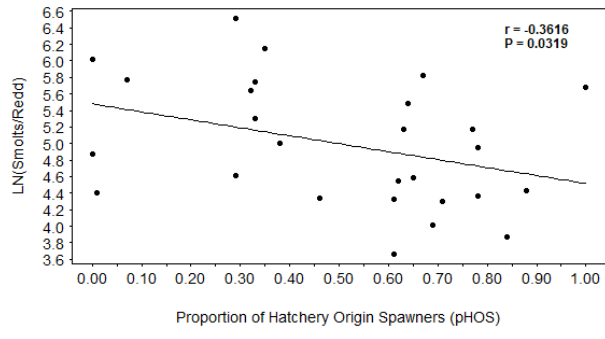
$$\ln(R/S) = \ln(55,479) - 0.0343P_{HOS} - \ln(117 + S).$$

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.

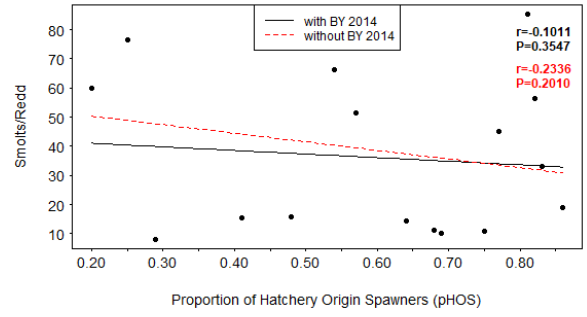
There was no evidence of a negative linear association between smolts per redd and the proportion of hatchery spawners (pHOS) in the other Spring Chinook salmon populations (Figure 5). There was evidence of post-spawning density dependence in Nason and Twisp (Figure 6) and of a linear association of 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.

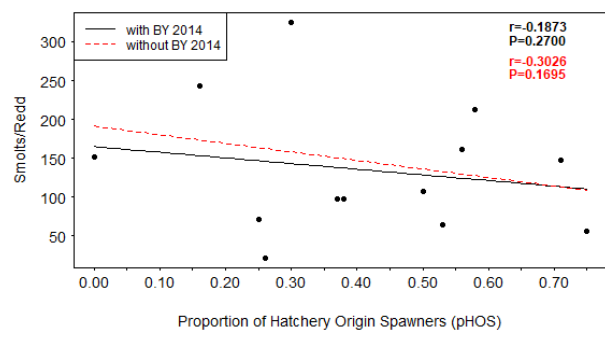
The analysis of the relationship of smolts per redd to pHOS suffered from the same limitations as the analysis of smolts versus pHOS (hypothesis H02.2.1.1). Sample sizes were small for all populations except the Chiwawa, and there was potentially large measurement error in the data for all populations. 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.



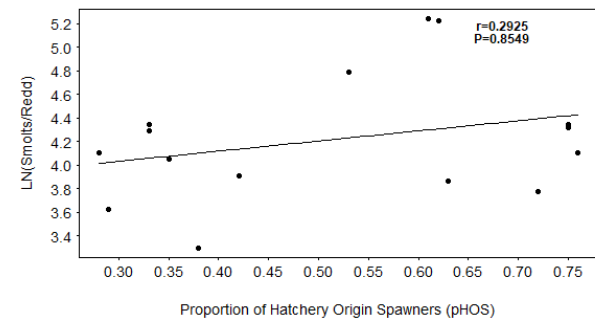
Chiwawa



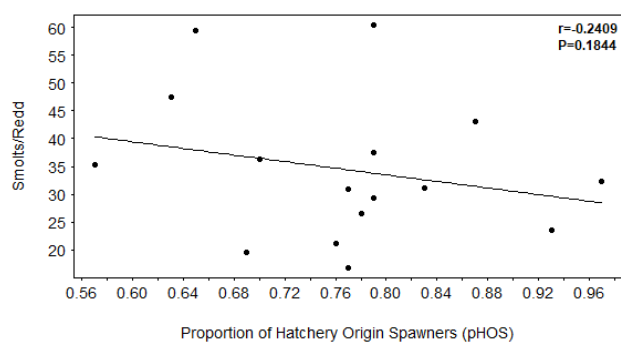
Nason



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.

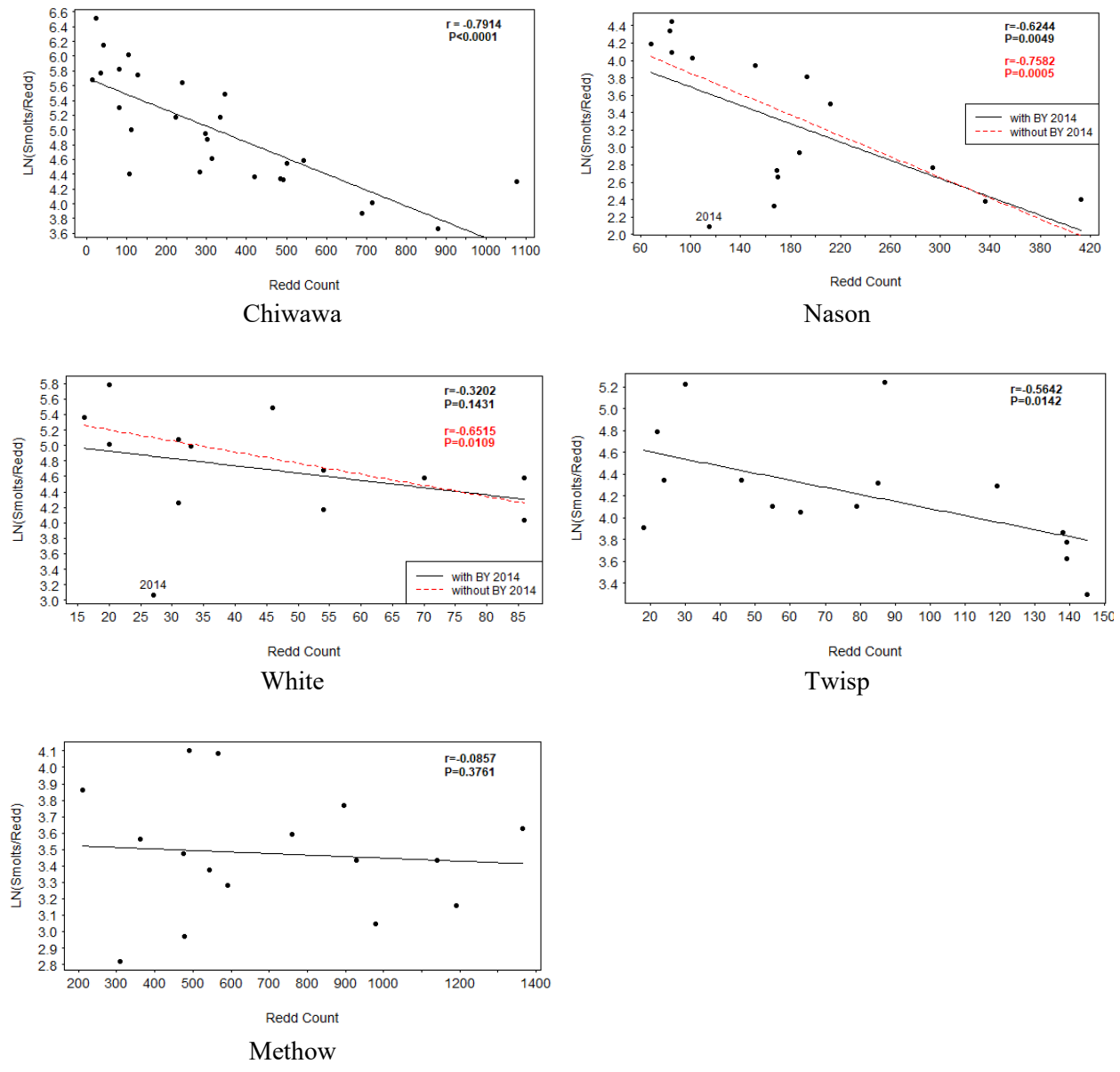


Figure 6. Smolts per redd (log scale) versus redd count for each population, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. Negative slope indicates post-spawning density dependence. Plots with and without the 2014 brood year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

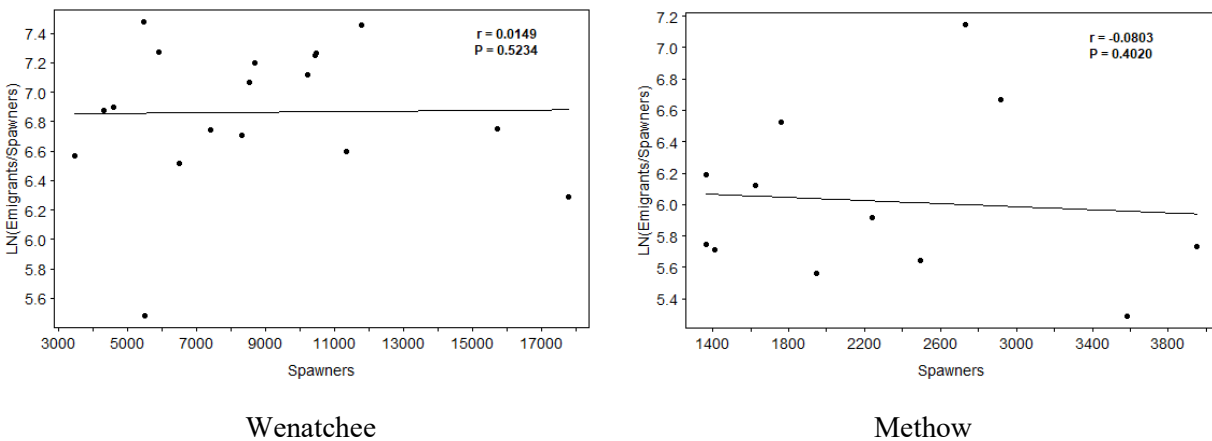


Figure 7. Emigrants per spawner (log scale) versus spawner abundance for Wenatchee and Methow Rivers Summer Chinook Salmon, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope.

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 ($\Delta AICc \leq 0.0072$); pHOS was not associated with the residuals from any of the models ($P \geq 0.7155$). 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 ($\Delta AICc \leq 0.1126$); model residuals were again not significantly associated with pHOS levels ($P \geq 0.6430$), and the likelihood ratio test of the pHOS was also not significant ($P \geq 0.6113$). 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 ($\Delta AICc \leq 0.02$), 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 ($P \geq 0.9838$). 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.

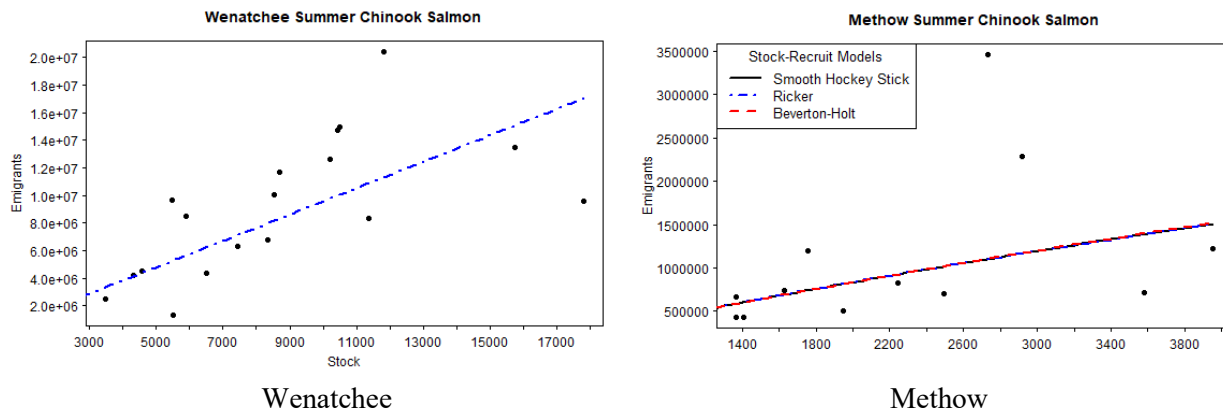


Figure 8. Stock-recruitment models fit to emigrant and spawner data for the Wenatchee and Methow River Summer Chinook Salmon. The Ricker stock-recruitment model is shown for the Wenatchee population.

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). $\Delta AICc$ 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*	$\Delta AICc$	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		0.00	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	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 $K=(\alpha/\beta)e^{-l}$ for the Ricker model.

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

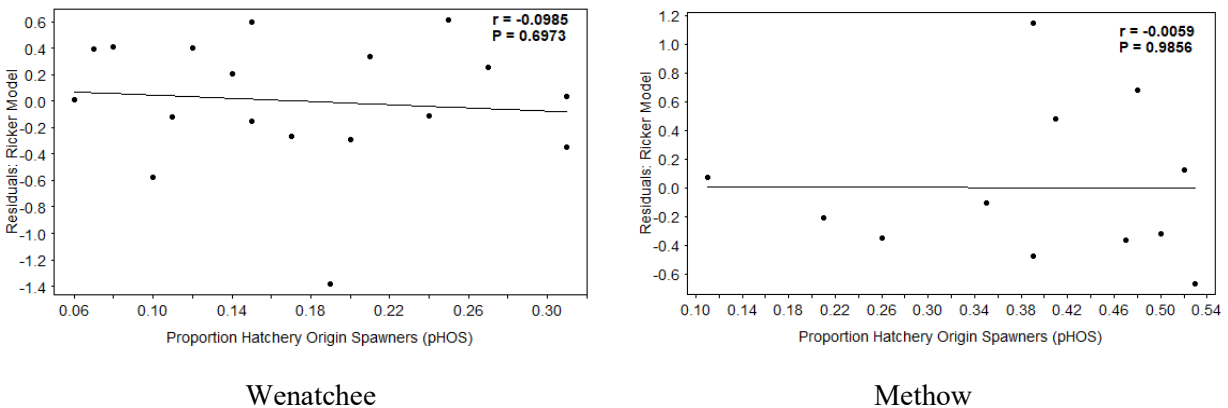


Figure 1. Residuals from Ricker Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using emigrant and spawner data from Wenatchee and Methow Rivers Summer 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 ($P \geq 0.3836$; 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 ($P \geq 0.2944$, 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 ($\Delta AICc \leq 0.10$) 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.

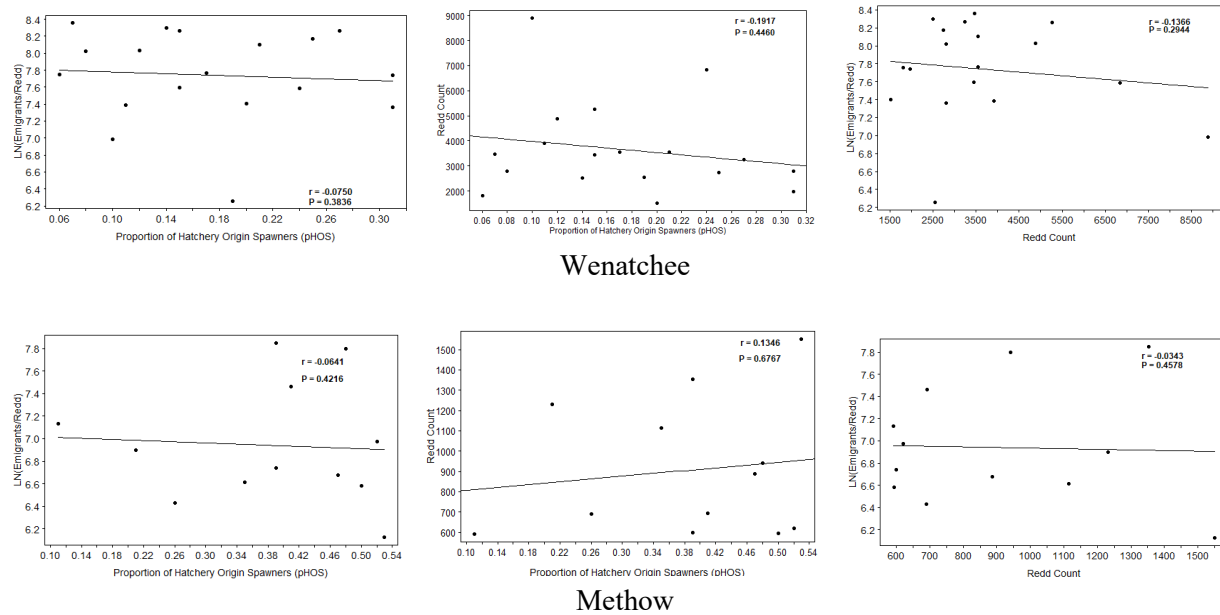


Figure 10. Emigrants per redd (log scale) versus proportion of hatchery origin spawners (pHOS) (left plots), redd count versus proportion of hatchery origin spawners (pHOS) (middle plots), and emigrants per redd versus redd count (right plots) for Wenatchee and Methow River Summer Chinook Salmon, with 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). $\Delta AICc$ represents change in AICc compared to model with minimum AICc for each population.

Population	Model	$\Delta AICc$	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	$\ln(\alpha)$	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	$\ln(\alpha)$	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.

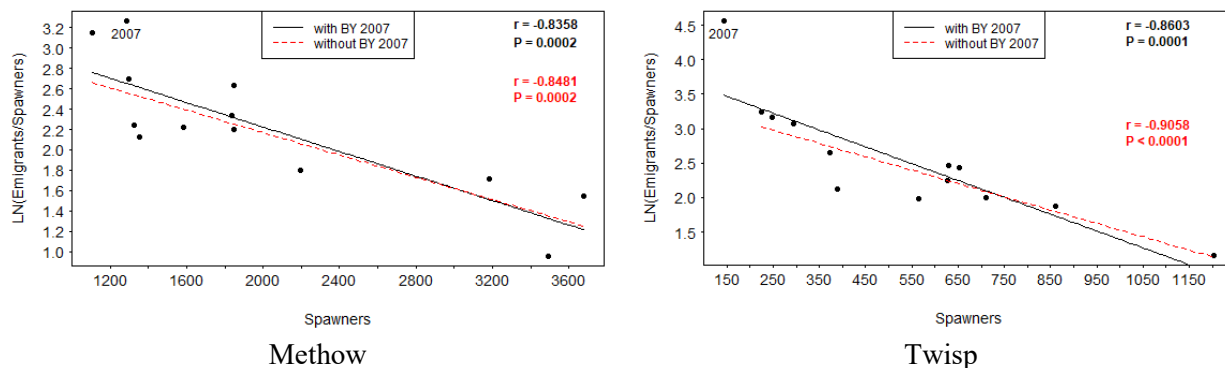


Figure 11. Emigrants per spawner (log scale) versus spawner abundance for Methow and Twisp Rivers Summer Steelhead, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope.

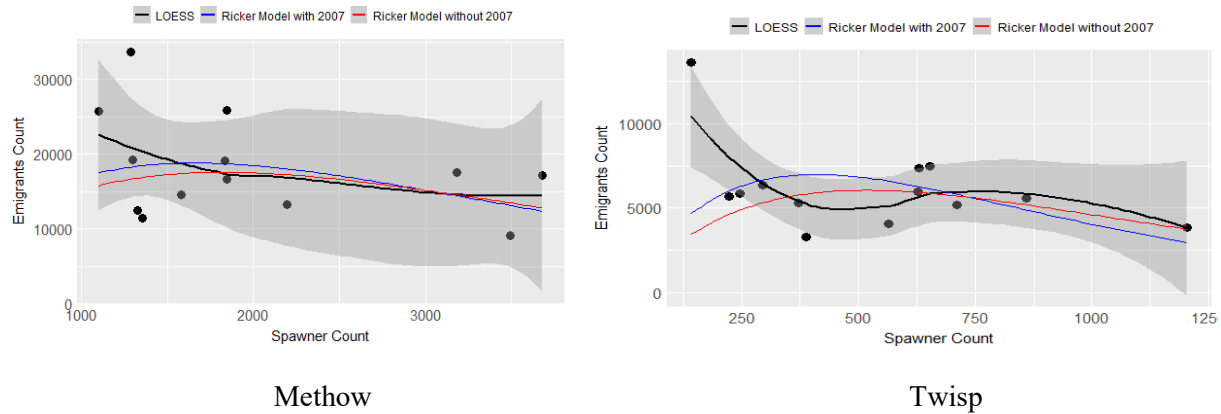


Figure 12. Stock and emigrant data with fitted LOESS curve and Ricker Model for Methow and Twisp Rivers Summer Steelhead.

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). $\Delta AICc$ 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*	$\Delta AICc$	Parameter ^a	Parameter		Correlation
				Estimates	95% CI	
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.

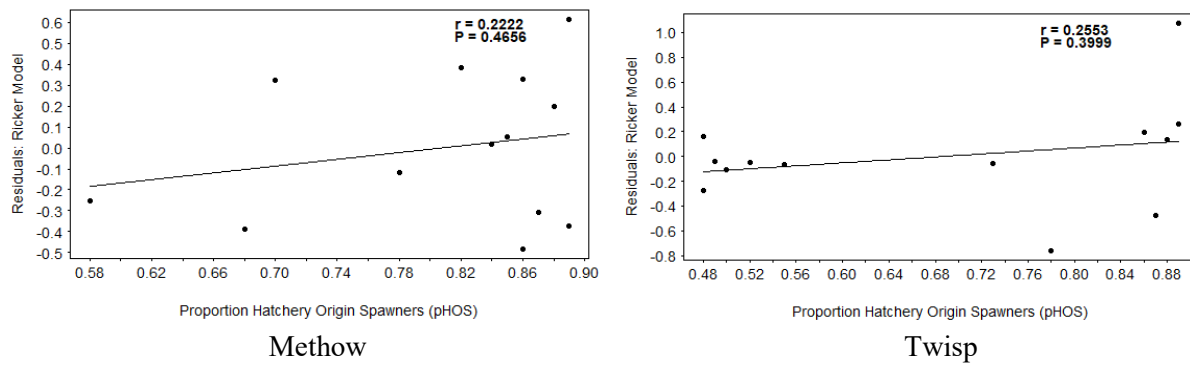


Figure 13. Residuals from the Ricker Model versus proportion of hatchery-origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using emigrant and spawner data from Methow and Twisp rivers Summer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

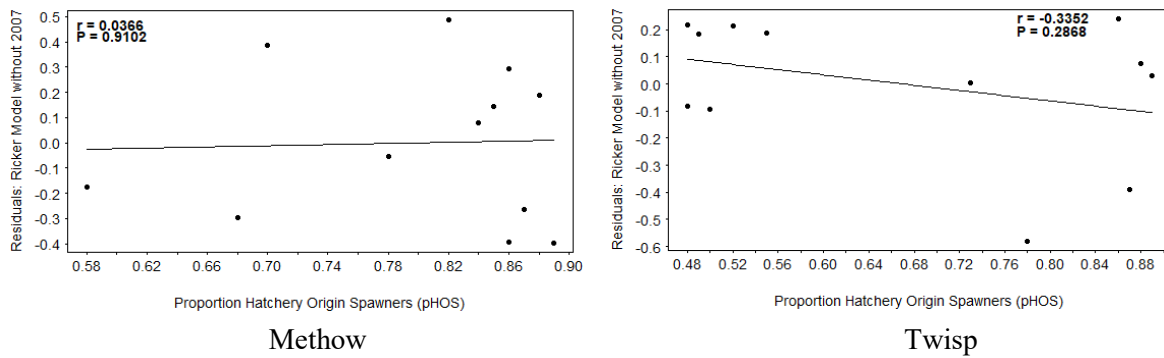


Figure 2. Residuals from the Ricker Model versus proportion of hatchery-origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using emigrant and spawner data from Methow and Twisp rivers Summer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

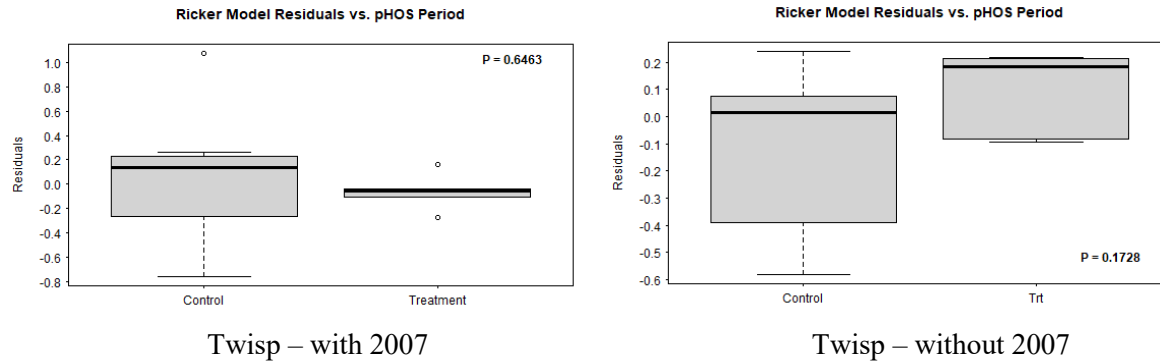


Figure 15. Distribution of residuals from the Ricker Model categorized by pHOS management period: Control = pre-2010, when pHOS levels were not restricted, and Treatment = 2010–2015, when pHOS levels were targeted at 0.5. Data used were emigrant and spawner counts from Twisp River Summer Steelhead, 2003–2015. 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≤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.

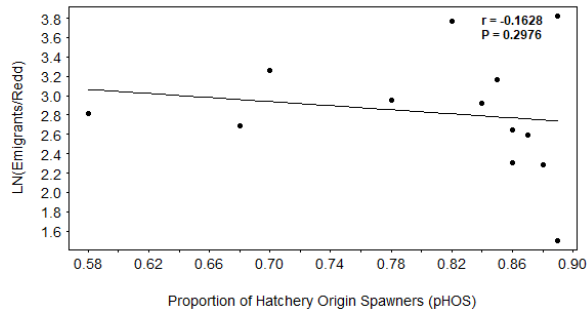
For the Twisp population, the residuals from the Ricker model agreed poorly with the model assumption of lognormal errors. The fitted Ricker model for Twisp River emigrants per redd was (Table 8):

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

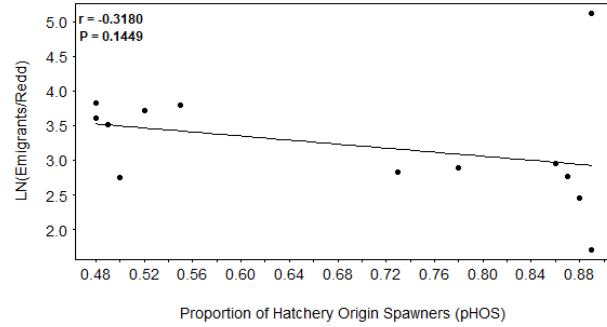
with a 95% bootstrap confidence interval of (-2.3366, 2.1443) for the effect of pHOS. Because the confidence interval for the effect of pHOS included both positive and negative values, we concluded that there was no evidence of a negative association between pHOS and emigrants per redd for Summer Steelhead 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.

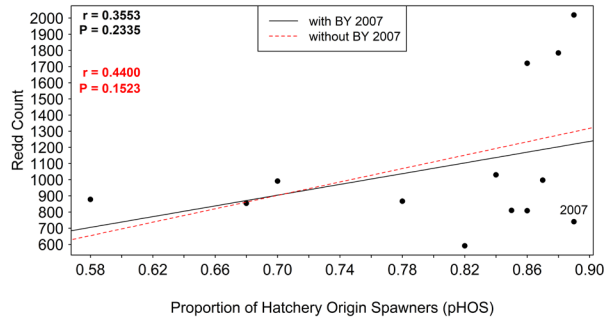


Methow

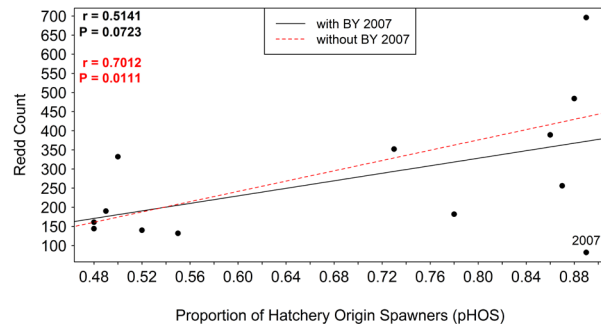


Twisp

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.

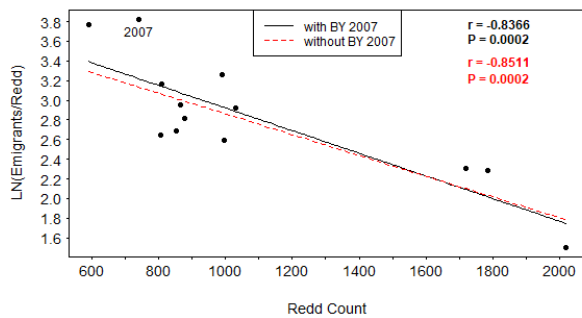


Methow

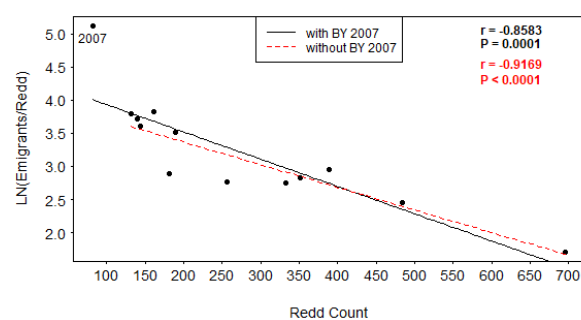


Twisp

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). Δ AICc 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*	Δ AICc	Parameter	Parameter Estimates	95% CI
Methow	Beverton-Holt	NA	α	NA	NA
			β	NA	NA
			β_2	NA	NA
	Ricker (with 2007)	NA	$\ln(\alpha)$	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	$\ln(\alpha)$	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	$\ln(\alpha)$	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	$\ln(\alpha)$	4.5239	3.8033 – 5.1740
			β	0.0027	0.0007 – 0.0049
			β_2	1.0323	-2.3915 – 1.0898

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

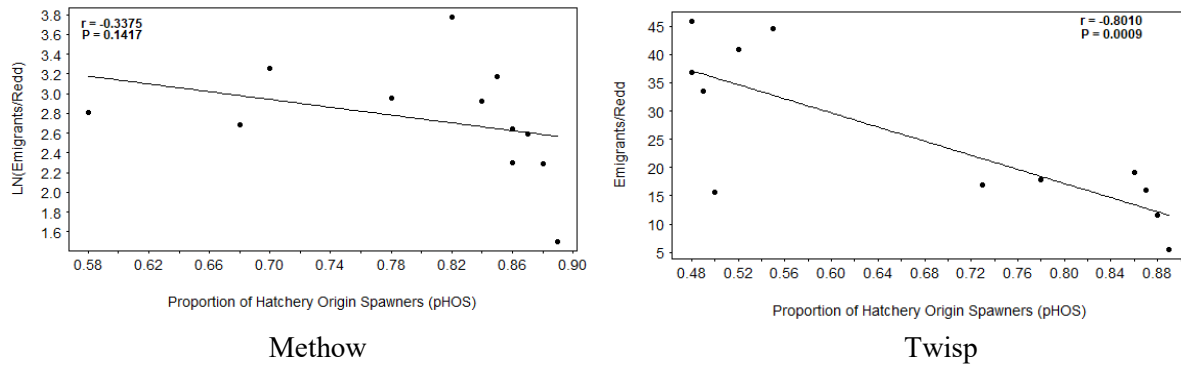
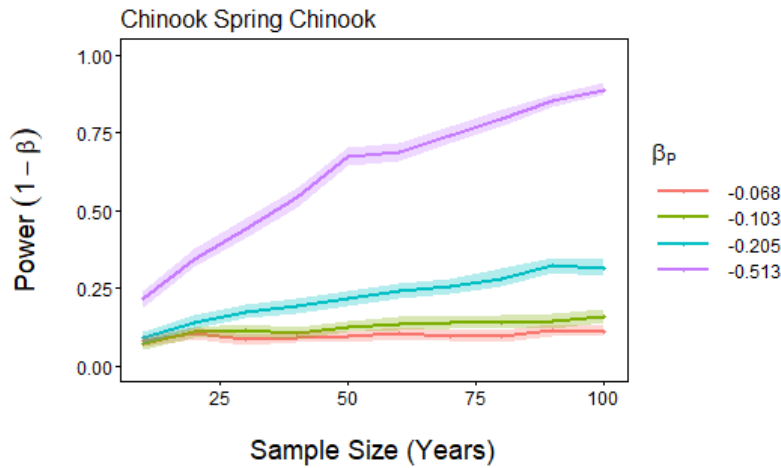


Figure 19. Emigrants per redd versus proportion of hatchery origin spawners (pHOS) for Methow and Twisp rivers Summer Steelhead, 2003–2015, omitting brood year 2007, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope.

Power Analysis

Simulated statistical power to detect a negative effect of pHOS was consistently ≤ 0.32 for all sample sizes considered ($N \leq 100$ 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 20). 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

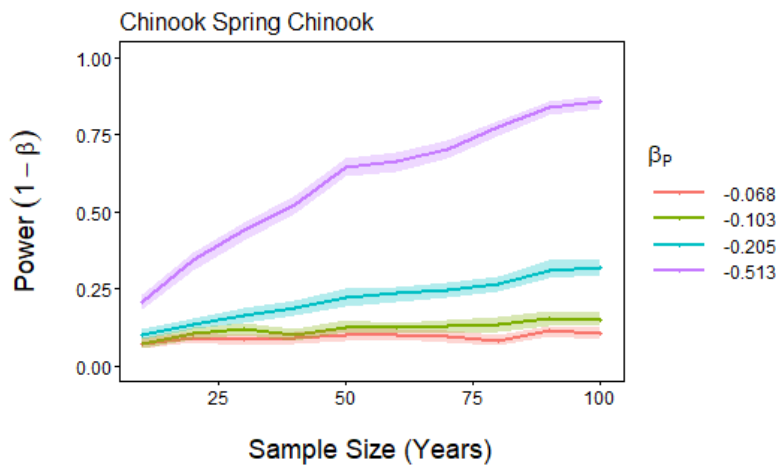


Figure 20. Statistical power of detecting a negative effect of pHOS for various levels of pHOS effect size β_P with (i) and without (ii) measurement error in stock and recruitment data. Power based on 1,000 simulations of stock (spawners) and juvenile recruitment data using Ricker stock-recruitment model fit to data from Chiwawa spring Chinook Salmon, 1991-2017: $a = 138$, $b = 0.0011$, $\sigma = 0.4386$ (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 alternative 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.

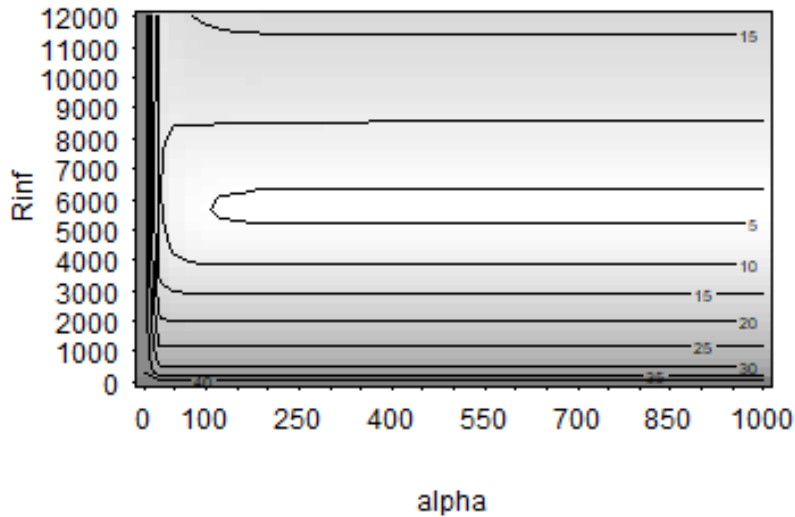


Figure 21. Negative log-likelihood surface and contour curves for the Smooth Hockey Stick model of emigrants and spawner counts. Lighter regions indicate higher likelihood values (lower negative log-likelihood values). The estimated parameter values occur where the negative log-likelihood is minimized.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

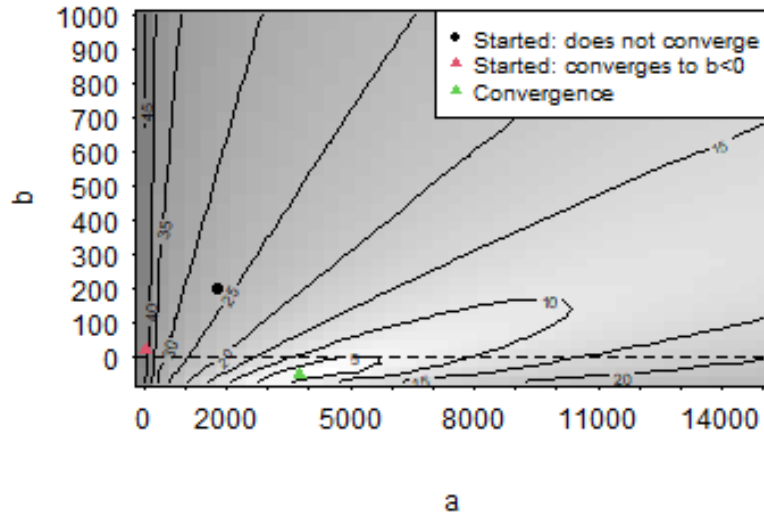


Figure 22. Negative log-likelihood surface and contour curves for Beverton-Holt model of emigrants, redd counts, and pHOS, using $\beta_2 = -0.1160$. Lighter regions indicate higher likelihood values (lower negative log-likelihood values). The estimated parameter values occur where the negative log-likelihood 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.

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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

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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 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 levels as spawners increase:

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

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:

$$R = \frac{\alpha S}{\beta + S} \quad (2)$$

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:

$$R = \alpha S e^{-\beta S} \quad (3)$$

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:

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

or equivalently

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

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:

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

or equivalently

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

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:

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

or equivalently

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

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 $\Delta AICc \leq 2$ 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

$$r_i = R_i - \hat{R}_i, \quad (10)$$

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

$$r_i = \beta_0 + \beta_1 \text{pHOS}_i + \epsilon_i, \quad (11)$$

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 H02.2.1.2

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:

$$\frac{R_i}{S_i} = \beta_0 + \beta_1 \text{pHOS}_i + \epsilon_i, \quad (12)$$

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).

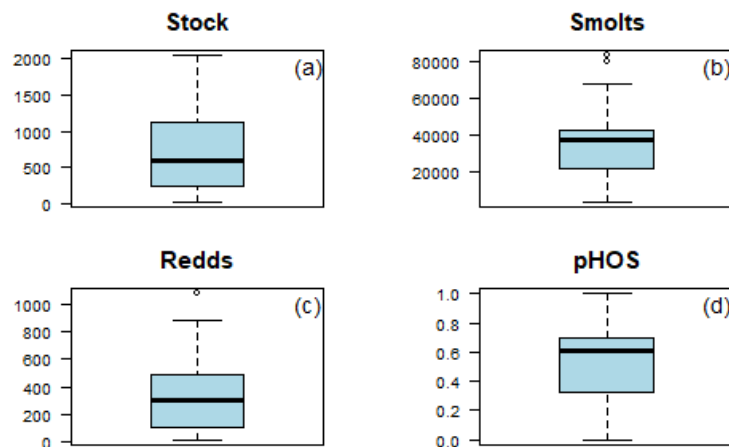


Figure 1. Chiwawa River Spring Chinook Salmon boxplots for Stock (spawner abundance), Smolts, Redd counts, and proportion of hatchery origin spawners (pHOS), 1991–2017. Box indicates interquartile range and thick horizontal bar is median. Whiskers indicate quartile $\pm 1.5 \times$ interquartile range.

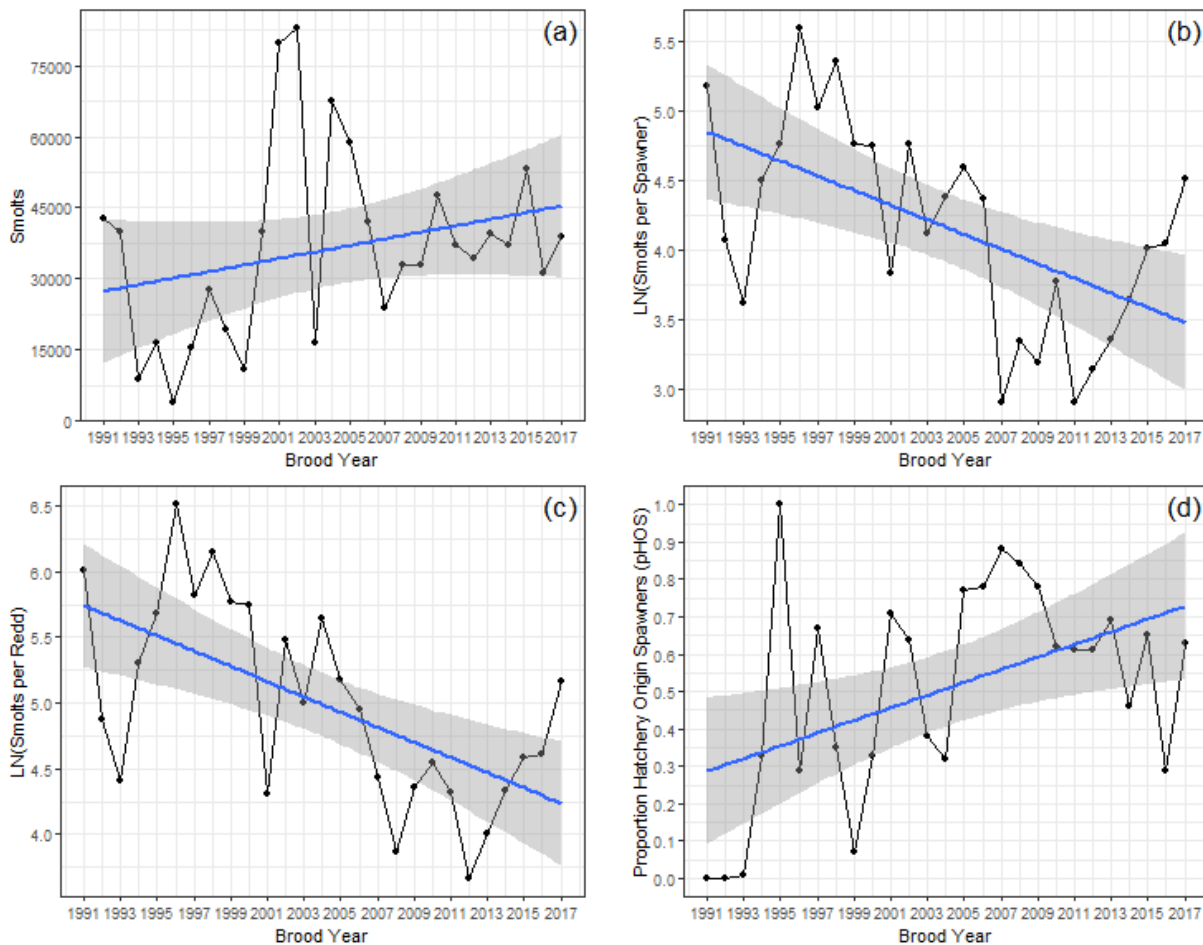


Figure 2. Chiwawa River Spring Chinook Salmon annual Smolt counts, Smolt/Spawner (log scale), Smolt/Redd (log scale), and proportion of hatchery origin spawners (pHOS), 1991–2017. Line indicates the linear trend. Shaded area is the estimated 95% confidence interval of the line.

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 ($\Delta AICc \leq 0.75$), 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.

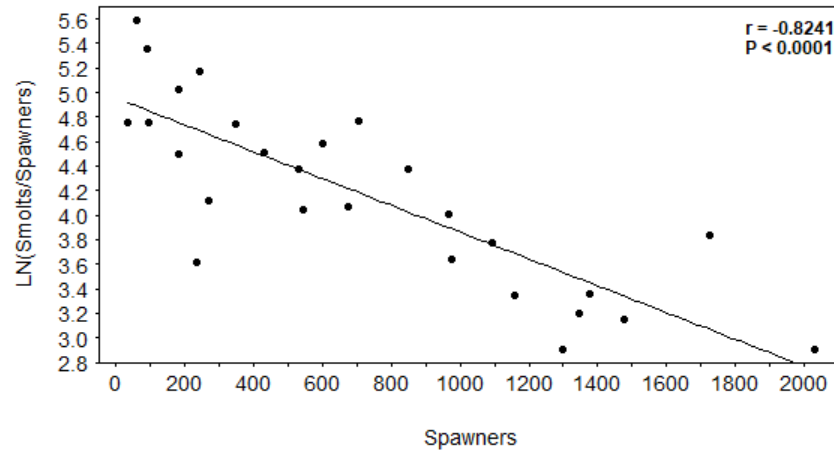


Figure 3. Smolts per spawner (log scale) versus spawner abundance for Chiwawa River Spring Chinook Salmon, 1991–2017, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope.

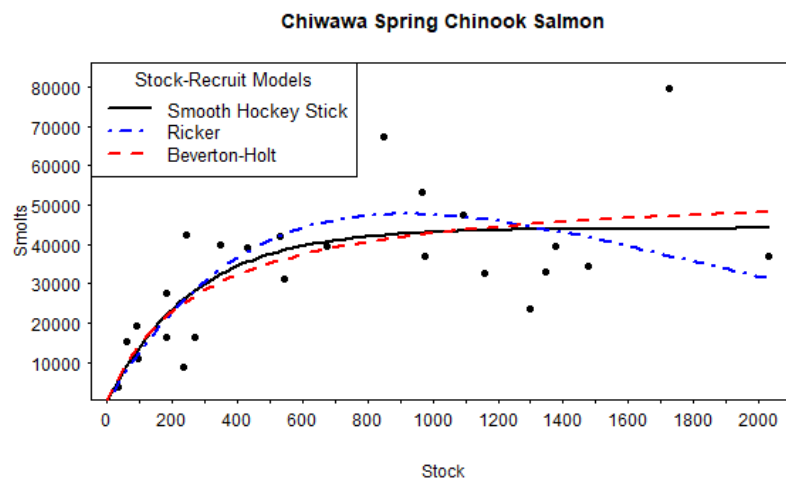


Figure 4. Stock-recruitment models fit to smolt and spawner data for Chiwawa River Spring Chinook Salmon, 1991–2017.

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.

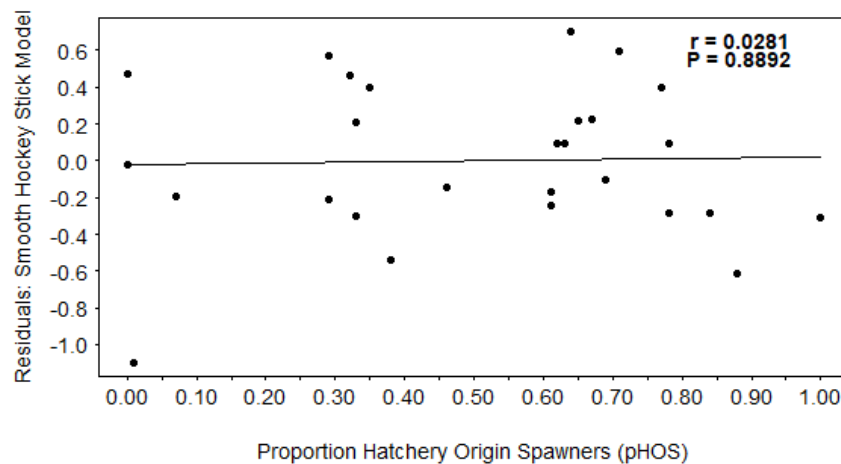


Figure 5. Residuals from Smooth Hockey Stick Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Chiwawa River Chinook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

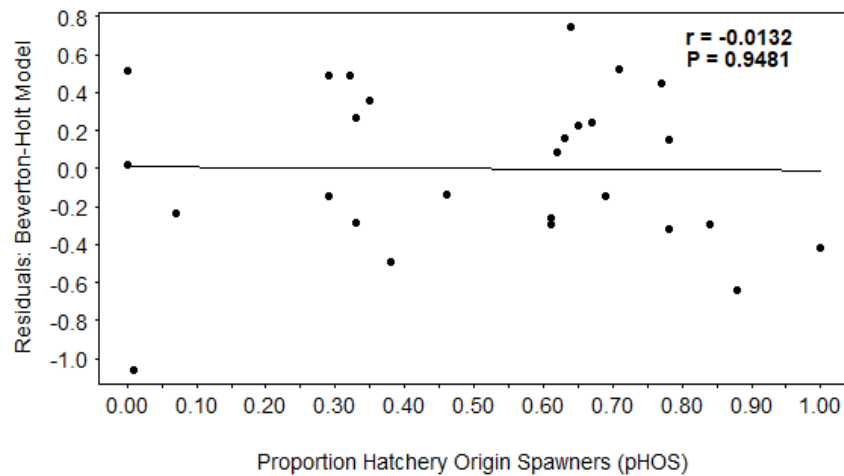


Figure 6. Residuals from Beverton-Holt Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Chiwawa River Chinook Salmon,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

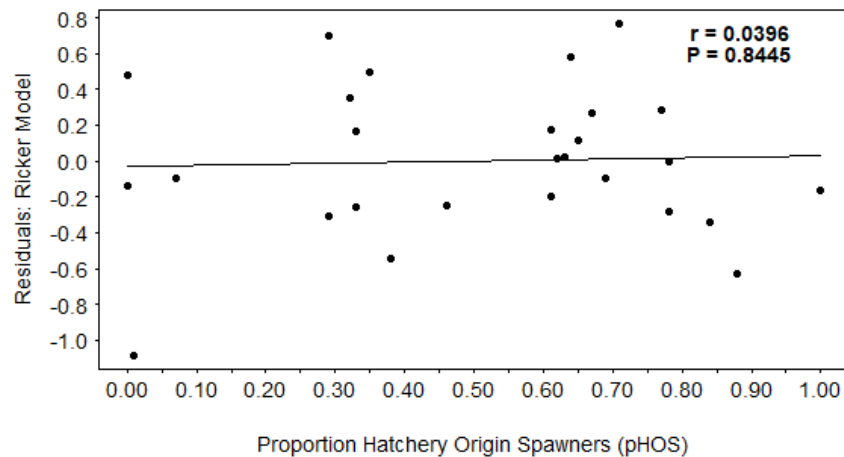


Figure 7. Residuals from Ricker Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Chiwawa River Chinook Salmon, 1991–2017.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

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 ($\Delta AICc = 5.81$ 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. $R^2 = 0.1256$.

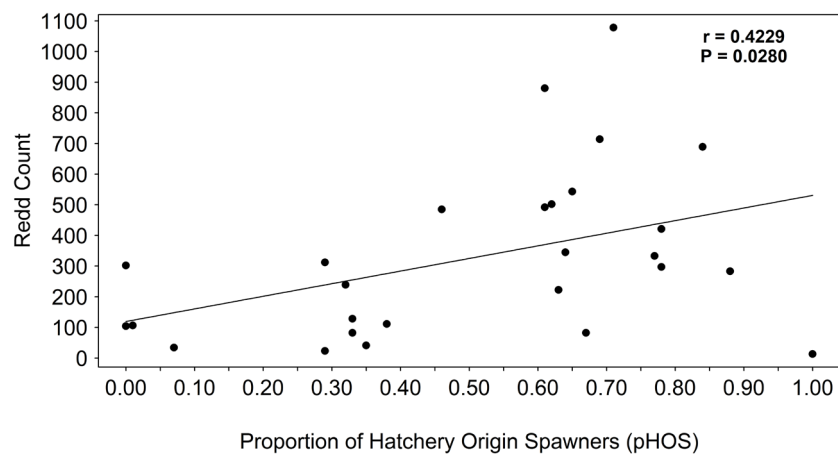


Figure 9. Redd count versus proportion of hatchery origin spawners (pHOS) for Chiwawa River Spring Chinook Salmon, 1991–2017, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope.

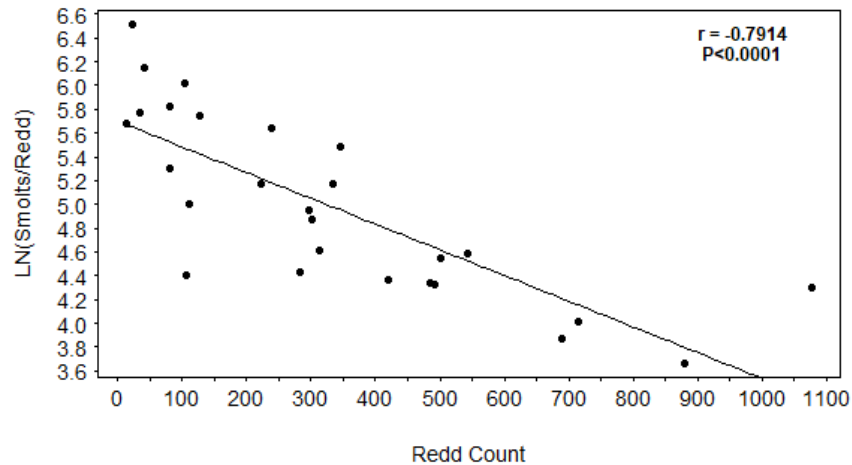


Figure 10. Smolts per redd versus redd count for Chiwawa River Spring Chinook Salmon, 1991–2017, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. Negative slope indicates post-spawning density dependence.

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.

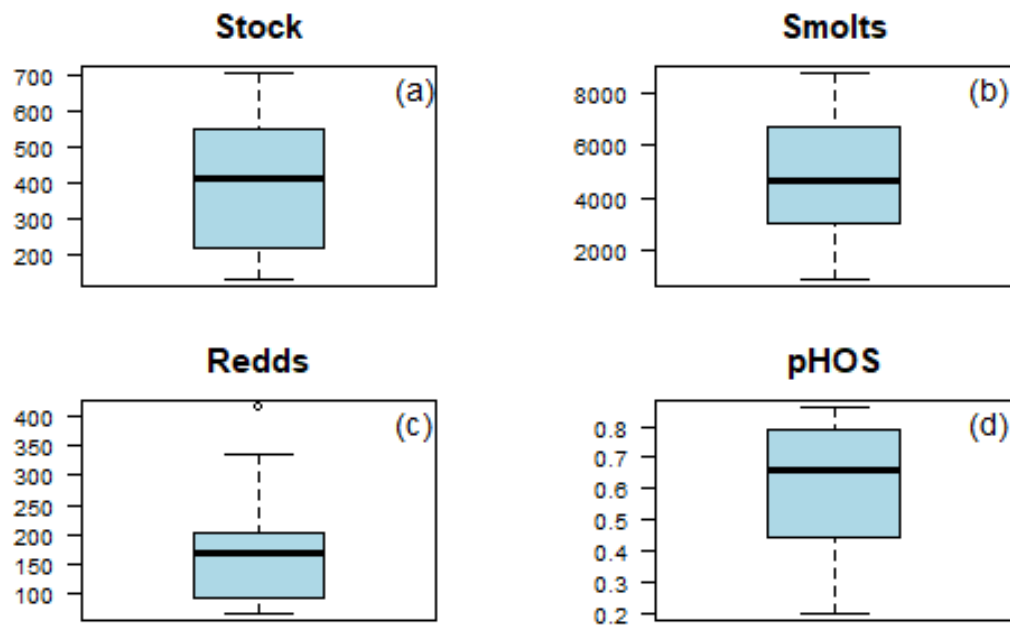


Figure 11. Nason Creek Spring Chinook Salmon boxplots for Stock (spawner abundance), Smolts, Redd counts, and proportion of hatchery origin spawners (pHOS), 2002–2017. Box indicates interquartile range and thick horizontal bar is median. Whiskers indicate quartile $\pm 1.5 \times$ interquartile range.

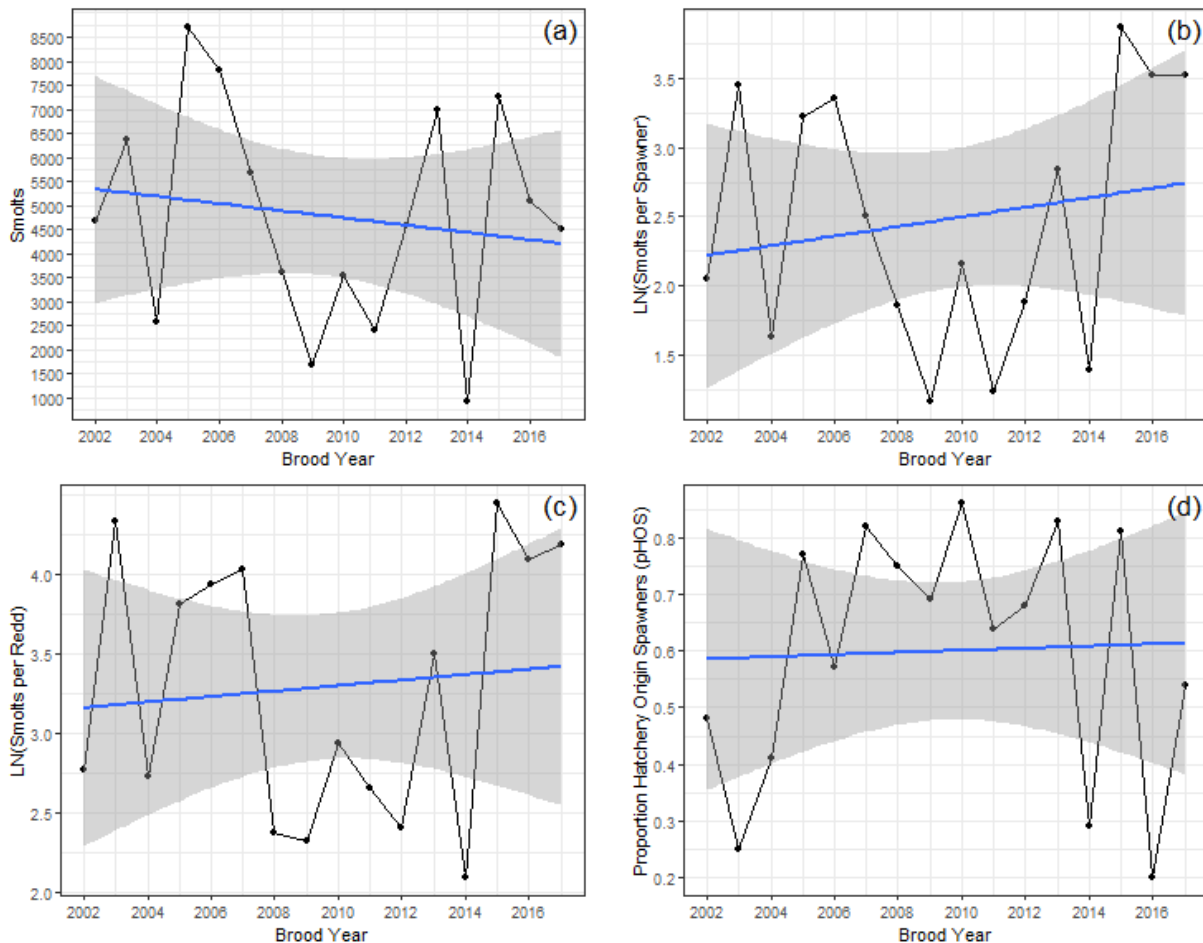


Figure 12. Nason Creek Spring Chinook Salmon annual Smolt counts, Smolt/Spawner (log scale), Smolt/Redd (log scale), and proportion of hatchery origin spawners (pHOS), 2002–2017. Line indicates the linear trend. Shaded area is the estimated 95% confidence interval of the line.

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.

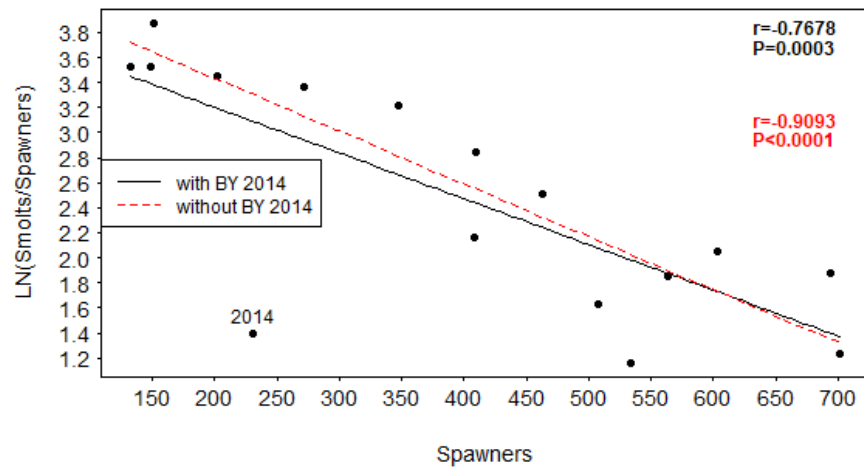


Figure 13. Smolts per spawner (log scale) versus spawner abundance for Nason Creek Spring Chinook Salmon, 2002–2017, with and without brood year 2014, with fitted linear regression line, Pearson correlation coefficient (r), and P -value from one-sided t -test of negative slope.

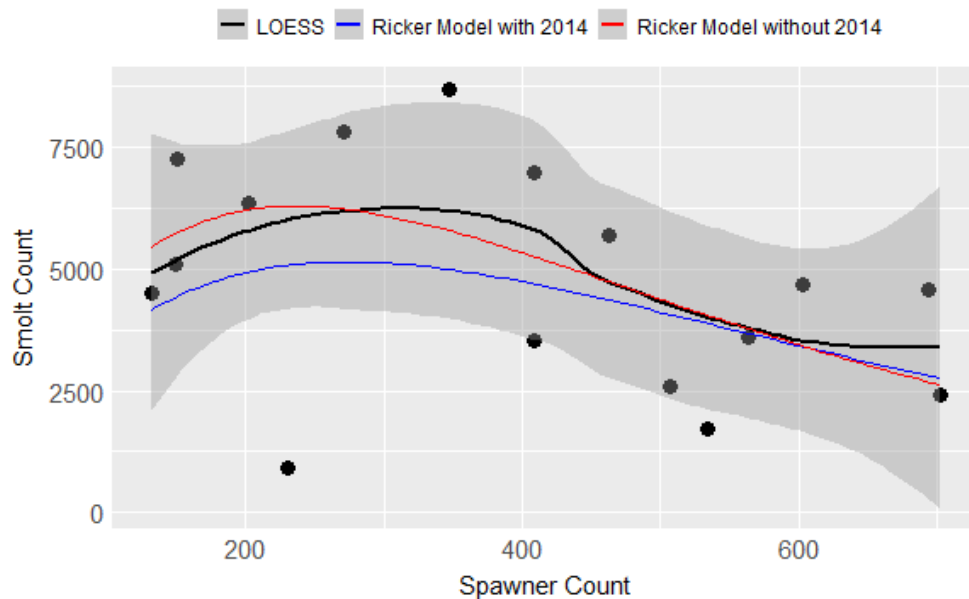


Figure 14. Stock and smolt data with fitted LOESS curve and Ricker Model (with and without data from 2014) for Nason Creek Spring Chinook Salmon, 2002–2017.

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.

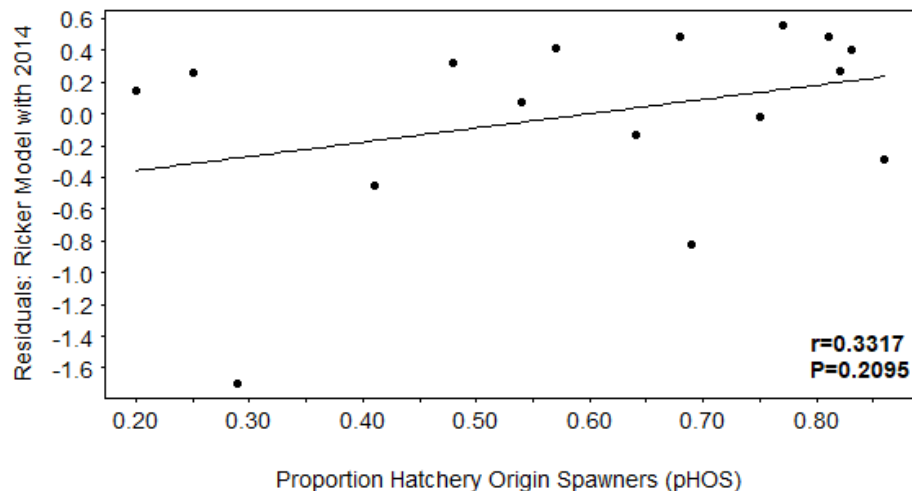


Figure 15. Residuals from the Ricker model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Nason Creek Chinook Salmon, 2002–2017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

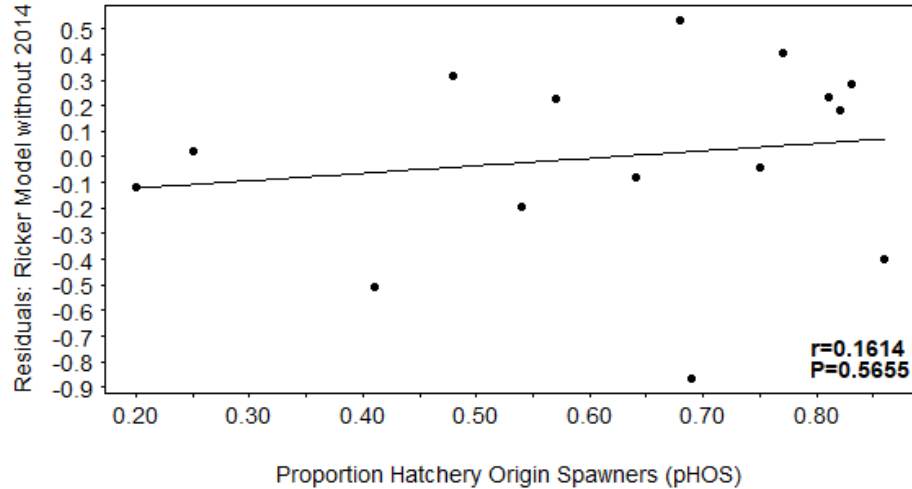


Figure 16. Residuals from the Ricker model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Nason Creek Chinook Salmon, 2002–2017 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.

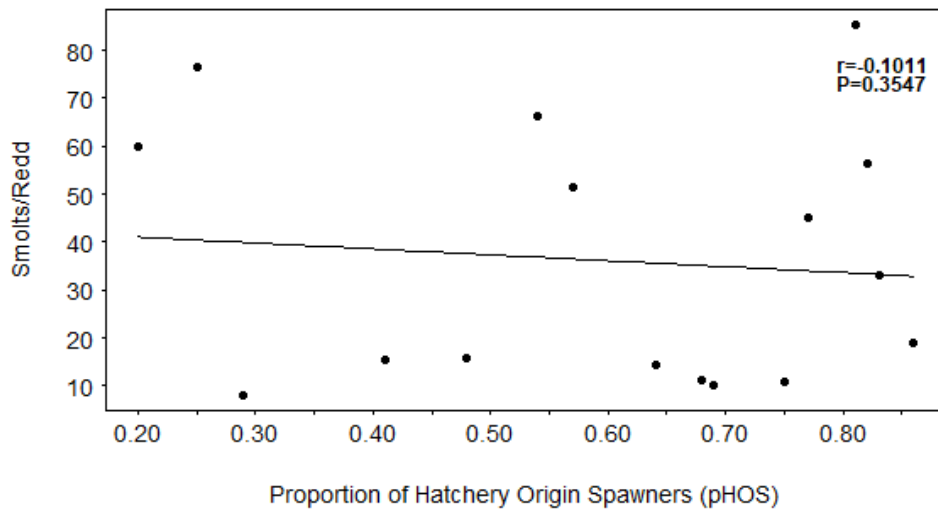


Figure 17. Smolts per redd versus proportion of hatchery origin spawners (pHOS) for Nason Creek Spring Chinook Salmon, 2002–2017, including brood year 2014, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. $R^2 = 0.0102$.

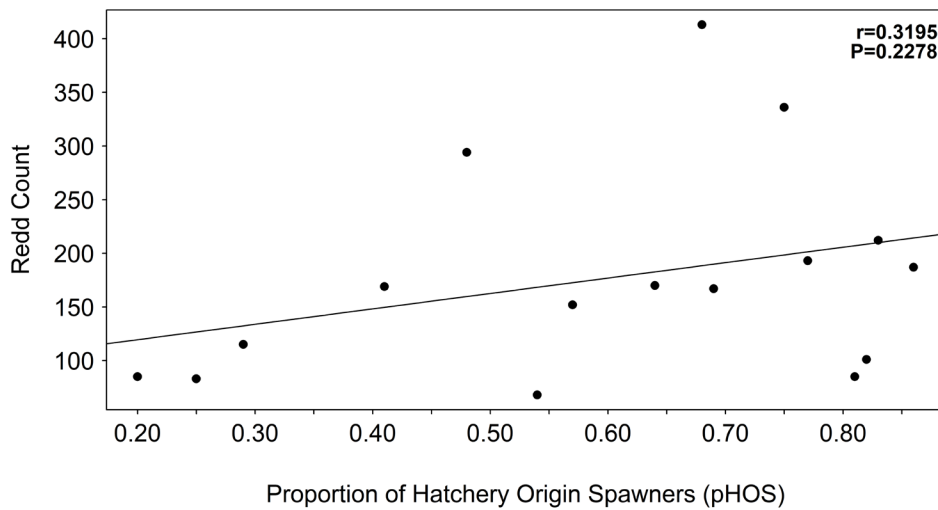


Figure 18. Redd count versus proportion of hatchery origin spawners (pHOS) for Nason Creek Spring Chinook Salmon, 2002–2017, including brood year 2014, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope.

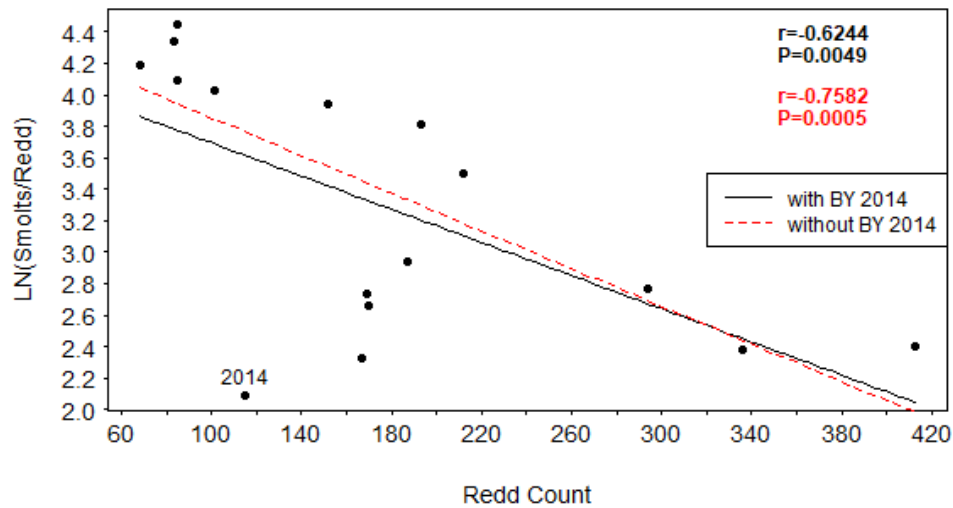


Figure 19. Smolts per redd (log scale) versus redd count for Nason Creek Spring Chinook Salmon, 2002–2017, with and without 2014, with fitted linear regression line, Pearson correlation coefficient (r), and P -value from one-sided t -test of negative slope. Negative slope indicates post-spawning density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

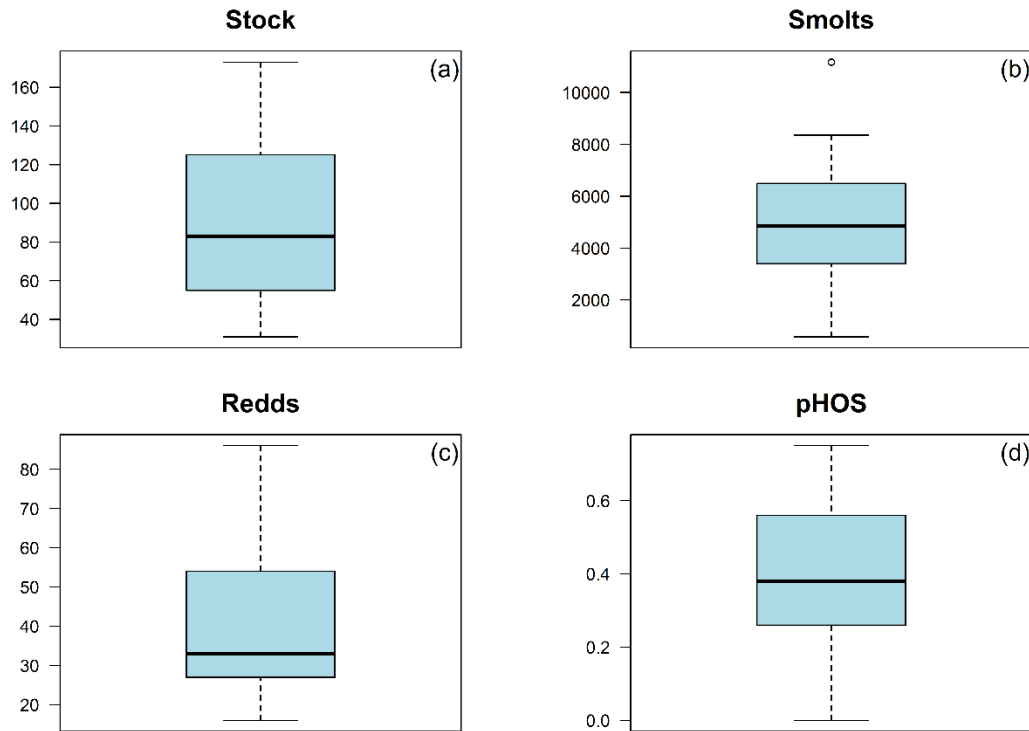


Figure 20. White River Spring Chinook Salmon boxplots for Stock (spawner abundance), Smolts, Redd counts, and proportion of hatchery origin spawners (pHOS), 2005–2017. Box indicates interquartile range and thick horizontal bar is median. Whiskers indicate quartile $\pm 1.5 \times$ interquartile range.

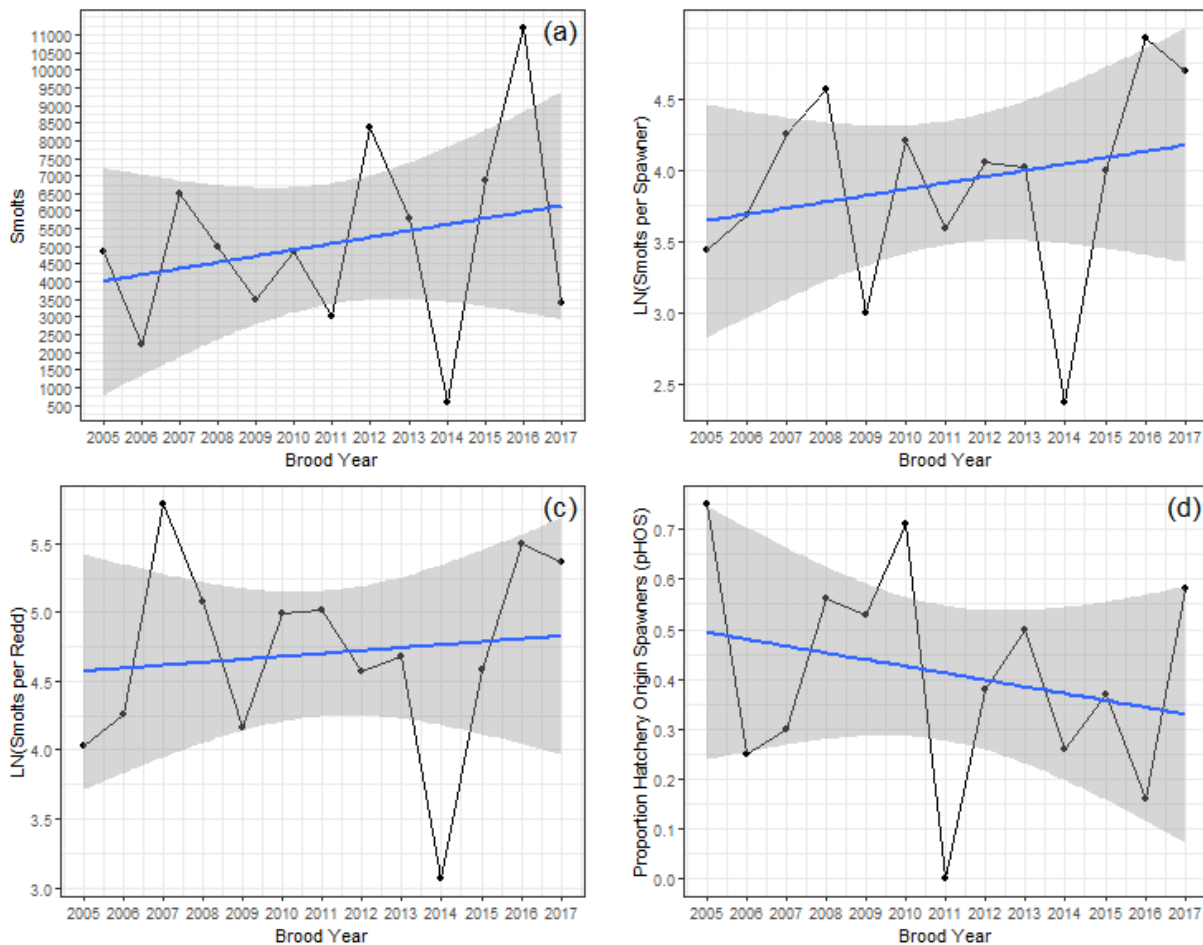


Figure 21. White River Spring Chinook Salmon annual Smolt counts, Smolt/Spawner (log scale), Smolt/Redd (log scale), and proportion of hatchery origin spawners (pHOS), 2005–2017. Line indicates the linear trend. Shaded area is the estimated 95% confidence interval of the line.

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 ($P \geq 0.6015$; Figure 24 – Figure 26). Additionally, likelihood ratio tests of the effect of pHOS on the Beverton-Holt and Ricker models were non-significant ($P \geq 0.5518$). 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 ($P \geq 0.8533$; Figure 28–Figure 30). Likelihood ratio tests of the effect of pHOS on the Beverton-Holt and Ricker models were also non-significant ($P \geq 0.7763$).

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.

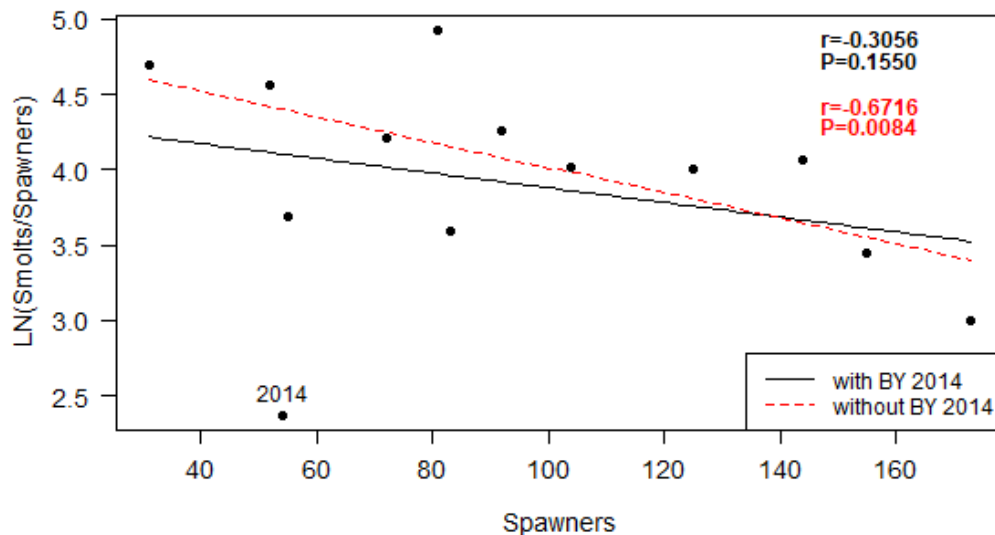


Figure 22. Smolts per spawner (log scale) versus spawner abundance for White River Spring Chinook Salmon, 2005–2017, with and without brood year 2014, with fitted linear regression line, Pearson correlation coefficient (r), and P -value from one-sided t -test of negative slope.

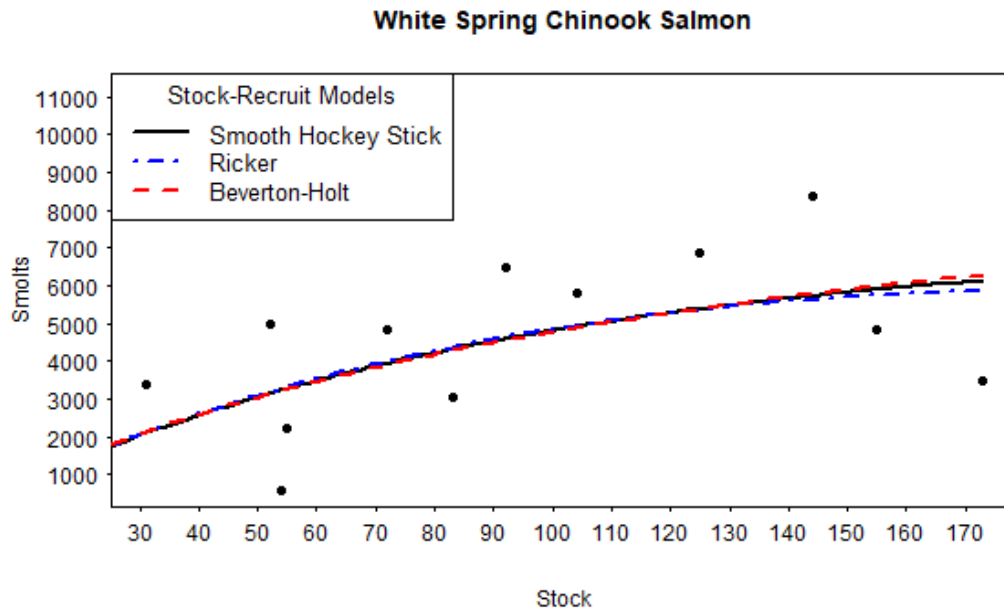


Figure 23. Stock-recruitment models fit to smolt and spawner data for White River Spring Chinook Salmon, 2005–2017, including brood year 2014.

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	$\alpha, R_\infty: -0.24^a$
			R_∞	7,183	3,516 – 60,989	
Beverton-Holt	34.12	0.14	α	11,011	5,286 – 185,892	$\alpha, \beta: 0.96$
			β	130	32 – 3,591	
Ricker	33.98	0.00	α	78.9	35.5 – 180.4	$\alpha, \beta: 0.90$
			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 $R_\infty = 0.6241$.

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.

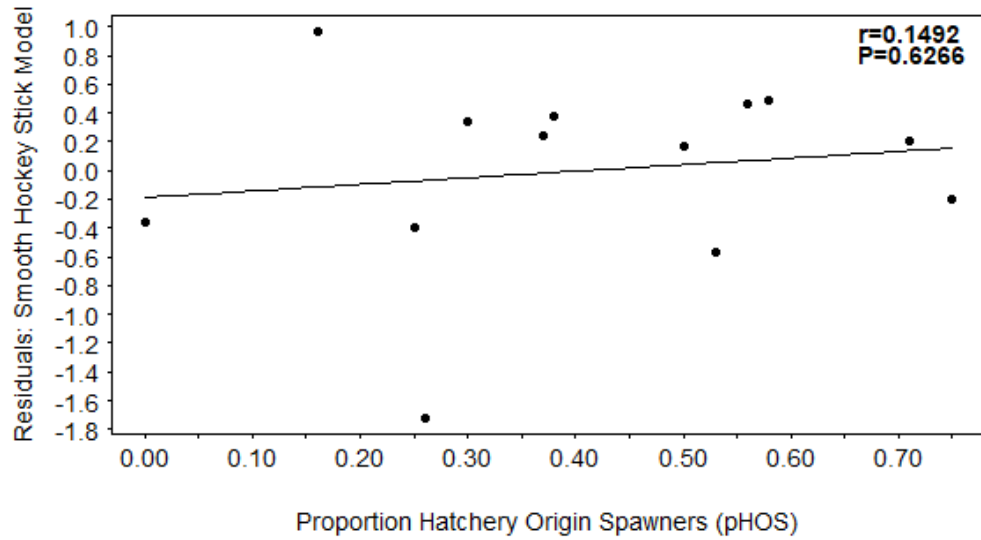


Figure 24. Residuals from Smooth Hockey Stick Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from White River Spring Chinook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

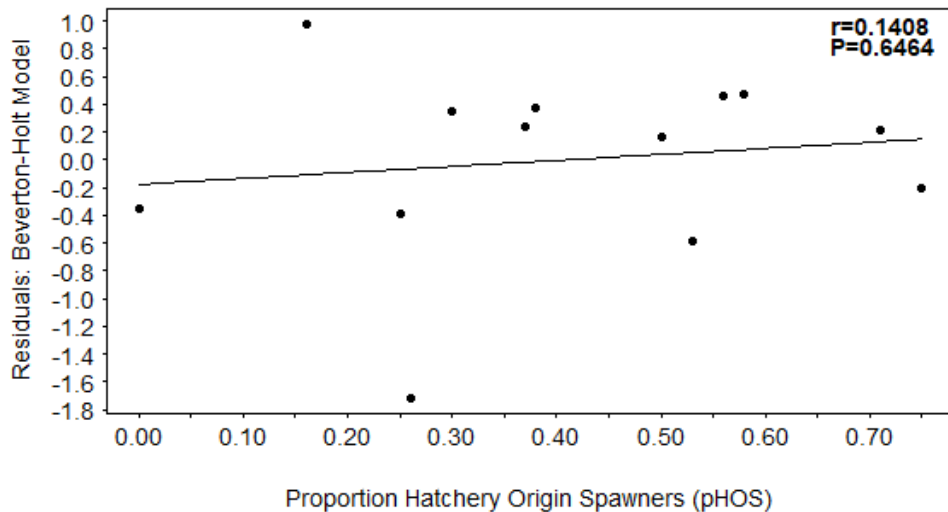


Figure 25. Residuals from the Beverton-Holt Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from White River Spring Chinook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

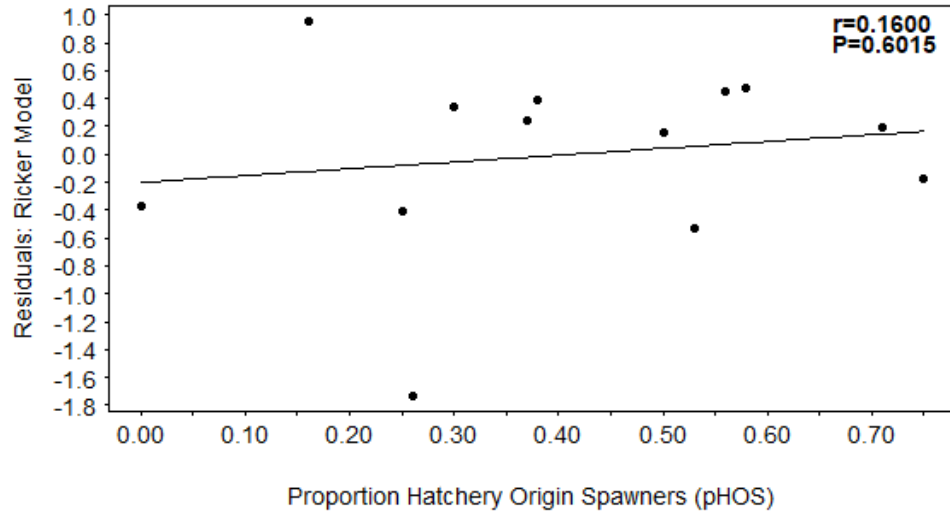


Figure 26. Residuals from the Ricker Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from White River Spring Chinook Salmon,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

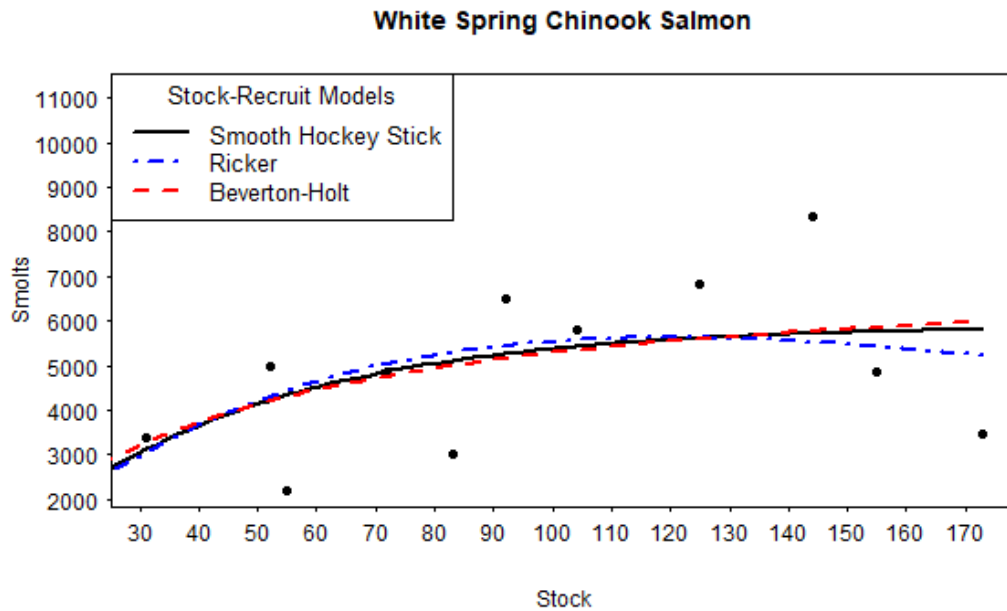


Figure 27. Stock-recruitment models fit to smolt and spawner data for White River Spring Chinook Salmon, 2005–2017, without brood year 2014.

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). Δ AICc represents change in AICc compared to model with minimum AICc.

Model	AICc	Δ AICc	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 $R_\infty = 0.5703$.

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.

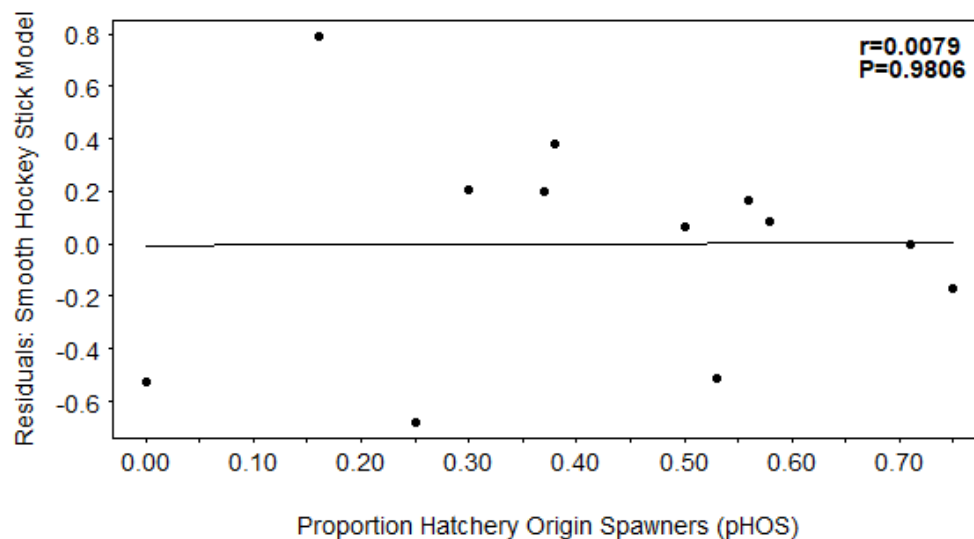


Figure 28. Residuals from Smooth Hockey Stick Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from White River Spring Chinook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

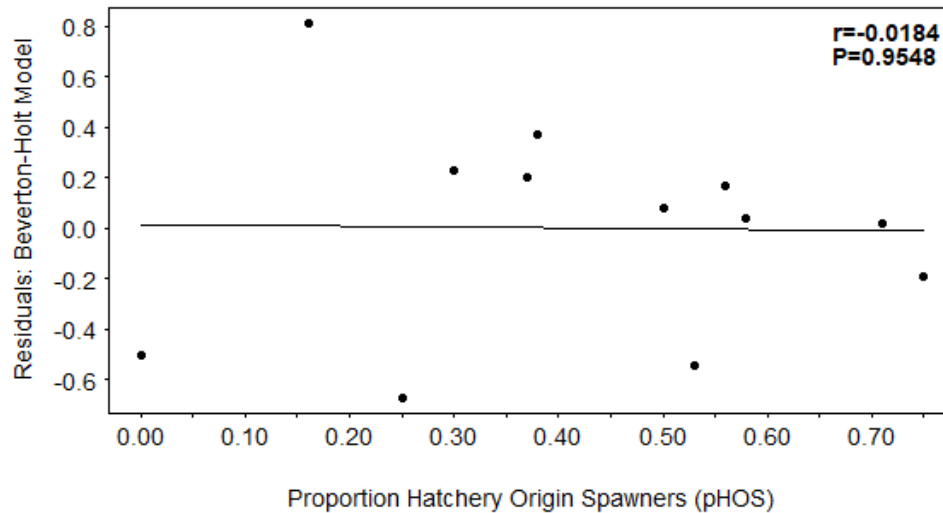


Figure 29. Residuals from the Beverton-Holt Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from White River Spring Chinook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

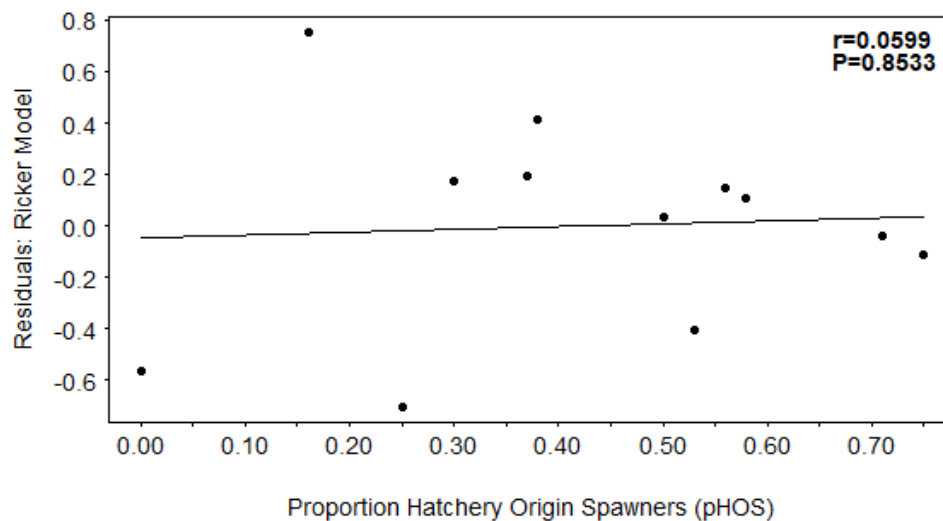


Figure 30. Residuals from the Ricker Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from White River Spring Chinook Salmon, 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.

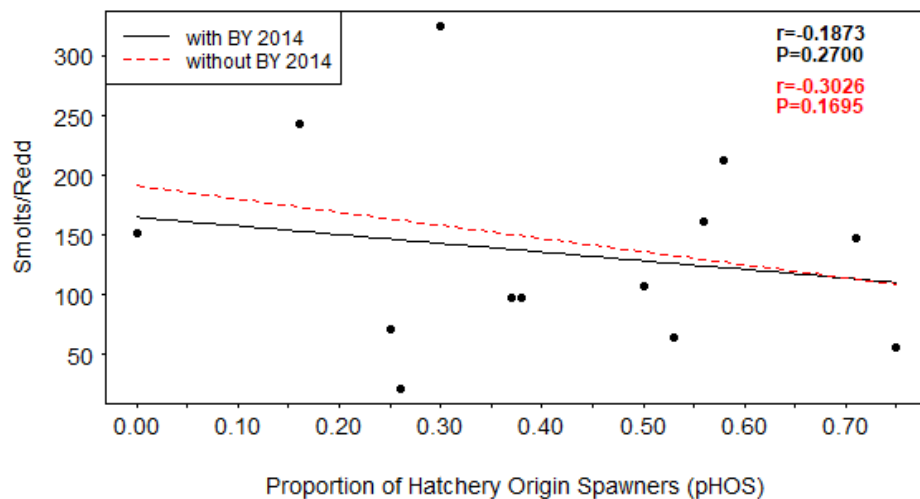


Figure 31. Smolts per redd versus proportion of hatchery origin spawners (pHOS) for White River Spring Chinook Salmon, 2005–2017, with and without brood year 2014, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. $R^2 = 0.0351$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

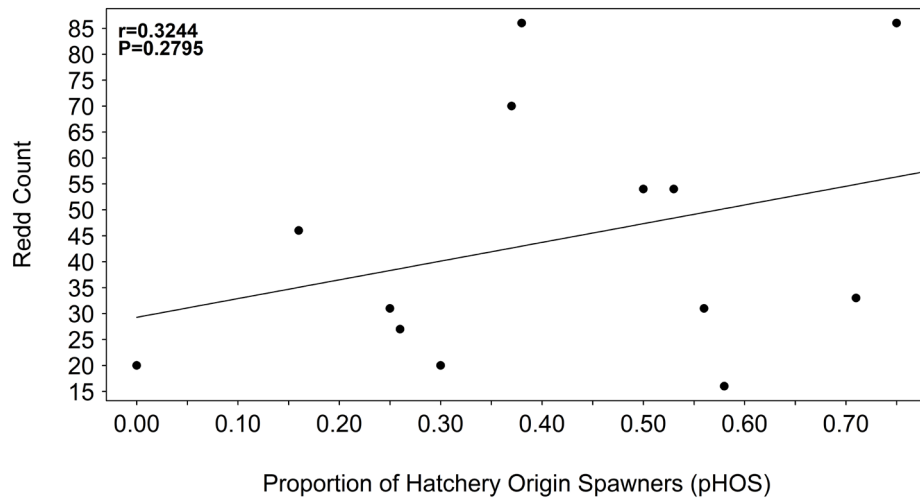


Figure 32. Redd count versus proportion of hatchery origin spawners (pHOS) for White River Spring Chinook Salmon, 2005–2017, including 2014 brood year, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope.

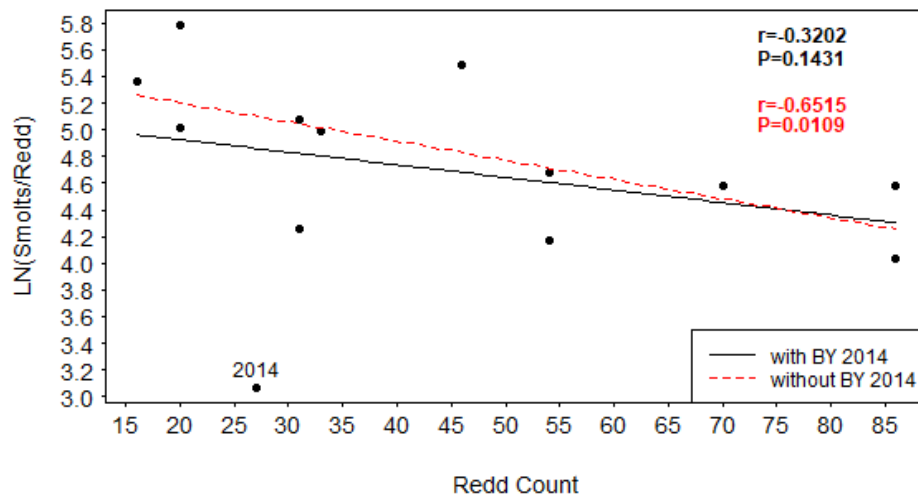


Figure 33. Smolts per redd (log scale) versus redd count for White River Spring Chinook Salmon, 2005–2017, with and without the 2014 brood year, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. Negative slope indicates post-spawning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

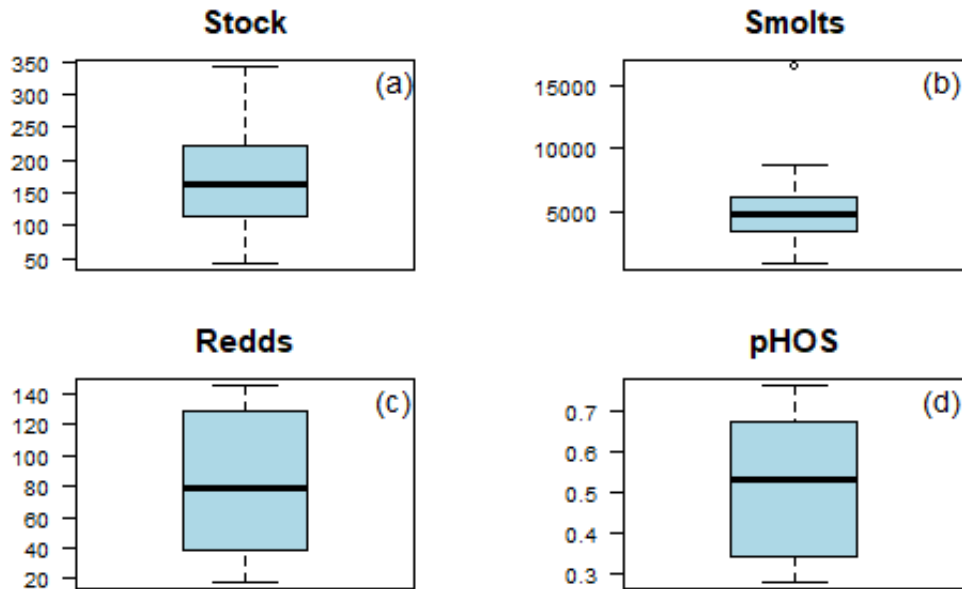


Figure 34. Twisp River Spring Chinook Salmon boxplots for Stock (spawner abundance), Smolts, Redd counts, and proportion of hatchery origin spawners (pHOS), 2003–2017. Box indicates interquartile range and thick horizontal bar is median. Whiskers indicate quartile $\pm 1.5 \times$ interquartile range.

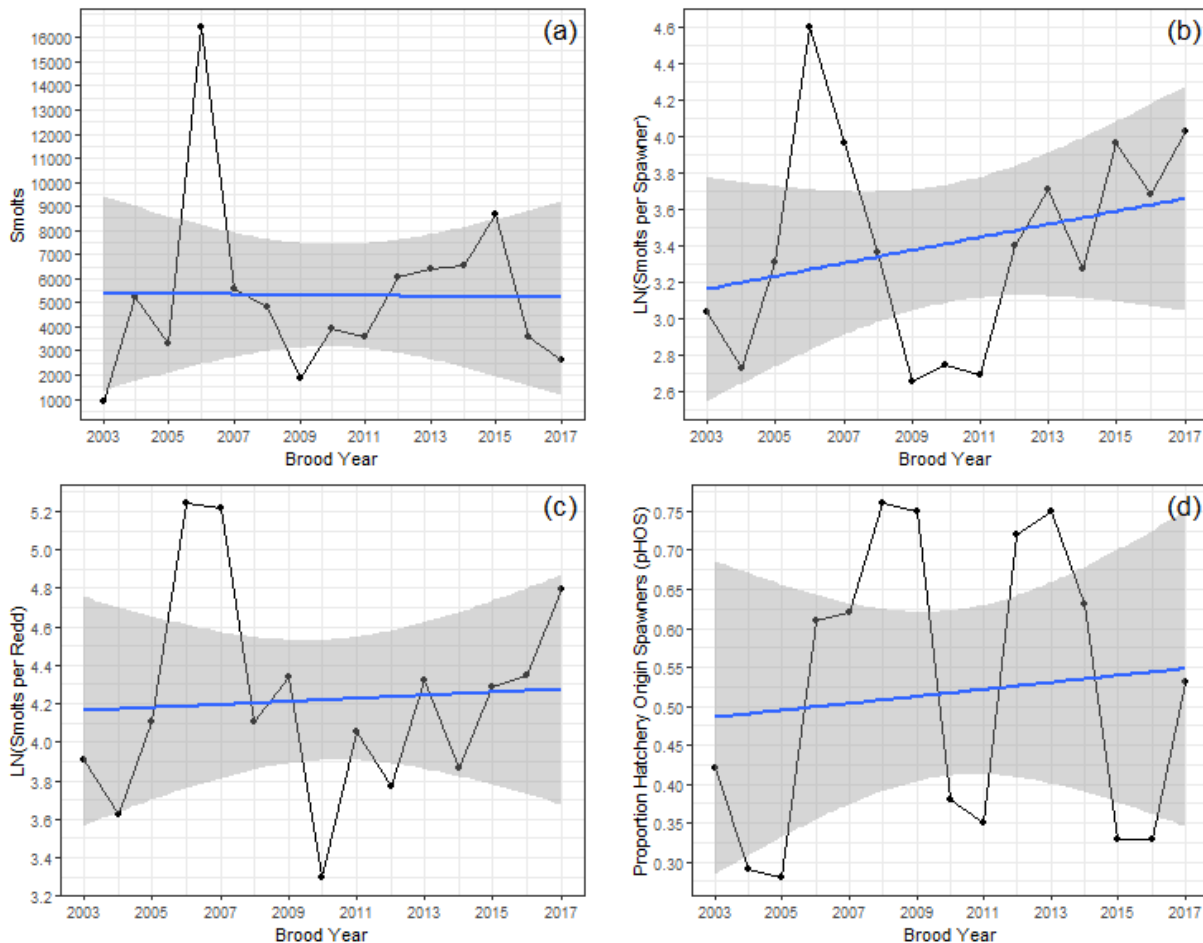


Figure 35. Twisp River Spring Chinook Salmon annual Smolt counts, Smolt/Spawner (log scale), Smolt/Redd (log scale), and proportion of hatchery origin spawners (pHOS), 2002–2017. Line indicates the linear trend. Shaded area is the estimated 95% confidence interval of the line.

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 $\Delta AICc \leq 0.62$ (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 ($P \geq 0.4470$). 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.

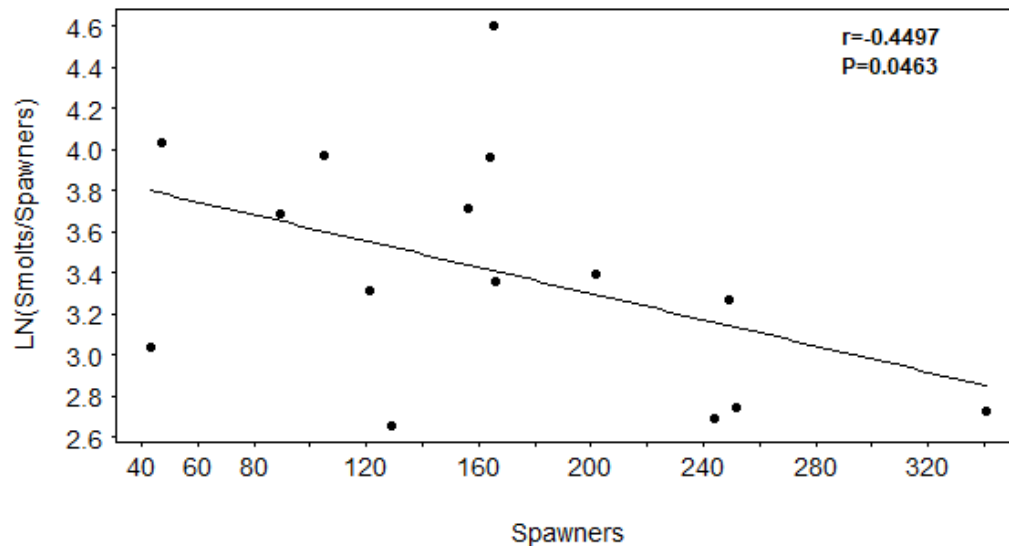


Figure 36. Smolts per spawner (log scale) versus spawner abundance for Twisp River Spring Chinook Salmon, 2003–2017, with fitted linear regression line, Pearson correlation coefficient (r), and P -value from one-sided t -test of negative slope.

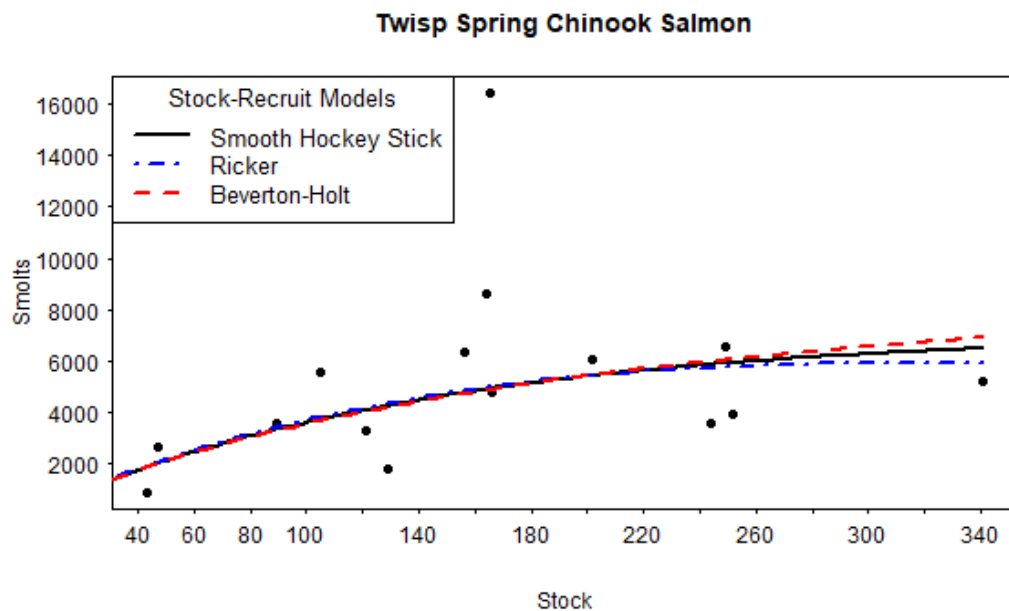


Figure 37. Stock-recruitment models fit to smolt and spawner data for Twisp River Spring Chinook Salmon, 2003–2017.

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 $R_\infty = 0.4951$.

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.

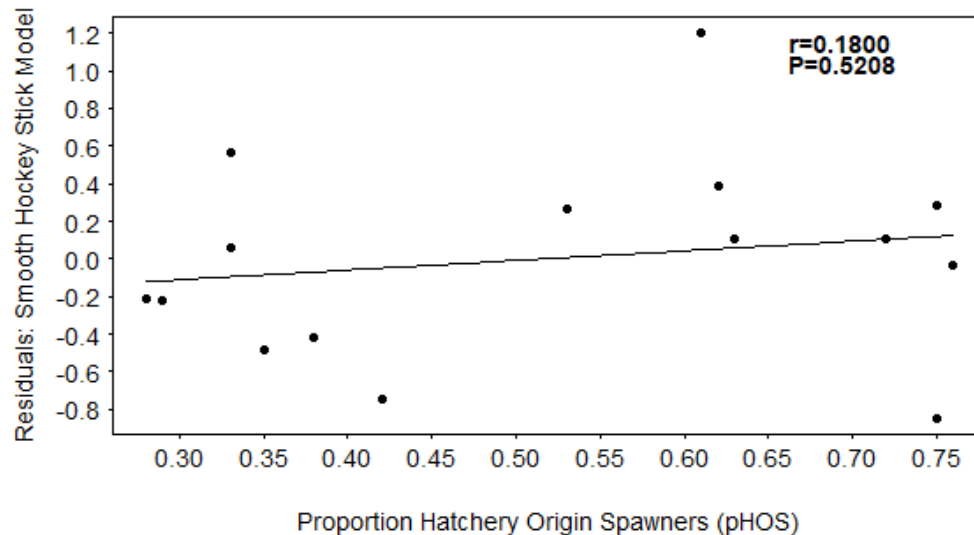


Figure 38. Residuals from Smooth Hockey Stick Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Twisp River Spring Chinook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

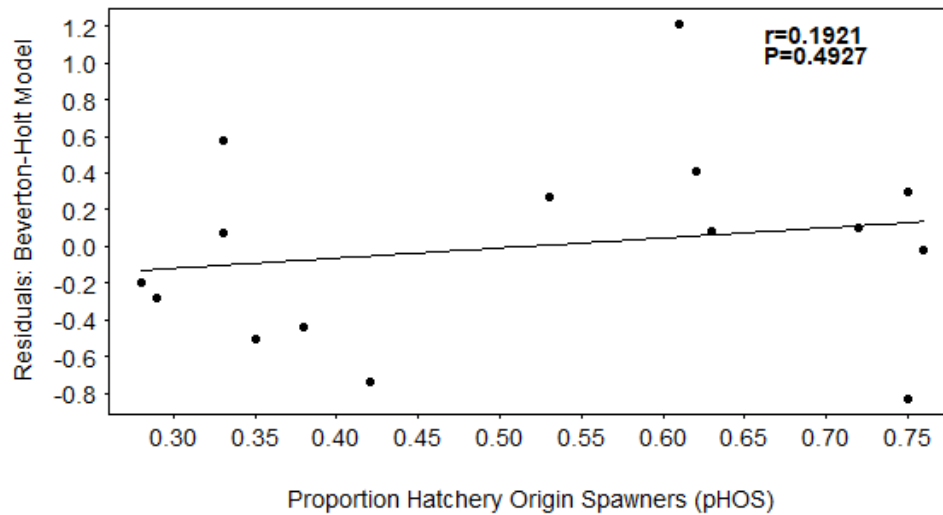


Figure 39. Residuals from the Beverton-Holt Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Twisp River Spring Chinook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

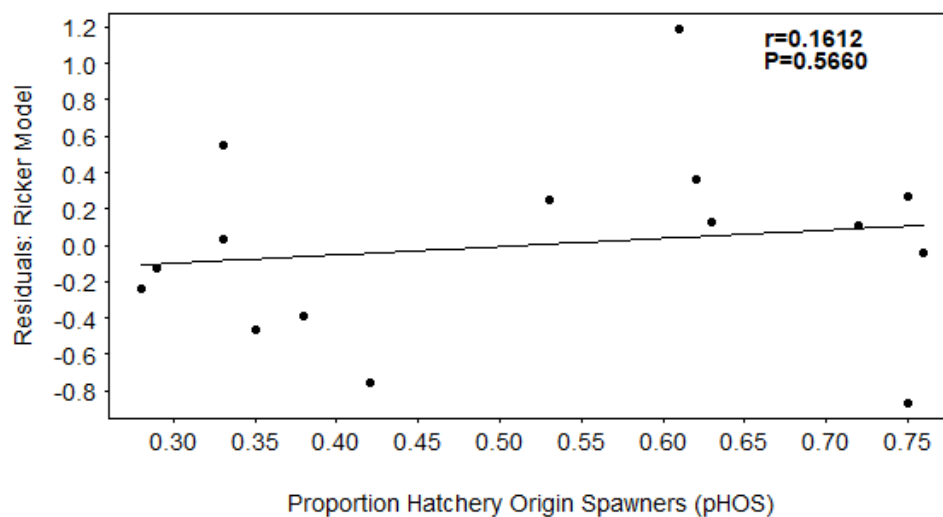


Figure 40. Residuals from the Ricker Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Twisp River Spring Chinook Salmon,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

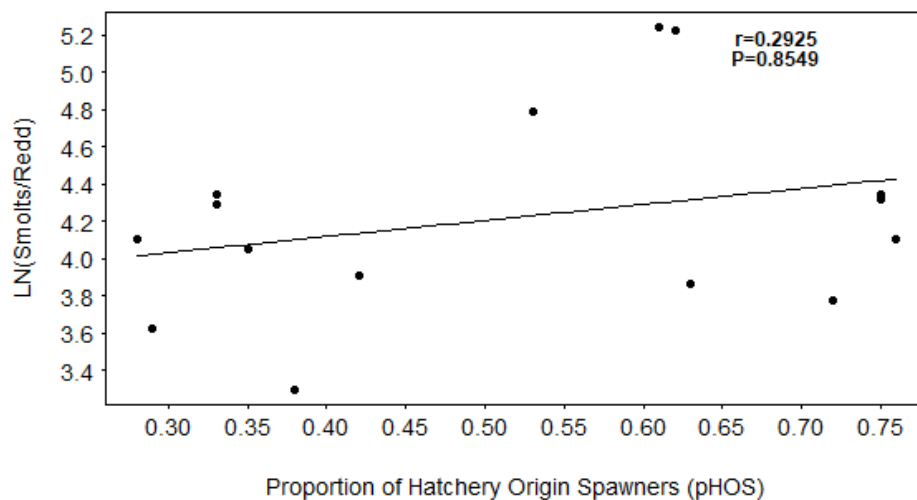


Figure 41. Smolts per redd (log scale) versus proportion of hatchery origin spawners (pHOS) for Twisp River Spring Chinook Salmon, 2003–2017, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. $R^2 = 0.0855$.

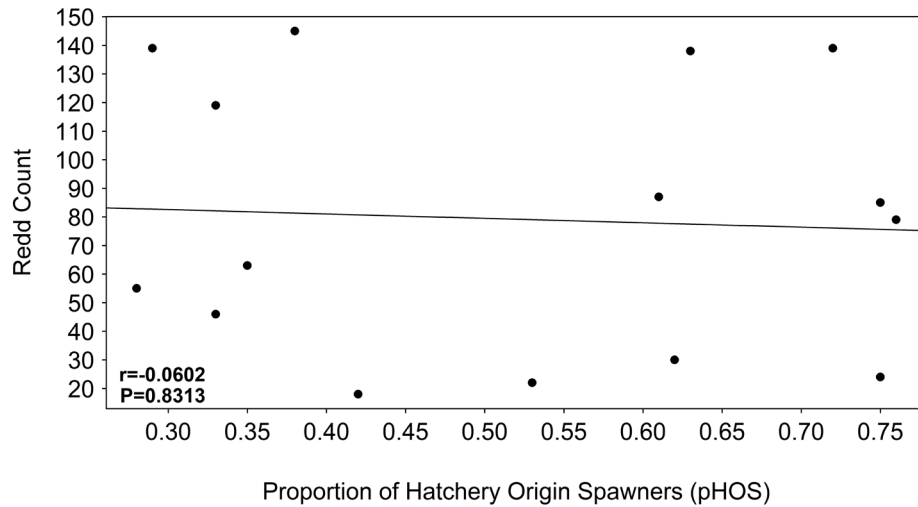


Figure 42. Redd count versus proportion of hatchery origin spawners (pHOS) for Twisp River Spring Chinook Salmon, 2003–2017, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope.

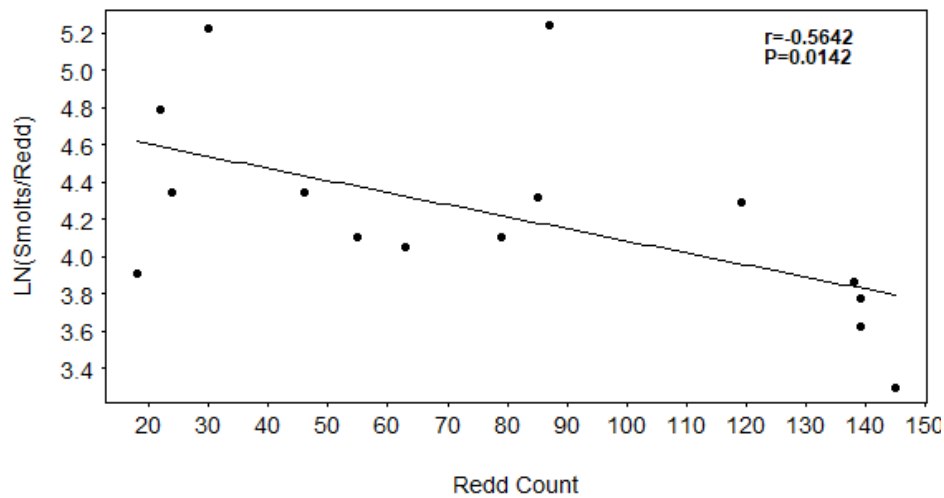


Figure 43. Smolts per redd (log scale) versus redd count for Twisp River Spring Chinook Salmon, 2003–2017, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. Negative slope indicates post-spawning density dependence.

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).

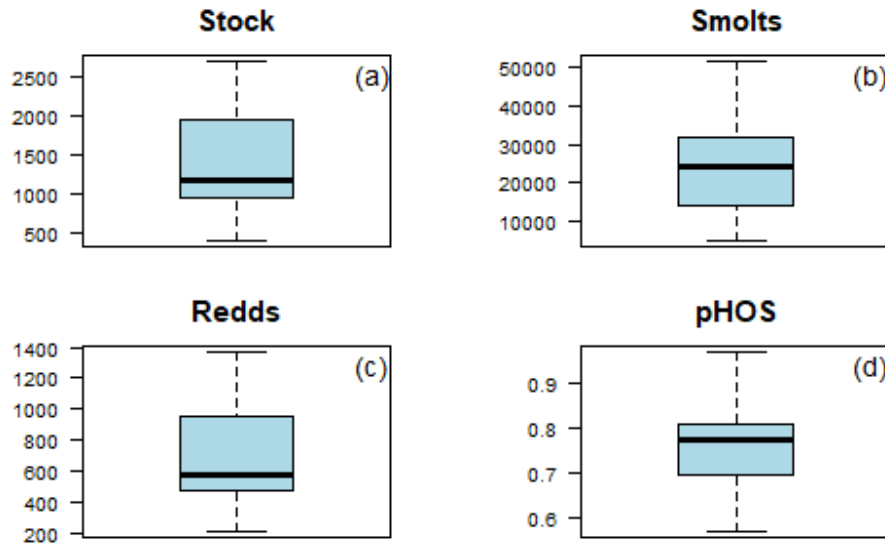


Figure 44. Methow River Spring Chinook Salmon boxplots for Stock (spawner abundance), Smolts, Redd counts, and proportion of hatchery origin spawners (pHOS), 2002–2017. Box indicates interquartile range and thick horizontal bar is median. Whiskers indicate quartile $\pm 1.5 \times$ interquartile range.

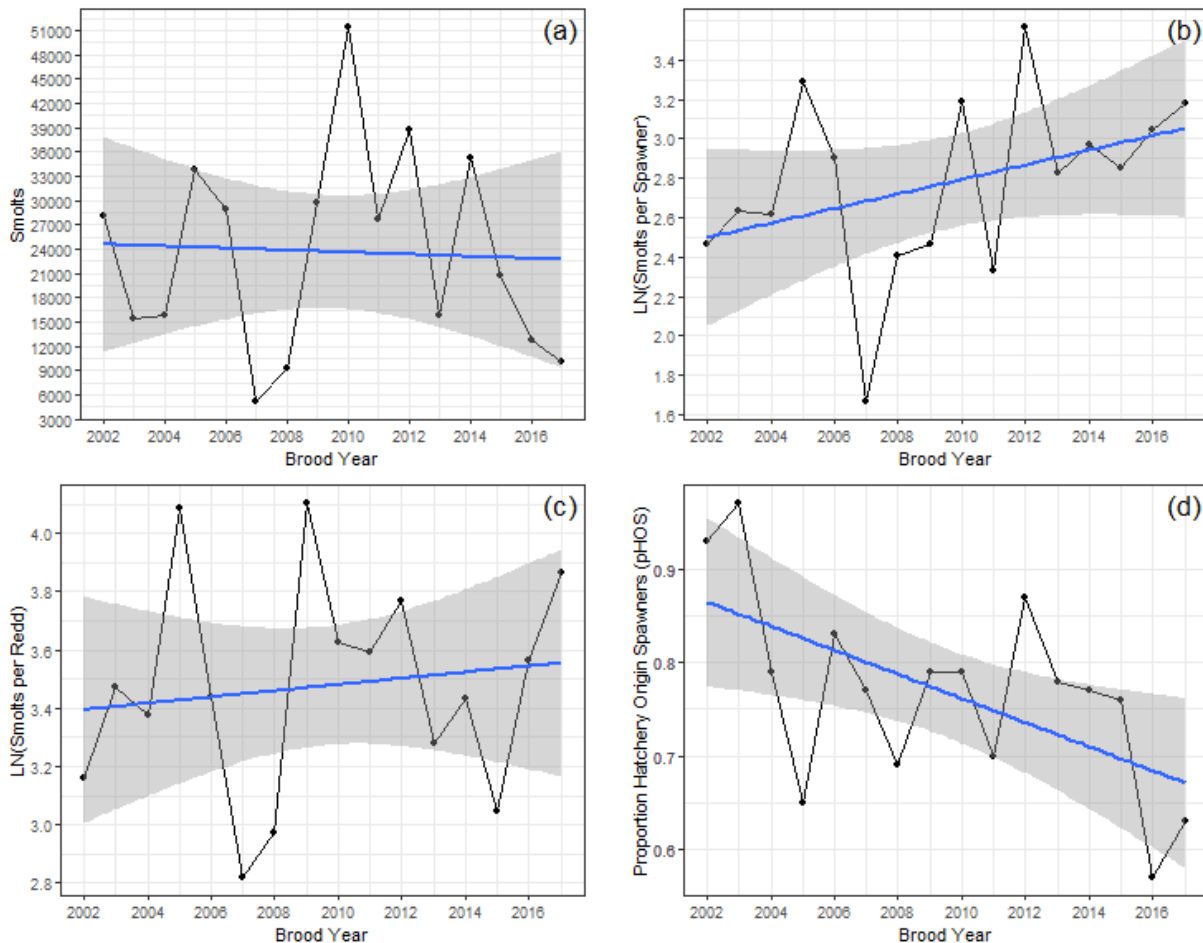


Figure 45. Methow River Spring Chinook Salmon annual Smolt counts, Smolt/Spawner (log scale), Smolt/Redd (log scale), and proportion of hatchery origin spawners (pHOS), 2002–2017. Line indicates the linear trend. Shaded area is the estimated 95% confidence interval of the line.

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 $\Delta AICc \leq 0.04$ 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 ($P \geq 0.7955$; Figure 48 – Figure 50). Additionally, likelihood ratio tests of the effect of pHOS on the Beverton-Holt and Ricker models were

non-significant ($P \geq 0.7635$). 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.

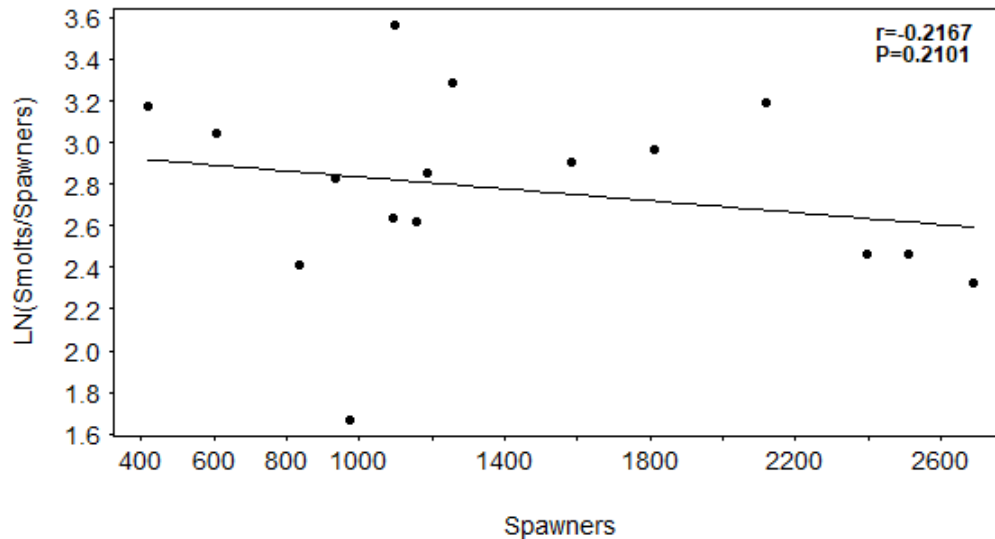


Figure 46. Smolts per spawner (log scale) versus spawner abundance for Methow River Spring Chinook Salmon, 2002–2017, with fitted linear regression line, Pearson correlation coefficient (r), and P -value from one-sided t -test of negative slope.

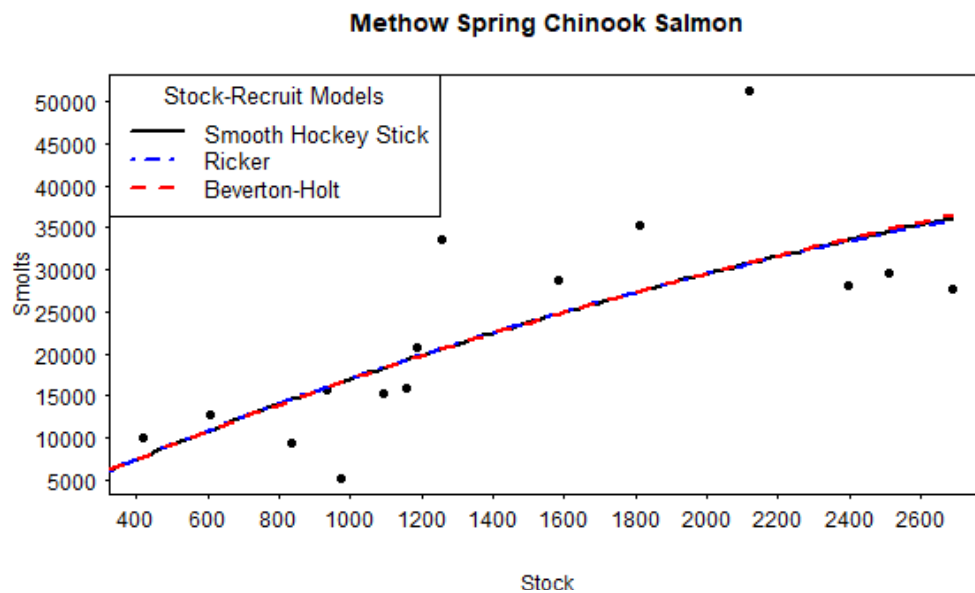


Figure 47. Stock-recruitment models fit to smolt and spawner data for Methow River Spring Chinook Salmon, 2002–2017.

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	$\alpha, R_\infty: -0.30^a$
			R_∞	65,051	23,577 – 549,603	
Beverton-Holt	26.66	0.04	α	115,394	32,755 – 1,382,406	$\alpha, \beta: 0.99$
			β	5,806	785 – 82,314	
Ricker	26.62	0.00	α	19.6	11.6 – 32.7	$\alpha, \beta: 0.88$
			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 $R_\infty = 0.7281$.

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.

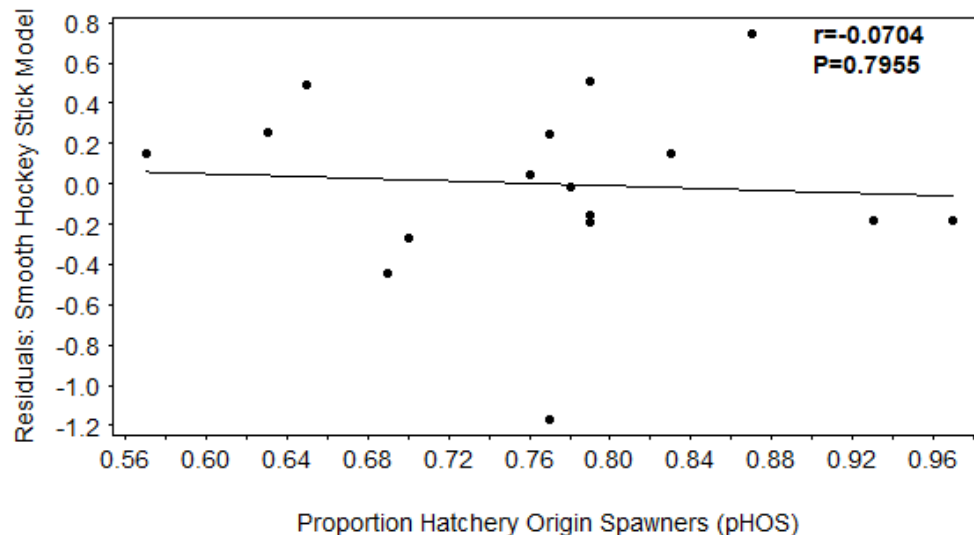


Figure 48. Residuals from Smooth Hockey Stick Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Methow River Spring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

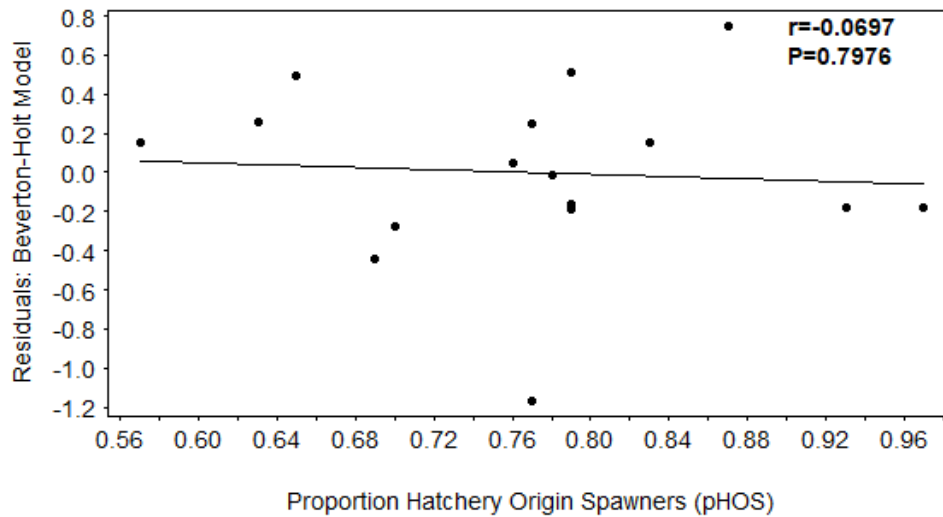


Figure 49. Residuals from the Beverton-Holt Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Methow River Spring Chinook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

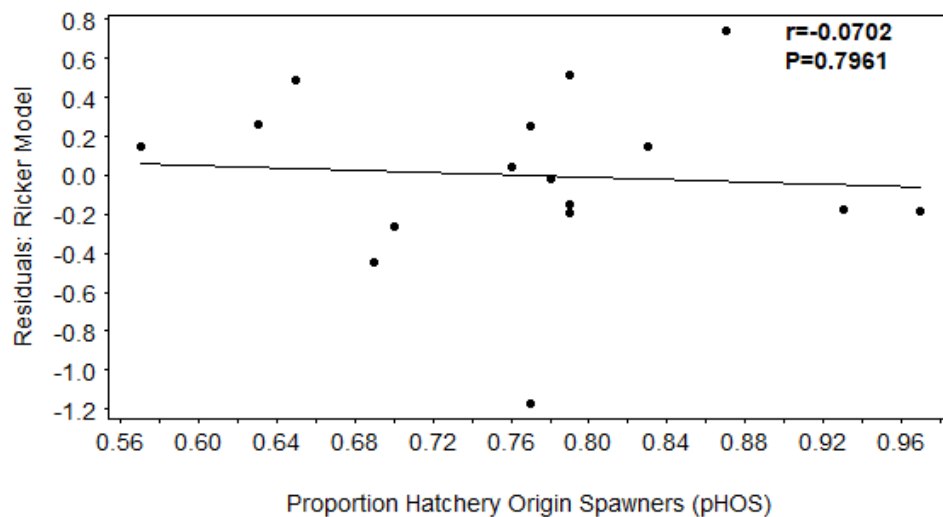


Figure 50. Residuals from the Ricker Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Methow River Spring Chinook Salmon,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

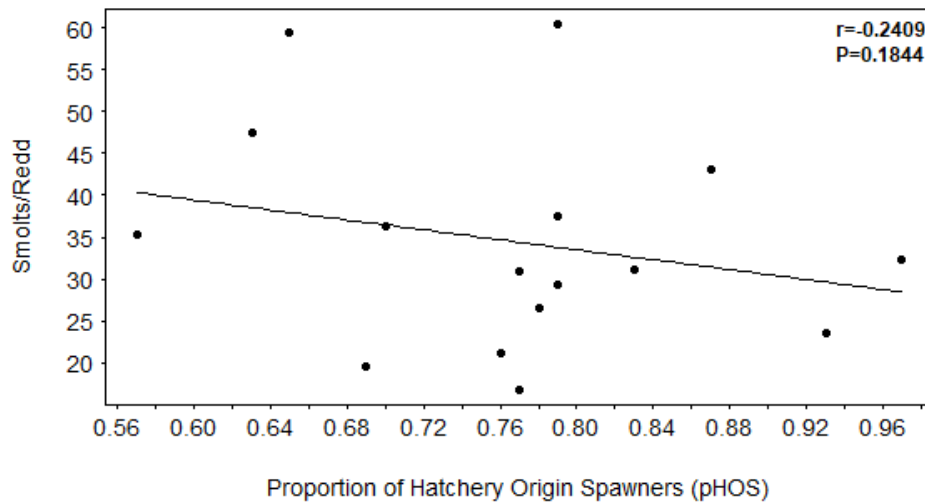


Figure 51. Smolts per redd versus proportion of hatchery origin spawners (pHOS) for Methow River Spring Chinook Salmon, 2002–2017, with fitted linear regression line, Pearson correlation coefficient (r), and P -value from one-sided t -test of negative slope. $R^2 = 0.0580$.

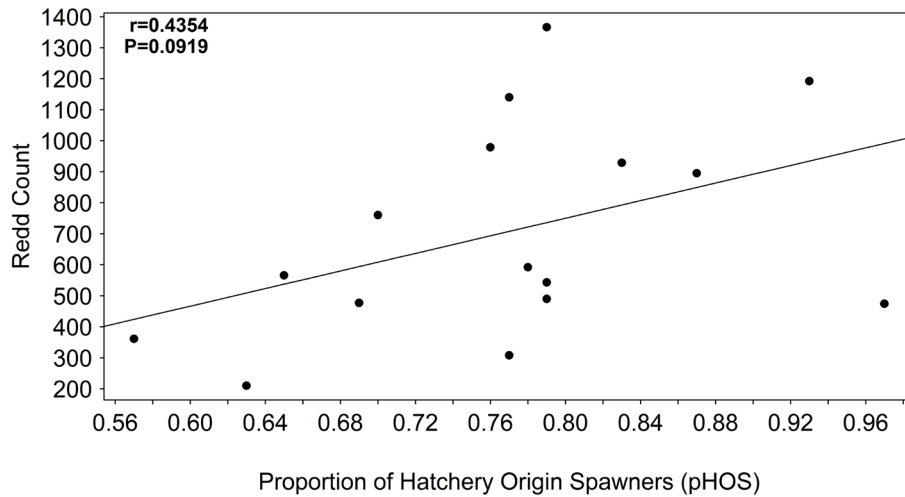


Figure 52. Redd count versus proportion of hatchery origin spawners (pHOS) for Methow River Spring Chinook Salmon, 2002–2017, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope.

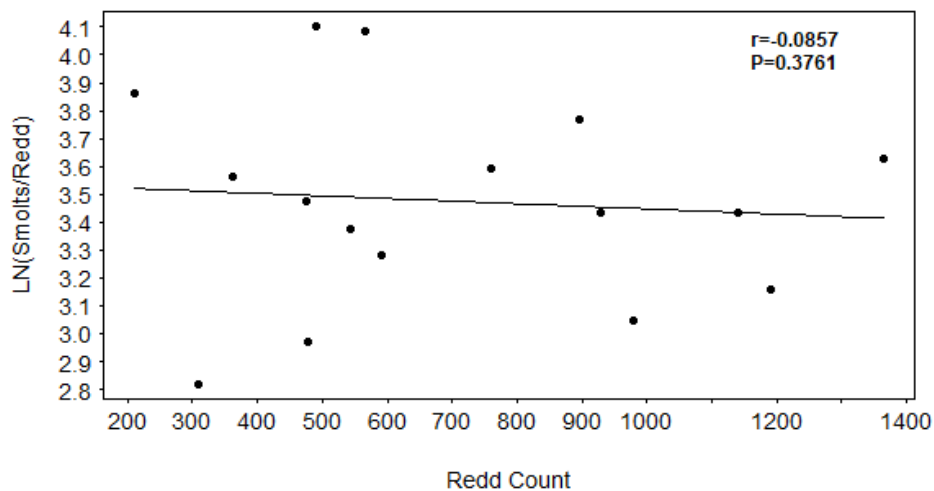


Figure 53. Smolts per redd (log scale) versus redd count for Methow River Spring Chinook Salmon, 2002–2017, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. Negative slope indicates post-spawning density dependence.

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.

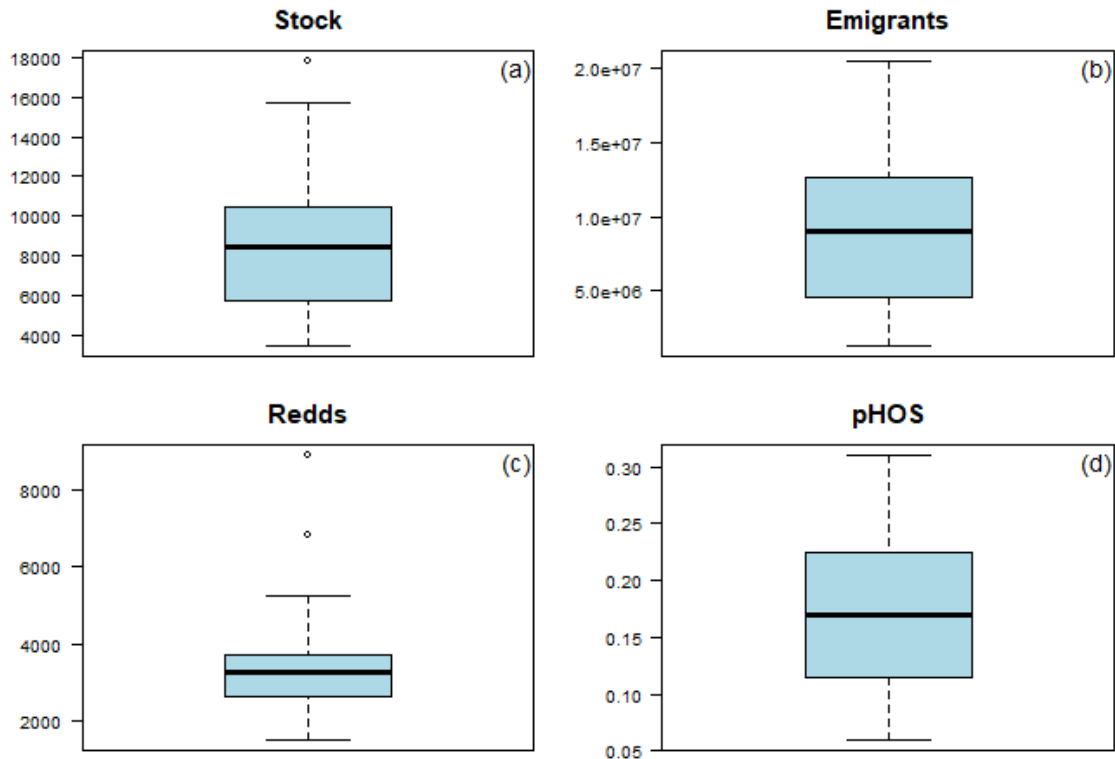


Figure 54. Wenatchee River Summer Chinook Salmon boxplots for Stock (spawner abundance), Emigrant counts, Redd counts, and proportion of hatchery origin spawners (pHOS), 1999–2018, without 2010 and 2011. Box indicates interquartile range and thick horizontal bar is median. Whiskers indicate quartile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

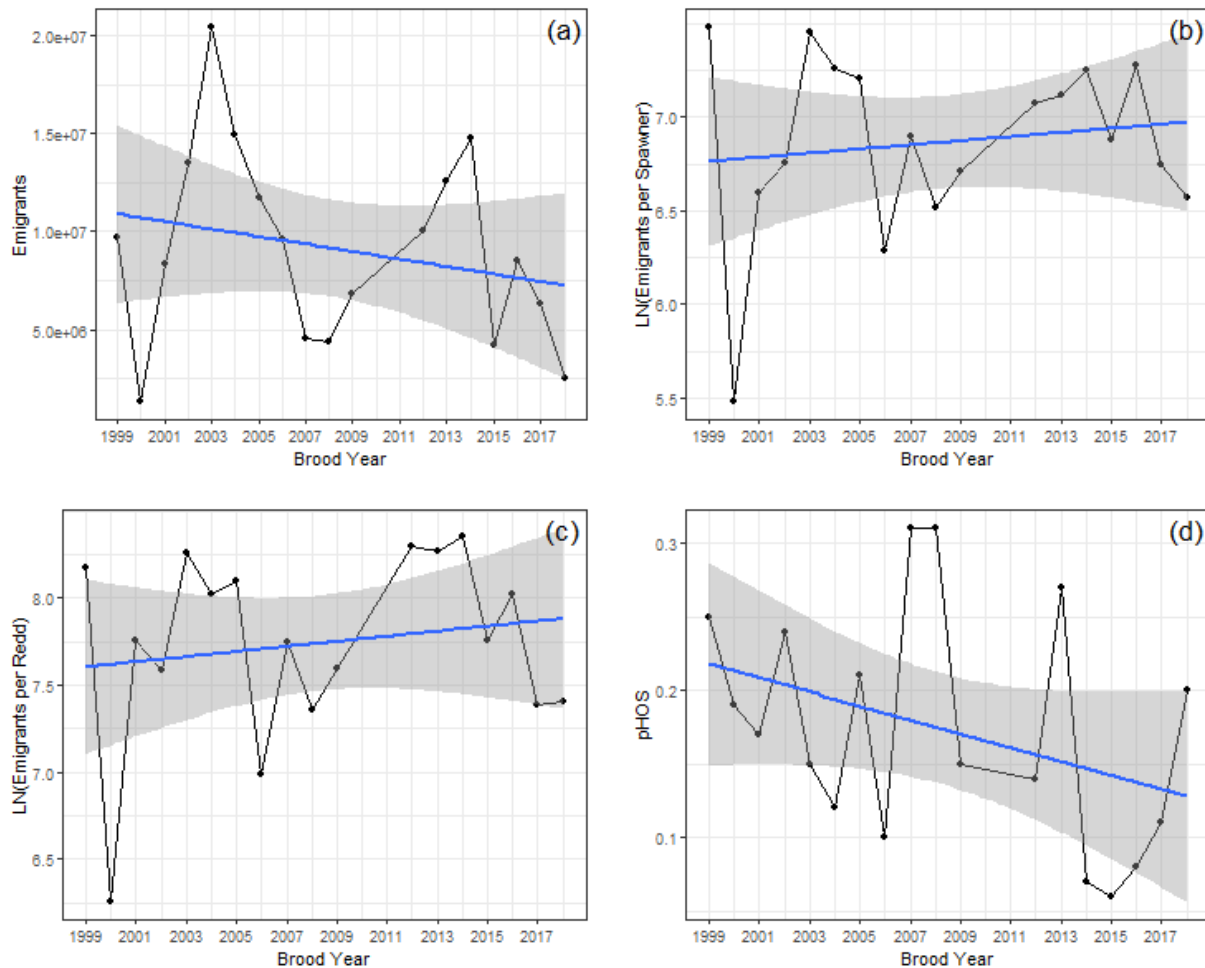


Figure 55. Wenatchee River Summer Chinook Salmon annual Emigrant counts, Emigrant/Spawner (log scale), Emigrant/Redd (log scale), and proportion of hatchery origin spawners (pHOS), 1999–2018 (without 2010, 2011). Line indicates the linear trend. Shaded area is the estimated 95% confidence interval of 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 ($\Delta AICc \leq 0.0072$); pHOS was not associated with the residuals from any of the models ($P \geq 0.7155$). 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 ($\Delta AICc \leq 0.1126$). Model residuals were again not significantly associated with

pHOS levels without the 2000 brood year ($P \geq 0.6430$; Figure F3 – Figure F6), and the likelihood ratio test of the pHOS was also not significant ($P \geq 0.6113$).

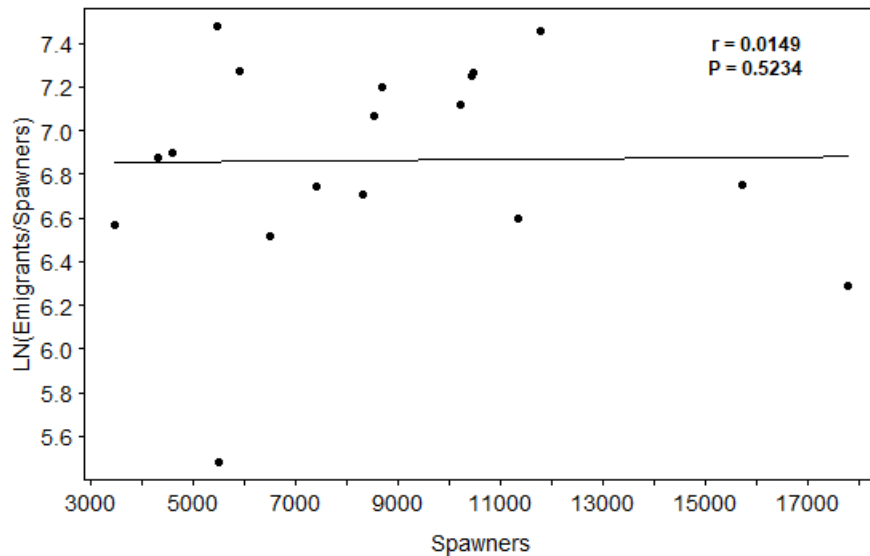


Figure 56. Emigrants per spawner (log scale) versus spawner abundance for Wenatchee River Summer Chinook Salmon, 1999–2018 (without 2010, 2011), with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope.

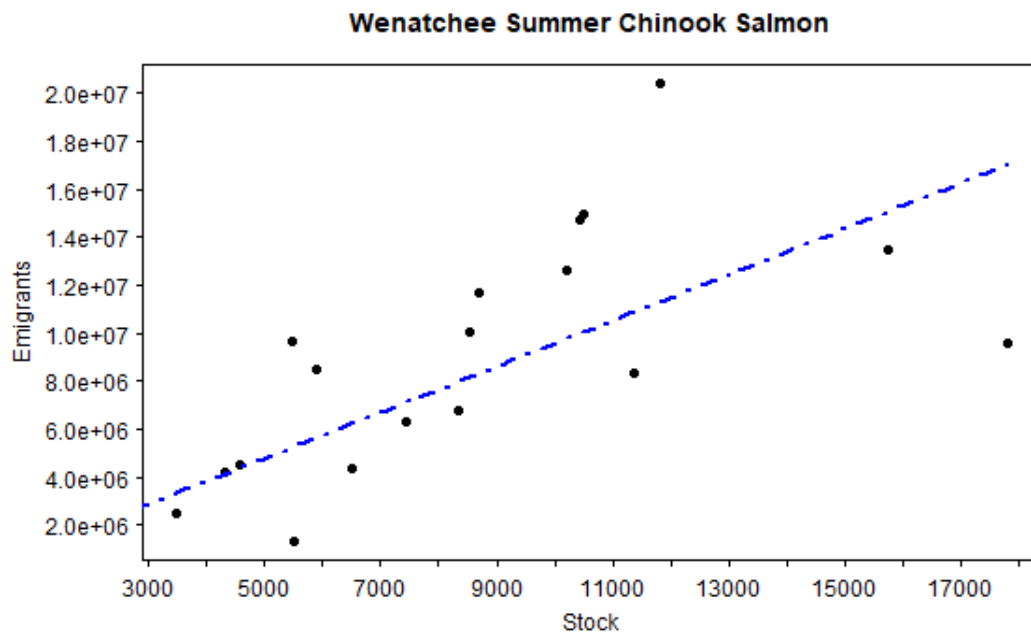


Figure 57. The Ricker stock-recruitment model fit to emigrants and spawner data for Wenatchee River Summer Chinook Salmon, 1999–2018 (without 2010, 2011).

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 $K=(a/\beta)e^{-l}$ for the Ricker model.

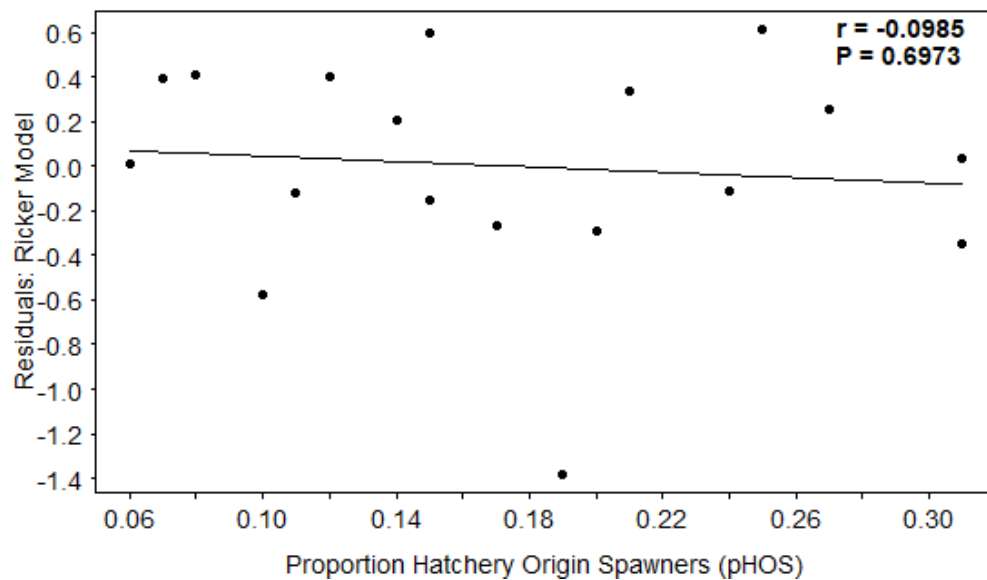


Figure 58. Residuals from Ricker Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using emigrant and spawner data from Wenatchee River Summer Chinook 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 ($\Delta AICc = 0.01$ 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).

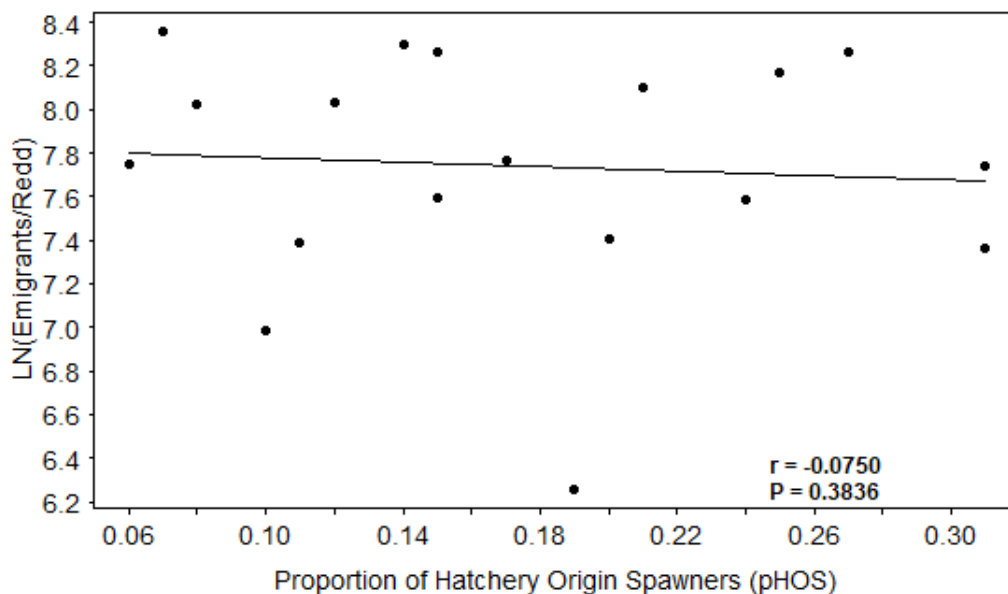


Figure 59. Emigrants per redd (log scale) versus proportion of hatchery origin spawners (pHOS) for Wenatchee River Summer Chinook Salmon, 1999–2018 (without 2010, 2011), with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. $R^2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

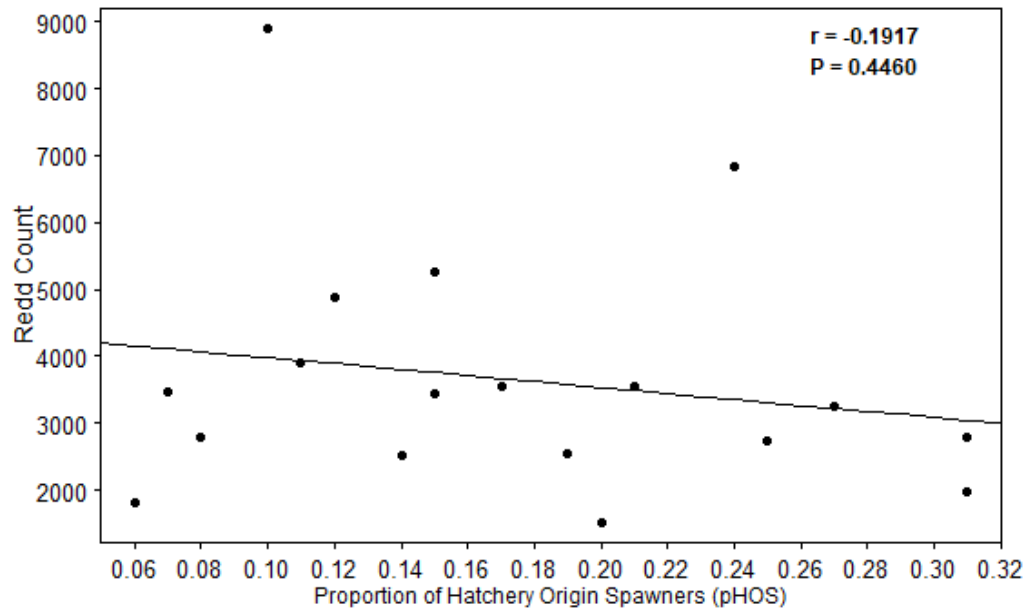


Figure 60. Redd count versus proportion of hatchery origin spawners (pHOS) for Wenatchee River Summer Chinook Salmon, 1999–2018 (without 2010, 2011), with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope.

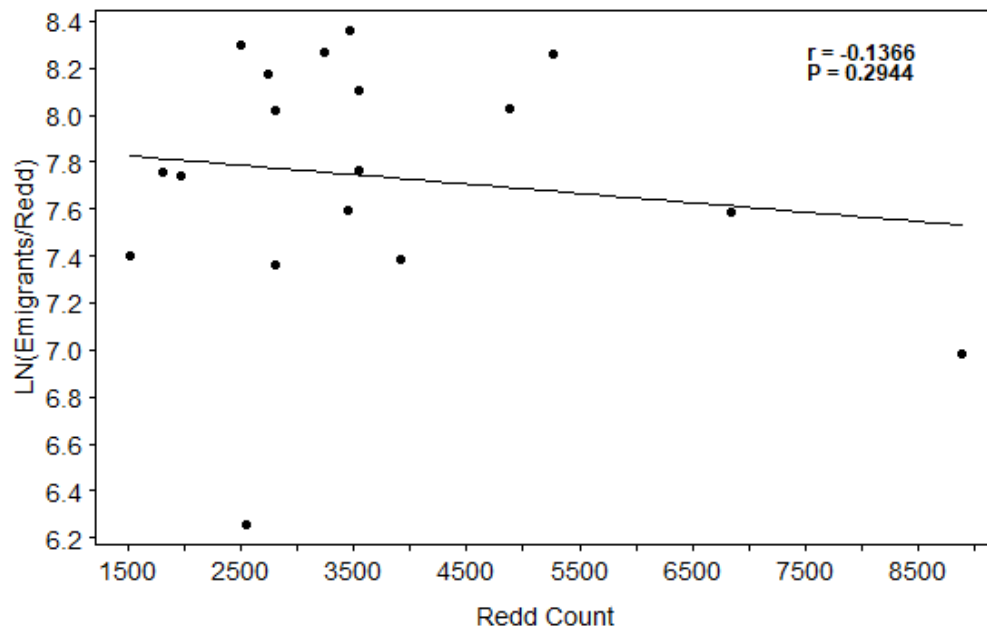


Figure 61. Emigrants per redd versus redd count for Wenatchee River Summer Chinook Salmon, 1999–2018 (without 2010, 2011), with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. Negative slope indicates post-spawning density dependence.

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).

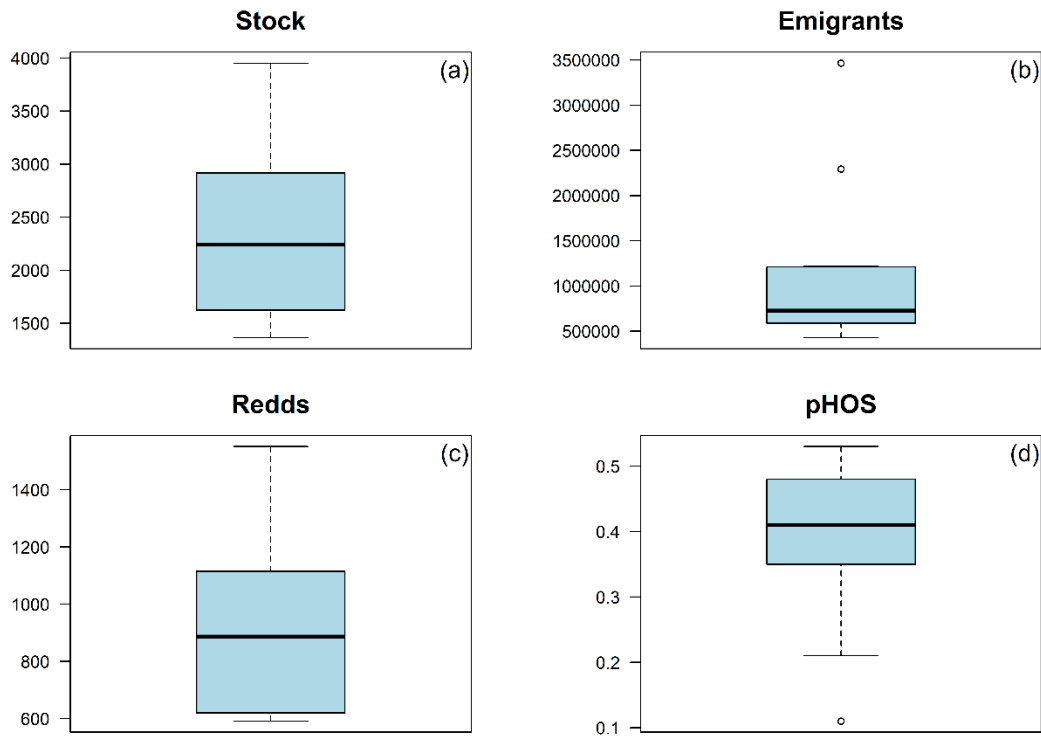


Figure 62. Methow River Summer Chinook Salmon boxplots for Stock (spawner abundance), Emigrant counts, Redd counts, and proportion of hatchery origin spawners (pHOS), 2006–2018. Box indicates interquartile range and thick horizontal bar is median. Whiskers indicate quartile $\pm 1.5 \times$ interquartile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

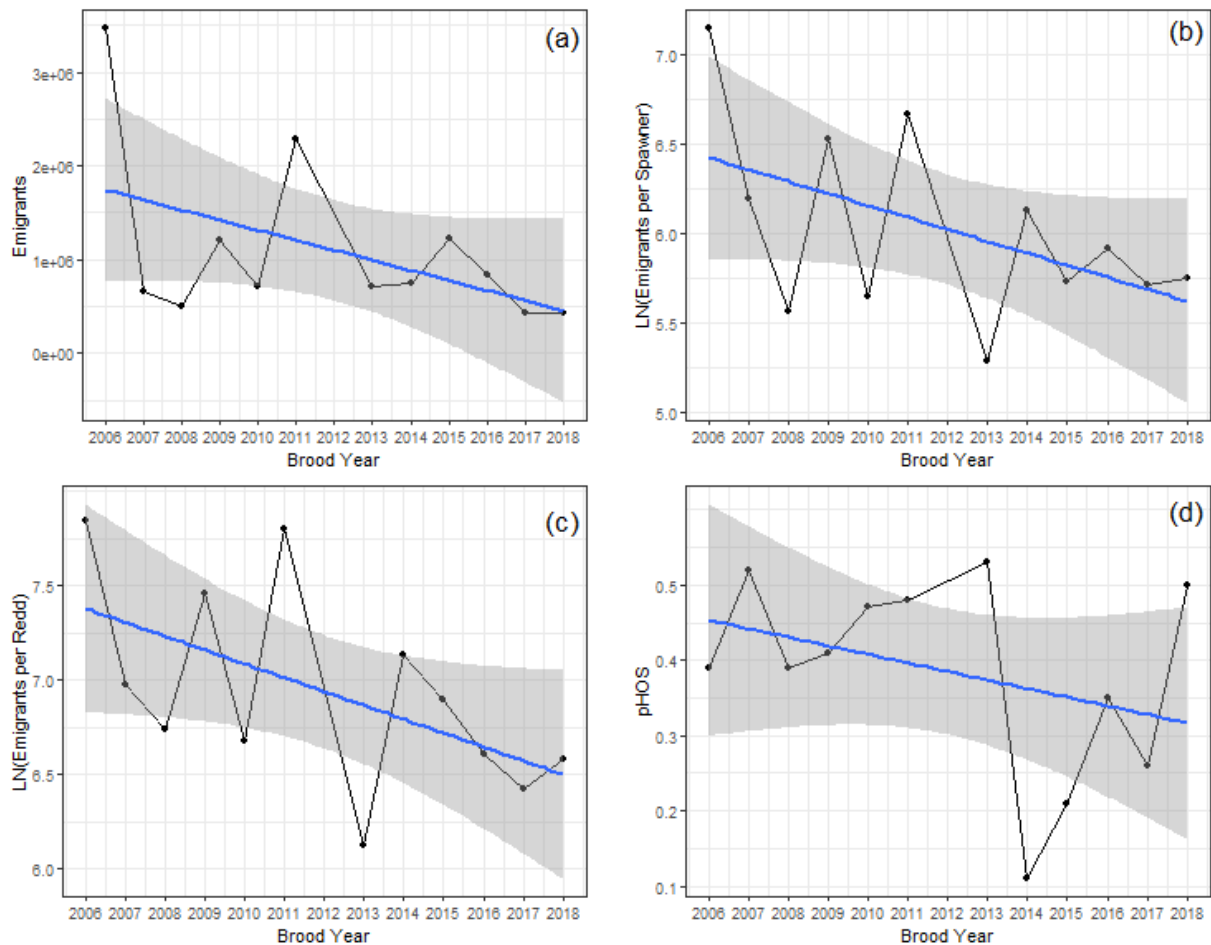


Figure 63. Methow River Summer Chinook Salmon annual Emigrant counts, Emigrant/Spawner (log scale), Emigrant/Redd (log scale), and proportion of hatchery origin spawners (pHOS), 2006–2018 (without 2012). Line indicates the linear trend. Shaded area is the estimated 95% confidence interval of the line.

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 ($\Delta AICc \leq 0.02$), 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 ($P \geq 0.9838$). 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.

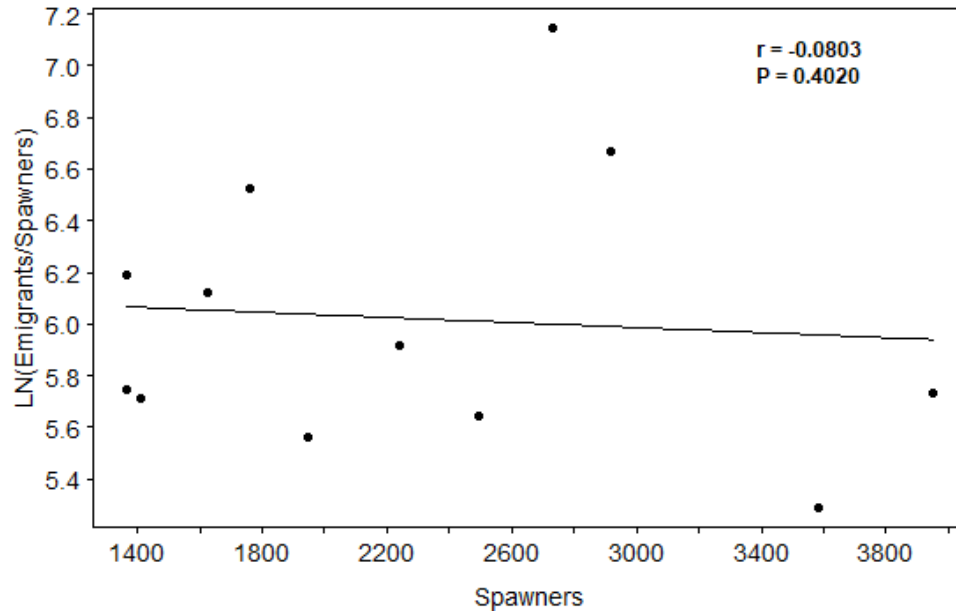


Figure 64. Emigrants per spawner (log scale) versus spawner abundance for Methow River Summer Chinook Salmon, 2006–2018 (without 2012), with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope.

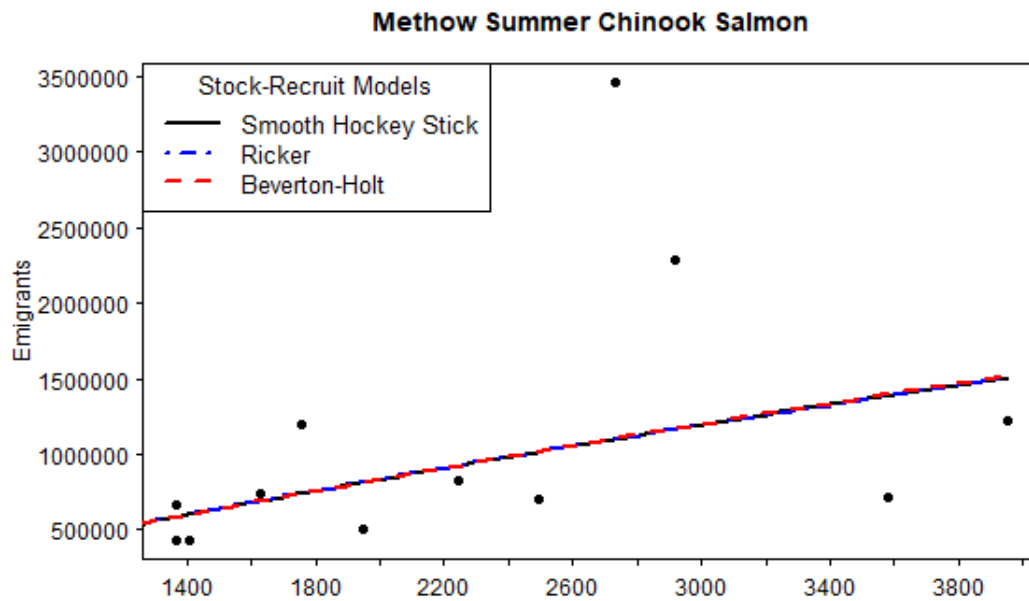


Figure 65. Stock-recruitment models fit to emigrants and spawner data for Methow River Summer Chinook Salmon, 2006–2018 (without 2012).

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	$\alpha, R_\infty: -0.23^a$
			R_∞	4,796,000	889,141 – 19,840,304	
Beverton-Holt	26.86	0.02	α	9,817,511	874,870 – 66,701,078	$\alpha, \beta: 0.99$
			β	21,552	-26.7 – 16,434.1	
Ricker	26.84	0.00	α	461	331.4 – 1032.5	$\alpha, \beta: 0.88$
			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.

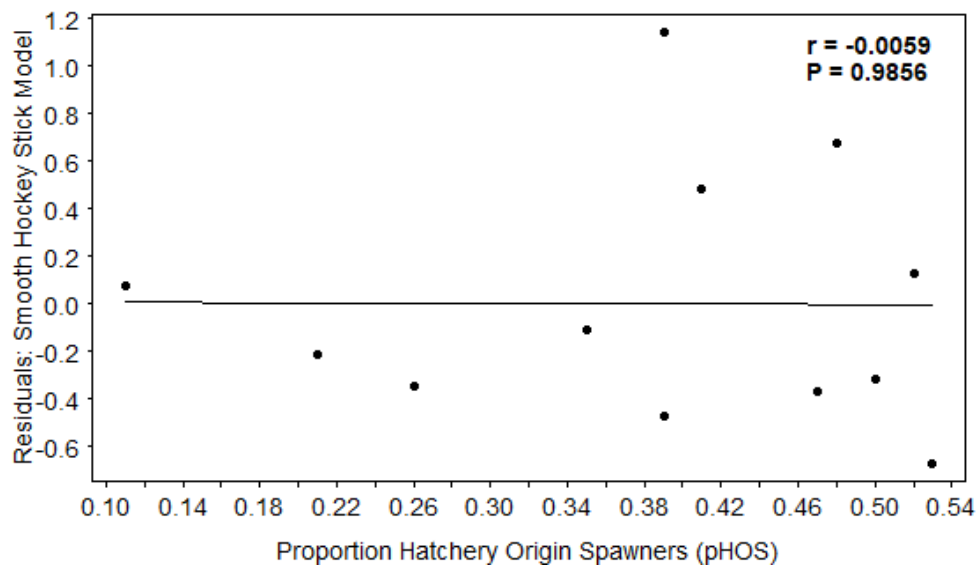


Figure 66. Residuals from Smooth Hockey Stick Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using emigrant and spawner data from Methow River Summer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

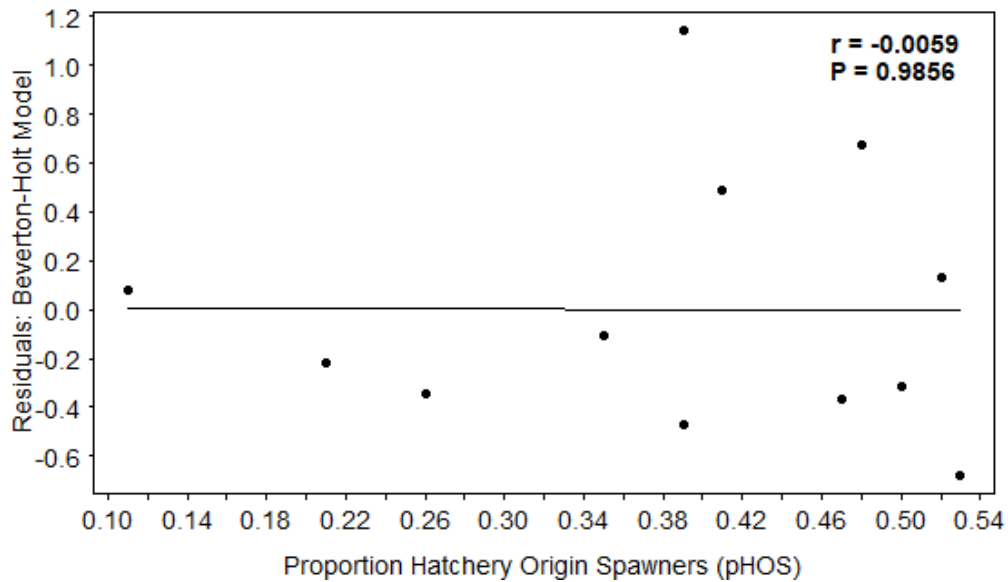


Figure 67. Residuals from Beverton-Holt Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using emigrant and spawner data from Methow River Summer Chinook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

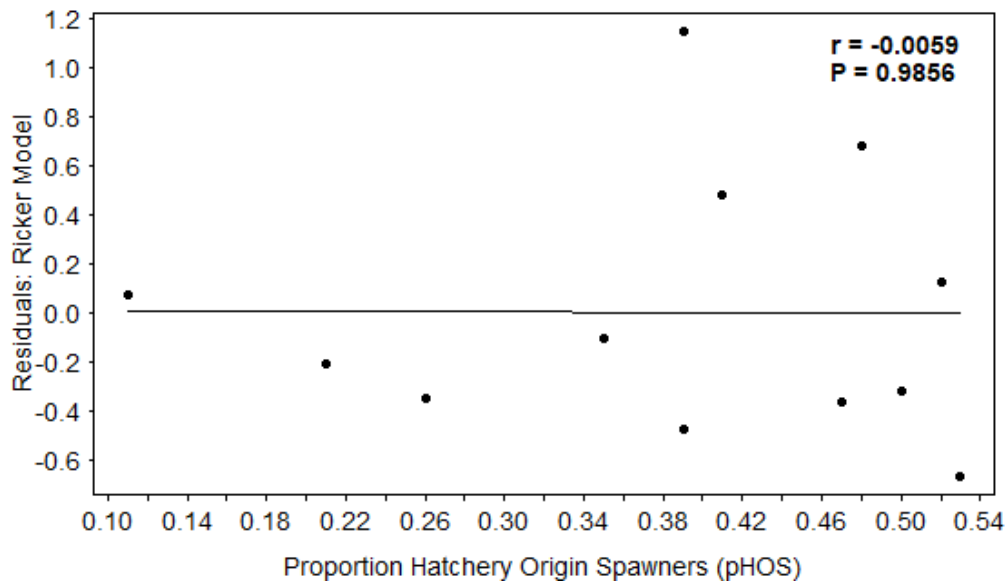


Figure 68. Residuals from Ricker Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using emigrant and spawner data from Methow River Summer Chinook Salmon,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

Hypothesis H02.2.1.2

There was a very weak and non-significant negative association between $\ln(\text{emigrants per redd})$ 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 ($\Delta\text{AICc} = 0.001$ 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.

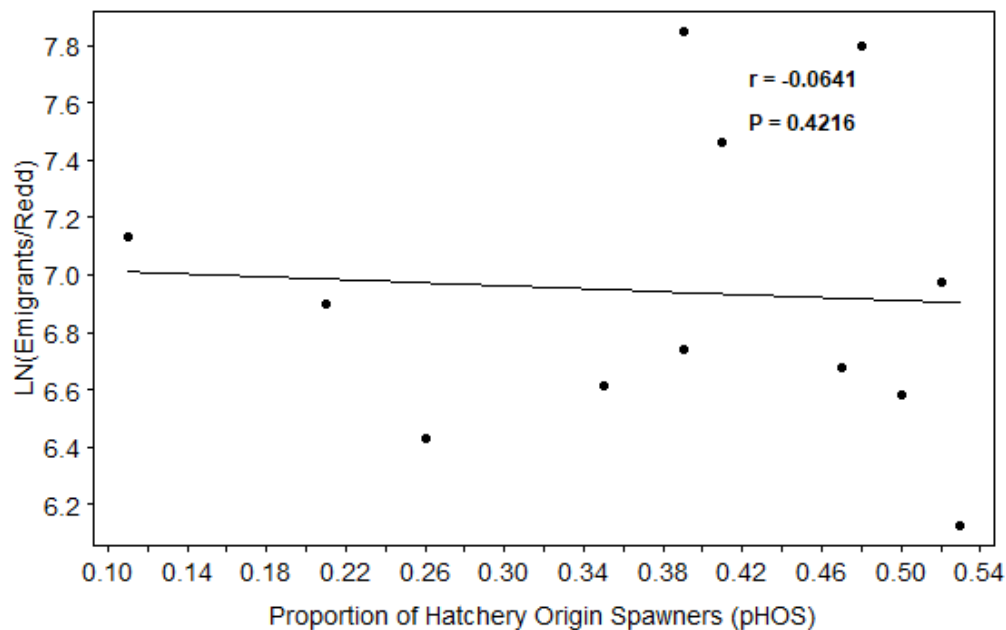


Figure 69. Emigrants per redd (log scale) versus proportion of hatchery origin spawners (pHOS) for Methow River Summer Chinook Salmon, 2006–2018 (without 2012), with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. $R^2 = 0.0041$.

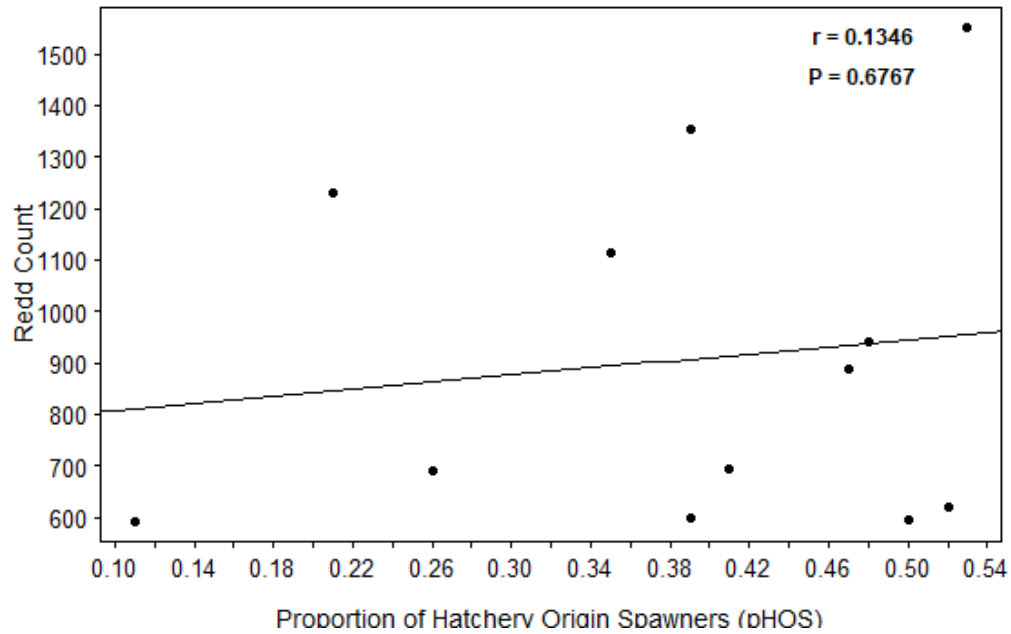


Figure 70. Redd count versus proportion of hatchery origin spawners (pHOS) for Methow River Summer Chinook Salmon, 2006–2018 (without 2012), with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope.

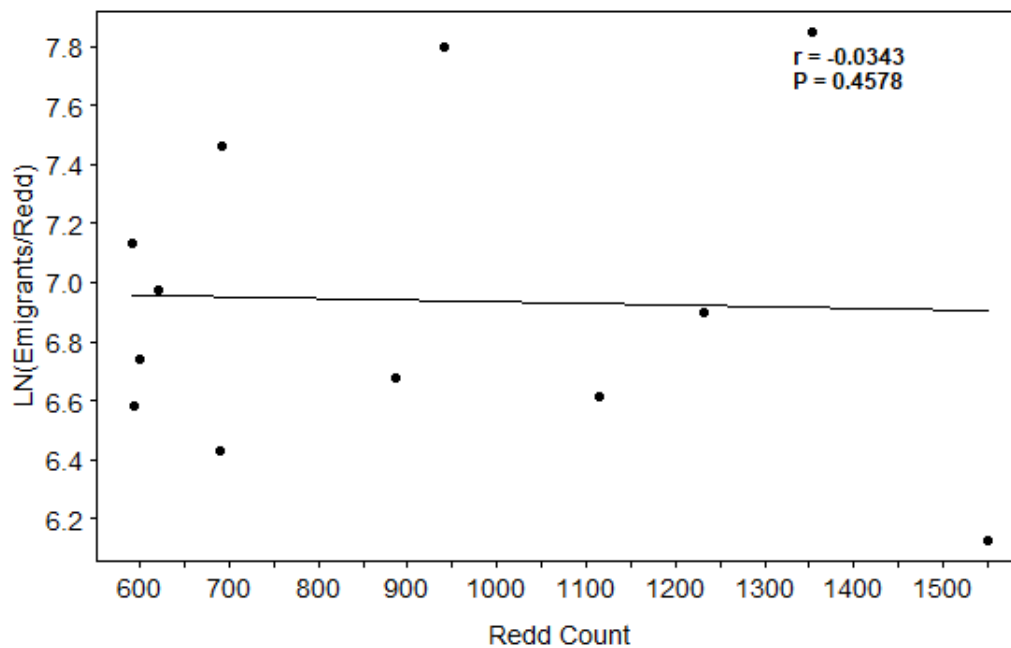


Figure 71. Emigrants per redd versus redd count for Methow River Summer Chinook Salmon, 2006–2018 (without 2012), with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. Negative slope indicates post-spawning density dependence.

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 $\geq 1,000$ 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).

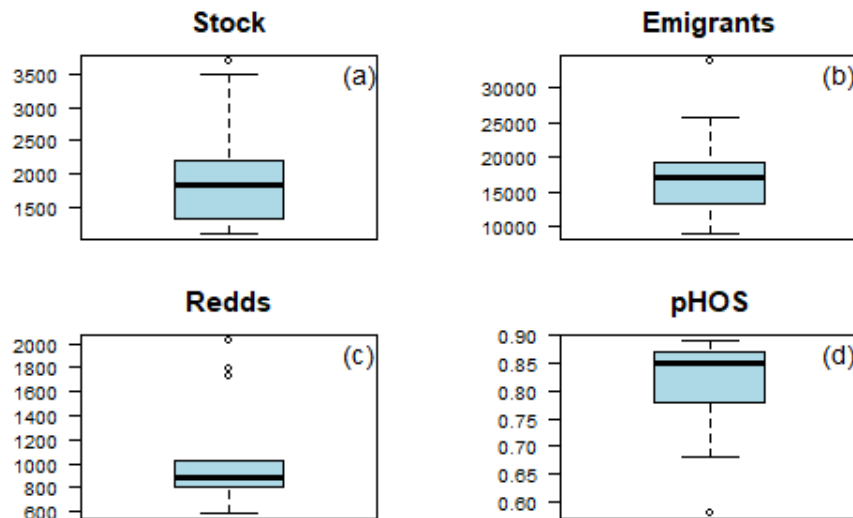


Figure 72. Methow River Summer Steelhead boxplots for Stock (spawner abundance), Emigrants, Redd counts, and proportion of hatchery origin spawners (pHOS), 2003–2015. Box indicates interquartile range and thick horizontal bar is median. Whiskers indicate quartile $\pm 1.5 \times$ interquartile range.

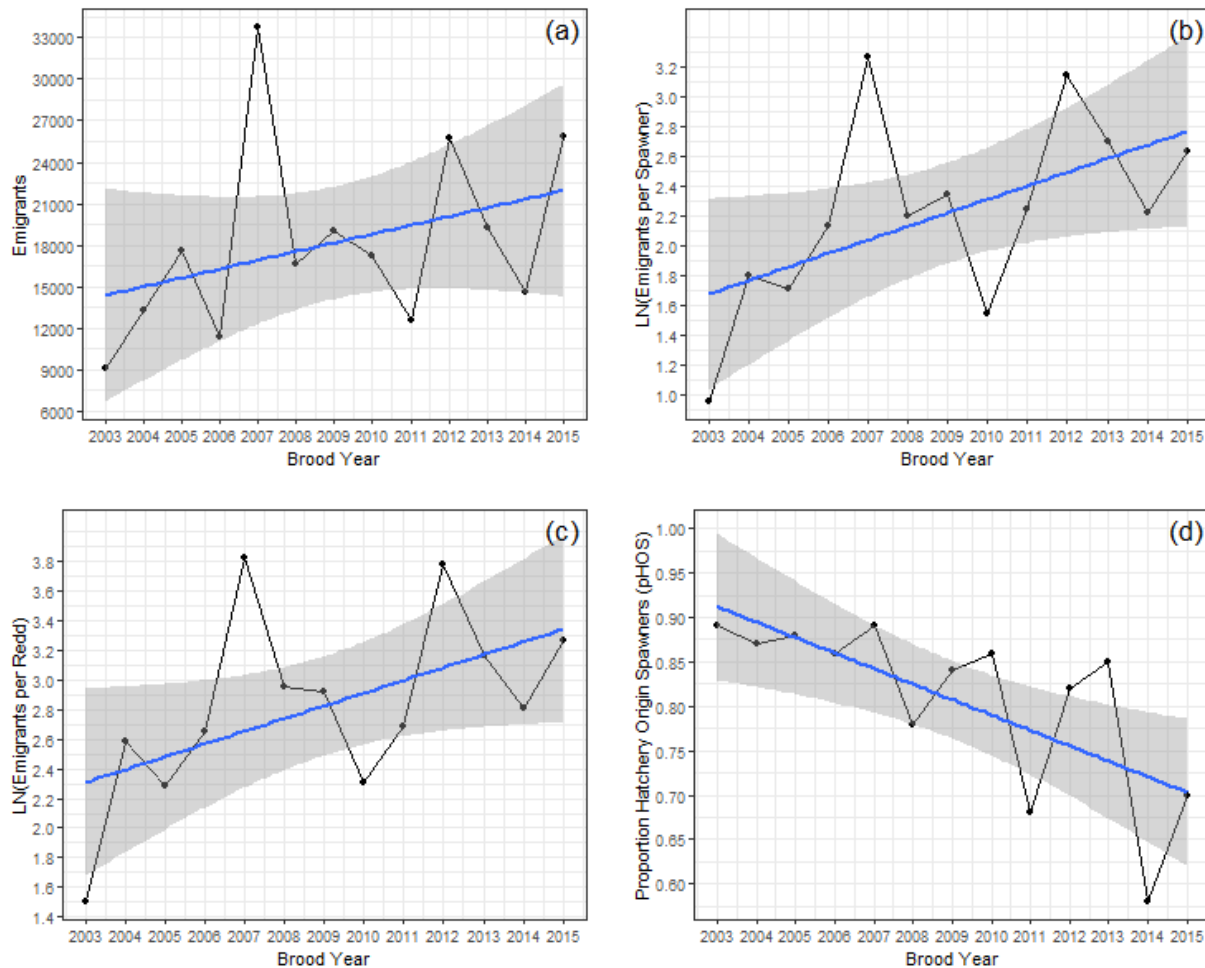


Figure 73. Methow River Summer Steelhead annual Emigrant counts, Emigrant/Spawner (log scale), Emigrant/Redd (log scale), and proportion of hatchery origin spawners (pHOS), 2003–2015. Line indicates the linear trend. Shaded area is the estimated 95% confidence interval of the line.

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.

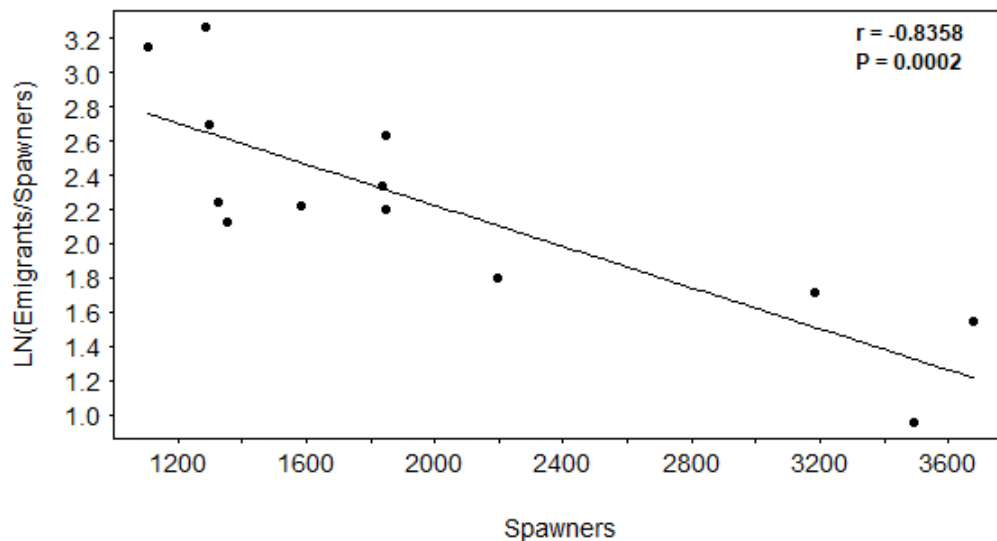


Figure 74. Emigrants per spawner (log scale) versus spawner abundance for Methow River Summer Steelhead, 2003–2015, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope.

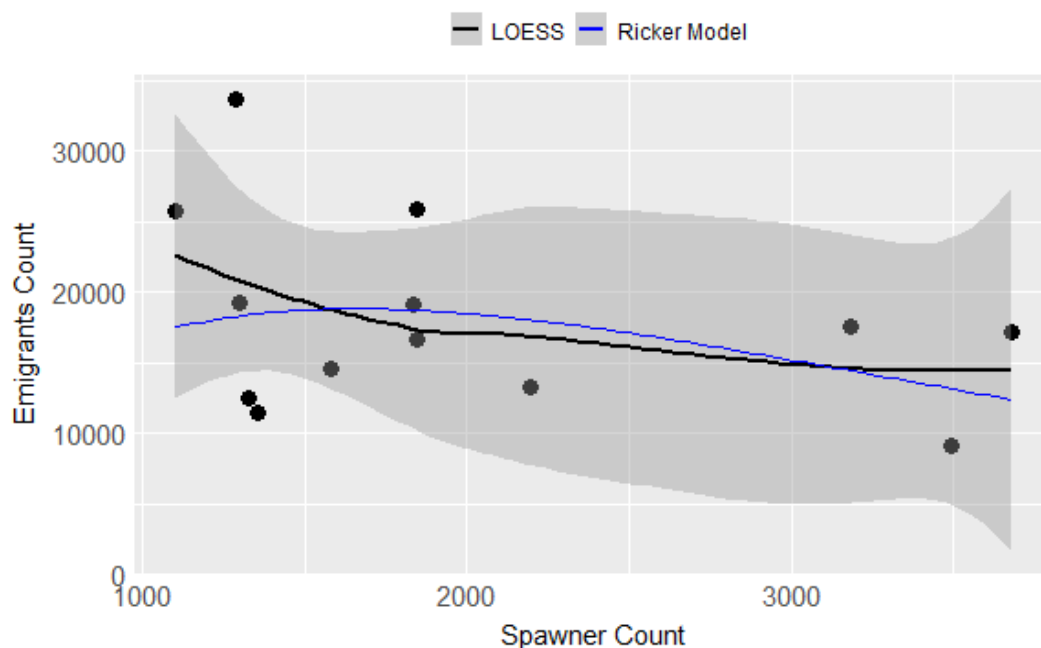


Figure 75. Stock and emigrant data with fitted LOESS curve and Ricker Model for Methow River Summer Steelhead, 2003–2015.

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.

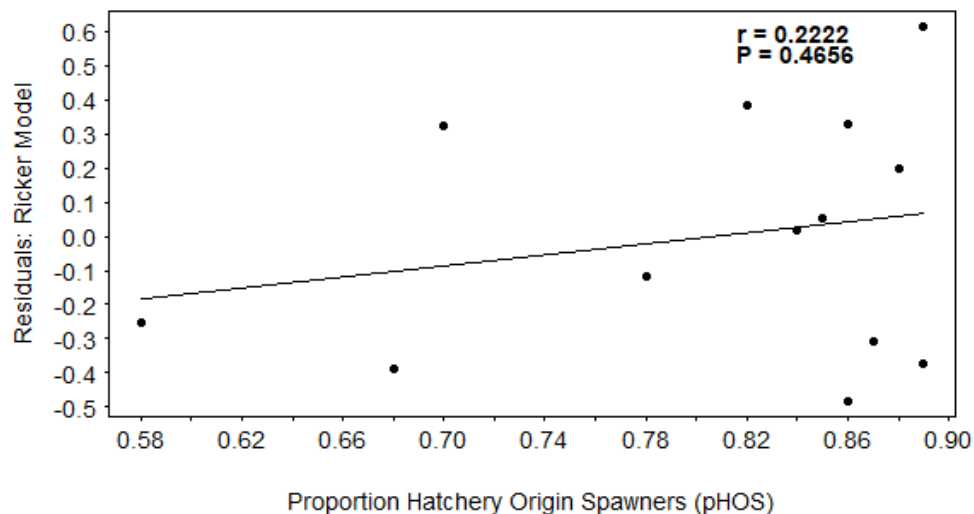


Figure 76. Residuals from the Ricker Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using emigrant and spawner data from Methow River Summer Steelhead,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

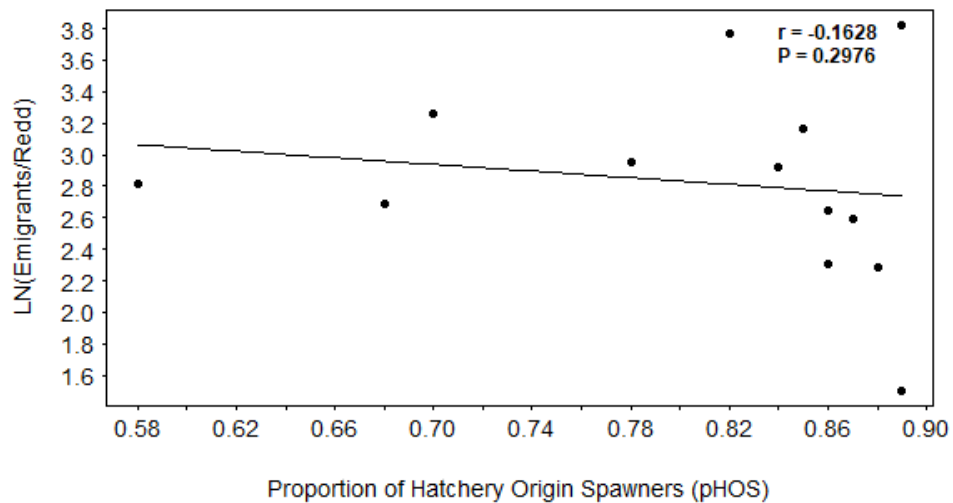


Figure 77. Emigrants per redd (log scale) versus proportion of hatchery origin spawners (pHOS) for Methow River Summer Steelhead, 2003–2015, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. $R^2 = 0.0265$.

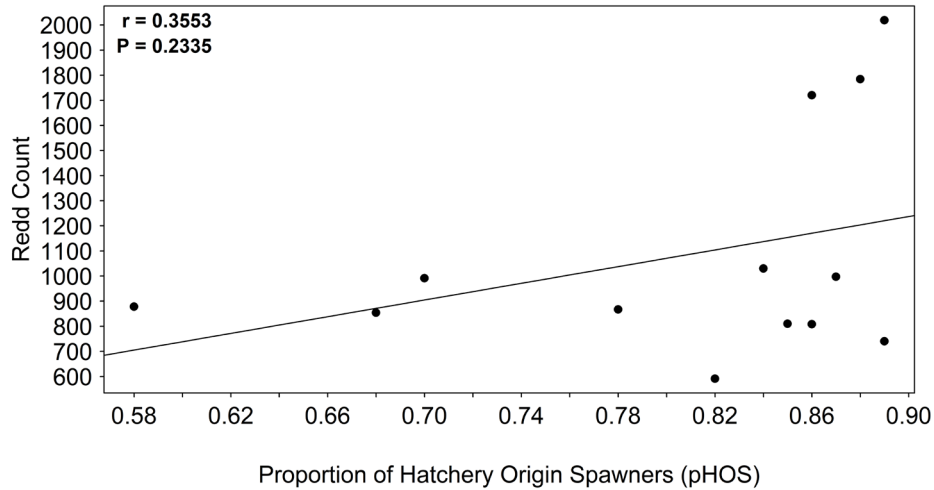


Figure 78. Redd count versus proportion of hatchery origin spawners (pHOS) for Methow River Summer Steelhead, 2003–2015, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope.

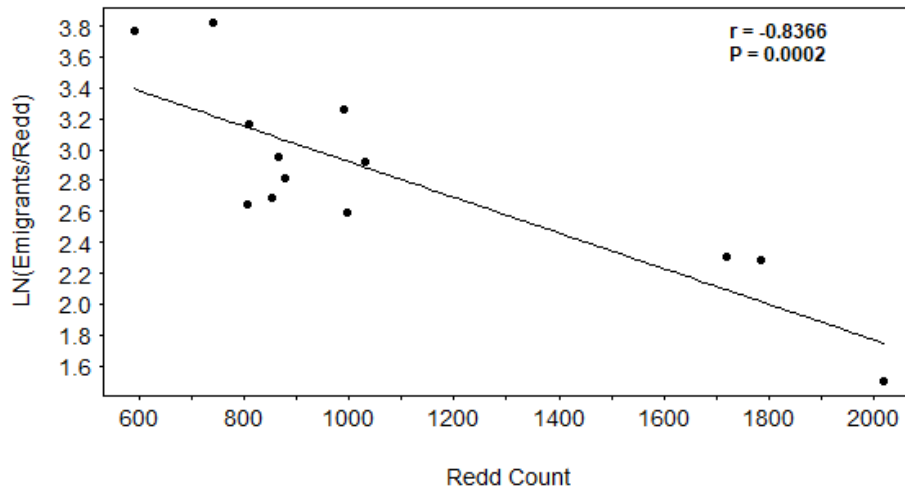


Figure 79. Emigrants per redd (log scale) versus redd count for Methow River Summer Steelhead, 2003–2015, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. Negative slope indicates post-spawning density dependence.

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).

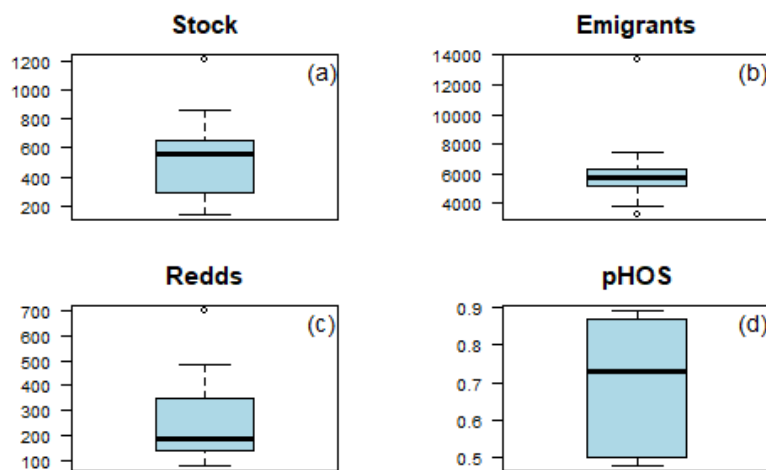


Figure 80. Twisp River Summer Steelhead boxplots for Stock (spawner abundance), Emigrants, Redd counts, and proportion of hatchery origin spawners (pHOS), 2003–2015. Box indicates interquartile range and thick horizontal bar is median. Whiskers indicate quartile $\pm 1.5 \times$ interquartile range.

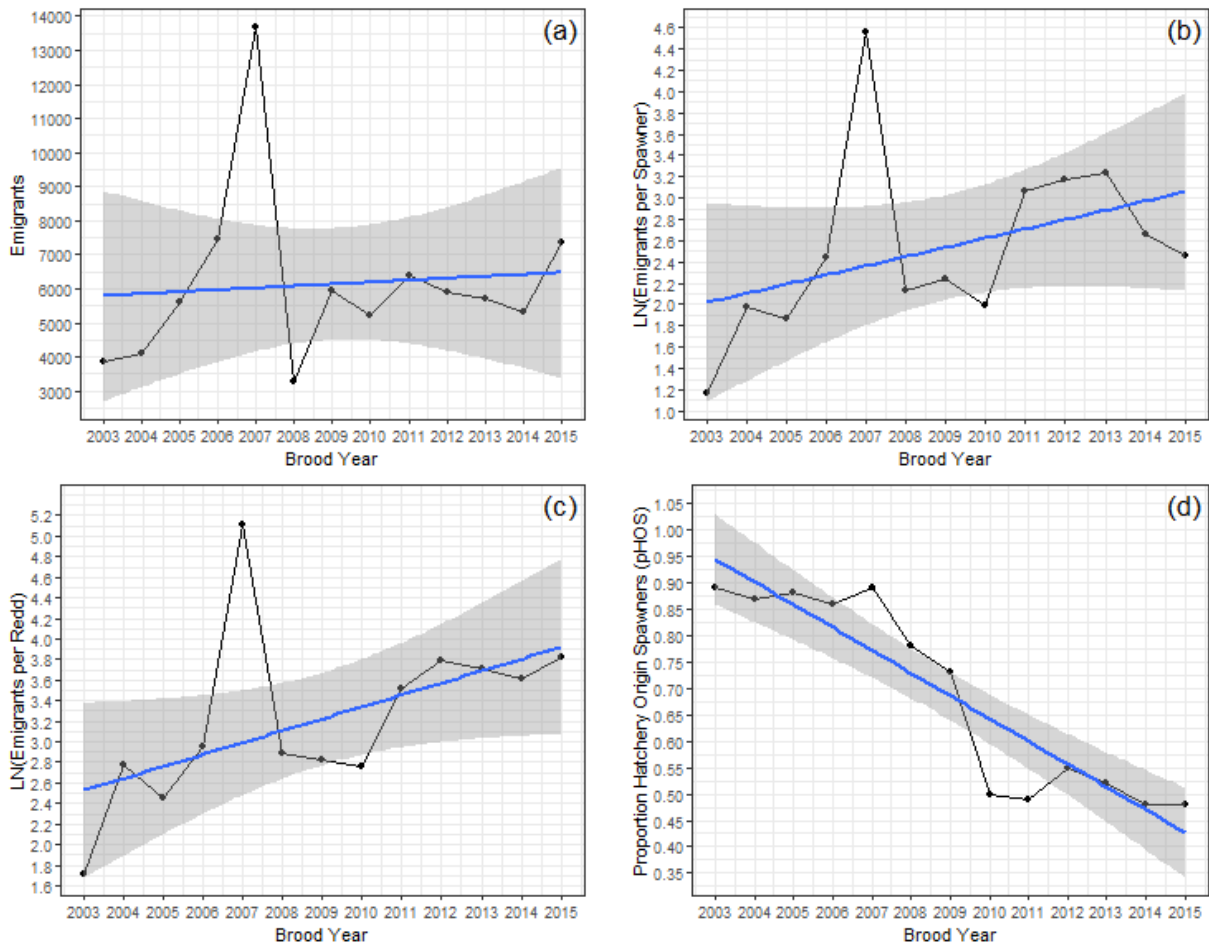


Figure 81. Twisp River Summer Steelhead annual Emigrant counts, Emigrant/Spawner (log scale), Emigrant/Redd (log scale), and proportion of hatchery origin spawners (pHOS), 2003–2015. Line indicates the linear trend. Shaded area is the estimated 95% confidence interval of the line.

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.

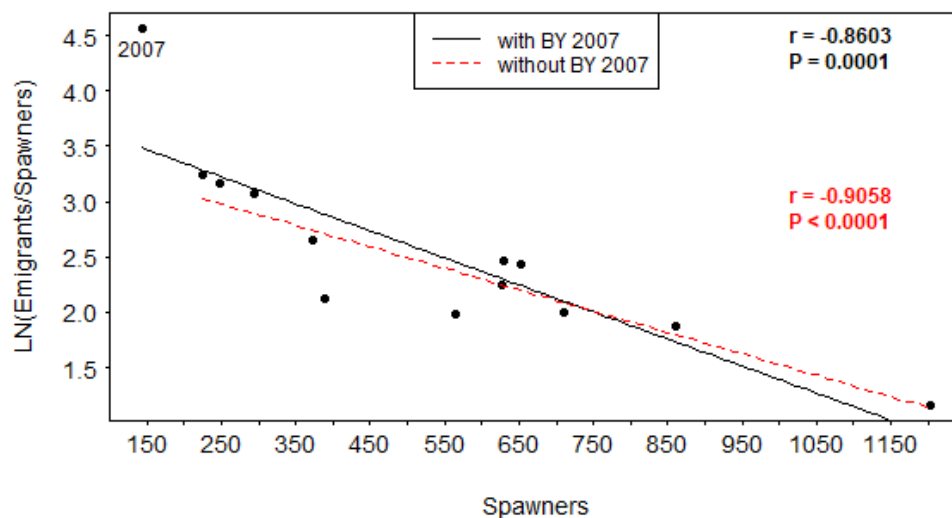


Figure 82. Emigrants per spawner (log scale) versus spawner abundance for Twisp River Summer Steelhead, 2003–2015, with and without brood year 2007, with fitted linear regression line, Pearson correlation coefficient (r), and P -value from one-sided t -test of negative slope.

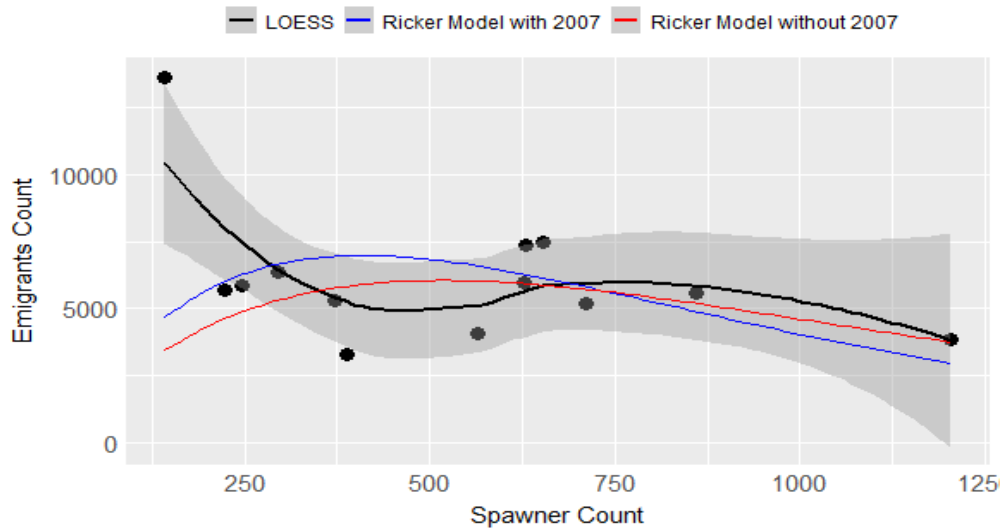


Figure 83. Stock and emigrant data with fitted LOESS curve and Ricker Model for Twisp River Summer Steelhead, 2003–2015, with and without brood year 2007.

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). $\Delta AICc$ 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	$\Delta AICc$	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.

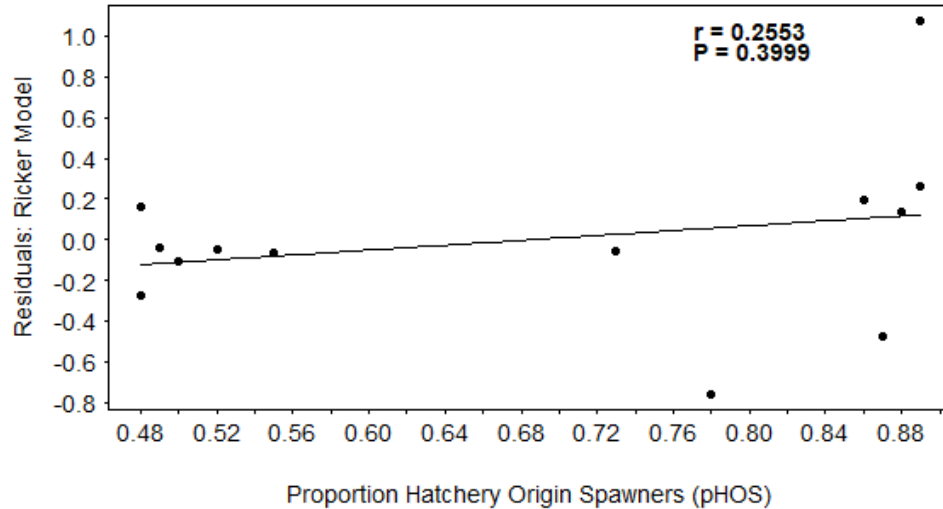


Figure 84. Residuals from the Ricker Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using emigrant and spawner data from Twisp River Summer Steelhead,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

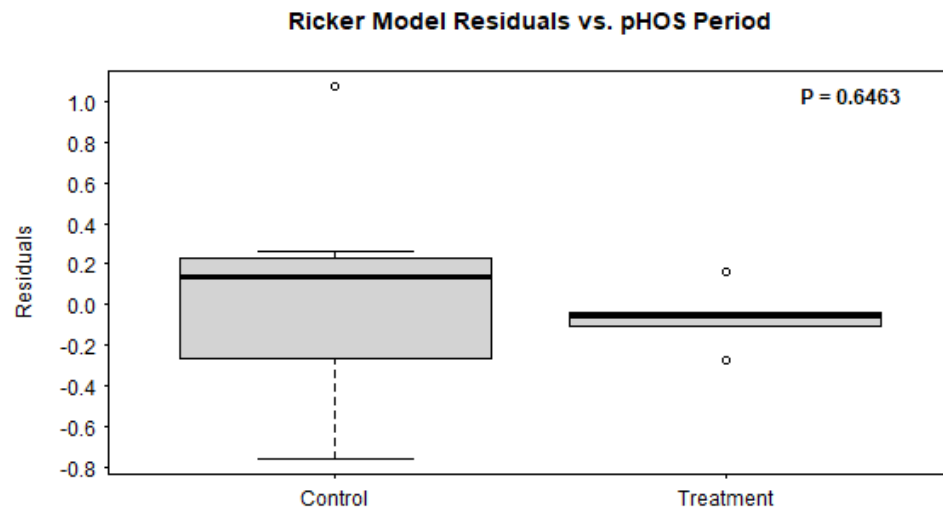


Figure 85. Distribution of residuals from the Ricker Model categorized by pHOS management period: Control = pre-2010, when pHOS levels were not restricted, and Treatment = 2010–2015, when pHOS levels were targeted at 0.5. P-value is from two-sided t-test: $t\text{-test} = -0.4717$, $df = 11$. Data used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

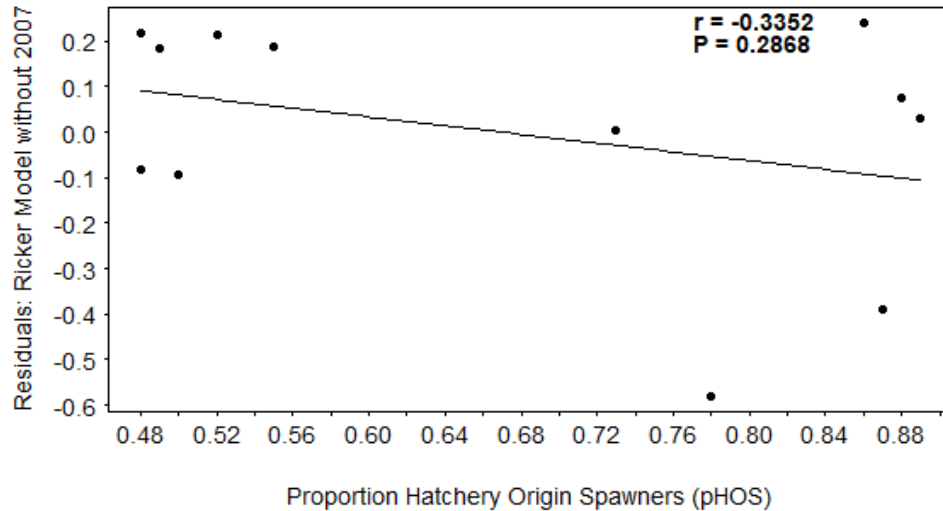


Figure 86. Residuals from the Ricker Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using emigrant and spawner data from Twisp River Summer Steelhead,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

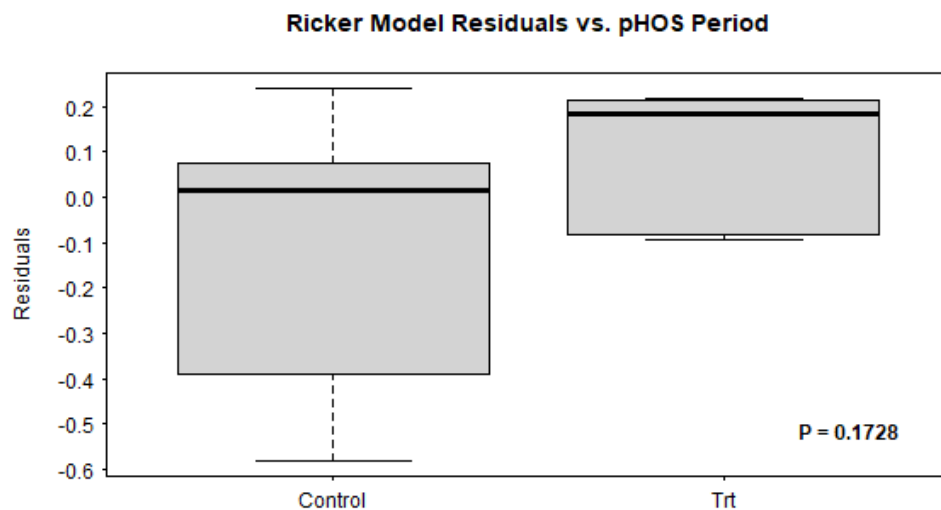


Figure 87. Distribution of residuals from the Ricker Model categorized by pHOS management period: Control = pre-2010, when pHOS levels were not restricted, and Treatment = 2010–2015, when pHOS levels were targeted at 0.5. P-value is from two-sided t-test: t -test = 1.4683, $df = 10$. Data used were emigrant 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).

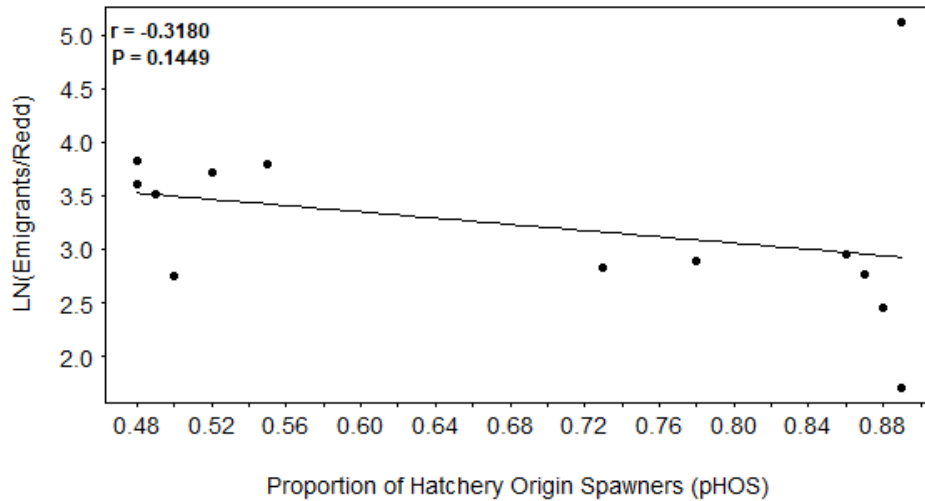


Figure 88. Emigrants per redd (log scale) versus proportion of hatchery origin spawners (pHOS) for Twisp River Summer Steelhead, 2003–2015, including brood year 2007, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. $R^2 = 0.1011$.

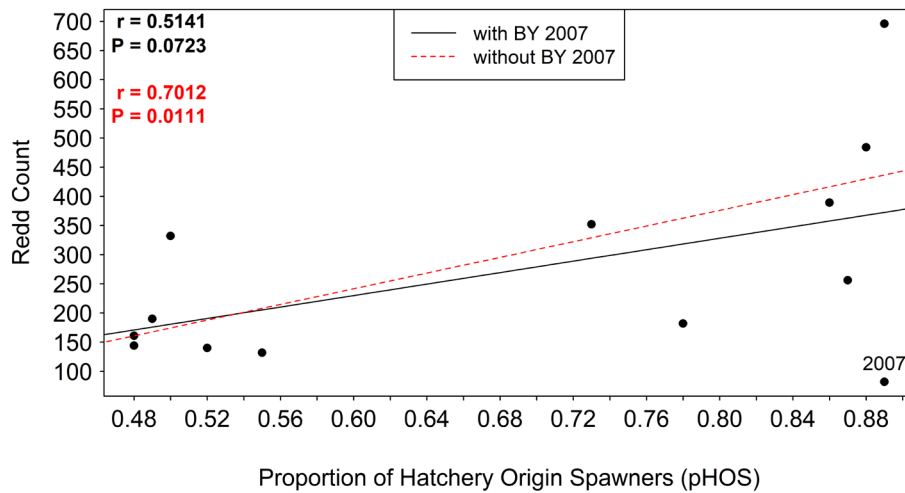


Figure 89. Redd count versus proportion of hatchery origin spawners (pHOS) for Twisp River Summer Steelhead, 2003–2015, with and without brood year 2007, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope.

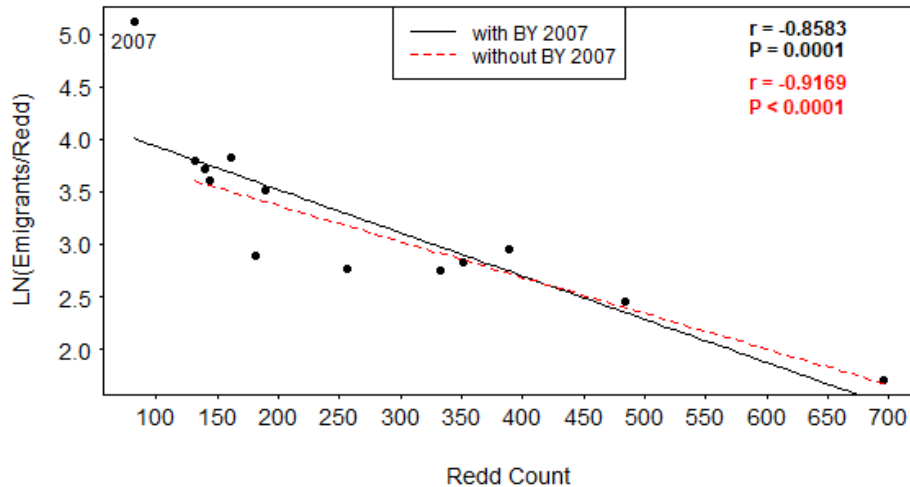


Figure 90. Emigrants per redd (log scale) versus redd count for Twisp River Summer Steelhead, 2003–2015, with and without brood year 2007, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. Negative slope indicates post-spawning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

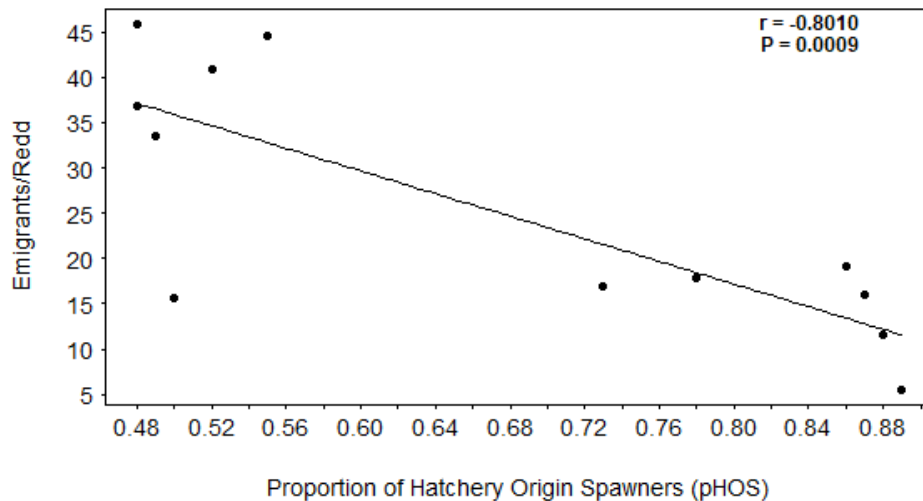


Figure 91. Emigrants per redd versus proportion of hatchery origin spawners (pHOS) for Twisp River Summer Steelhead, 2003–2015, omitting brood year 2007, with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope. $R^2 = 0.6417$.

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.

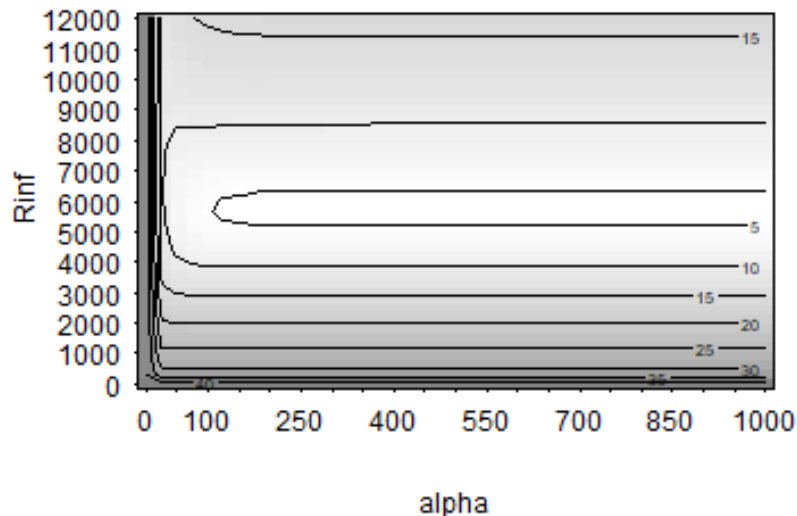


Figure 92. Negative log-likelihood surface and contour curves for the Smooth Hockey Stick model of emigrants and spawner counts. Lighter regions indicate higher likelihood values (lower negative log-likelihood values). The estimated parameter values occur where the negative log-likelihood is minimized.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

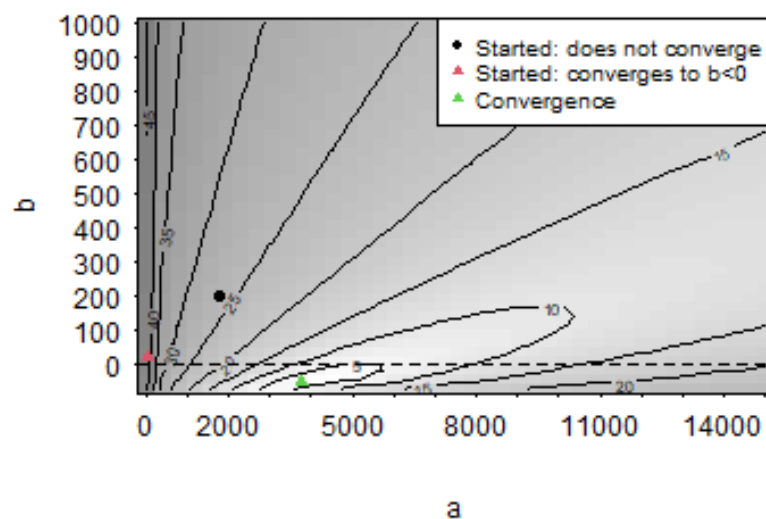


Figure 93. Negative log-likelihood surface and contour curves for Beverton-Holt model of emigrants, redd counts, and pHOS, using $\beta_2 = -0.1160$. Lighter regions indicate higher likelihood values (lower negative log-likelihood values). The estimated parameter values occur where the negative log-likelihood 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.

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Appendices: Evaluation of Modeling Assumptions

Appendix A: Chiwawa River Spring Chinook Salmon

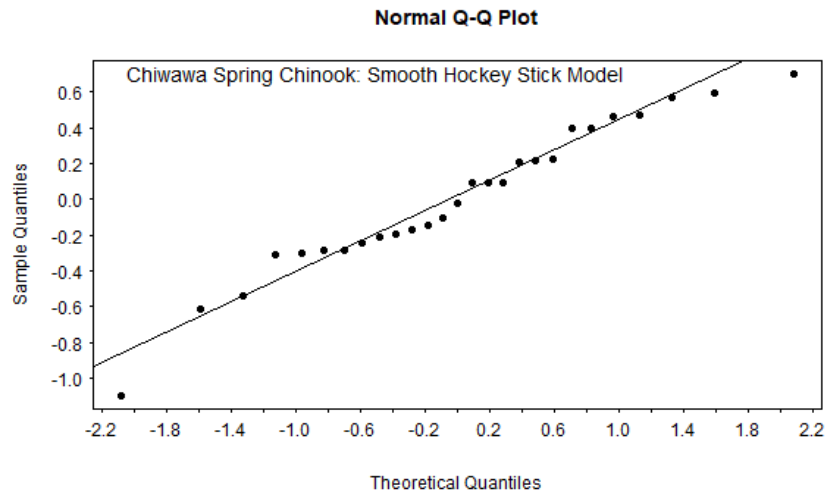


Figure A1. Normal quantile-quantile plot of residual from Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for Chiwawa River Spring Chinook, 1991–2017. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: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

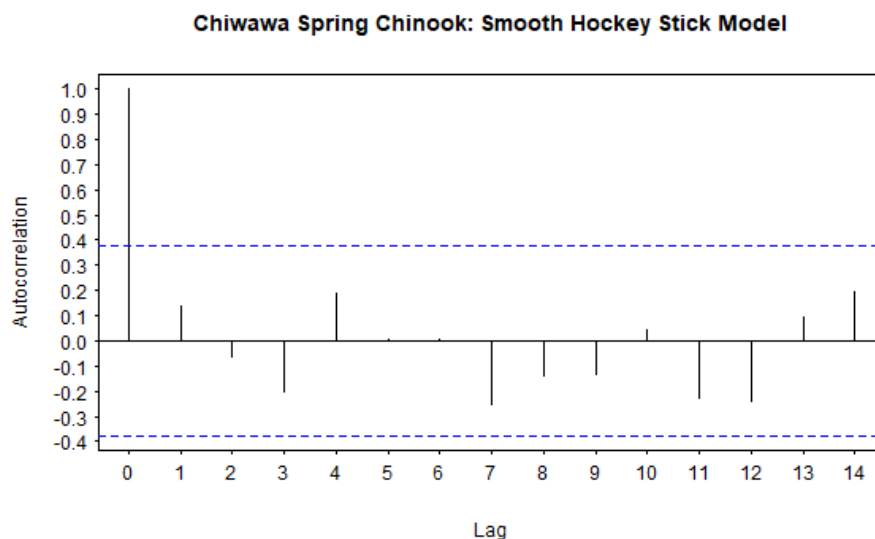


Figure A2. Autocorrelation plot of residuals for Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for Chiwawa River Spring Chinook, 1991–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

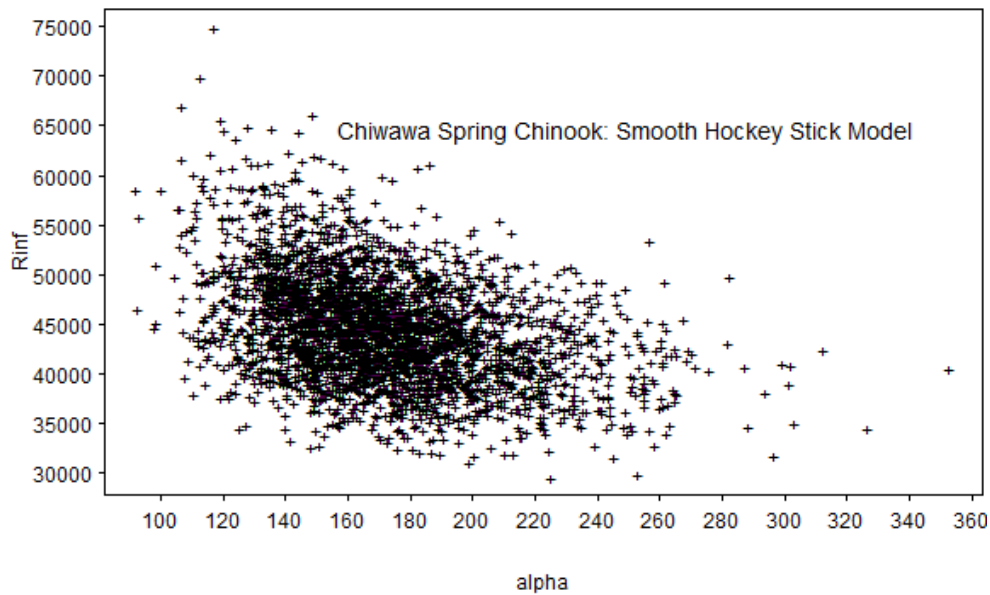


Figure A3. Correlation plot of bootstrap parameter estimates from the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for Chiwawa River Spring Chinook, 1991–2017, based on 3,000 bootstrap samples.

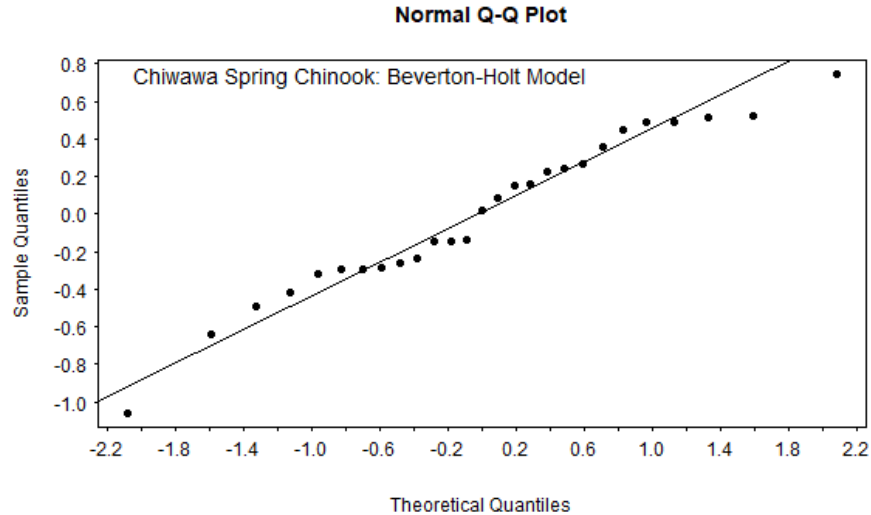


Figure A4. Normal quantile-quantile plot of residual from Beverton-Holt model of smolt recruitment as a function of spawner abundance (stock) for Chiwawa River Spring Chinook, 1991–2017. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: $W=0.9672$,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

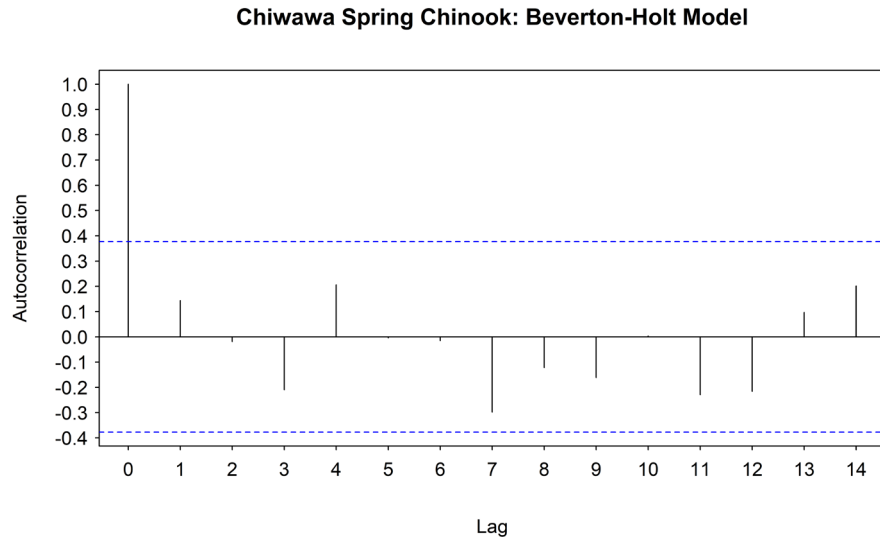


Figure A5. Autocorrelation plot of residuals for Beverton-Holt model of smolt recruitment as a function of spawner abundance (stock) for Chiwawa River Spring Chinook, 1991–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

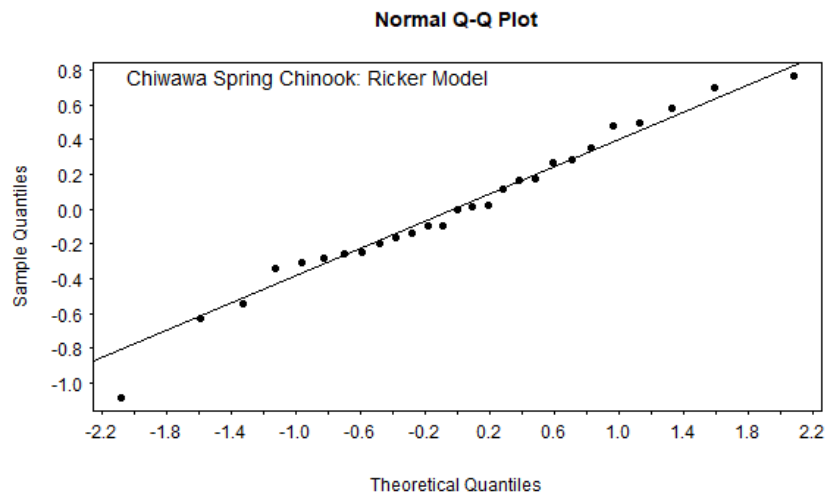


Figure A6. Normal quantile-quantile plot of residual from Ricker model of smolt recruitment as a function of spawner abundance (stock) for Chiwawa River Spring Chinook, 1991–2017. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: $W=0.9788$,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

Chiwawa Spring Chinook: Ricker Model

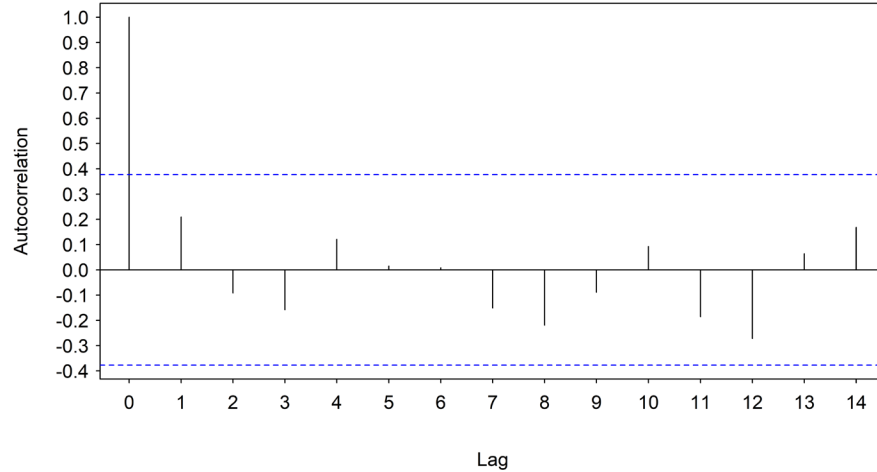


Figure A7. Autocorrelation plot of residuals for Ricker model of smolt recruitment as a function of spawner abundance (stock) for Chiwawa River Spring Chinook, 1991–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

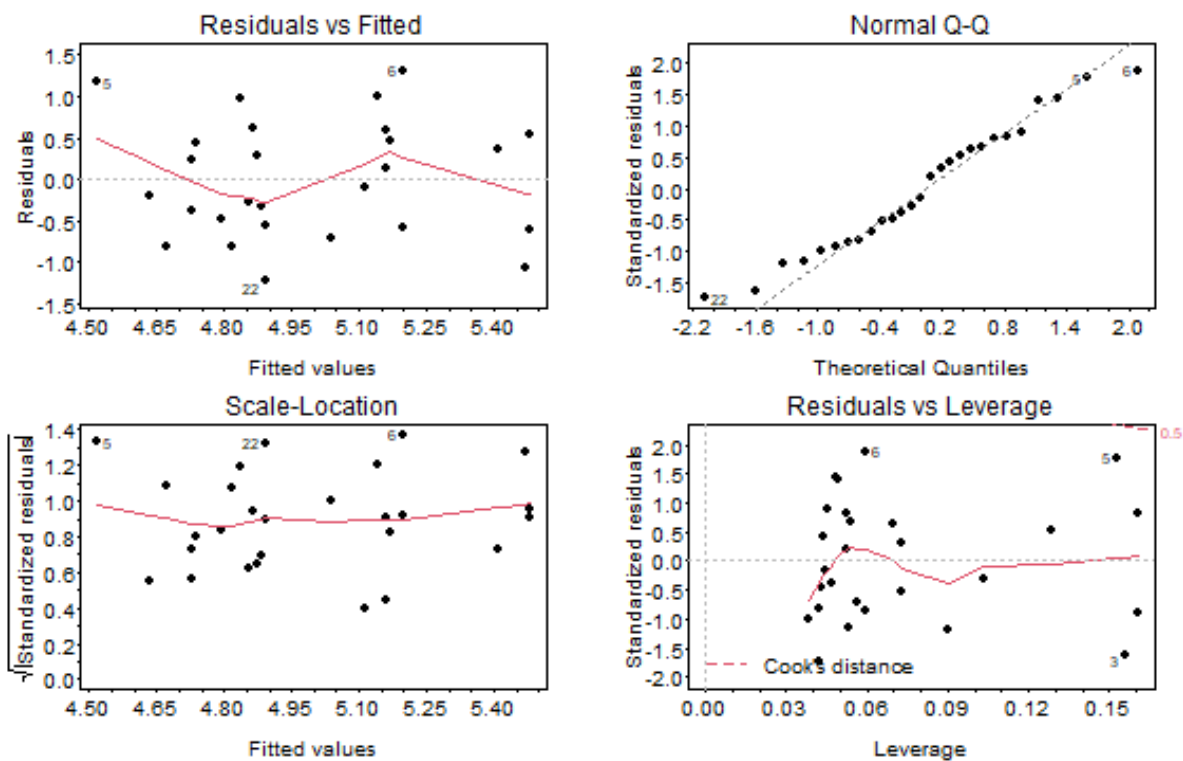


Figure A8. Residual plots for linear model of smolts per redd as a function of pHOS for Chiwawa River Spring Chinook, 1991–2017. Shapiro-Wilk test of normality of residuals: $W=0.9672$, $P=0.5302$.

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	

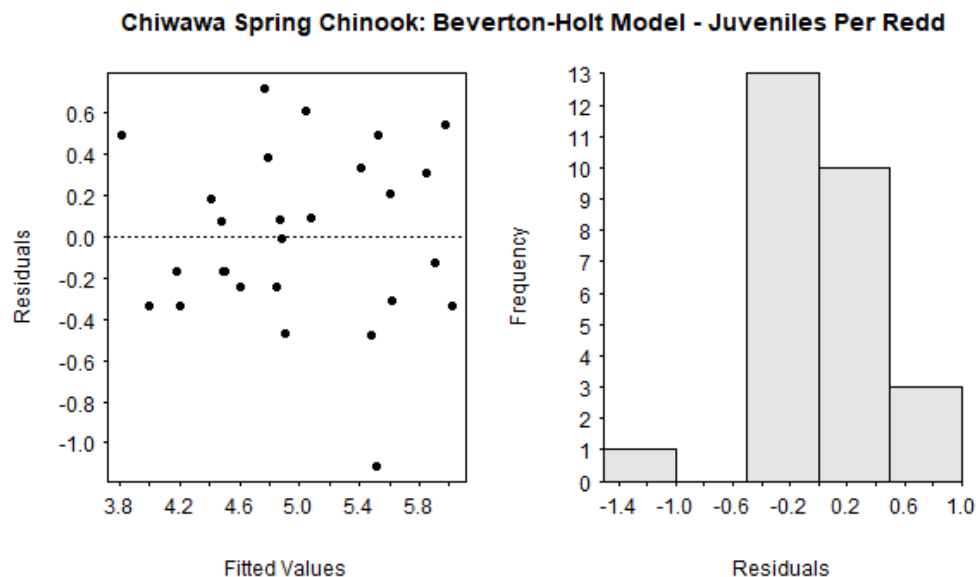


Figure A9. Residual plots for Beverton-Holt model of smolts per redd as a function of redd count and pHOS for Chiwawa River Spring Chinook, 1991–2017. Shapiro-Wilk test of normality of residuals: $W=0.9608$, $P=0.3864$.

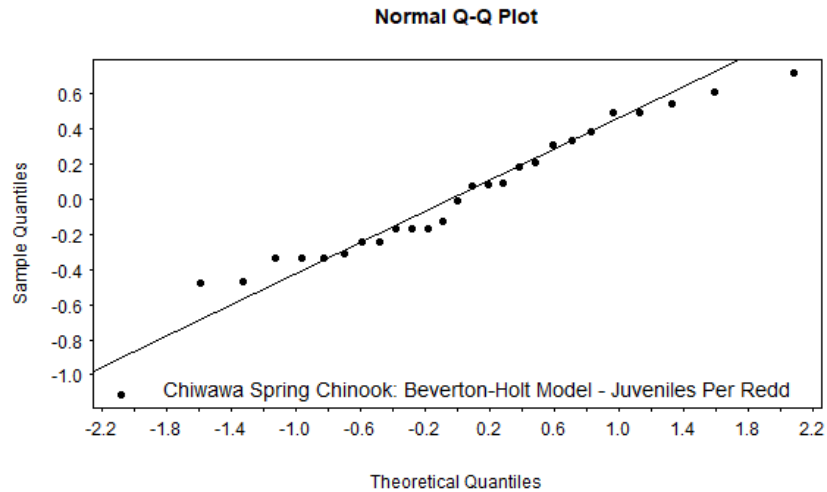


Figure A10. Normal quantile-quantile plot of residual from Beverton-Holt model of smolts per redd as a function of redd count and pHOS for Chiwawa River Spring Chinook, 1991–2017. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: $W=0.9608$,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

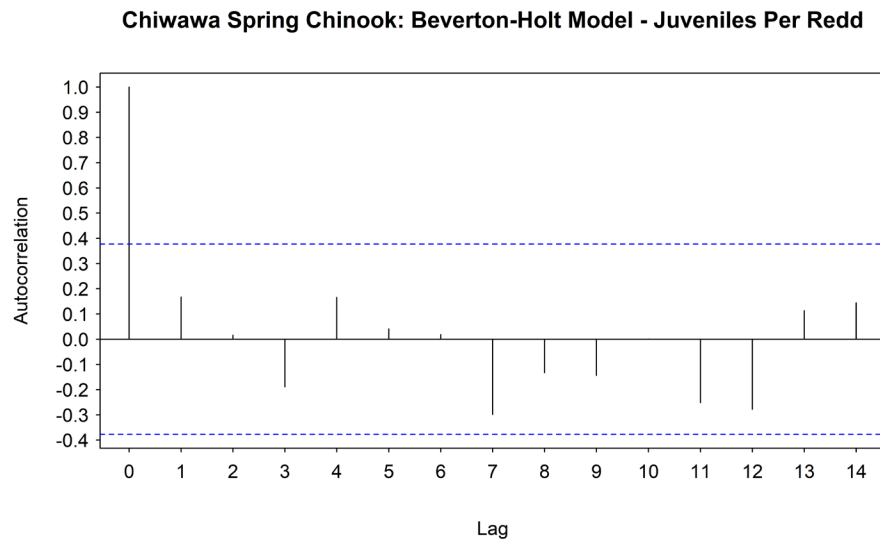


Figure A11. Autocorrelation plot of residuals for Beverton-Holt model of smolts per redd as a function of redd count and pHOS for Chiwawa River Spring Chinook, 1991–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

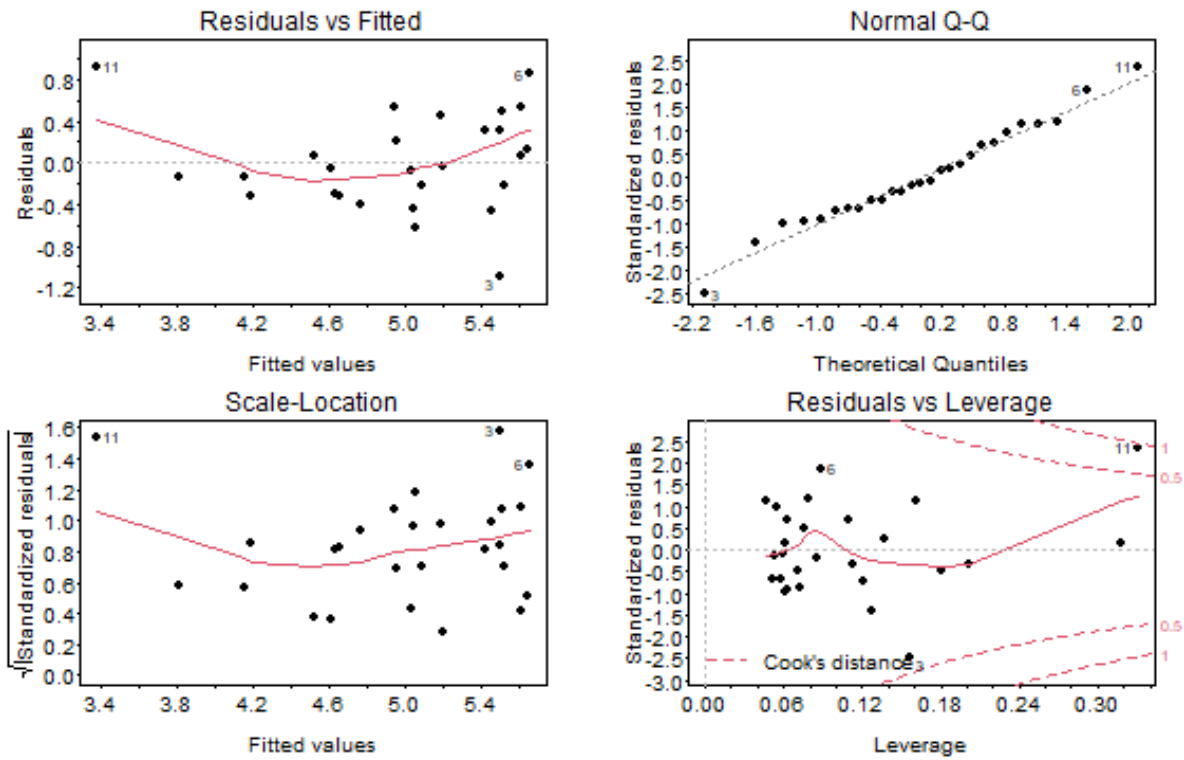


Figure A12. Residual plots for Ricker model of smolts per redd as a function of redd count and pHOS for Chiwawa River Spring Chinook, 1991–2017. Shapiro-Wilk test of normality of residuals: $W=0.9801$, $P=0.8656$.

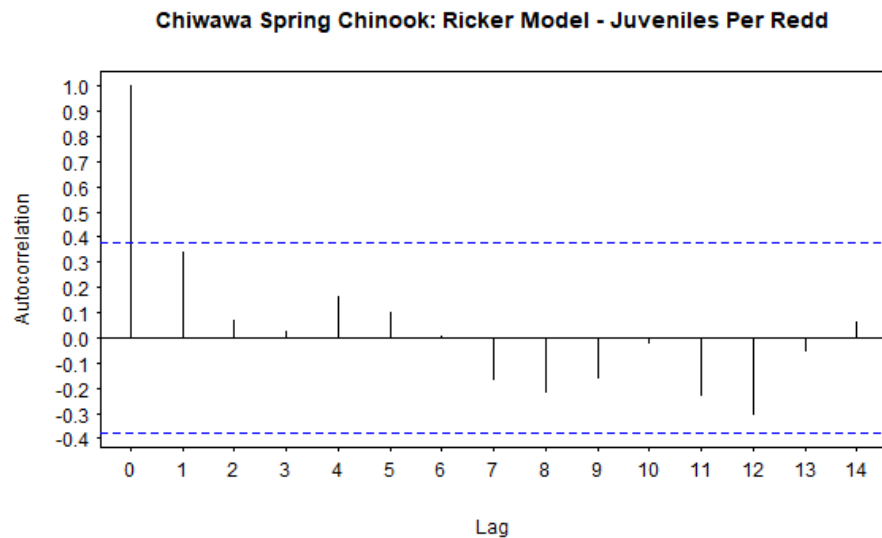


Figure A13. Autocorrelation plot of residuals for Ricker model of smolts per redd as a function of redd count and pHOS for Chiwawa River Spring Chinook, 1991–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

Appendix B: Nason Creek Spring Chinook Salmon

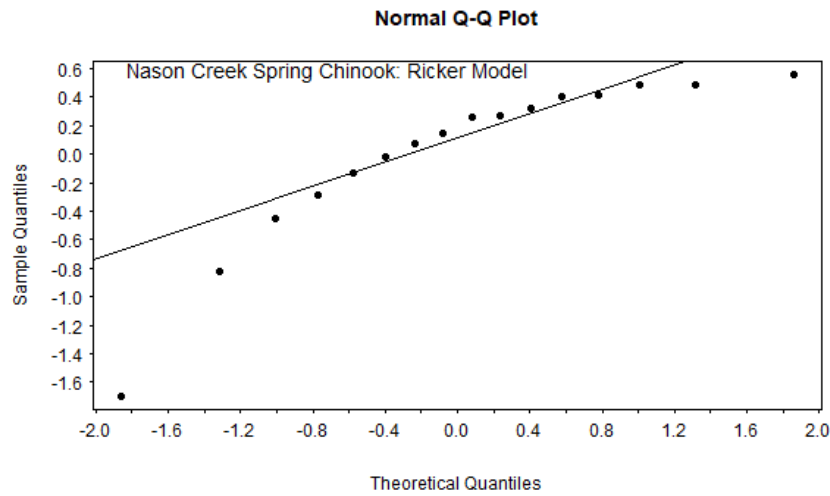


Figure B1. Normal quantile-quantile plot of residual from Ricker model of smolt recruitment as a function of spawner abundance (stock) for Nason Creek Spring Chinook, 2002–2017, including brood year 2014. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality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

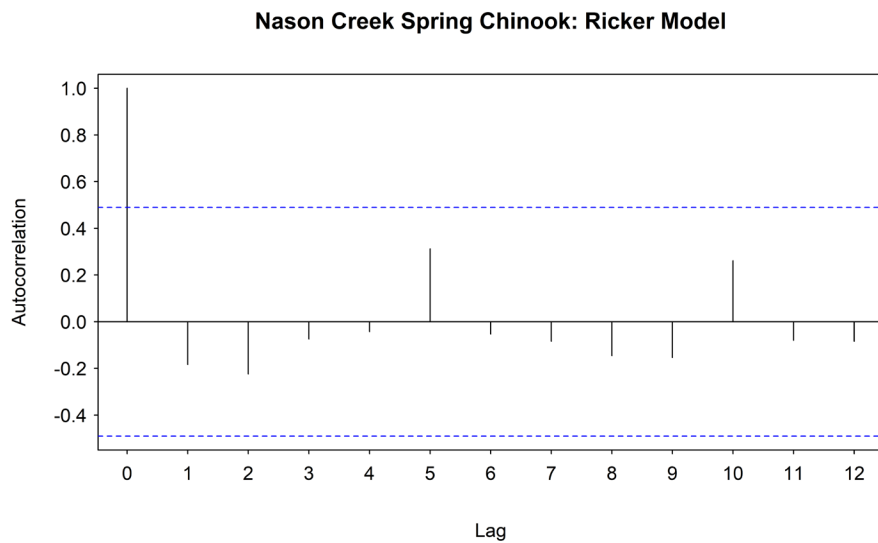


Figure B2. Autocorrelation plot of residuals for Ricker model of smolt recruitment as a function of spawner abundance (stock) for Nason Creek Spring Chinook, 2002–2017, including brood year 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

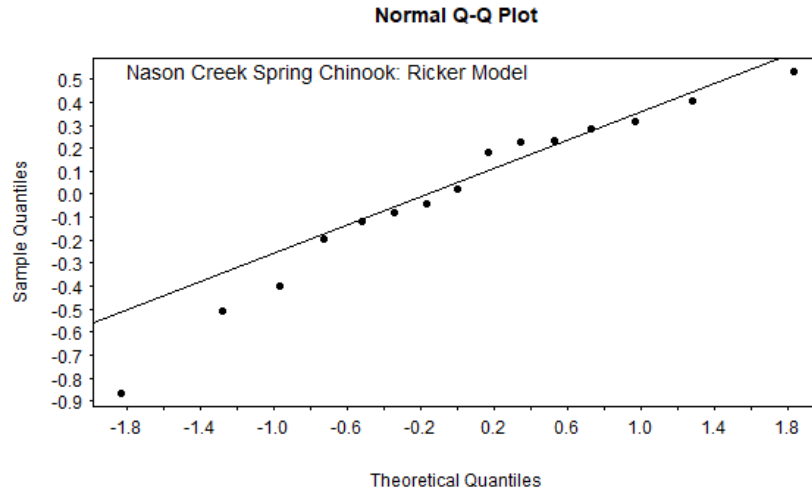


Figure B3. Normal quantile-quantile plot of residual from Ricker model of smolt recruitment as a function of spawner abundance (stock) for Nason Creek Spring Chinook, 2002–2017 without brood year 2014. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of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

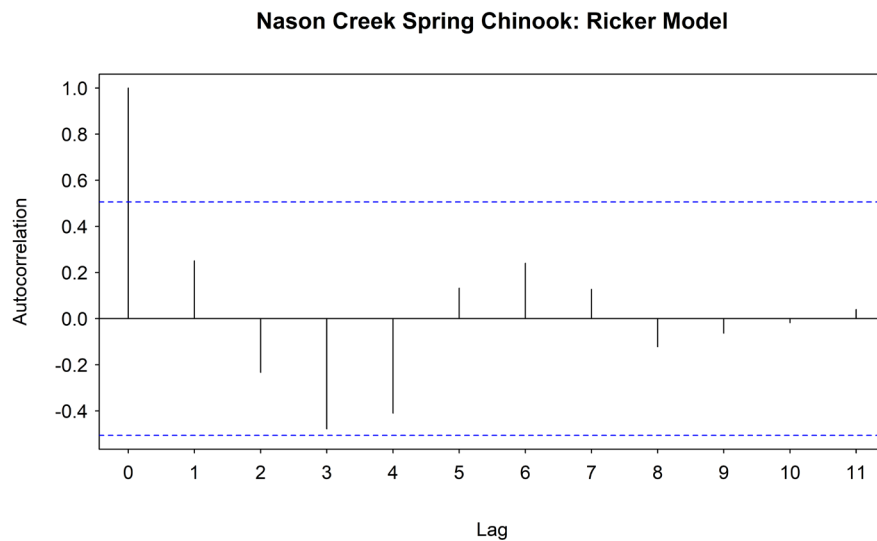


Figure B4. Autocorrelation plot of residuals for Ricker model of smolt recruitment as a function of spawner abundance (stock) for Nason Creek Spring Chinook, 2002–2017 without brood year 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

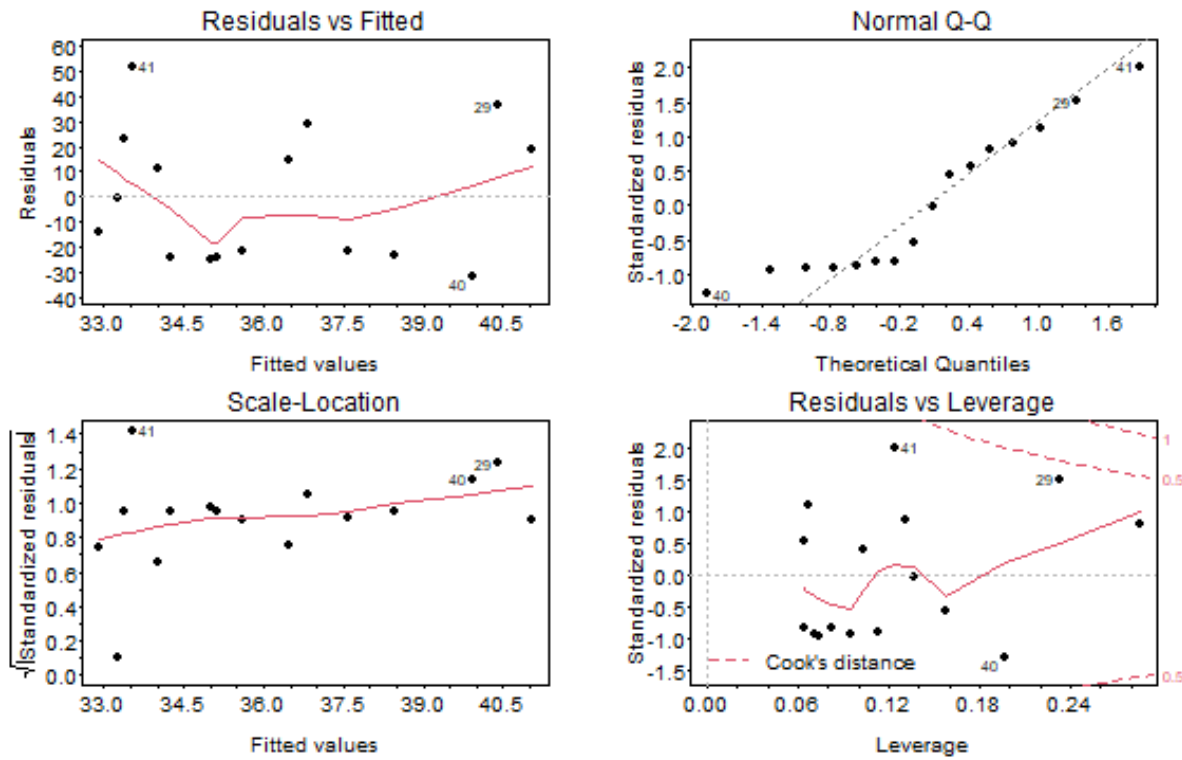


Figure B5. Residual plots for linear model of smolts per redd as a function of pHOS for Nason Creek Spring Chinook, 2002–2017 (including brood year 2014). Shapiro-Wilk test of normality of residuals: $W=0.8923$, $P=0.0606$.

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	

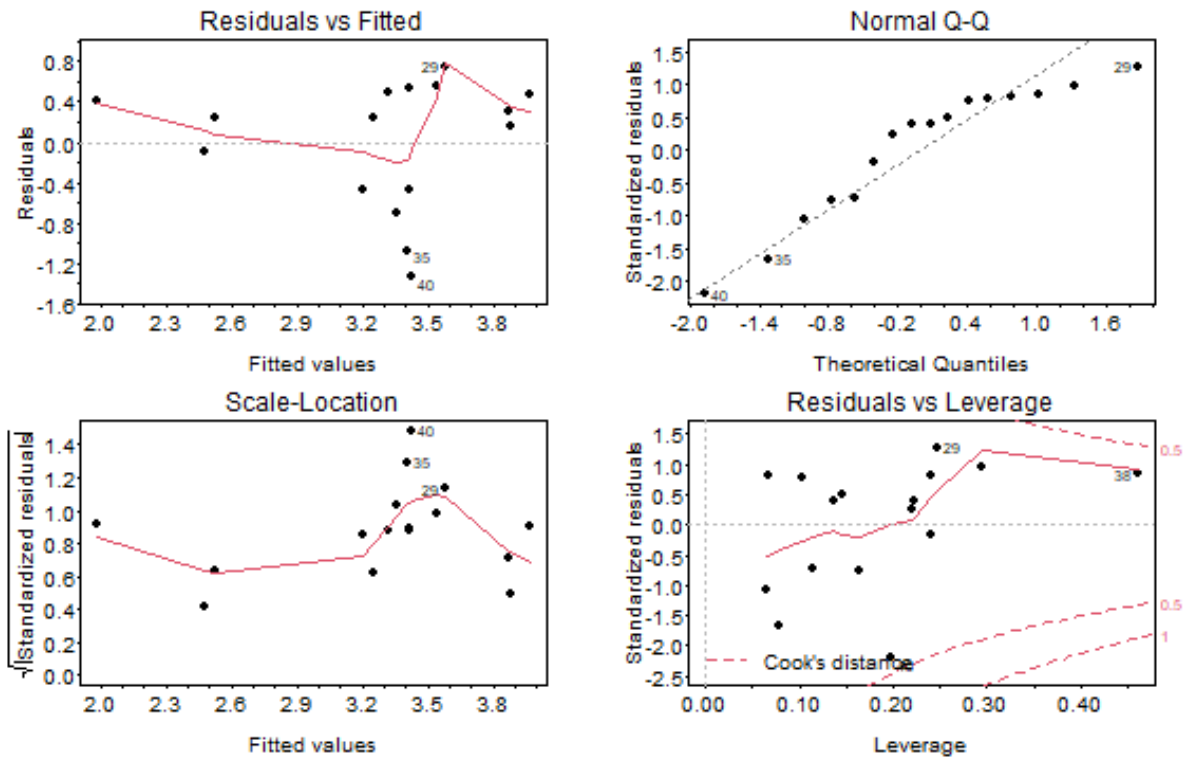


Figure B6. Residual plots for Ricker model of smolts per redd as a function of redd count and pHOS for Nason Creek Spring Chinook, 1991–2017, with brood year 2014. Shapiro-Wilk test of normality of residuals: $W=0.8831$, $P=0.0434$.

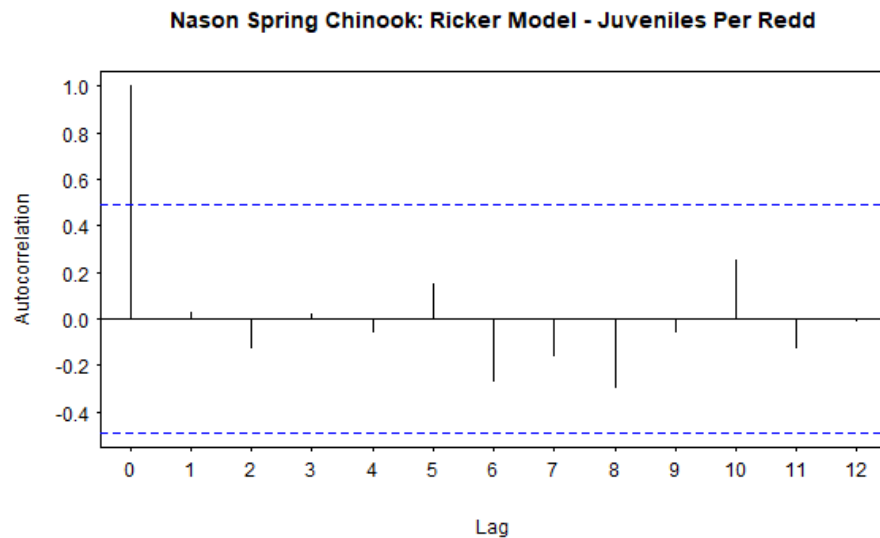


Figure B7. Autocorrelation plot of residuals for Ricker model of smolts per redd as a function of redd count and pHOS for Nason Creek Spring Chinook, 2002–2017, with brood year 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

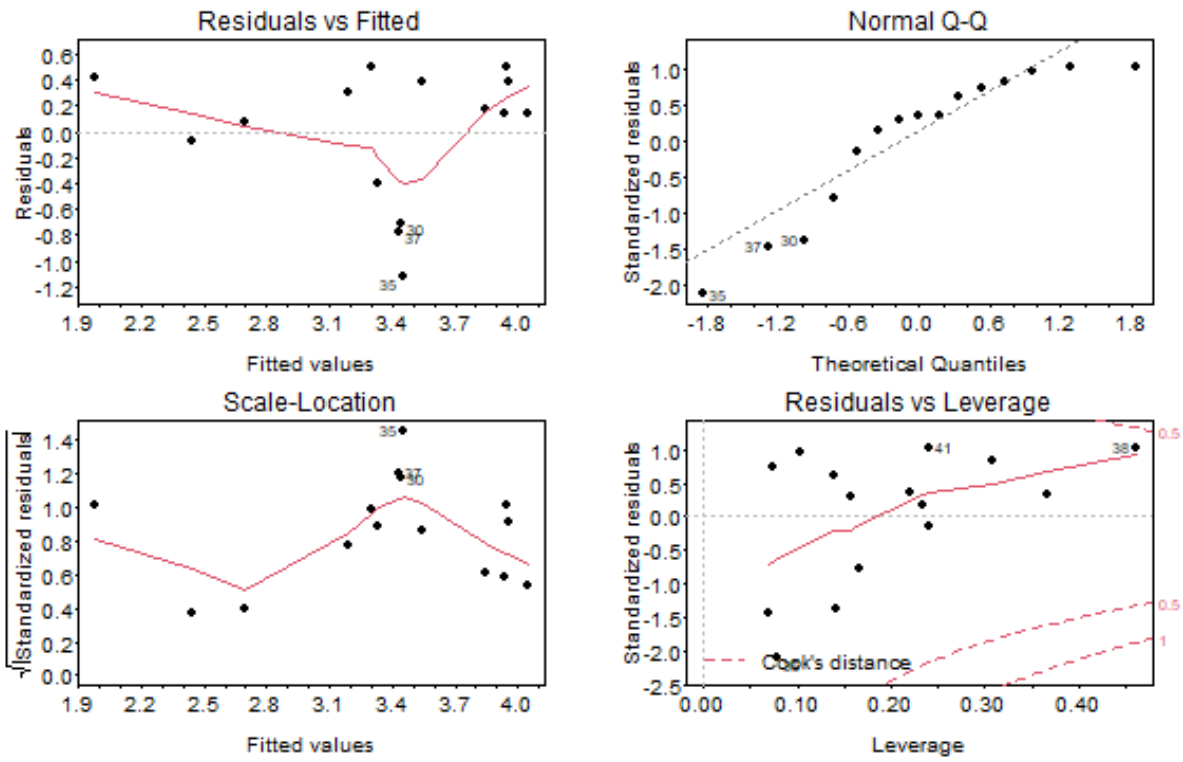


Figure B8. Residual plots for Ricker model of smolts per redd as a function of redd count and pHOS for Nason Creek Spring Chinook, 1991–2017, without brood year 2014. Shapiro-Wilk test of normality of residuals: $W=0.8533$, $P=0.0193$.

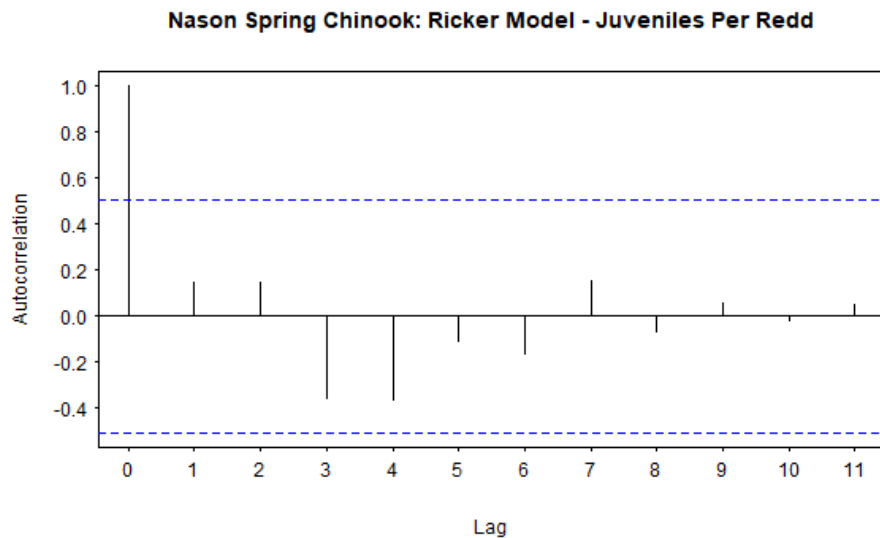


Figure B9. Autocorrelation plot of residuals for Ricker model of smolts per redd as a function of redd count and pHOS for Nason Creek Spring Chinook, 2002–2017, without brood year 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

Appendix C: White River Spring Chinook Salmon

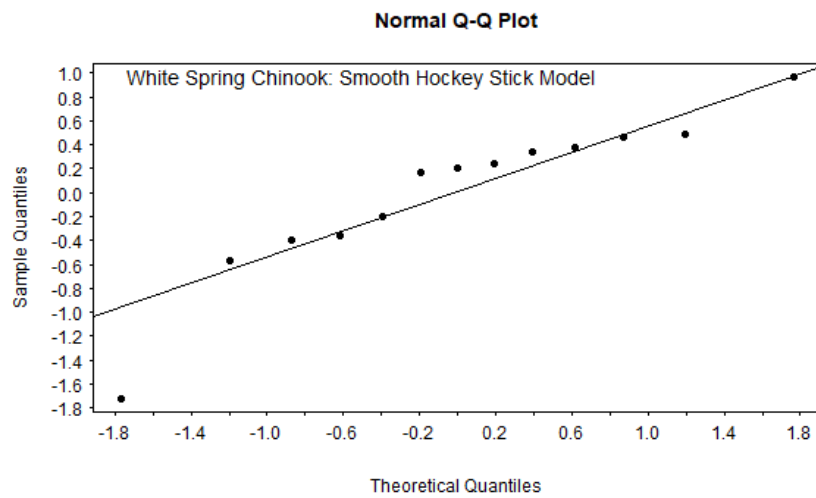


Figure C1. Normal quantile-quantile plot of residual from the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017, including brood year 2014. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test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

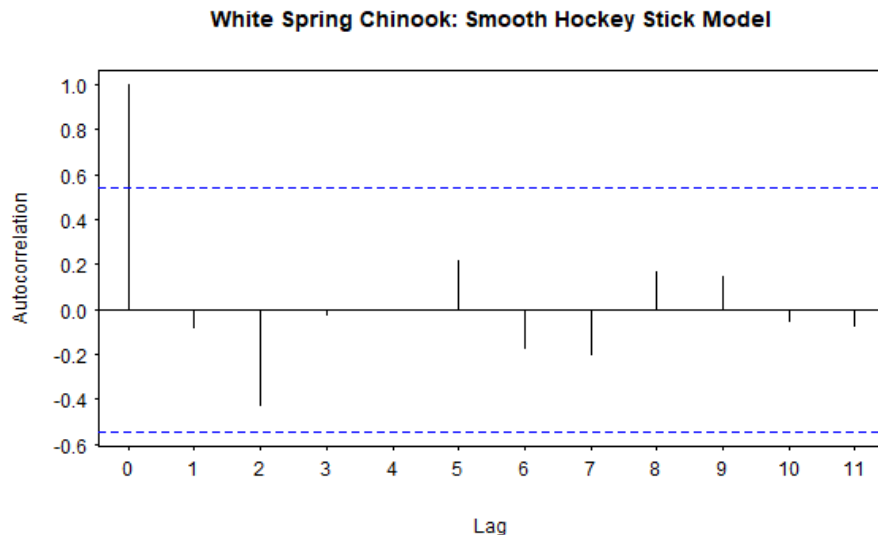


Figure C2. Autocorrelation plot of residuals for the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017, including brood year 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

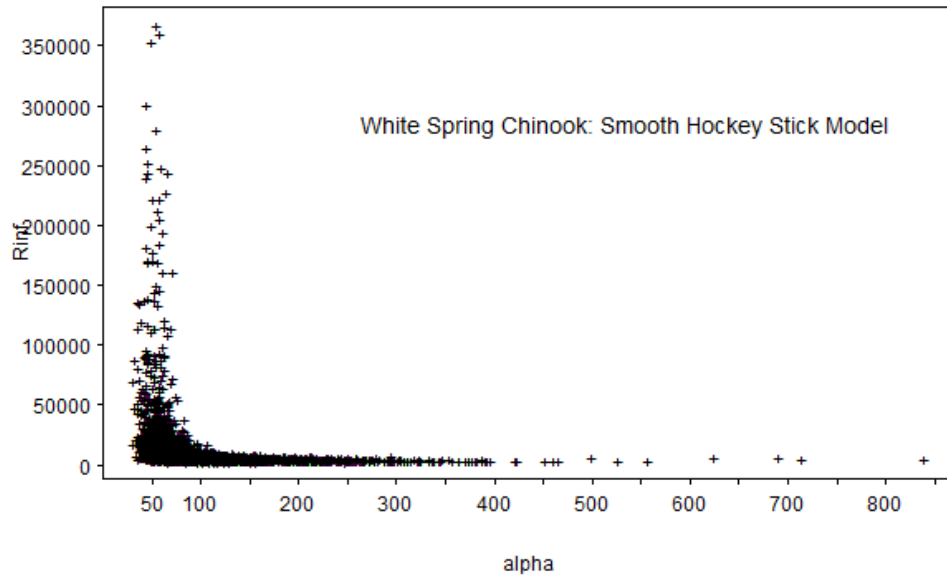


Figure C3. Correlation plot of bootstrap parameter estimates from the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017, including brood year 2014, based on 3,291 bootstrap samples.

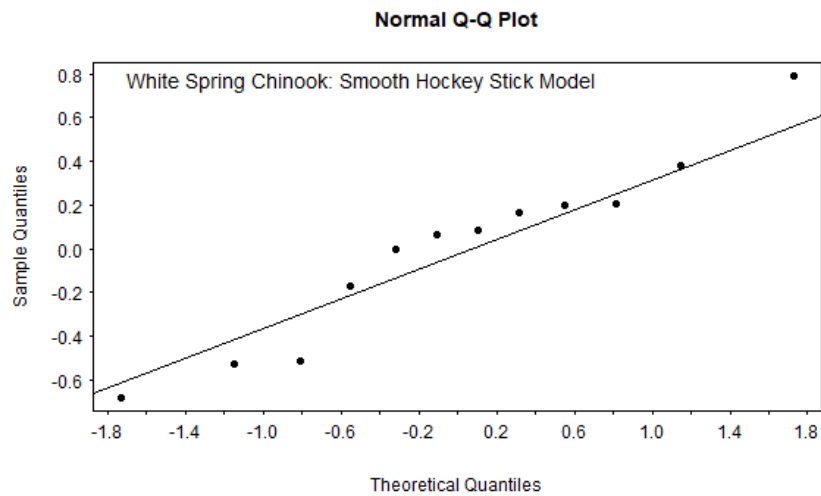


Figure C4. Normal quantile-quantile plot of residual from the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017 without brood year 2014. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test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

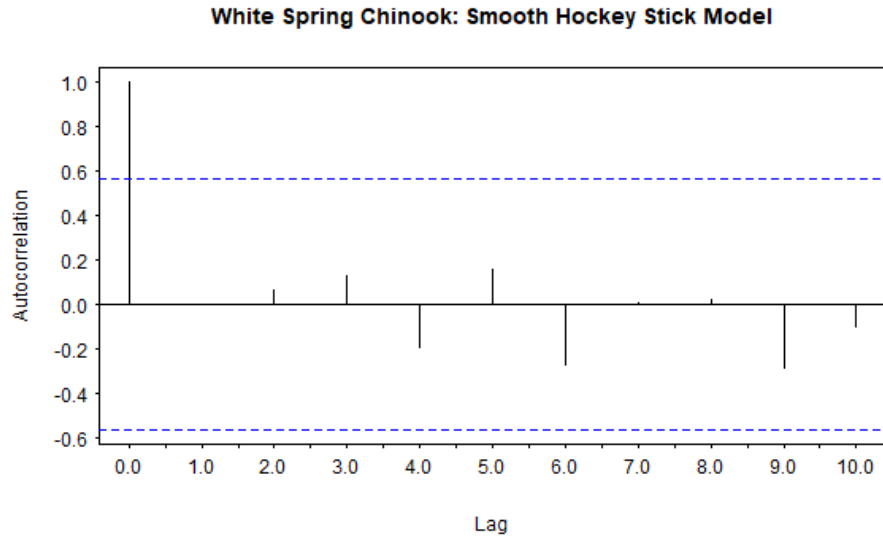


Figure C5. Autocorrelation plot of residuals for the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017 without brood year 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

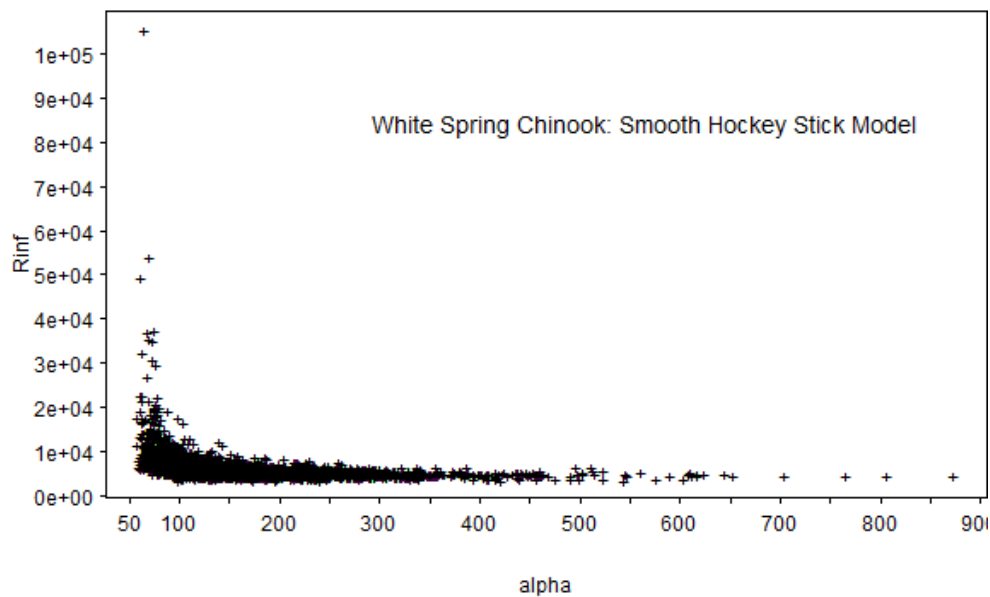


Figure C6. Correlation plot of bootstrap parameter estimates from the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017, without brood year 2014, based on 3,618 bootstrap samples.

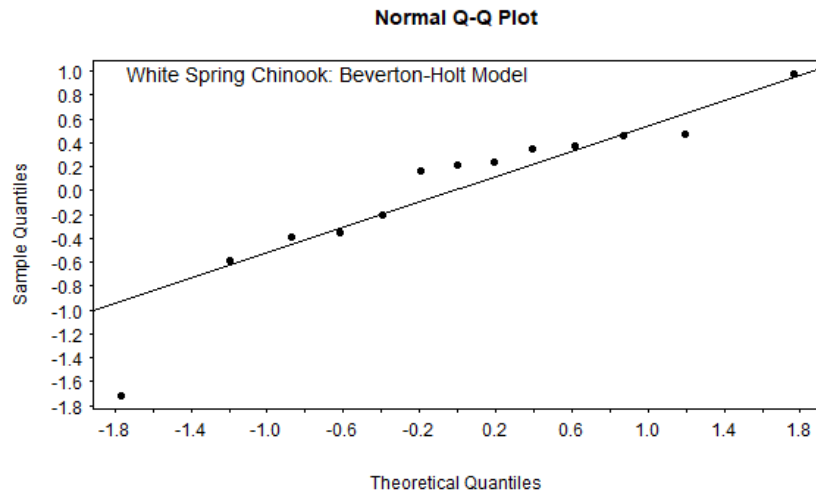


Figure C7. Normal quantile-quantile plot of residual from Beverton-Holt model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017, including brood year 2014. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality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

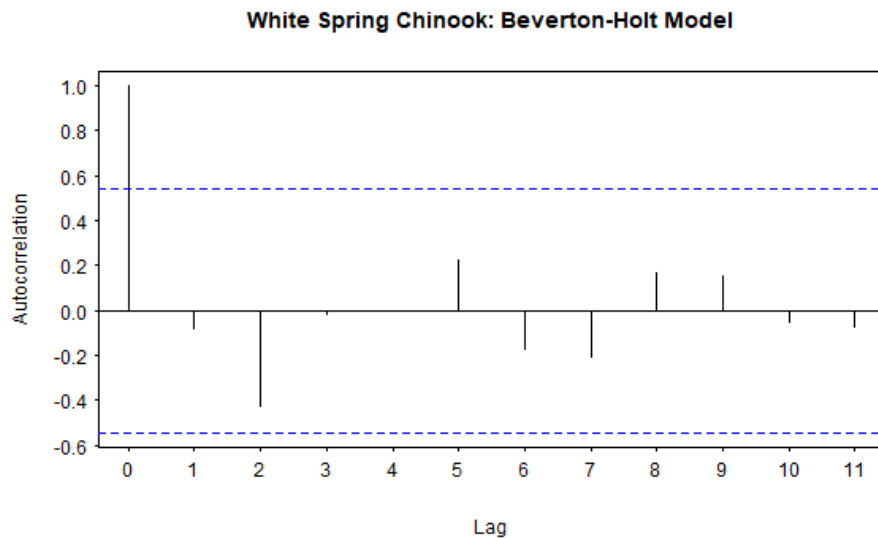


Figure C8. Autocorrelation plot of residuals for Beverton-Holt model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017, including brood year 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

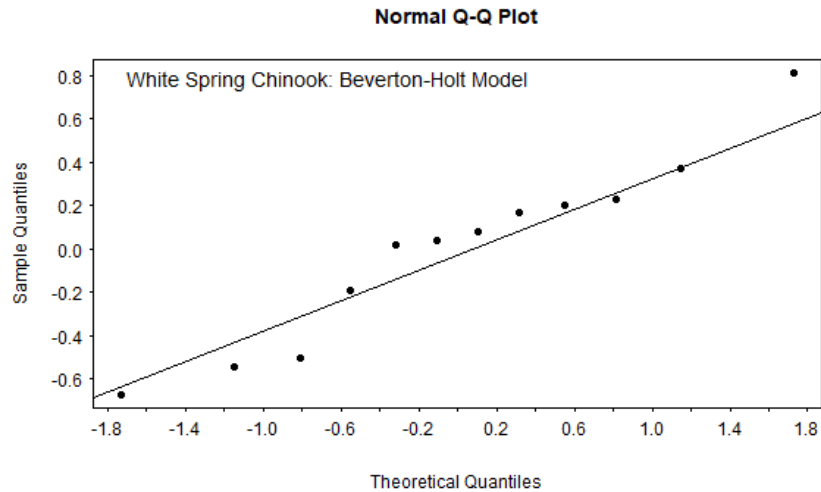


Figure C9. Normal quantile-quantile plot of residual from Beverton-Holt model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017 without brood year 2014. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality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

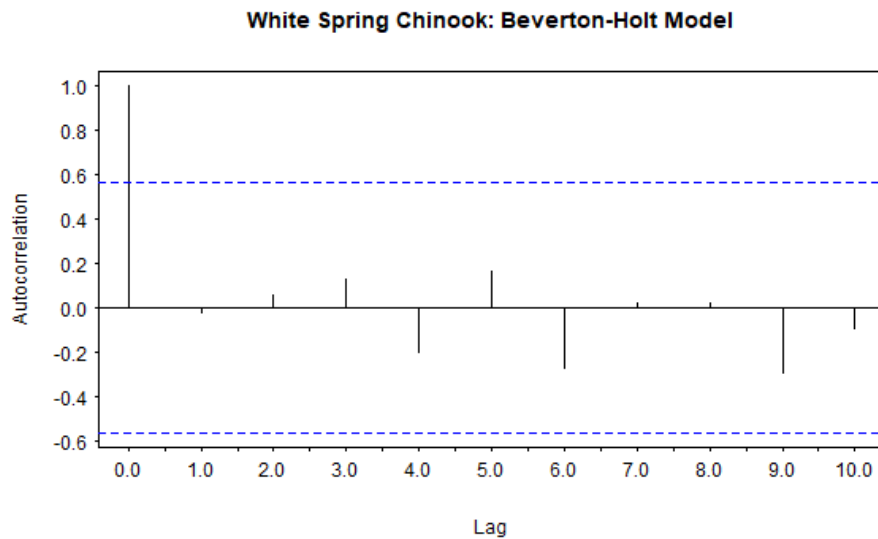


Figure C10. Autocorrelation plot of residuals for Beverton-Holt model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017 without brood year 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

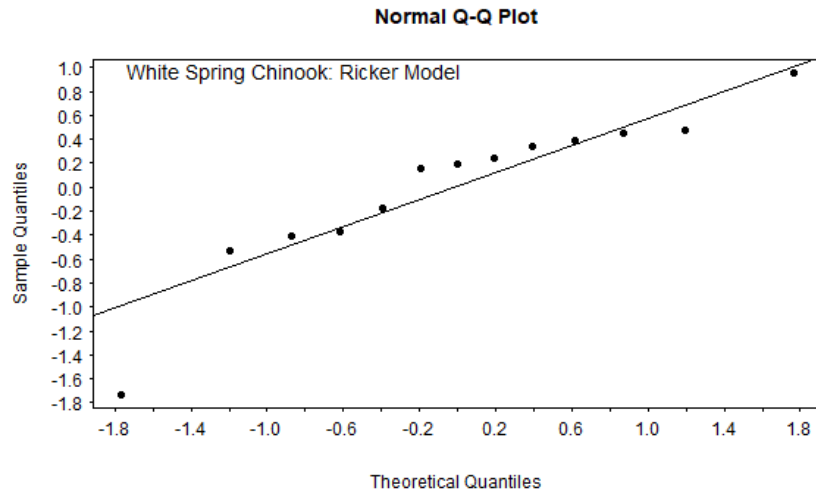


Figure C11. Normal quantile-quantile plot of residual from Ricker model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017, including brood year 2014. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality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

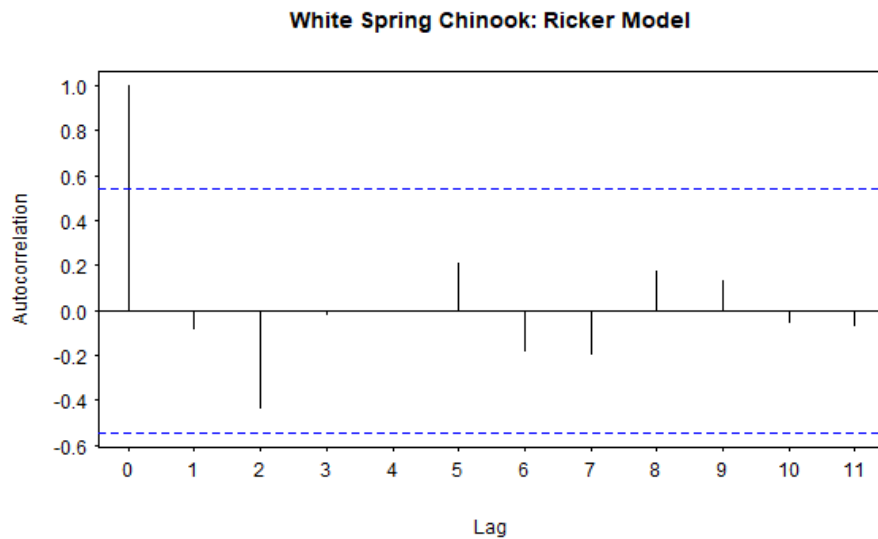


Figure C12. Autocorrelation plot of residuals for Ricker model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017, including brood year 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

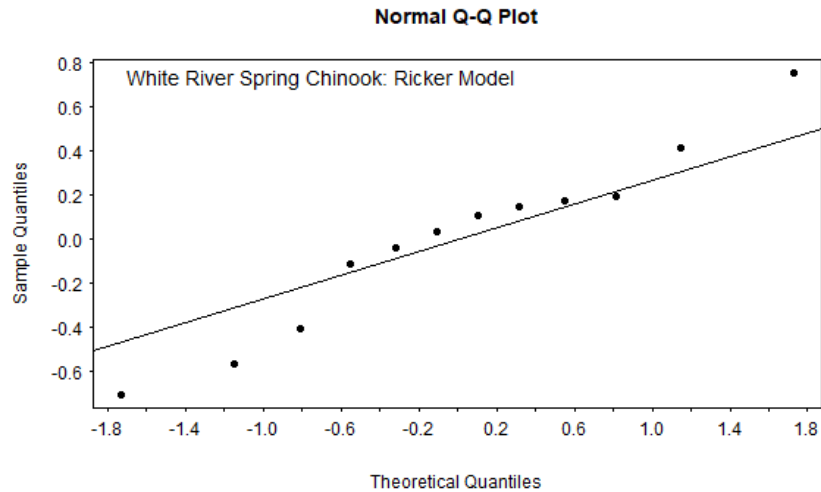


Figure C13. Normal quantile-quantile plot of residual from Ricker model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017 without brood year 2014. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of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

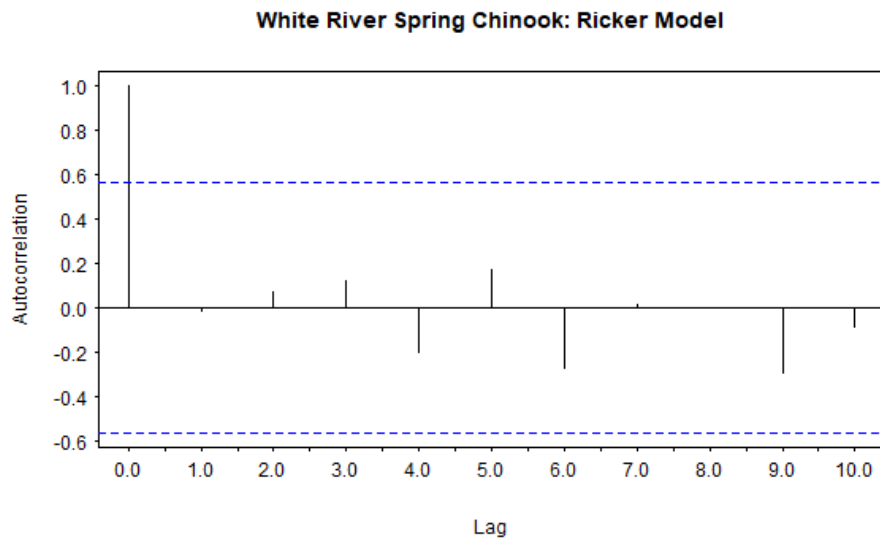


Figure C14. Autocorrelation plot of residuals for Ricker model of smolt recruitment as a function of spawner abundance (stock) for White River Spring Chinook, 2005–2017 without brood year 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

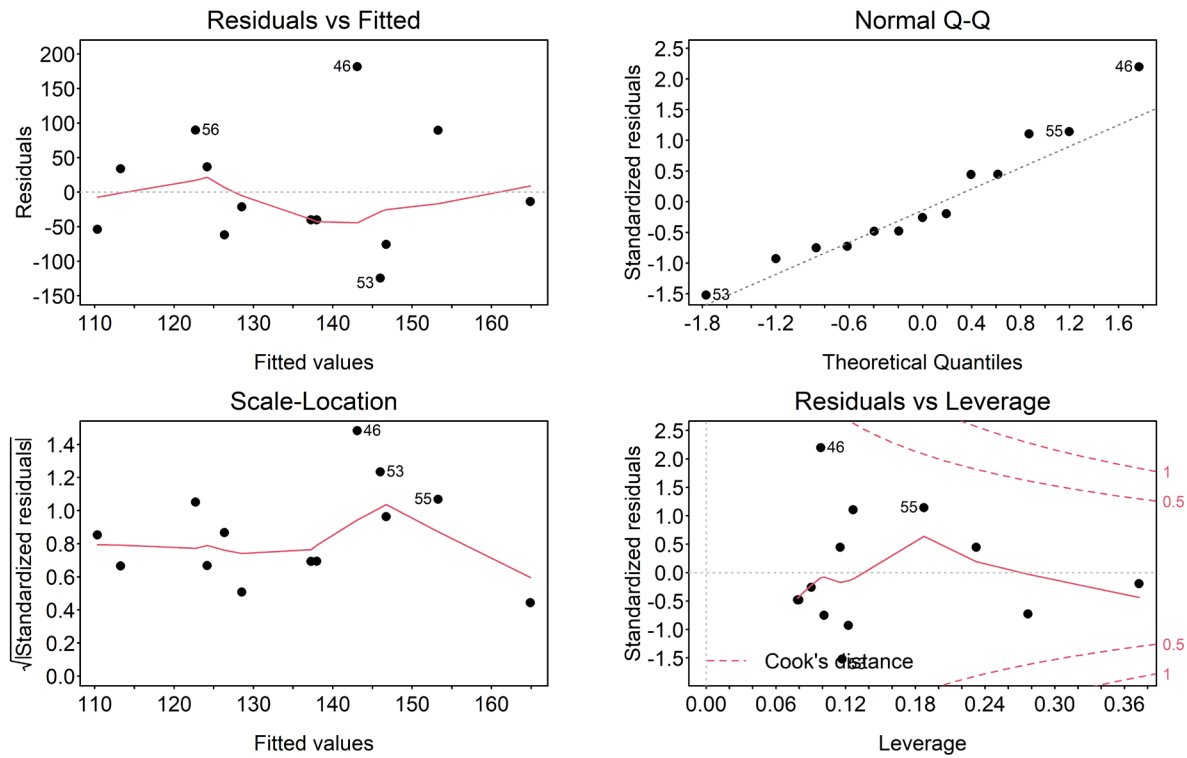


Figure C15. Residual plots for linear model of smolts per redd as a function of pHOS for White River Spring Chinook, 2005–2017 (including brood year 2014). Shapiro-Wilk test of normality of residuals: $W=0.9443$, $P=0.5150$.

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 ($\geq 3,000$ 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 ($\geq 3,000$ 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	

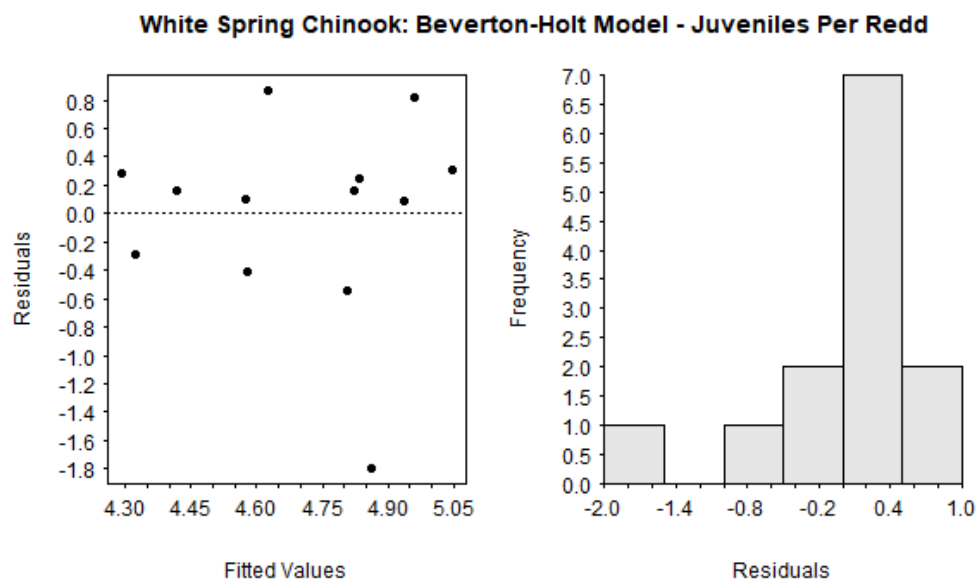


Figure C16. Residual plots for Beverton-Holt model of smolts per redd as a function of redd count and pHOS for White River Spring Chinook, 2005–2017, with 2014. Shapiro-Wilk test of normality of residuals: $W=0.8585$, $P=0.3681$.

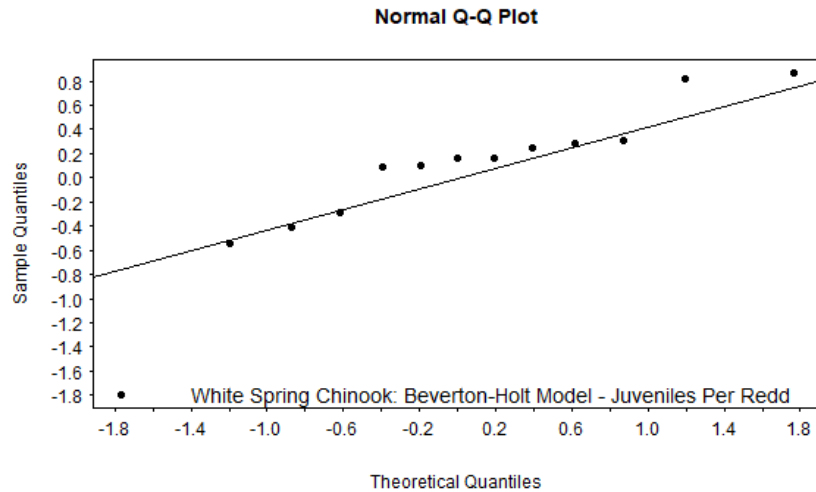


Figure C17. Normal quantile-quantile plot of residual from Beverton-Holt model of smolts per redd as a function of redd count and pHOS for White River Spring Chinook, 2005–2017, with 2014. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: $W=0.8585$,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

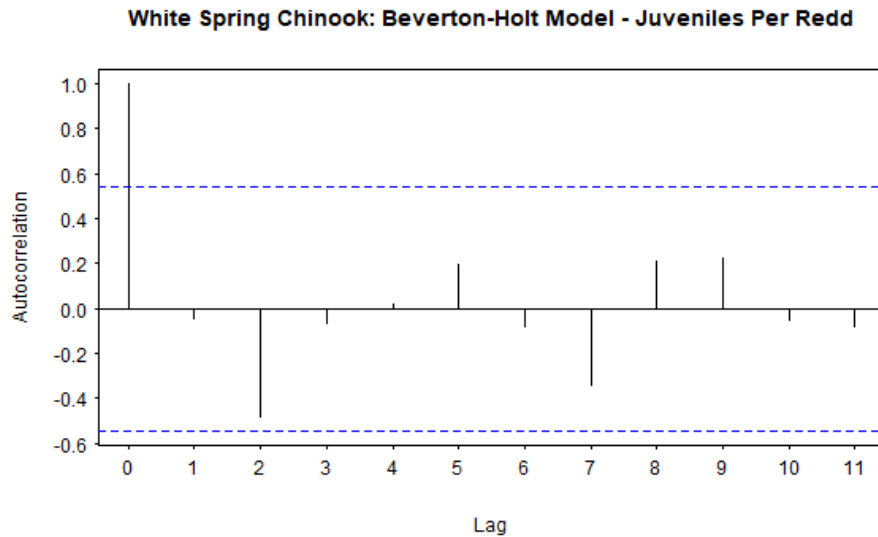


Figure C18. Autocorrelation plot of residuals for Beverton-Holt model of smolts per redd as a function of redd count and pHOS for White River Spring Chinook, 2005–2017, with 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

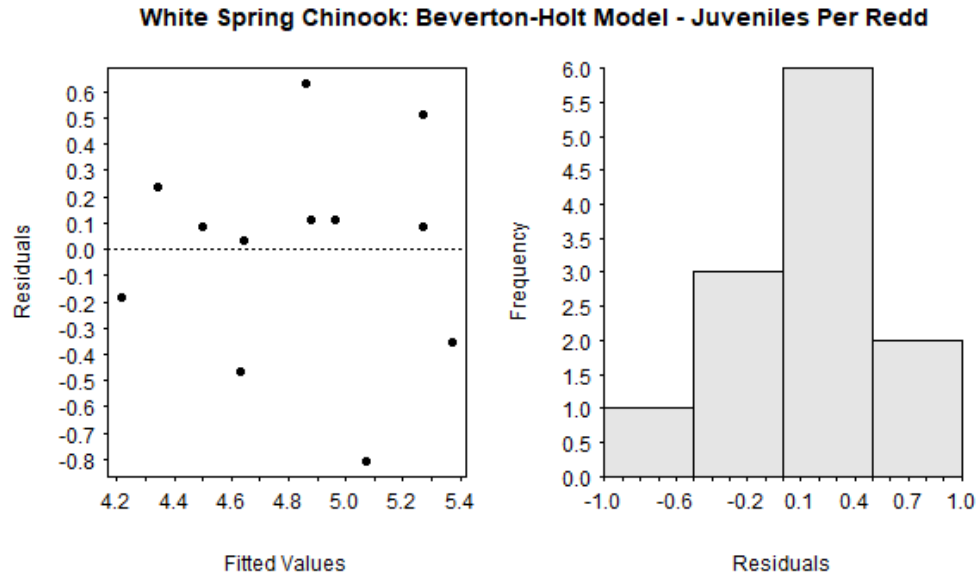


Figure C19. Residual plots for Beverton-Holt model of smolts per redd as a function of redd count and pHOS for White River Spring Chinook, 2005–2017, without 2014. Shapiro-Wilk test of normality of residuals: $W=0.9549$, $P=0.7099$.

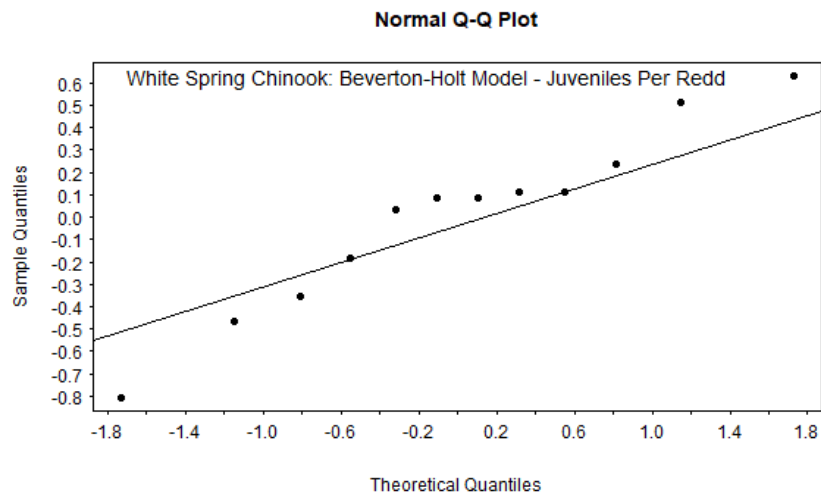


Figure C20. Normal quantile-quantile plot of residual from Beverton-Holt model of smolts per redd as a function of redd count and pHOS for White River Spring Chinook, 2005–2017, without 2014. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: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

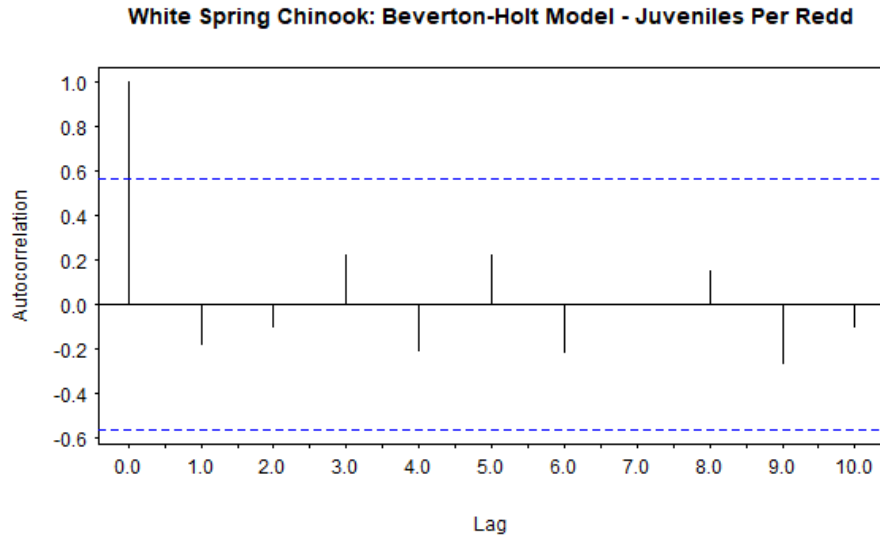


Figure C21. Autocorrelation plot of residuals for Beverton-Holt model of smolts per redd as a function of redd count and pHOS for White River Spring Chinook, 2005–2017, without 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

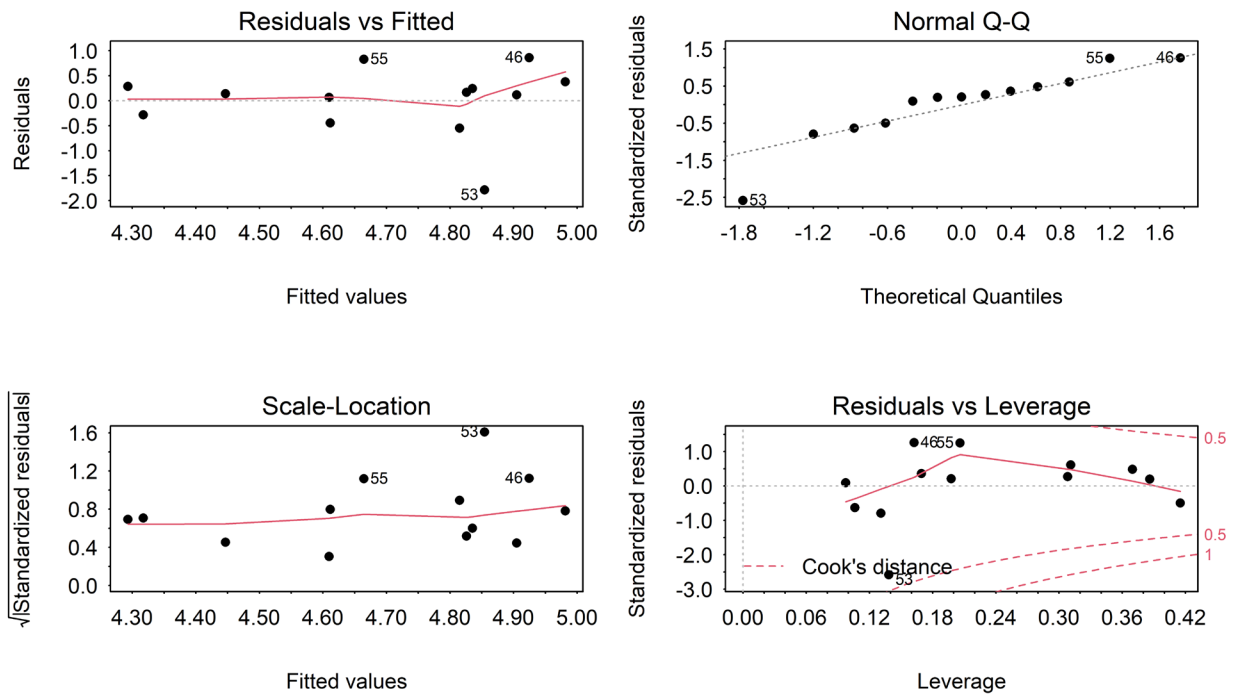


Figure C22. Residual plots for Ricker model of smolts per redd as a function of redd count and pHOS for White River Spring Chinook, 2005–2017, including brood year 2014. Shapiro-Wilk test of normality of residuals: $W=0.8682$, $P=0.0495$.

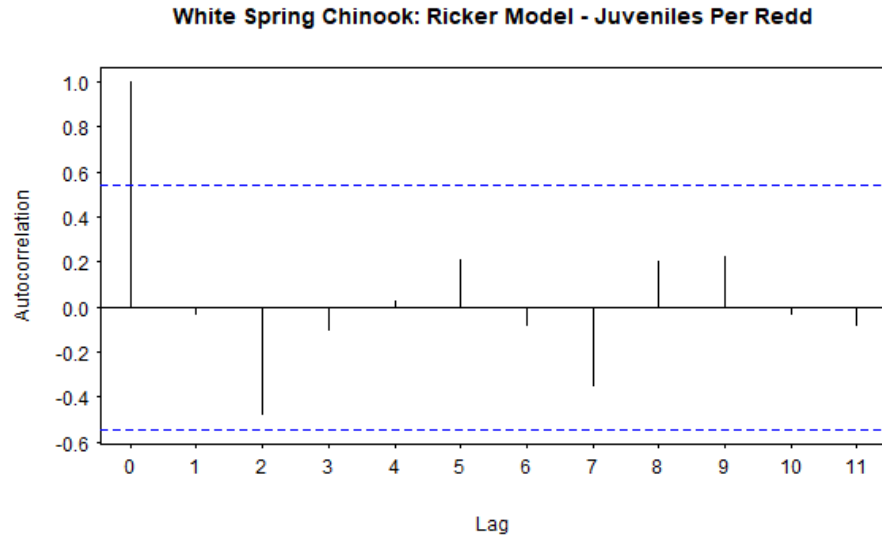


Figure C23. Autocorrelation plot of residuals for Ricker model of smolts per redd as a function of redd count and pHOS for White River Spring Chinook, 2005–2017, including brood year 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

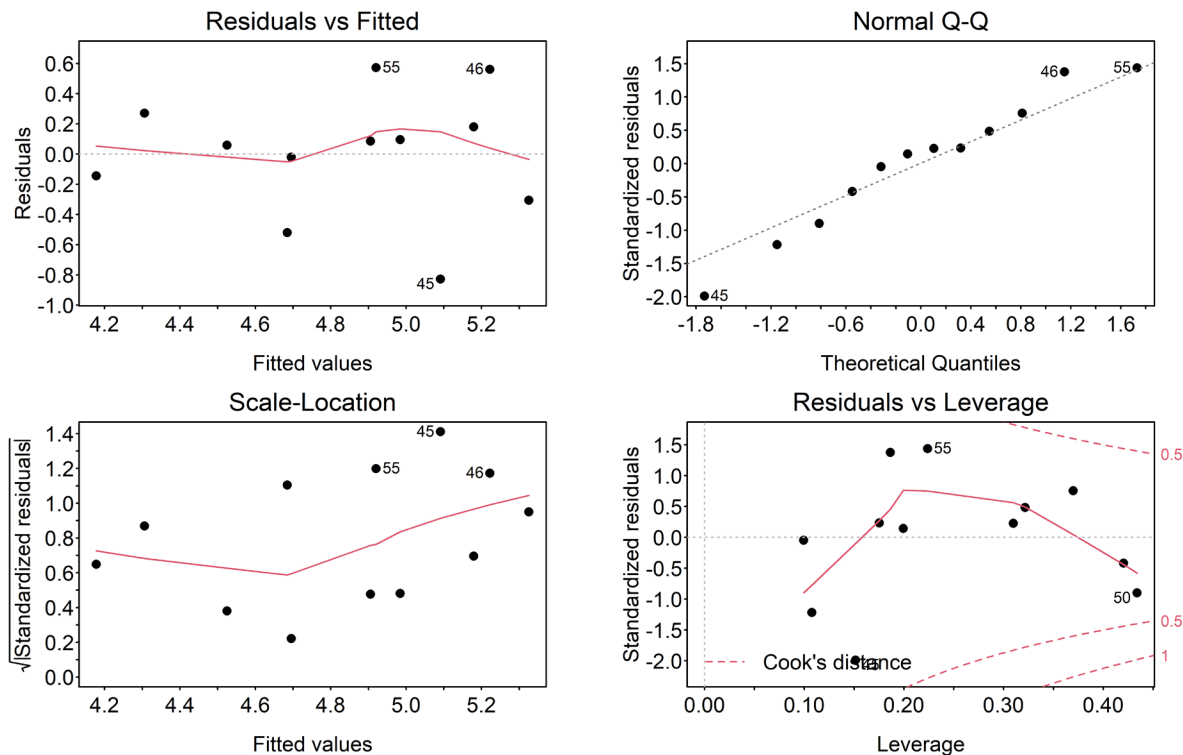


Figure C24. Residual plots for Ricker model of smolts per redd as a function of redd count and pHOS for White River Spring Chinook, 2005–2017, omitting brood year 2014. Shapiro-Wilk test of normality of residuals: $W=0.9540$, $P=0.6956$.

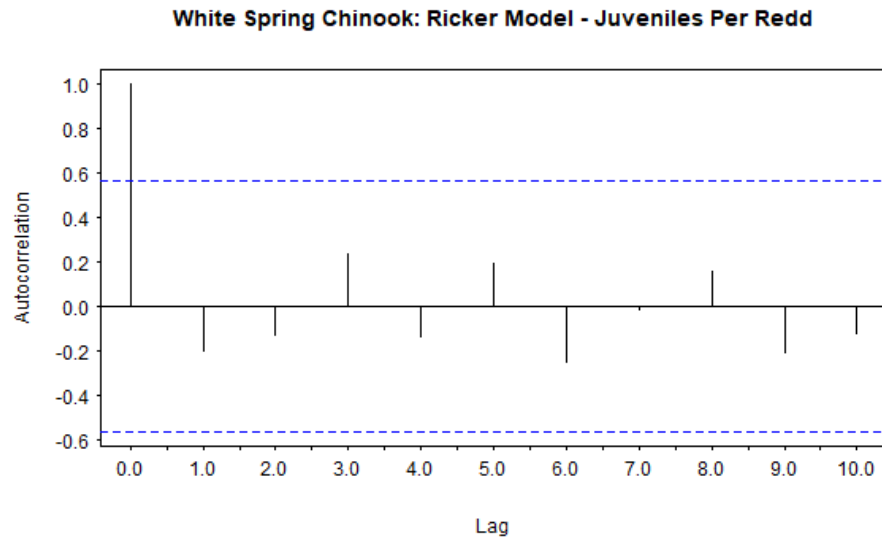


Figure C25. Autocorrelation plot of residuals for Ricker model of smolts per redd as a function of redd count and pHOS for White River Spring Chinook, 2005–2017, omitting brood year 2014. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

Appendix D: Twisp River Spring Chinook Salmon

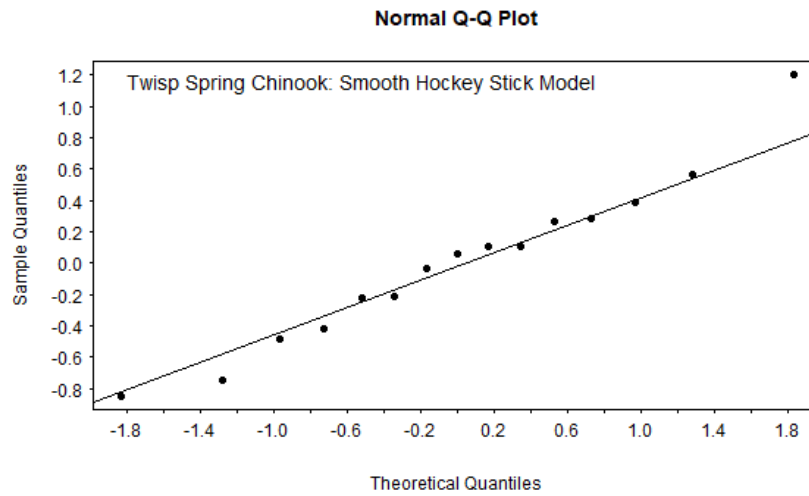


Figure D1. Normal quantile-quantile plot of residual from the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for Twisp River Spring Chinook, 2003–2017. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: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

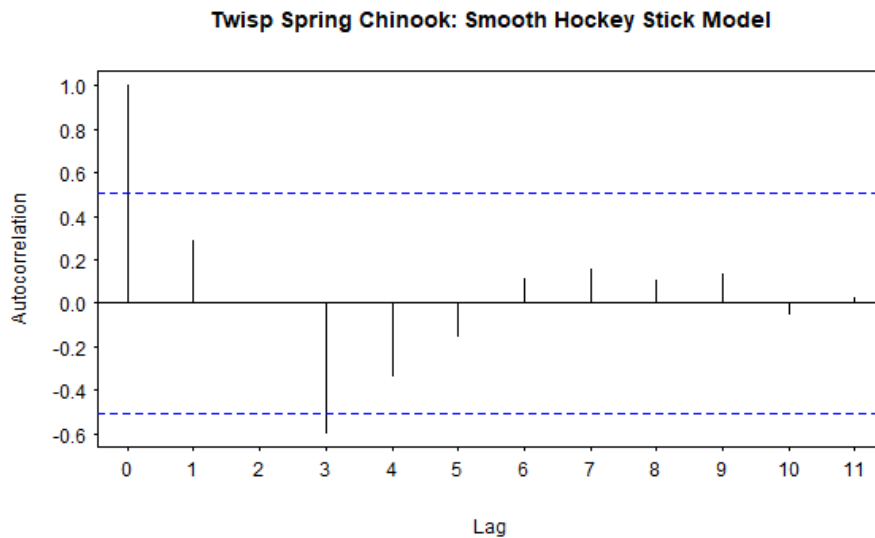


Figure D2. Autocorrelation plot of residuals for the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for Twisp River Spring Chinook, 2003–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

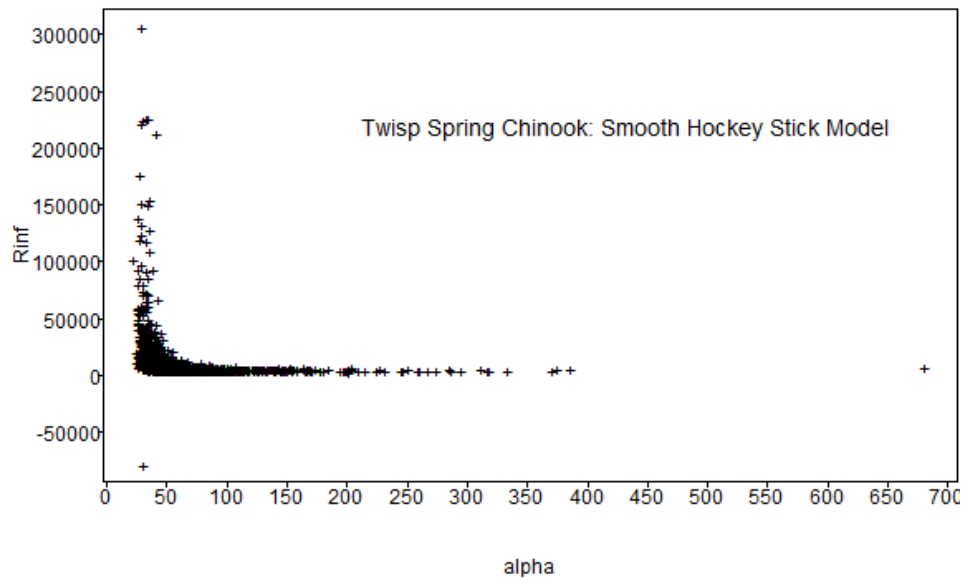


Figure D3. Correlation plot of bootstrap parameter estimates from the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for Twisp River Spring Chinook, 2003–2017, based on 2,813 bootstrap samples.

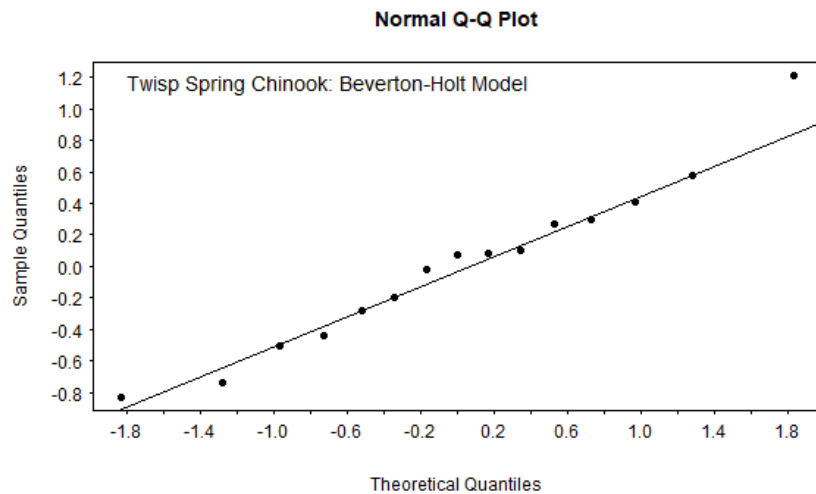


Figure D4. Normal quantile-quantile plot of residual from Beverton-Holt model of smolt recruitment as a function of spawner abundance (stock) for Twisp River Spring Chinook, 2003–2017. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: $W=0.9700$,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

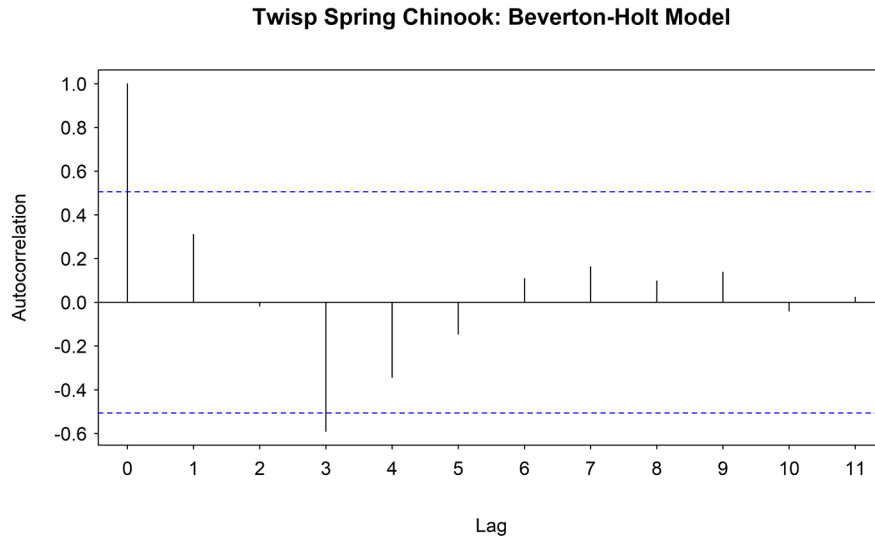


Figure D5. Autocorrelation plot of residuals for Beverton-Holt model of smolt recruitment as a function of spawner abundance (stock) for Twisp River Spring Chinook, 2003–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

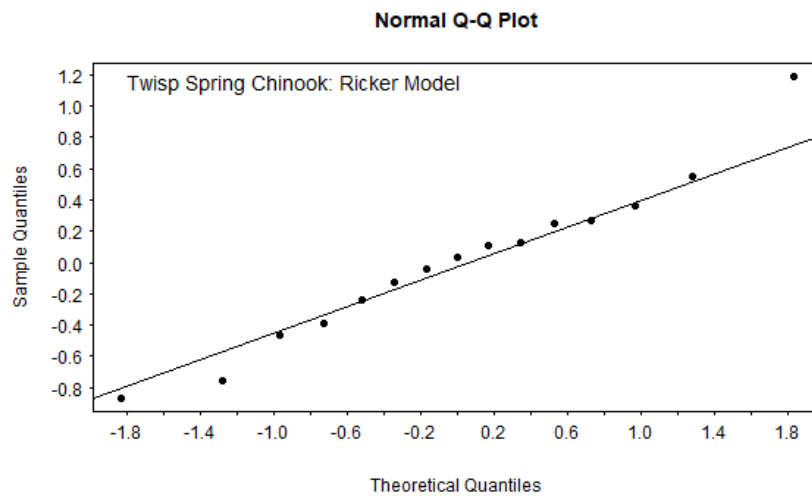


Figure D6. Normal quantile-quantile plot of residual from Ricker model of smolt recruitment as a function of spawner abundance (stock) for Twisp River Spring Chinook, 2003–2017. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: $W=0.9815$, $P=0.8831$.

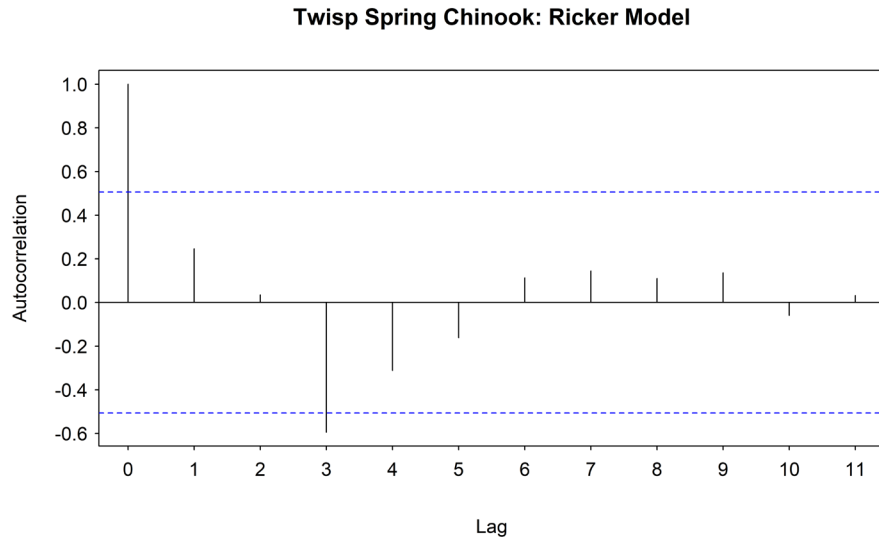


Figure D7. Autocorrelation plot of residuals for Ricker model of smolt recruitment as a function of spawner abundance (stock) for Twisp River Spring Chinook, 2003–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

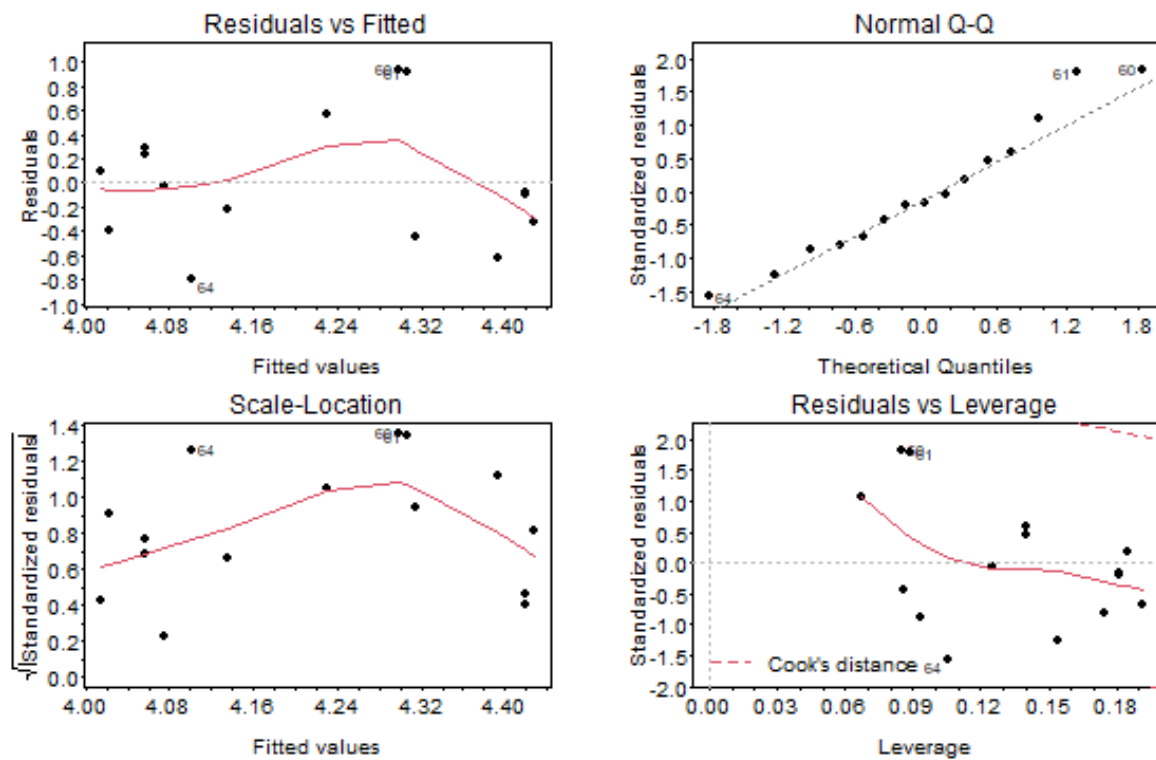


Figure D8. Residual plots for linear model of smolts per redd (log scale) as a function of pHOS for Twisp River Spring Chinook, 2003–2017. Shapiro-Wilk test of normality of residuals: $W=0.9575$, $P=0.6489$.

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	

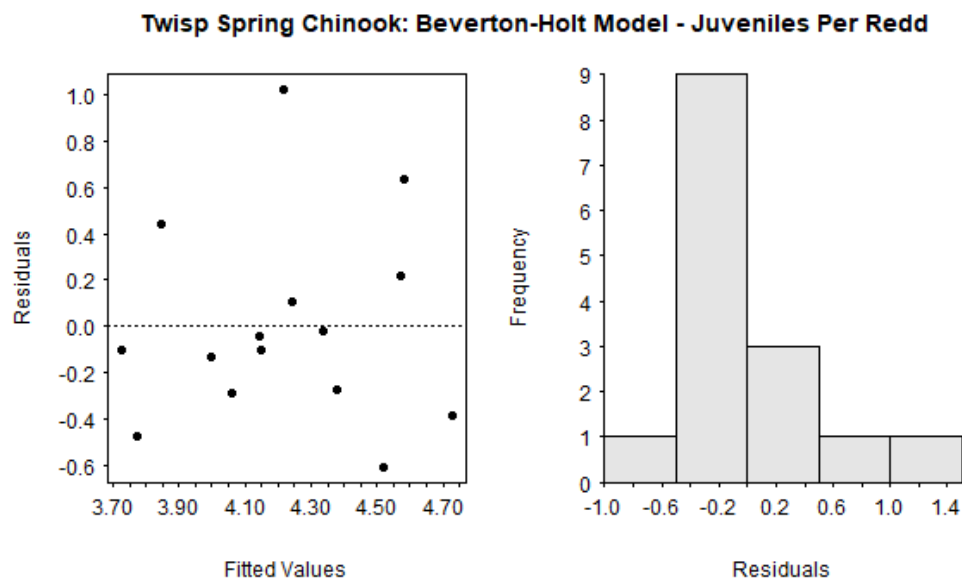


Figure D9. Residual plots for Beverton-Holt model of smolts per redd as a function of redd count and pHOS for Twisp River Spring Chinook, 2003–2017. Shapiro-Wilk test of normality of residuals: $W=0.9345$, $P=0.3185$.

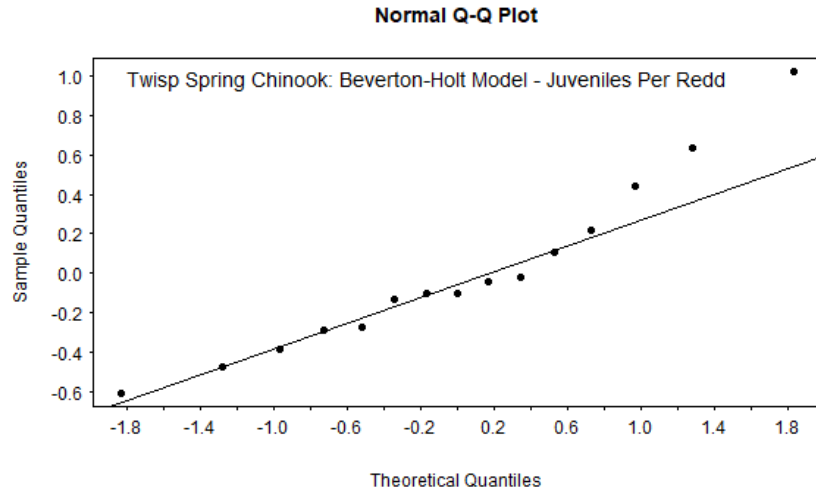


Figure D10. Normal quantile-quantile plot of residual from Beverton-Holt model of smolts per redd as a function of redd count and pHOS for Twisp River Spring Chinook, 2003–2017. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: $W=0.9345$, $P=0.3185$.

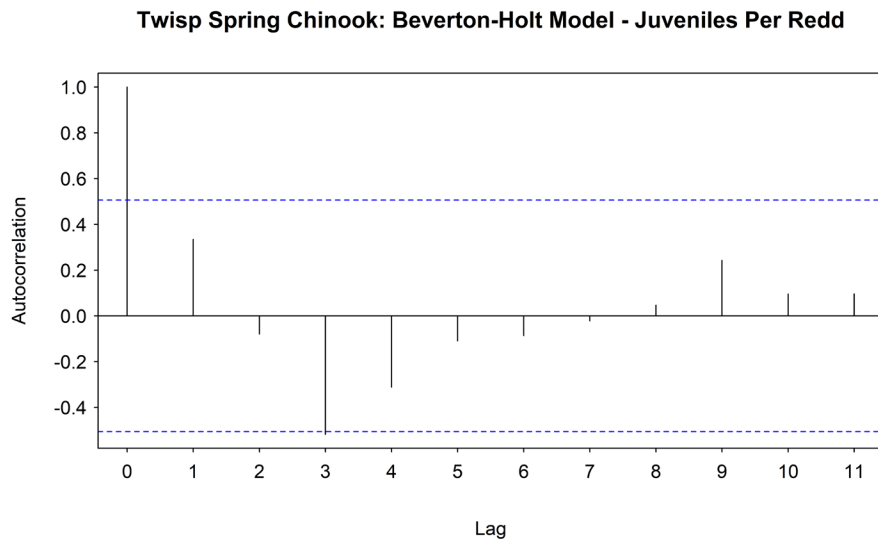


Figure D11. Autocorrelation plot of residuals for Beverton-Holt model of smolts per redd as a function of redd count and pHOS for Twisp River Spring Chinook, 2003–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

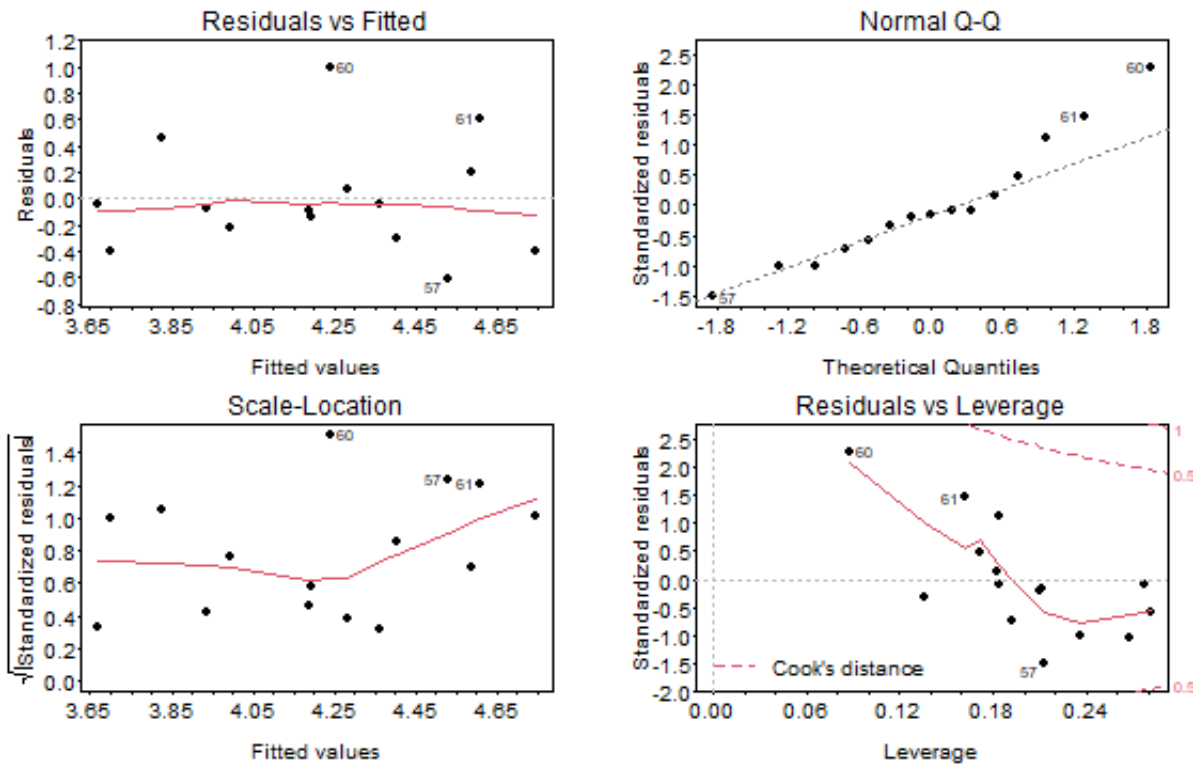


Figure D12. Residual plots for Ricker model of smolts per redd as a function of redd count and pHOS for Twisp River Spring Chinook, 2003–2017. Shapiro-Wilk test of normality of residuals: $W=0.9284$, $P=0.2587$.

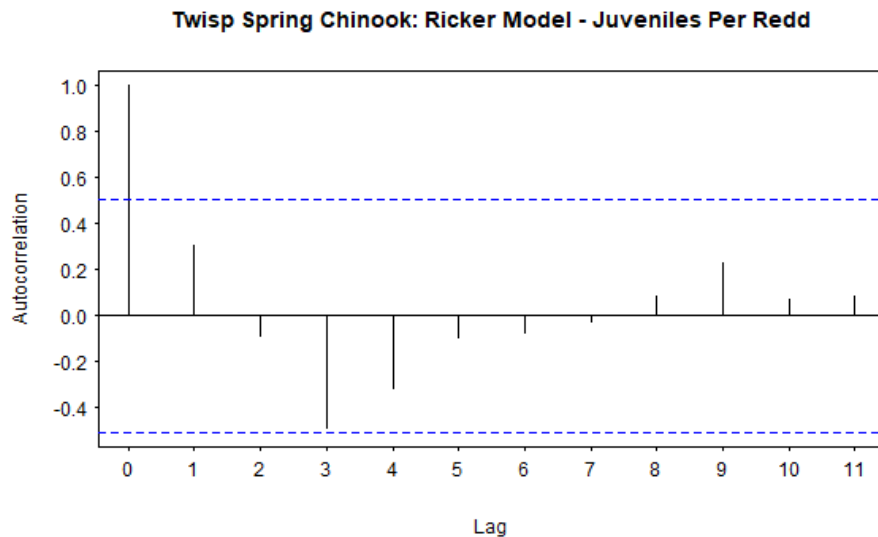


Figure D13. Autocorrelation plot of residuals for Ricker model of smolts per redd as a function of redd count and pHOS for Twisp River Spring Chinook, 2003–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

Appendix E: Methow River Spring Chinook Salmon

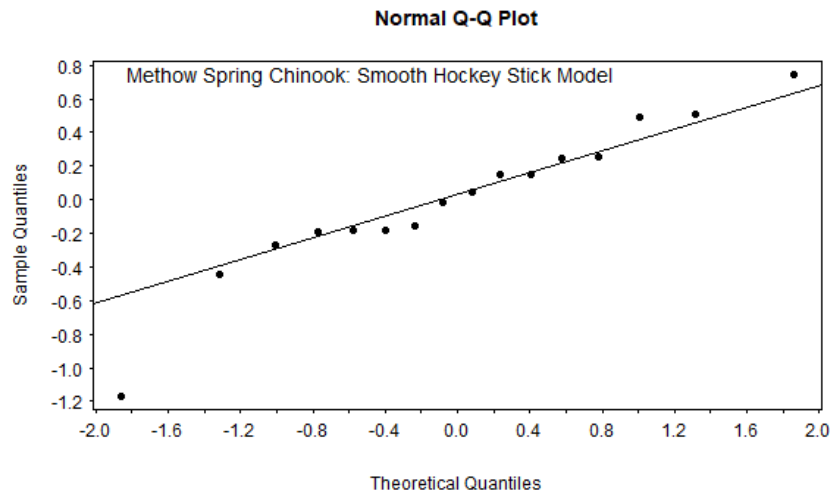


Figure E1. Normal quantile-quantile plot of residual from the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for Methow River Spring Chinook, 2002–2017. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: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

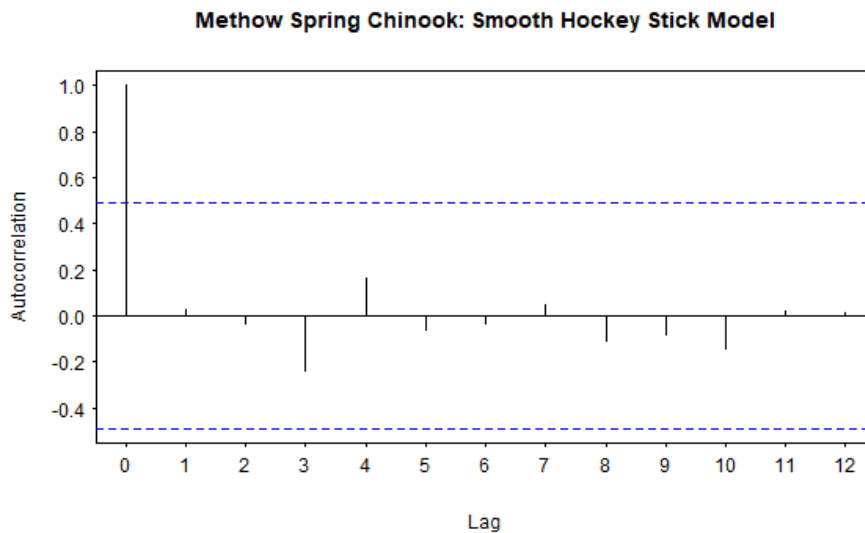


Figure E2. Autocorrelation plot of residuals for the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for Methow River Spring Chinook, 2002–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

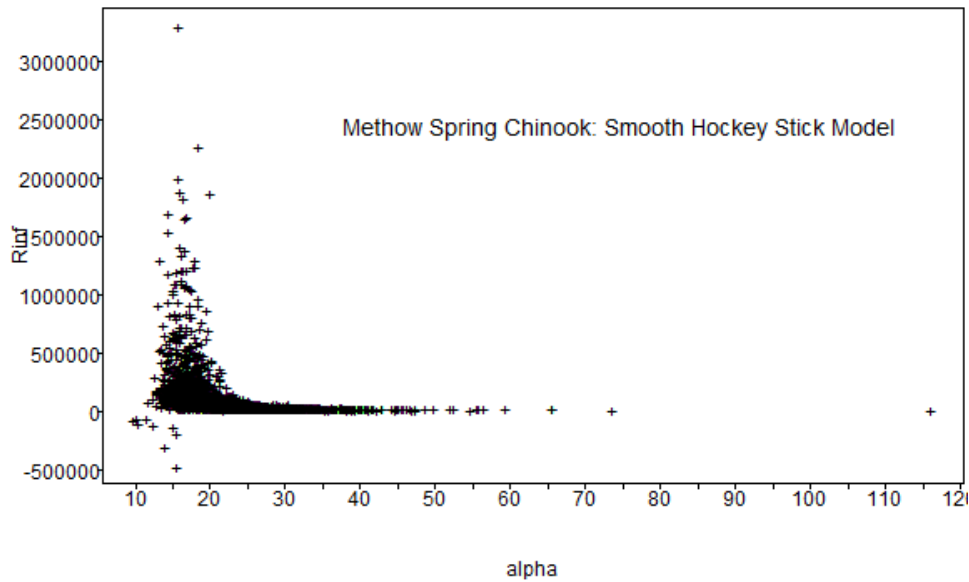


Figure E3. Correlation plot of bootstrap parameter estimates from the Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for Methow River Spring Chinook, 2002–2017, based on 3,182 bootstrap samples.

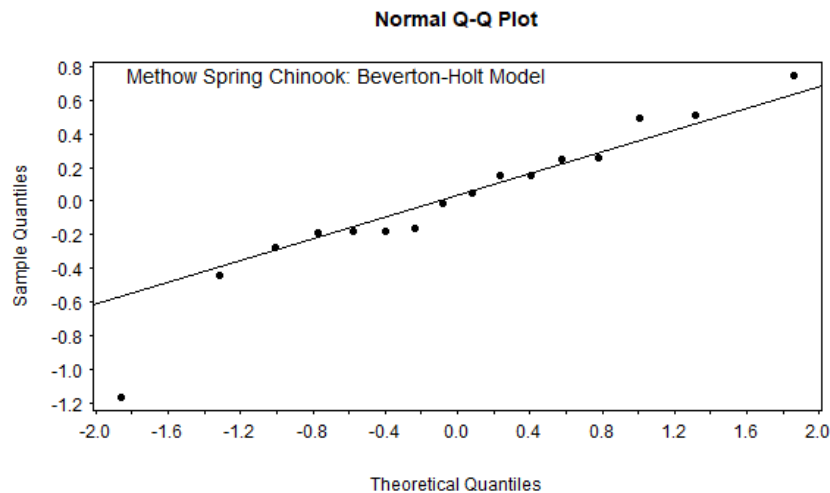


Figure E4. Normal quantile-quantile plot of residual from Beverton-Holt model of smolt recruitment as a function of spawner abundance (stock) for Methow River Spring Chinook, 2002–2017. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: $W=0.9382$,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

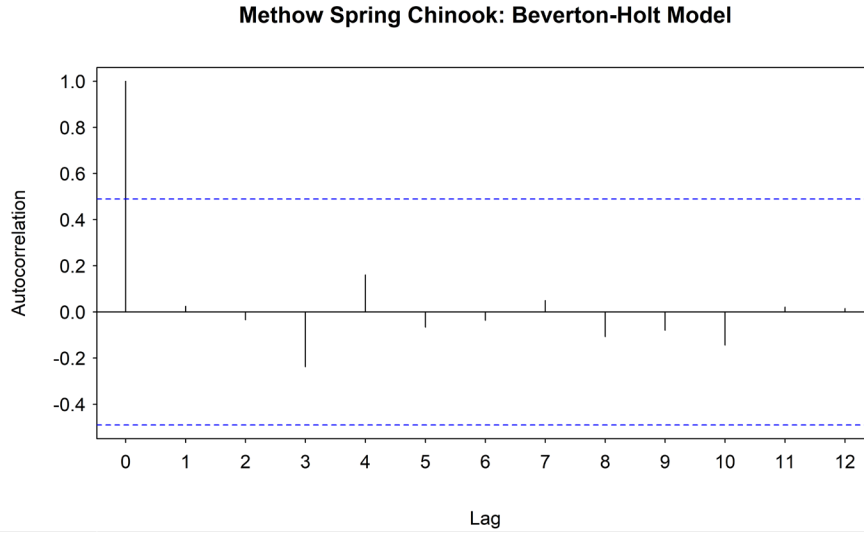


Figure E5. Autocorrelation plot of residuals for Beverton-Holt model of smolt recruitment as a function of spawner abundance (stock) for Methow River Spring Chinook, 2002–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

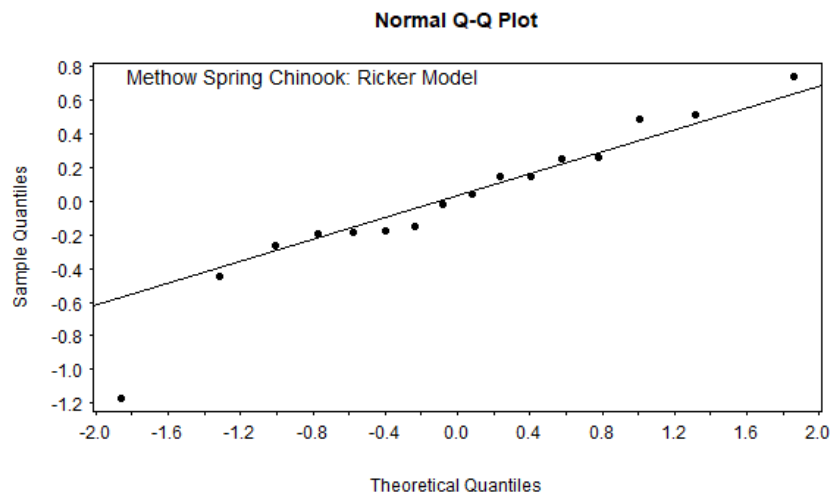


Figure E6. Normal quantile-quantile plot of residual from Ricker model of smolt recruitment as a function of spawner abundance (stock) for Methow River Spring Chinook, 2002–2017. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: $W=0.9370$,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

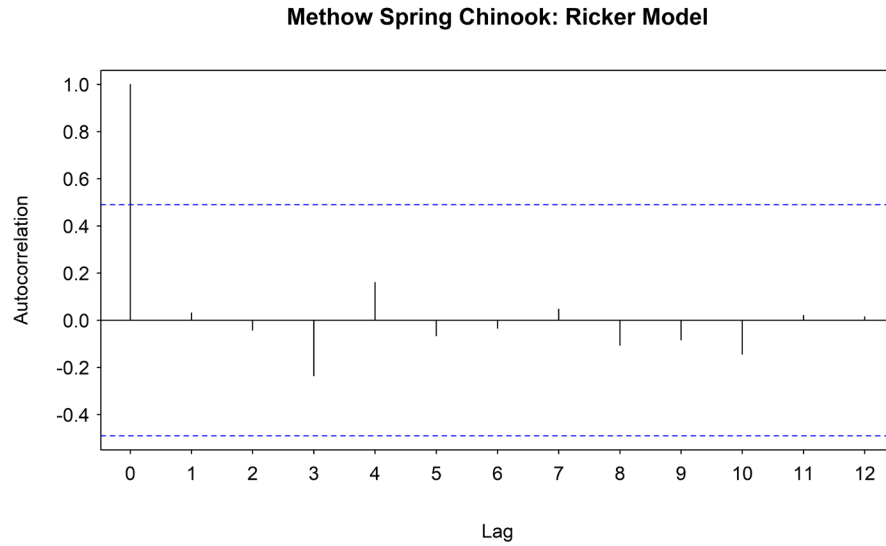


Figure E7. Autocorrelation plot of residuals for Ricker model of smolt recruitment as a function of spawner abundance (stock) for Methow River Spring Chinook, 2002–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

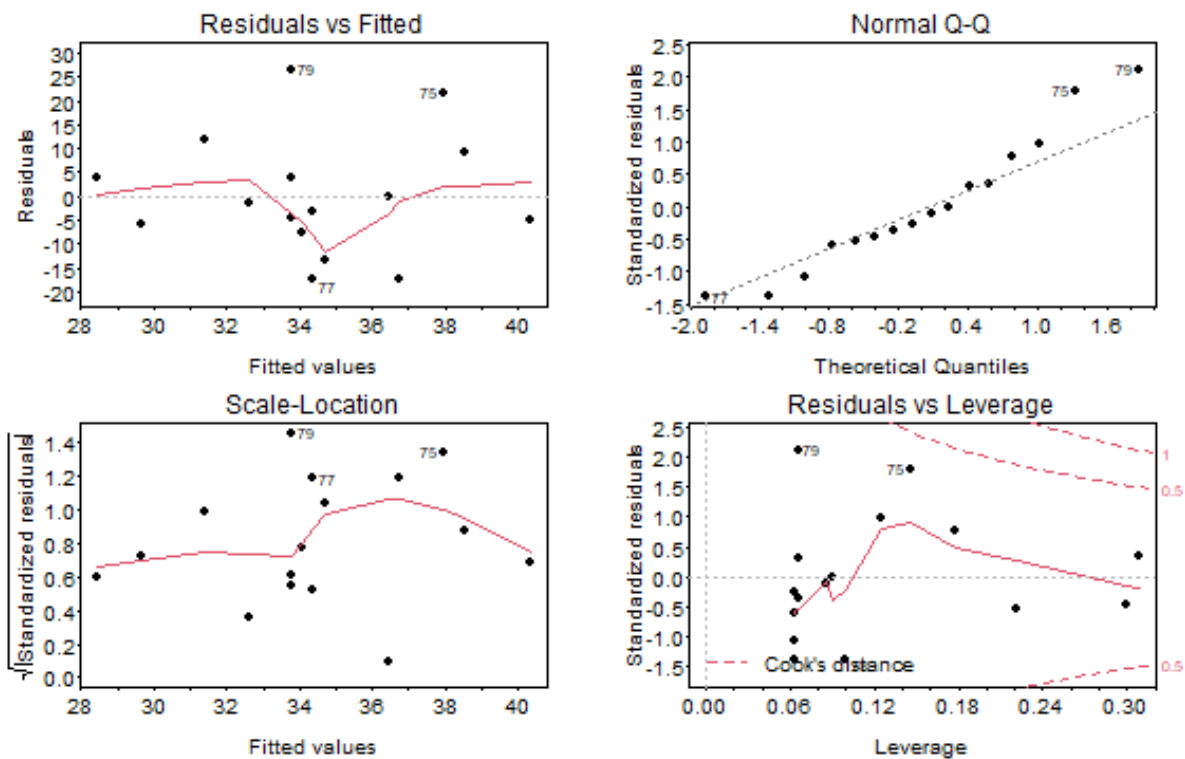


Figure E8. Residual plots for linear model of smolts per redd as a function of pHOS for Methow River Spring Chinook, 2002–2017. Shapiro-Wilk test of normality of residuals: $W=0.9467$, $P=0.4400$.

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	

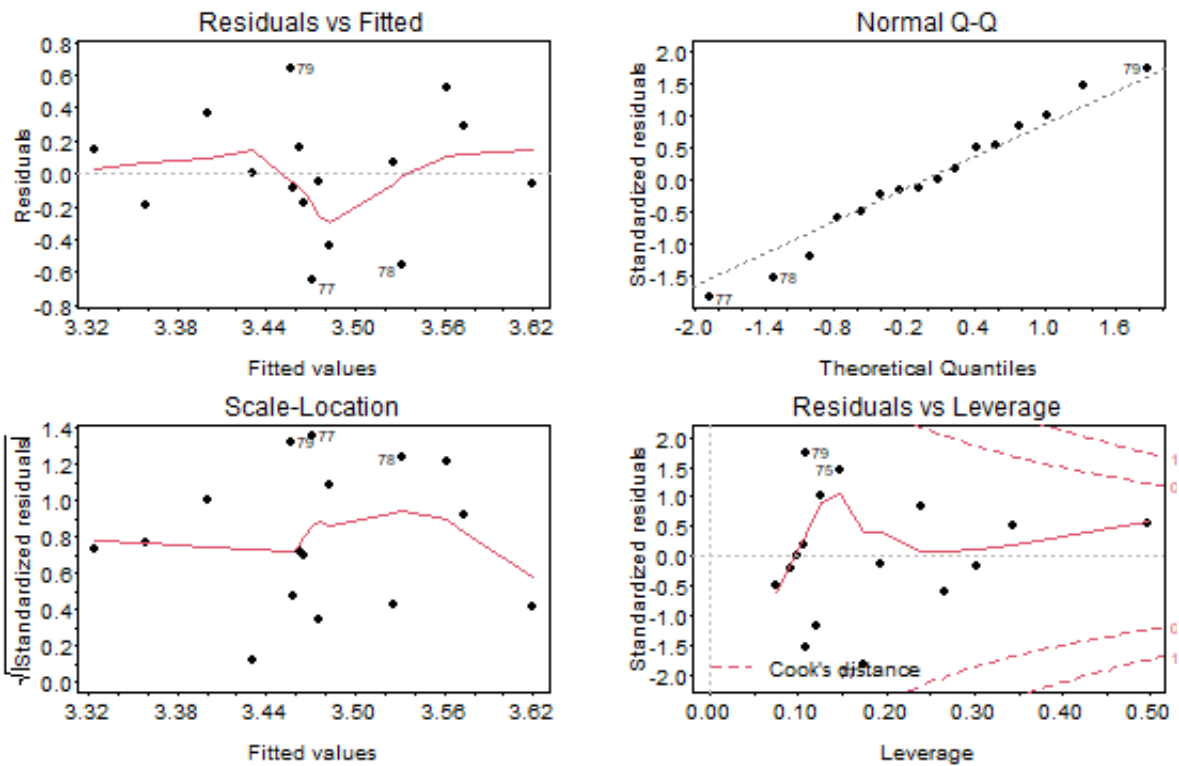


Figure E9. Residual plots for Ricker model of smolts per redd as a function of redd count and pHOS for Methow River Spring Chinook, 2002–2017. Shapiro-Wilk test of normality of residuals: $W=0.9794$, $P=0.9589$.

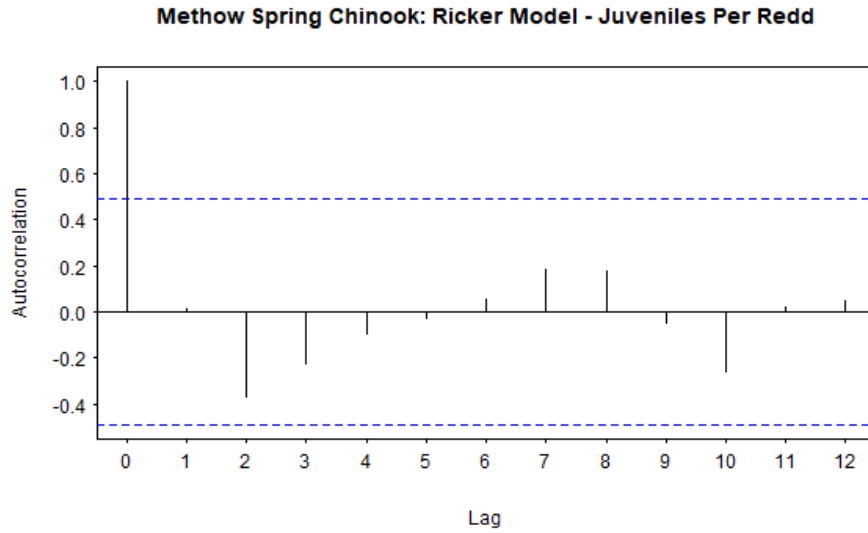


Figure E10. Autocorrelation plot of residuals for Ricker model of smolts per redd as a function of redd count and pHOS for Methow River Spring Chinook, 2002–2017. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

Appendix F: Wenatchee River Summer Chinook Salmon

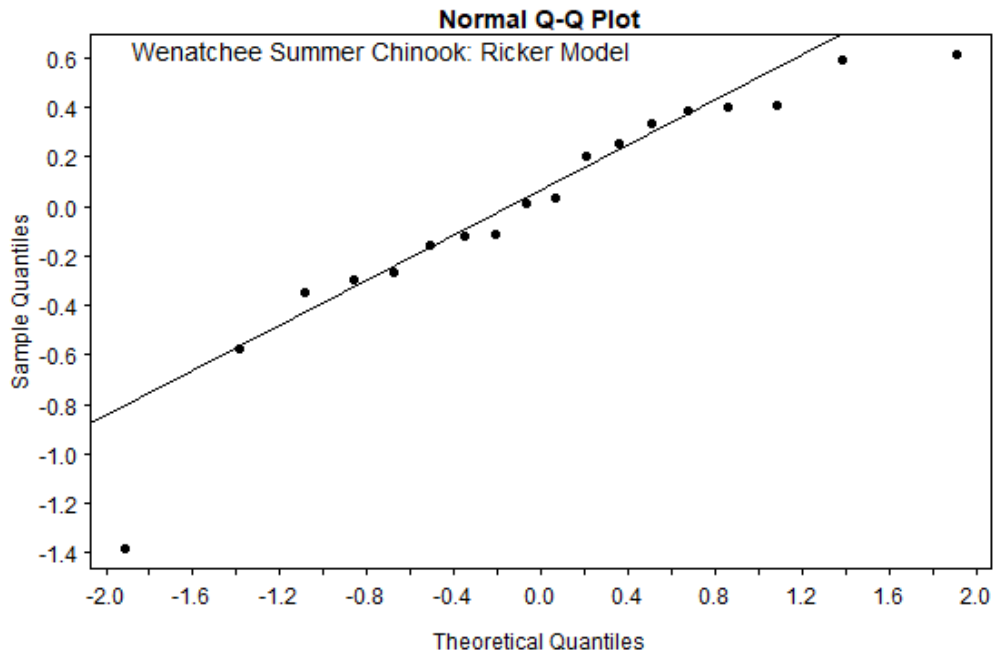


Figure F1. Normal quantile-quantile plot of residual from Ricker model of emigrant count as a function of spawner abundance (stock) for Wenatchee River Summer Chinook, 1999–2018 (without 2010, 2011). Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: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

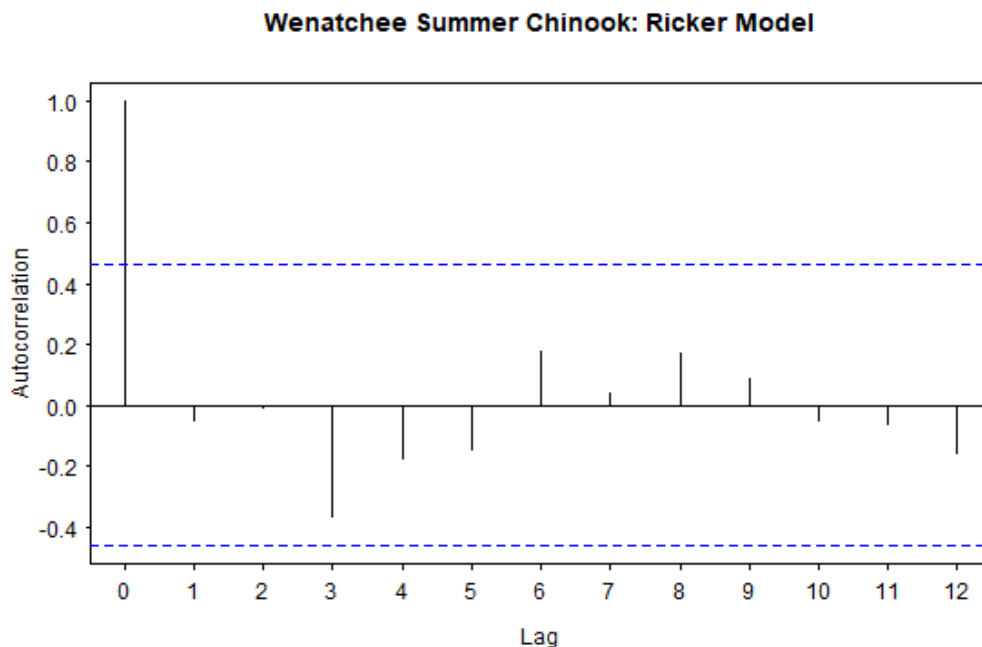


Figure F2. Autocorrelation plot of residuals for Ricker model of smolt recruitment as a function of spawner abundance (stock) for Wenatchee River Summer Chinook, 1999–2018 (without 2010, 2011). Blue lines mark 95% confidence interval under assumption of no autocorrelation.

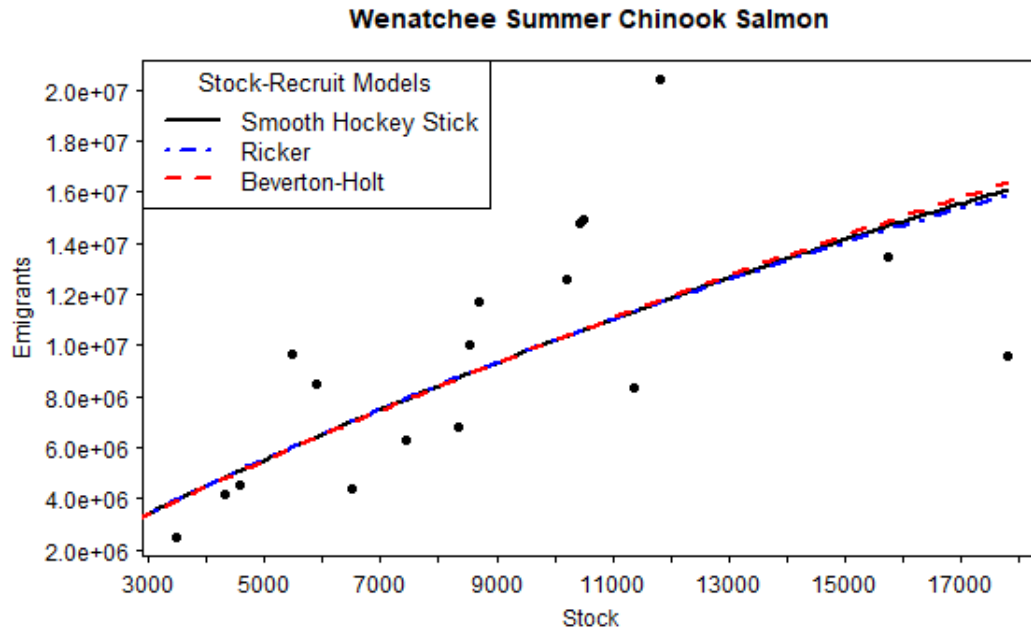


Figure F3. The Smooth Hockey Stick, Beverton-Holt, and Ricker stock-recruitment model fit to emigrants and spawner data for Wenatchee River Summer Chinook Salmon, 1999–2018 (without 2000, 2010, 2011).

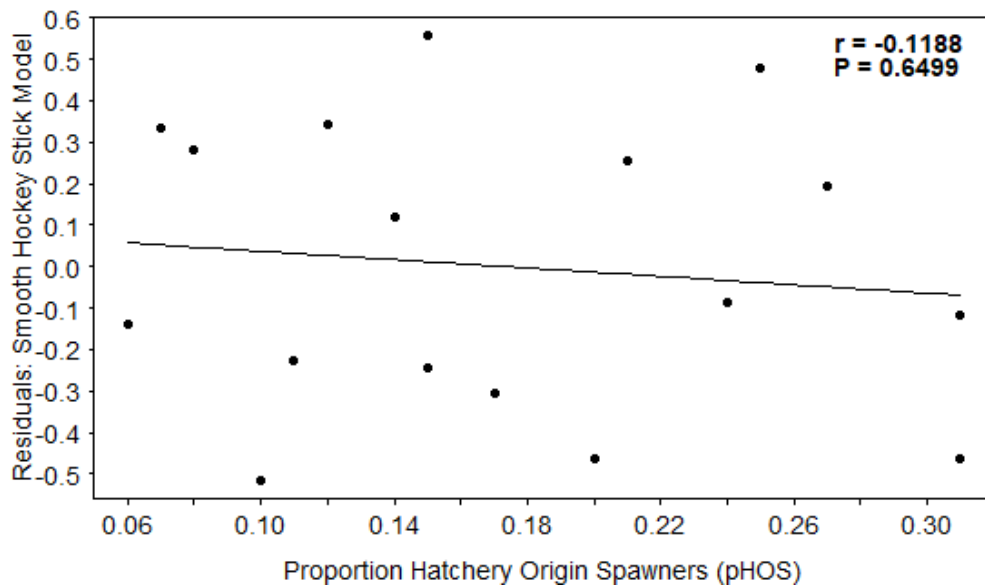


Figure F4. Residuals from the Smooth Hockey Stick Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Wenatchee River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

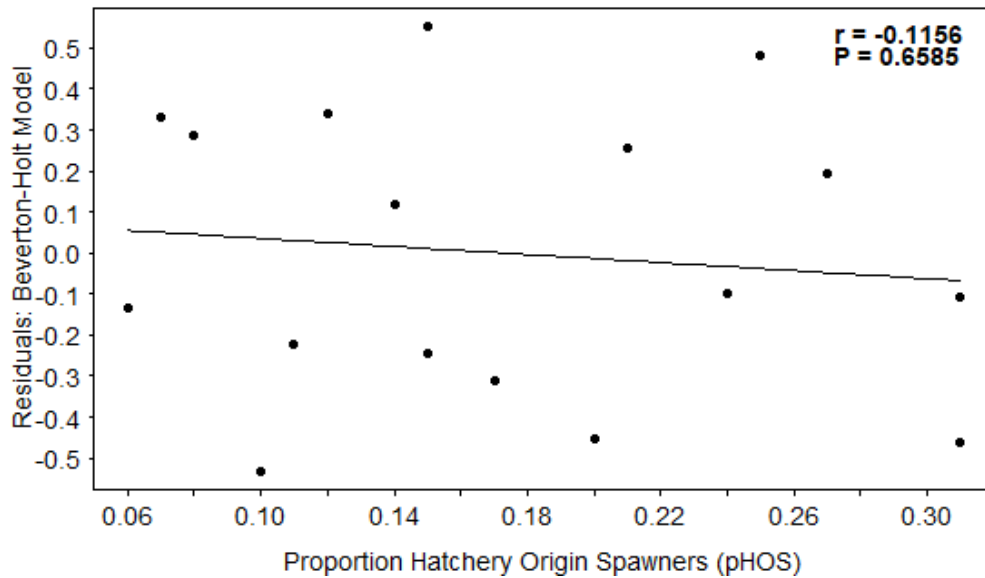


Figure F5. Residuals from the Beverton-Holt Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Wenatchee River Summer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

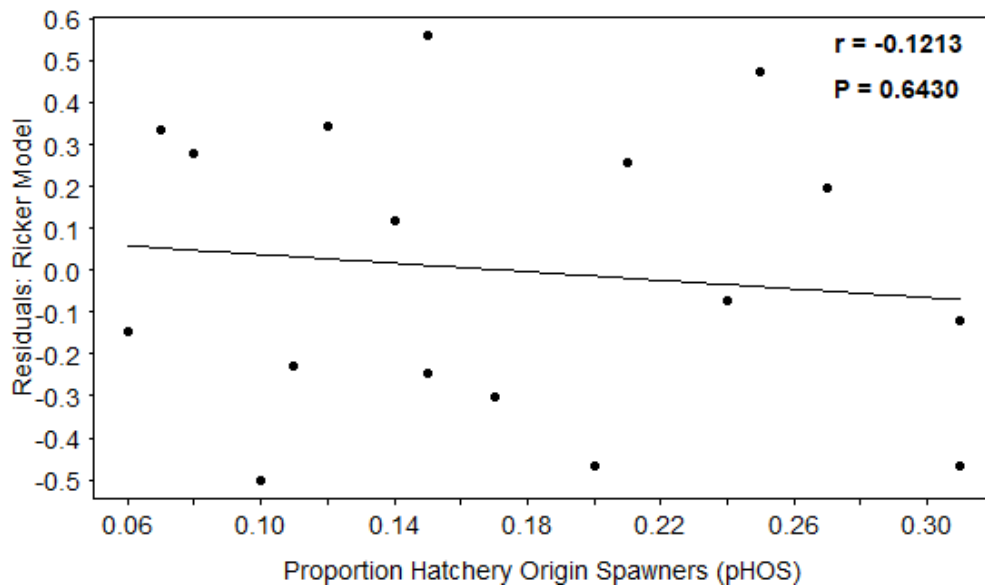


Figure F6. Residuals from Ricker Model versus proportion of hatchery origin spawners (pHOS) with fitted linear regression line, Pearson correlation coefficient (r), and P-value from two-sided t-test of slope of linear regression line using smolt and spawner data from Wenatchee River Summer Chinook Salmon,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

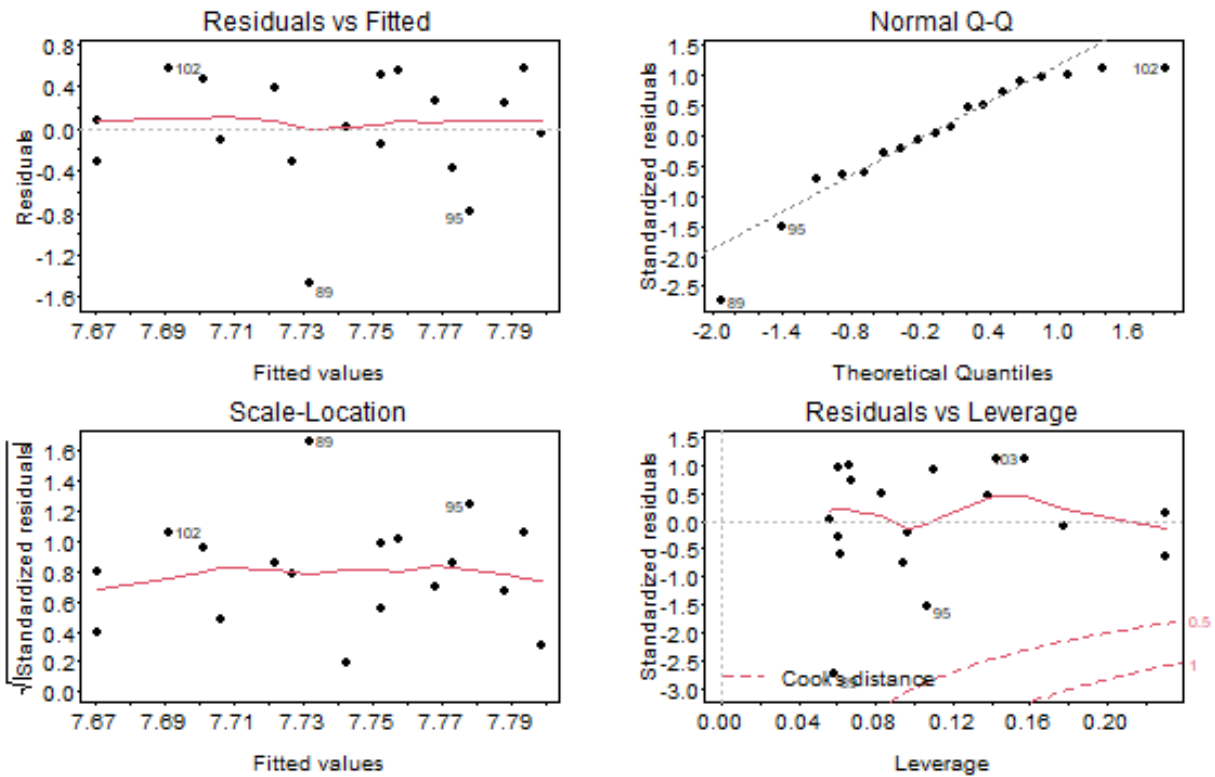


Figure F7. Residual plots for linear model of emigrants (log scale) per redd as a function of pHOS for Wenatchee River Summer Chinook, 1999–2018 (without 2010, 2011). Shapiro-Wilk test of normality of residuals: $W=0.8877$, $P=0.0353$.

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	

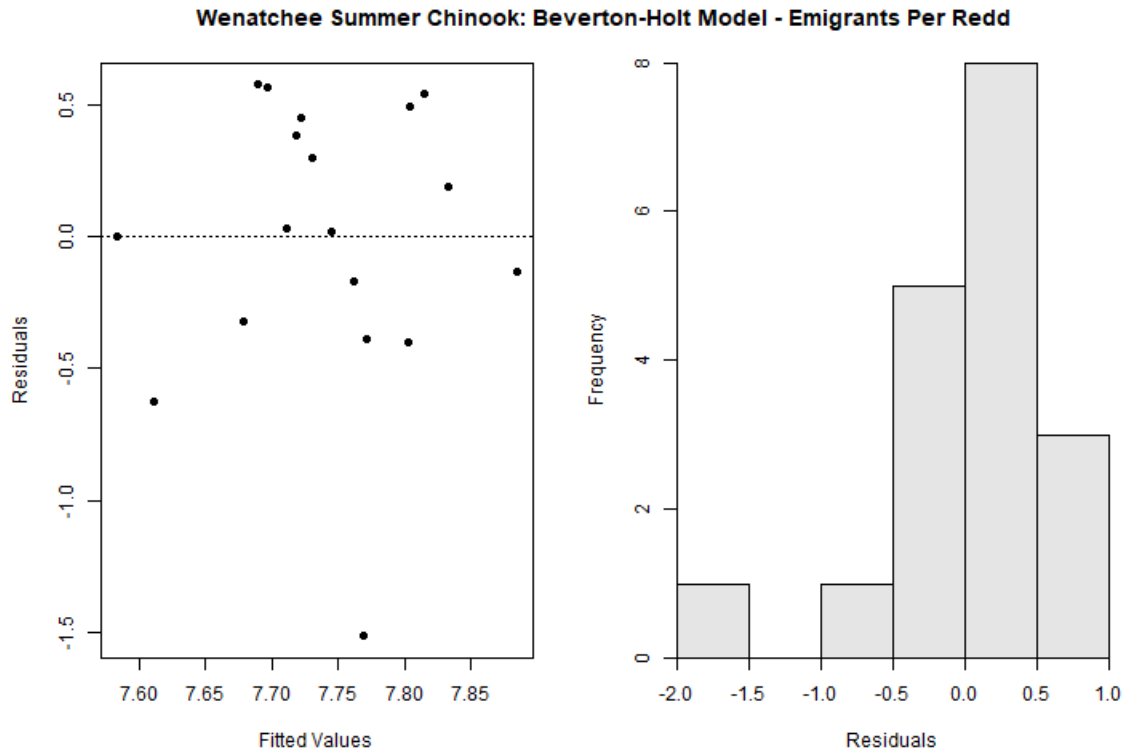


Figure F8. Residual plots for Beverton-Holt model of emigrants per redd as a function of redd count and pHOS for Wenatchee River Summer Chinook, 1999–2018 (without 2010, 2011). Shapiro-Wilk test of normality of residuals: $W=0.8845$, $P=0.0311$.

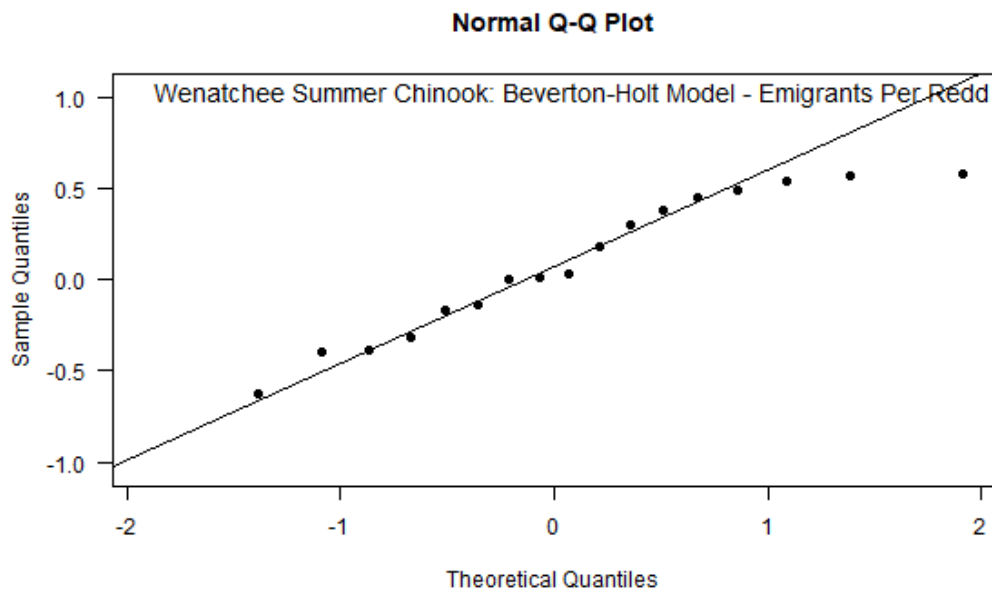


Figure F9. Normal quantile-quantile plot of residual from Beverton-Holt model of emigrants per redd as a function of redd count and pHOS for Wenatchee River Summer Chinook, 1999–2018 (without 2010, 2011). Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality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

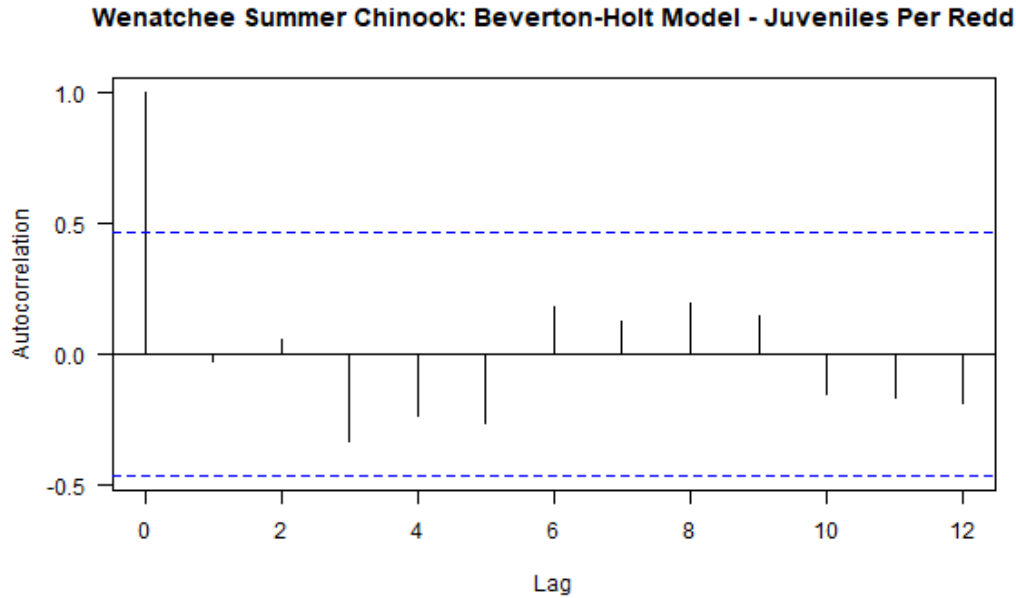


Figure F10. Autocorrelation plot of residuals for Beverton-Holt model of emigrants per redd as a function of redd count and pHOS for Wenatchee River Summer Chinook, 1999–2018 (without 2010, 2011). Blue lines mark 95% confidence interval under assumption of no autocorrelation.

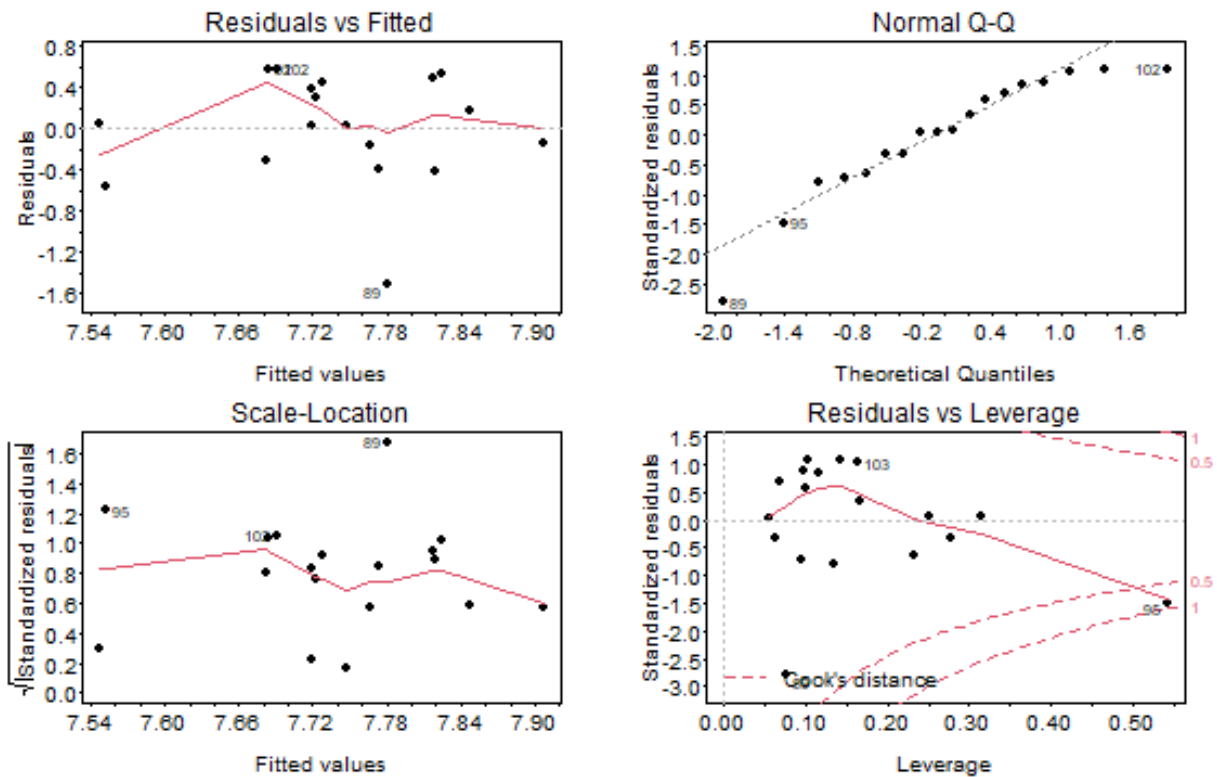


Figure F11. Residual plots for Ricker model of emigrants per redd as a function of redd count and pHOS for Wenatchee River Summer Chinook, 1999–2018 (without 2010, 2011). Shapiro-Wilk test of normality of residuals: $W=0.8822$, $P=0.0284$.

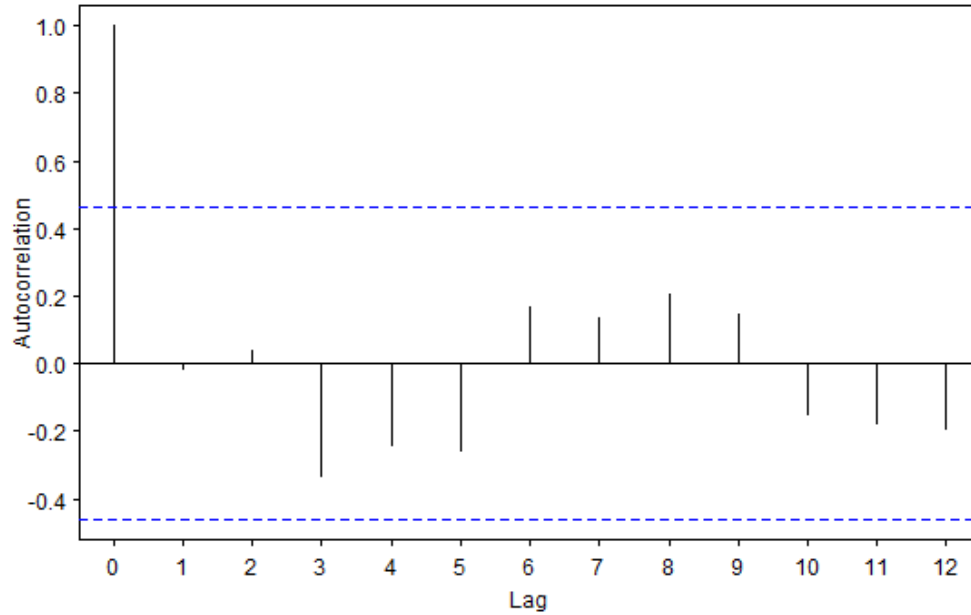


Figure F12. Autocorrelation plot of residuals for Ricker model of smolts per redd as a function of redd count and pHOS for Wenatchee River Summer Chinook, 1999–2018 (without 2010, 2011). Blue lines mark 95% confidence interval under assumption of no autocorrelation.

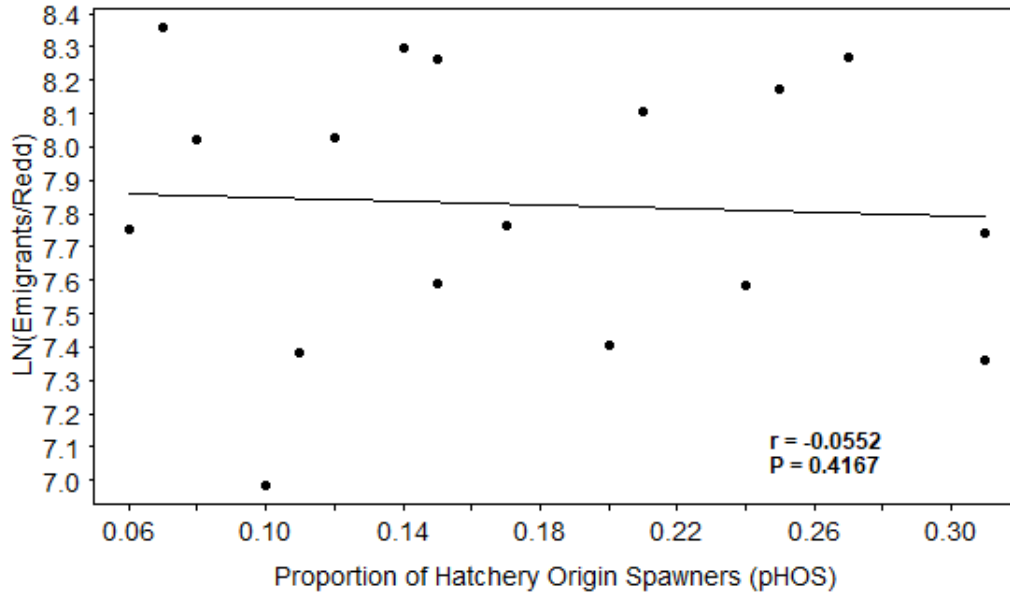


Figure F13. Emigrants per redd (log scale) versus proportion of hatchery origin spawners (pHOS) for Wenatchee River Summer Chinook Salmon, 1999–2018 (without 2000, 2010, 2011), with fitted linear regression line, Pearson correlation coefficient (r), and P-value from one-sided t-test of negative slope.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

Appendix G: Methow River Summer Chinook Salmon

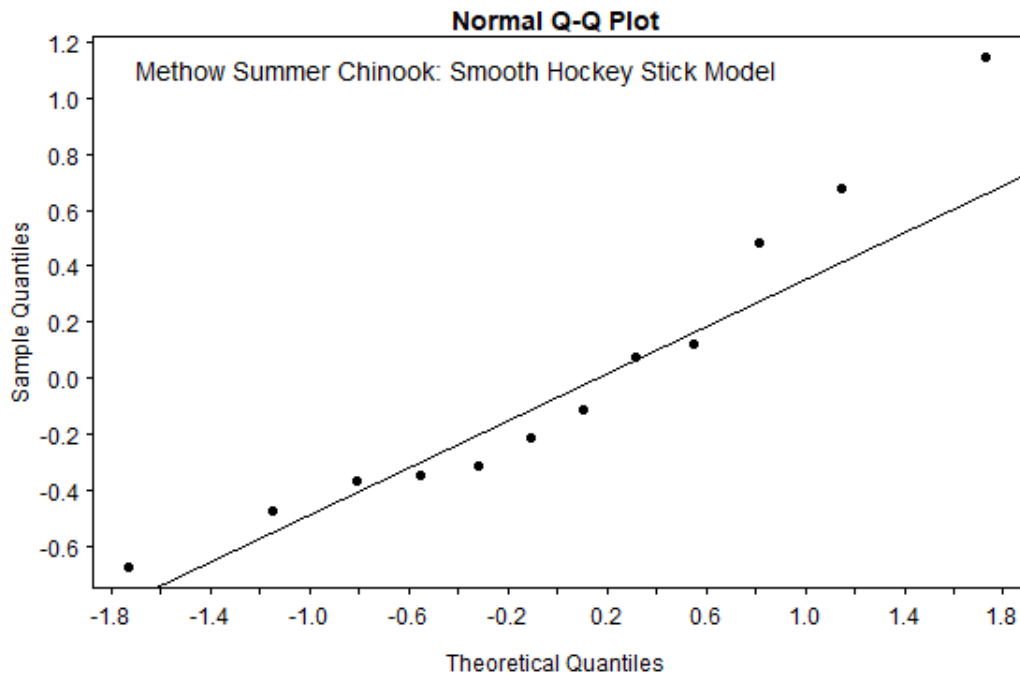


Figure G1. Normal quantile-quantile plot of residual from Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for Methow River Summer Chinook, 2006–2018 (without 2012). Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality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

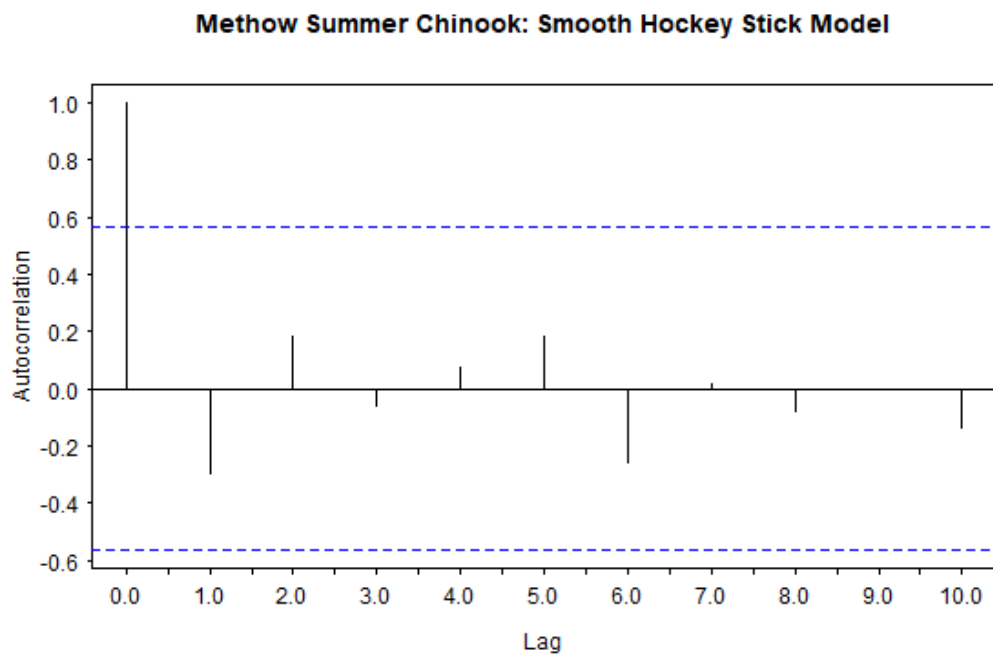


Figure G2. Autocorrelation plot of residuals for Smooth Hockey Stick model of smolt recruitment as a function of spawner abundance (stock) for Methow River Summer Chinook, 2006–2018 (without 2012). Blue lines mark 95% confidence interval under assumption of no autocorrelation.

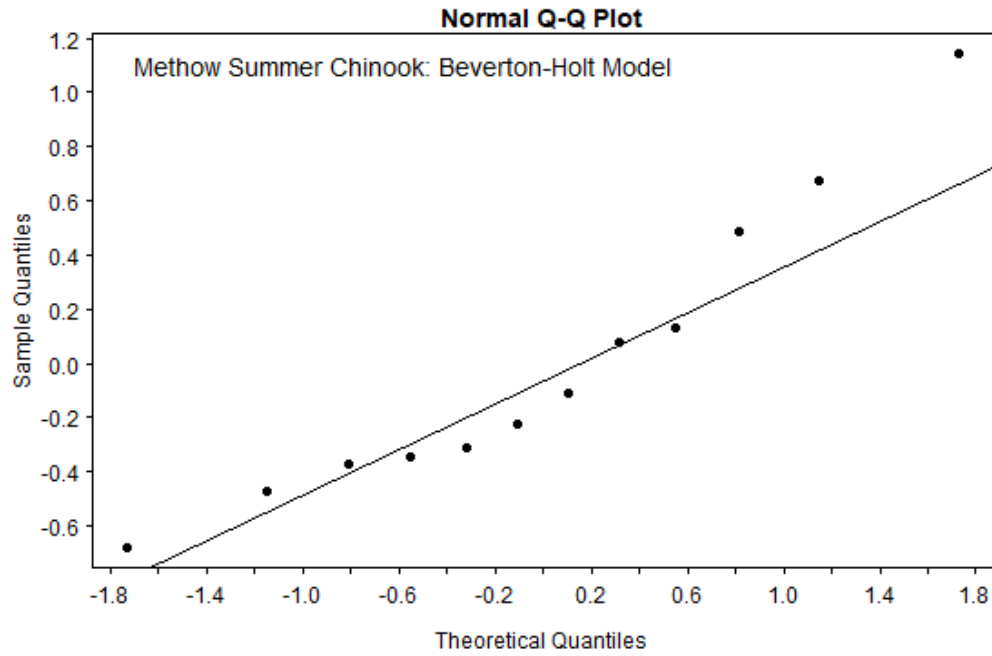


Figure G3. Normal quantile-quantile plot of residual from Beverton-Holt model of emigrant count as a function of spawner abundance (stock) for Methow River Summer Chinook, 2006–2018 (without 2012). Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: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

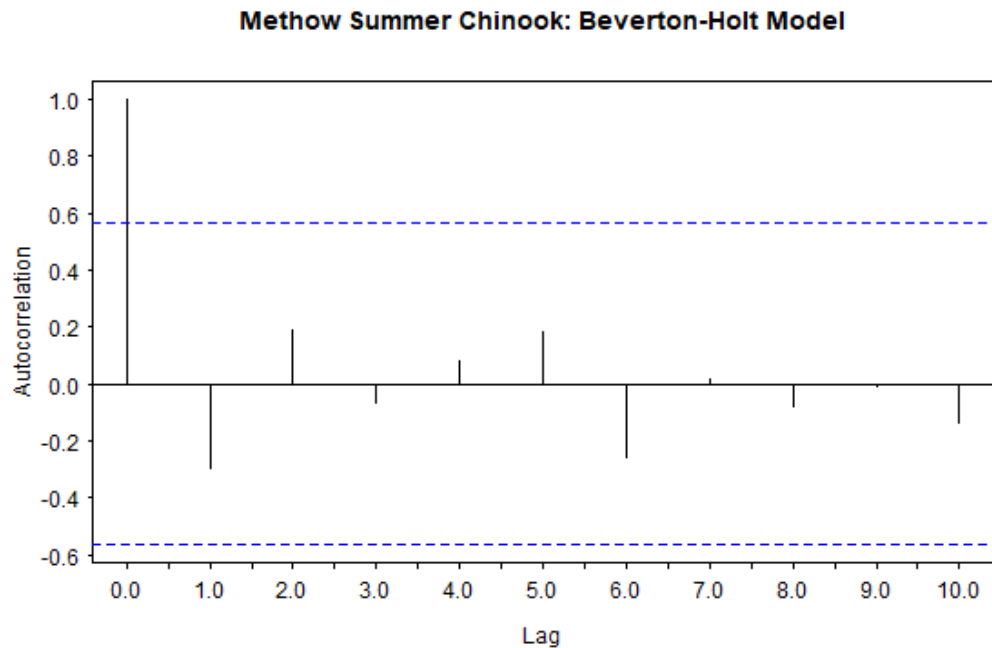


Figure G4. Autocorrelation plot of residuals for Beverton-Holt model of smolt recruitment as a function of spawner abundance (stock) for Methow River Summer Chinook, 2006–2018 (without 2012). Blue lines mark 95% confidence interval under assumption of no autocorrelation.

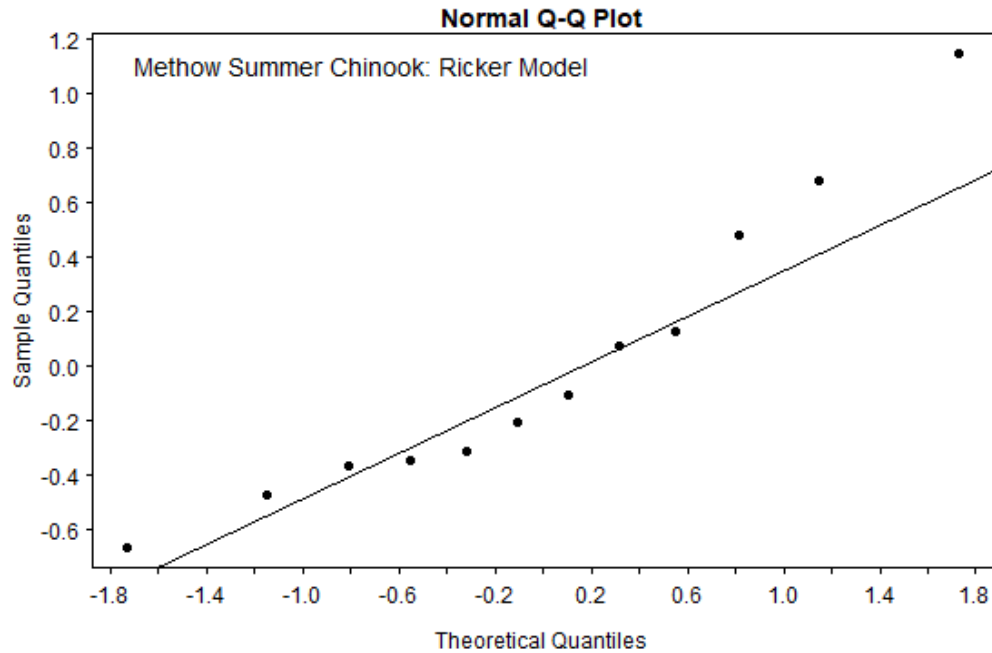


Figure G5. Normal quantile-quantile plot of residual from Ricker model of emigrant count as a function of spawner abundance (stock) for Methow River Summer Chinook, 2006–2018 (without 2012). Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: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

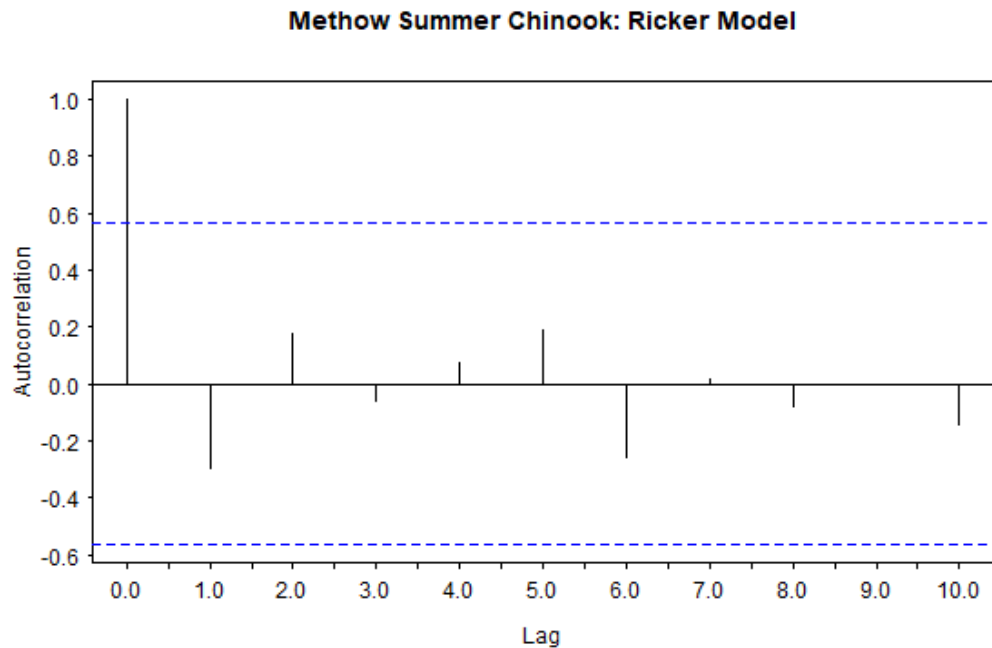


Figure G6. Autocorrelation plot of residuals for Ricker model of smolt recruitment as a function of spawner abundance (stock) for Methow River Summer Chinook, 2006–2018 (without 2012). Blue lines mark 95% confidence interval under assumption of no autocorrelation.

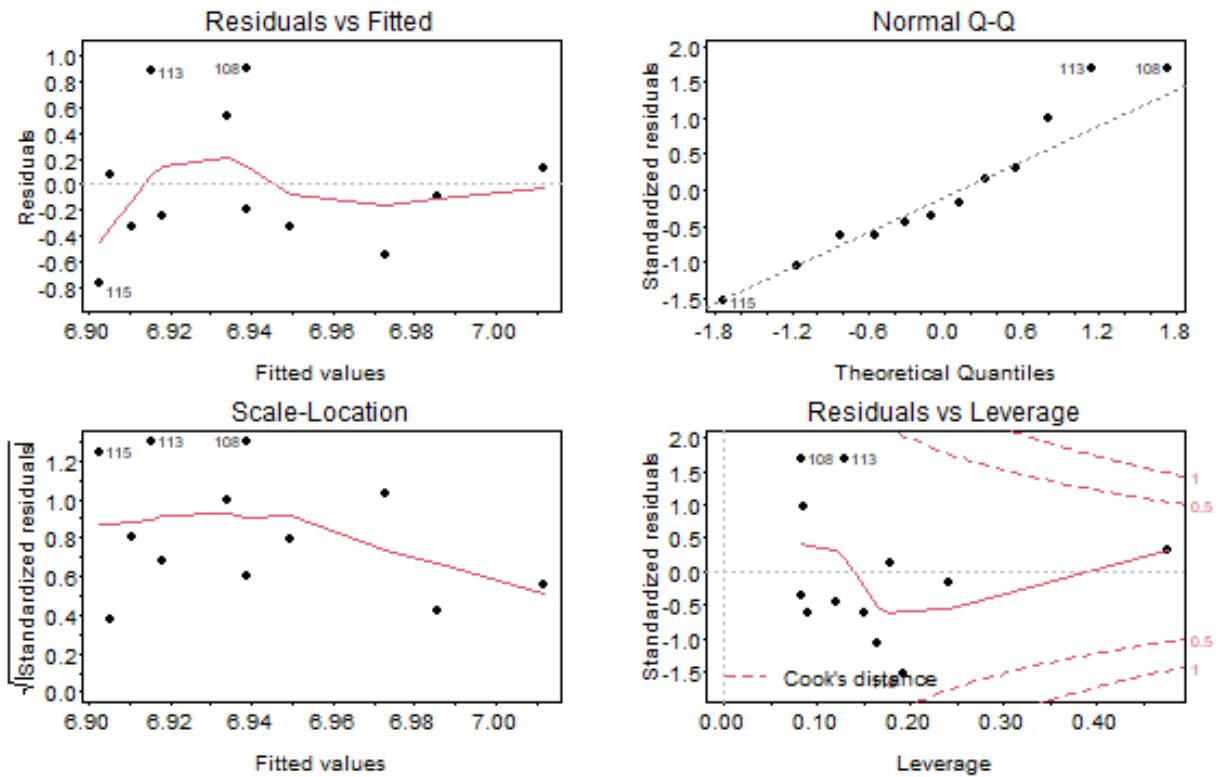


Figure G7. Residual plots for linear model of smolts per redd as a function of pHOS for Methow River Summer Chinook, 2006–2018 (without 2012). Shapiro-Wilk test of normality of residuals: $W=0.9284$, $P=0.3632$.

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	

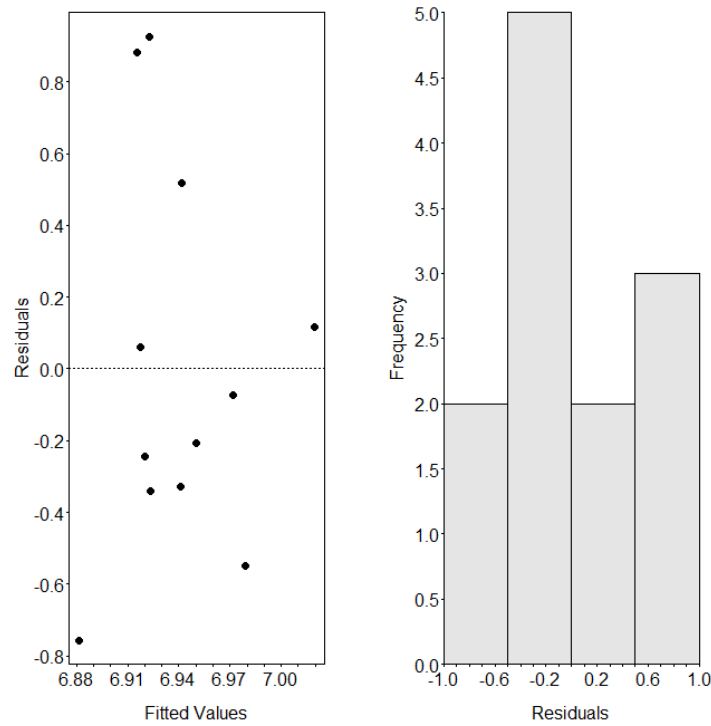


Figure G8. Residual plots for Beverton-Holt model of emigrants per redd as a function of redd count and pHOS for Methow River Summer Chinook, 2006–2018 (without 2012). Shapiro-Wilk test of normality of residuals: $W=0.9255$, $P=0.3352$.

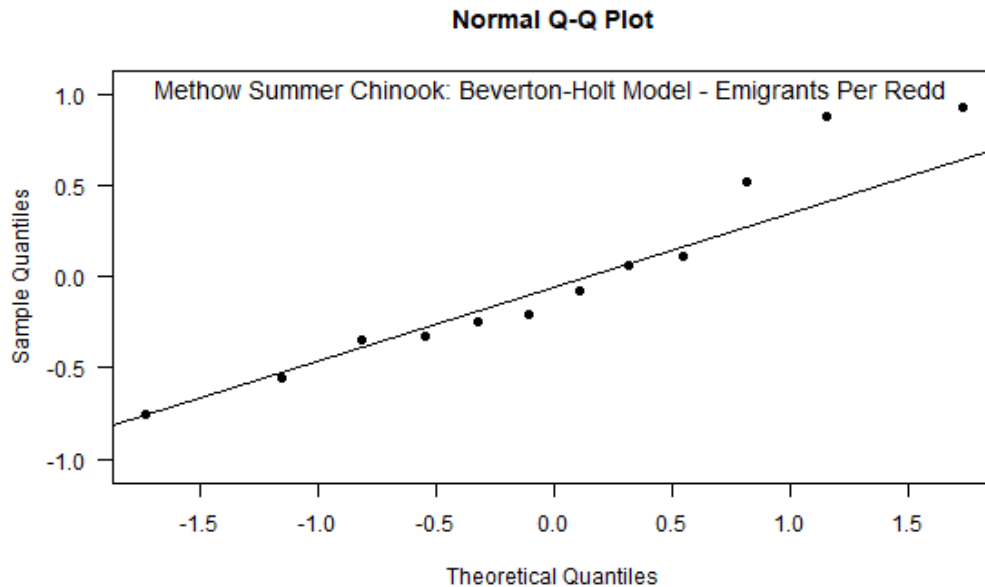


Figure G9. Normal quantile-quantile plot of residual from Beverton-Holt model of emigrants per redd as a function of redd count and pHOS for Methow River Summer Chinook, 2006–2018 (without 2012). Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: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

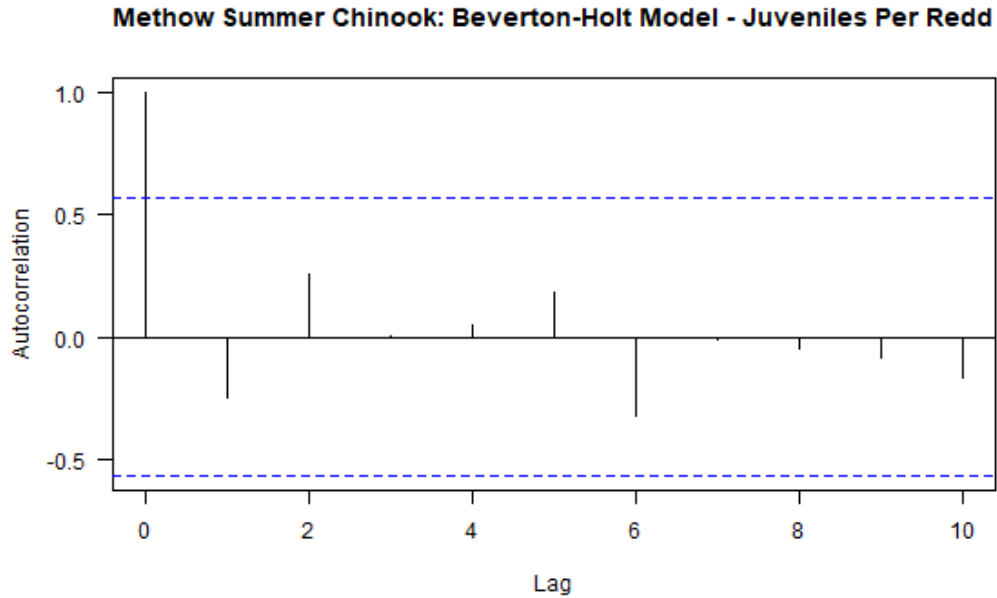


Figure G10. Autocorrelation plot of residuals for Beverton-Holt model of emigrants per redd as a function of redd count and pHOS for Methow River Summer Chinook, 2006–2018 (without 2012). Blue lines mark 95% confidence interval under assumption of no autocorrelation.

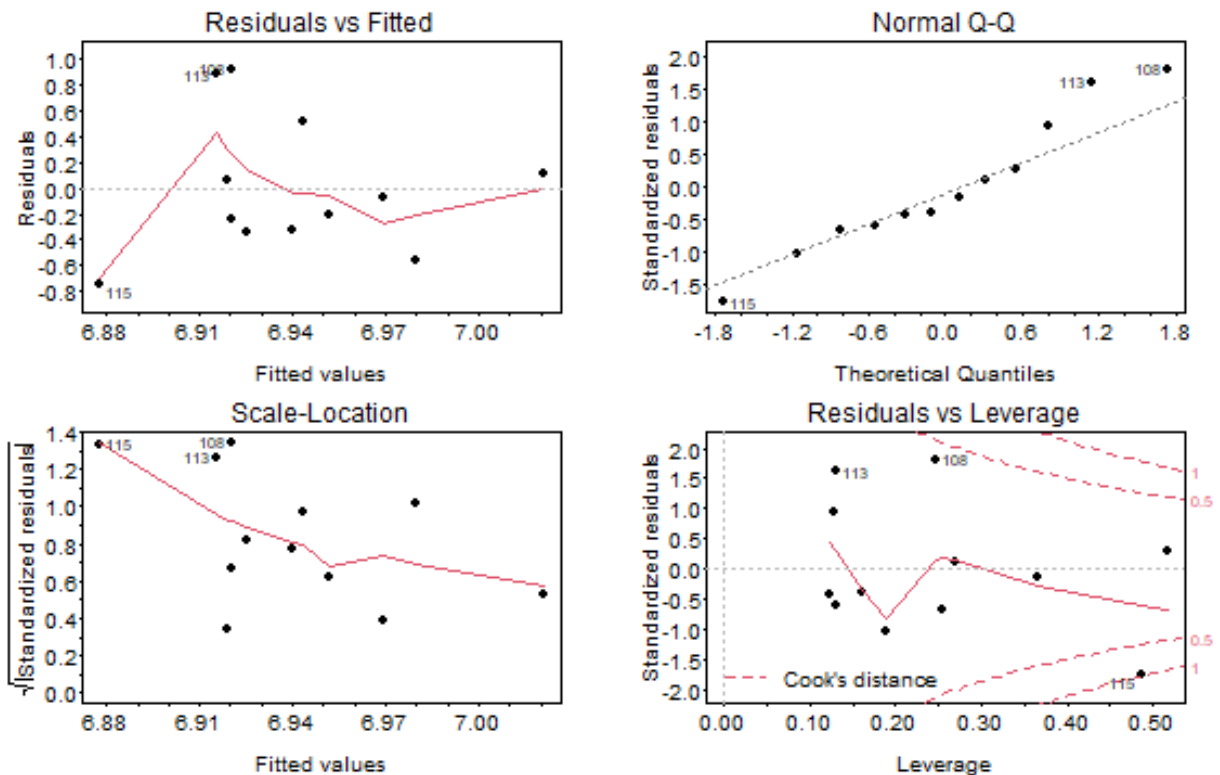


Figure G11. Residual plots for Ricker model of emigrants per redd as a function of redd count and pHOS for Methow River Summer Chinook, 2006–2018 (without 2012). Shapiro-Wilk test of normality of residuals: $W=0.9251$, $P=0.3313$.

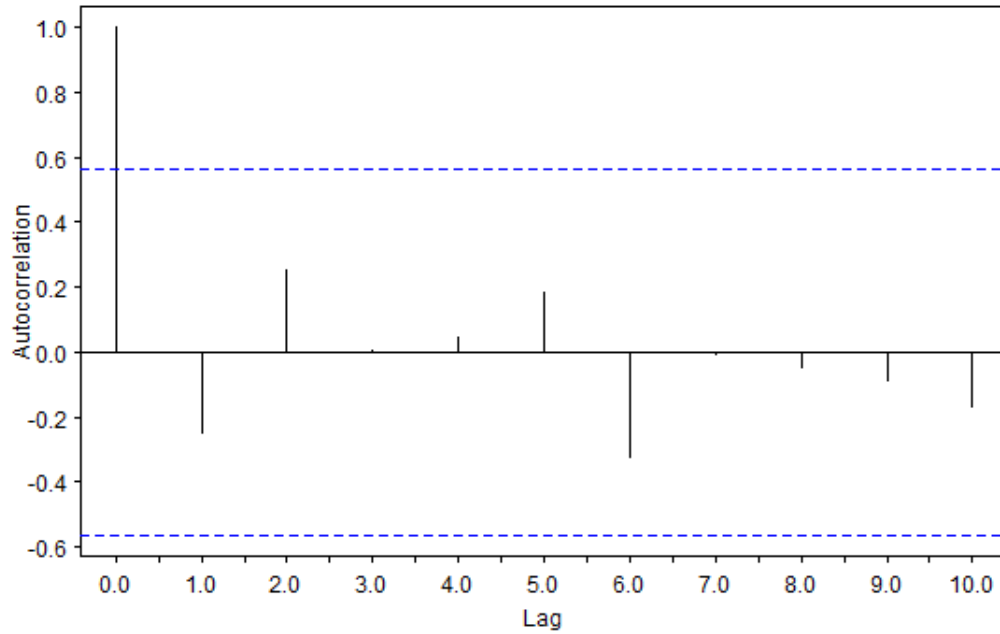


Figure G12. Autocorrelation plot of residuals for Ricker model of smolts per redd as a function of redd count and pHOS for Methow River Summer Chinook, 2006–2018 (without 2012). Blue lines mark 95% confidence interval under assumption of no autocorrelation.

Appendix H: Methow River Summer Steelhead

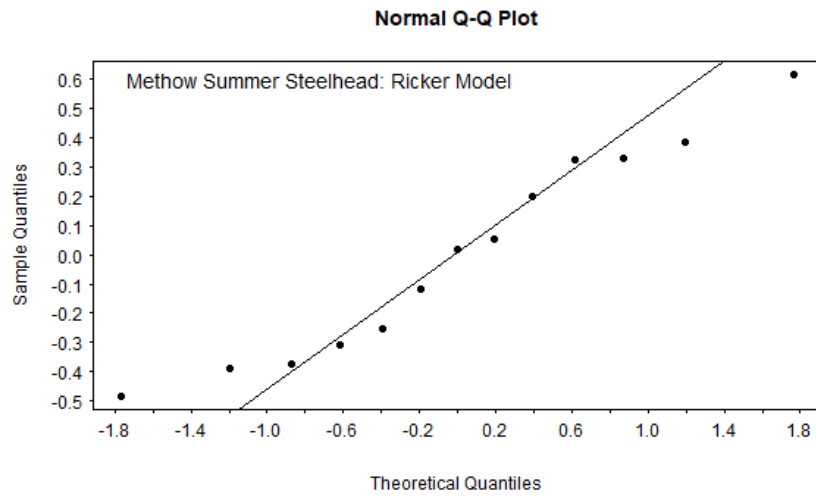


Figure H1. Normal quantile-quantile plot of residual from Ricker model of emigrant recruitment as a function of spawner abundance (stock) for Methow River Summer Steelhead, 2003–2015. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality of residuals: $W=0.9445$,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

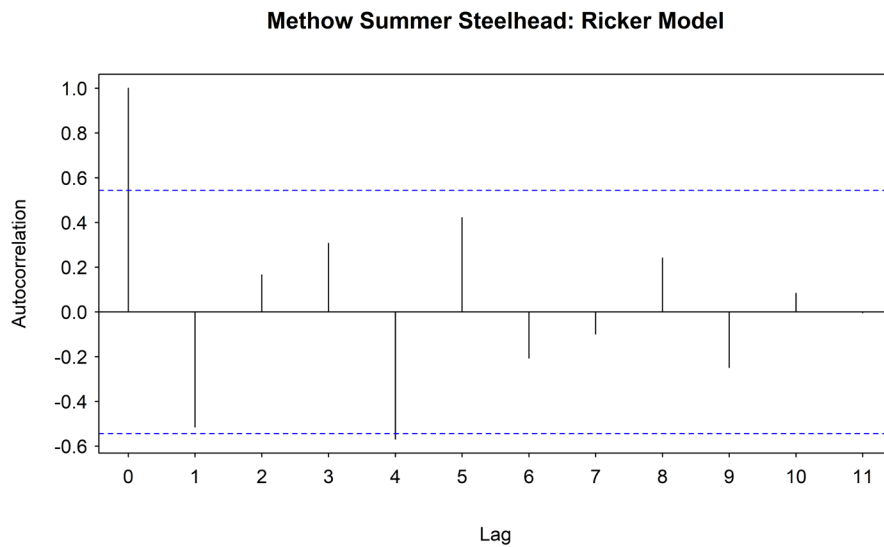


Figure H2. Autocorrelation plot of residuals for Ricker model of emigrant recruitment as a function of spawner abundance (stock) for Methow River Summer Steelhead, 2003–2015. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

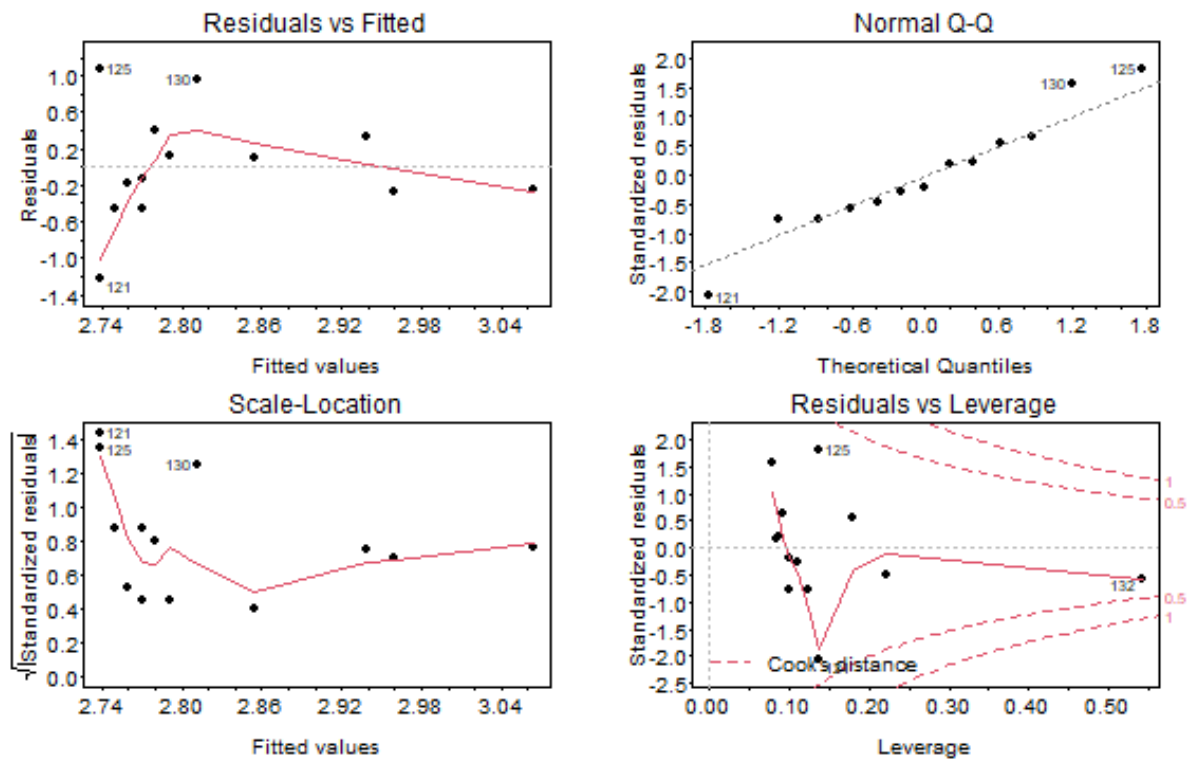


Figure H3. Residual plots for linear model of emigrants per redd (log scale) as a function of pHOS for Methow River Summer Steelhead, 2003–2015. Shapiro-Wilk test of normality of residuals: $W=0.9579$, $P=0.7205$.

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	

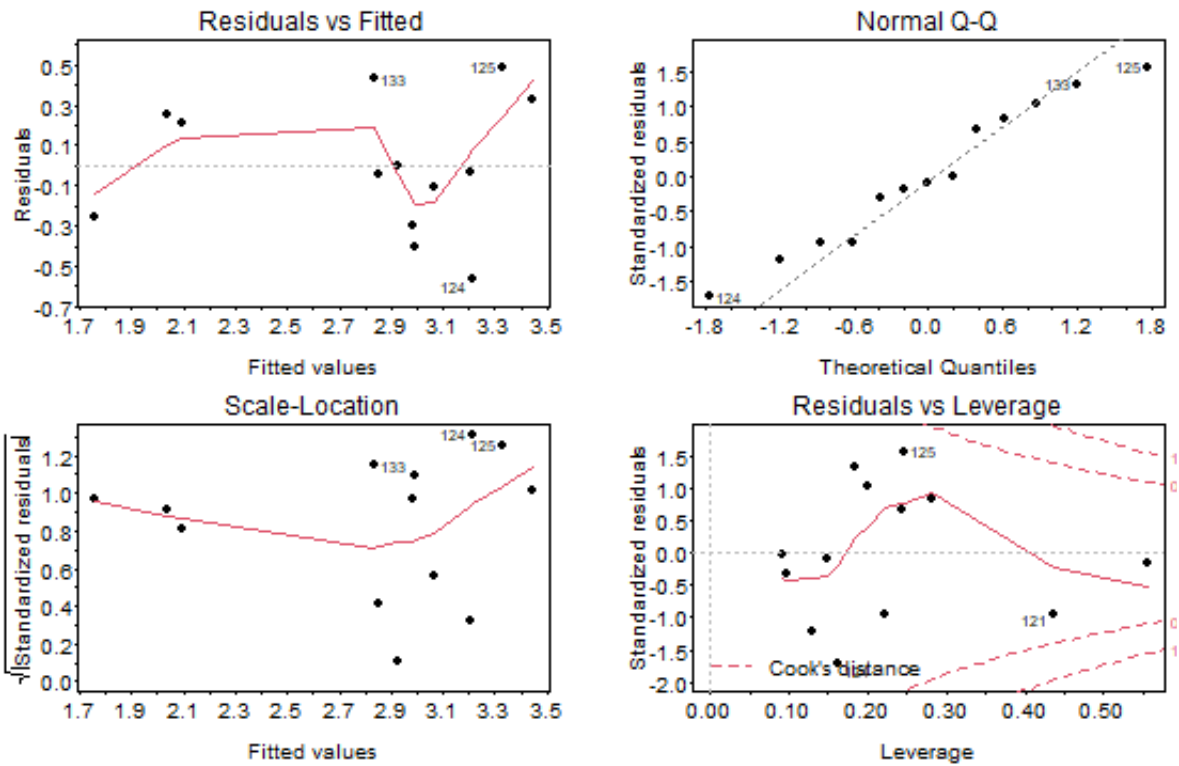


Figure H4. Residual plots for Ricker model of emigrants per redd as a function of redd count and pHOS for Methow River Summer Steelhead, 2003–2015. Shapiro-Wilk test of normality of residuals: $W=0.9671$, $P=0.8578$.

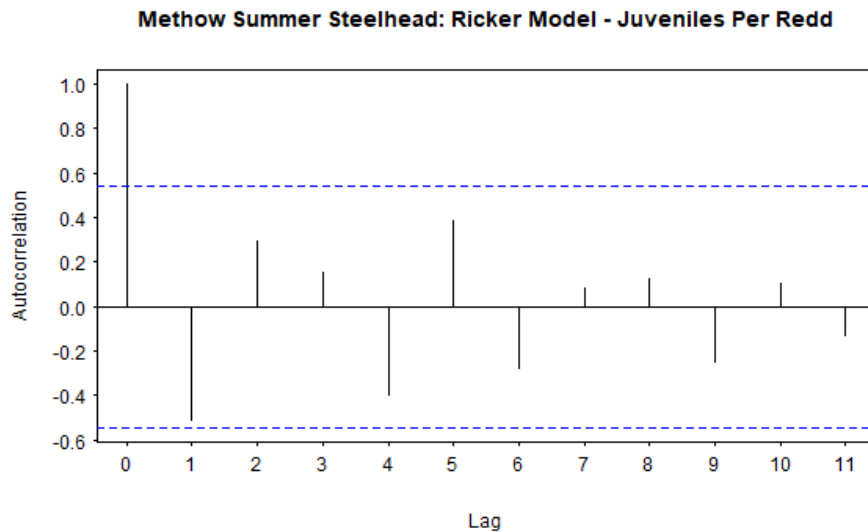


Figure H5. Autocorrelation plot of residuals for Ricker model of emigrants per redd as a function of redd count and pHOS for Methow River Summer Steelhead, 2003–2015. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

Appendix I: Twisp River Summer Steelhead

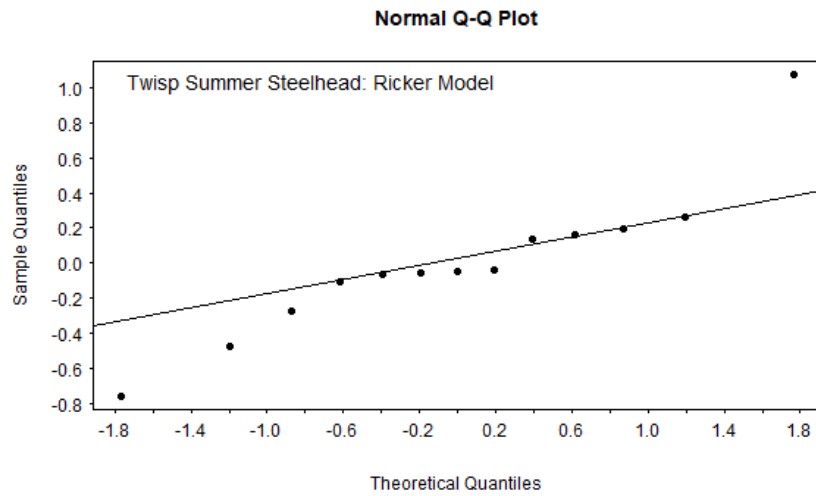


Figure I1. Normal quantile-quantile plot of residual from Ricker model of emigrant recruitment as a function of spawner abundance (stock) for Twisp River Summer Steelhead, 2003–2015, including brood year 2007. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality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

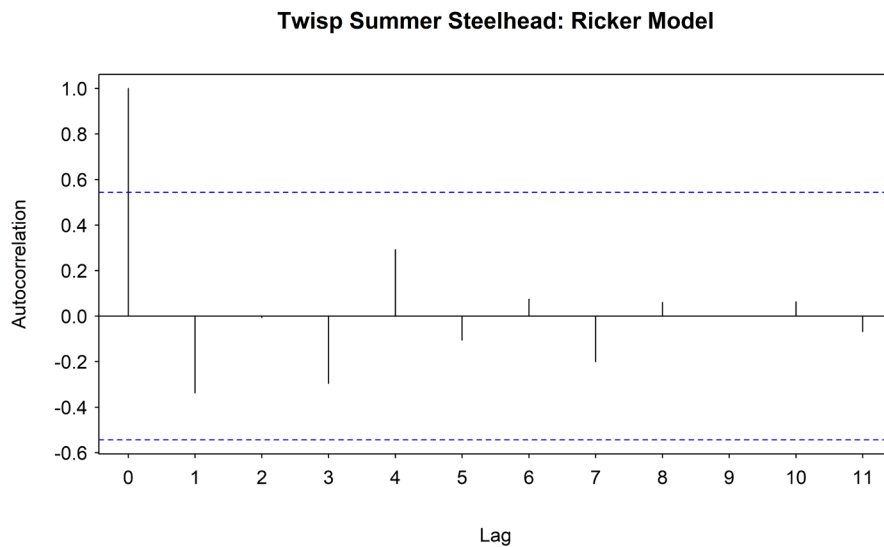


Figure I2. Autocorrelation plot of residuals for Ricker model of emigrant recruitment as a function of spawner abundance (stock) for Twisp River Summer Steelhead, 2003–2015, including brood year 2007. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

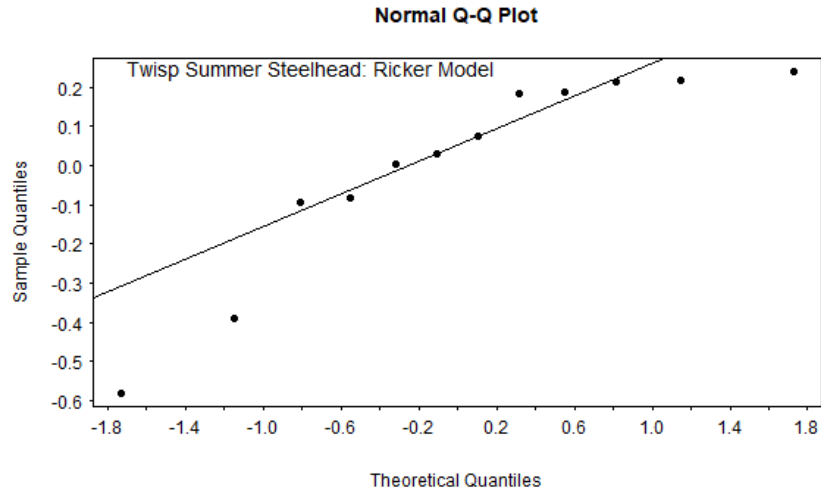


Figure I3. Normal quantile-quantile plot of residual from Ricker model of emigrant recruitment as a function of spawner abundance (stock) for Twisp River Summer Steelhead, 2003–2015, without brood year 2007. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality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

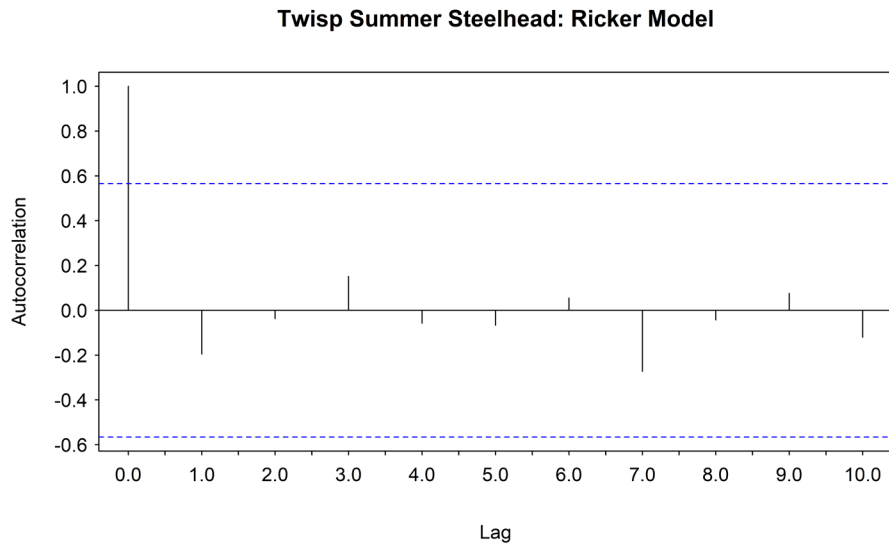


Figure I4. Autocorrelation plot of residuals for Ricker model of emigrant recruitment as a function of spawner abundance (stock) for Twisp River Summer Steelhead, 2003–2015, without brood year 2007. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

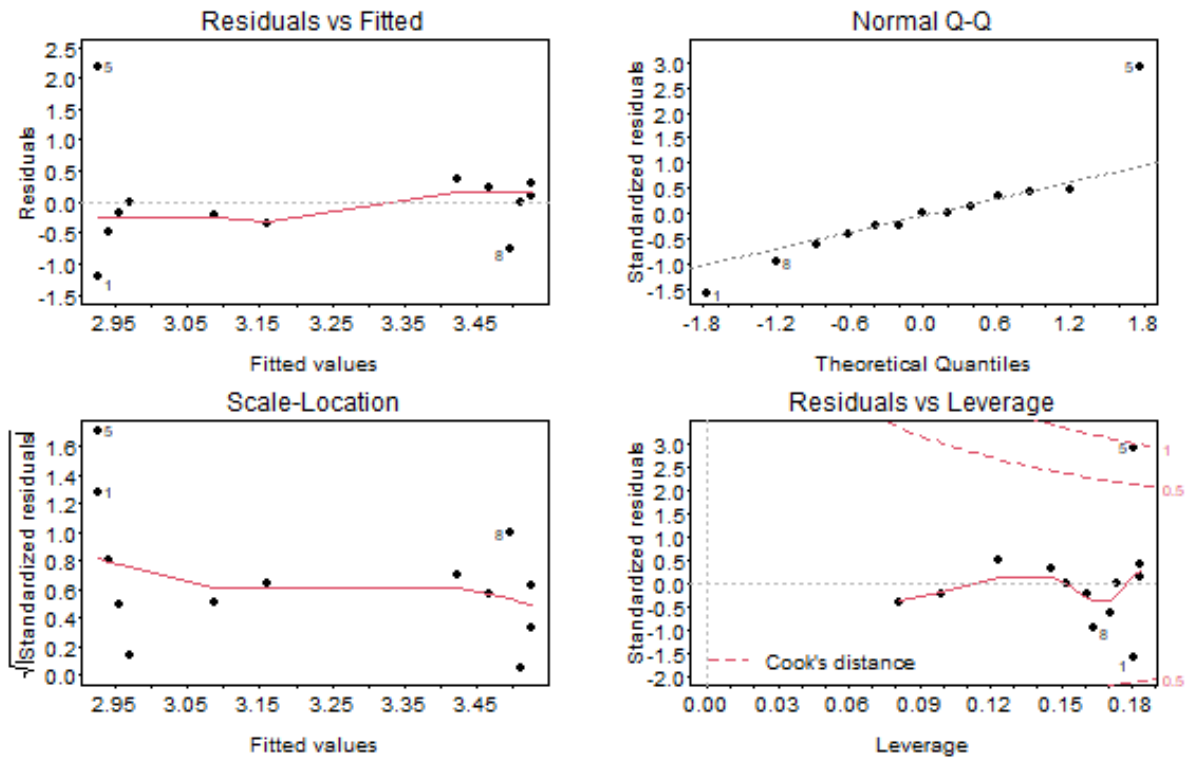
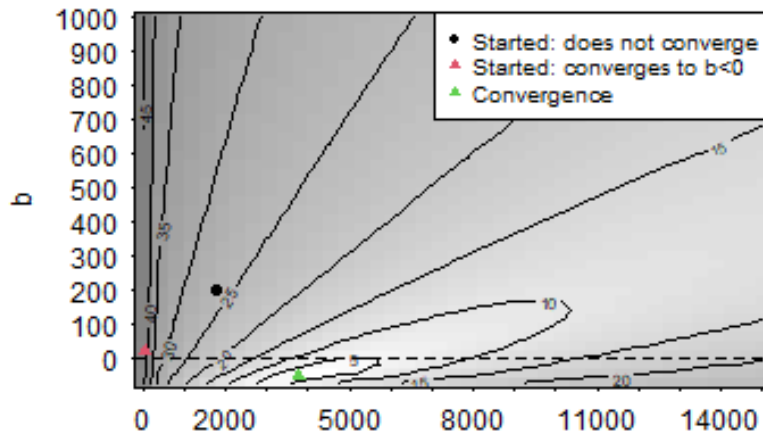


Figure I5. Residual plots for linear model of emigrants per redd (log scale) as a function of pHOS for Twisp River Summer Steelhead, 2003–2015, including brood year 2007. Shapiro-Wilk test of normality of residuals: $W=0.8461$, $P=0.0254$.



a

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 II. 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	

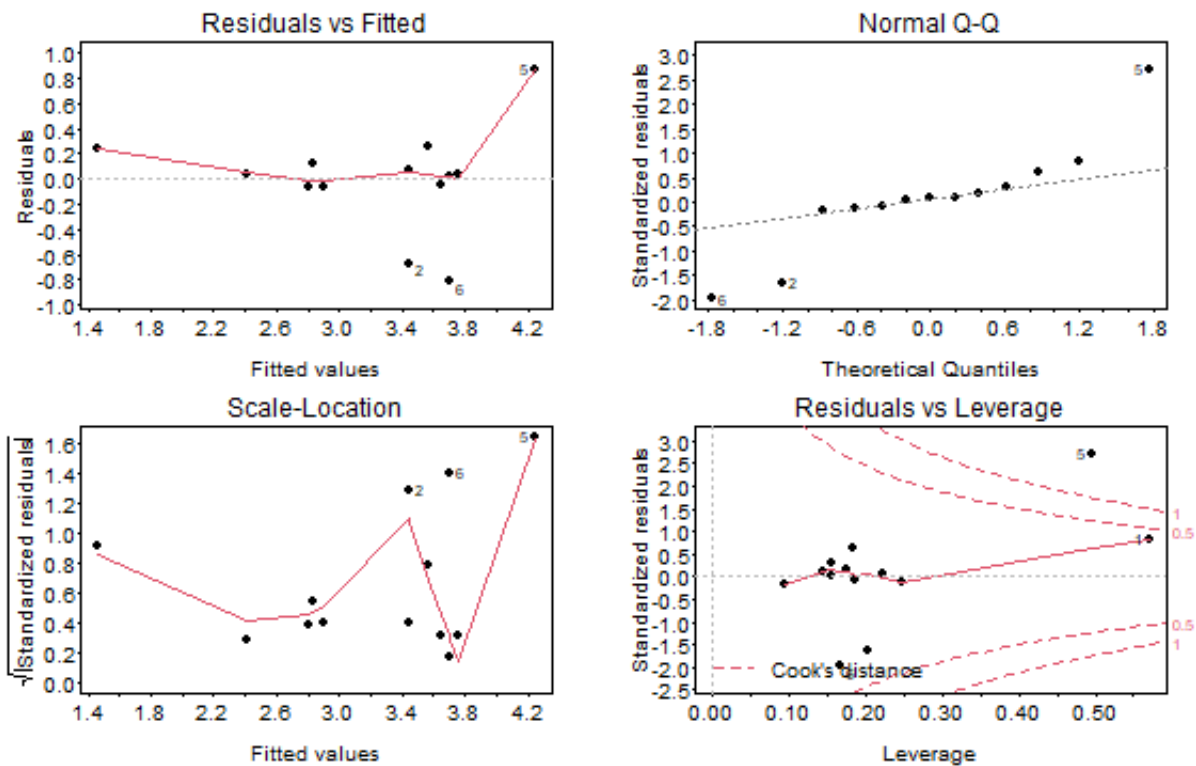


Figure I7. Residual plots for Ricker model of emigrants per redd as a function of redd count and pHOS for Twisp River Summer Steelhead, 2003–2015, including 2007. Shapiro-Wilk test of normality of residuals: $W=0.8740$, $P=0.0592$.

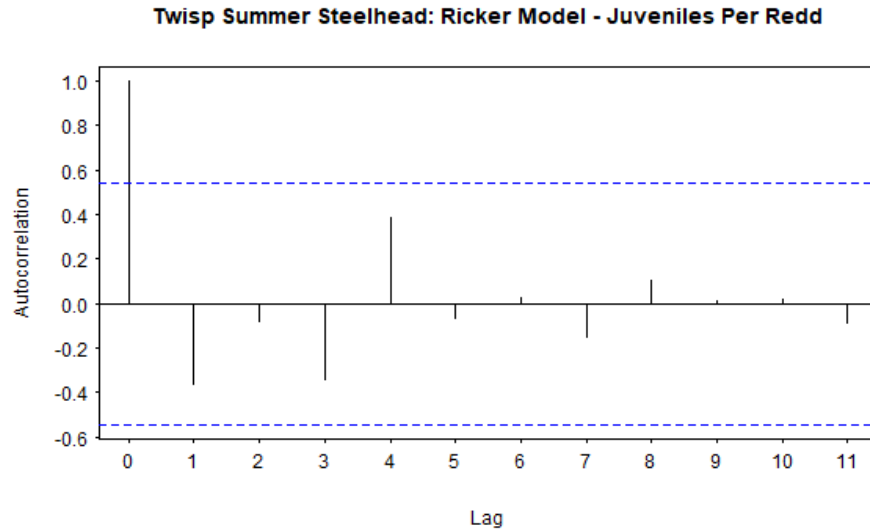


Figure I8. Autocorrelation plot of residuals for Ricker model of emigrants per redd as a function of redd count and pHOS for Twisp River Summer Steelhead, 2003–2015, including 2007. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

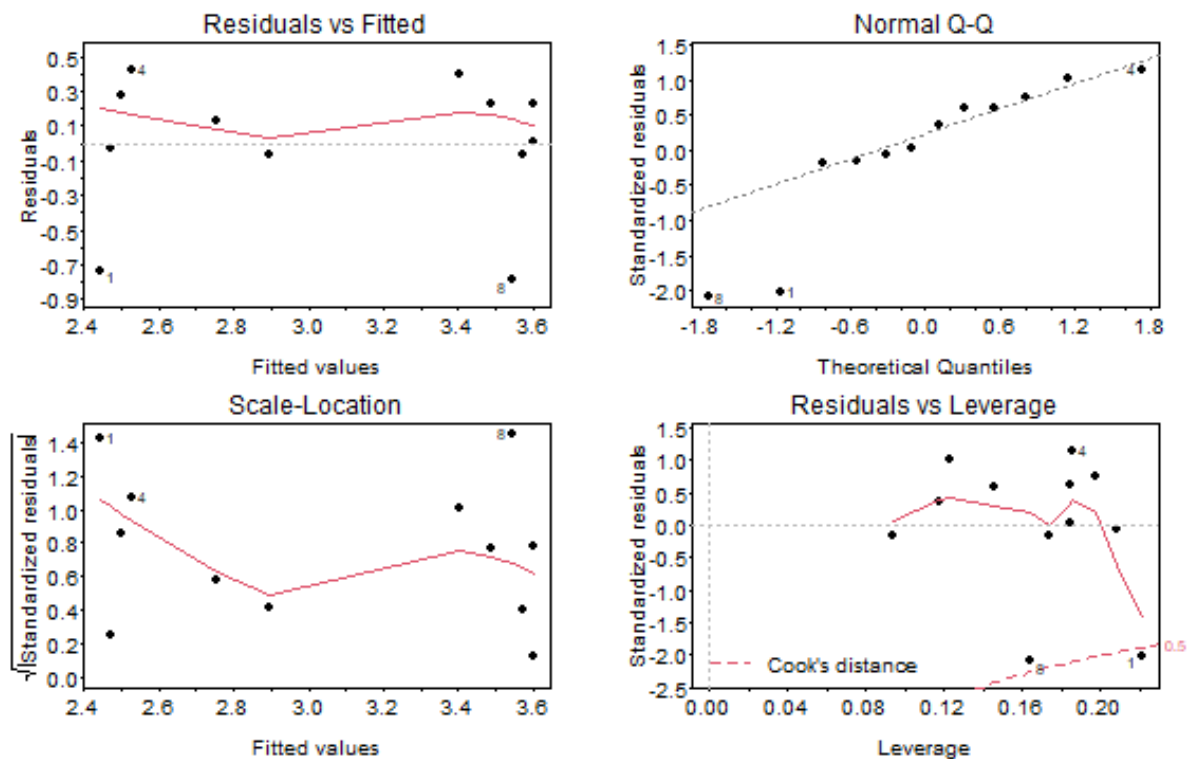


Figure I9. Residual plots for linear model of emigrants per redd as a function of pHOS for Twisp River Summer Steelhead, 2003–2015, omitting brood year 2007. Shapiro-Wilk test of normality of residuals: $W=0.9230$, $P=0.3116$.

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	

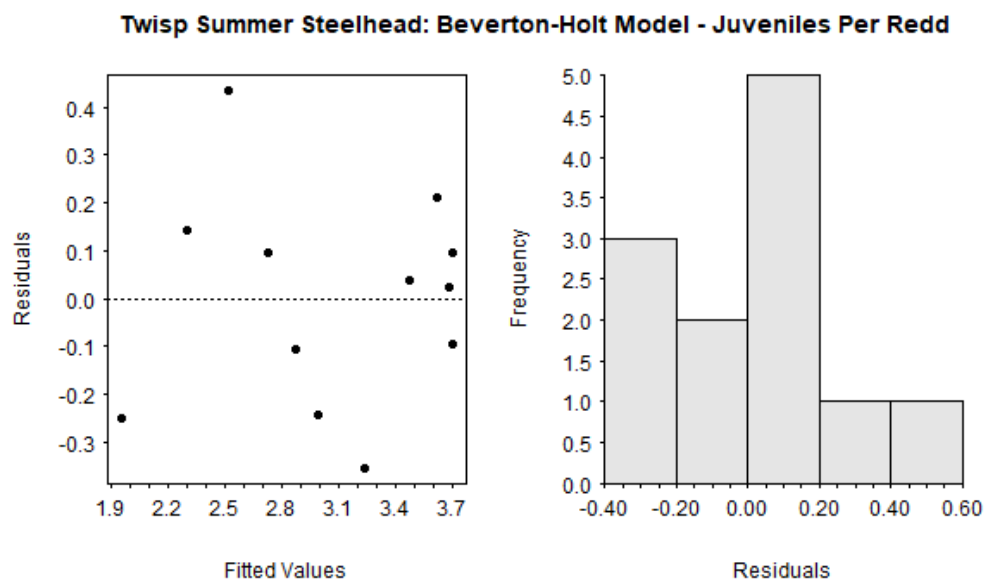


Figure I10. Residual plots for Beverton-Holt model of smolts per redd as a function of redd count and pHOS for Twisp River Summer Steelhead, 2003–2015, omitting brood year 2007. Shapiro-Wilk test of normality of residuals: $W=0.9728$, $P=0.9377$.

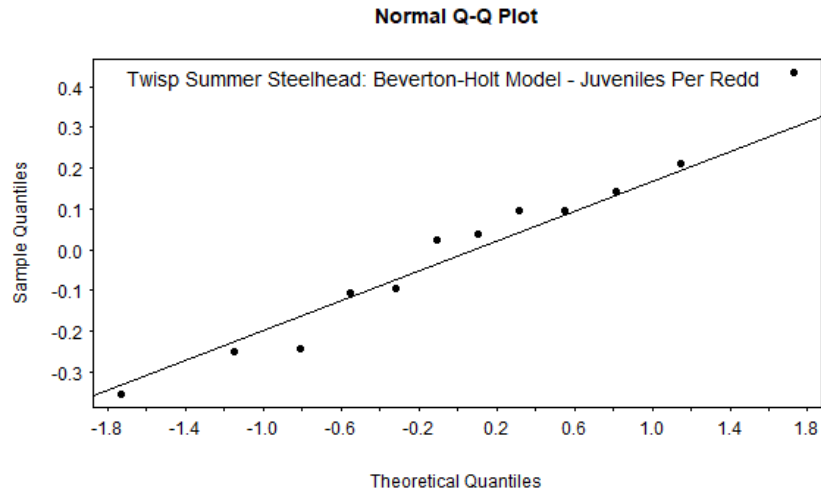


Figure I11. Normal quantile-quantile plot of residual from Beverton-Holt model of smolts per redd as a function of redd count and pHOS for Twisp River Summer Steelhead, 2003–2015, omitting brood year 2007. Points should lie on the line under assumption of normal errors. Shapiro-Wilk test of normality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

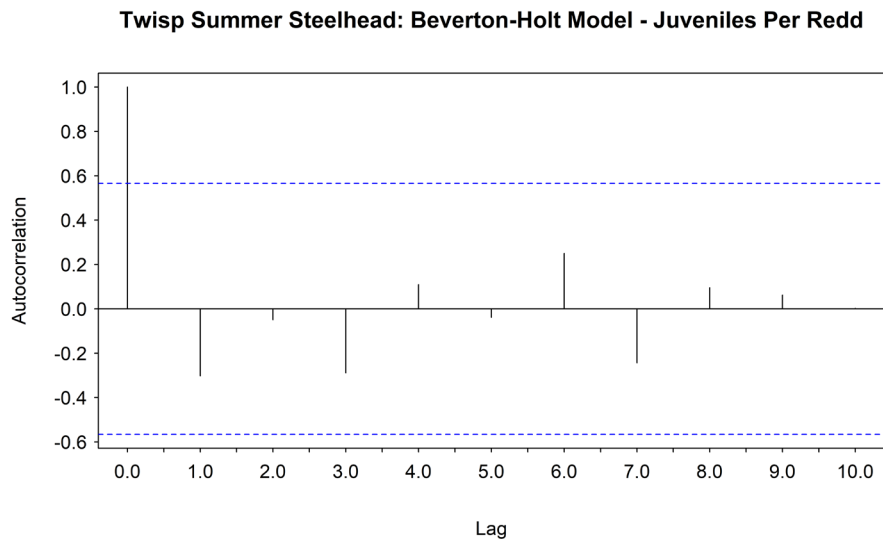


Figure I12. Autocorrelation plot of residuals for Beverton-Holt model of smolts per redd as a function of redd count and pHOS for Twisp River Summer Steelhead, 2003–2015, omitting brood year 2007. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

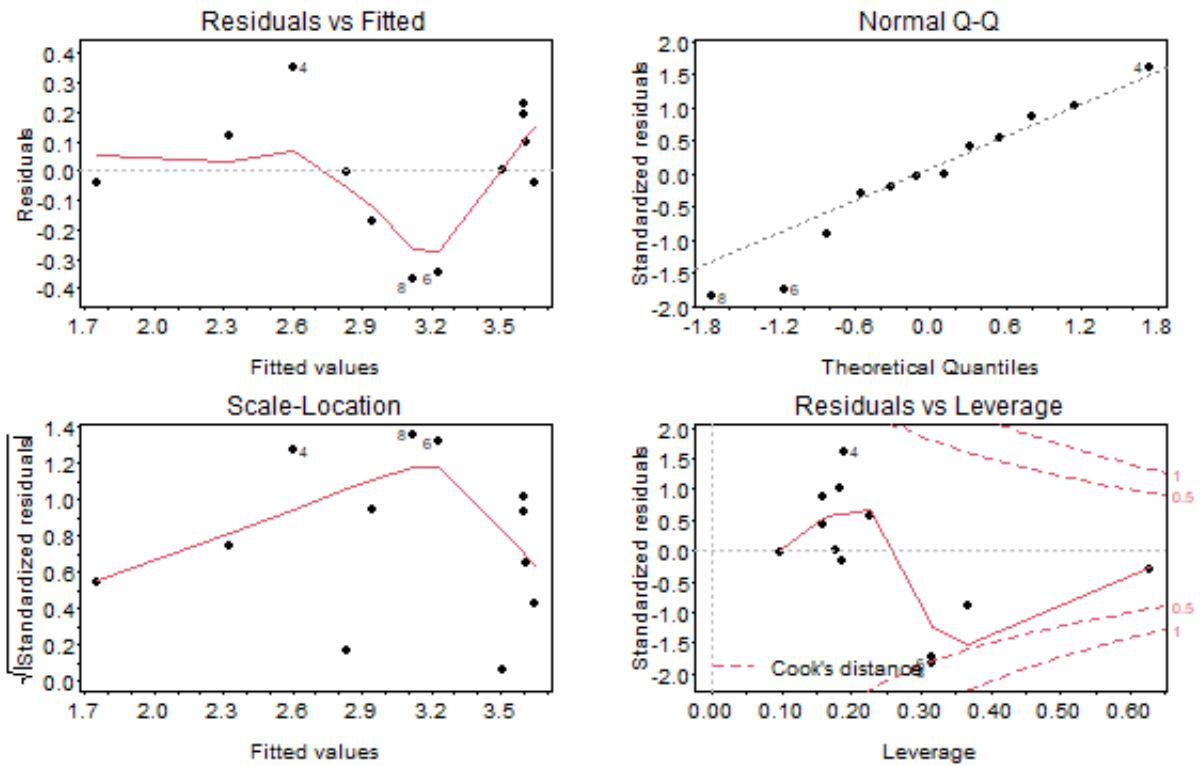


Figure I13. Residual plots for Ricker model of emigrants per redd as a function of redd count and pHOS for Twisp River Summer Steelhead, 2003–2015, omitting brood year 2007. Shapiro-Wilk test of normality of residuals: $W=0.9588$, $P=0.7658$.

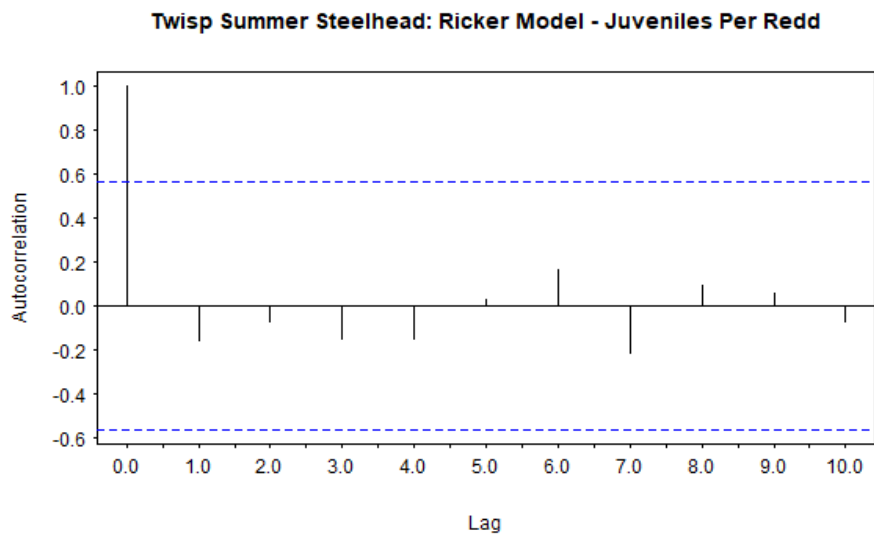


Figure I14. Autocorrelation plot of residuals for Ricker model of emigrants per redd as a function of redd count and pHOS for Twisp River Summer Steelhead, 2003–2015, omitting brood year 2007. Blue lines mark 95% confidence interval under assumption of no autocorrelation.

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Appendix B

Power Analysis for Effect of pHOS on Juvenile Productivity

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Power Analysis for effect of pHOS on juvenile productivity

5 August 2021

TO: GREG MACKEY

PUD No. 1 of Douglas County

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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:

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

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:

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

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 $i = 1, \dots, 1000$, the total number of spawners S_{iy} and the number of natural origin spawners NOS_{iy} were simulated for each year y ($y = 1, \dots, N$) 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 $pHOS_{iy} = \frac{HOS_{iy}}{S_{iy}}$, 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

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

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: $\widehat{NOS}_{iy} = NOS_{ij} + e_{NOS,iy}$ where $e_{NOS,iy}$ is randomly generated from the $N(0, \sigma_{NOS,iy}^2)$ distribution with $\sigma_{NOS,iy}^2 = NOS_{iy}^2 \times CV_{NOS}^2$

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

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

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

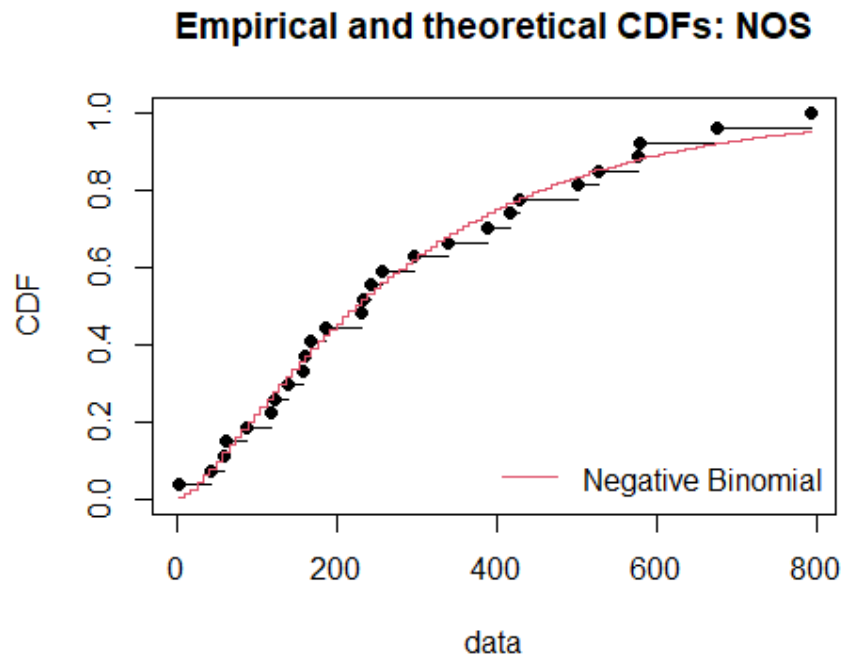
Observed R: $\tilde{R}_{iy} = R_{ij} + e_{R,iy}$ where $e_{R,iy}$ is randomly generated from the $N(0, \sigma_{R,iy}^2)$ distribution for $\sigma_{R,iy}^2 = R_{iy}^2 \times CV_R^2$.

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 $S \cdot p\text{HOS}$, and value of NOS was calculated as $S \cdot \text{HOS}$.

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

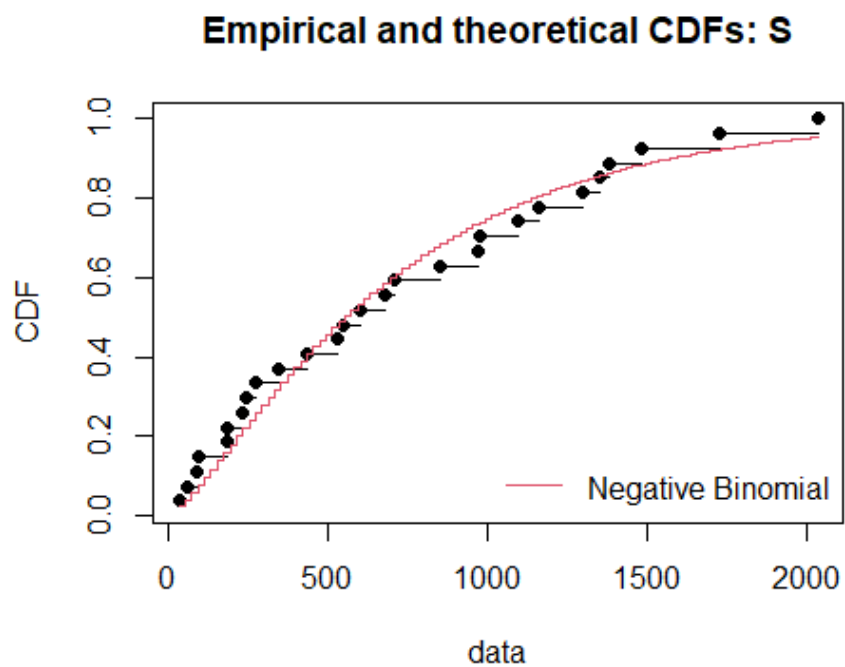


Figure 1. Comparison of empirical and fitted negative binomial cumulative distribution functions (CDFs) for natural origin spawners (NOS) data (a) and total spawners (S) data (b). Black dots represent observed data, and horizontal lines represent the distance between observations in empirical step-wise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

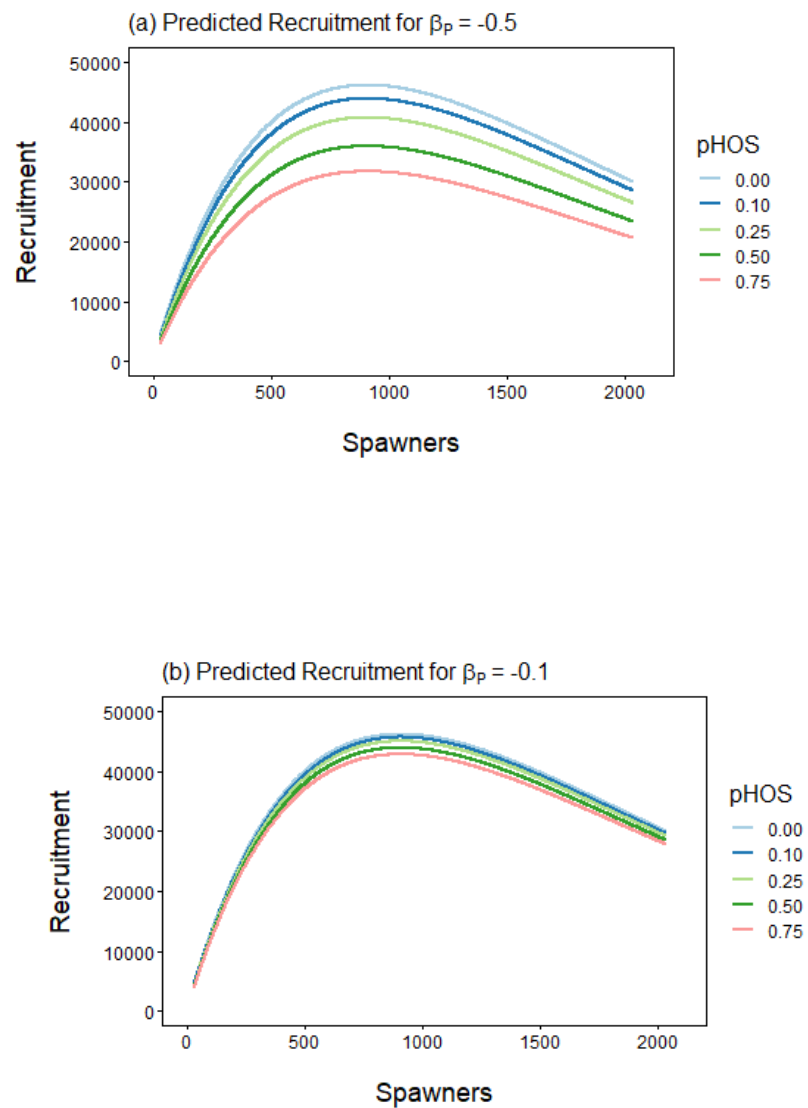


Figure 2. Predicted juvenile recruitment from Ricker model (2) at various levels of spawners S and pHOS for (a) $\beta_p = -0.5$ and (b) $\beta_p = -0.1$. Ricker model parameters: $a = 138$, $b = 0.0011$.

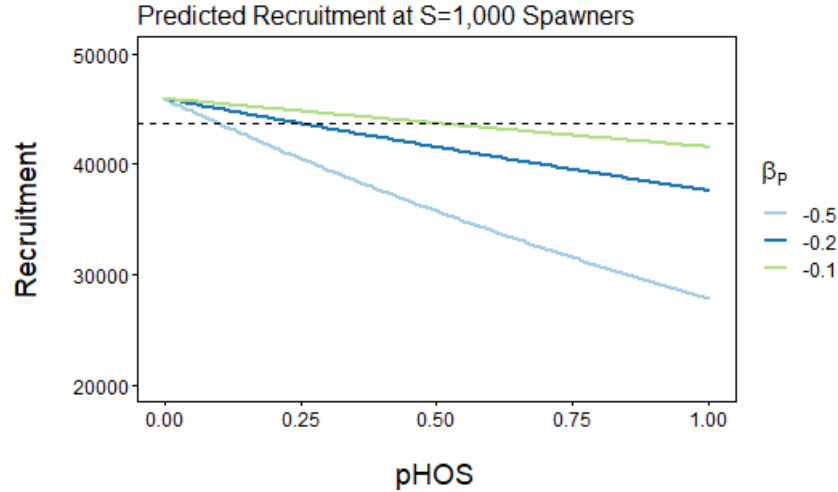


Figure 3. Predicted juvenile recruitment from Ricker model at $S=1,000$ spawners for various levels of pHOS and β_p , the effect of pHOS on recruitment. Dashed line indicates 5% reduction in recruitment compared to pHOS=0. Ricker model parameters: $a = 138$, $b = 0.0011$.

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:

$$R_1 = ae^{\beta_p P_1} S e^{-bS}$$

and

$$R_2 = ae^{\beta_p P_2} S e^{-bS}.$$

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

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

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:

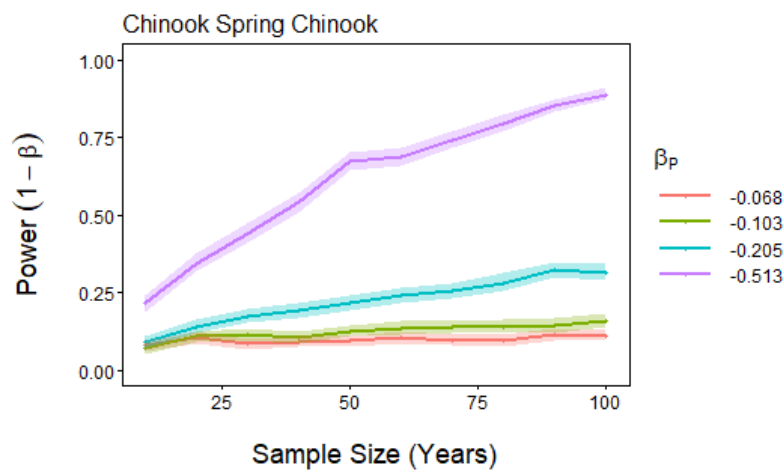
$$\beta_p = \frac{\ln(0.95)}{\Delta P_{HOS}}. \quad (6)$$

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

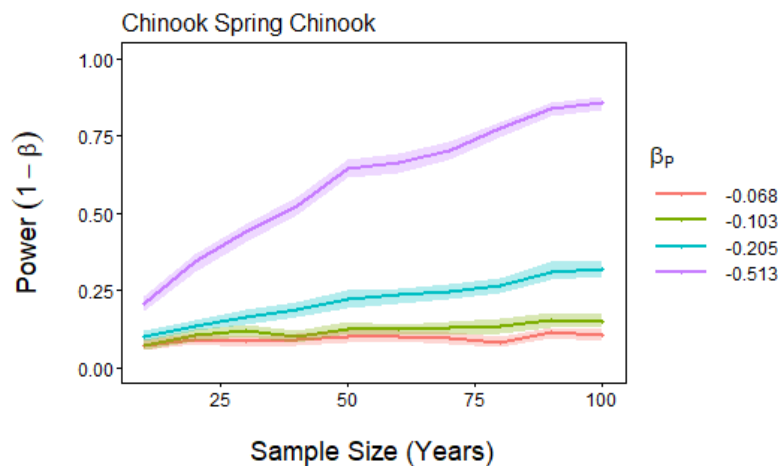


Figure 4. Statistical power of detecting a negative effect of pHOS for various levels of pHOS effect size β_p with (i) and without (ii) measurement error in stock and recruitment data. Power based on 1,000 simulations of stock (spawners) and juvenile recruitment data using Ricker stock-recruitment model fit to data from Chiwawa spring Chinook Salmon, 1991-2017: $a = 138$, $b = 0.0011$, $\sigma = 0.4386$ (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 alternative 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; Moberg 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 $PNI \geq 0.67$. 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 $PNI \geq 0.67$. 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
<i>Average^b</i>	<i>355</i>	<i>406</i>	<i>0.51</i>	<i>76</i>	<i>73</i>	<i>0.51</i>	<i>0.52</i>	<i>0.51</i>
<i>Median^b</i>	<i>351</i>	<i>350</i>	<i>0.50</i>	<i>77</i>	<i>69</i>	<i>0.55</i>	<i>0.51</i>	<i>0.51</i>
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
<i>Average^c</i>	<i>524</i>	<i>391</i>	<i>0.41</i>	<i>62</i>	<i>64</i>	<i>0.49</i>	<i>0.55</i>	<i>0.55</i>
<i>Median^c</i>	<i>456</i>	<i>272</i>	<i>0.39</i>	<i>62</i>	<i>66</i>	<i>0.48</i>	<i>0.57</i>	<i>0.55</i>

^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 $PNI \geq 0.67$ 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
<i>Average</i>	<i>0.56</i>	<i>0.15</i>	<i>0.30</i>	<i>0.44</i>	<i>0.31</i>	<i>0.25</i>	<i>0.44</i>	<i>0.69</i>	<i>0.50</i>	<i>0.64</i>
<i>Median</i>	<i>0.61</i>	<i>0.14</i>	<i>0.26</i>	<i>0.39</i>	<i>0.29</i>	<i>0.19</i>	<i>0.50</i>	<i>0.71</i>	<i>0.50</i>	<i>0.56</i>

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	
<i>Average</i>	<i>307</i>	<i>407</i>	<i>0.48</i>	<i>55</i>	<i>66</i>	<i>0.57</i>	<i>0.56</i>	
<i>Median</i>	<i>238</i>	<i>274</i>	<i>0.61</i>	<i>58</i>	<i>44</i>	<i>0.45</i>	<i>0.53</i>	

^aPNI 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 _N	HOS _S	pHOS _N	pHOS _{N+S}	NOB _N	HOB _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
<i>Average**</i>	<i>95</i>	<i>19</i>	<i>94</i>	<i>0.12</i>	<i>0.48</i>	<i>49</i>	<i>42</i>	<i>0.64</i>	<i>0.62</i>
<i>Median**</i>	<i>95</i>	<i>6</i>	<i>53</i>	<i>0.04</i>	<i>0.42</i>	<i>57</i>	<i>59</i>	<i>0.52</i>	<i>0.63</i>

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	<i>1.00</i>	1.00
2000	22	0	0	0.00	0.00	0	0	<i>0.48</i>	1.00
<i>Average*</i>	<i>48</i>	<i>0</i>	<i>1</i>	<i>0.00</i>	<i>0.00</i>	<i>0</i>	<i>0</i>	<i>0.79</i>	<i>1.00</i>
<i>Median*</i>	<i>32</i>	<i>0</i>	<i>0</i>	<i>0.00</i>	<i>0.00</i>	<i>0</i>	<i>0</i>	<i>1.00</i>	<i>1.00</i>
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
<i>Average**</i>	<i>57</i>	<i>12</i>	<i>30</i>	<i>0.12</i>	<i>0.27</i>	<i>162</i>	<i>16</i>	<i>0.94</i>	<i>0.60</i>
<i>Median**</i>	<i>54</i>	<i>5</i>	<i>23</i>	<i>0.07</i>	<i>0.30</i>	<i>116</i>	<i>0</i>	<i>1.00</i>	<i>0.61</i>

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
<i>Average</i>	575	665	0.45	131	77	0.64	0.60
<i>Median</i>	562	472	0.50	86	52	0.61	0.57

^aPNI 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
<i>Average</i>	<i>7,764</i>	<i>1,233</i>	<i>0.14</i>	<i>297</i>	<i>30</i>	<i>0.93</i>	<i>0.87</i>
<i>Median</i>	<i>7,687</i>	<i>1,058</i>	<i>0.15</i>	<i>275</i>	<i>5</i>	<i>0.99</i>	<i>0.87</i>

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
<i>Average</i>	<i>1,169</i>	<i>708</i>	<i>0.34</i>	<i>358</i>	<i>139</i>	<i>0.76</i>	<i>0.71</i>
<i>Median</i>	<i>1,076</i>	<i>655</i>	<i>0.38</i>	<i>294</i>	<i>71</i>	<i>0.86</i>	<i>0.69</i>

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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Adult Migration and Spawn Timing of Steelhead in the Wenatchee and Methow River Subbasins

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Abstract

Success of integrated hatchery programs relies, in part, on similar migration and spawn timing of hatchery- and natural-origin conspecifics. Synchronous migration timing between hatchery- and natural-origin steelhead ensures that hatchery- and natural-origin fish experience comparable migration conditions to allow for similar arrival timing at the spawning grounds. An overlap in spawn timing ensures that hatchery- and natural-origin fish are, at minimum, present on the spawning grounds at similar times to allow interbreeding among these groups. This study uses Passive Integrated Transponders (PIT) tag data to evaluate adult migration and spawn timing between hatchery-origin and natural-origin summer steelhead originating from the Wenatchee and Methow sub-basins in Washington State. Migration timing was evaluated at PIT-tag interrogation systems located within adult fishways at dams. Paired t-tests, comparing the mean day of year (DOY) that 10%, 50%, and 90% of hatchery- and natural-origin steelhead passed interrogation sites, indicated that natural-origin steelhead tended to arrive slightly earlier than hatchery-origin adults in their migration through Bonneville and Priest Rapids Dams located on the Columbia River, although these differences were not significant, generally indicating similar migration timing. However, as these populations moved farther up the Columbia River approaching their spawning grounds, migration timing between hatchery- and natural-origin steelhead began to differentiate. Wenatchee hatchery-origin steelhead arrived earlier at Rock Island Dam for the latter (90%) portion of the run. Migration through Tumwater Dam showed a bimodal distribution where, at 50% of the run, natural-origin steelhead arrived 12 days earlier than their hatchery conspecifics. Methow natural-origin steelhead arrived earlier than their hatchery-origin counterparts at Priest Rapids Dam (50% of the run) and at Wells Dam (10% and 50% of run). Spawn timing, evaluated at instream PIT-tag interrogation array systems located within spawning tributaries, indicated similar arrival timing to spawning grounds between hatchery- and natural-origin steelhead for both the Wenatchee and Methow populations. Further analysis is needed to evaluate year-specific patterns and mechanisms causing observed differences, especially given the large variation observed in the pooled analysis.

Introduction

Migration timing, spawn timing, and spawning distribution for adult salmonids are heritable traits subject to environmental conditions and human induced pressures (Abadia-Cardoso et al. 2013; Quinn et al. 2002; Kovach et al. 2013; Carlson and Seamons 2008). Integrated hatchery programs incorporate naturally returning adults into the hatchery broodstock and are designed to supplement natural populations with the goal of increasing natural reproduction, while preventing the deleterious effects of a domesticated hatchery stock and affecting the fitness of the supplemented population (Goodman 2004; Reisenbichler 2003). Mismatches between mean values of traits in supplemented populations and environmental conditions to which the natural population was initially adapted can cause decreases in fitness (Utter 1998; Frankham 2008; Palkovacs et al. 2012). Successful integration requires, at minimum, spatial and temporal overlap in spawn timing and spawn location of hatchery-origin adults (i.e., fish spawned in a hatchery) with natural-origin adults (i.e., fish spawned in the wild). Differences in migration and spawn timing of hatchery- and natural-origin fish may result in differences in survival and reproductive success (Kostow 2009). Hatchery steelhead have consistently been found to have lower relative reproductive success than their natural-origin counterparts (Chilcote et al. 1986; Leider et al. 1990; McLean et al. 2003; Araki et al. 2007a; Araki et al. 2007b; Berntson et al. 2011; Ford et al. 2016).

Synchronous migration timing between hatchery- and natural-origin steelhead ensures that hatchery- and natural-origin fish experience comparable migration conditions to allow for similar arrival timing at the spawning grounds. Disparities in adult migration timing may expose steelhead to different selection pressures of environmental stressors, predation, and harvest along their migration route. For example, earlier run individuals may be exposed to higher harvest pressure than later run fish leading to increased mortality of the earlier portion of the run. Intra- and interannual changes in freshwater temperature can cause shifts in migration rates, where increasing temperatures cause slower migration timing (Keefer et al. 2004; Kovach et al. 2013). Intra-annual migration timing of adult steelhead slowed dramatically when summer water temperatures peaked, and then increased as rivers cooled in the fall (Keefer et al. 2004). Over a larger time scale, Kovach et al. (2013) showed that salmonid migration events in Alaskan streams have shifted earlier and become more contracted over the last 3-5 decades due to warming freshwater temperatures. Over-wintering behavior in stream-maturing steelhead has been hypothesized as one of a suite of traits allowing migration to spawning habitats that would otherwise be inaccessible because of flow and/or temperature conditions (Robards and Quinn 2002; Trudel et al. 2004). Overwintering mortality has been attributed to a variety of mechanisms (Keefer et al. 2008; Bowerman et al. 2016) and potentially includes indirect fishing mortality of natural-origin steelhead when winter distributions of non-harvestable and harvestable steelhead overlap (Feeken et al. 2019). If migration timing influences spawn timing, then differences in migration timing can lead to differences in spawn timing between hatchery- and natural-origin fish, ultimately compromising the success of integrated hatchery programs.

Overlap in spawn timing and distribution of hatchery-origin and natural-origin spawners is one component necessary to achieve the goals of integrated hatchery programs. 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). Hatchery adults that spawn at different times or locations than natural-origin fish would be reproductively isolated from the natural population, and this could potentially lead to reduced fitness of the population.

This study evaluates differences in adult migration timing and spawn timing between hatchery-origin and natural-origin summer steelhead originating from the Wenatchee Sub-basin and the Methow Sub-basin in Washington State. These programs operate as conservation hatchery programs where the intention is for hatchery- and natural-origin fish to spawn together in similar locations (Hillman et al. 2019). Consistent with the goals of the Monitoring and Evaluation Plan for PUD Hatchery Programs (Hillman et al. 2019), we used Passive Integrated Transponders (PIT) tag data to assess whether mean adult migration timing differed among similar aged hatchery-origin and natural-origin steelhead along their migration route through the Columbia River (WA). Additionally, PIT-tag data were used to evaluate differences in cumulative spawn timing between hatchery-origin and natural-origin steelhead in each of the sub-basins and their spawning tributaries.

Methods

Study Area and Populations

The Wenatchee and Methow sub-basins are located in north-central Washington State and drain 3,439 and 4,727 km² of the Cascade Mountain eastern slope, respectively. Adult steelhead bound for the Wenatchee Sub-basin must travel 754 river kilometers (rkm) and pass through seven dams along the mainstem Columbia River to reach the Wenatchee River confluence, located between Rock Island and Rocky Reach Dams. The Wenatchee Sub-basin contains 332 km of major streams with 207 km accessible to anadromous salmonids (Mullan et al. 1992). Steelhead returning to the Methow Sub-basin must travel 843 rkm and pass through nine dams along the Columbia River to reach the Methow River confluence, located between Wells Dam and the confluence of the Okanogan River. The Methow Sub-basin contains 270 km of major streams with 239 km accessible to anadromous salmonids (Mullan et al. 1992). Steelhead in the Wenatchee and Methow sub-basins are classified as summer-run and are listed as threatened under the Endangered Species Act (NMFS 2016) as part of the Upper Columbia River Distinct Population Segment. Summer-run steelhead enter freshwater the year prior to spawning, typically April through November. All populations overwinter upstream from Priest Rapids Dam in the Columbia River or its major tributaries. Steelhead complete their migration to their natal watershed, where they become sexually mature and spawn the following spring, typically between March through June.

Over the time period captured in this study, hatchery-origin steelhead were produced from natural-origin x natural-origin (WxW), hatchery-origin x natural-origin (HxW), and hatchery-origin x hatchery-origin (HxH) parental crosses within each sub-basin (Hillman et al. 2020). Over 90% of the hatchery-origin fish were marked with coded wire tags (CWTs) and HxH juveniles received an adipose fin clip; additionally, a proportion of the juvenile steelhead smolts were PIT tagged annually before release. Starting with Wenatchee brood year 2010, only WxW and HxH crosses were used for hatchery production. All broodstock for the Wenatchee

program were collected within the Wenatchee Sub-basin from the run-at-large at the right- and left-bank traps at Dryden Dam, and at Tumwater Dam if the weekly quotas cannot be achieved at Dryden Dam. Before 2012, the goal was to collect 50% natural-origin and 50% hatchery-origin steelhead for broodstock. After 2012, goals were similar but in addition, broodstock collected could not exceed 33% of the natural-origin Wenatchee steelhead population. The intent of the current program is to target adults necessary to meet a 50% natural-origin conservation-oriented program and a 50% hatchery-origin safety-net program. Before 2012, adult steelhead were held and spawned at Wells Hatchery and juvenile steelhead were reared at a combination of facilities including Eastbank Hatchery, Chelan Hatchery, Turtle Rock Acclimation Pond, Blackbird Acclimation Pond, and Chiwawa Acclimation Facility and released in the Wenatchee River, Chiwawa River, and Nason Creek. After 2012, adult steelhead were spawned at Eastbank Fish Hatchery and juveniles were overwinter-acclimated at the Chiwawa Acclimation Facility; all fish were truck planted into the Wenatchee River, Chiwawa River, and Nason Creek. Beginning in 2010 and consistent with ESA Section 10(a)(1)(A) permit 18583, adult management activities have been conducted to remove excess hatchery-origin steelhead before they spawn in the natural environment. This was accomplished through removal at Tumwater Dam and/or through conservation fisheries.

Prior to brood year 2011, broodstock for the entire Methow summer steelhead program was collected from the run at-large at the fishway traps at Wells Dam and from Wells Hatchery volunteer channel, with the broodstock comprising 80% to 90% hatchery-origin fish. Spawning, incubation, and rearing all occurred at Wells Hatchery, and smolts were trucked to and released in roughly equal proportions to the Twisp, Chewuch, and upper Methow rivers. Additionally, a variable component (typically 100,000 smolts) of that Methow River production spawned at Wells Hatchery was transferred as eyed eggs to Winthrop National Fish Hatchery (WNFH) for incubation, rearing, acclimation, and release directly from that facility. Beginning in brood year 2011, the Twisp River program was separated from the Methow River program with a distinct brood source and release strategy, and the Methow River program continued with broodstock collection from the run-at-large at Wells Dam and Hatchery for brood year 2012. From brood years 2011 to 2016, natural-origin broodstock for the Twisp River program were collected from the Twisp River weir and spawned at Methow Hatchery. The progeny of those WxW crosses were incubated and reared to the fry stage at Methow Hatchery, transferred to Wells Hatchery for rearing, then spring-acclimated in the Twisp Acclimation Pond until volitional release to the Twisp River. Beginning with brood year 2013 and continuing to the present, WNFH has functioned as the conservation hatchery program for the Methow Basin, excluding the Twisp River (until BY 2017), and used natural-origin broodstock collected via hook-and-line angling in the Methow River, and (for brood years 2013 and 2014) hatchery-origin returns to Wells Dam or Hatchery as necessary to fill the program. Also in brood year 2013, the Methow safety-net program (HxH) began with brood comprising F1 returns from the Twisp and WNFH programs collected at the Twisp River weir and WNFH, and spawning and incubation at Methow Hatchery, and rearing occurring at Wells Hatchery. Methow safety-net pre-smolts from brood years 2013 and 2014 were spring-acclimated at and released from Methow Hatchery, but progeny from brood years 2015-2017 remained at Wells Hatchery until release and were trucked to the lower Methow River for release at the lower Burma Bridge.

Adult Migration Timing

Hatchery- and natural-origin steelhead migration timing was evaluated at PIT-tag interrogation systems located within adult fishways at dams. For Wenatchee River steelhead, migration timing was assessed at Bonneville (Rkm 234), Priest Rapids (Rkm 639), and Rock Island (Rkm 730) dams on the Columbia River and at Tumwater Dam (Rkm 44) on the Wenatchee River (Figure 1). Video monitoring and trapping of hatchery- and natural-origin steelhead at Tumwater Dam was also used to assess migration timing there. During video monitoring, adults with adipose fins were identified as natural-origin fish, while adults without adipose fins were identified as hatchery-origin fish. Fallback and re-ascension of steelhead was assumed to be low at Tumwater Dam; therefore, there was no adjustment for fallback and re-ascension. For Methow River steelhead, migration timing was assessed at Bonneville, Priest Rapids, and Wells (Rkm 830) dams (Figure 1).

Migration timing was based on day of the year (DOY; 1-365 days) each PIT-tagged steelhead was first detected at a PIT-tag interrogation array. First detection at each project was used as the indicator of migration timing to eliminate subsequent detections related to fallback or multiple ladder system detections at the same project. Fish used to evaluate migration timing included only hatchery- and natural-origin steelhead PIT tagged as juveniles and released within the Wenatchee and Methow sub-basins. This eliminated the potential of including steelhead tagged as juveniles or adults that originated from hatchery programs or natural production areas outside the Wenatchee or Methow River sub-basins.

Spawn Timing

Hatchery- and natural-origin steelhead spawn timing was evaluated at instream PIT-tag interrogation array systems located within spawning tributaries in the Wenatchee and Methow River sub-basins. Within the Wenatchee River sub-basin, we evaluated spawn timing within the Chiwawa River and Nason Creek (locations where hatchery-origin steelhead are released; Figure 2). Within the Methow River sub-basin, we evaluated spawn timing within the Twisp and Chewuch rivers.¹ We also evaluated spawn timing within the Twisp River based on steelhead encounters at the Twisp River weir (Figure 3).

The lowermost PIT-tag detection array within a spawning tributary was used to assess spawn timing in spawning tributaries with multiple interrogation arrays. Spawn timing was based on DOY each PIT-tagged steelhead was first detected by a tributary instream PIT-tag interrogation array. To maintain consistency with past evaluations, first detection within a tributary was used as the indicator of spawn timing across all locations and years included within the evaluation. This is a rough estimate of spawn timing because some adult steelhead may

¹ PIT arrays within Gold Creek, Libby Creek, Beaver Creek, Wolf Creek, Early Winters Creek, and the Lost River in the Methow sub-basin and within Mission Creek, Peshastin Creek, Chumstick Creek, Icicle Creek, Chiwaukum Creek, White River, and Little Wenatchee River in the Wenatchee sub-basin allowed us to estimate steelhead spawn timing within those tributaries. Those results are available upon request.

remain in spawning tributaries for an extended period of time before spawning. PIT-tagged juvenile steelhead and resident or residual *O. mykiss* were excluded from the evaluation by only accepting PIT-tagged steelhead first detected as returning adults at Bonneville Dam. In addition, steelhead tagged as returning adults (i.e., Priest Rapids Dam, Tumwater Dam, and Wells Dam) were included in the evaluation of spawn timing. Stray hatchery- and natural-origin steelhead were removed from the evaluation if they originated from hatchery programs or natural production areas outside the Wenatchee and Methow sub-basins.



Figure 1. Locations on the Columbia River where adult Steelhead migration timing was assessed from PIT-tag detections of hatchery- and natural-origin Steelhead.

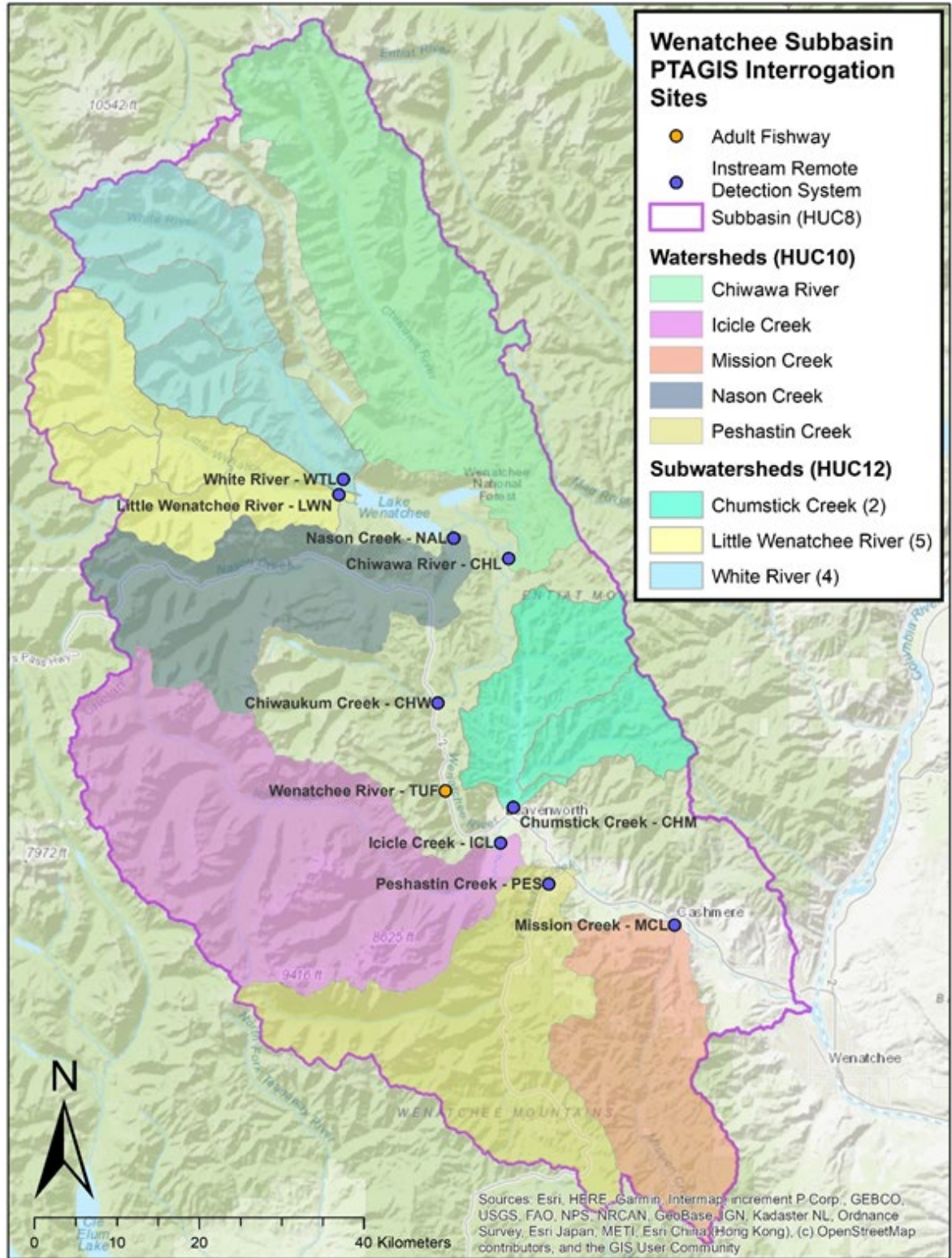


Figure 2. Locations in the Wenatchee River sub-basin where spawn timing was assessed from PIT-tag detections of hatchery- and natural-origin steelhead. Migration timing was assessed at Tumwater Dam.

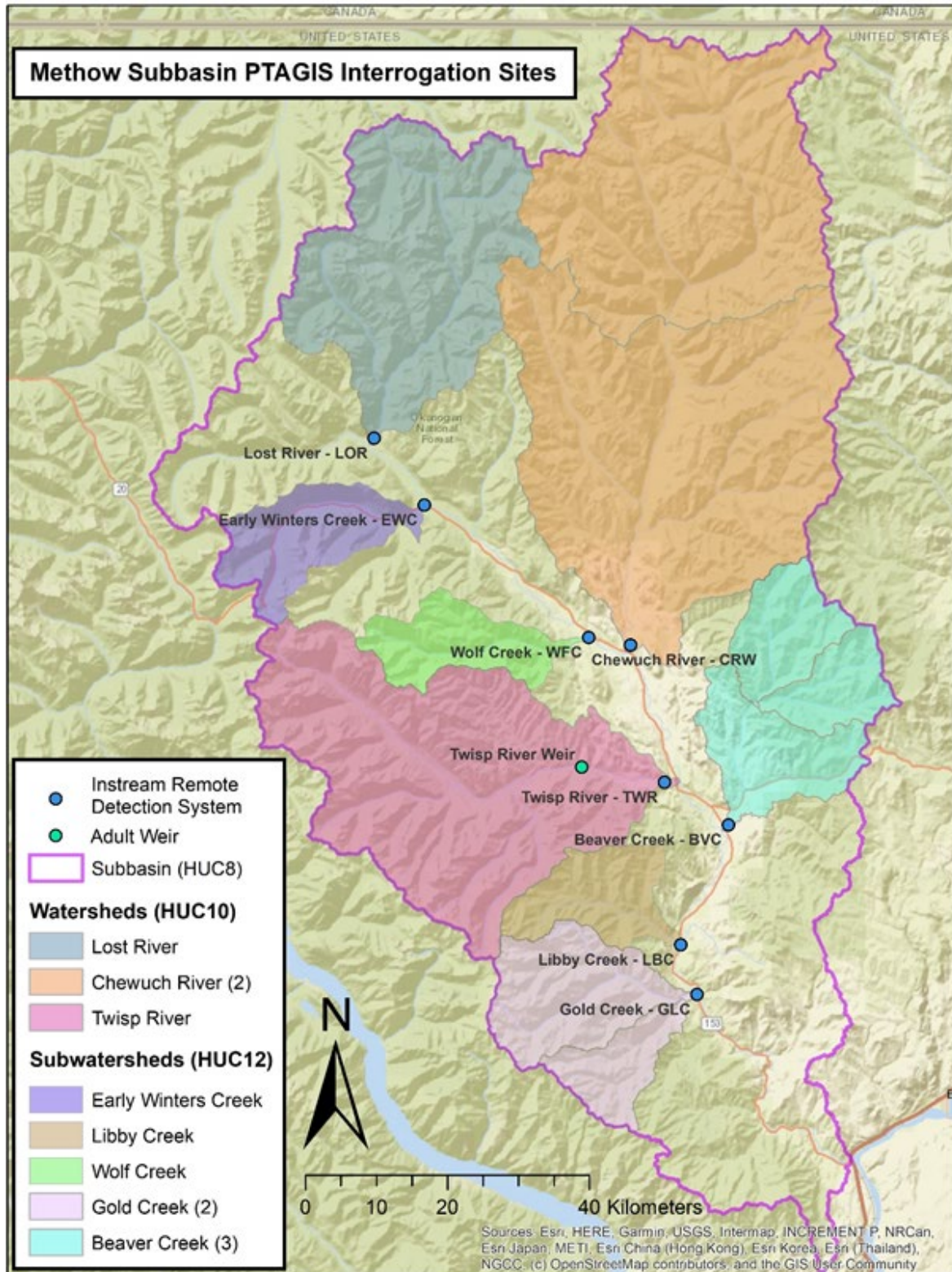


Figure 3. Locations in the Methow River sub-basin where spawn timing was assessed from PIT-tag detections of hatchery- and natural-origin steelhead.

Data Analysis:

For both migration timing and spawning timing, we developed cumulative frequency polygons for hatchery- and natural-origin adult steelhead. For migration timing, we used DOY that PIT-tagged fish were first detected at various interrogation sites to construct cumulative frequency polygons. As noted above, first detection at each dam or spawning stream was used as the indicator of migration or spawn timing to eliminate multiple passage events. We also examined cumulative frequency polygons for hatchery- and natural-origin steelhead detected at Tumwater Dam (based on video monitoring and trapping) and the Twisp River weir. At these sites, fish were sampled for salt (ocean) age and therefore we were able to evaluate migration patterns based on age. Paired t-tests compared the mean DOY that 10%, 50%, and 90% of hatchery- and natural-origin steelhead passed interrogation sites.

Differences in spawn timing were determined by comparing the DOY that hatchery- and natural-origin steelhead were identified in spawning tributaries. We used cumulative frequency polygons to assess differences in spawn timing between hatchery- and natural-origin fish and paired t-tests to compare the mean DOY that 10%, 50%, and 90% of hatchery- and natural-origin steelhead were detected in spawning tributaries. Results were considered statistically significant if the P value ≤ 0.05 .

Results

Migration Timing

Wenatchee Sub-basin – Based on PIT-tag analyses for the period 2003-2018 (return years), hatchery- and natural-origin Wenatchee River steelhead arrived at Bonneville Dam at about the same time throughout the run (Figure 4). Although natural-origin steelhead arrived slightly earlier than did hatchery-origin steelhead at Bonneville Dam, mean differences in the DOY for the 10th, 50th, and 90th percentiles were less than five days, and these differences were not statistically significant (all t-test values < 2.039 and P values > 0.066). As Wenatchee River steelhead moved upstream, differences in migration timing increased between hatchery and natural-origin fish (Figure 4). Natural-origin steelhead generally arrived at upstream dams (Priest Rapids and Rock Island Dams) earlier than hatchery-origin fish and mean differences in the DOY for the 10th, 50th, and 90th percentiles ranged from 5-26 days, but only the 90th percentile at Rock Island Dam was significant (26 days; t-test = -4.030; P value = 0.002).

Based on PIT-tag interrogations at Tumwater Dam, hatchery-origin steelhead arrived earlier than did natural-origin steelhead, but that trend reversed later in the run as natural-origin steelhead completed the run earlier than did hatchery-origin fish (Figure 4). Mean differences in the DOY for the 10th and 90th percentiles were relatively small (7 days), but there was a larger significant difference at the 50th percentile (12 days; t-test = 4.119; P value = 0.002). A similar migration pattern was observed at Tumwater Dam based on video monitoring and trapping (Figure 5). Mean differences in the DOY for the 10th and 90th percentiles based on video monitoring and trapping were again relatively small (6 days), and again there was a larger significant difference at the 50th percentile (15 days; t-test = 2.711; P value = 0.013). For both hatchery- and natural-origin steelhead sampled at Tumwater Dam, salt-1 fish arrived earlier than

did salt-2 fish, and salt-2 fish arrived earlier than did salt-3 fish (Figure 5; Table 1). This pattern decreased over the period of the run, with little difference in migration timing between ages during the middle and later half of the run.

Methow Sub-basin – Based on PIT-tag analyses for the period 2003-2018 (return years), hatchery- and natural-origin Methow River steelhead arrived at Bonneville Dam at about the same time throughout the run (Figure 6). Although natural-origin steelhead arrived slightly earlier than hatchery-origin steelhead at Bonneville Dam, mean differences in the DOY for the 10th, 50th, and 90th percentiles were less than seven days, and these differences were not statistically significant (all t-test values < 1.521 and P values > 0.186). As Methow River steelhead moved upstream, differences in migration timing increased between hatchery and natural-origin fish (Figure 6). Natural-origin steelhead generally arrived at upstream dams earlier than hatchery-origin fish and mean differences in the DOY for the 10th, 50th, and 90th percentiles ranged from 0-14 days, but only the 50th percentile at Priest Rapids was significant (10 days; t-test = 3.403; P value = 0.006), while both the 10th and 50th percentiles were significant at Wells Dam (10th percentile: 14 days; t-test = 3.142; P value = 0.009; 50th percentile: 11 days; t-test = 2.963; P value = 0.013).

Table 1. Sample sizes and descriptive statistics of different salt-age hatchery- and natural-origin steelhead sampled at Tumwater Dam during 1998-2018. Descriptive statistics include the mean DOY, standard deviation (SD), and minimum and maximum DOY.

Salt age	Natural-origin steelhead					Hatchery-origin steelhead				
	Sample size	Mean	SD	Min	Max	Sample size	Mean	SD	Min	Max
1	1,803	235	67	49	343	2,598	231	80	62	343
2	2,768	241	63	48	342	2,608	233	70	49	346
3	45	246	47	107	312	25	238	70	79	313
4	12	257	31	208	300	0	--	--	--	--

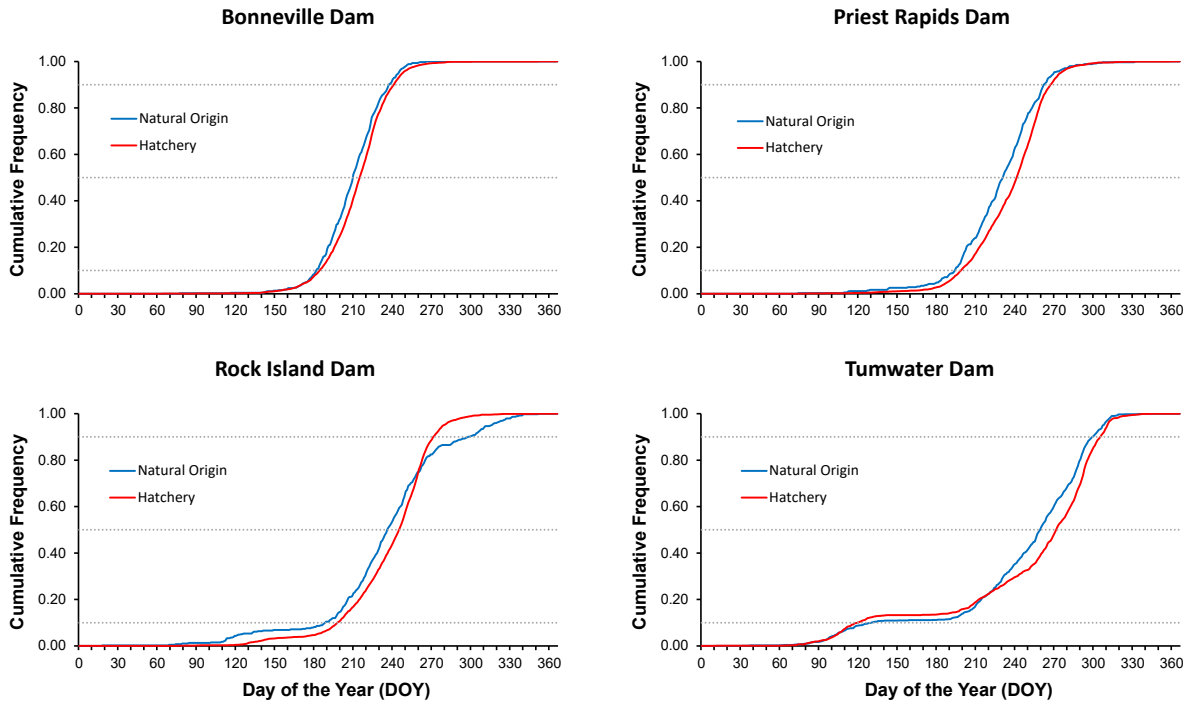


Figure 4. Cumulative frequency polygons of migration timing of adult hatchery- and natural-origin Wenatchee steelhead passing Bonneville, Priest Rapids, Rock Island, and Tumwater dams. Migration timing was based on detection of PIT tags during the period 2003-2018 (return years). Horizontal dashed lines indicate the 10th, 50th, and 90th percentiles. Sample sizes = 456 natural-origin and 4,831 hatchery-origin steelhead at Bonneville Dam, 352 natural-origin and 3,719 hatchery-origin steelhead at Priest Rapids Dam, 393 natural-origin and 3,269 hatchery-origin steelhead at Rock Island Dam, and 946 natural-origin and 1,655 hatchery-origin steelhead at Tumwater Dam.

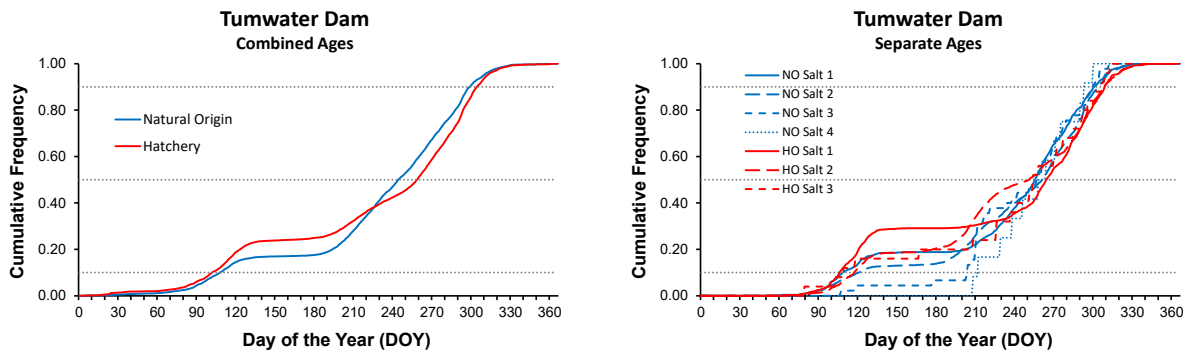


Figure 5. Cumulative frequency polygons of migration timing of adult hatchery- and natural-origin Wenatchee steelhead passing Tumwater Dam. Migration timing was based on video monitoring and trapping, and includes analyses based on salt (ocean) age and pooled (combined) ages during the period 1998-2018 (return years). Horizontal dashed lines indicate the 10th, 50th, and 90th percentiles. Sample sizes = 12,837 natural-origin and 16,301 hatchery-origin steelhead.

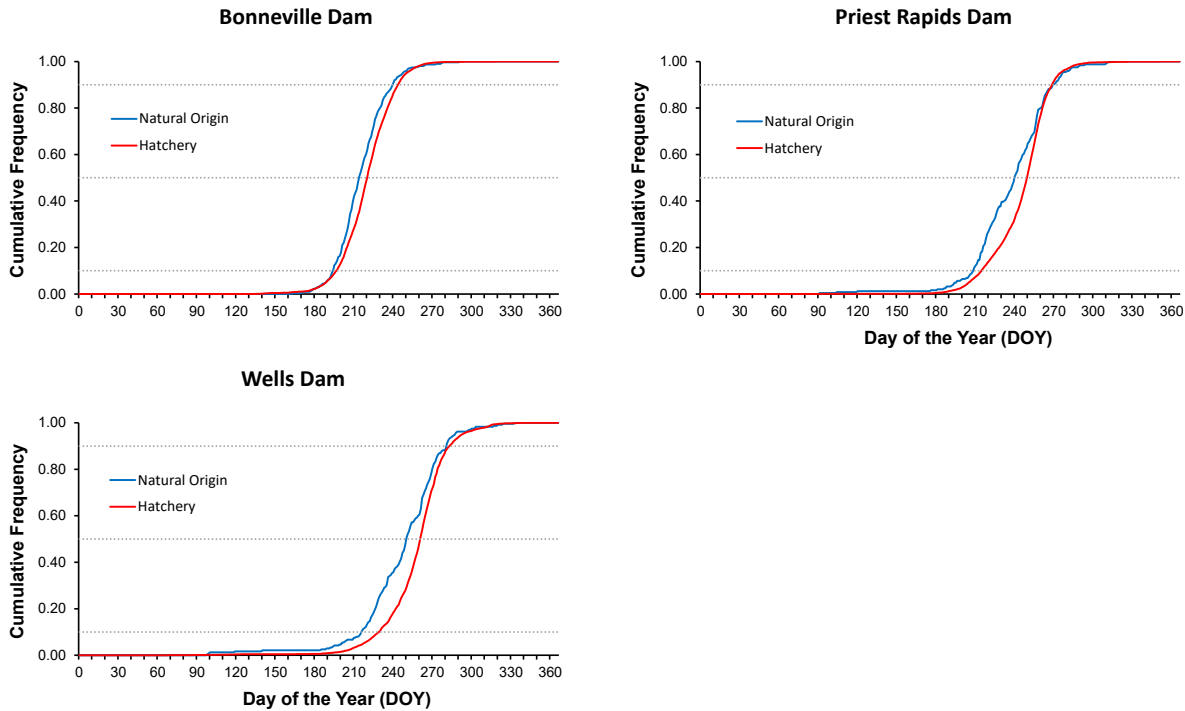


Figure 6. Cumulative frequency polygons of migration timing of adult hatchery- and natural-origin Methow steelhead passing Bonneville, Priest Rapids, and Wells dams. Migration timing was based on detection of PIT tags during the period 2003-2018 (return years). Horizontal dashed lines indicate the 10th, 50th, and 90th percentiles. Sample sizes = 314 natural-origin and 6,333 hatchery-origin steelhead at Bonneville Dam, 247 natural-origin and 4,820 hatchery-origin steelhead at Priest Rapids Dam, and 238 natural-origin and 4,603 hatchery-origin steelhead at Wells Dam.

Spawn Timing

Wenatchee River Sub-basin – There were differences in the spawn timing of hatchery- and natural-origin steelhead in the Wenatchee River sub-basin (Figure 7). On average, hatchery- and natural-origin steelhead in the Chiwawa River spawned within three days of each other early in the spawning period (10th and 50th percentiles). Near the end of spawning, however, differences increased with 90% of the hatchery-origin fish completing their spawning about 15 days earlier than natural-origin steelhead. This difference was not significant because of the large variation in the DOY that hatchery- and natural-origin steelhead completed spawning within the Chiwawa River (t-test = 1.030; P value = 0.327). Over the years of evaluation, spawn timing for hatchery-origin steelhead at the 90th percentile ranged from DOY 117-302, while natural-origin steelhead at the same percentile ranged from DOY 110-293.

Unlike within the Chiwawa River, spawn timing of hatchery- and natural-origin steelhead within Nason Creek differed initially, but those differences decreased later in the spawning period (Figure 7). On average, natural-origin steelhead began spawning earlier than did hatchery-origin steelhead in Nason Creek. The mean difference in DOY at the 10th percentile was 21 days; however, this was not statistically significant because of the large variation in DOY among

evaluation years (t-test = 1.604; P value = 0.139). That is, over the years of evaluation, spawn timing for hatchery-origin steelhead at the 10th percentile ranged from DOY 41-112, while natural-origin steelhead at the same percentile ranged from DOY 42-109. Natural-origin steelhead spawned on average four days earlier than hatchery-origin steelhead at the 50th and 90th percentiles. These differences were not significant (t-test < 1.866; P values > 0.092).

Methow Sub-basin – There were minor differences in the spawn timing of hatchery- and natural-origin steelhead in the Methow River sub-basin (Figure 8). On average, natural-origin steelhead spawned earlier than did hatchery-origin steelhead in the Chewuch River, but the differences were relatively small. Mean differences in the DOY for the 10th, 50th, and 90th percentiles were 10 days or less, and these differences were not statistically significant (all t-test values < 1.531 and P values > 0.164). The difference was greatest during the initial spawning period (mean DOY difference = 10 days) with differences decreasing later in the spawning period.

Within the Twisp River, hatchery- and natural-origin steelhead spawned at about the same time throughout the spawning period (Figure 8). Based on PIT-tag evaluations, mean differences in the DOY for the 10th, 50th, and 90th percentiles were three days or less, and these differences were not statistically significant (all t-test values < 2.077 and P values > 0.168). Evaluation of steelhead at the Twisp River weir also indicated little difference in spawn timing of steelhead in the Twisp River (Figure 9). Based on evaluations at the weir, mean differences in the DOY for the 10th, 50th, and 90th percentiles were three days or less, and these differences were not statistically significant (all t-test values < 1.418 and P values > 0.189). For both hatchery- and natural-origin steelhead sampled at the weir, salt-2 fish arrived earlier than did salt-1 fish (Figure 9; Table 2). This pattern decreased over the period of the spawning period, with little difference in spawn timing between ages during the middle and later half of the period.

Table 2. Sample sizes and descriptive statistics of different salt-age hatchery- and natural-origin steelhead sampled at the Twisp River Wier during 2009-2018. Descriptive statistics include the mean DOY, standard deviation (SD), and minimum and maximum DOY.

Salt age	Natural-origin steelhead					Hatchery-origin steelhead				
	Sample size	Mean	SD	Min	Max	Sample size	Mean	SD	Min	Max
1	493	108	12	67	161	949	108	11	69	161
2	387	105	13	78	151	637	107	12	72	161

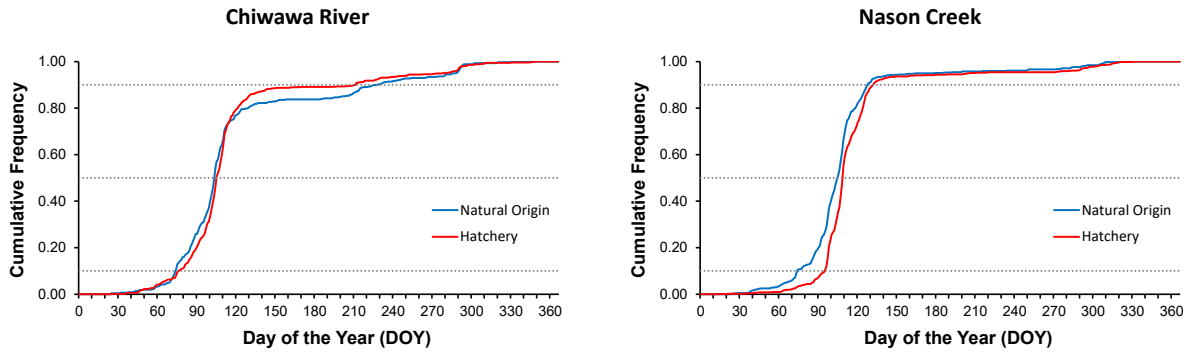


Figure 7. Cumulative frequency polygon of spawn timing of hatchery- and natural-origin Wenatchee steelhead in the Chiwawa River and Nason Creek. Spawn timing was based on the day of year (DOY) of first detection of Steelhead at the lowest PIT-tag array within each tributary during the period 2005-2018 (return years). Horizontal dashed lines indicate the 10th, 50th, and 90th percentiles. Sample sizes = 456 natural origin and 808 hatchery-origin steelhead in the Chiwawa River and 596 natural-origin and 963 hatchery-origin steelhead in Nason Creek.

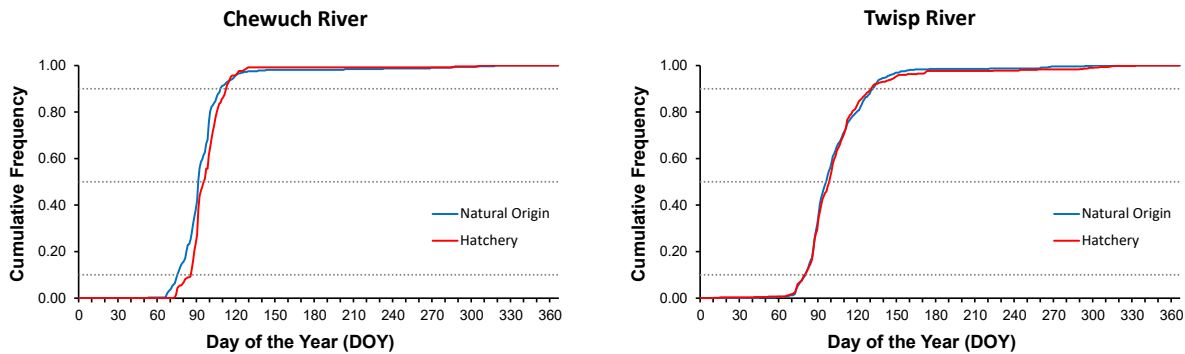


Figure 8. Cumulative frequency polygon of spawn timing of hatchery- and natural-origin Methow steelhead in the Chewuch and Twisp rivers. Spawn timing was based on the day of year (DOY) of first detection of steelhead at the lowest PIT-tag array within each tributary. Horizontal dashed lines indicate the 10th, 50th, and 90th percentiles. Sample sizes = 327 natural origin and 257 hatchery-origin steelhead in the Chewuch River and 488 natural-origin and 602 hatchery-origin steelhead in the Twisp River.

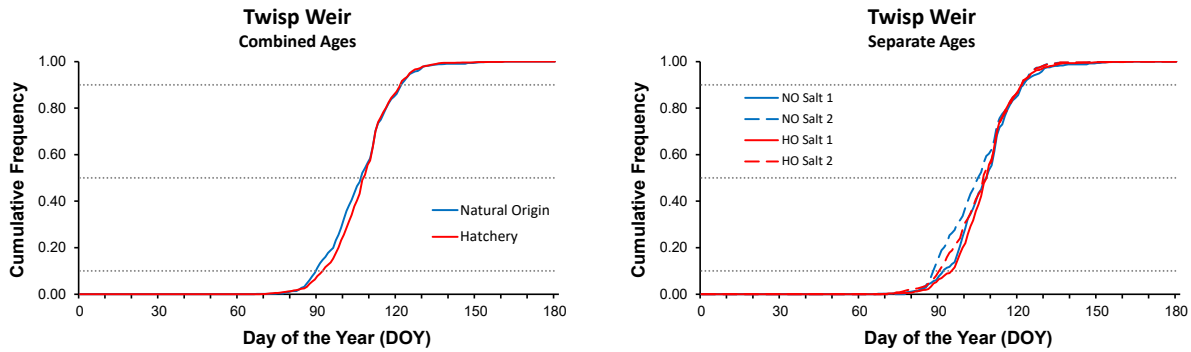


Figure 9. Cumulative frequency polygons of spawn timing of adult hatchery- and natural-origin Methow steelhead sampled at the Twisp River weir. Analyses included evaluations based on salt (ocean) age and pooled (combined) ages during the period 2009-2018 (return years). Horizontal dashed lines indicate the 10th, 50th, and 90th percentiles. Sample sizes = 880 natural-origin steelhead and 1,586 hatchery-origin steelhead.

Discussion

Migration timing was similar between hatchery- and natural-origin fish for each of the Wenatchee and Methow steelhead populations in the lower sections of the Columbia River system. Natural- and hatchery-origin fish arrived at Bonneville Dam at similar times for both the Wenatchee and Methow populations, and to Priest Rapids Dam for the Wenatchee population. However, as these populations moved farther up the Columbia River approaching their spawning grounds, migration timing between hatchery- and natural-origin steelhead began to differentiate. Differences observed in migration timing could indicate that hatchery- and natural-origin steelhead were exposed to different environmental conditions, harvest pressures, and predation pressures. Although not tested statistically, both natural- and hatchery-origin steelhead from the Wenatchee population arrived at the lower dams (Bonneville and Priest Rapids) earlier than steelhead from the Methow population likely resulting in different selection pressures and adult survival through this stretch of their migratory route.

Different patterns for the early (10th percentile), middle (50th percentile) and later (90th percentile) portion of the run were observed for Wenatchee steelhead migrating from Rock Island Dam to Tumwater Dam, encompassing much of their migration through the lower mainstem Wenatchee River. Steelhead do return to spawn in Peshastin Creek, Mission Creek, or Chumstick Creek, all tributaries downstream of Tumwater Dam. These fish would have been detected at Rock Island, but not at Tumwater Dam, likely influencing migration and spawn timing patterns observed if natural- and hatchery origin fish are disproportionately represented in these tributaries. Results indicate that natural-origin steelhead have a more contracted migration timing from the Columbia River confluence through the lower Wenatchee River (from Rock Island to Tumwater Dams) than hatchery-origin fish. For the earlier portion of the run (10th percentile), although not significant, trends showed natural-origin fish arrived slightly earlier at Rock Island Dam, but later at Tumwater Dam than hatchery-origin fish. This indicates that natural-origin fish were slower at migrating through the lower Wenatchee River than hatchery-origin fish, or that the earlier component could have been steelhead returning to Peshastin Creek,

Mission Creek or Chumstick Creek (which were not evaluated in this study). This earlier portion arrives at Tumwater at the end of April, when flows are typically beginning to rise (the Wenatchee River hydrograph typically peaks in mid- to late-May). Towards the middle of the run (50th percentile), natural-origin fish arrive slightly earlier than hatchery-origin fish at Rock Island and significantly earlier than hatchery-origin fish at Tumwater (12-15 days), indicating the natural-origin fish are starting to move faster than hatchery-origin fish as they exit the Columbia River and migrate through the lower Wenatchee River. This middle portion comprises the most significant difference in migration timing between hatchery- and natural-origin steelhead arriving at Tumwater in early September, coinciding with the highest annual water temperatures and lowest annual flows in the Wenatchee River. At the latter portion of the run (90th percentile), natural-origin fish arrived significantly later at Rock Island Dam, but earlier at Tumwater Dam than hatchery-origin fish, indicating that natural-origin fish are traveling faster through the lower Wenatchee River than their hatchery conspecifics. This later portion of the run arrives at Tumwater in early November, when fall rain events typically decrease water temperature and increase flows. Keefer et al. (2004) found that steelhead migrations through the Columbia River slowed dramatically when summer temperatures peaked within each year, and then increased as rivers cooled in the fall. As river temperatures and flows are highly variable from year to year in the mainstem Wenatchee, further analysis exploring correlations of year-specific migration timing between hatchery- and natural-origin steelhead with temperature and flows would yield better understanding.

Trapping and video data, which yielded higher data quality at Tumwater Dam with age-specific data and higher sample sizes, further support the conclusions made with PIT-tag-only migration data. These data indicate that steelhead migrate throughout the year; however, the migration distribution is bimodal. The first pulse occurs during the summer/autumn of the year before spawning and consists of more hatchery-origin than natural-origin fish, although this difference was not significant. The second pulse occurs during the winter/spring of the year of spawning and consists of significantly more natural-origin than hatchery-origin fish. For the Wenatchee population at Tumwater, the earlier portion of the run consists of younger fish (salt age-1) returning earlier than salt age-2 and salt age-3 steelhead for both hatchery- and natural-origin steelhead, consistent in most years with trends that hatchery-fish tend to return at a younger age than natural-origin fish. Towards the middle and end of the run, steelhead of all ages start to return at similar times presumably because the older, natural-origin fish start to return in higher numbers than hatchery-origin fish.

Similar to the Wenatchee population, hatchery- and natural-origin Methow steelhead began to differentiate as they moved farther up the Columbia River. While no significant difference in migration timing were observed at Bonneville Dam, natural-origin steelhead arrived, on average, 10 days earlier to Priest Rapids Dam for the middle portion of the run (50th percentile). Similarly, natural-origin steelhead arrived earlier to Wells Dam for the earlier (10th percentile; 14 days) and middle (50th percentile; 11 days) portion of the run. These results are consistent with a radio-telemetry study that found Upper Columbia natural-origin steelhead returning slightly earlier to Priest Rapid Dam than hatchery-origin steelhead (Nathaniel Fuchs, personal communication). Increasing temperature and decreasing flow could have played a role in earlier arrival of natural-origin fish higher up in the system.

Fallback, overwintering mortality, and harvest rates were not measured as a part of this study and could cause differential impact to survival (and detection) of hatchery- and natural-origin steelhead, especially if they experience those events at different rates. Overwintering in the mainstem Columbia River was more likely for later-arriving steelhead (Fuchs et al. 2021). Winter tributary use for overwintering has been documented in the Wenatchee (26% in 2016) and in the Methow (18% in 2015) rivers, where overwintering mortality was slightly higher for hatchery-origin steelhead (Fuchs et al. 2021). Fallback occurs when an adult passes through a dam (or detection site) and then later migrates back downstream past that detection point. Fuchs et al. (2021) documented 20% (n = 165 of 807) of steelhead fell back at Priest Rapids Dam and did not reascend. However, proportions of steelhead fallbacks that were hatchery- and natural-origin were similar to the proportions of fish tagged, suggesting no difference in rates between hatchery- and natural-origin fish. A recreational steelhead fishery for hatchery-origin steelhead has occurred in some (but not all) years included in this analysis in the Columbia River (upstream and downstream of Priest Rapids Dam), Wenatchee River, and Methow River (Hillman et al. 2019). Differences in harvest rates and timing between years could potentially influence the number of hatchery-origin fish reaching the spawning grounds. For example, in 2015, harvest reduced the survival of radio-tagged steelhead above Priest Rapids Dam by 18%, resulting in a relatively larger difference in survival to spawning between hatchery- and natural-origin conspecifics (Fuchs et al. 2021).

No significant differences were observed in DOY of entry (“spawn timing”) between hatchery- and natural-origin steelhead into their spawning tributaries of the Wenatchee sub-basin (Chiwawa River and Nason Creek) or the Methow sub-basin (Chewuch River and Twisp River). On average, natural-origin steelhead tended to have an earlier DOY of entry than hatchery-origin fish; however, none of these comparisons were statistically significant, indicating that both hatchery- and natural-origin steelhead were present on the spawning grounds in each of these tributaries at similar times throughout all portions of the run. Spawn timing reported here is based on DOY each PIT-tagged steelhead was first detected by the lowest instream PIT-tag interrogation array in a respective tributary. Using this data source, we were not able to get exact spawning dates for individuals, so we used DOY first detected as a surrogate for this analysis. Because data were collected at time of entry into the tributary, given the large variance observed in some portions of the run, and the potential for steelhead to overwinter in tributaries and mainstem rivers (Fuchs et al. 2021), further data collection and analyses are recommended should it be necessary to evaluate differences more accurately between spawn timing of hatchery- and natural-origin steelhead.

Based on these data, DOY of entry may not accurately reflect spawn timing for all spawning locations. Mean date of first entry for both hatchery- and natural-origin steelhead into the Chiwawa River ranged from approximately 1 February (DOY 32) to 5 November (DOY 310); however, approximately 85% of the run entered by 29 May (DOY 150). The typical observed spawn timing for steelhead in the Wenatchee sub-basin based on redd surveys in the mainstem Wenatchee River spans from March through May. Therefore, it is likely that steelhead detected in the last 15% of the run were not actively spawning but could have entered into the Chiwawa River to either hold until the next spring spawning season or entered into the Chiwawa River and later left to hold in the Wenatchee River. The range in the approximate mean date of first entry into other tributaries (Nason Creek: 1 February – 9 May, Chewuch River: 10 March –

29 April, Twisp: 10 March – 9 May) were more consistent with the typical spawning window observed during spawning ground surveys.

Despite differences in mean date of entry between hatchery- and natural-origin steelhead for some portions of the run that could have indicated biologically significant differences in spawn timing, no significant differences were found because there was large variation in date of entry among individuals. For example, for the latter portion (90th percentile) of the Chiwawa run, DOY of entry spanned 185 days for hatchery-origin fish and 183 days for natural-origin steelhead. Despite a mean difference of 15 days and considering the protracted timing associated with this portion of run (discussed above), results indicated no significant difference between DOY of entry between hatchery- and natural-origin steelhead. Additionally, for the early portion (10th percentile) of the Nason Creek run, DOY of entry spanned 71 days for hatchery-origin fish and 67 days for natural-origin steelhead. Despite a mean difference of 21 days, results indicated no significant difference between DOY of entry between hatchery- and natural-origin steelhead. For the Chewuch and Twisp spawning tributaries in the Methow sub-basin, all mean differences of DOY of first entry between hatchery- and natural-origin steelhead were 10 days or less. Further confirming no biological difference in spawn timing, Goodman et al. (2021) tracked anchor-tagged steelhead in the Twisp River from 2009-2020 and found that natural-origin females spawned an average of only 1.7 days earlier than hatchery-origin females across years, however, this difference varied among years.

Sex-specific differences in migration and spawn timing may also exist but were not tested in this analysis. Natural-origin females arrived at the Twisp River weir significantly earlier than their hatchery-origin females, while no significant differences were found between natural- and hatchery-origin males (Goodman et al. 2021). Further analysis including sex-specific data could be important in explaining variation and contributing to observed patterns.

Overlap in spawning distribution between hatchery- and natural-origin steelhead is another useful metric and objective to evaluate success of these integrated hatchery programs (Hillman et al. 2019). We were not able to evaluate overlap in spawning distribution of hatchery- and natural-origin steelhead in the Wenatchee and Methow sub-basins with the available data. PIT-tag data used in this study only provide information on when individuals enter into each tributary, not on exact spawning location. In the Twisp River, identification of anchor-tagged individuals showed that mean spawning location of natural-origin females was 1.9 rkms farther upstream than that of hatchery-origin females for pooled data (2009-2020), however, this finding was not biologically significant as no differences were found within individual year comparisons (Goodman et al. 2021). Differences in the spatial distribution of spawning hatchery- and natural-origin steelhead could be due to low abundance of natural- or hatchery-produced fish (i.e., vacant habitat), improper smolt release locations (Murdoch et al. 2007; Hoffnagle et al. 2008), or inadequate homing of hatchery fish (Murdoch et al. 2007). Additional data collection and analysis would need to occur to identify specific spawning locations of hatchery- and natural-origin steelhead.

Throughout the years analyzed in this study, the origin of broodstock and parental crosses (HxH, HxW, WxW) used to create hatchery fish varied. The use of hatchery broodstock in supplementation programs can cause domestication selection, reducing rates of survival and

reproductive success in steelhead (McLean et al. 2003; Chilcote et al. 2011). In the Wenatchee population, hatchery fish originating from two prior generation hatchery parents had <20% of the reproductive success of natural-origin spawners, where hatchery females originating from a cross between two natural-origin parents of the prior generation had equivalent or better reproductive success than natural-origin females (Ford et al. 2016). More recently, efforts have been made to reduce the use of hatchery-origin broodstock in supplementation programs to reduce the effects of domestication selection. A year-specific analysis, identifying proportions of parental crosses, may possibly identify the effect that these different hatchery practices have had on migration and spawn timing.

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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; Moberg 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%).

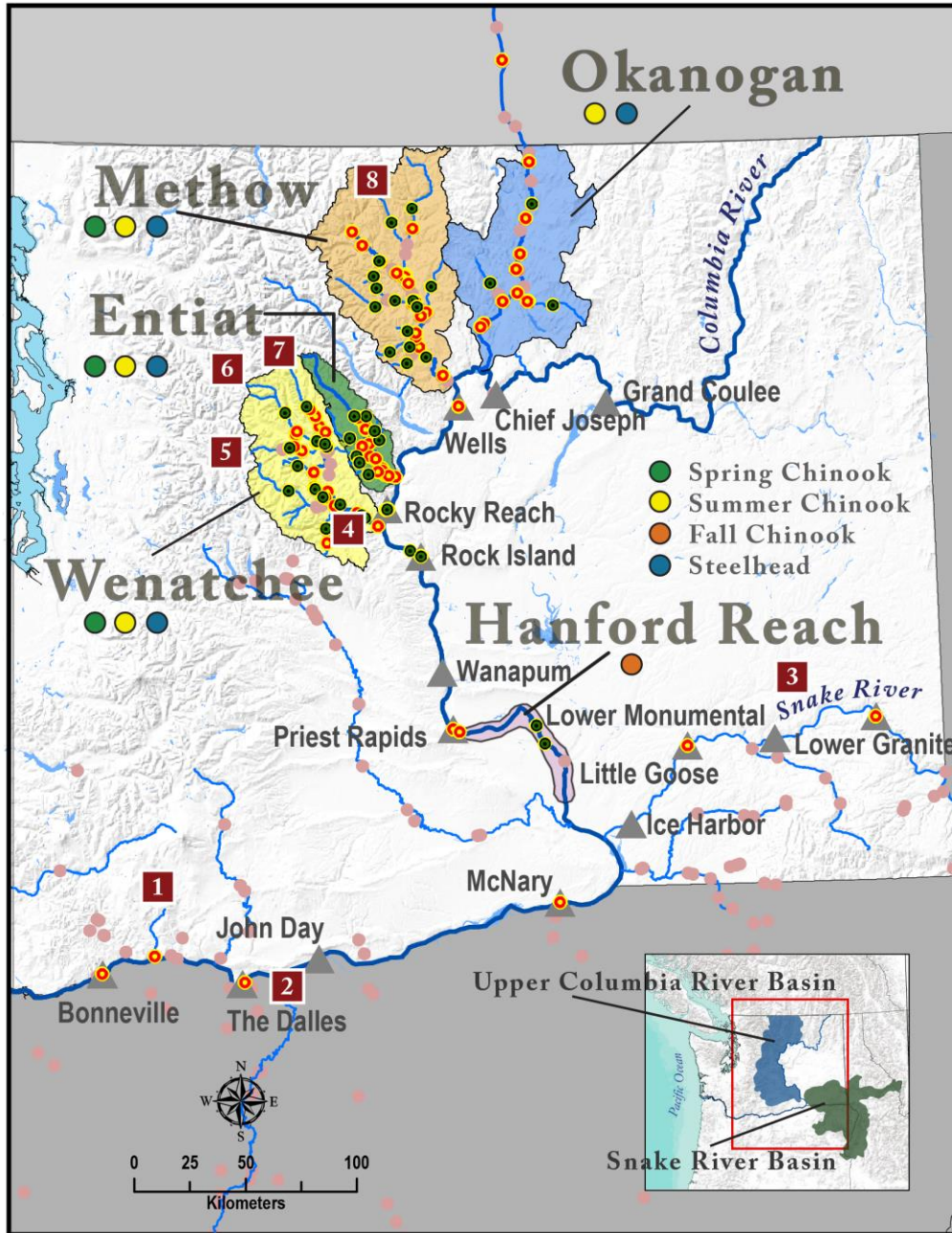


FIGURE 1. Release locations (green bullseye) and final PIT tag detection locations (yellow bullseye) of Chinook Salmon and steelhead originating from the upper Columbia River Basin. Other PIT tag detection sites are displayed as shaded dots for reference. Hydropower dams are denoted with triangles. The 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%	

¹Strays were last detected outside the subbasins from which they originated.

²Fall Chinook were released into the Hanford Reach of the Columbia River and not into the Wenatchee, Entiat, Methow, or Okanogan rivers.

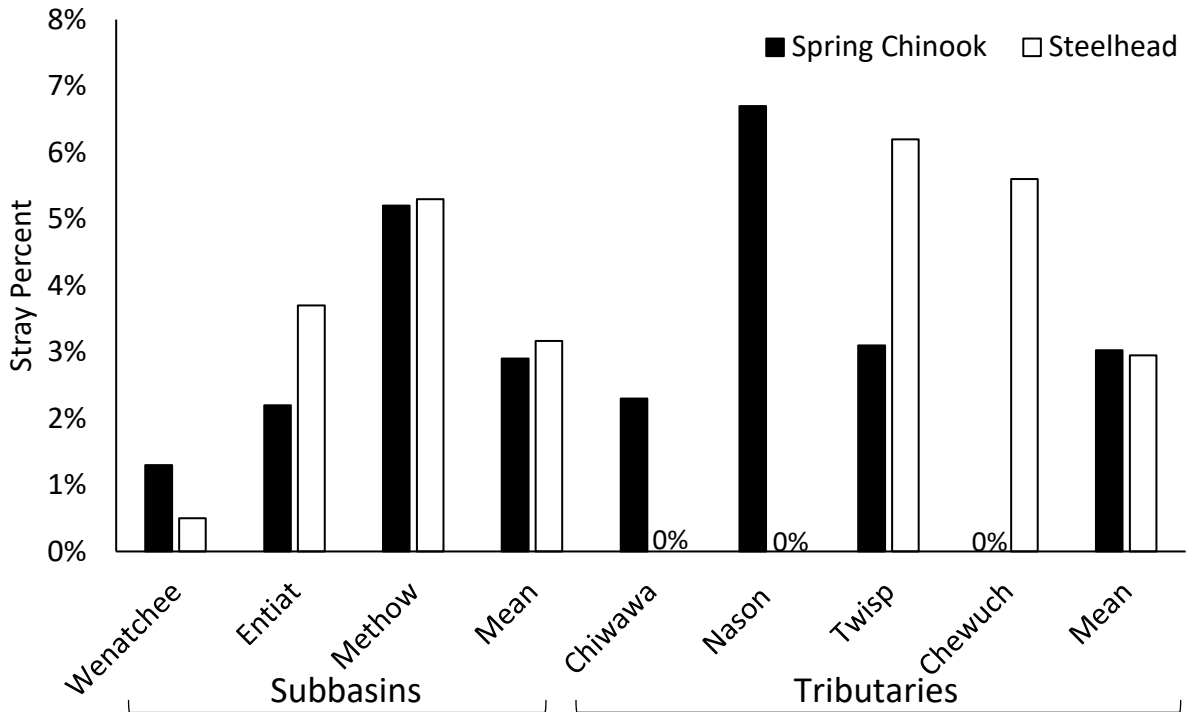


Figure 2. The percent of PIT-tagged natural-origin spring Chinook Salmon and steelhead that strayed away from their subbasins and tributaries of origin.

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; Mobernd 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; Moberg 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; Moberg 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*,

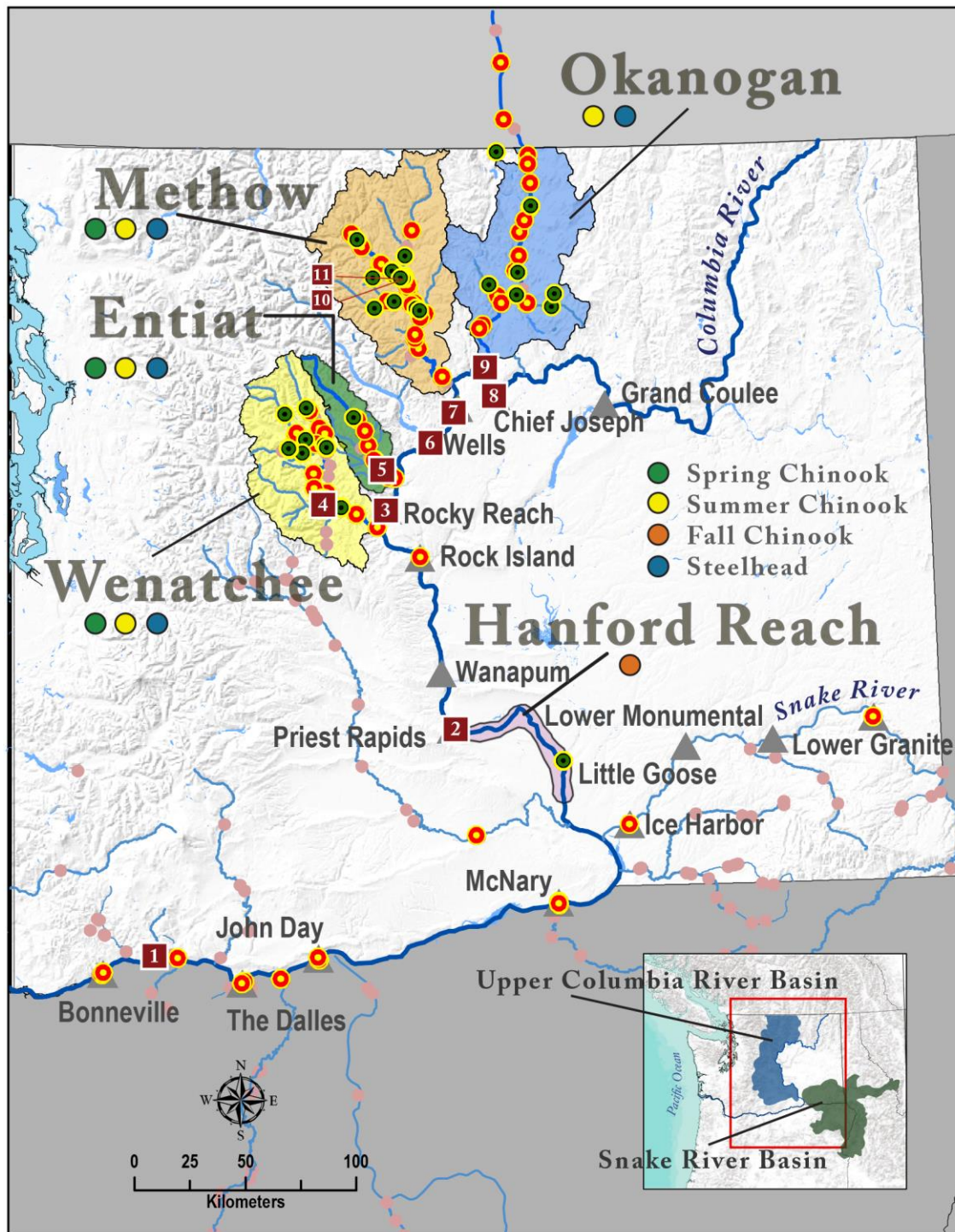


Figure 1. Release locations (green bullseye) and final detection locations (orange bullseye) of spring, summer, and fall Chinook Salmon and steelhead from the upper Columbia River Basin. Other points along rivers indicate PIT tag detection arrays. Numbered boxes represent locations of subject hatcheries 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 Cassimer Bar	Winthrop Cassimer Bar	Chewuch River Omak Creek	2010, 2012 2005, 2007-2011	996 88,332
Cassimer Bar	Cassimer Bar	Stapaloop Creek	2004, 2006	23,334
Wells	Saint Mary's	Omak Creek	2003-2005, 2012-2017	90,249
Wells	Wells	Salmon Creek	2012, 2017	11,310
Wells	Wells	Similkameen River	2003-2005, 2012, 2017	93,613
Total				4,379,563

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

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

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

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

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

Analysis

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

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

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

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

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

Results

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

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

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

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

Steelhead trout

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

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

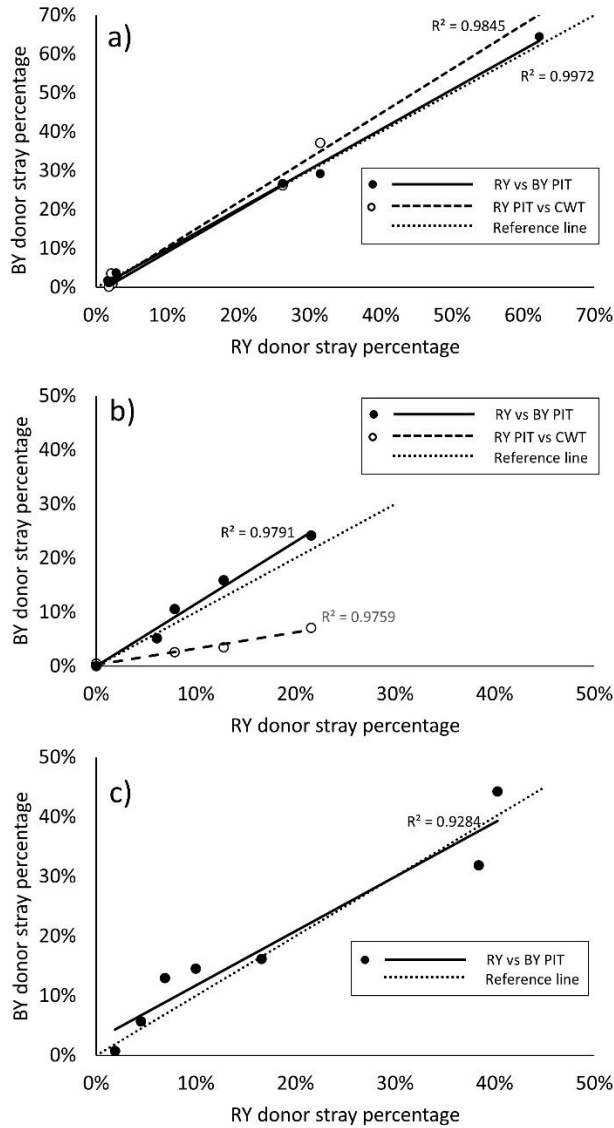


Figure 2. PIT-tag-based return-year (RY, spawn year) stray estimates versus brood-year (BY) stray estimates using either PIT tags or BY coded wire tags (CWT) for upper Columbia watershed a) spring Chinook Salmon, b) summer Chinook Salmon, and c) steelhead.

Spatial scale and taxa

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

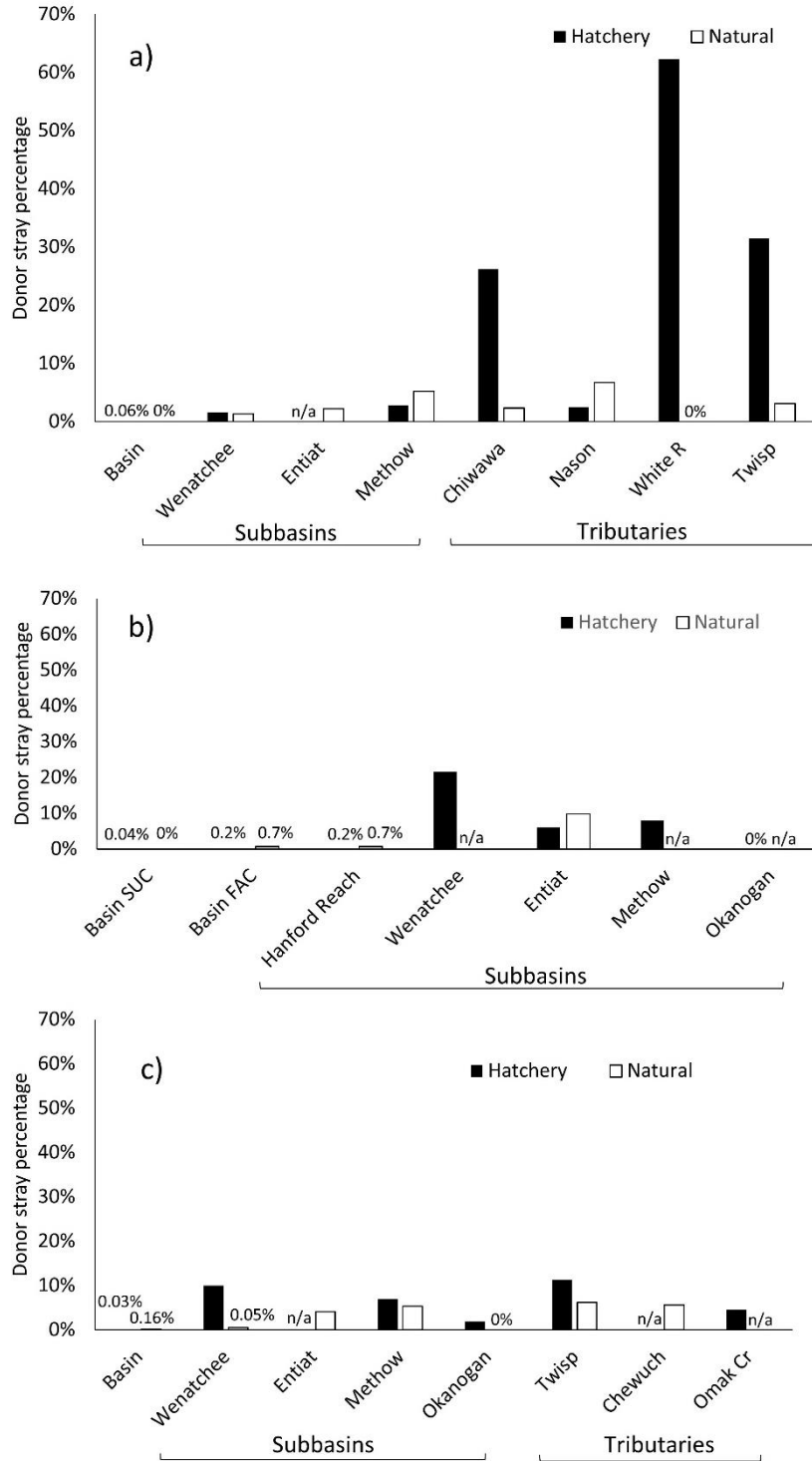


Figure 3. Donor stray percentages of hatchery- and natural-origin a) spring Chinook Salmon, b) summer Chinook Salmon (SUC) and fall Chinook Salmon, (FAC) and c) steelhead at basin, subbasin, and tributary scales.

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

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

Stray direction

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

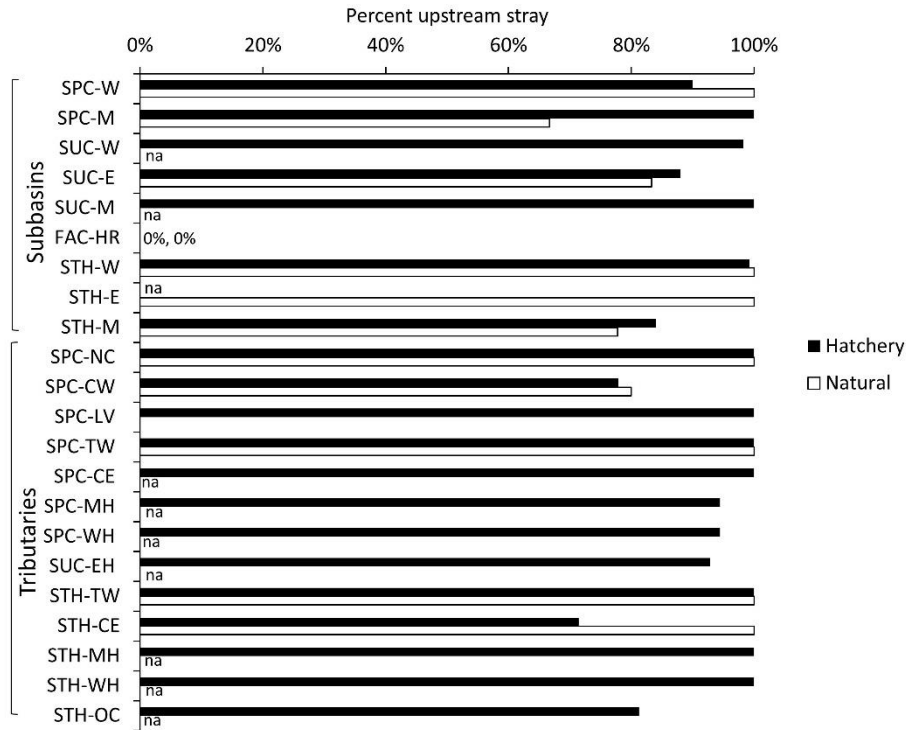


Figure 4. Direction of hatchery- and natural-origin straying. Abbreviations: SPC spring Chinook Salmon, SUC summer Chinook Salmon, FAC fall Chinook Salmon, STH steelhead. W Wenatchee River, M Methow River, E Entiat River, HR Hanford Reach, NC Nason Creek, CW Chiwawa River, LV Leavenworth Nation Fish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

Movement for remote acclimation

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

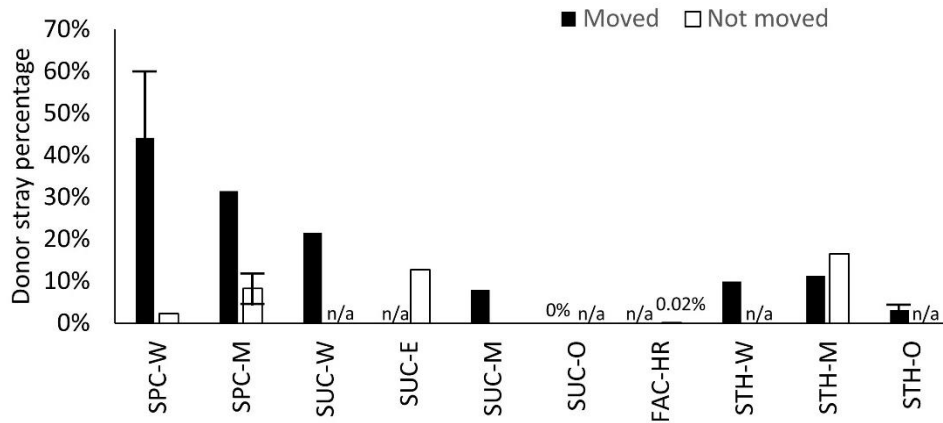


Figure 5. Mean donor stray percentages of hatchery-origin fish that were moved as juveniles among facilities prior to release (moved) or those that were incubated, reared, acclimated and released from a single facility (not moved). Error bars represent the range of values when more than one value was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

Management changes

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

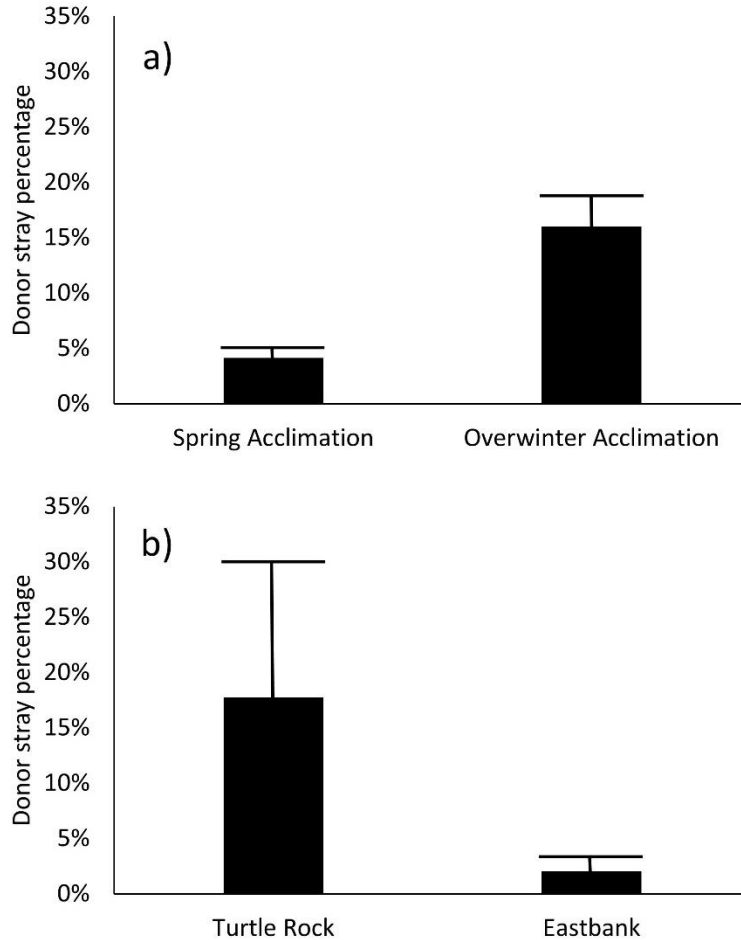


Figure 6. Mean donor stray percentages in periods of differing management regimes for a) summer Chinook Salmon released from the Carlton Acclimation Facility on the Methow River, and b) steelhead released into the Wenatchee River after being raised at either Turtle Rock or Eastbank Hatchery. Bars represent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

Discussion

Spatial scale (size of the target) and risk

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

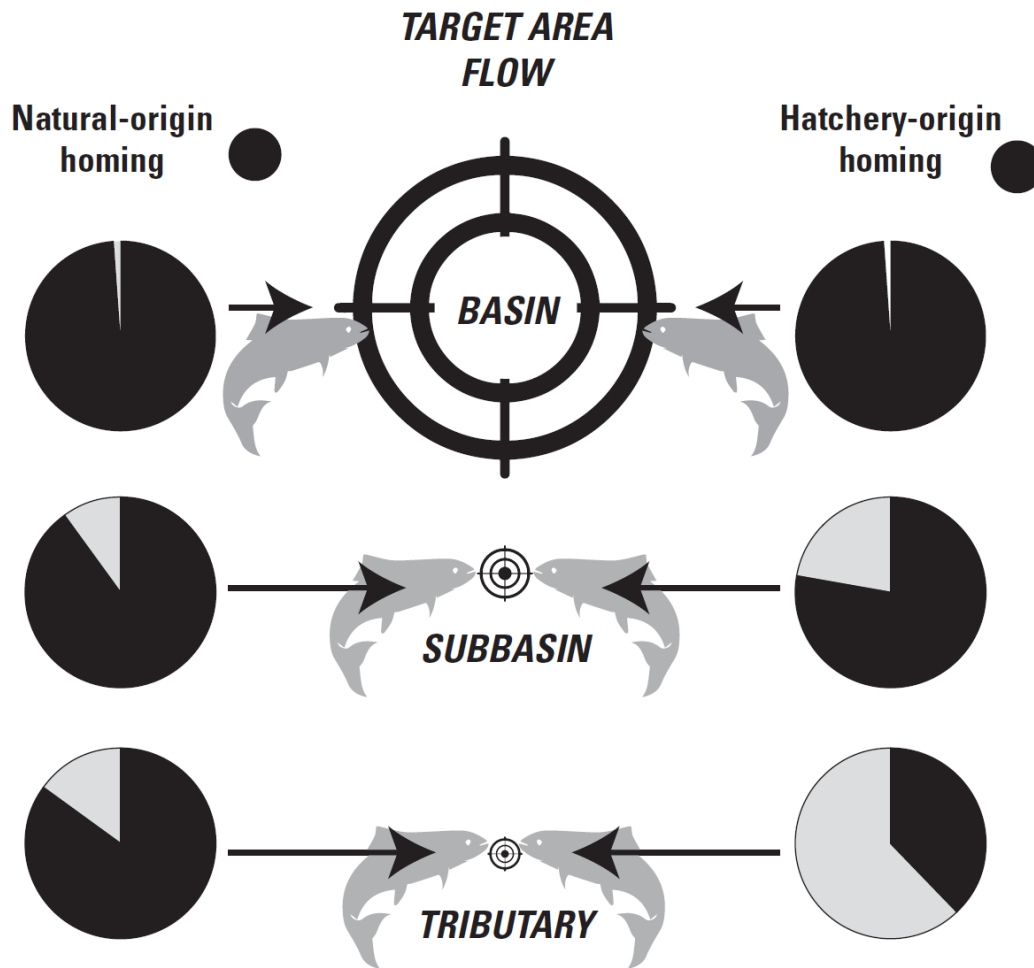


Figure 7. Comparisons of homing rates (minimums in black) and straying (maximums in grey) between hatchery- and natural-origin Salmon and steelhead at three spatial scales in the upper Columbia subregion. The size of the targets was scaled to the fall discharges of the upper Columbia River (basin), the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

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

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

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

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

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

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

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

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

Factors influencing straying

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

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

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

Stray direction

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

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

Moved vs. non-moved

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

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

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

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

Responses to management actions

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

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

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

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

Tag methods and influence on conclusions

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

Applications

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

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

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

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

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Abstract

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

Introduction

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

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

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

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

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

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

Methods

Study Area

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

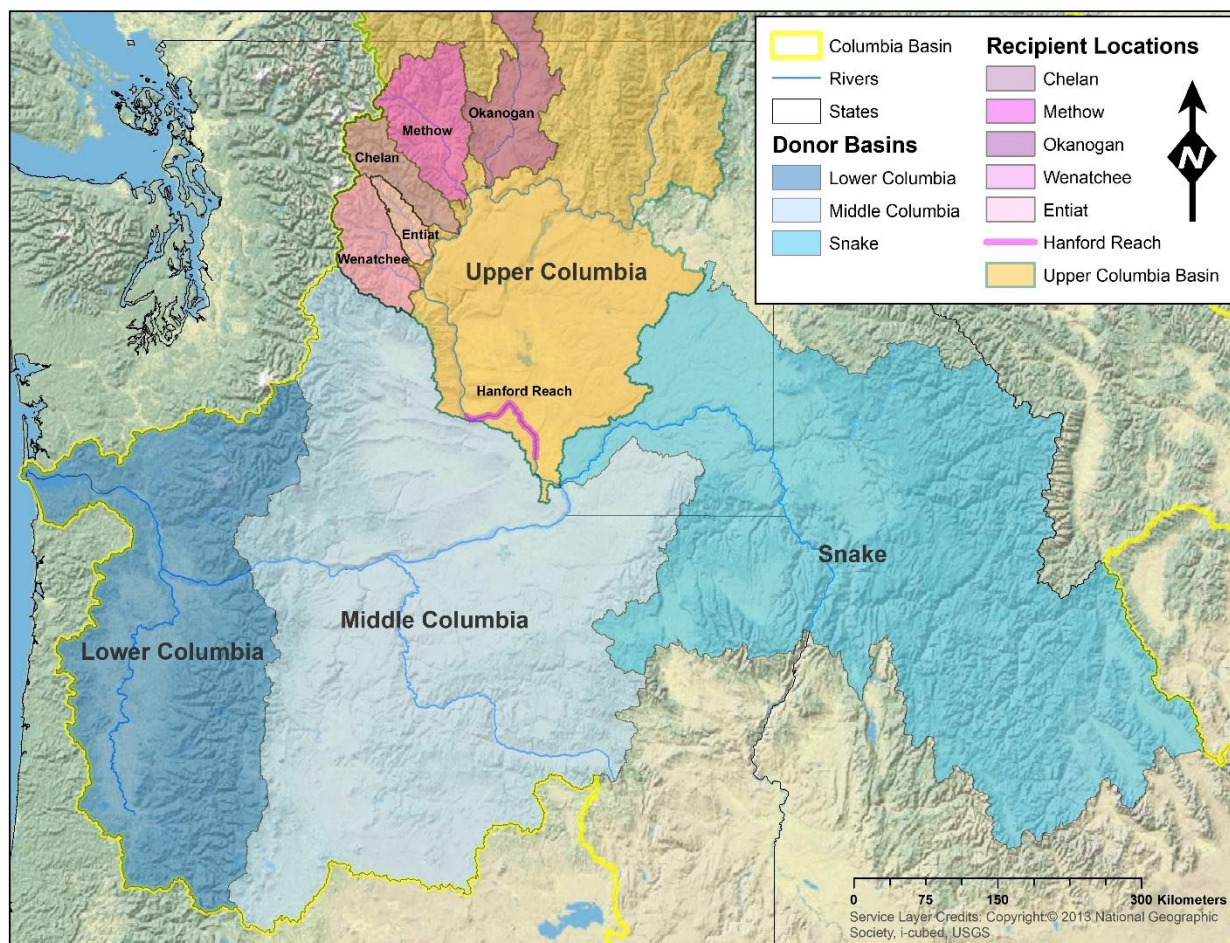


Figure 1. Map of the study area of the upper Columbia Basin and areas outside of the upper Columbia Basin that contributed strays to recipient populations within the upper Columbia Basin.

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

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

Hatchery description and tagging

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

Spawning escapement and composition

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

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

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

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

Field Methods

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

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

Analysis

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

Results

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

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

Spawn year	Upper Columbia Basin escapement	Natural-origin recruits		Target Hatchery-origin recruits		Non-target strays Hatchery-origin recruits	
		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.

Spawn year	Subbasin escapement	Natural-origin recruits		Target		Non-target strays	
		Number	Percent	Hatchery-origin		Hatchery-origin	
				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.

Spawn year	Escapement	Natural-origin recruits		Target		Non-target strays	
		Number	Percent	Hatchery-origin recruits Number	Percent	Hatchery-origin recruits 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).

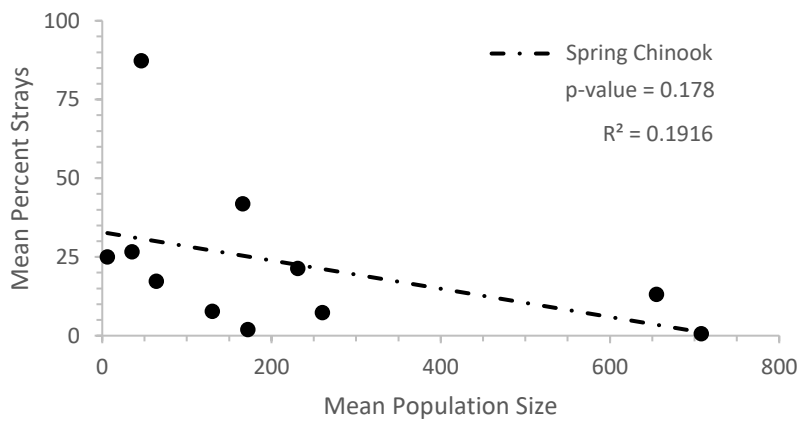
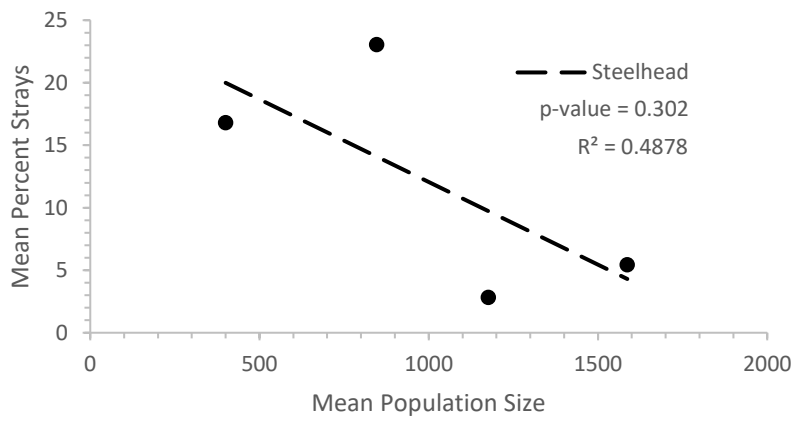
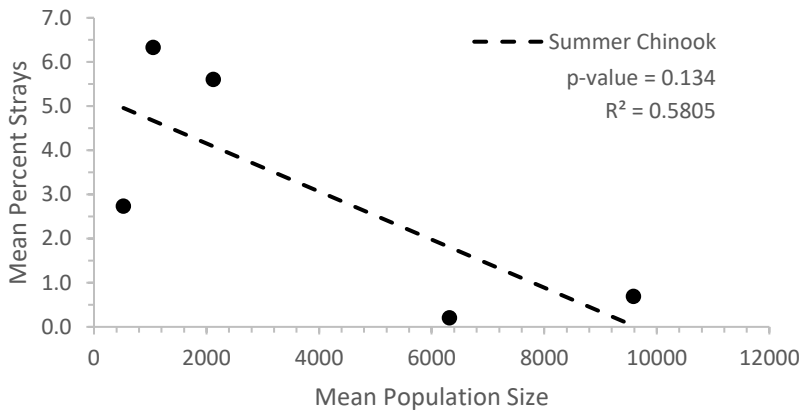


Figure 2. The relationship between recipient population size and mean stray rate for summer Chinook Salmon, steelhead, and spring Chinook Salmon.

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).

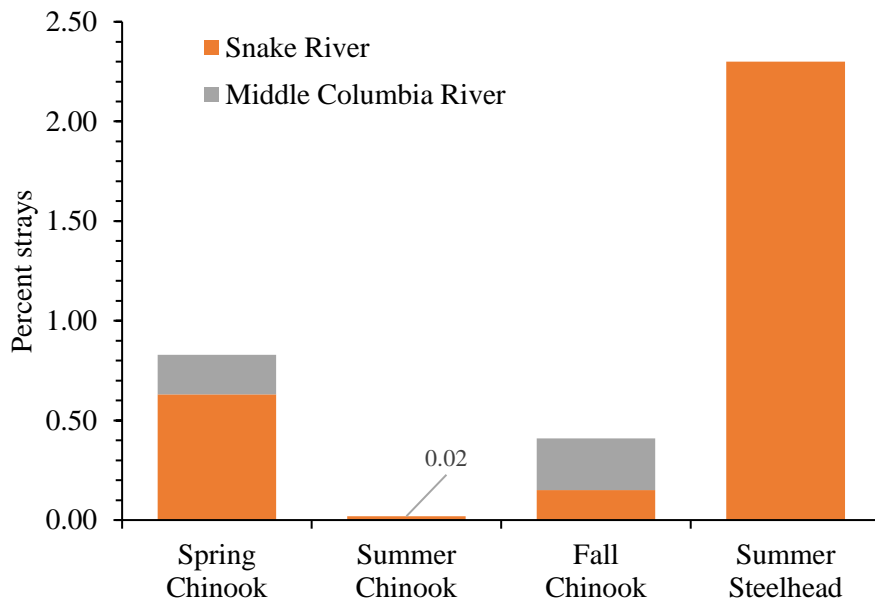


Figure 3. Mean percent hatchery stray Chinook Salmon and steelhead observed in the Upper Columbia River Basin from other regions of the Columbia River Basin from 2014 to 2018.

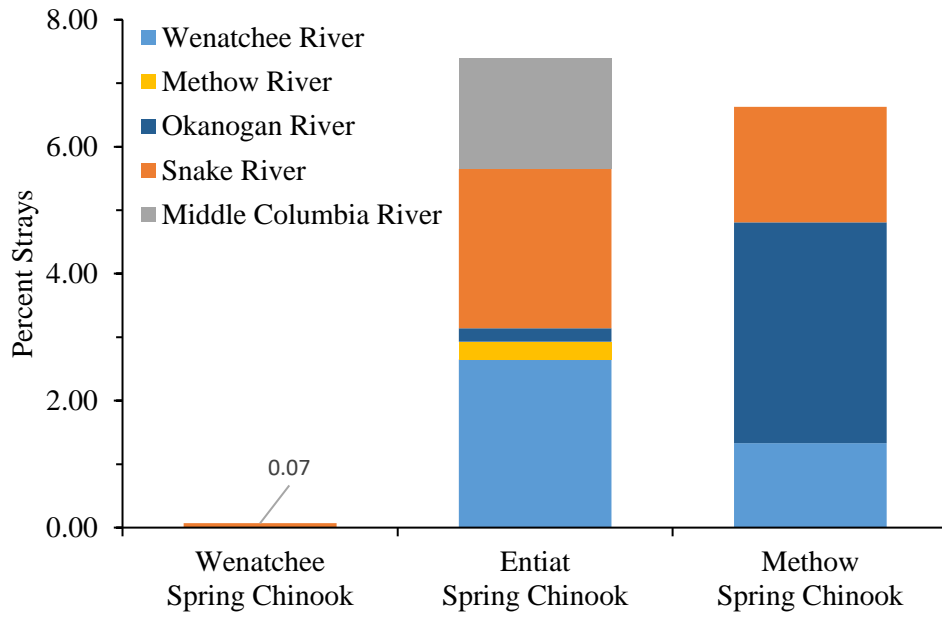


Figure 4. Mean percent hatchery stray spring Chinook Salmon observed in the Upper Columbia River subbasins from other regions of the Columbia River Basin from 2014 to 2018. The management target is <5%.

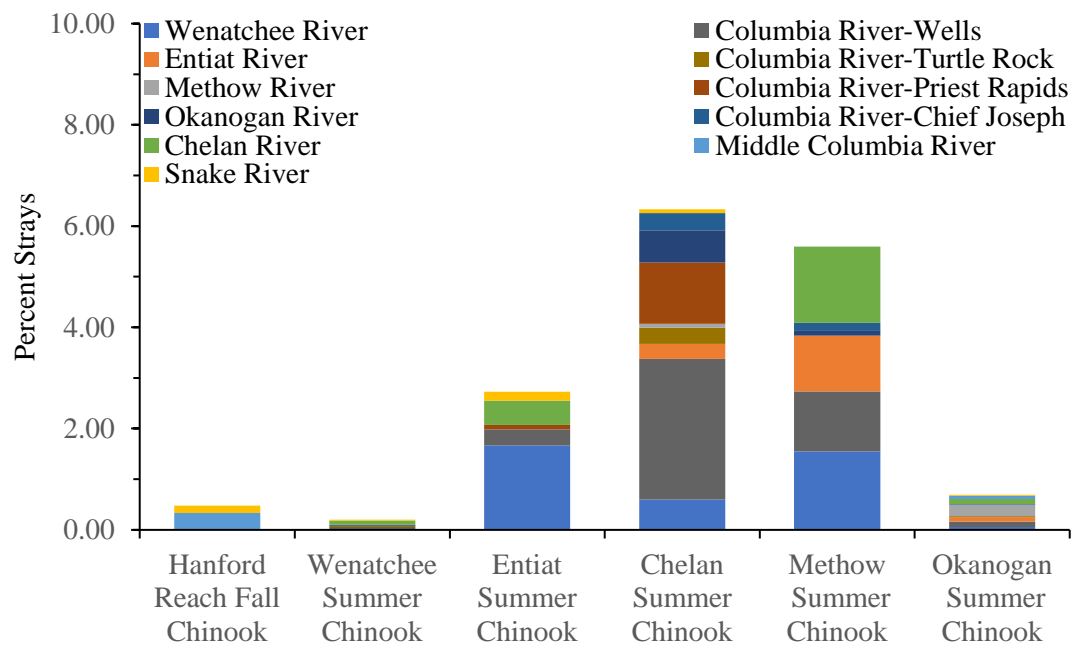


Figure 5. Mean percent hatchery stray summer and fall Chinook Salmon observed in subbasins of the Upper Columbia River basin from 2014 to 2018. The management target is <5%.

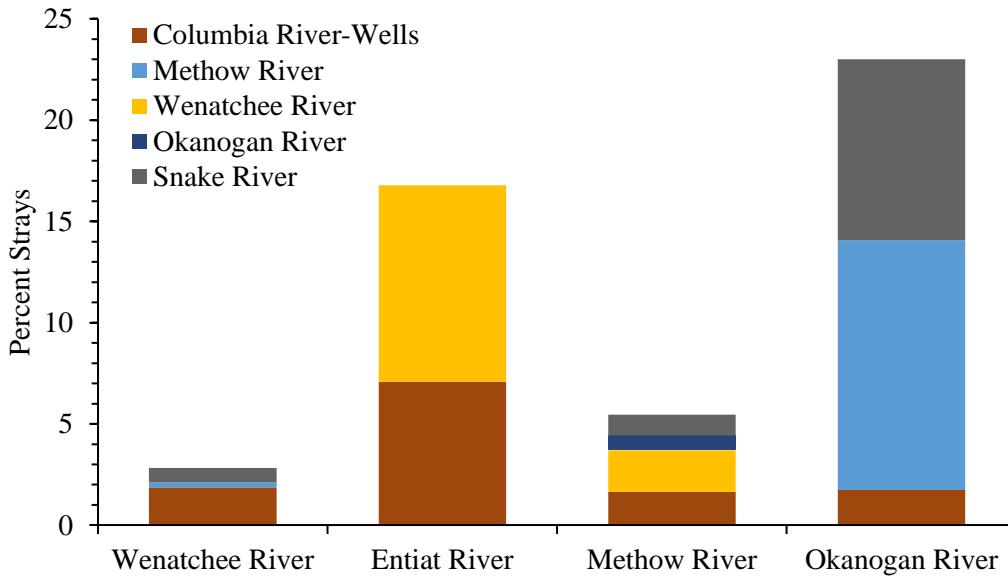


Figure 6. Mean percent hatchery stray steelhead observed in subbasins of the Upper Columbia River basin from 2014 to 2018. The management target is <5%.

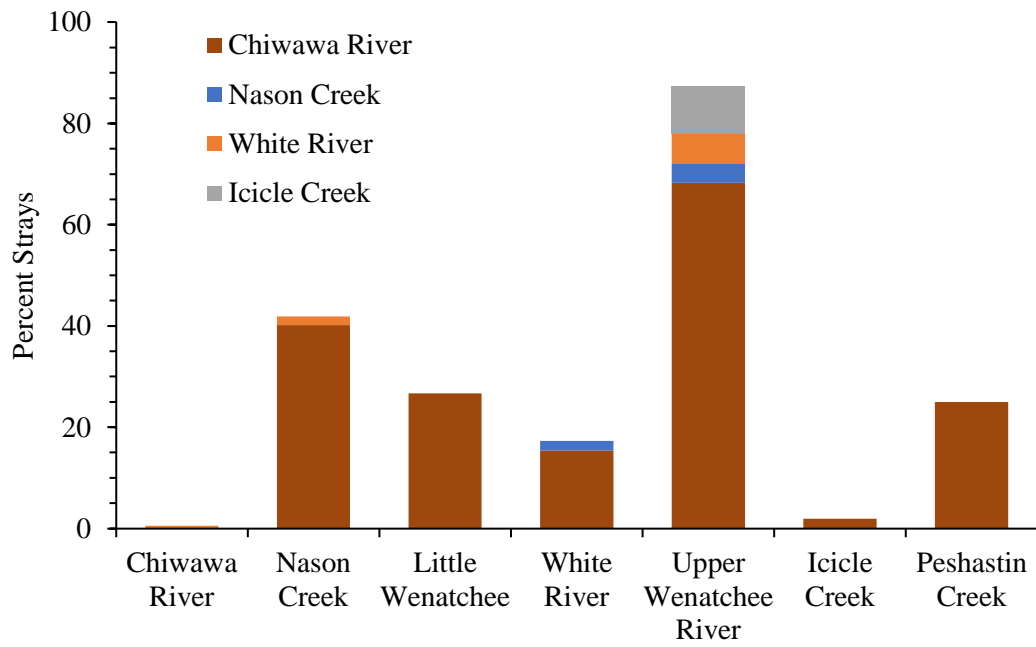


Figure 7. Mean percent hatchery stray spring Chinook Salmon observed in tributaries of the Wenatchee subbasin from 2014 to 2018. The management target is <10%.

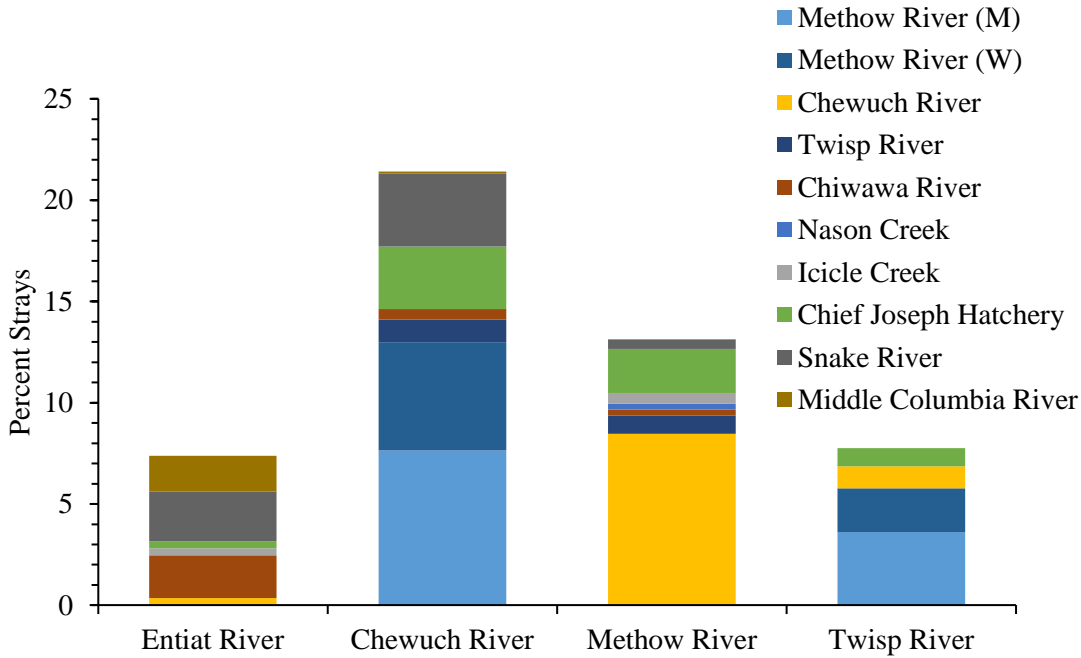


Figure 8. Mean percent hatchery stray spring Chinook Salmon observed in the Entiat River and Methow River and tributaries (Chewuch and Twisp rivers) from 2014 to 2018. The management target is <10% except for the Entiat River which is <5%.

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 counterparts (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.

Acknowledgments

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Evaluation of Genetic Metrics of Adult Hatchery- and Natural-Origin Steelhead in the Upper Columbia Basin

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Abstract

In 1997, the upper Columbia River summer steelhead evolutionarily significant unit (ESU), was listed as threatened under the Endangered Species Act (ESA). Hatchery programs already underway were used to supplement wild steelhead populations in the Wenatchee, Methow, and Okanogan rivers for conservation and fishery benefits. Hatchery propagation comes with genetic risks to wild populations of reduced within- and among-population diversity and domestication. 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 steelhead. Current hatchery programs are integrated and broodstock are collected locally within each population. Hatchery collections (baseline or contemporary) had higher levels of linkage disequilibrium and lower estimates of effective number of breeders (N_b) than collections from natural-origin fish due to strong family structure and small number of parents spawned. In addition, contemporary hatchery collections were genetically distant from natural baseline and contemporary collections. This indicates genetic drift is occurring in the hatchery collections to a higher degree than in the naturally spawning population. This pattern is likely mostly due to the low number of steelhead used as broodstock in upper Columbia River steelhead hatchery programs. Contemporary hatchery collections from 2018 tended to be quite different from all other collections likely due to low number of broodstock and decreased survival of the 2014 cohort due to poor ocean conditions. These results run counter to long-term conservation goals and may impact the long-term viability of these populations. Management for increased abundance and Proportionate Natural Influence (PNI) goals may exacerbate these shifts by removing natural-origin adults from the spawning grounds for use as broodstock, releasing numbers of juvenile fish that annually exceed pHOS targets upon returning as adults, and use of already small broodstock populations.

Introduction

The use of hatchery propagation comes with significant genetic risks to naturally spawning populations which generally fall under one of three categories: reduction in within-population diversity, reduction of among-population diversity, and domestication (Anderson et al. 2020; Busack and Currens 1995; Naish et al. 2007). The long-term fitness of natural populations is related to their genetic diversity (Forsman and Wennersten 2016). Metapopulation viability and stability depends in part on among-population diversity (Braun et al. 2016; Greene et al. 2010; Schindler et al. 2015). Selection for alleles favorable in domestic settings may reduce the fitness of wild populations (Hagen et al. 2019; White et al. 2013).

These negative impacts occur when hatchery- and natural-origin fish interbreed, which may or may not be intentional. Interbreeding can be intentional and substantial such as when the objective of the hatchery program is to increase natural production (Ford et al. 2015a; Williamson et al. 2010). Interbreeding can also be an unintentional byproduct of operating a hatchery program when hatchery-origin fish stray to non-target spawning populations (Ford et al. 2015b; Keefer and Caudill 2014; see Pearsons and O'Connor and Pearsons and Miller chapters in this report). Hatchery programs select a subset of individuals whose probability of passing on genetic material to the next generation is increased by reducing mortality associated with freshwater rearing and development. This subset is often a relatively small number of individuals that then produce a large number of adult offspring and thus these programs can change allele frequencies and reduce effective population size (Ryman and Laikre 1991). Thus, it is important to monitor the genetic status of the natural populations to determine if there are signs of changes in within- and among-population genetic diversity, and to the degree possible, domestication.

Background

The National Marine Fisheries Service (NMFS) recognizes 15 Evolutionary Significant Units (ESU) for west coast steelhead (*Oncorhynchus mykiss*). The Upper Columbia River (UCR) ESU, which comprises steelhead in the Wenatchee, Entiat, Methow, and Okanogan subbasins, was listed as endangered under the Endangered Species Act (ESA) in 1997 and reclassified as threatened in 2006 (threatened status reaffirmed in 2009 and 2014). Included in this listing were the Wells Hatchery steelhead (program initiated in the late 1960s) that originated from a mixed group of native steelhead that are considered genetically similar to natural spawning populations above Wells Dam. Wells Fish Hatchery was the primary source of juvenile steelhead released into the Wenatchee River from 1982-1996 (Murdoch et al. 2003) and the Methow and Okanogan rivers (Mullan et al. 1992). The 1998 steelhead 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). The Biological Review Team (BRT) further identified the relationship between the resident and anadromous forms of *O. mykiss* and possible changes in the population structure ('genetic heritage of the naturally spawning fish') in the basin as two areas requiring additional study. Furthermore, the West Coast Steelhead BRT (2003) recommended that stocks in the Wenatchee, Entiat, and Methow rivers, within the Upper Columbia ESU, be managed as separate populations.

In addition to the mixed ancestry Wells Hatchery steelhead, Skamania Hatchery (Washougal River steelhead ancestry) steelhead were also released into the Wenatchee River basin between 1977 and 1989 and into the Methow River basin prior to 1975 (Mullan et al. 1992; Peven and Hays 1989; Peven et al. 1994). In 1996, broodstock for the Wenatchee River steelhead program were collected from Priest Rapids Dam and Dryden (rkm 24.9) and Tumwater (rkm 52.6) dams on the Wenatchee River. Because of the ESA listing, broodstock collection after 1996 was restricted to the Wenatchee River in an effort to develop a localized broodstock (Murdoch et al. 2003). Thus, starting in 1998, all juvenile steelhead released into the Wenatchee River and Wenatchee River tributaries were offspring of only Wenatchee River-captured broodstock. Similarly, since 1975, releases to the Methow and Okanogan rivers originated entirely from Wells Hatchery, which obtained broodstock from the fishways of Wells Dam (Mullan et al. 1992).

Objectives

In response to the need for evaluation of the supplementation programs mitigating for the operation of Rock Island, Rocky Reach, and Wells dams, both a monitoring and evaluation plan (Murdoch and Peven 2005) and the associated analytical framework (Hays et al. 2006) were developed for the Habitat Conservation Plans Hatchery Committee through the joint effort of the fishery co-managers (Confederated Tribes of the Colville Reservation [CCT], NMFS, U.S. Fish and Wildlife Service [USFWS], Washington Department of Fish and Wildlife [WDFW], and Yakama Nation [YN]) and Chelan, Douglas, and Grant counties public utility districts. This plan was updated multiple times, most recently in 2019 (Hillman et al. 2020b), and includes twelve objectives to be applied to various species, assessing the impacts of mitigation hatchery operations. This report pertains to UCR steelhead and associated steelhead supplementation programs as addressed by Objective 7, evaluating population genetics to determine whether genetic diversity, population structure, and effective population size have changed in naturally spawning steelhead as a result of the conservation and safety-net hatchery programs and assess genetic changes of hatchery-origin returns.

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

Methods

Sample collections

Baseline collections were genotyped for this project by WDFW MGL. 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, mostly collected in the 1990s, except for the Wenatchee steelhead samples (Table 1). The previous Wenatchee steelhead assessment described genetic changes occurring during the transition from the old composite segregated hatchery program to a Wenatchee-specific integrated hatchery program (Seamons et al. 2012). Rather than use the oldest available collections, which represented a hatchery program that hasn't existed for several steelhead generations, we used two collections taken in 2006 (fish spawning in 2007) and 2010 after the transition to the new integrated program had been completed. Both baseline collections were used in the previous genetic monitoring project (Seamons et al. 2012). Most baseline collections were taken from adult fish. Okanogan baseline collections were taken from smolts at a smolt trap in Omak Creek in 2007 and 2008. Omak Creek is the area that produces most naturally produced steelhead in the Okanogan sub-basin and has been the focus of supplementation efforts. In Okanogan baseline collections, previous genetic assessments had identified deviations from Hardy-Weinberg proportions and significant levels of linkage disequilibrium associated with high relatedness among samples in the collections (Blankenship et al. 2008). Before genotyping at SNP panels, family structure in Okanogan baseline collections was identified using the microsatellite data of Blankenship et al. (2008) and sibship analysis algorithms of COLONY v2.0.6.6 (Wang 2004; Wang 2013). One to three members of each family were randomly selected for genotyping. Samples to be genotyped were chosen to balance representation of all identified full-sibling families. All baseline collections had been used in previous genetic monitoring projects (Blankenship et al. 2008; Seamons et al. 2012).

Contemporary steelhead collections consisted of hatchery- and natural-origin broodstock captured and/or spawned in 2017 and 2018 at Eastbank Fish Hatchery, Wells Fish Hatchery, Twisp River weir, and Winthrop Fish Hatchery (Table 1). These steelhead broodstock had previously been genotyped by Columbia River Inter-tribal Fish Commission (CRITFC) or Idaho Fish and Game (IDFG) geneticists for parentage-based tagging (PBT) projects, with the exception of the Twisp River samples, which were genotyped by WDFW MGL.

The Wells Hatchery Methow Safety-Net program used only hatchery-origin fish as broodstock, but they were one generation removed from natural fish, i.e., broodstock consist of fish produced for the Winthrop National Fish Hatchery (WNFH) steelhead and the Twisp Conservation steelhead hatchery programs using predominantly natural-origin Methow Basin fish for broodstock. Wells Hatchery produced fish were not used as broodstock in this program. The Wells Hatchery Twisp River Conservation program used Twisp River natural-origin fish as broodstock. For most hatchery programs, the origin (hatchery or natural) of each fish was recorded and could be associated with its genotype, in which case hatchery- and natural-origin broodstock were considered different collections. For the Winthrop and Okanogan programs, we failed to find individual origin information, in which case the entire sample was considered a single collection. The broodstock for the current Okanogan program has been collected exclusively from the Okanogan Basin, however in previous years broodstock has also been collected from the volunteer channel at Wells Dam. Genotypes were obtained directly from CRITFC (S. Harmon, CRITFC, pers. comm), or from an online genetics repository database (<https://FishGen.net>).

Table 1. Collections of adult and juvenile upper Columbia River steelhead used for genetic monitoring and evaluation. Samples Total were the number of samples processed and Samples Final were the number of samples with at least 70% genotypic data that were included in the study.

Population	Category	Origin	Year spawned	Samples Total (n)	Samples Final (n)	
Wenatchee	Baseline	Natural	2007	74	71	
		Natural	2010	90	87	
	Contemporary	Natural	2017	53	53	
		Hatchery	2017	66	66	
		Natural	2018	67	67	
		Hatchery	2018	74	74	
	Total				424	418
	Methow/Wells/ Winthrop/Twisp	Baseline	Natural	1995	50	47
Natural			1997	54	54	
Hatchery			1997	48	48	
Hatchery			1998	48	46	
Contemporary		Natural	2017	139	83	
		Natural	2018	193	111	
		Hatchery	2017	183	147	
		Hatchery	2018	201	149	
Total				916	685	
Okanogan		Baseline	Natural	2007	50	50
	Natural		2008	50	48	
	Contemporary	Mixed	2017	27	27	
		Mixed	2018	60	60	
	Total				187	185

Samples and their genotypes were grouped together into collections to be analyzed as a unit (Analysis units, Table 2). Analysis units were organized based on population, origin, spawn year, and hatchery program. When appropriate, analysis units were combined and analyzed (noted below for those tests).

Table 2. Population, origin, and hatchery information for collections used in genetic analysis of Upper Columbia steelhead.

Analysis Unit/collection	WDFW code ¹	Population	Sub-Population	Origin ²	Hatchery	Hatchery Program	Sample Type
Wenatchee-Eastbank-natural-2007	06CX	Wenatchee	Wenatchee	N	NA	NA	Baseline
Wenatchee-Eastbank-natural-2010	10FD	Wenatchee	Wenatchee	N	NA	NA	Baseline
Wenatchee-Eastbank-natural-2017	16IQ	Wenatchee	Wenatchee	N	NA	NA	Contemporary
Wenatchee-Eastbank-natural-2018	16IQ	Wenatchee	Wenatchee	N	NA	NA	Contemporary
Wenatchee-Eastbank-hatchery-2017	17GK	Wenatchee	Wenatchee	H	Eastbank	Wenatchee	Contemporary
Wenatchee-Eastbank-hatchery-2018	17GK	Wenatchee	Wenatchee	H	Eastbank	Wenatchee	Contemporary
Methow-Wells-natural-1995	95AA, 95AB	Methow	Methow	N	NA	NA	Baseline
Methow-Wells-hatchery-1997	97AB	Methow	Methow	H	Wells	Wells	Baseline
Methow-Wells-natural-1997	97AC	Methow	Methow	N	NA	NA	Baseline
Methow-Wells-hatchery-1998	98AA	Methow	Wells Stock	H	Wells	Wells	Baseline
Methow-Twisp-natural-2017	17EK	Methow	Twisp	N	Wells	NA	Contemporary
Methow-Twisp-natural-2018	18FS	Methow	Twisp	N	Wells	NA	Contemporary
Methow-Winthrop-natural-2017	17EN	Methow	Methow	N	NA	NA	Contemporary
Methow-Winthrop-natural-2018	18FV, NA	Methow	Methow	N	NA	NA	Contemporary
Methow-Twisp-hatchery-2017	17EK, 17EL	Methow	Twisp	H	Wells	Twisp Conservation	Contemporary
Methow-Twisp-hatchery-2018	18FT	Methow	Twisp	H	Wells	Twisp Conservation.	Contemporary
Methow-Wells-hatchery-2017	NA	Methow	Methow	H	Wells	Methow Safety-Net	Contemporary
Methow-Wells-hatchery-2018	NA	Methow	Methow	H	Wells	Methow Safety-Net	Contemporary
Wells-Wells-hatchery-2017	NA	U. Columbia	Wells Stock	H	Wells	Columbia Safety-Net	Contemporary
Wells-Wells-hatchery-2018	NA	U. Columbia	Wells Stock	H	Wells	Columbia Safety-Net	Contemporary
Okanogan-Okanogan-natural-2007	07AR	Okanogan	Okanogan	N	NA	NA	Baseline
Okanogan-Okanogan-natural-2008	08CL	Okanogan	Okanogan	N	NA	NA	Baseline
Okanogan-Wells-hatchery-2017	NA	Okanogan	Okanogan/Wells	Unk	Wells	Okanogan	Contemporary
Okanogan-Wells-hatchery-2018	NA	Okanogan	Okanogan/Wells	Unk	Wells	Okanogan	Contemporary

¹ – Collections genotyped by CRITFC do not have a WDFW code.

² – “Unk” indicates unknown origin.

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

Data processing

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

Only neutral loci were used in further analysis. SNP marker designations, neutral or adaptive, were established by testing in multiple laboratories, including CRITFC and WDFW laboratories, during development of the SNP panel or by designation as adaptive by CRITFC for markers CRITFC ascertained (J. Stephenson – CRITFC, pers. comm.). Neutral loci were evaluated for missing data, deviations from Hardy-Weinberg expectations (HWE), and diversity. 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 exploratory analysis using Principal Component Analysis (PCA) on allele frequencies of collections and graphed the first two axes and separately calculated and graphed average allelic richness among all loci within a collection. To evaluate whether collections had different allele frequencies we statistically evaluated allele frequency similarity

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

Question 3, Genetic Distance – To estimate genetic distance among collections we calculated pairwise F_{ST} and 95% confidence intervals with the R package *hierfstat* using default parameters (Goudet 2005). F_{ST} estimates the genetic variance due to structure among collections. It ranges from 0 (no variance, i.e., no genetic distance) to 1 (all variation is among collections). 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 were not a representative sample 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 – The effective population size (N_e) of a population is an important metric for populations that roughly indicates the amount of within-population genetic variation that exists because genetic variation generally increases with the effective number of spawners. There is 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_e for each collection separately was estimated using the LDNE algorithms employed by the software NE ESTIMATOR (Do et al. 2014). Using this method with the available tissue collections, LDNE is estimating N_b , the effective number of breeders, rather than N_e ; N_b is a better metric for monitoring (Luikart et al. 2021). Because subject hatchery programs are integrated programs or safety-net programs, hatchery- and natural-origin fish belong to the same population. Thus, we also estimated N_b with the contemporary hatchery- and natural-origin components combined for each of the two years

of samples. Loci with very low minor allele frequencies (MAF; in particular, loci where only one copy of the minor allele exists) cause an upward bias in N_b estimates using LDNE (Waples and Do 2008). Inclusion or exclusion of such loci is accomplished by setting a MAF critical value. Because of variable sample sizes and missing data, problem loci have different MAFs. To choose a critical value, for several collections we evaluated the MAF and counted the number of loci that would be dropped at various critical values. Setting the critical value at 0.02 eliminated all or nearly all problem loci, whereas significantly higher numbers of loci that had higher MAFs were dropped when the critical value was set at 0.05. Thus, we report results based on the critical value of 0.02. We report the jack-knife 95% confidence interval (CI) for each collection. Statistical significance of comparisons was evaluated by overlapping CIs. All previous generations impact N_b estimates to some degree and N_b estimates may be biased due to overlapping generations (Waples et al. 2014). To calculate unbiased N_b/N ratios, we estimated the impacts of multiple generations of influence and corrected bias due to overlapping generations (Waples et al. 2014; *c.f.*, Waters et al. 2015) using escapement estimates for as many spawn years prior to the spawn years of our collections as were available in the WDFW SCoRE database (<https://fortress.wa.gov/dfw/score/score/>). To calculate expected bias, we assumed a 6-year maximum life span with youngest age at maturity of 3-years old.

Results

Sample collections

Table 1 lists sample sizes summarized by population and origin; Table 2 lists sample sizes analyzed by collection. One hundred fifty-eight of 164 Wenatchee natural-origin baseline samples from spawn years 2007 and 2010 were successfully genotyped and used for analysis. Contemporary Wenatchee collections consisted of 260 hatchery- and natural-origin contemporary samples from spawn years 2017 and 2018. Baseline Methow collections consisted of 200 hatchery- and natural-origin samples from spawn years 1995, 1997, and 1998. Genotypes were successfully obtained from 195. Methow contemporary collections consisted of 716 samples from hatchery- and natural-origin fish, from which 490 were randomly selected for further analysis. Baseline Okanogan collections consisted of 100 samples from natural-origin smolts from sample years 2007 and 2008. Ninety-eight were available for further analysis. Contemporary Okanogan collections taken in the Okanogan sub-basin, mainly Omak Creek, consisted of 87 samples of unknown-origin adults from spawn years 2017 and 2018. All were used in further analysis. All contemporary samples came from fish that had been used as broodstock for the steelhead hatchery programs.

Evaluation of loci

Of 384 SNP loci amplified, 129 were identified as adaptive markers and were removed from further analysis as were the three species ID SNPs and the sex ID SNP. Of 251 neutral loci, 239 were used in the final analysis. Removed loci included invariant loci ($n=1$), loci with too much missing data ($n=7$), and loci with excess deviations from Hardy-Weinberg equilibrium ($n=4$).

Data analysis

Allele frequencies – Question 7.1.1 and 7.1.2

PCA based on allele frequencies of steelhead populations of the UCR ESU showed some structure, primarily between Wenatchee and Methow steelhead (Figure 1), which was entirely due to family structure in contemporary hatchery collections (Figure 2). Based on the number of fixed loci (i.e., only a single allele present) and allelic richness, contemporary collections in all three populations had lower diversity than their baseline counterparts. Wenatchee and Okanogan steelhead had more fixed loci than Methow steelhead (Table 3). Baseline collections in all three populations had fewer fixed loci (more allelic diversity) than their contemporary counterparts, and although one contemporary Methow collection had the most recorded fixed loci (2017 Twisp hatchery, $n = 22$ fixed loci) the average difference between baseline and contemporary was much lower in the Methow. Allelic richness of contemporary collections was slightly lower than baseline, but that difference was mostly driven by lower allelic richness of contemporary hatchery collections (average N_A natural = 1.81, average N_A hatchery = 1.79; Table 3). Pairwise AMOVA based on allele frequencies among collections within populations showed contemporary collections had less diversity than baseline collections, and most hatchery-origin collections had less diversity than natural-origin collections (not shown). Observed and expected heterozygosity were similar among baseline and contemporary collections in all populations and among hatchery-origin and natural-origin collections (Table 3). Based on pairwise comparisons of expected heterozygosity among collections within populations, no general pattern was detected (not shown). No significant difference in average expected heterozygosity was detected among baseline and contemporary collections in Wenatchee steelhead. In Okanogan steelhead, the 2008 natural collection had higher heterozygosity than the 2018 contemporary collection, but no other pairwise comparison was statistically significant. In Methow steelhead, most pairwise comparisons were not statistically significant. Among those pairwise tests that were significant, expected heterozygosity of natural-origin collections was higher than that of hatchery-origin collections, but there was no pattern regarding baseline vs. contemporary.

Table 3. Genetic summary statistics for upper Columbia River steelhead.

Analysis Unit	N		Avg Rich	Het obs	Het exp	Avg % HWE % Pair LD			$\widehat{N}b^a$	95% CI		$\widehat{N}b/\widehat{N}^b$
	Sample N	Fixed loci				F_{IS}	$p < 0.05$	$p < 0.05$		Jackknife	on samples	
Wenatchee-Eastbank-natural-2007	71	7	1.82	0.277	0.279	0.274	3.93	4.44	430.8	238.6	1786.9	0.153
Wenatchee-Eastbank-natural-2010	87	11	1.81	0.283	0.278	0.291	5.24	5.04	356.2	199.6	1271.2	0.148
Wenatchee-Eastbank-natural-2017	53	18	1.79	0.266	0.273	0.265	4.80	4.19	531.4	254.7	Infinite	0.244
Wenatchee-Eastbank-natural-2018	67	15	1.81	0.274	0.280	0.274	7.42	4.20	600	338.3	2256.5	0.386
Wenatchee-Eastbank-hatchery-2017	66	12	1.80	0.276	0.281	0.276	11.35	9.31	39	27.8	57.7	0.287
Wenatchee-Eastbank-hatchery-2018	74	13	1.78	0.284	0.277	0.283	8.73	14.22	18	14.2	22.9	0.132
Methow-Wells-natural-1995	47	8	1.81	0.269	0.279	0.269	5.24	3.62	746.1	215.6	Infinite	0.807
Methow-Wells-hatchery-1997	48	5	1.82	0.277	0.282	0.277	7.42	4.32	154.2	83.6	612.4	0.066
Methow-Wells-natural-1997	54	12	1.81	0.279	0.279	0.279	4.37	3.95	639.3	252	Infinite	0.396
Methow-Wells-hatchery-1998	46	9	1.80	0.276	0.281	0.276	4.37	4.18	218.2	126.1	671.2	0.181
Methow-Twisp-natural-2017	33	14	1.81	0.275	0.279	0.275	4.80	3.33	794.7	103.1	Infinite	2.114
Methow-Twisp-natural-2018	61	13	1.81	0.265	0.277	0.265	9.17	5.11	149.7	87.7	396.6	0.474
Methow-Winthrop-natural-2017	50	6	1.82	0.281	0.282	0.281	4.37	4.09	624.2	246.7	Infinite	0.236
Methow-Winthrop-natural-2018	50	6	1.80	0.274	0.279	0.274	5.24	3.93	1,030.1	439.4	Infinite	0.437
Methow-Twisp-hatchery-2017	56	22	1.76	0.271	0.264	0.271	11.35	13.63	13.1	8.6	19.5	0.546
Methow-Twisp-hatchery-2018	43	11	1.76	0.276	0.263	0.276	6.55	9.65	17.3	12.4	24.6	0.721
Methow-Wells-hatchery-2017	41	7	1.80	0.267	0.274	0.267	6.11	5.73	48.1	27.4	116.8	0.273
Methow-Wells-hatchery-2018	56	10	1.79	0.269	0.272	0.269	6.99	6.62	54.4	34	104	0.309
Wells-Wells-hatchery-2017	50	9	1.80	0.272	0.278	0.272	5.68	4.86	139.4	83.9	341.8	0.792
Wells-Wells-hatchery-2018	50	8	1.80	0.276	0.277	0.276	5.24	4.54	170.8	98.3	504.7	0.970
Okanogan-Okanogan-natural-2007	50	9	1.81	0.267	0.277	0.267	7.42	6.41	40.7	28.4	63.7	0.018
Okanogan-Okanogan-natural-2008	48	8	1.81	0.281	0.282	0.281	4.80	4.89	116.7	73.1	251.3	0.069
Okanogan-Wells-hatchery-2017	27	16	1.80	0.264	0.275	0.264	5.68	3.55	126	64.7	920.6	0.067
Okanogan-Wells-hatchery-2018	60	18	1.76	0.271	0.268	0.271	7.86	8.12	36.7	24.3	60.6	0.041

^a – N_b estimated using LDNE

^b – Estimated census steelhead spawner abundance

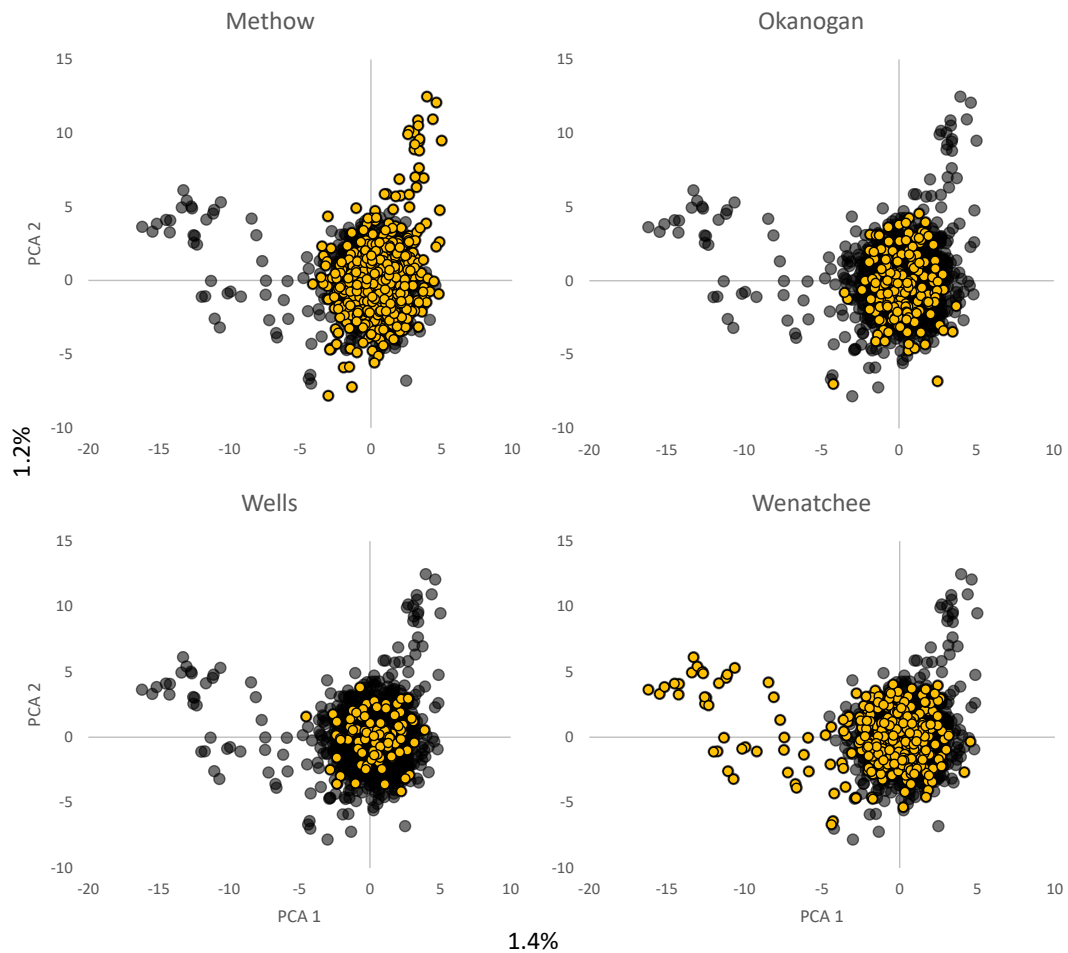


Figure 1. Graph of the first two axes of Principal Components Analysis (PCA) of upper Columbia River steelhead allele frequencies. Two of three loci that were in linkage disequilibrium in most collections were removed to produce these results. All graphs are the same data, but with the groups named above each graph highlighted. There is no apparent structure except within Methow and Wenatchee collections, which was entirely due to family structure within the contemporary hatchery-origin collections.

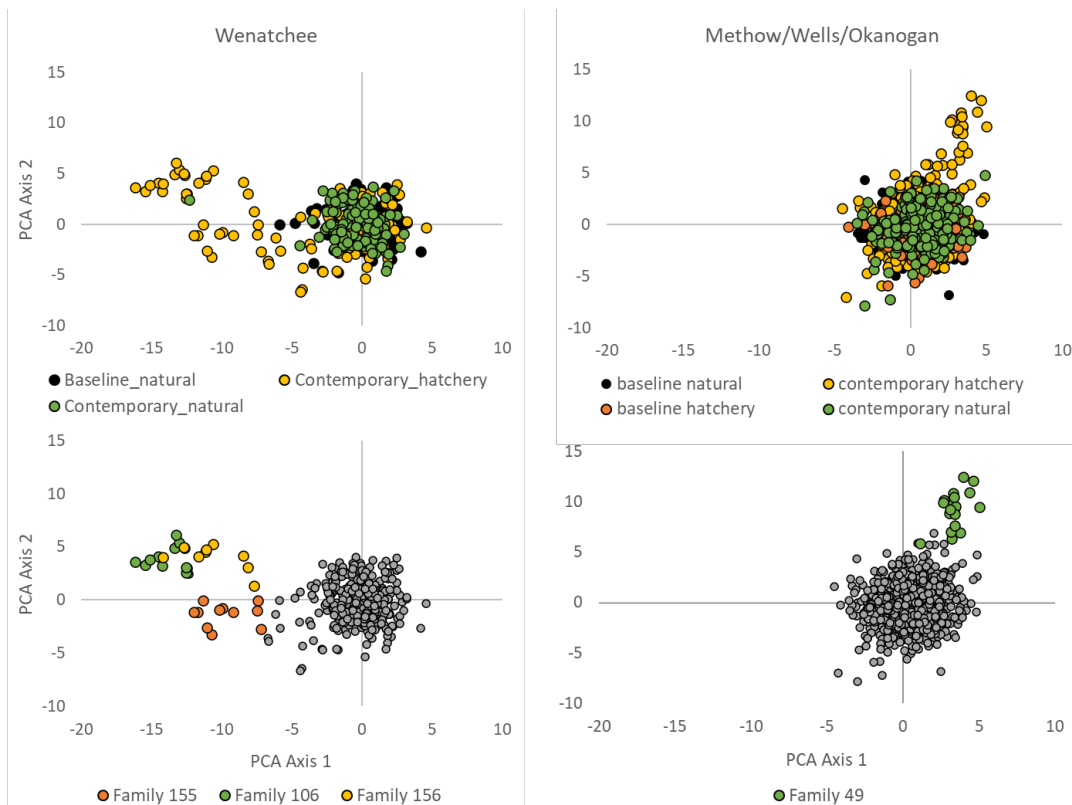


Figure 2. Graph of the first two axes of Principal Components Analysis (PCA) of upper Columbia River steelhead. The data are the same as in Figure 1 but focused on Wenatchee steelhead (left) and Methow/Wells/Okanogan steelhead (right). The top and bottom graphs are the same data, but with different groups highlighted. In the top graph, baseline and contemporary hatchery- and natural-origin groups are highlighted. Apparent structure was entirely due to family structure within the contemporary hatchery-origin collections. The bottom graphs highlight some of the full-sibling families that were identified by sibship analysis using COLONY v2.0.6.6. Additional family structure was also obvious in graphs of PCA axes 3 and 4 (not shown). These graphs also apparently identify an individual Wenatchee steelhead that was identified in the field as natural-origin but based on PCA and sibship analysis is likely a member of one of the hatchery-origin full-sibling families (the green point among the yellow in the upper left graph, gray among the green in the lower left graph).

Linkage Disequilibrium – Question 7.2.1 and 7.2.2

Stronger linkage disequilibrium existed within hatchery-origin collections than within natural-origin collections (natural collections average $r^2 = 0.022$, hatchery collections average $r^2 = 0.029$), especially the contemporary hatchery-origin collections (average $r^2 = 0.03$, max $r^2 = 0.043$). This was also reflected in the frequency of significant probability tests, with many more significant pairwise tests of LD among loci in contemporary hatchery-origin collections (Table 3). Most pairwise comparisons of the amount of LD per collection were statistically significant (Mann-Whitney tests of the distribution of P values; results not shown). In Wenatchee steelhead, the amount of LD was different among all collections. In Okanogan steelhead, the baseline 2008 collection had similar LD as the 2018 contemporary collection, but all other pairwise

comparisons were significantly different. In Methow steelhead, three of four baseline collections were not different from one another or from the 2018 Wells hatchery collection. The 1997 baseline natural-origin collection was different from the other baseline collections, but not from the 2018 Winthrop natural-origin collection. All other pairwise comparisons were significantly different.

Genetic Distance – Question 7.3.1

Genetic structure among populations of Upper Columbia River ESU steelhead was evident (Figure 3). Genetic distance, as estimated by F_{ST} , was greater between Wenatchee steelhead and Methow and Okanogan steelhead (average F_{ST} s = 0.013 and 0.015, respectively) than between Methow and Okanogan steelhead (average F_{ST} = 0.009) and was greater than the genetic distance among collections within populations (average F_{ST} = 0.009, 0.007, and 0.008 for Wenatchee, Methow, and Okanogan respectively). Within and among collections, the largest F_{ST} s were those found when comparing hatchery-origin collections to any other collections. The largest F_{ST} (i.e., greatest genetic distance, F_{ST} = 0.045) was found between the 2018 Wenatchee hatchery-origin collection and the 2018 Twisp hatchery-origin collection (Figure 3).

Within the Wenatchee population, contemporary hatchery-origin adults were genetically different from baseline and contemporary natural-origin adults. Baseline collections were not significantly different from one another nor were they significantly different from almost all contemporary natural-origin collections. Contemporary hatchery-origin collections were significantly different from one another and from all other collections. Genetic distance of the 2018 hatchery-origin collection was an order of magnitude larger than distances among other Wenatchee collections (average F_{ST} = 0.021 vs 0.002). Within the Methow population, genetic distances among collections were generally small, averaging less than 1%. Pairwise genetic distances of contemporary Twisp hatchery-origin steelhead to any other Methow steelhead collection were the highest observed in the Methow, averaging 2%. Genetic distances of baseline and contemporary Okanogan collections were small (1% or less), but statistically significant. As with the Wenatchee and Methow populations, the largest genetic distances were seen in pairwise comparisons of the 2018 contemporary hatchery-origin collection with the other Okanogan collections, but were roughly half that seen in the Methow and Wenatchee (average F_{ST} = 0.011).

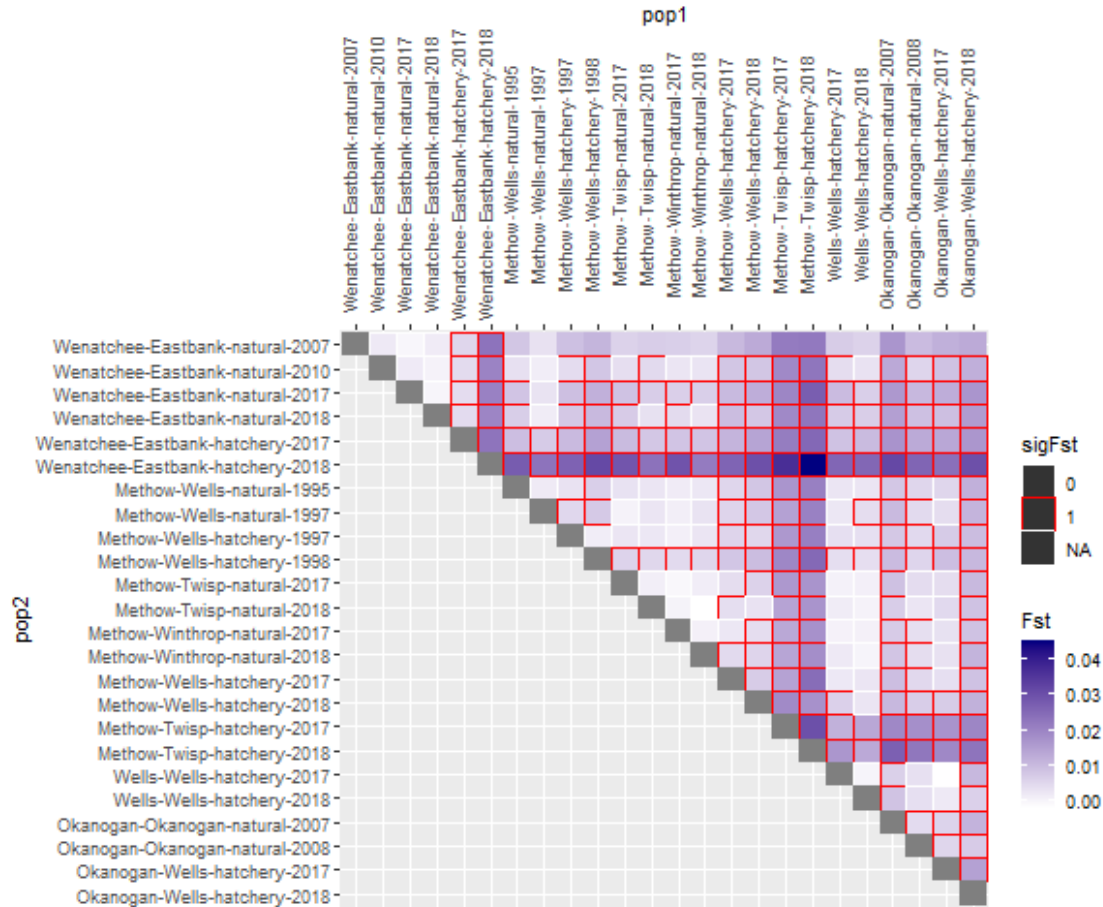


Figure 3. Heatmap of pairwise F_{ST} values for upper Columbia River steelhead. 95% confidence intervals were estimated. Those F_{ST} estimates whose 95% confidence intervals lower bound was larger than zero were deemed significantly different from zero and are shown with red outline (1 = significant), F_{ST} estimates not different than zero have a white outline (0 = not significant). The largest F_{ST} s (dark blue) were found in comparisons with the 2018 Wenatchee hatchery-origin fish and with 2017 and 2018 Twisp hatchery-origin fish. This was likely entirely due to genetic drift, of which hatchery programs are particularly susceptible due to the small number of broodstock spawned.

Effective Population Size (N_e) – Question 7.4.1

Estimates of N_b for Wenatchee and Methow steelhead baseline and contemporary natural-origin collections were similar to one another, and all had overlapping 95% confidence intervals (Figure 4 and Figure 5, left panels). Baseline Methow hatchery-origin collections and the 2018 Twisp natural-origin collection all had much lower N_b estimates, but confidence intervals overlapped those of the baseline and contemporary natural-origin collections (Figure 5). Contemporary Wenatchee and Methow hatchery-origin collections had very low estimates of N_b ; Wenatchee hatchery-origin estimates were significantly different from those of baseline and contemporary natural-origin collections. In the Methow, Twisp contemporary hatchery-origin N_b estimates were significantly different from all other N_b estimates, Methow contemporary hatchery-origin N_b estimates were significantly less than the baseline natural-origin collections,

and Wells contemporary hatchery-origin N_b estimates were low, but overlapped baseline and contemporary natural-origin confidence intervals (Figure 5). Combined Wenatchee hatchery- and natural-origin contemporary collections had low estimates of N_b , but only the 2018 contemporary N_b estimate was significantly lower than the baseline estimates (Figure 4). Combined Methow hatchery- and natural-origin contemporary collections had low estimates of N_b ; both were significantly lower than baseline natural-origin collections, but overlapped baseline and contemporary hatchery-origin collections (Figure 5). Okanogan N_b estimates were all similar, though the 2007 baseline collection and the 2018 contemporary collection were the smallest and were significantly different from the 2008 baseline and 2017 contemporary collection (Figure 6).

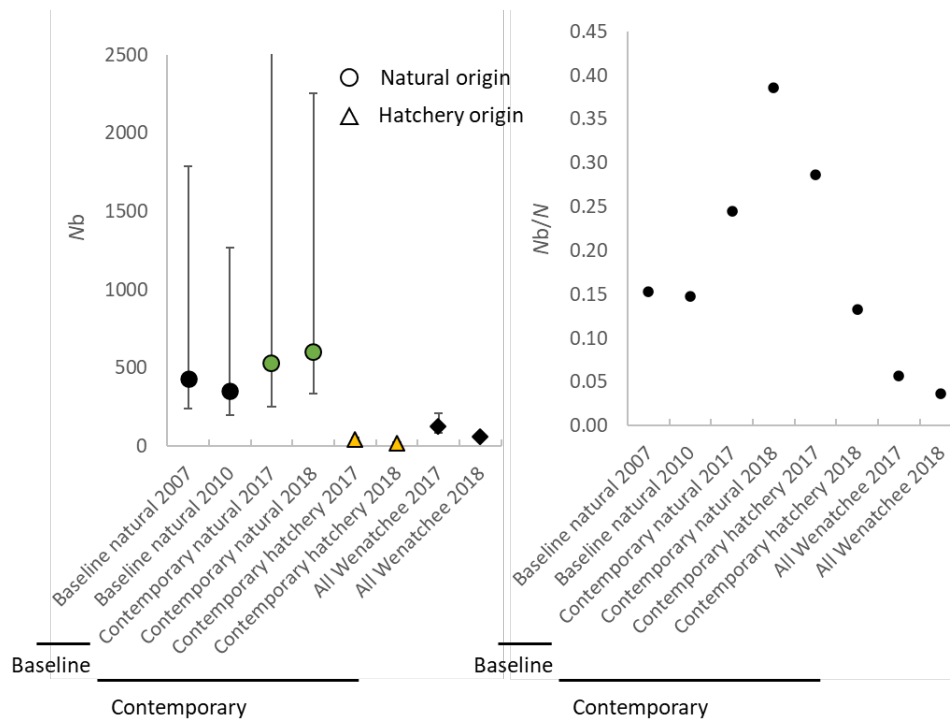


Figure 4. Estimated effective number of breeders (N_b ; left) and ratio of N_b to abundance (N_b/N ; right) for Wenatchee steelhead baseline and contemporary collections. Because hatchery programs are integrated, contemporary hatchery- and natural-origin collections were combined for a total population estimate (far right of each graph; diamonds on left graph are hatchery and natural combined). Baseline and contemporary natural-origin collections showed much higher estimates of N_b than contemporary hatchery-origin collections (left). No clear pattern in baseline N_b/N ratios compared to contemporary was evident (right). However, combined contemporary hatchery- and natural-origin collections were lower than baseline (right, far right data points). Error bars extending past the graph boundary were infinite indicating not enough linkage disequilibrium existed to estimate the upper bound, i.e., N_b was large. N_b was estimated using LDNE (Do et al. 2014). Abundance was escapement estimates of hatchery- and natural-origin fish as found in the WDFW SCoRE database. Since N_b estimates refer to parental generations, abundance from one generation prior was used assuming 5-year generation for natural-origin and 4-year generation for hatchery-origin.

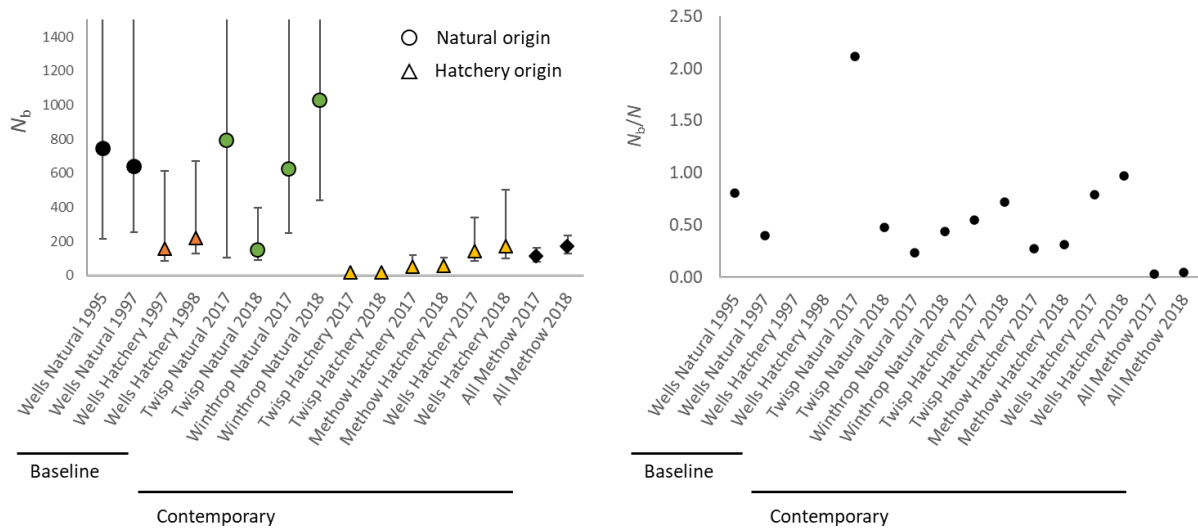


Figure 5. Estimated effective number of breeders (N_b ; left) and ratio of N_b to abundance (N_b/N ; right) for Methow/Wells steelhead baseline and contemporary collections. Because hatchery programs are integrated, contemporary hatchery- and natural-origin collections were combined for a total population estimate (far right of each graph; diamonds on left graph are hatchery and natural combined). Baseline and contemporary natural-origin collections showed much higher estimates of N_b than contemporary hatchery-origin collections (left). No clear pattern in baseline N_b/N ratios compared to contemporary was evident (right). However, combined contemporary hatchery- and natural-origin collections were lower than baseline (right, far right data points). Error bars extending past the graph boundary were infinite indicating not enough linkage disequilibrium existed to estimate the upper bound, i.e., N_b was large. N_b was estimated using LDNE (Do et al. 2014). Abundance was escapement estimates of hatchery- and natural-origin fish as found in the WDFW SCoRE database. Since N_b estimates refer to parental generations, abundance from one generation prior was used assuming 4-year generation for natural-origin and 3-year generation for hatchery-origin.

Wenatchee contemporary natural-origin collection N_b/N ratios were higher than baseline and those of contemporary hatchery-origin collections were comparable to baseline, but combined hatchery- and natural-origin contemporary collections were lower than all others (Figure 4, right panel). Methow baseline and contemporary N_b/N estimates were variable, but comparable (Figure 5, right panel). Natural-origin collection N_b/N estimates were typically, but not always, higher than those of hatchery-origin collections. The Twisp contemporary natural-origin 2017 collection was more than twice as high as all other estimates. As with Wenatchee steelhead, combined contemporary Methow collections had the lowest N_b/N ratios. Okanogan N_b/N estimates followed the same pattern as the N_b estimates with the 2007 baseline and 2018 collections having lower estimates than the 2008 baseline and 2017 contemporary collections (Figure 6). Notably, Okanogan steelhead N_b/N ratios were all quite low, similar to the combined contemporary Wenatchee and Methow estimates.

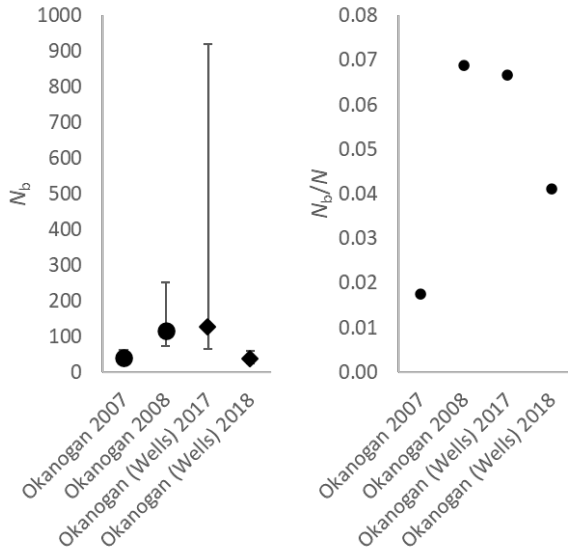


Figure 6. Estimated effective number of breeders (N_b ; left) and ratio of N_b to abundance (N_b/N ; right) for Okanogan steelhead baseline and contemporary collections. No individual origin data was available for the contemporary Okanogan samples. Because hatchery programs are integrated, these likely represent a combined hatchery- and natural-origin collection (diamonds). Baseline 2007 and contemporary 2018 N_b estimates were less than the baseline 2008 and contemporary 2017 estimates (left) and that same general trend was found in the N_b/N ratios (right). However, estimates for both baseline estimates were likely biased high due to the removal of full-sibling family members prior to genotyping. Thus, contemporary estimates of N_b were likely higher than baseline. Error bars extending past the graph boundary were infinite indicating not enough linkage disequilibrium existed to estimate the upper bound, i.e., N_b was large. N_b was estimated using LDNE (Do et al. 2014). Abundance was escapement estimates of hatchery- and natural-origin fish as found in the WDFW SCoRE database. Since N_b estimates refer to parental generations, abundance from one generation prior was used assuming 4-year generation for natural-origin and 3-year generation for hatchery-origin.

Discussion

To evaluate genetic impacts of upper Columbia River steelhead hatchery programs on the steelhead populations in the UCR ESU, we compared genetic data from baseline and contemporary natural- and hatchery-origin collections, evaluated genetic metrics, and, when appropriate, compared those findings to the previous genetic evaluations (Blankenship et al. 2008; Seamons et al. 2012). Contemporary hatchery-origin collections had lower allelic richness and allele frequencies, higher levels of linkage disequilibrium, and lower estimates of N_b than baseline collections. In addition, contemporary hatchery-origin collections were genetically distant from natural-origin baseline and contemporary collections. This pattern is likely mostly due to the low number of steelhead used as broodstock in upper Columbia River steelhead hatchery programs and a high proportion of hatchery produced spawners on the spawning grounds. Paired with higher egg-to-smolt survival than natural-origin fish, low broodstock numbers reduce diversity due to Ryman-Laikre effects (Ryman and Laikre 1991). This greatly depresses the effective size of the overall population as seen in Figure 4. These results are

similar to previous monitoring results, to the degree that they can be directly compared. These results run counter to long-term conservation goals and may impact the long-term viability of these populations.

Contemporary hatchery-origin collections showed significantly higher levels of genetic drift. Average pairwise F_{ST} estimates for most contemporary hatchery-origin collections were up to four times higher than those of other collections, N_b and N_b/N ratios for the same collections were the lowest of all estimates, and contemporary hatchery-origin collections showed high levels of family structure (Figure 1, lower). These results are remarkably similar to those found in a study of Hood River steelhead (Christie et al. 2012) and to a lesser degree the previous evaluations of upper Columbia steelhead (Blankenship et al. 2008; Seamons et al. 2012). The exception to this pattern was the Wells program. The Wells program may draw broodstock from all hatchery populations upstream (Twisp, Winthrop, and Okanogan), and, unintentionally, possibly downstream of Wells Dam (Wenatchee and Ringold). Almost all 2018 Wenatchee hatchery-origin fish were age 3, coming from brood year 2015. Though age data for other collections were unavailable at the time of writing, this was highly likely to have occurred in all three populations. While hatchery production of steelhead tends to result in decreased life history diversity, hatchery returns typically have at least two age classes, which reduce the rate of loss of genetic diversity due to drift. Fish produced in 2014 were subject to poor smolt-to-adult survival, due to impacts of low, warm water during outmigration and poor ocean conditions (a.k.a., the blob; Bond et al. 2015; Hillman et al. 2020a) essentially eliminating a cohort and dramatically reducing life-history diversity even further and subjecting the population to increased risk of genetic drift.

Hatchery-origin collections had higher levels of LD than did natural-origin collections, a pattern evident but unreported in an earlier evaluation of Methow Basin steelhead (Table 1 of Blankenship et al. 2008; LD was not evaluated in previous analysis of Wenatchee steelhead Seamons et al. 2012). Steelhead hatchery programs are relatively small; when coupled with variability in survival among families the number of families represented in returning adult offspring is very small compared to naturally spawning populations, even with overlapping generations (McLean et al. 2008; Naish et al. 2013). Mann-Whitney tests showed significant differences among most pairwise comparisons of collections within population in the amount of linkage disequilibrium, which was not informative. This was likely a statistical power issue; with 239 SNP loci we had sufficient power to detect small differences between collections. Small differences may not be of conservation concern. In the future, different methods of comparing LD may need to be evaluated to provide findings that are useful for conservation purposes.

Estimates of N_b for Wenatchee baseline collections were similar to previous estimates using the same samples but different genetic markers (Seamons et al. 2012). However, N_b/N ratios were quite different because of using different estimates of abundance. Methow baseline natural-origin N_b estimates were similar to the previously estimated Methow steelhead N_b estimate ($N_b \sim 370$; Blankenship et al. 2008), but direct comparison is difficult due to different markers and methods being used to generate that estimate. Okanogan steelhead N_b and N_b/N were among the lowest estimated in the upper Columbia River. This could occur if abundance is chronically low or a bottleneck occurred in the populations, or both. However, census

abundance estimates are similar in magnitude to those of the Wenatchee steelhead populations and no evidence of a severe bottleneck exists in the available abundance data. Nevertheless, the naturally produced population in the Okanogan Basin has been chronically low and most spawners are of hatchery-origin. Omak Creek smolt-trap samples showed high levels of relatedness among individuals, likely a reflection of the low spawner numbers. Thus, Okanogan estimates of N_b are likely biased high, and thus the N_b/N ratios even lower, due to the removal of most related individuals prior to genotyping and analysis (Waples and Anderson 2017). It is well known that rainbow trout produce migratory offspring and steelhead produce non-migratory offspring (Kendall et al. 2015), so rainbow trout are genetically part of the same population as the steelhead. Thus, N_b estimates include the genetic contribution of rainbow trout, and, while informative, ratios of N_b/N for natural-origin collections from all three populations are likely biased high due to the exclusion of non-anadromous rainbow trout from census abundance estimates. The amount of bias is unknown and rainbow trout numbers could vary among populations, so the amount of bias for each population could be different.

Hatchery-origin collections had much lower N_b estimates than natural-origin collections and this low N_b reduced the N_b/N ratio in the entire population, which was not unexpected due to the nature of demographic and genetic trade-offs associated with hatchery programs (Bingham et al. 2014; Christie et al. 2012; McLean et al. 2008; Perrier et al. 2016; Small et al. 2014). Several factors may influence the N_b of the hatchery-origin fish. Small hatchery programs will always be challenged with low estimates of N_b , regardless of which fish are selected for broodstock or how they are spawned. For example, in the previous evaluation of Wenatchee steelhead, Seamons et al. (2012) showed a decline in the N_b of hatchery broodstock as the hatchery program transitioned from a larger composite broodstock to a smaller locally derived broodstock. However, there are techniques that can be used to maximize N_b for a given number of broodstock. How fish are chosen for broodstock and how they are mated may increase or significantly decrease N_b (Bartron et al. 2018; Fisch et al. 2015). Variance in reproductive success reduces N_b in hatchery populations (Christie et al. 2012; McLean et al. 2008). The impact of variance in reproductive success may be ameliorated by equalizing variance in family contributions from hatchery-origin fish. The logistically easiest way to equalize family contributions would be to equalize family size at the egg stage. Managing family size prior to release of juveniles from the hatchery would require rearing each family in a separate vessel, which is impractical. In addition, smolt-to-adult survival varies among families in hatchery fish (McLean et al. 2008). Equalizing family contributions at the returning adult stage would be more effective, but logistically difficult and expensive, requiring differential marking of families, for example by using parentage based tagging (PBT; Anderson and Garza 2005). PBT not only allows for high-precision identification of family membership, but also could aid in identifying unmarked hatchery-origin fish, such as the suspected fish in Figure 2 (Hargrove et al. 2021). Management of hatchery programs to achieve genetic and demographic goals requires addressing opposing strategies and logistical constraints.

A high proportion of hatchery-origin fish on the spawning grounds (pHOS) can dramatically reduce the N_b of the entire (hatchery and wild) population through the Ryman-Laikre Effect (Christie et al. 2012; Hagen et al. 2020; Ryman and Laikre 1991). Christie et al. (2012) found that reduction in N_b was most pronounced when pHOS, was > 0.10 . Reducing pHOS could help reduce impacts from hatchery fish. Indeed, ESA consultations require

managers to help control pHOS in order to achieve target Proportionate Natural Influence (PNI) values, including removing hatchery fish at weirs and dams and mandatory retention of hatchery-origin fish during recreational fisheries (NMFS 2017). However, removal of hatchery-origin fish reduces the intended positive demographic impact on the naturally spawning population. Sufficient removal of hatchery-origin spawners to achieve low pHOS goals in most systems is very difficult, so systems typically have hatchery-origin spawner escapement that exceeds that required to meet the PNI target (Hillman et al. 2020a; Snow et al. 2020; see also PNI chapter of this report).

Hatcheries can alter among-population genetic structure, and though the monitoring plan did not specifically call for evaluating among-population structure, we were able to evaluate it. In the upper Columbia, beginning in 1939 as part of the Grand Coulee Fish Maintenance Program, hatchery broodstock were once collected in traps at mainstem Columbia River dams, spawned, and were spread throughout all three populations, promoting genetic homogenization. Broodstock for Wenatchee steelhead have been collected in the Wenatchee River since 1998 and baseline collections for this study were specifically chosen to reflect the current broodstock selection protocols. Similarly, the broodstock for the Okanogan program has changed to collect only fish from the Okanogan sub-basin (though protocols allow for filling in with fish captured at Wells Dam, which could be from any population upstream). Straying of hatchery-origin fish has likely genetically homogenized some tributary populations, particularly those that are small and adjacent to large hatchery programs (see recipient population stray chapter of this report). For example, both the Entiat and Okanogan steelhead populations had recipient stray rates that exceeded 15%. Unfortunately, Entiat steelhead were not included in the current genetic analysis to directly evaluate their genetic attributes. Our F_{ST} results suggest that some genetic structure currently exists among the three populations; within the Wenatchee average F_{ST} s are less than average F_{ST} comparisons to Methow and Okanogan steelhead (Figure 3), likely a result of genetic drift and a lack of straying. Pearsons and O'Connor (2020) measured donor stray rates (rate of fish originating in a population that stray to a different location) of natural-origin steelhead in the UCR ESU. Donor stray rates among basins was very low; most movement was within basin and from downstream to upstream locations. Straying only impacts among-population diversity if strays successfully interbreed with the recipient population (effective strays). Recipient stray rates and effective stray rates for UCR ESU NOR steelhead are unknown, but likely low at the population level. Effective stray rates are likely lower than estimated recipient stray rates due to local adaptation reducing the reproductive success of stray fish, which may also drive divergence. Here, however, we used putatively neutral markers, so the divergence we observed is likely due to random changes in allele frequencies, i.e., genetic drift. Hatcheries, however, eliminate or minimize the impacts of local adaptation by making all broodstock successful. Straying of natural-origin fish or unmarked hatchery-origin fish into hatchery broodstocks is unknown. For a more complete understanding of genetic structure, future monitoring could explicitly include evaluation of among-population genetic structure and monitor the use of strays in hatchery broodstock.

Domestication represents a significant genetic risk to wild populations that we have not addressed in our analysis. Currently, relative reproductive success studies (i.e., comparing the spawning success of hatchery- and natural-origin fish spawning in the wild) are used to infer impacts of domestication. Two such studies in upper Columbia River steelhead have been

published (Wenatchee steelhead; Ford et al. 2016) or are ongoing (Twisp steelhead; Douglas PUD and WDFW unpublished). Similar to the well-known Hood River study of steelhead relative reproductive success (Araki et al. 2007), Ford et al. (2016) found that Wenatchee hatchery-origin steelhead had reduced reproductive success when spawning naturally compared to their natural-origin counterparts. Ongoing Twisp steelhead studies are finding similar results (B. Goodman WDFW, personal communication). Thus, domestication impacts, in addition to reductions in diversity, represent a significant concern for viability of upper Columbia River steelhead.

The monitoring plan and the current implementation of the monitoring plan have limitations, but we are not aware of any other large-scale monitoring of hatchery genetic effects on natural populations that has been developed or implemented. The monitoring plan has been extensively reviewed by science and genetic experts (e.g., ISAB and genetic expert panel) and has been adapted based on evaluation of reviews. One of the challenges associated with long-term genetic monitoring is changes in genetic techniques. Over the years, upper Columbia hatchery evaluations have utilized allozyme, microsatellite, and SNP markers making direct comparisons of results problematic. Adding larger sample sizes to the M&E program may be appropriate when final analyses or specific issues need resolution, but interim evaluations may not need such level of precision, particularly if new and more powerful techniques are available for future monitoring work. The monitoring plan lacks monitoring of adaptive genetic diversity that utilize genetic techniques. SNP markers associated with adaptive traits have been discovered and developed (e.g., run-timing, Hess et al. 2016; Micheletti et al. 2018; anadromy/residency, Pearse et al. 2014) and could be used to evaluate the impacts of hatchery propagation on allele frequencies at these markers. Surprisingly, instead of having polygenic associations with important traits, some of these adaptive traits are associated with single gene regions with only a few variant alleles (Ford et al. 2020). Under this simpler system, variability can be rapidly lost from a population. Monitoring allele frequencies of these few available marker-trait associations may be important for those traits but also would serve as model data for other undiscovered marker-trait associations that may have a similar genetic architecture. The full PUD monitoring and evaluation plan includes many additional metrics that help evaluate adaptive traits (see other chapters in this report), including straying, productivity, age at maturity, size at age, run and spawn time, spawn distribution, and PNI. Evaluating genetic and other metrics together would provide the most comprehensive means of evaluating the hatchery programs, but it is unclear how additional metrics would influence adaptive management decisions.

This evaluation should be considered within the larger context of the long-term monitoring and evaluation plan. This evaluation was the second timestep of the monitoring plan following initial baseline sampling (i.e., a total of 3 collection times representing multiple brood years) and represented a large effort in genotyping and analysis to characterize patterns of genetic variation in hatchery- and natural-origin samples from different time points. Future assessments will occur at 10-year intervals and will result in an increase of brood years included (i.e., evaluations in 2031, 2041, 2051). Definitive conclusions may not be possible with work done each timestep, but cumulative assessments should provide useful information to adaptively manage the hatchery programs. One of the biggest challenges of this evaluation, and for future evaluations, was how to compare data and findings from the previous evaluations that used

different genetic and analytical techniques. We reprocessed baseline samples using current genetic markers so that we could make direct comparisons to baseline collections, but even so, we were able to compare results of only a subset of data and findings from the last evaluation. Future work would benefit by developing standardized approaches that would facilitate comparisons across timesteps. Toward that end, analyses used here were developed within R scripts that make transparent the methods used and which easily accommodate future analyses. Another improvement would be to evaluate the sample sizes, cohorts, and timesteps necessary to detect genetic changes of interest to managers. The sample sizes and cohorts used in this evaluation were chosen by considering standard genetic sample sizes and inclusion of the most recent cohorts to provide maximum contrast while minimizing cost. For example, early detection of any future negative trends in N_b would allow for changes to be made to hatchery programs preventing further decline. This might be particularly important if census sizes, which are monitored annually, decrease substantially. The power to detect declines in N_b is in part determined by the number of cohorts analyzed (Luikart et al. 2021). They found that the power to detect a declining trend in N_b nearly doubled when the number of consecutive cohorts analyzed went from five to ten. Power also increased, up to a point, when the number of samples and loci used increased. Having this kind of analysis for all metrics of interest would be extremely valuable. However, the benefits of such an analysis will be limited if genetic methods and markers continue to substantially change between timesteps.

Summary – The generally small size of the steelhead hatchery programs appears to have resulted in lower allelic richness and allele frequencies, higher levels of linkage disequilibrium, reduced N_b , and divergence of hatchery-origin collections from baseline and contemporary collections. Genetic drift is likely occurring at a higher rate in the hatchery programs than in the natural populations. Management for increased abundance and PNI goals may exacerbate these shifts by removing natural-origin adults from the spawning grounds for use as broodstock, releasing numbers of juvenile fish that annually exceed pHOS targets upon returning as adults, and use of already small broodstock populations. Goals of the programs should be revised and clearly stated, and management strategies structured to meet these updated program goals.

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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
OmyY1_2SEXY	Sex ID	X	Y	(Brunelli et al. 2008)
Ocl_gshpx-357	species ID	G	T	(Campbell et al. 2009)
Omy_Omyclmk438-96	species ID	A	C	(Sprowles et al. 2006)
Omy_myclarp404-111	species ID	T	G	Campbell - unpubl.
M09AAC.055	Neutral	C	T	WDFW - S. Young unpubl.
M09AAD.076	Neutral	T	C	WDFW - S. Young unpubl.
M09AAE.082	Neutral	T	G	WDFW - S. Young unpubl.
M09AAJ.163	Neutral	T	C	WDFW - S. Young unpubl.
OMGH1PROM1-SNP1	Neutral	A	T	(Abadía-Cardoso et al. 2011)
OMS00002	Neutral	T	C	(Sánchez et al. 2009)
OMS00003	Neutral	T	G	(Sánchez et al. 2009)
OMS00006	Neutral	T	C	(Sánchez et al. 2009)
OMS00008	Neutral	T	C	(Sánchez et al. 2009)
OMS00013	Neutral	A	G	(Sánchez et al. 2009)
OMS00014	Neutral	T	C	(Sánchez et al. 2009)
OMS00015	Neutral	A	T	(Sánchez et al. 2009)
OMS00017	Neutral	A	G	(Sánchez et al. 2009)
OMS00018	Neutral	T	G	(Sánchez et al. 2009)
OMS00024	Neutral	T	G	(Sánchez et al. 2009)
OMS00030	Neutral	T	C	(Sánchez et al. 2009)
OMS00039	Neutral	T	C	(Sánchez et al. 2009)
OMS00041	Neutral	G	C	(Sánchez et al. 2009)
OMS00048	Neutral	T	C	(Sánchez et al. 2009)
OMS00052	Neutral	T	G	(Sánchez et al. 2009)
OMS00053	Neutral	T	C	(Sánchez et al. 2009)
OMS00056	Neutral	T	C	(Sánchez et al. 2009)
OMS00057	Neutral	T	G	(Sánchez et al. 2009)
OMS00058	Neutral	T	C	(Sánchez et al. 2009)
OMS00061	Neutral	T	C	(Sánchez et al. 2009)
OMS00062	Neutral	T	C	(Sánchez et al. 2009)
OMS00064	Neutral	T	G	(Sánchez et al. 2009)
OMS00068	Neutral	A	G	(Sánchez et al. 2009)
OMS00070	Neutral	T	C	(Sánchez et al. 2009)
OMS00071	Neutral	A	G	(Sánchez et al. 2009)
OMS00072	Neutral	A	G	(Sánchez et al. 2009)
OMS00074	Neutral	T	G	(Sánchez et al. 2009)
OMS00077	Neutral	C	G	(Sánchez et al. 2009)
OMS00078	Neutral	T	C	(Sánchez et al. 2009)
OMS00079	Neutral	T	C	(Sánchez et al. 2009)

Locus Name	Purpose	Allele 1	Allele 2	Reference
OMS00087	Neutral	A	G	(Sánchez et al. 2009)
OMS00089	Neutral	A	G	(Sánchez et al. 2009)
OMS00090	Neutral	T	C	(Sánchez et al. 2009)
OMS00092	Neutral	A	C	(Sánchez et al. 2009)
OMS00095	Neutral	T	C	(Sánchez et al. 2009)
OMS00096	Neutral	T	G	(Sánchez et al. 2009)
OMS00101	Neutral	A	G	(Sánchez et al. 2009)
OMS00103	Neutral	A	T	(Sánchez et al. 2009)
OMS00105	Neutral	T	G	(Sánchez et al. 2009)
OMS00106	Neutral	T	G	(Sánchez et al. 2009)
OMS00111	Neutral	T	C	(Sánchez et al. 2009)
OMS00112	Neutral	A	T	(Sánchez et al. 2009)
OMS00114	Neutral	T	C	(Sánchez et al. 2009)
OMS00116	Neutral	T	A	(Sánchez et al. 2009)
OMS00118	Neutral	T	G	(Sánchez et al. 2009)
OMS00119	Neutral	A	T	(Sánchez et al. 2009)
OMS00120	Neutral	A	G	(Sánchez et al. 2009)
OMS00121	Neutral	T	C	(Sánchez et al. 2009)
OMS00127	Neutral	T	G	(Sánchez et al. 2009)
OMS00128	Neutral	T	G	(Sánchez et al. 2009)
OMS00129	Neutral	T	C	(Sánchez et al. 2009)
OMS00132	Neutral	A	T	(Sánchez et al. 2009)
OMS00133	Neutral	A	G	(Sánchez et al. 2009)
OMS00134	Neutral	A	G	(Sánchez et al. 2009)
OMS00138	Neutral	T	C	(Sánchez et al. 2009)
OMS00143	Neutral	T	C	(Sánchez et al. 2009)
OMS00149	Neutral	T	G	(Sánchez et al. 2009)
OMS00151	Neutral	T	C	(Sánchez et al. 2009)
OMS00153	Neutral	T	G	(Sánchez et al. 2009)
OMS00154	Neutral	A	T	(Sánchez et al. 2009)
OMS00156	Neutral	A	T	(Sánchez et al. 2009)
OMS00164	Neutral	T	G	(Sánchez et al. 2009)
OMS00169	Neutral	A	G	(Sánchez et al. 2009)
OMS00173	Neutral	T	C	(Sánchez et al. 2009)
OMS00174	Neutral	T	C	(Sánchez et al. 2009)
OMS00175	Neutral	T	C	(Sánchez et al. 2009)
OMS00176	Neutral	T	G	(Sánchez et al. 2009)
OMS00179	Neutral	A	C	(Sánchez et al. 2009)
OMS00180	Neutral	T	G	(Sánchez et al. 2009)
Omy_1004	Neutral	A	T	(Hansen et al. 2011)
Omy_101554-306	Neutral	T	C	(Abadía-Cardoso et al. 2011)
Omy_101832-195	Neutral	A	C	(Abadía-Cardoso et al. 2011)

Locus Name	Purpose	Allele 1	Allele 2	Reference
Omy_101993-189	Neutral	A	T	(Abadía-Cardoso et al. 2011)
Omy_102505-102	Neutral	A	G	(Abadía-Cardoso et al. 2011)
Omy_102867-443	Neutral	T	G	(Abadía-Cardoso et al. 2011)
Omy_103705-558	Neutral	T	C	(Abadía-Cardoso et al. 2011)
Omy_104519-624	Neutral	T	C	(Abadía-Cardoso et al. 2011)
Omy_104569-114	Neutral	A	C	(Abadía-Cardoso et al. 2011)
Omy_105075-162	Neutral	T	G	(Abadía-Cardoso et al. 2011)
Omy_105105-448	Neutral	C	T	(Abadía-Cardoso et al. 2011)
Omy_105385-406	Neutral	T	C	(Abadía-Cardoso et al. 2011)
Omy_105714-265	Neutral	C	T	(Abadía-Cardoso et al. 2011)
Omy_107031-704	Neutral	C	T	(Abadía-Cardoso et al. 2011)
Omy_107285-69	Neutral	C	G	(Abadía-Cardoso et al. 2011)
Omy_107336-170	Neutral	C	G	(Abadía-Cardoso et al. 2011)
Omy_107806-34	Neutral	C	T	(Abadía-Cardoso et al. 2011)
Omy_108007-193	Neutral	A	G	(Abadía-Cardoso et al. 2011)
Omy_109243-222	Neutral	A	C	(Abadía-Cardoso et al. 2011)
Omy_109525-403	Neutral	A	G	(Abadía-Cardoso et al. 2011)
Omy_109894-185	Neutral	T	C	(Abadía-Cardoso et al. 2011)
Omy_110064-419	Neutral	T	G	(Abadía-Cardoso et al. 2011)
Omy_110201-359	Neutral	T	G	(Abadía-Cardoso et al. 2011)
Omy_110362-585	Neutral	G	A	(Abadía-Cardoso et al. 2011)
Omy_110689-148	Neutral	A	C	(Abadía-Cardoso et al. 2011)
Omy_111084-526	Neutral	A	C	(Abadía-Cardoso et al. 2011)
Omy_111383-51	Neutral	C	T	(Abadía-Cardoso et al. 2011)
Omy_111666-301	Neutral	T	A	(Abadía-Cardoso et al. 2011)
Omy_112301-202	Neutral	T	G	(Abadía-Cardoso et al. 2011)
Omy_112820-82	Neutral	G	A	(Abadía-Cardoso et al. 2011)
Omy_113490-159	Neutral	C	T	(Abadía-Cardoso et al. 2011)
Omy_114315-438	Neutral	T	G	(Abadía-Cardoso et al. 2011)
Omy_114587-480	Neutral	T	G	(Abadía-Cardoso et al. 2011)
Omy_114976-223	Neutral	T	G	(Abadía-Cardoso et al. 2011)
Omy_116733-349	Neutral	C	T	(Abadía-Cardoso et al. 2011)
Omy_116938-264	Neutral	A	G	(Abadía-Cardoso et al. 2011)
Omy_117286-374	Neutral	A	T	(Abadía-Cardoso et al. 2011)
Omy_117370-400	Neutral	A	G	(Abadía-Cardoso et al. 2011)
Omy_117540-259	Neutral	T	G	(Abadía-Cardoso et al. 2011)
Omy_117815-81	Neutral	C	T	(Abadía-Cardoso et al. 2011)
Omy_118175-396	Neutral	T	A	(Abadía-Cardoso et al. 2011)
Omy_118205-116	Neutral	A	G	(Abadía-Cardoso et al. 2011)
Omy_118654-91	Neutral	A	G	(Abadía-Cardoso et al. 2011)
Omy_120255-332	Neutral	A	T	(Abadía-Cardoso et al. 2011)
Omy_128693-455	Neutral	T	C	(Abadía-Cardoso et al. 2011)

Locus Name	Purpose	Allele 1	Allele 2	Reference
Omy_128923-433	Neutral	T	C	(Abadía-Cardoso et al. 2011)
Omy_128996-481	Neutral	T	G	(Abadía-Cardoso et al. 2011)
Omy_129870-756	Neutral	C	T	(Abadía-Cardoso et al. 2011)
Omy_130524-160	Neutral	C	G	(Abadía-Cardoso et al. 2011)
Omy_131460-646	Neutral	C	T	(Abadía-Cardoso et al. 2011)
Omy_187760-385	Neutral	A	T	(Abadía-Cardoso et al. 2011)
Omy_96222-125	Neutral	T	C	(Abadía-Cardoso et al. 2011)
Omy_97077-73	Neutral	T	A	(Abadía-Cardoso et al. 2011)
Omy_97660-230	Neutral	T	C	(Abadía-Cardoso et al. 2011)
Omy_97865-196	Neutral	T	C	(Abadía-Cardoso et al. 2011)
Omy_97954-618	Neutral	C	T	(Abadía-Cardoso et al. 2011)
Omy_98683-165	Neutral	A	C	(Abadía-Cardoso et al. 2011)
Omy_99300-202	Neutral	T	C	(Abadía-Cardoso et al. 2011)
Omy_ada10-71	Neutral	T	C	(Narum et al. 2010)
Omy_aldB-165	Neutral	T	C	(Campbell et al. 2009)
Omy_anp-17	Neutral	C	A	(Narum et al. 2010)
Omy_aromat-280	Neutral	T	C	WSU - J. DeKoning unpubl.
Omy_arp-630	Neutral	G	A	(Campbell et al. 2009)
Omy_aspAT-123	Neutral	T	C	(Campbell et al. 2009)
Omy_b1-266	Neutral	T	C	(Sprowles et al. 2006)
Omy_b9-164	Neutral	T	C	(Sprowles et al. 2006)
Omy_BAC-B4-324	Neutral	T	C	WDFW - S. Young unpubl.
Omy_BAC-F5.284	Neutral	C	T	(Limborg et al. 2012)
Omy_BAMBI2.312	Neutral	T	C	WDFW - S. Young unpubl.
Omy_BAMBI4.238	Neutral	T	C	WDFW - S. Young unpubl.
Omy_bcAKala-380rd	Neutral	G	A	(Narum et al. 2010)
Omy_ca050-64	Neutral	T	C	(Narum et al. 2010)
Omy_carban1-264	Neutral	T	C	(Narum et al. 2010)
Omy_cd28-130	Neutral	T	C	WSU - J. DeKoning unpubl.
Omy_cd59-206	Neutral	T	C	WSU - J. DeKoning unpubl.
Omy_cd59b-112	Neutral	C	T	WSU - J. DeKoning unpubl.
Omy_cin-172	Neutral	C	T	CRITFC - N. Campbell unpubl.
Omy_colla1-525	Neutral	C	T	WSU - J. DeKoning unpubl.
Omy_cox1-221	Neutral	T	C	(Campbell et al. 2009)
Omy_cox2-335	Neutral	T	G	WSU - J. DeKoning unpubl.
Omy_crb-106	Neutral	T	C	(Sprowles et al. 2006)
Omy_CRBF1-1	Neutral	T	C	(Aguilar and Garza 2008)
Omy_cyp17-153	Neutral	C	T	WSU - J. DeKoning unpubl.
Omy_e1-147	Neutral	G	T	(Sprowles et al. 2006)
Omy_ftzf1-217	Neutral	A	T	WSU - J. DeKoning unpubl.
Omy_g1-103	Neutral	T	C	(Stephens et al. 2009)
Omy_g12-82	Neutral	T	C	WSU - J. DeKoning unpubl.

Locus Name	Purpose	Allele 1	Allele 2	Reference
Omy_G3PD_2.246	Neutral	C	T	WDFW - S. Young unpubl.
Omy_G3PD_2-371	Neutral	C	A	CRITFC - N. Campbell unpubl.
Omy_gadd45-332	Neutral	T	C	CRITFC - unpubl.
Omy_gdh-271	Neutral	C	T	(Campbell et al. 2009)
Omy_GH1P1_2	Neutral	C	T	(Aguilar and Garza 2008)
Omy_gh-475	Neutral	C	T	(Campbell et al. 2009)
Omy_GHSR-121	Neutral	T	C	CRITFC - unpubl.
Omy_gluR-79	Neutral	C	T	CRITFC - unpubl.
Omy_gsdf-291	Neutral	T	C	WSU - J. DeKoning unpubl.
Omy_hsc715-80	Neutral	C	A	WDFW - S. Young unpubl.
Omy_hsf1b-241	Neutral	T	C	(Campbell and Narum 2009)
Omy_hsf2-146	Neutral	T	C	(Campbell and Narum 2009)
Omy_hsp47-86	Neutral	T	A	WDFW - S. Young unpubl.
Omy_hsp70aPro-329	Neutral	A	G	(Campbell and Narum 2009)
Omy_hsp90BA-193	Neutral	C	T	(Campbell and Narum 2009)
Omy_hus1-52	Neutral	T	C	(Narum et al. 2010)
Omy_IL17-185	Neutral	G	A	WSU - J. DeKoning unpubl.
Omy_Il-1b_.028	Neutral	T	C	WDFW - S. Young unpubl.
Omy_IL1b-163	Neutral	T	G	WSU - J. DeKoning unpubl.
Omy_I11b-198	Neutral	T	C	WDFW - S. Young unpubl.
Omy_IL6-320	Neutral	T	C	WSU - J. DeKoning unpubl.
Omy_imp1-55	Neutral	T	C	(Narum et al. 2010)
Omy_inos-97	Neutral	C	A	WSU - J. DeKoning unpubl.
Omy_LDHB-1_i2	Neutral	T	C	(Aguilar and Garza 2008)
Omy_LDHB-2_e5	Neutral	T	C	(Aguilar and Garza 2008)
Omy_LDHB-2_i6	Neutral	T	C	(Aguilar and Garza 2008)
Omy_lpl-220	Neutral	T	C	(Narum et al. 2010)
Omy_mapK3-103	Neutral	A	T	CRITFC - N. Campbell unpubl.
Omy_mcsf-268	Neutral	T	C	WSU - J. DeKoning unpubl.
Omy_metA-161	Neutral	T	G	WSU - J. DeKoning unpubl.
Omy_metB-138	Neutral	T	A	WSU - J. DeKoning unpubl.
Omy_MYC_2	Neutral	T	C	(Aguilar and Garza 2008)
Omy_myoD-178	Neutral	A	C	(Campbell et al. 2009)
Omy_nach-200	Neutral	A	T	WSU - J. DeKoning unpubl.
Omy_NaKATPa3-50	Neutral	T	C	(Campbell et al. 2009)
Omy_ndk-152	Neutral	A	G	CRITFC - N. Campbell unpubl.
Omy_nips-299	Neutral	T	Deletion	(Campbell et al. 2009)
Omy_nkef-241	Neutral	C	A	(Campbell et al. 2009)
Omy_ntl-27	Neutral	G	A	(Campbell et al. 2009)
Omy_nxt2-273	Neutral	T	C	(Campbell et al. 2009)
Omy_Ogo4-212	Neutral	T	C	(Campbell et al. 2009)
Omy_OmyP9-180	Neutral	C	G	(Sprowles et al. 2006)

Locus Name	Purpose	Allele 1	Allele 2	Reference
Omy_Ots249-227	Neutral	C	T	(Campbell et al. 2009)
Omy_oxct-85	Neutral	A	T	WSU - J. DeKoning unpubl.
Omy_p53-262	Neutral	T	C	CRITFC - unpubl.
Omy_pad-196	Neutral	T	C	CRITFC - unpubl.
Omy_ppie-232	Neutral	T	C	(Narum et al. 2010)
Omy_RAD17632-23	Neutral	T	C	CRITFC - unpubl.
Omy_RAD26080-69	Neutral	T	C	CRITFC - unpubl.
Omy_RAD29700-18	Neutral	T	C	CRITFC - unpubl.
Omy_RAD36848-7	Neutral	T	C	CRITFC - unpubl.
Omy_RAD38269-10	Neutral	T	C	CRITFC - unpubl.
Omy_RAD43612-42	Neutral	T	C	CRITFC - unpubl.
Omy_RAD45104-18	Neutral	T	C	CRITFC - unpubl.
Omy_RAD47444-53	Neutral	T	C	CRITFC - unpubl.
Omy_RAD48799-69	Neutral	T	C	CRITFC - unpubl.
Omy_RAD52812-28	Neutral	T	C	CRITFC - unpubl.
Omy_RAD58213-70	Neutral	T	C	CRITFC - unpubl.
Omy_RAD58835-15	Neutral	T	C	CRITFC - unpubl.
Omy_RAD62596-38	Neutral	T	C	CRITFC - unpubl.
Omy_RAD69583-33	Neutral	T	C	CRITFC - unpubl.
Omy_RAD7210-8	Neutral	T	C	CRITFC - unpubl.
Omy_RAD74691-49	Neutral	T	C	CRITFC - unpubl.
Omy_RAD88122-32	Neutral	T	C	CRITFC - unpubl.
Omy_rapd-167	Neutral	T	C	(Sprowles et al. 2006)
Omy_rbm4b-203	Neutral	Deletion	T	(Narum et al. 2010)
Omy_redd1-410	Neutral	C	T	(Narum et al. 2010)
Omy_sast-264	Neutral	T	C	(Narum et al. 2010)
Omy_SECC22b-88	Neutral	T	C	CRITFC - unpubl.
Omy_srp09-37	Neutral	C	T	(Narum et al. 2010)
Omy_sSOD-1	Neutral	T	C	(Brunelli et al. 2008)
Omy_star-206	Neutral	A	G	WSU - J. DeKoning unpubl.
Omy_stat3-273	Neutral	G	Deletion	WSU - J. DeKoning unpubl.
Omy_sys1-188	Neutral	C	A	(Narum et al. 2010)
Omy_tlr3-377	Neutral	C	T	WSU - J. DeKoning unpubl.
Omy_tlr5-205	Neutral	T	A	WSU - J. DeKoning unpubl.
Omy_txnip-343	Neutral	T	C	(Narum et al. 2010)
Omy_u07-79-166	Neutral	G	T	(Limborg et al. 2012)
Omy_u09-52.284	Neutral	T	G	(Limborg et al. 2012)
Omy_u09-53.469	Neutral	T	C	(Limborg et al. 2012)
Omy_u09-54-311	Neutral	C	T	WDFW - S. Young unpubl.
Omy_u09-56.119	Neutral	T	C	(Limborg et al. 2012)
Omy_u09-61.043	Neutral	A	T	WDFW - S. Young unpubl.
Omy_U11_2b-154	Neutral	T	C	WDFW - S. Young unpubl.

Locus Name	Purpose	Allele 1	Allele 2	Reference
Omy_UBA3b	Neutral	A	T	(Hansen et al. 2011)
Omy_UT16_2-173	Neutral	C	T	WDFW - S. Young unpubl.
Omy_vamp5-303	Neutral	A	Deletion	(Narum et al. 2010)
Omy_vatf-406	Neutral	T	C	(Narum et al. 2010)
Omy_zg57-91	Neutral	T	C	(Narum et al. 2010)
OMY1011SNP	Neutral	C	A	(Hansen et al. 2011)
Omy_GREB1_05	Adaptive	T	C	(Micheletti et al. 2018)
Omy_GREB1_09	Adaptive	T	C	(Micheletti et al. 2018)
Omy28_11607954	Adaptive	G	A	(Micheletti et al. 2018)
Omy28_11625241	Adaptive	A	G	(Micheletti et al. 2018)
Omy28_11632591	Adaptive	G	A	(Micheletti et al. 2018)
Omy28_11658853	Adaptive	A	C	(Micheletti et al. 2018)
Omy28_11667578	Adaptive	T	C	(Micheletti et al. 2018)
Omy28_11671116	Adaptive	C	T	(Micheletti et al. 2018)
Omy28_11676622	Adaptive	T	G	(Micheletti et al. 2018)
Omy28_11683204	Adaptive	G	T	(Micheletti et al. 2018)
Omy28_11773194	Adaptive	A	T	(Micheletti et al. 2018)
Omy_RAD103359-45	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD10733-10	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD10945-51	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD116-59	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD1186-59	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD12439-64	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD12566-14	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD13034-67	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD13073-16	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD13499-13	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD14033-46	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD14269-30	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD14541-72	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD15709-53	Adaptive	T	C	CRITFC - unpubl.
Omy_RAD16104-20	Adaptive	T	C	(Hess et al. 2016)
Omy_RAD1751-18	Adaptive	T	C	CRITFC - unpubl.
Omy_RAD17849-16	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD18903-48	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD1919-22	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD19340-24	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD19578-59	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD20917-11	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD22123-69	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD2277-7	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD23354-66	Adaptive	T	C	(Micheletti et al. 2018)

Locus Name	Purpose	Allele 1	Allele 2	Reference
Omy_RAD23577-43	Adaptive	T	C	(Hess et al. 2016)
Omy_RAD23894-58	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD24287-74	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD24343-29	Adaptive	T	C	CRITFC - unpubl.
Omy_RAD25042-68	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD25266-23	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD2567-8	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD25907-57	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD26691-36	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD27740-55	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD28236-38	Adaptive	T	C	CRITFC - unpubl.
Omy_RAD29352-6	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD29559-69	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD2976-26	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD30230-25	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD30243-74	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD30392-17	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD30619-61	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD31079-58	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD31408-67	Adaptive	T	C	CRITFC - unpubl.
Omy_RAD3209-10	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD32139-58	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD33122-47	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD33798-24	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD35005-13	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD35149-9	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD35417-9	Adaptive	T	C	(Hess et al. 2016)
Omy_RAD3651-48	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD366-7	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD36952-53	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD37492-53	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD37816-68	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD38406-19	Adaptive	T	C	CRITFC - unpubl.
Omy_RAD39156-33	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD3926-22	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD40132-55	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD40520-48	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD40641-58	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD41594-34	Adaptive	T	C	CRITFC - unpubl.
Omy_RAD42465-32	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD42793-59	Adaptive	T	C	(Hess et al. 2016)
Omy_RAD43117-55	Adaptive	T	C	(Micheletti et al. 2018)

Locus Name	Purpose	Allele 1	Allele 2	Reference
Omy_RAD43573-37	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD43694-41	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD45246-10	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD46314-35	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD46452-51	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD46672-27	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD47080-54	Adaptive	T	C	(Hess et al. 2016)
Omy_RAD47955-51	Adaptive	T	C	(Hess et al. 2016)
Omy_RAD4848-14	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD49111-35	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD49637-74	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD49827-67	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD50632-21	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD52458-17	Adaptive	T	C	(Hess et al. 2016)
Omy_RAD5374-56	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD54441-29	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD55404-54	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD55997-10	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD57916-29	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD59758-41	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD59950-44	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD60135-12	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD619-59	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD65808-68	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD65959-69	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD66218-58	Adaptive	T	C	CRITFC - unpubl.
Omy_RAD66402-36	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD66834-17	Adaptive	T	C	(Hess et al. 2016)
Omy_RAD68634-40	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD7016-31	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD72528-44	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD73204-63	Adaptive	T	C	(Hess et al. 2016)
Omy_RAD7384-50	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD739-59	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD73963-73	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD76060-20	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD76570-62	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD76882-63	Adaptive	T	C	(Hess et al. 2016)
Omy_RAD77789-54	Adaptive	T	C	(Hess et al. 2016)
Omy_RAD78147-27	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD78502-57	Adaptive	T	C	(Micheletti et al. 2018)
Omy_RAD78776-10	Adaptive	T	C	(Micheletti et al. 2018)

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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 SequalPrep™ 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 Qubit™dsDNA 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 Illumina 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.

References for Appendix B

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.

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 facilities 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 facilities 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 ($\pm 10\%$) 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.

Wenatchee Steelhead

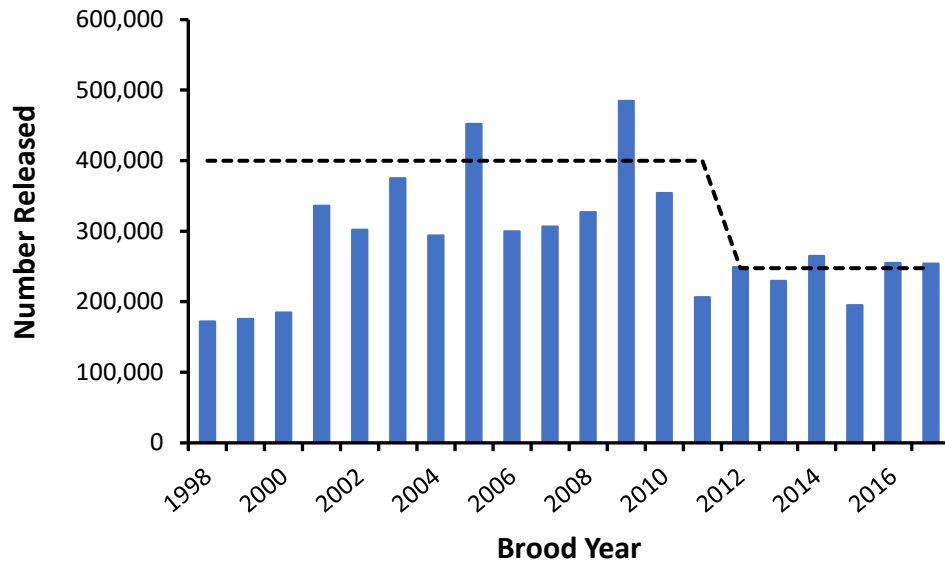


Figure 1. Number of juvenile Steelhead released in the Wenatchee River Subbasin for brood years 1998-2017. The dashed horizontal line represents the target release number (400,000 from 1998-2011 and 247,300 from 2012-2017).

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).

Wenatchee Steelhead Hatchery Releases

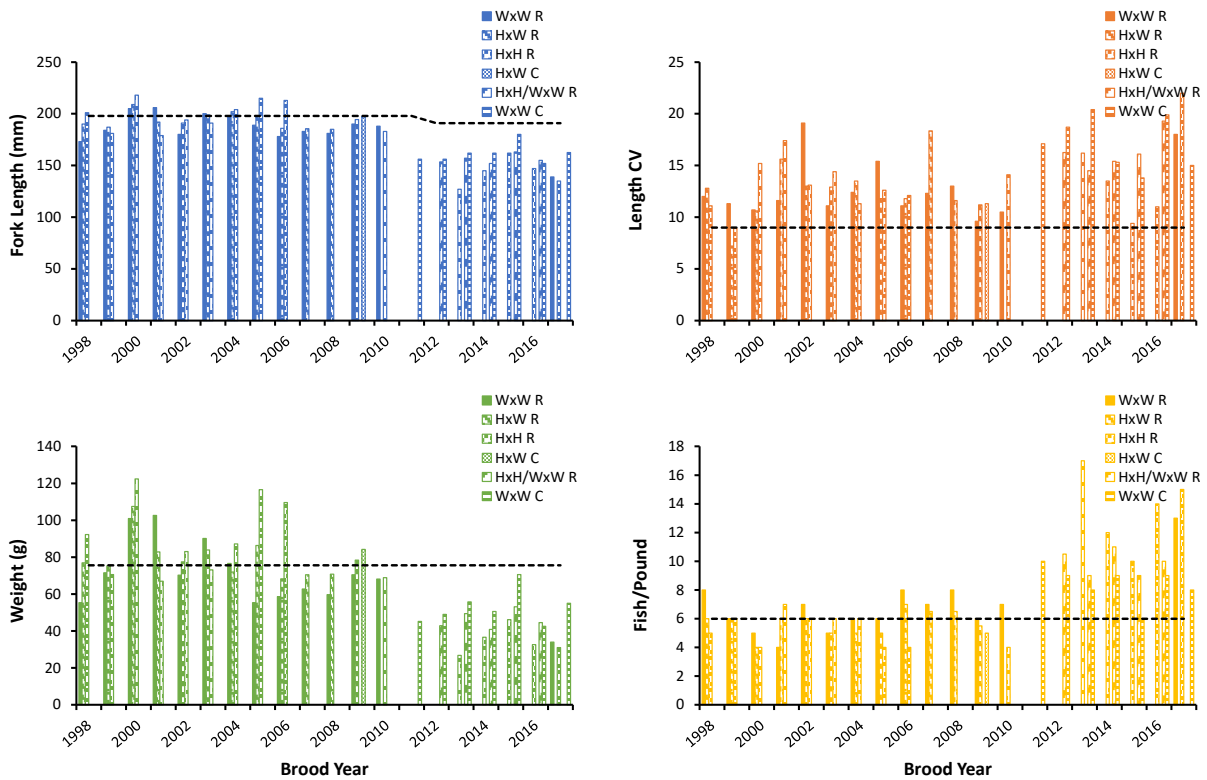


Figure 2. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of juvenile Steelhead released in the Wenatchee River Subbasin for brood years 1998-2017. The dashed horizontal lines represent the target length (198 mm from 1998-2011 and 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).

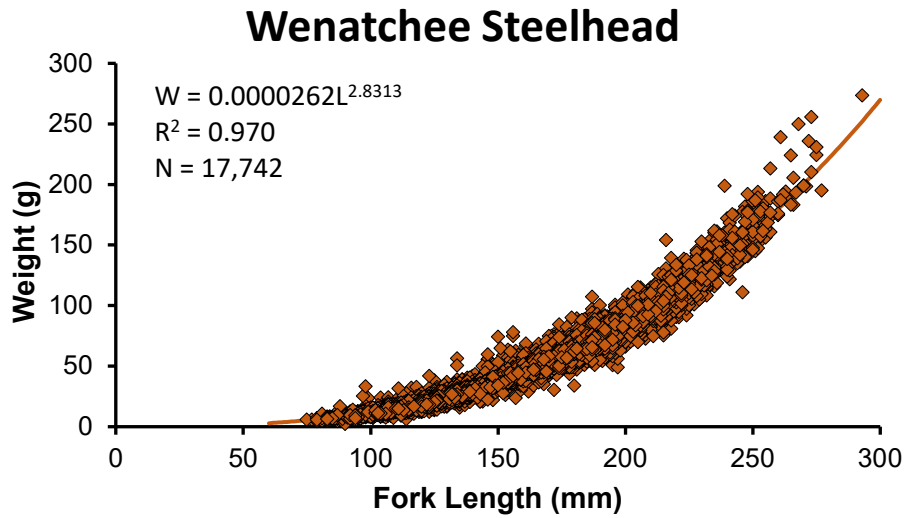


Figure 3. Relationship between fork length (mm) and weight (g) of juvenile Wenatchee River Steelhead sampled before release during 2003-2018.

Methow River Safety-Net Summer Steelhead

Number Released—The recent goal of the supplementation program is to release 100,000 ($\pm 10\%$) 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.

Methow Steelhead

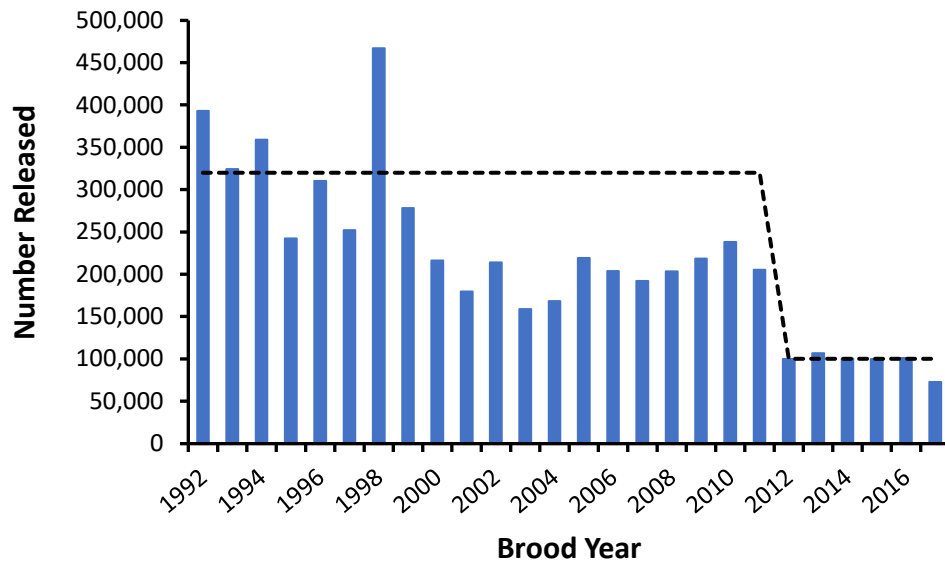


Figure 4. Number of juvenile steelhead released in the Methow River for brood years 1992-2017. The dashed horizontal line represents the target release number (320,000 from 1992-2011 and 100,000 from 2012-2017).

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).

Methow Steelhead Hatchery Releases

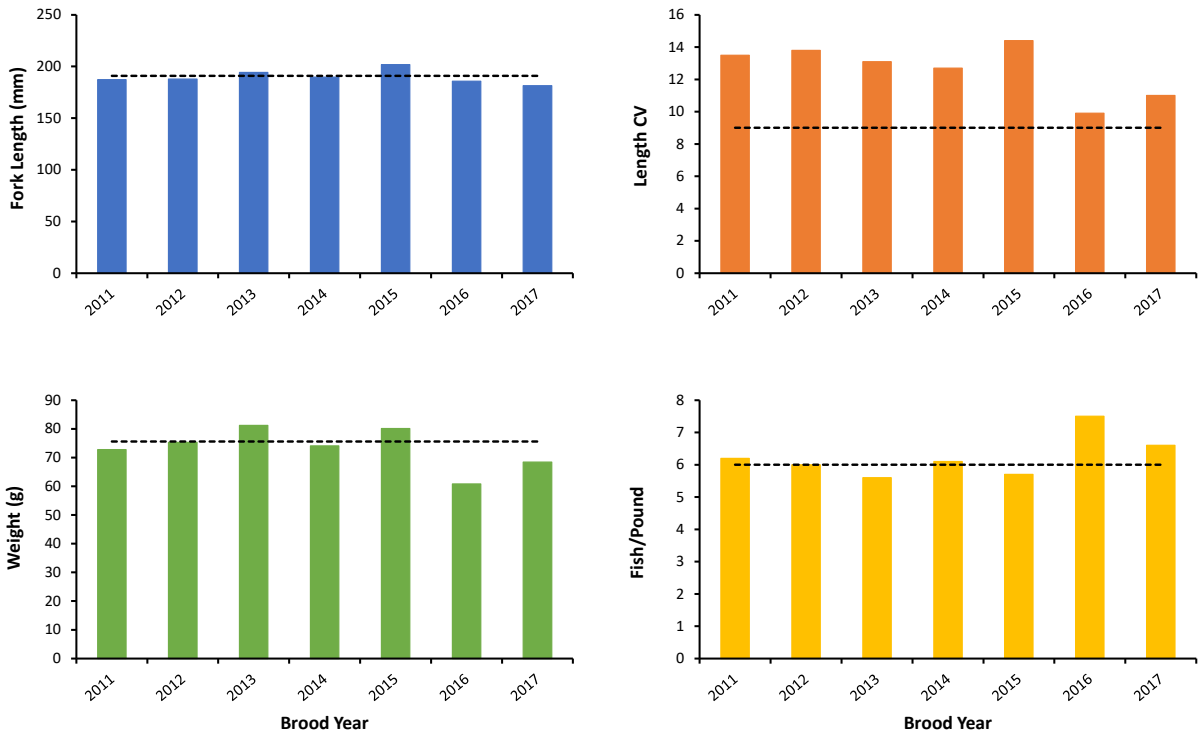


Figure 5. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of juvenile steelhead released in the Methow River for brood years 2011-2017. The dashed horizontal lines represent the target length (191 mm), length CV (9), weight (75.6 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).

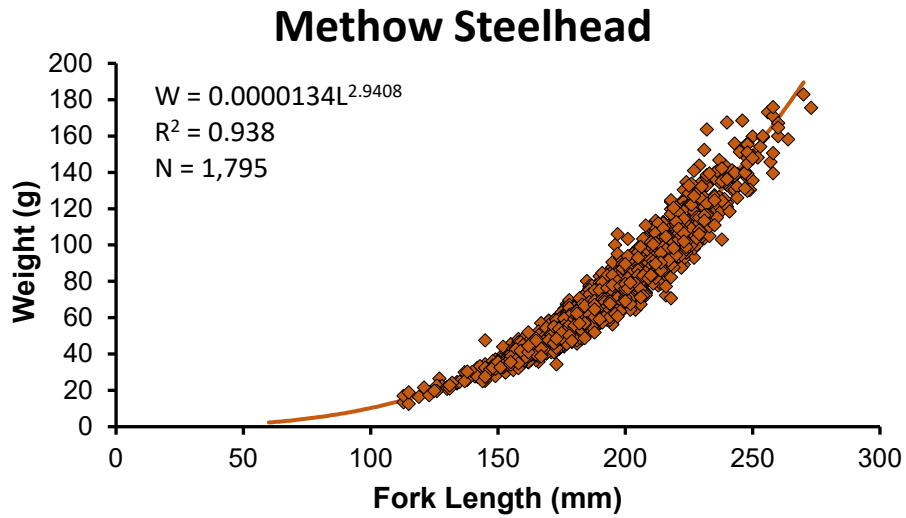


Figure 6. Relationship between fork length (mm) and weight (g) of juvenile Methow River steelhead sampled before release during 2013-2018.

Twisp River Conservation Summer Steelhead

Number Released—The recent goal of the conservation program is to release 48,000 ($\pm 10\%$) 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.

Twisp Steelhead

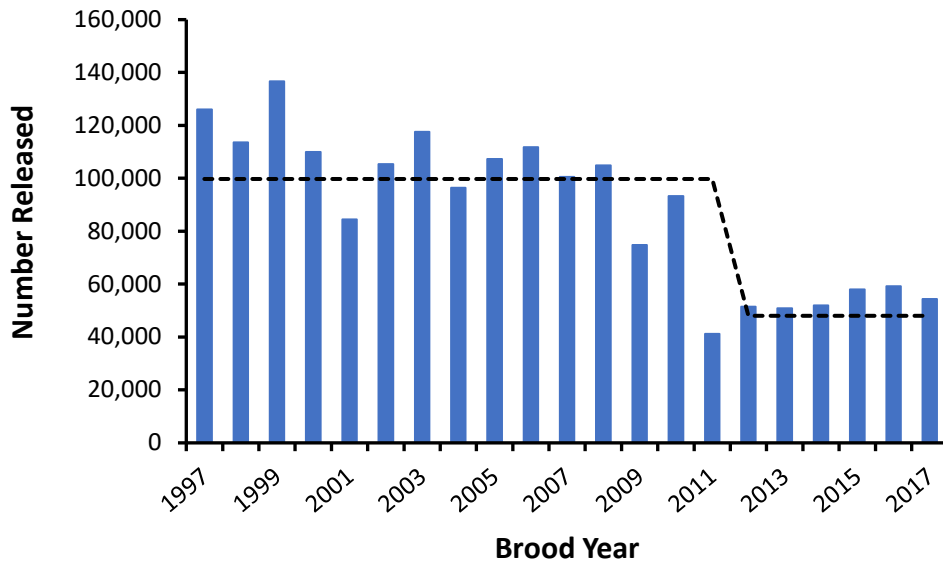


Figure 7. Number of juvenile Steelhead released in the Twisp River for brood years 1997-2017. The dashed horizontal line represents the target release number (99,666 from 1997-2011 and 48,000 from 2012-2017).

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

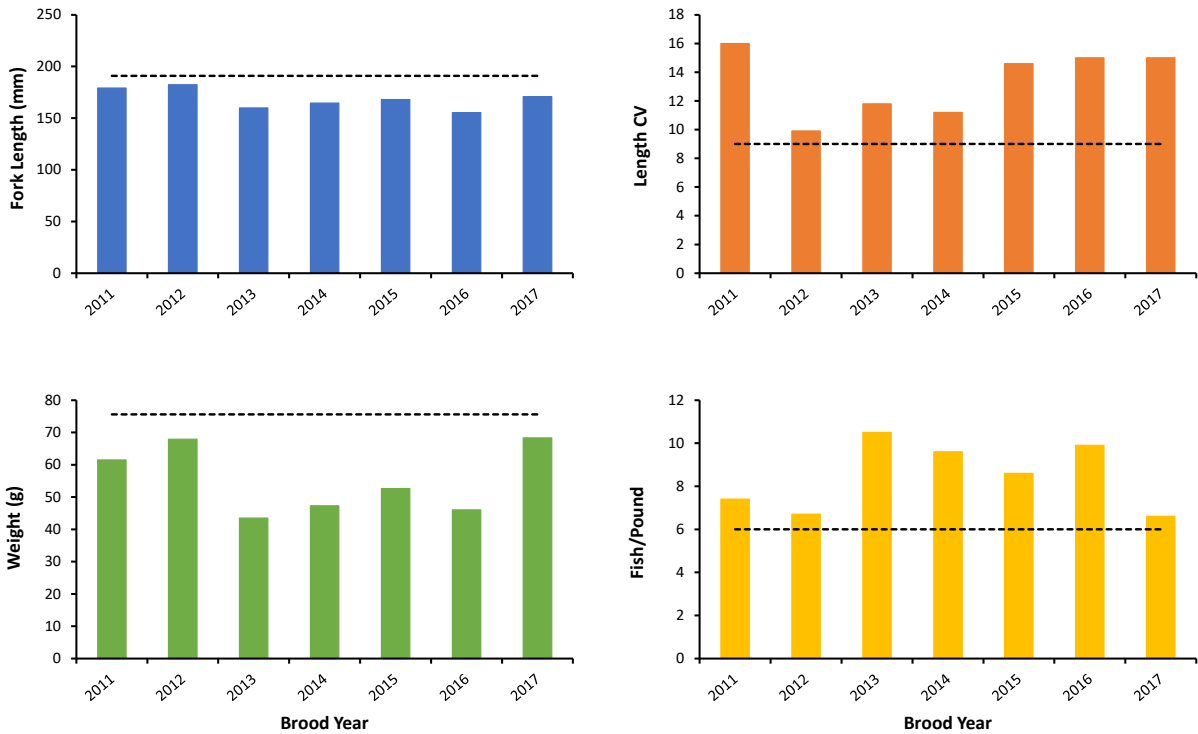


Figure 8. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of juvenile steelhead released in the Twisp River for brood years 2011-2017. The dashed horizontal lines represent the target length (191 mm), length CV (9), weight (75.6 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).

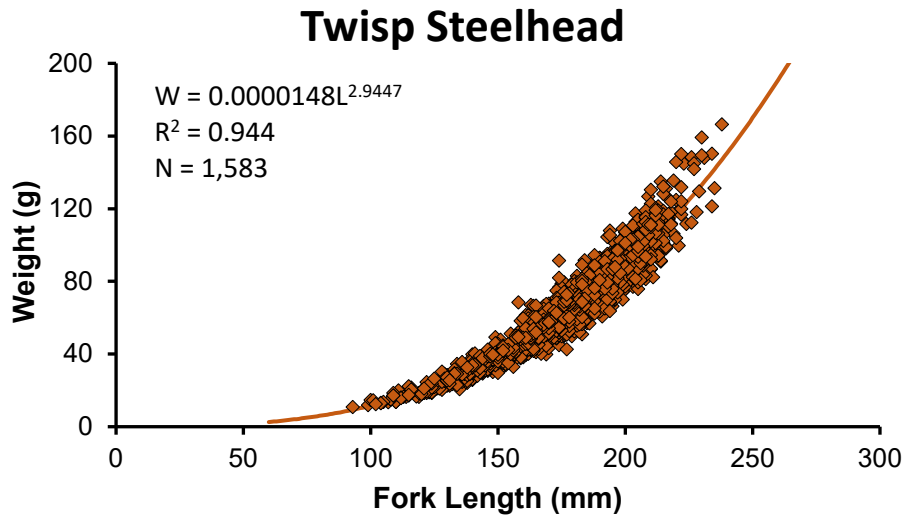


Figure 9. Relationship between fork length (mm) and weight (g) of juvenile Twisp River steelhead sampled before release during 2011-2018.

Columbia River (Wells) Safety-Net Summer Steelhead

Number Released—The recent goal of the safety-net program is to release 160,000 ($\pm 10\%$) 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.

Wells Steelhead

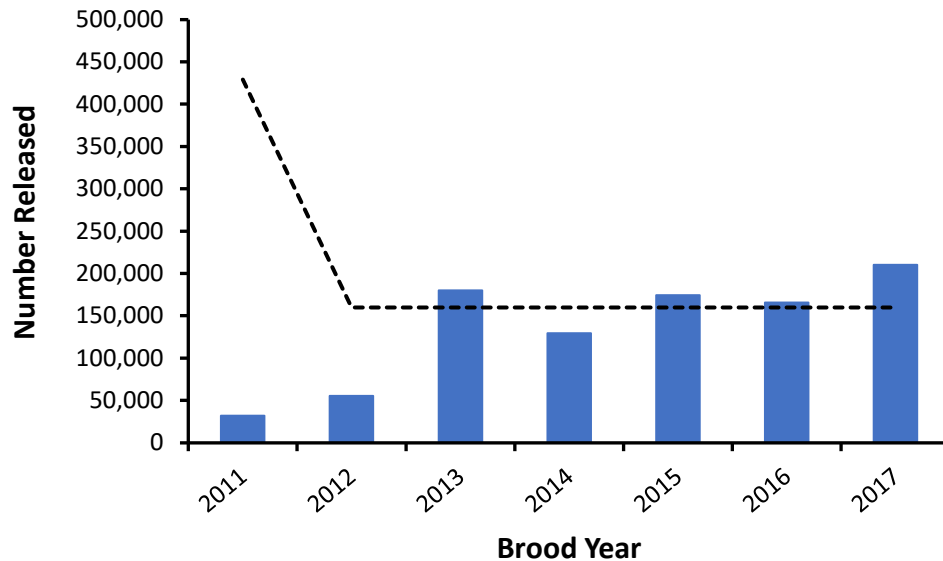


Figure 10. Number of juvenile steelhead released from the Wells Hatchery to the Columbia River for brood years 2011-2017. Note that the current Columbia Safety-Net program (160,000) began releases with brood year 2013. The dashed horizontal line represents the target release number (429,000 before 2012 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 ($\pm 10\%$) 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.

Chiwawa Spring Chinook

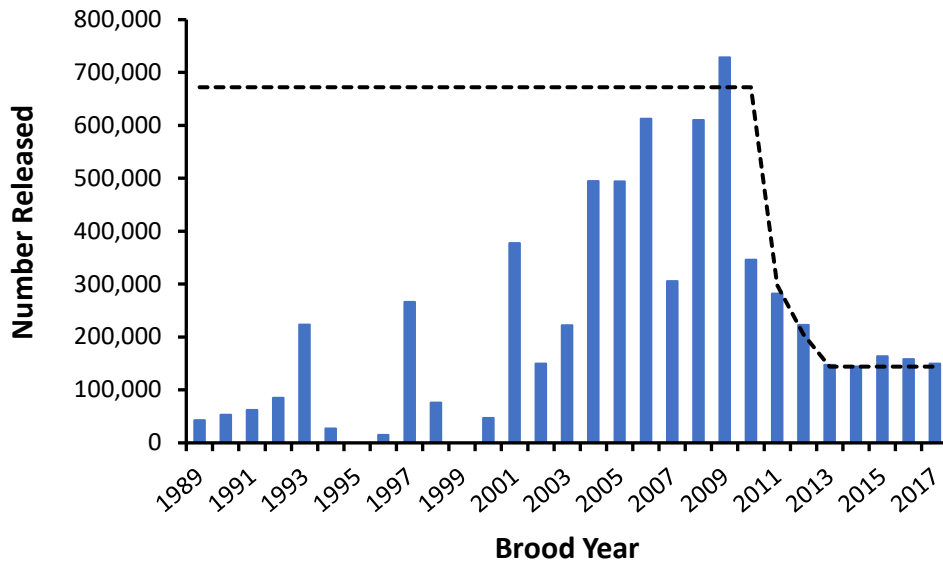


Figure 11. Number of juvenile spring Chinook Salmon released in the Chiwawa River for brood years 1989-2017. The dashed horizontal line represents the target release number (672,000 from 1989-2010, 298,000 in 2011, 205,000 in 2012, and 144,026 from 2013-2017).

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

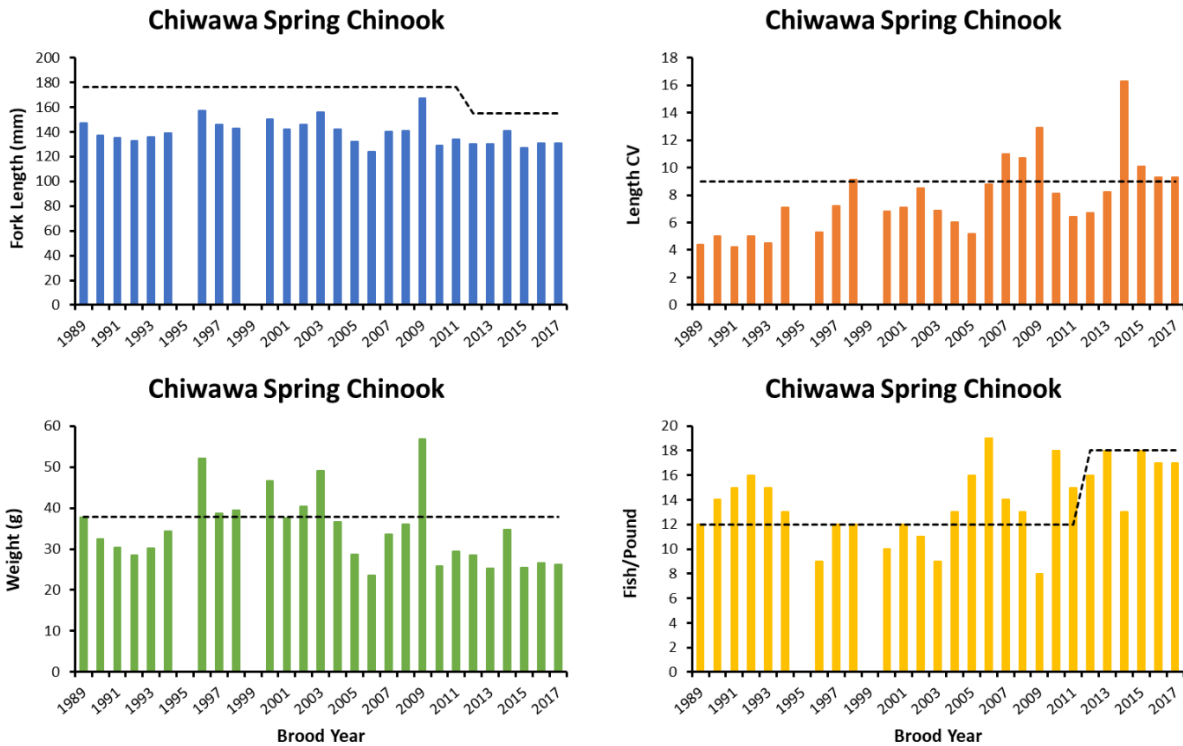


Figure 12. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of juvenile spring Chinook Salmon released in the Chiwawa River for brood years 1989-2017. The dashed horizontal lines represent the target length (176 mm from 1989-2011 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).

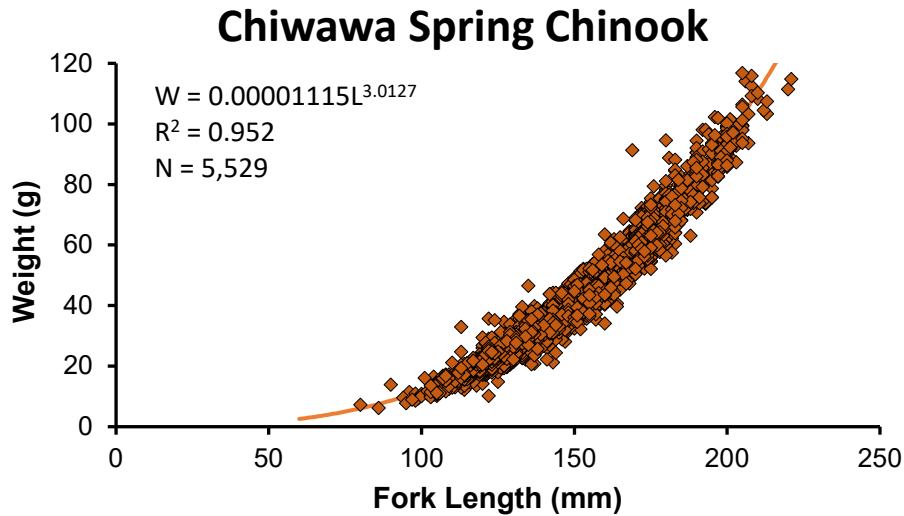


Figure 13. Relationship between fork length (mm) and weight (g) of juvenile Chiwawa River spring Chinook Salmon sampled before release during 2003-2018.

Nason Creek Spring Chinook Salmon

Number Released—The goal of the supplementation program is to release 223,670 ($\pm 10\%$) 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.

Nason Creek Spring Chinook

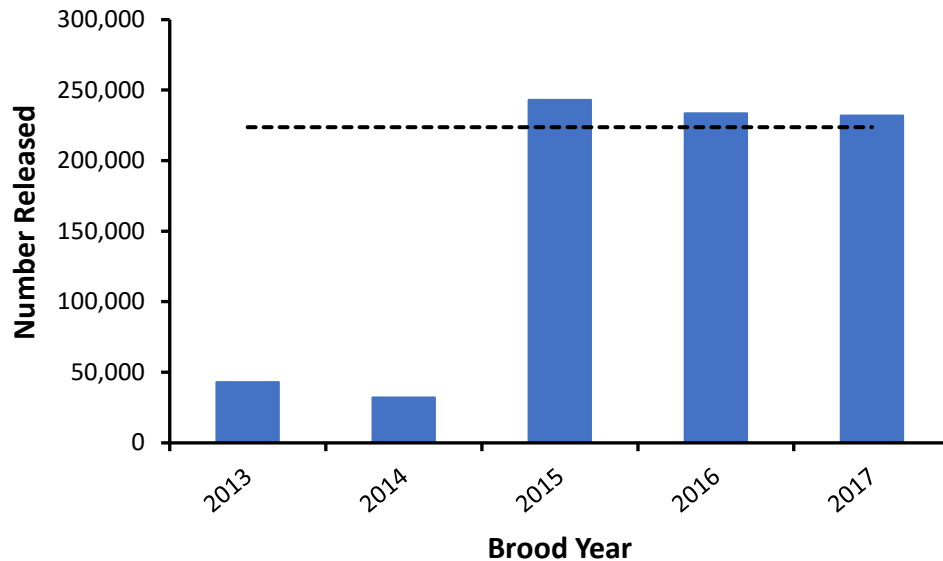


Figure 14. Number of juvenile spring Chinook Salmon released in Nason Creek for brood years 2013-2017. The dashed horizontal line represents the target release number (223,670). For brood year 2014, most of the Nason Creek program was transferred to the Chiwawa Acclimation Facility and 196,866 of these 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.

Nason Creek Spring Chinook Salmon Hatchery Releases

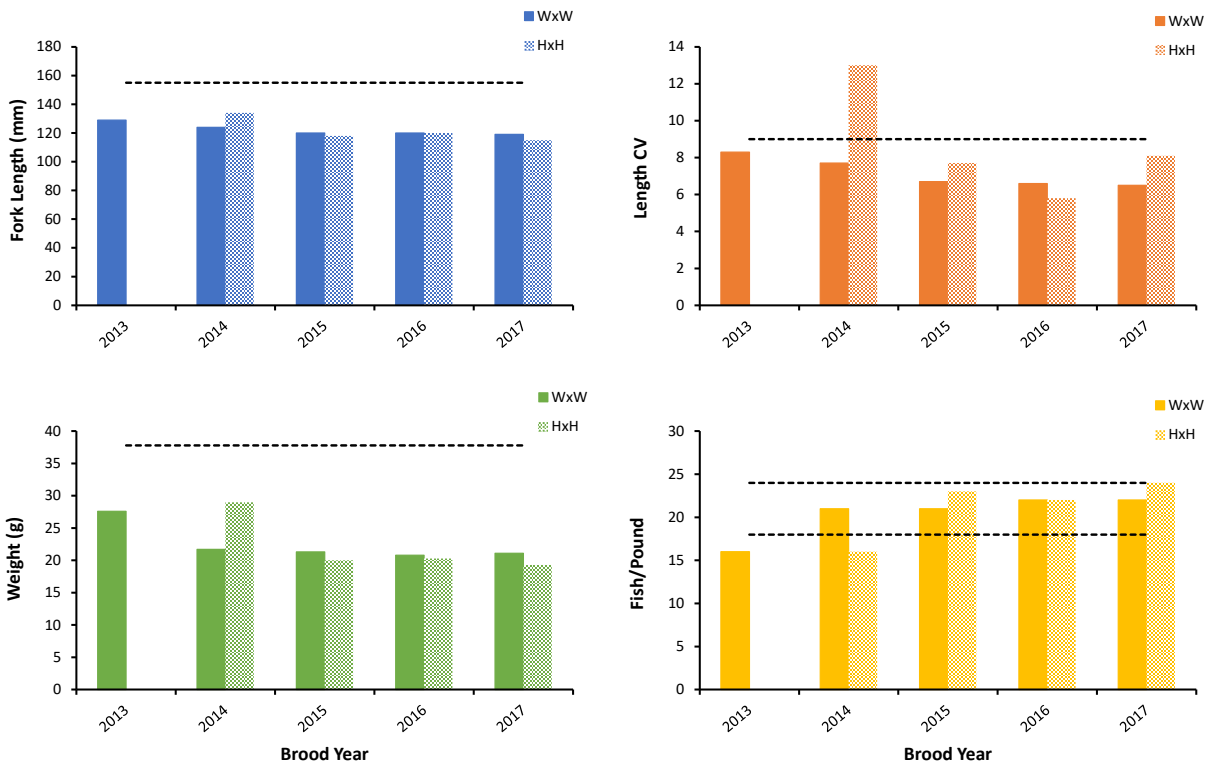


Figure 15. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of juvenile spring Chinook Salmon released in Nason Creek for brood years 2013-2017. The dashed horizontal lines represent the target length (155 mm), length CV (9), weight (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).

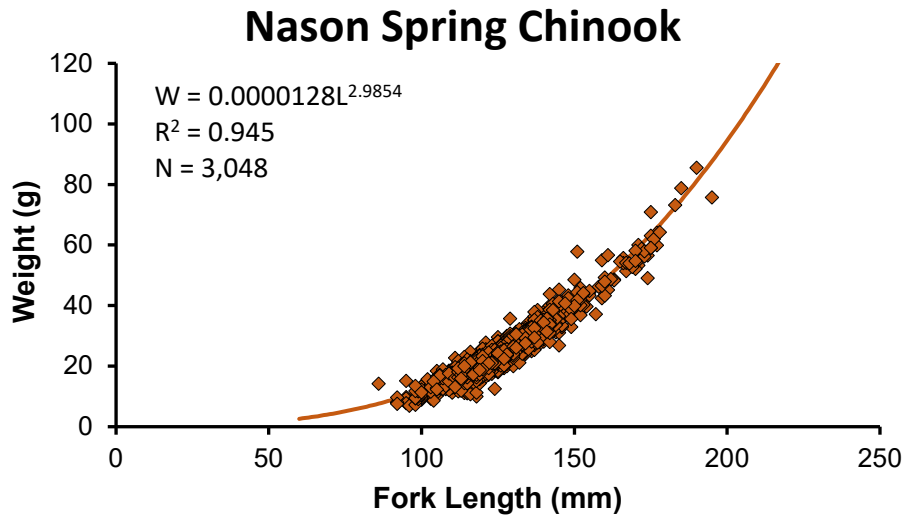


Figure 16. Relationship between fork length (mm) and weight (g) of juvenile Nason Creek spring Chinook Salmon sampled before release during 2013-2018.

White River Spring Chinook Salmon

Number Released—The goal of the supplementation program was to release 150,000 ($\pm 10\%$) 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

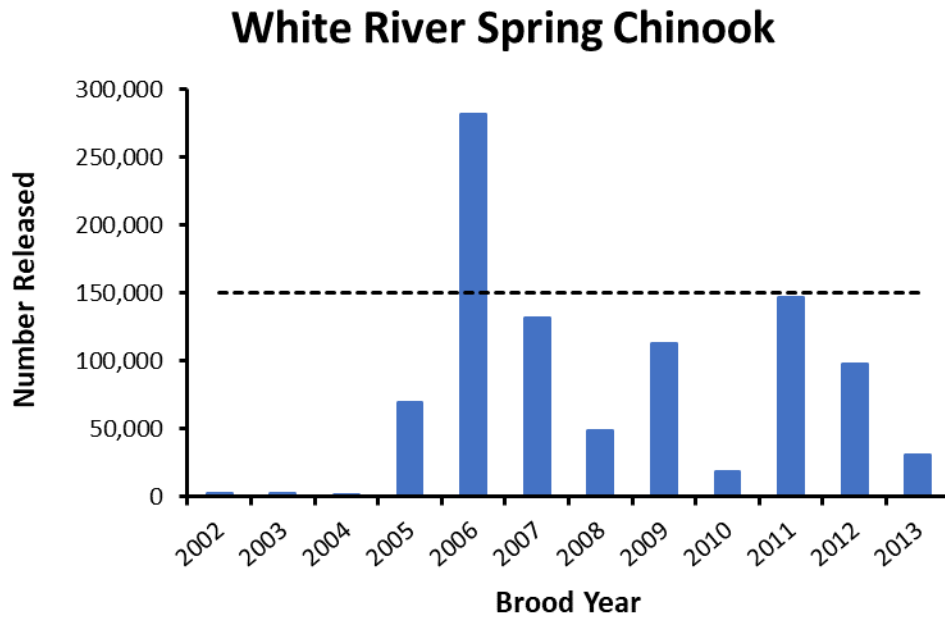


Figure 17. Number of juvenile spring Chinook Salmon released in White River, Lake Wenatchee, and Wenatchee River for brood years 2002-2013. The dashed horizontal line represents the target release number (150,000).

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).

White River Spring Chinook Salmon Hatchery Releases

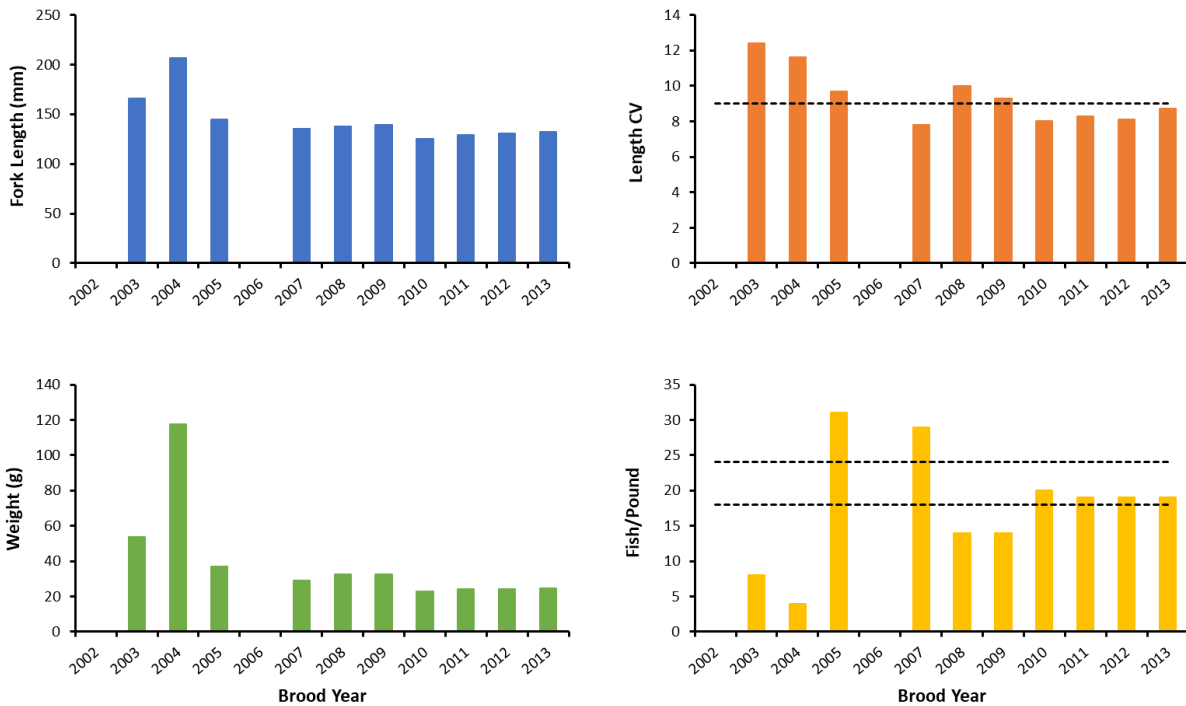


Figure 18. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of juvenile spring Chinook Salmon released in White River for brood years 2002-2013. The dashed horizontal lines represent the target length CV (9; provided for reference – 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 ($\pm 10\%$) 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.

Methow Spring Chinook

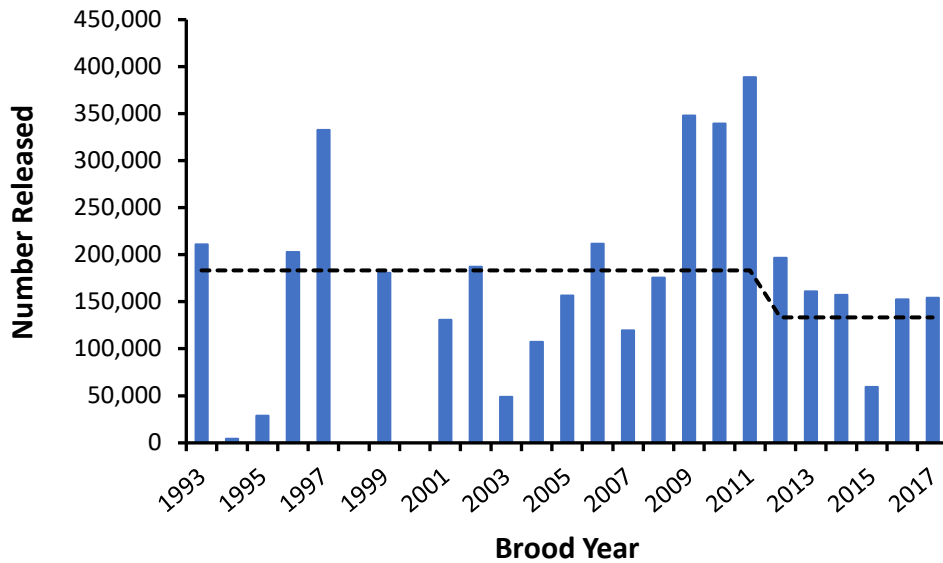


Figure 19. Number of juvenile spring Chinook Salmon released in the Methow River for brood years 1993-2017. The dashed horizontal line represents the target release number (183,334 from 1993-2011 and 133,249 from 2012-2017).

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).

Methow Spring Chinook Salmon Hatchery Releases

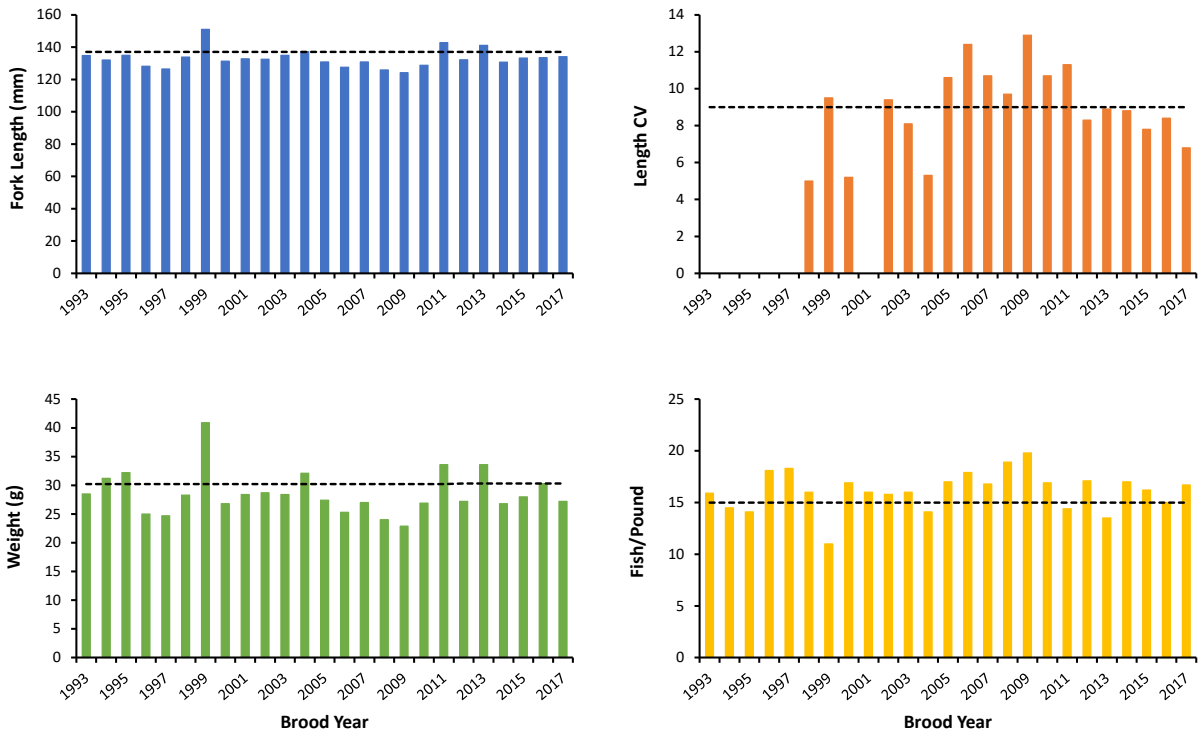


Figure 20. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of juvenile spring Chinook Salmon released in the Methow River for brood years 1993-2017. The dashed horizontal lines represent the target length (137 mm), length CV (9.0), 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).

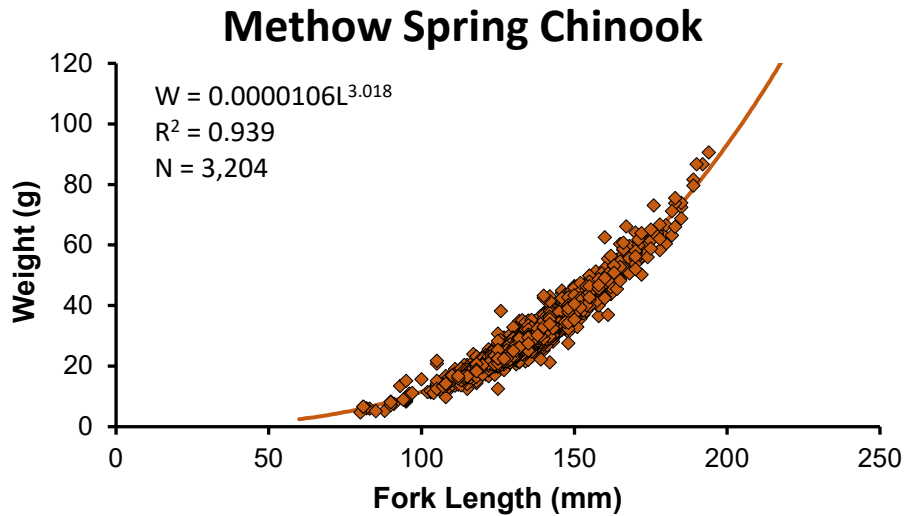


Figure 21. Relationship between fork length (mm) and weight (g) of juvenile Methow River spring Chinook Salmon sampled before release during 2003-2018.

Chewuch River Spring Chinook Salmon

Number Released—The recent goal of the conservation program is to release 60,516 ($\pm 10\%$) 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 exceeded 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.

Chewuch Summer Chinook

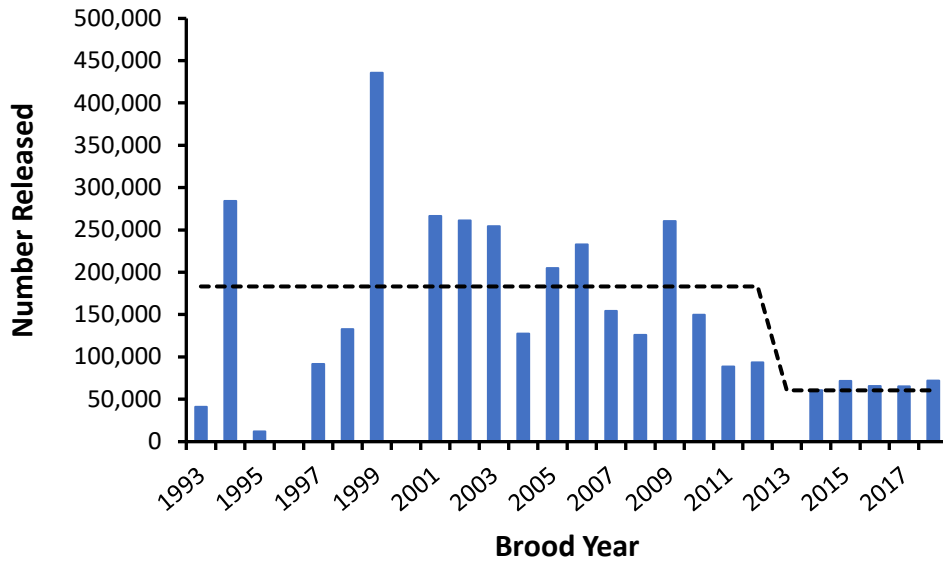


Figure 22. Number of juvenile spring Chinook Salmon released in the Chewuch River for brood years 1994-2017. The dashed horizontal line represents the target release number (183,333 from 1994-2011 and 60,516 from 2012-2017).

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).

Chewuch Spring Chinook Salmon Hatchery Releases

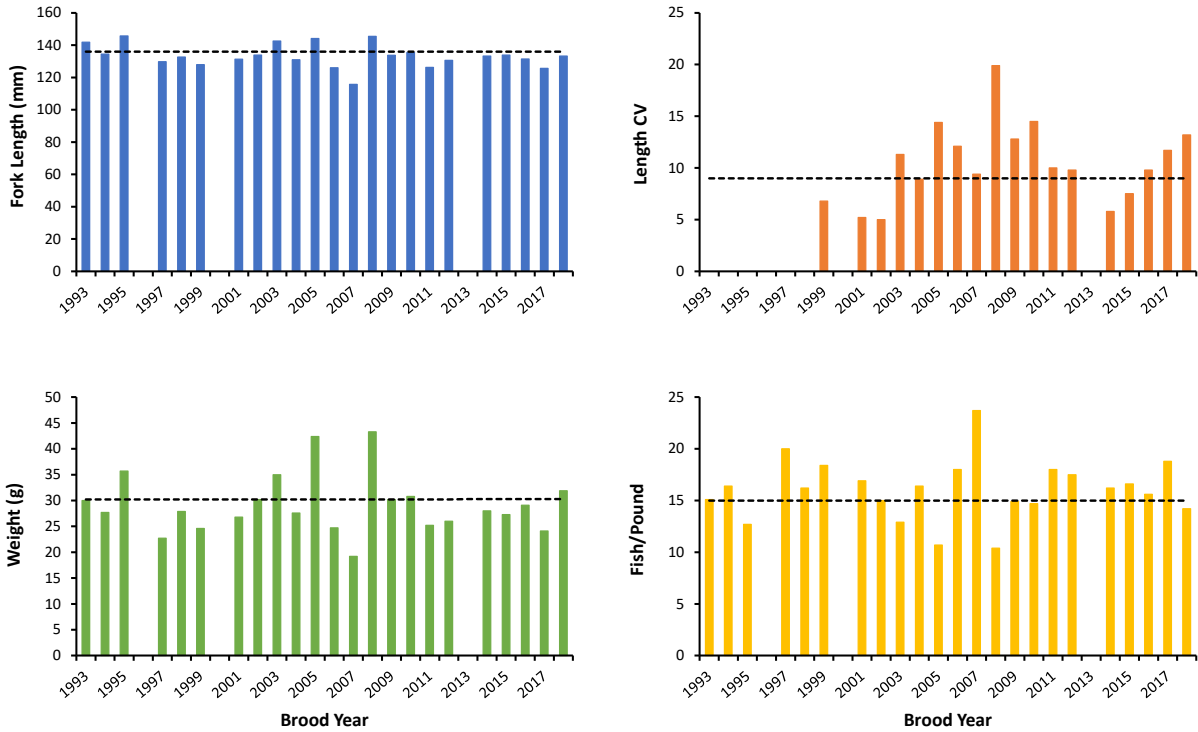


Figure 23. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of juvenile spring Chinook Salmon released in the Chewuch River for brood years 1992-2017. The dashed horizontal lines represent the target length (137 mm), length CV (9.0), 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).

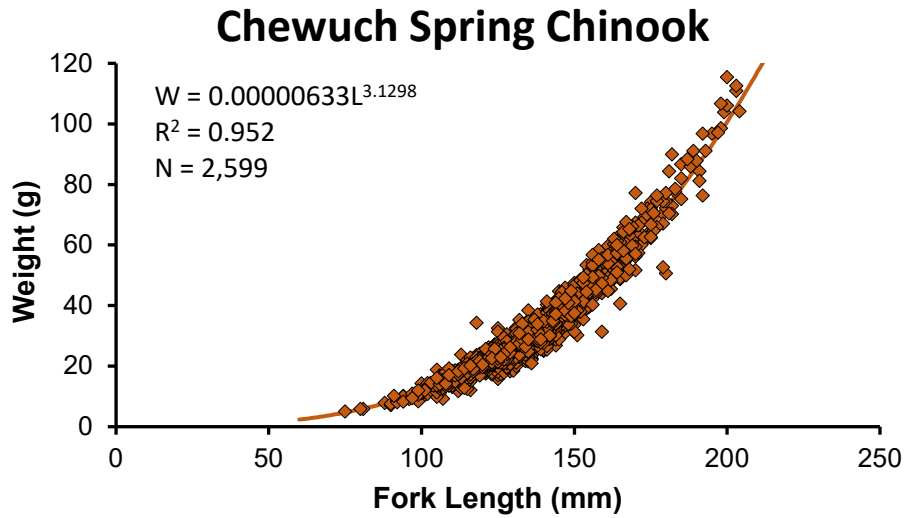


Figure 24. Relationship between fork length (mm) and weight (g) of juvenile Chewuch River spring Chinook Salmon sampled before release during 2003-2018.

Twisp River Spring Chinook Salmon

Number Released—The recent goal of the conservation program is to release 30,000 ($\pm 10\%$) 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.

Twisp Spring Chinook

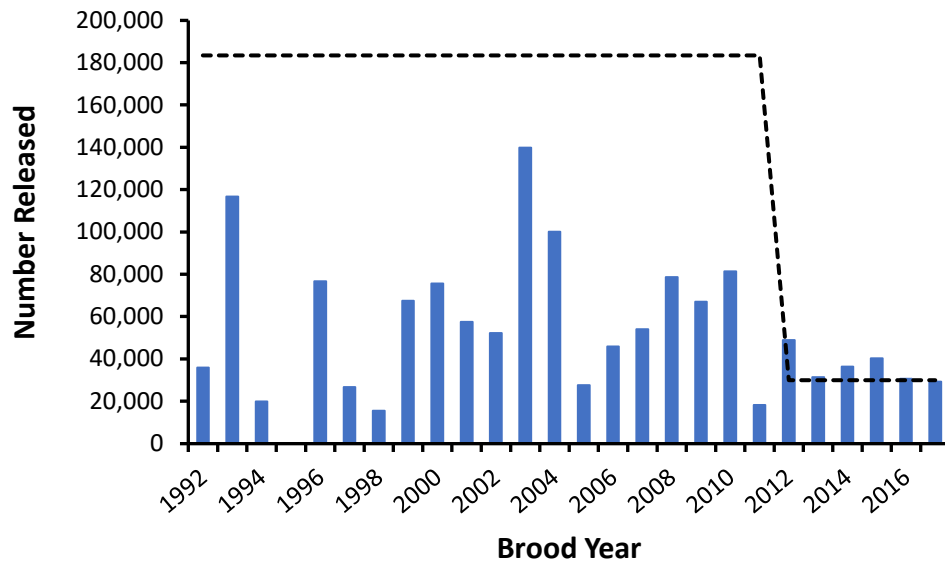


Figure 25. Number of juvenile spring Chinook Salmon released in the Twisp River for brood years 1992-2017. The dashed horizontal line represents the target release number (183,333 from 1992-2011 and 30,000 from 2012-2017).

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).

Twisp Spring Chinook Salmon Hatchery Releases

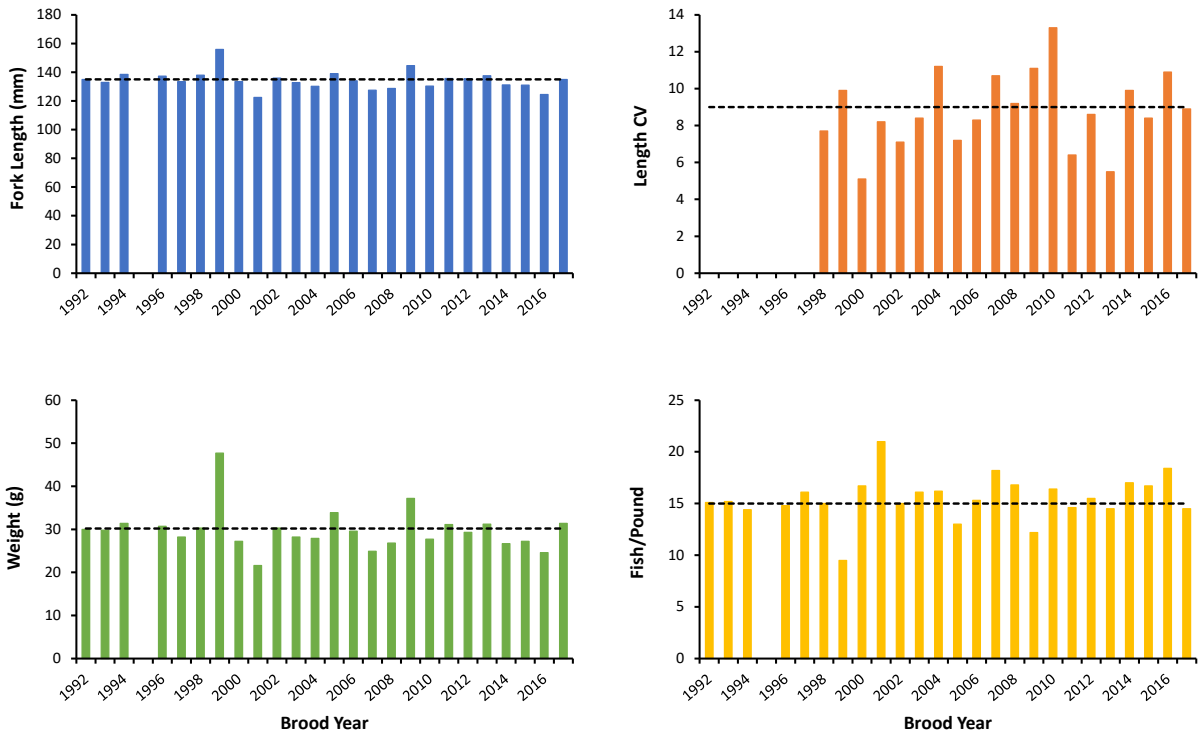


Figure 26. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of juvenile spring Chinook Salmon released in the Twisp River for brood years 1992-2017. The dashed horizontal lines represent the target length (135 mm), length CV (9.0), 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).

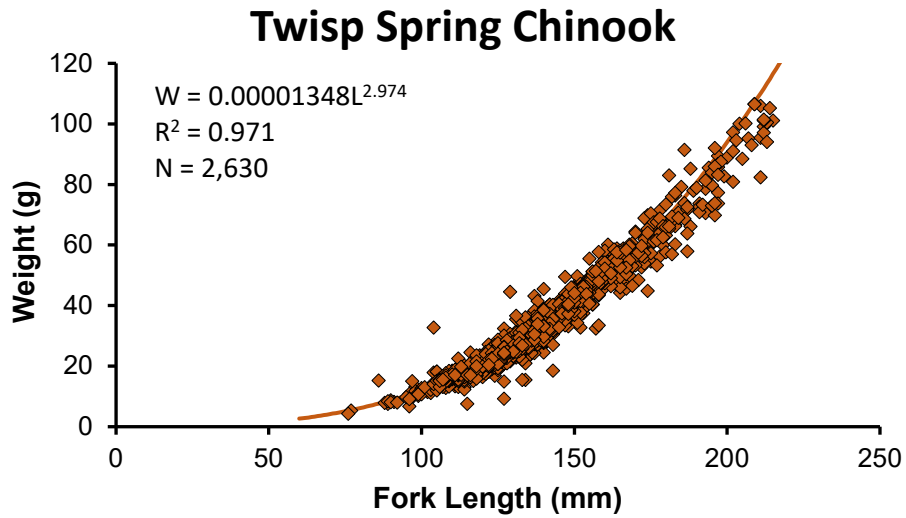


Figure 27. Relationship between fork length (mm) and weight (g) of juvenile Twisp River spring Chinook Salmon sampled before release during 2003-2018.

Wenatchee River Summer Chinook Salmon

Number Released—The recent goal of the supplementation program is to release 500,001 ($\pm 10\%$) 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.

Wenatchee Summer Chinook

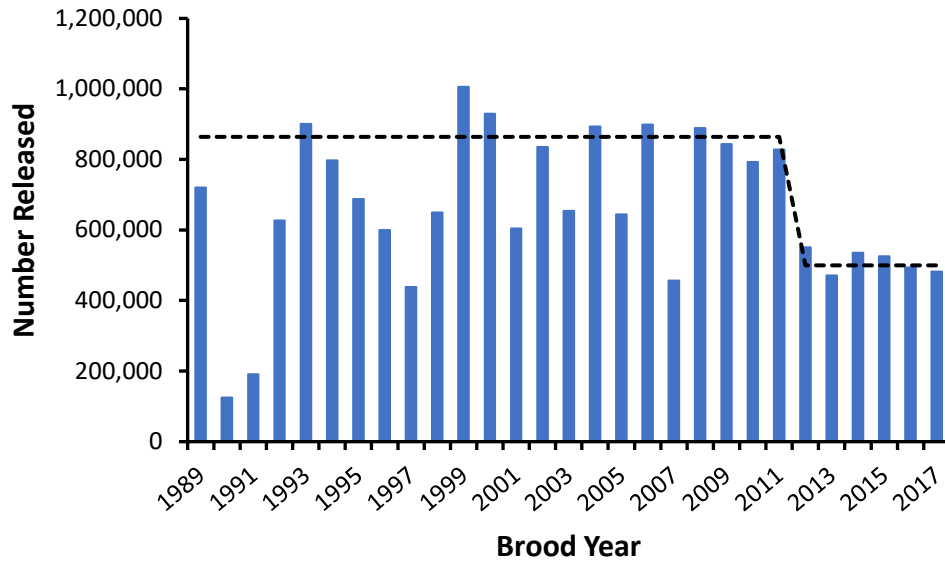


Figure 28. Number of juvenile summer Chinook Salmon released in the Wenatchee River for brood years 1989-2017. The dashed horizontal line represents the target release number (864,000 from 1989-2011 and 500,001 from 2012-2017).

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).

Wenatchee Summer Chinook Salmon Hatchery Releases

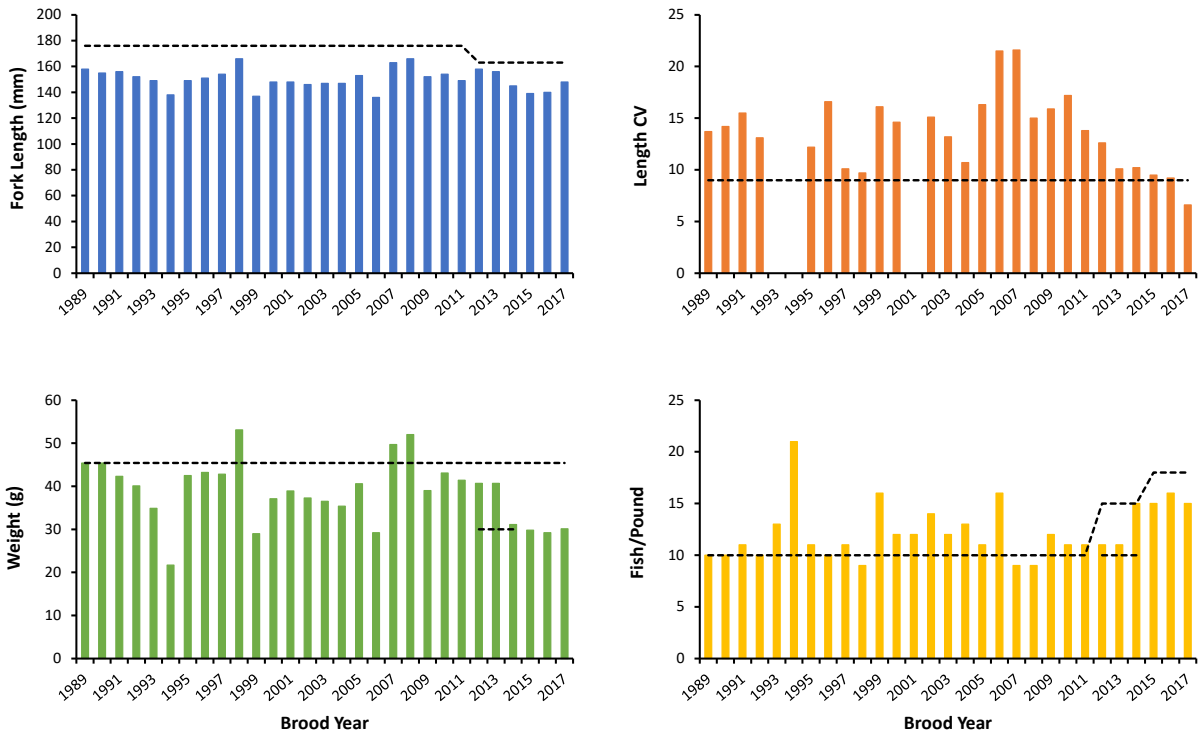


Figure 29. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of juvenile summer Chinook Salmon released in the Wenatchee River for brood years 1989-2017. The dashed horizontal lines represent the target length (135 mm from 1989-2011 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).

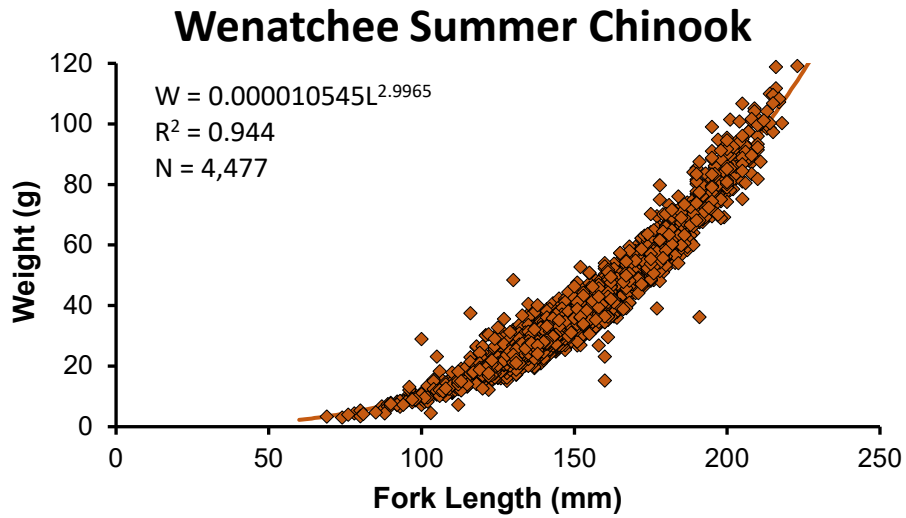


Figure 30. Relationship between fork length (mm) and weight (g) of juvenile Wenatchee River summer Chinook Salmon sampled before release during 2003-2018.

Chelan Falls Summer Chinook Salmon

Number Released—The goal of the supplementation program is to release 576,000 ($\pm 10\%$) 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.

Chelan Falls Summer Chinook

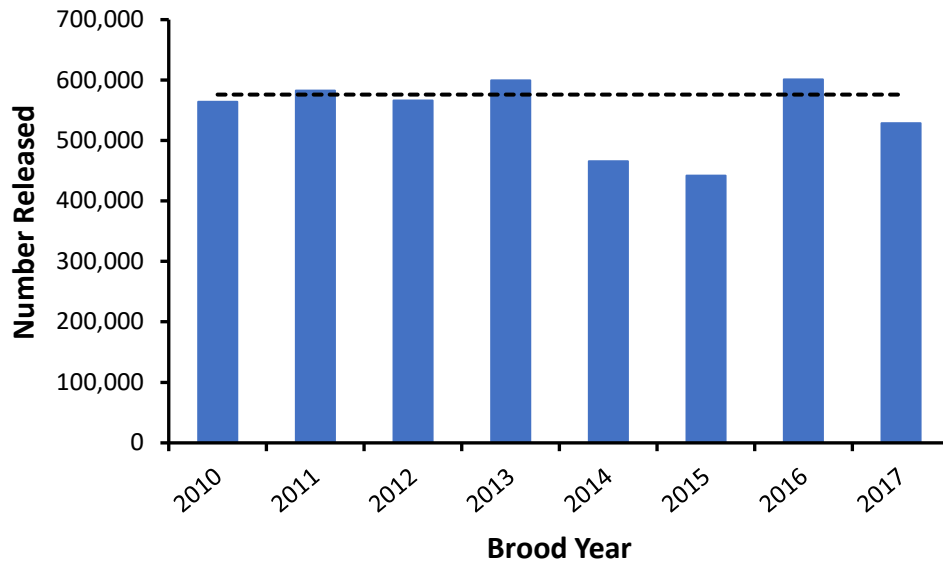


Figure 31. Number of juvenile summer Chinook Salmon released in the Chelan River for brood years 2010-2017. The dashed horizontal line represents the target release number (576,000).

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).

Chelan Falls Summer Chinook Salmon Hatchery Releases

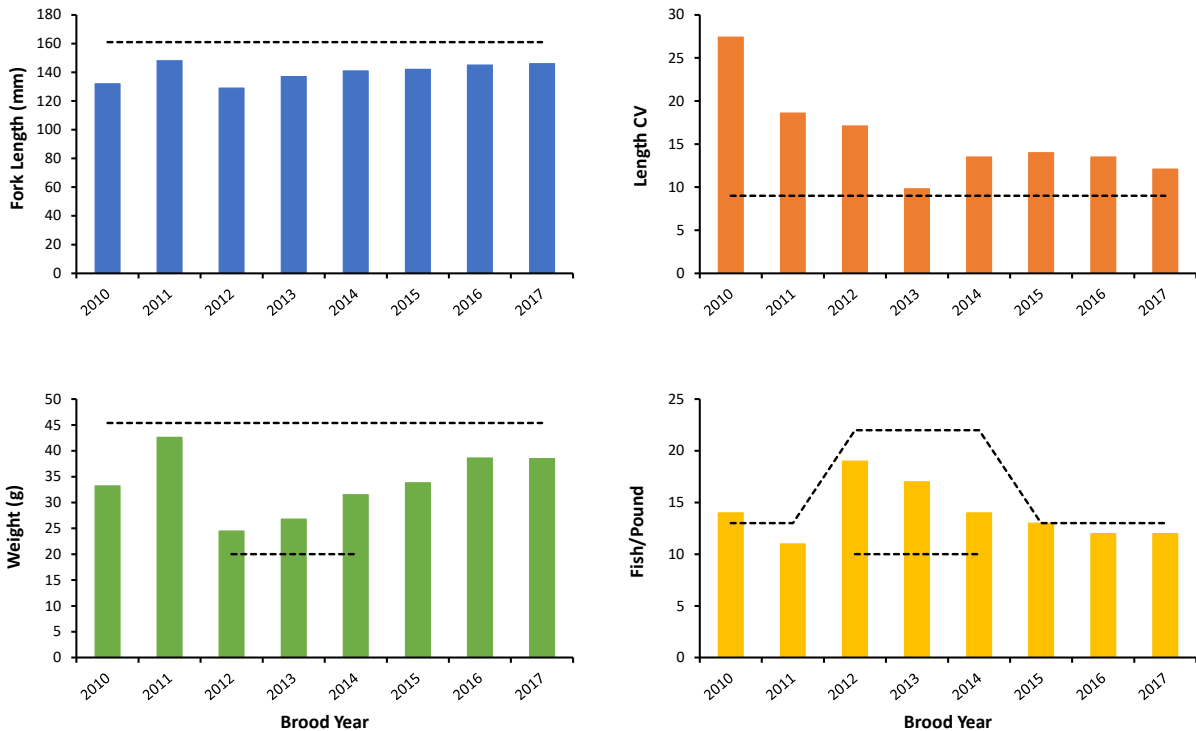


Figure 32. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of juvenile summer Chinook Salmon released in the Chelan River for brood years 2010-2017. The dashed horizontal lines represent the target length (161 mm), length CV (9.0), 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).

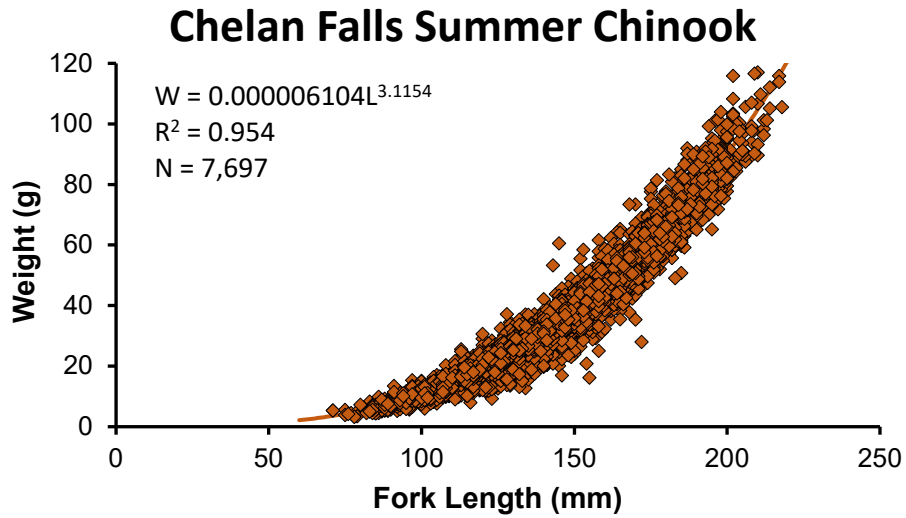


Figure 33. Relationship between fork length (mm) and weight (g) of juvenile Chelan Falls summer Chinook Salmon sampled before release during 2010-2018.

Methow River Summer Chinook Salmon

Number Released—The recent goal of the supplementation program is to release 200,000 ($\pm 10\%$) 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.

Methow Summer Chinook

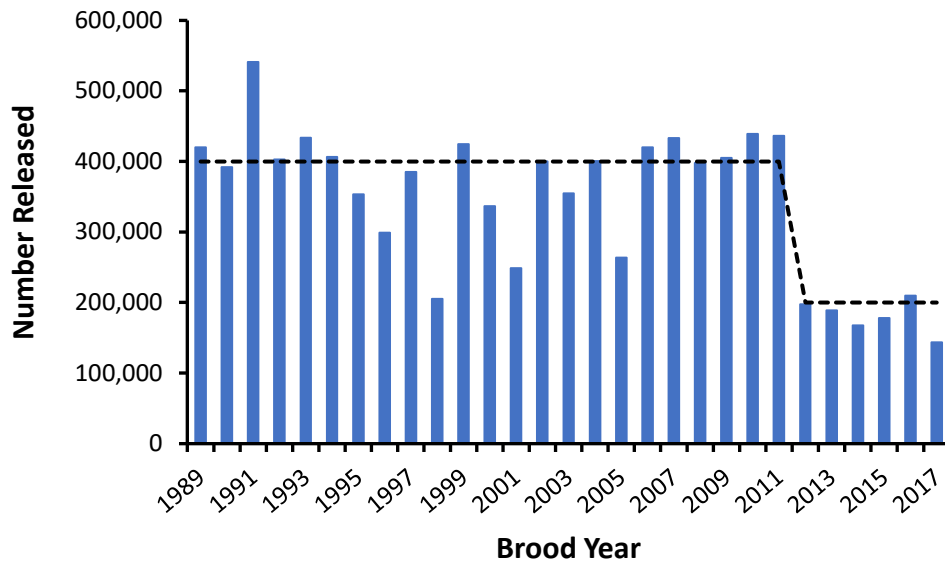


Figure 34. Number of juvenile summer Chinook Salmon released in the Methow River for brood years 1989-2017. The dashed horizontal line represents the target release number (400,000 from 1989-2011 and 200,000 from 2012-2017).

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).

Methow Summer Chinook Salmon Hatchery Releases

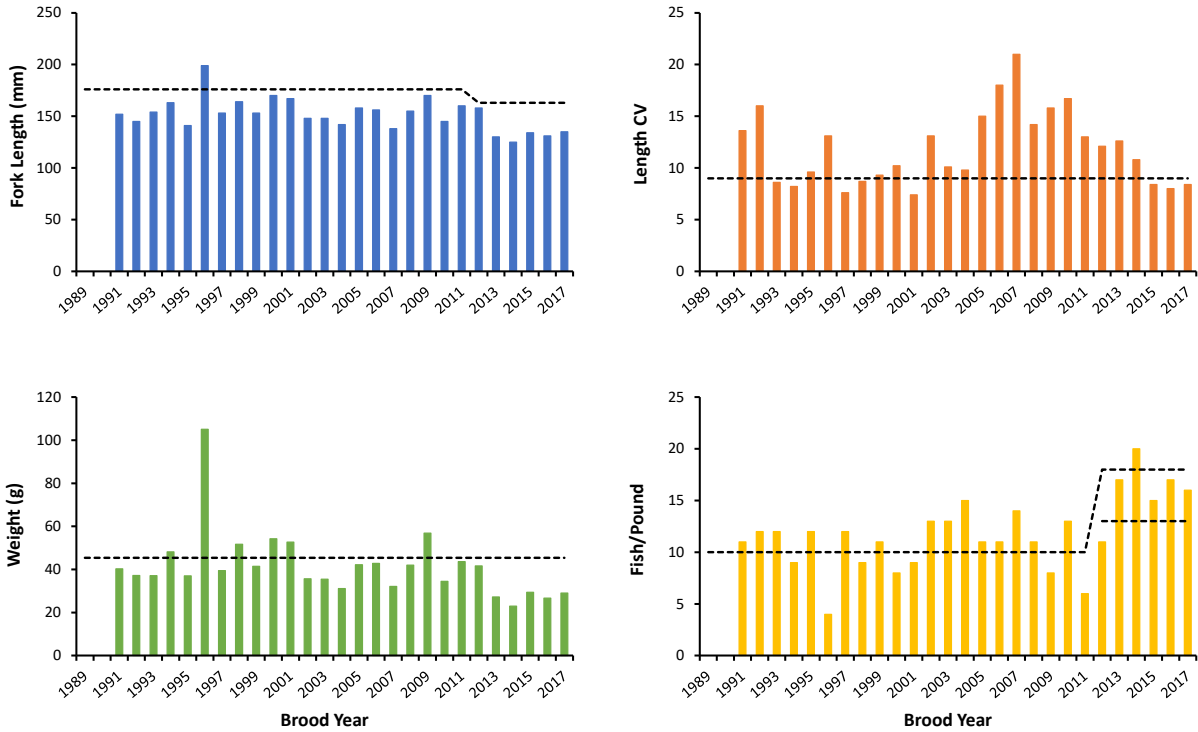


Figure 35. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of juvenile summer Chinook Salmon released in the Methow River for brood years 1989-2017. The dashed horizontal lines represent the target length (176 mm from 1989-2011 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).

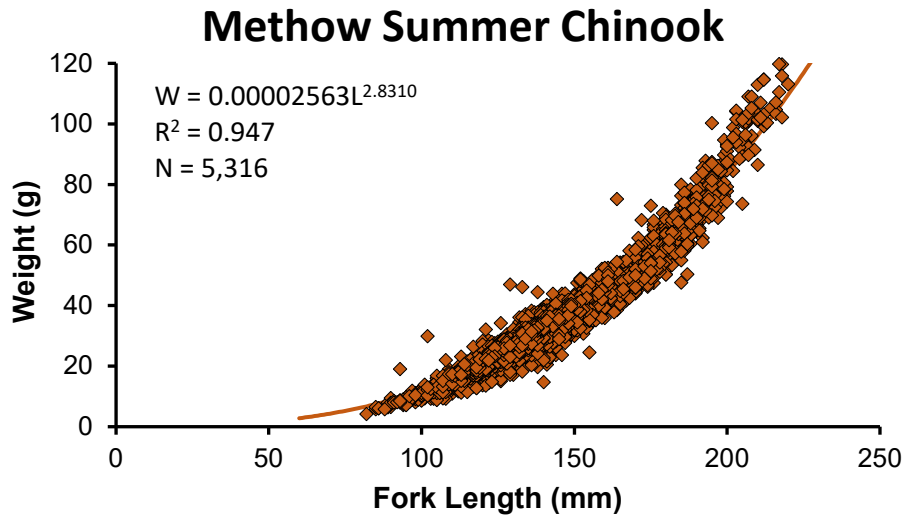


Figure 36. Relationship between fork length (mm) and weight (g) of juvenile Methow River summer Chinook Salmon sampled before release during 2003-2018.

Wells Subyearling Summer Chinook Salmon

Number Released—The goal of the supplementation program is to release 484,000 ($\pm 10\%$) 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.

Wells Subyearling Summer Chinook

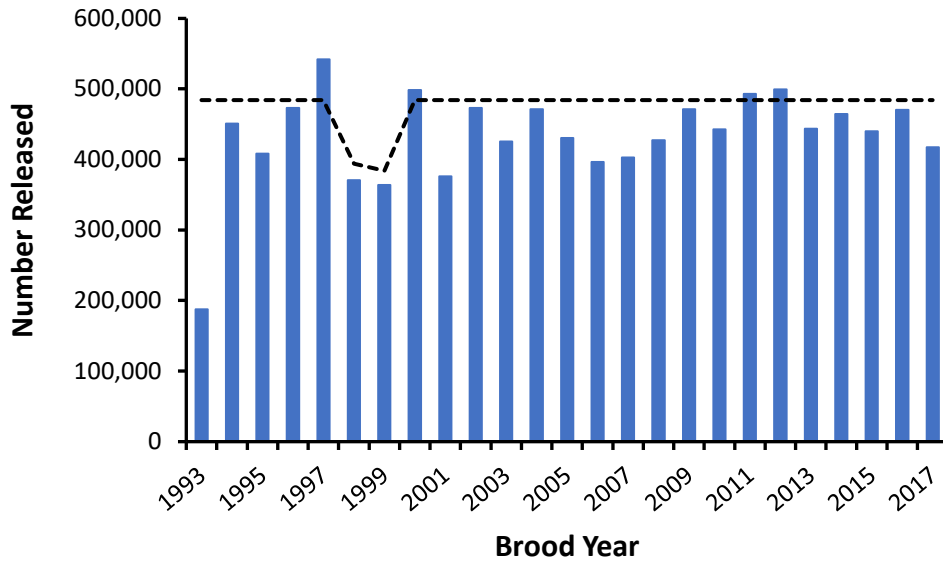


Figure 37. Number of subyearling summer Chinook Salmon released from the Wells Fish Hatchery for brood years 1993-2017. The dashed horizontal line represents the target release number (484,000 except for 1998-1999).

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

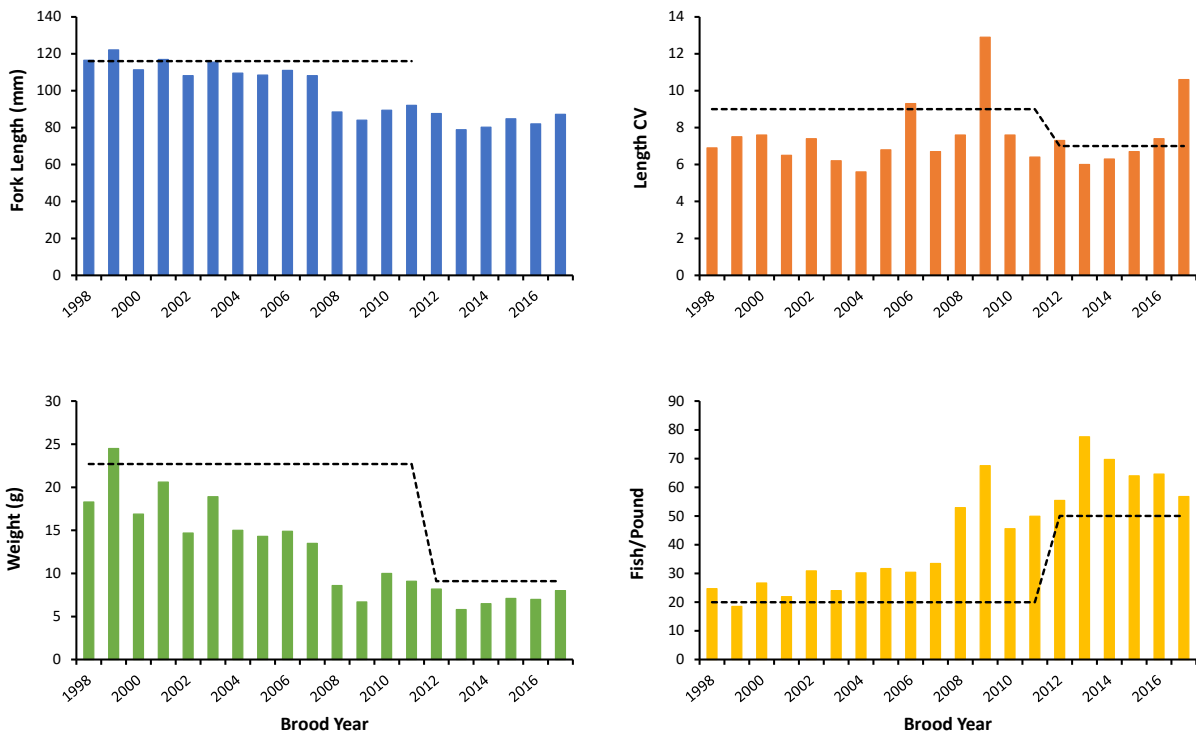


Figure 38. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of subyearling summer Chinook Salmon released from the Wells Fish Hatchery for brood years 1998-2017. The dashed horizontal lines represent the target length (116 mm from 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).

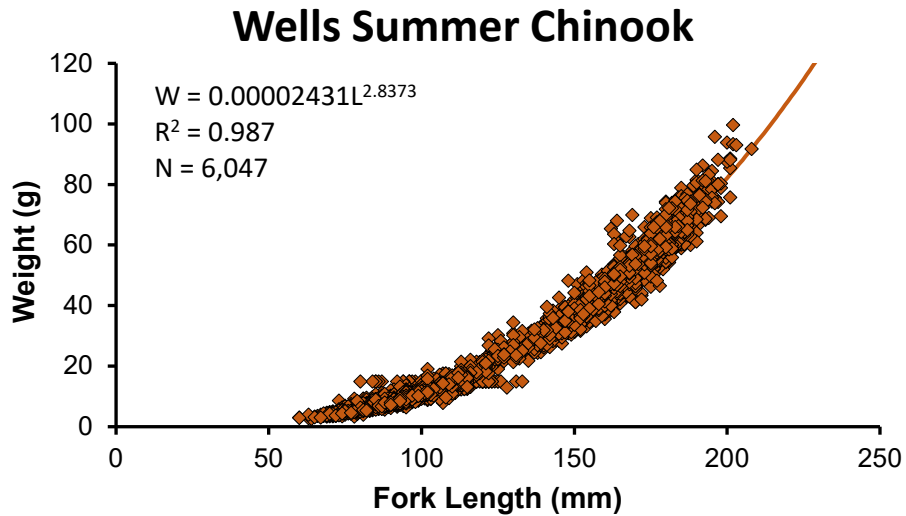


Figure 39. Relationship between fork length (mm) and weight (g) of juvenile Wells summer Chinook Salmon sampled before release during 2003-2018.

Wells Yearling Summer Chinook Salmon

Number Released—The goal of the supplementation program is to release 320,000 ($\pm 10\%$) 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.

Wells Yearling Summer Chinook

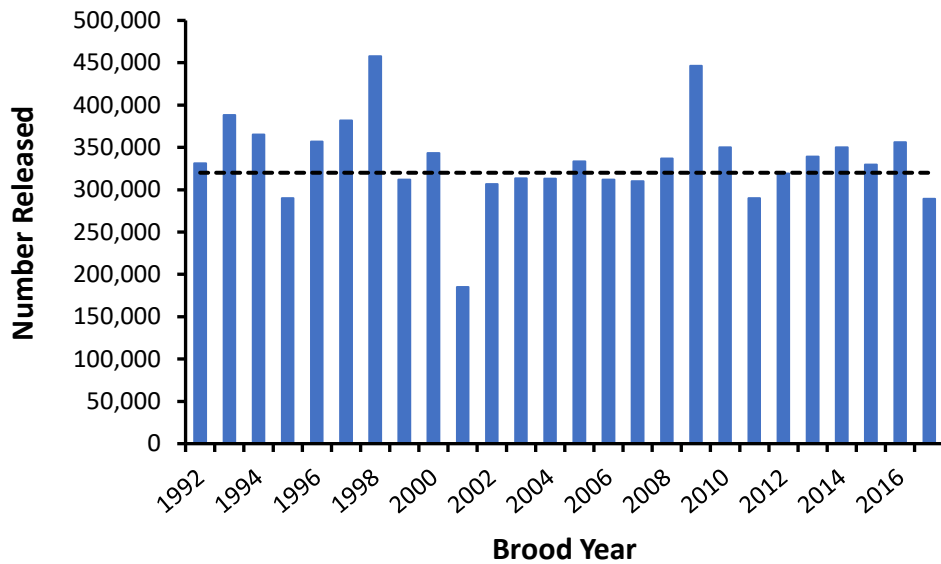


Figure 40. Number of yearling summer Chinook Salmon released from the Wells Fish Hatchery for brood years 1992-2017. The dashed horizontal line represents the target release number (320,000).

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).

Wells Yearling Summer Chinook Salmon Hatchery Releases

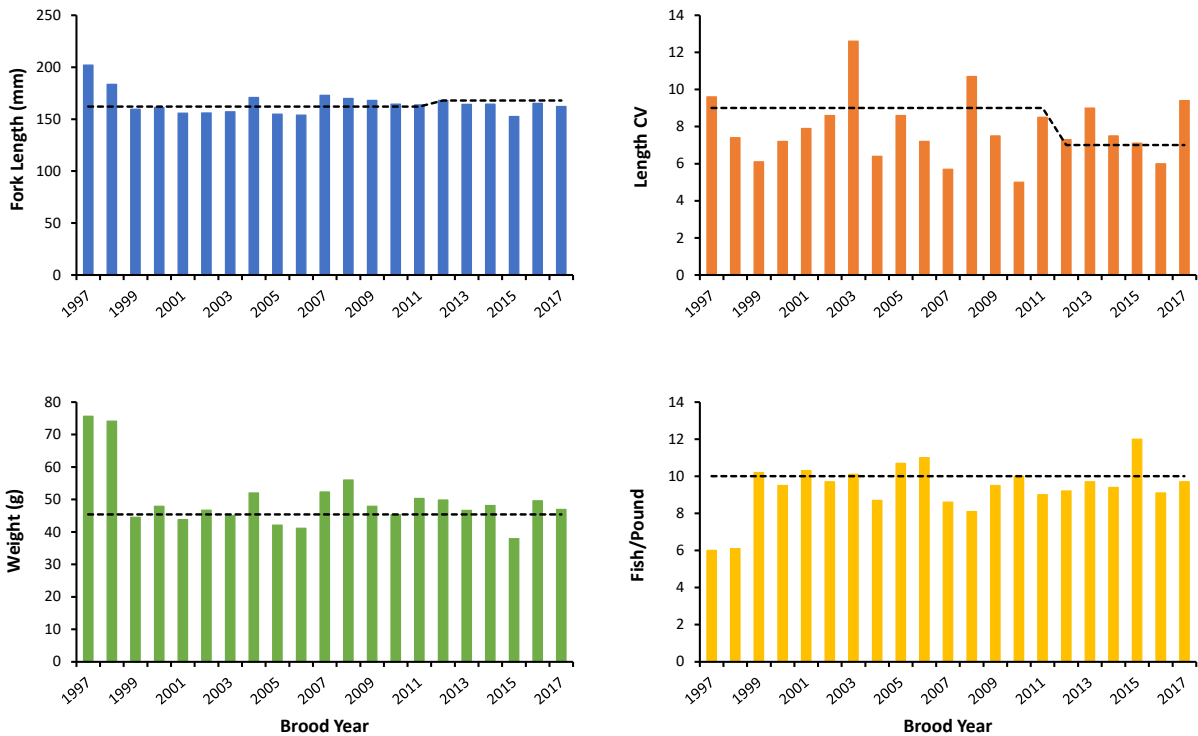


Figure 41. Average fork length (mm), coefficient of variation (CV) of fork length, average weight (g), and number of fish per pound of yearling summer Chinook Salmon released from the Wells Fish Hatchery for brood years 1997-2017. The dashed horizontal lines represent the target length (162 mm from 1997-2011 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.

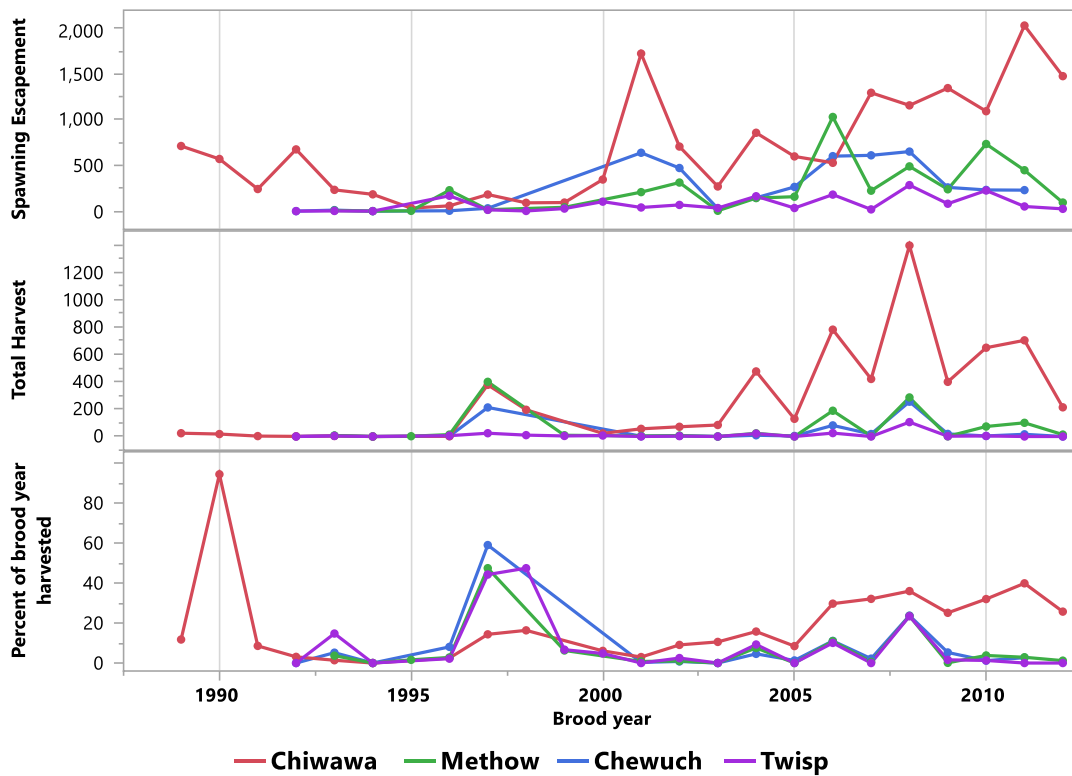
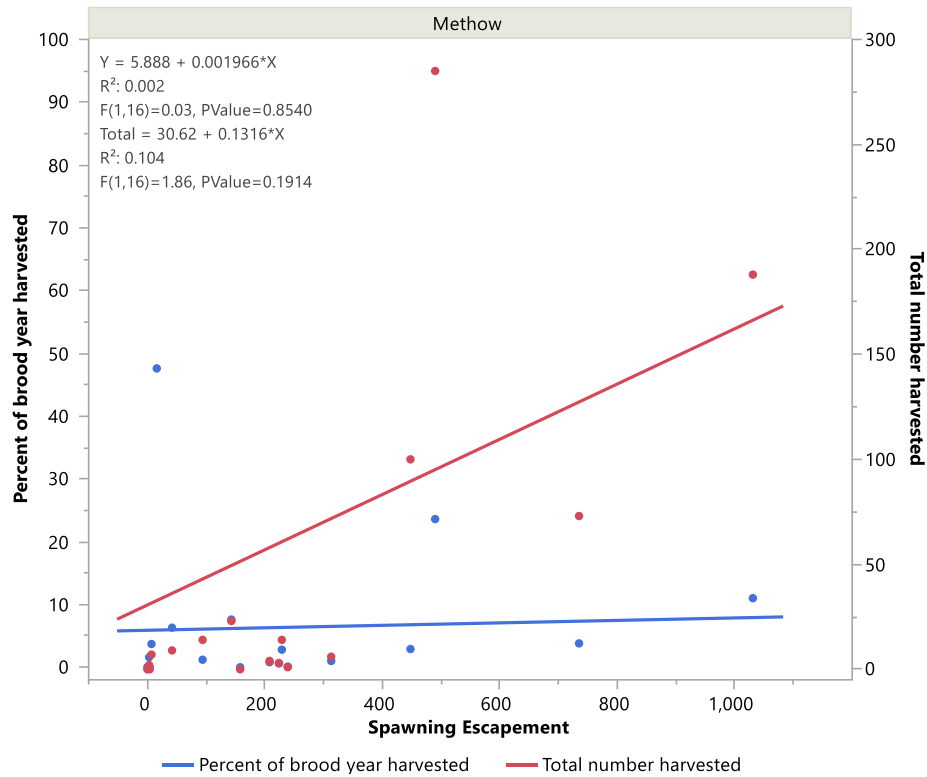
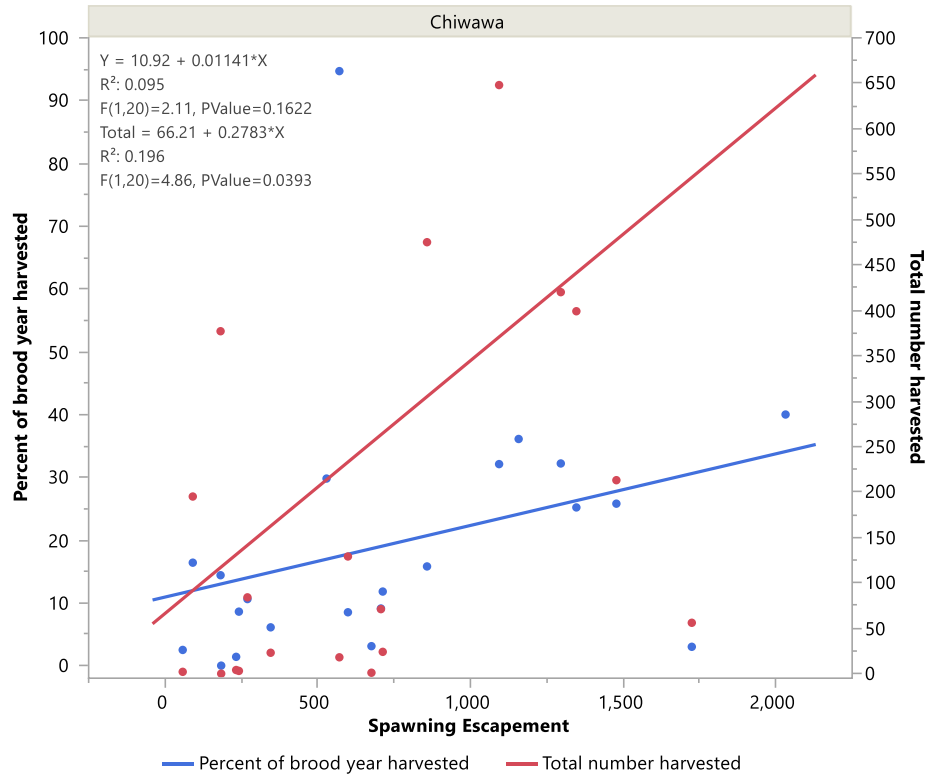


Figure 1. Spawning escapement, total harvest, and percent of brood year harvested for hatchery spring Chinook Salmon from the Chiwawa ($\bar{x} = 25.6\%$), Methow ($\bar{x} = 5.1\%$), Chewuch ($\bar{x} = 5.8\%$), and Twisp ($\bar{x} = 4.6\%$) rivers (averages represent percent of brood year harvested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



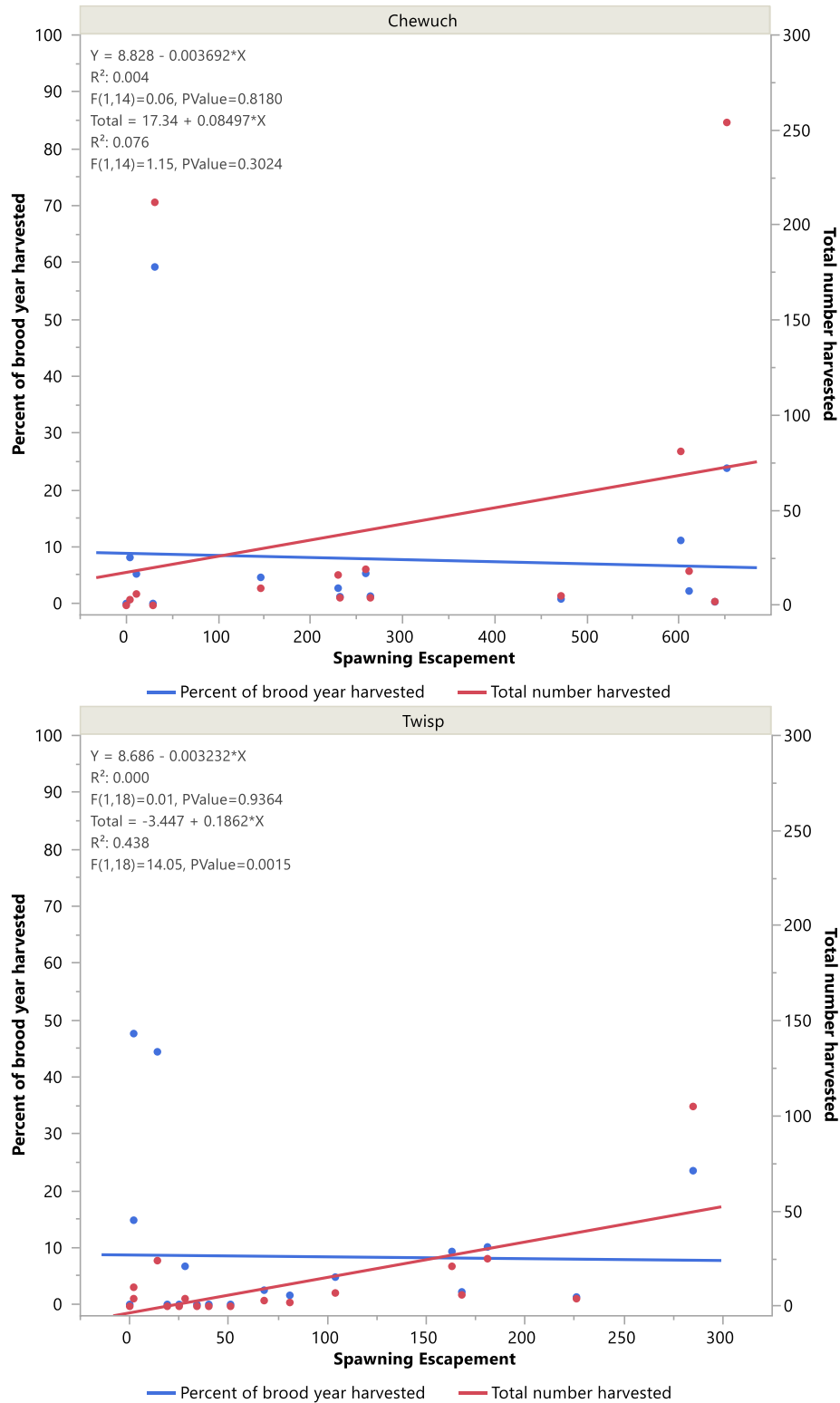


Figure 2. Spawning escapement versus percent of brood year harvested and total number of hatchery fish harvested for spring Chinook Salmon from the Chiwawa, Methow, Chewuch, and Twisp rivers.

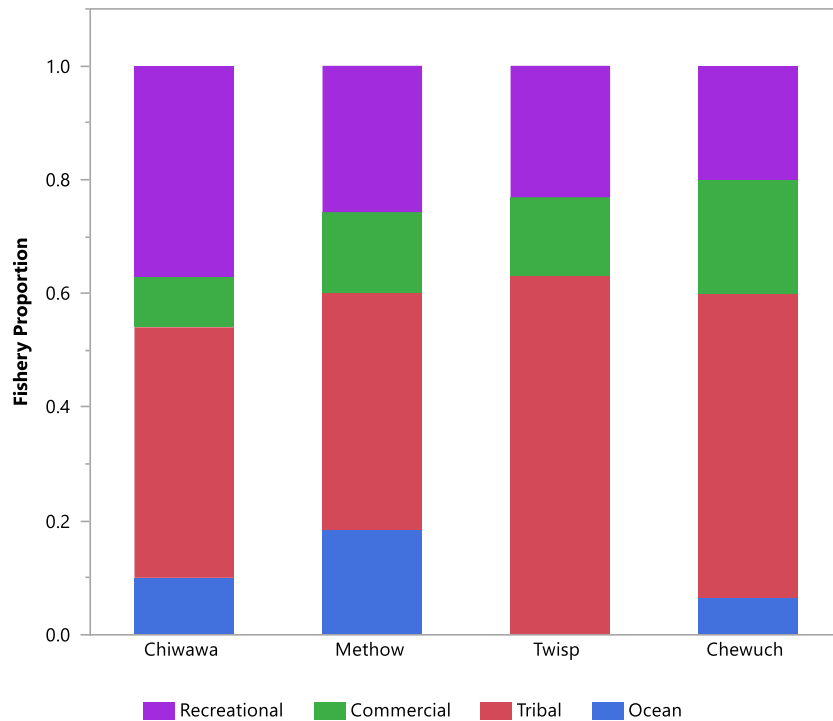


Figure 3. Fishery proportions (mean values) for spring Chinook Salmon harvested from the Chiwawa, Methow, Twisp, and Chewuch rivers.

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.

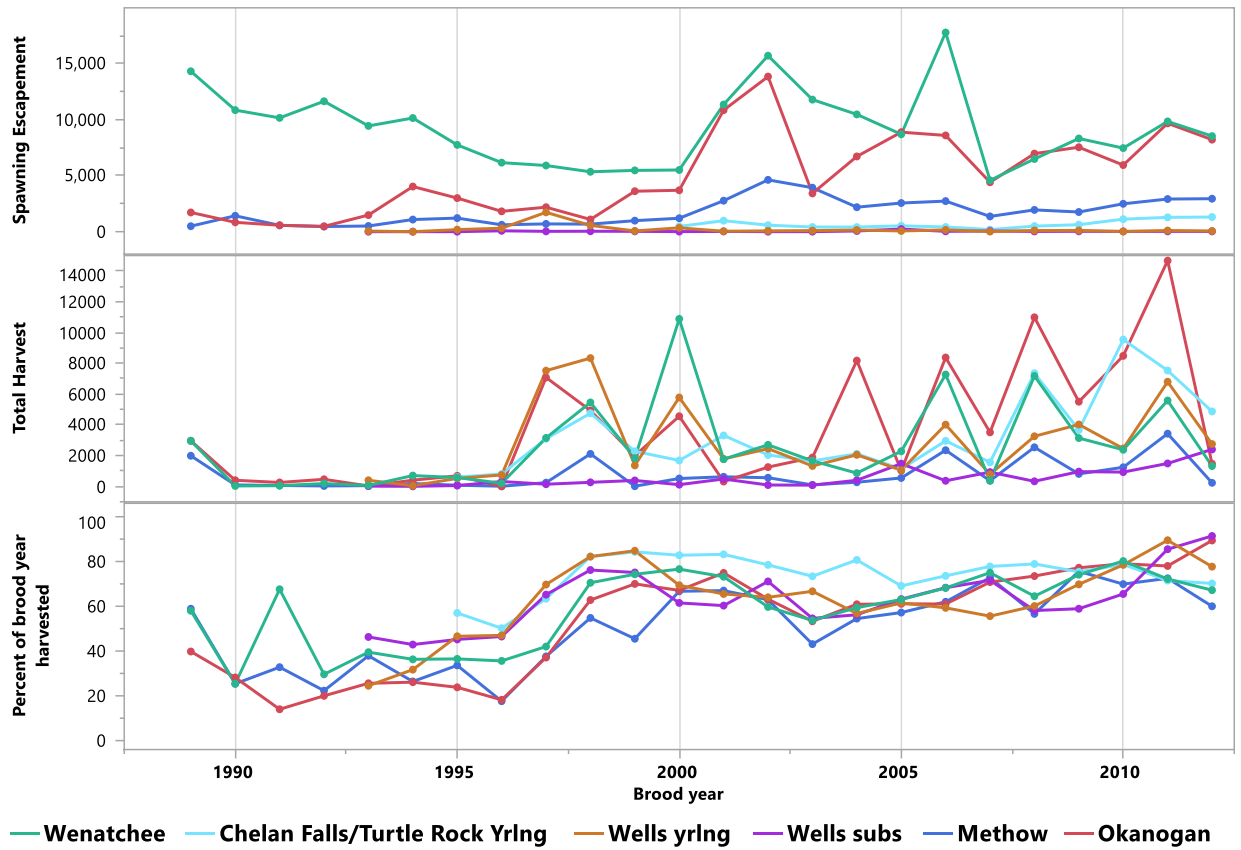


Figure 4. Spawning escapement, total harvest, and percent of brood year harvested for hatchery-origin summer Chinook Salmon from the Wenatchee River ($\bar{x} = 67.8\%$), Chelan Falls/Turtle Rock yearling program ($\bar{x} = 74.6\%$), Wells Hatchery yearling program ($\bar{x} = 67.6\%$), Wells Hatchery 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).

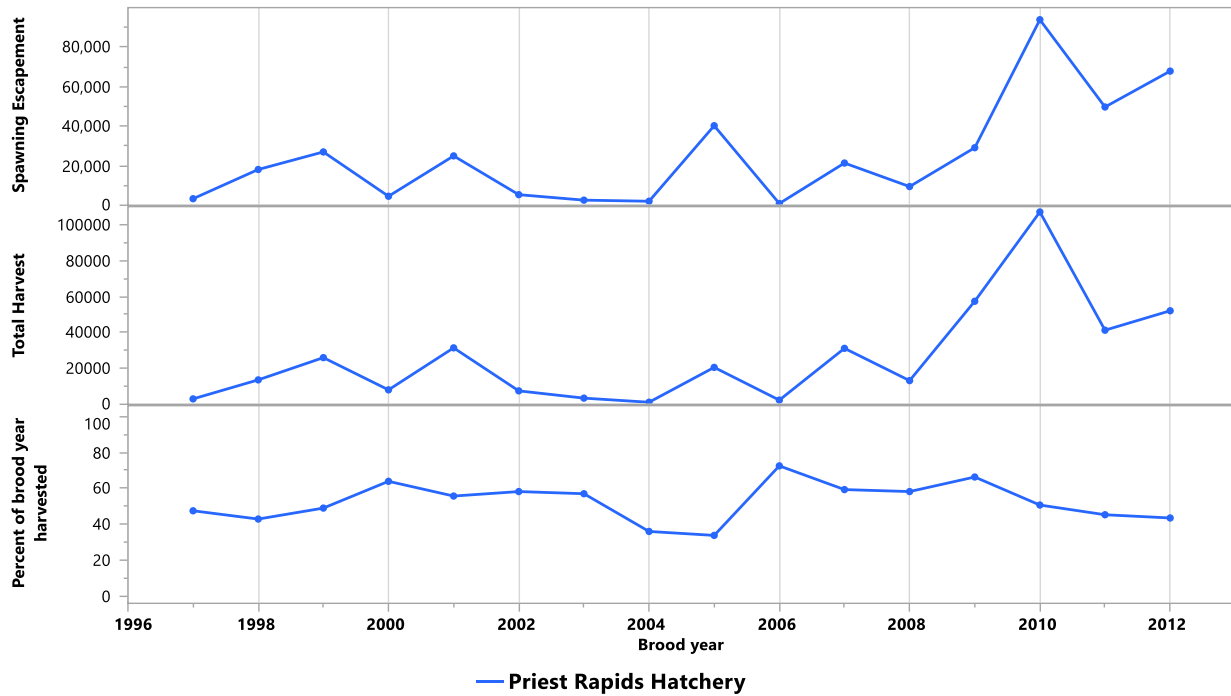
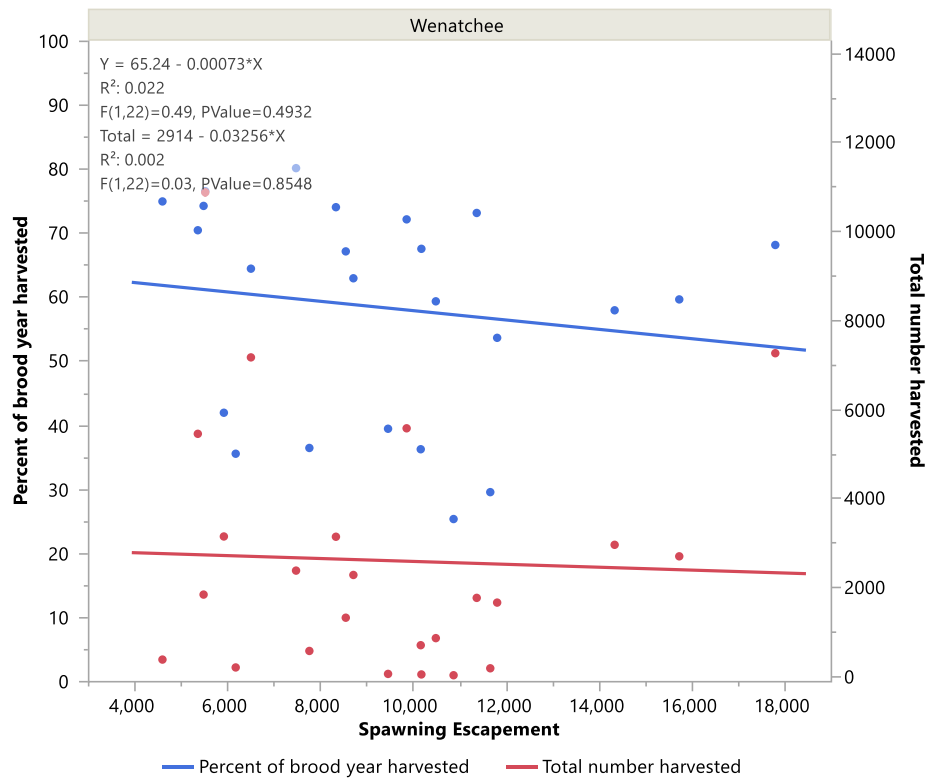
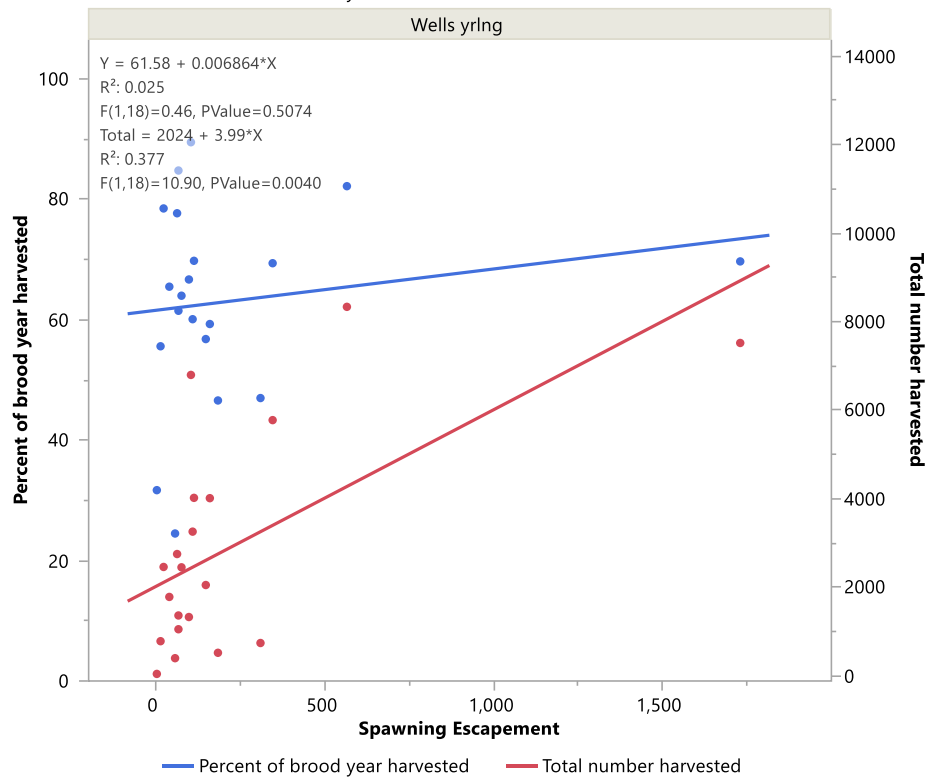
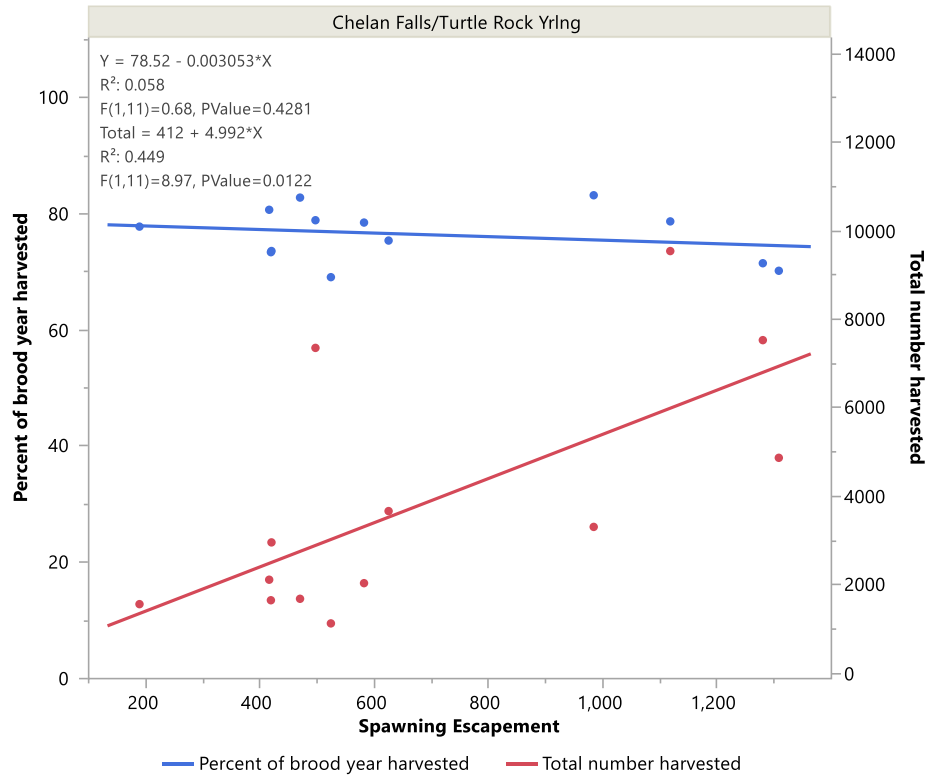
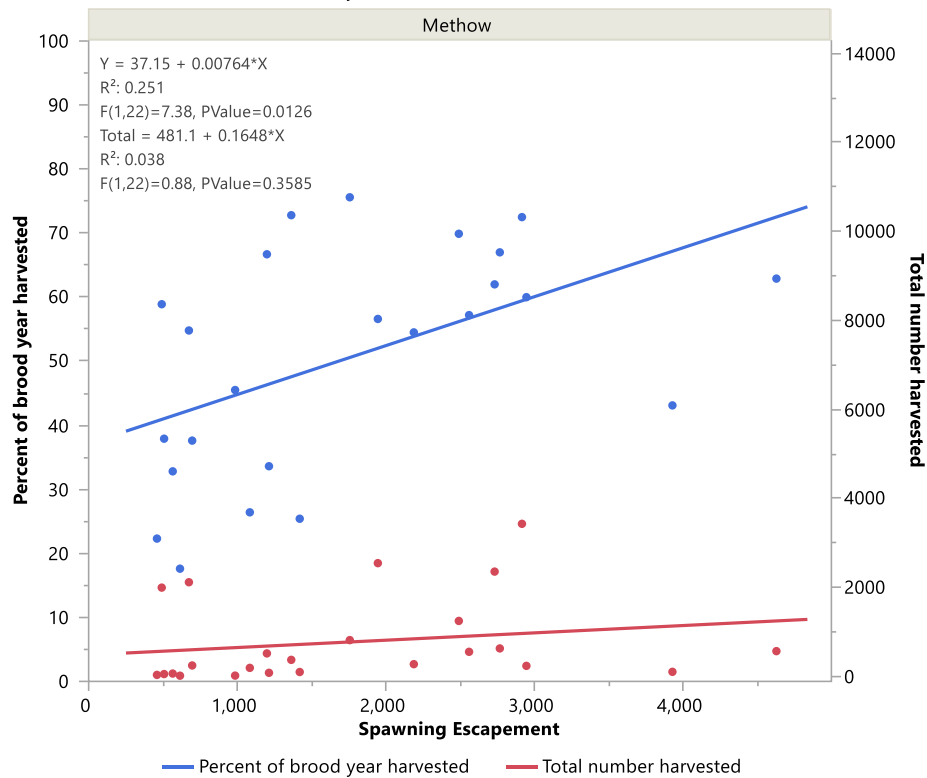
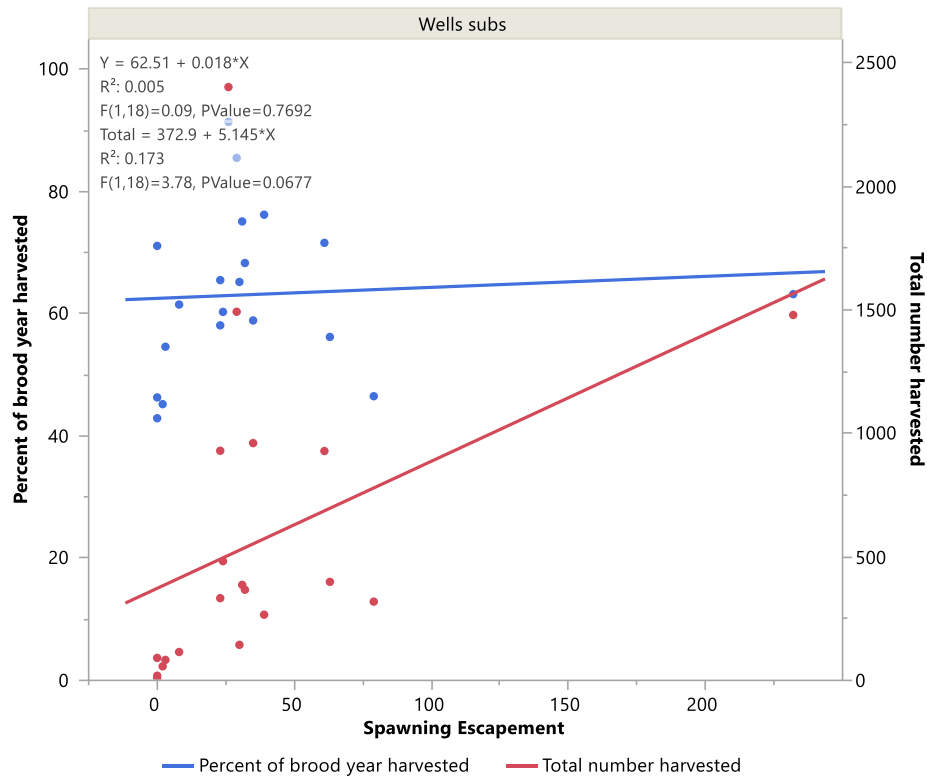


Figure 5. Spawning escapement, total harvest, and percent of brood year harvested for hatchery fall Chinook Salmon from Priest Rapids Hatchery ($\bar{x} = 52.5\%$) program (average represent percent of brood year harvested over brood years 2004-2012).







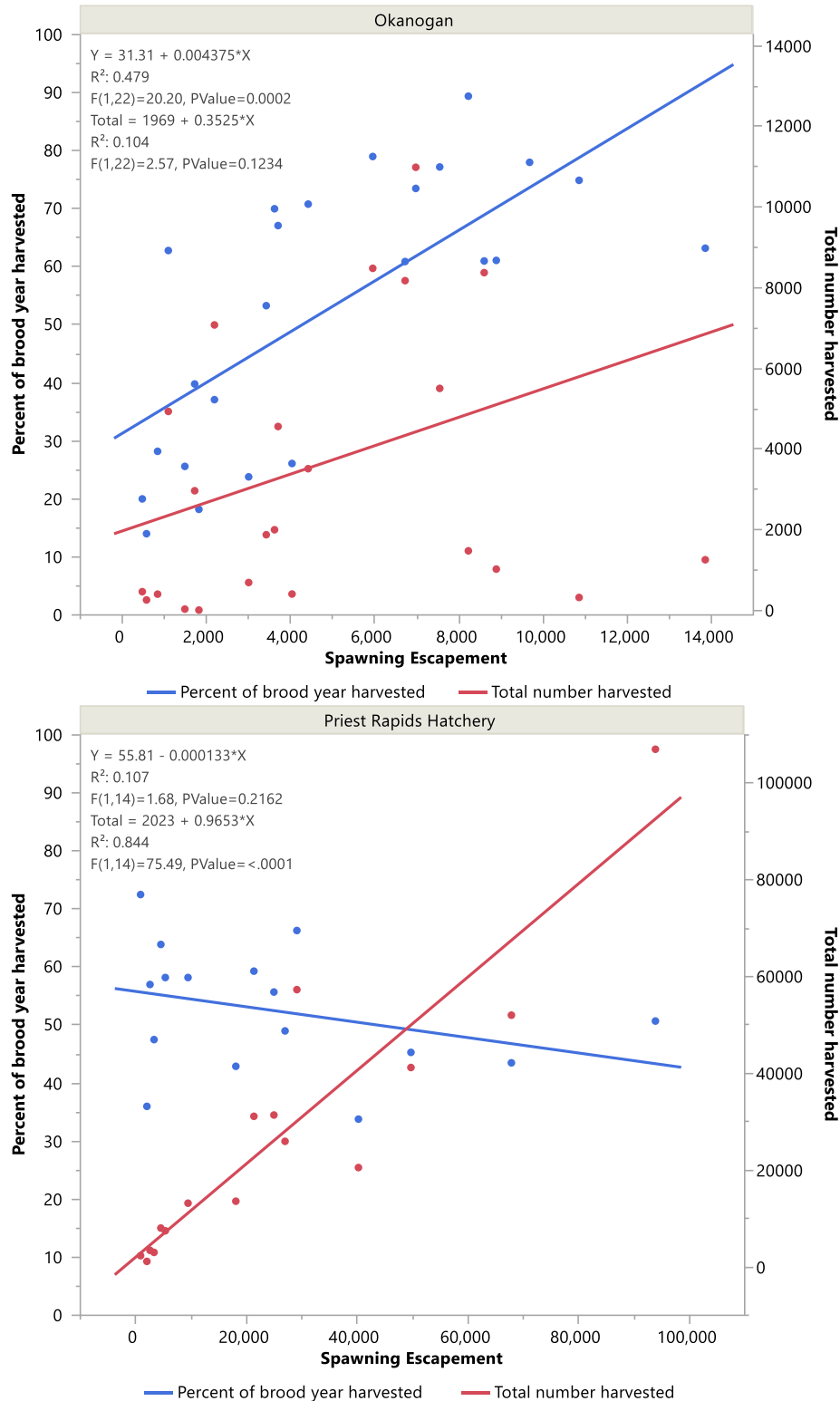


Figure 6. Spawning escapement versus percent of brood year harvested and number harvested for hatchery-origin summer Chinook Salmon from the Wenatchee River, Chelan Falls/Turtle Rock yearling program, Wells Hatchery yearling program, Wells Hatchery subyearling program, Methow River, Okanogan River, and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

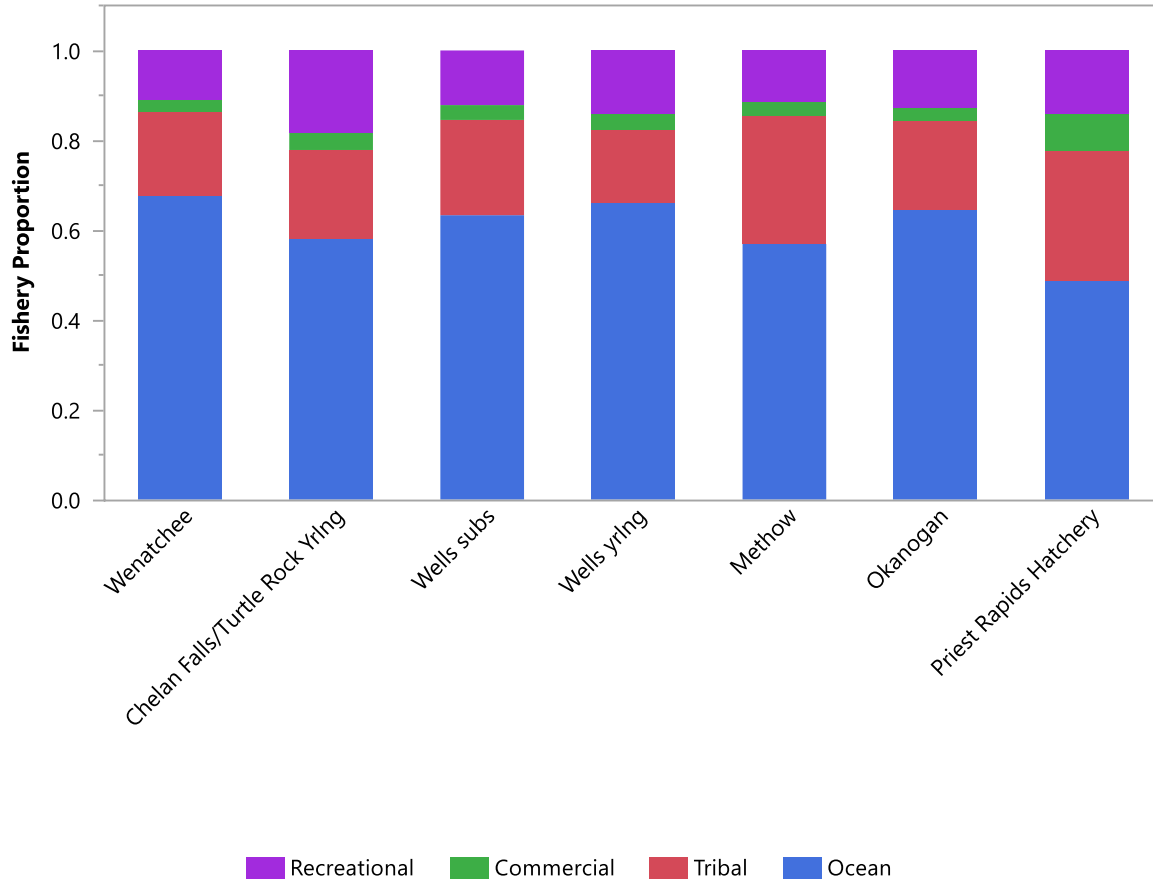


Figure 7. Fishery proportions (mean values) for summer Chinook Salmon harvested from the Wenatchee River, Chelan Falls/Turtle Rock yearling program, Wells Hatchery subyearling program, Wells Hatchery yearling program, Methow River, Okanogan River, and fall Chinook Salmon from Priest Rapids Hatchery.

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.

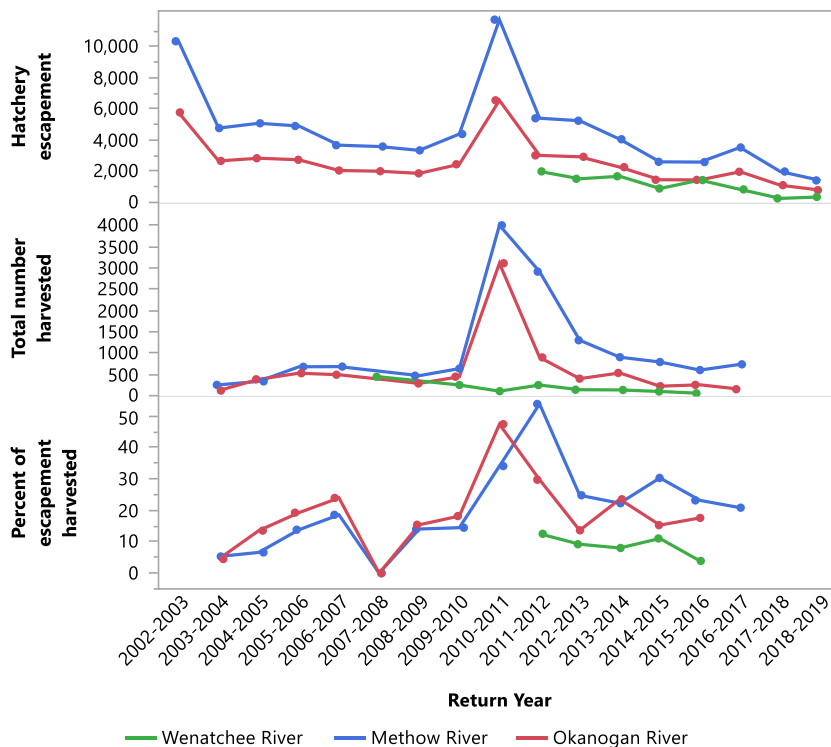
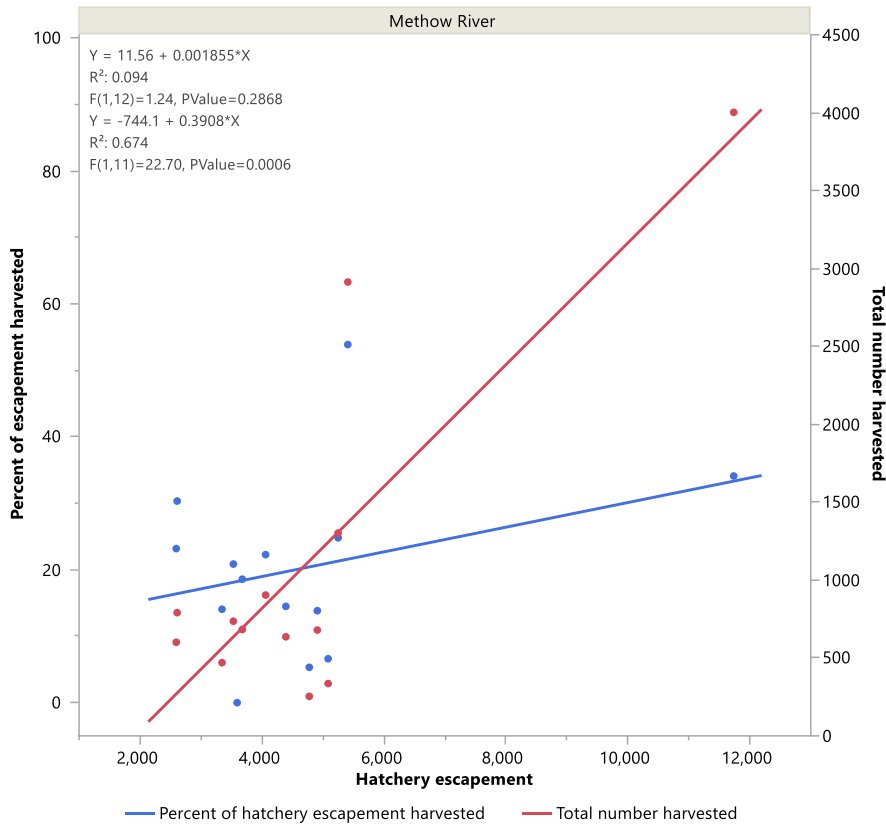
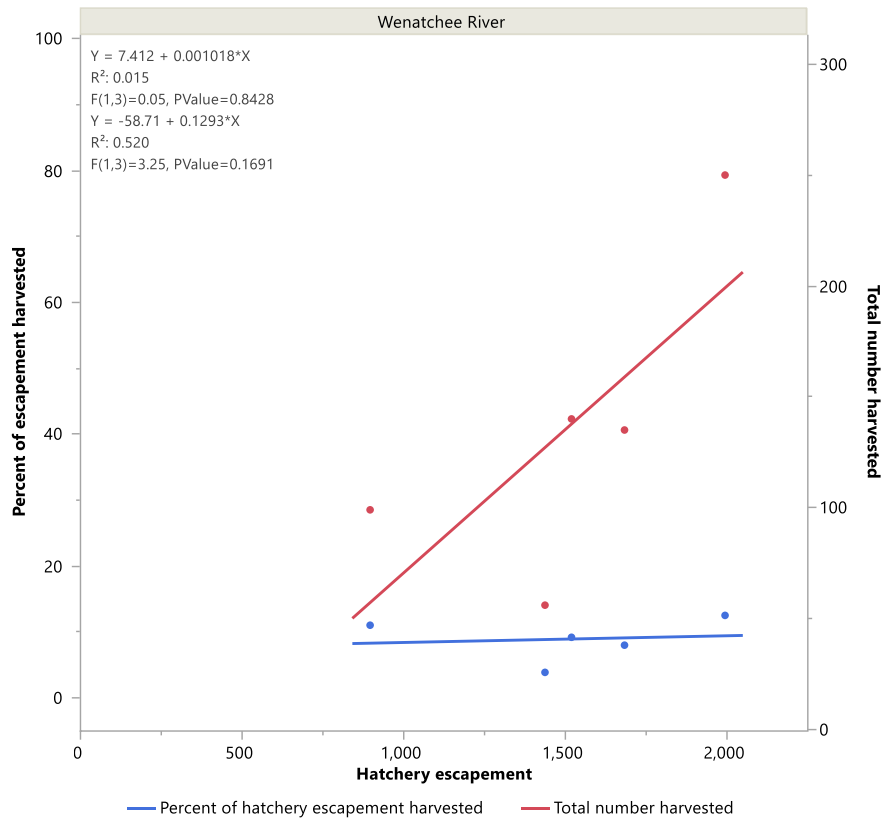


Figure 8. Escapement, total number harvested, and percent harvest of hatchery-origin steelhead escapement to the Wenatchee ($\bar{x} = 8.7\%$), Methow ($\bar{x} = 20.2\%$), Okanogan ($\bar{x} = 18.6\%$) rivers (averages represent return years 2003-2017 for the Methow and Okanogan rivers and 2011-2016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



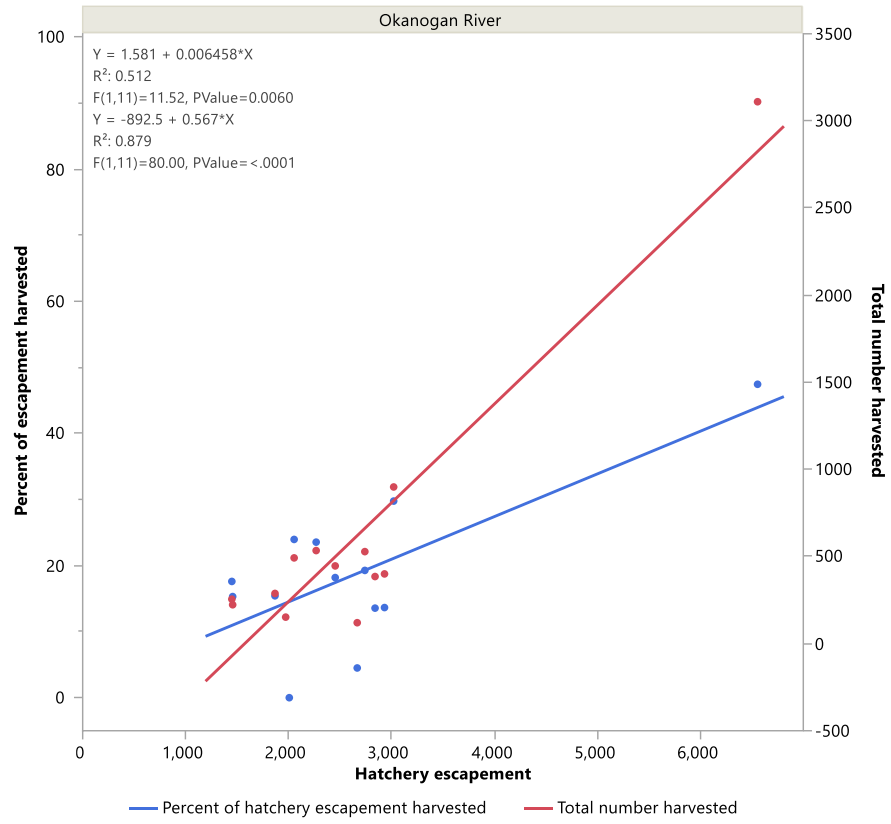


Figure 9. Escapement versus percent of escapement harvested and number harvested of hatchery-origin steelhead from the Wenatchee, Methow, and Okanogan rivers.

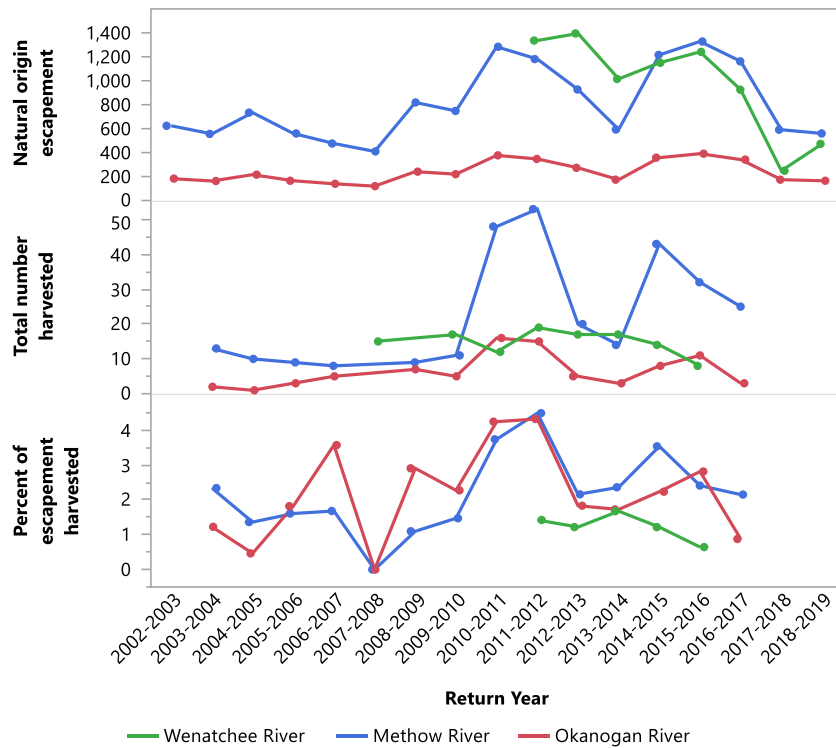
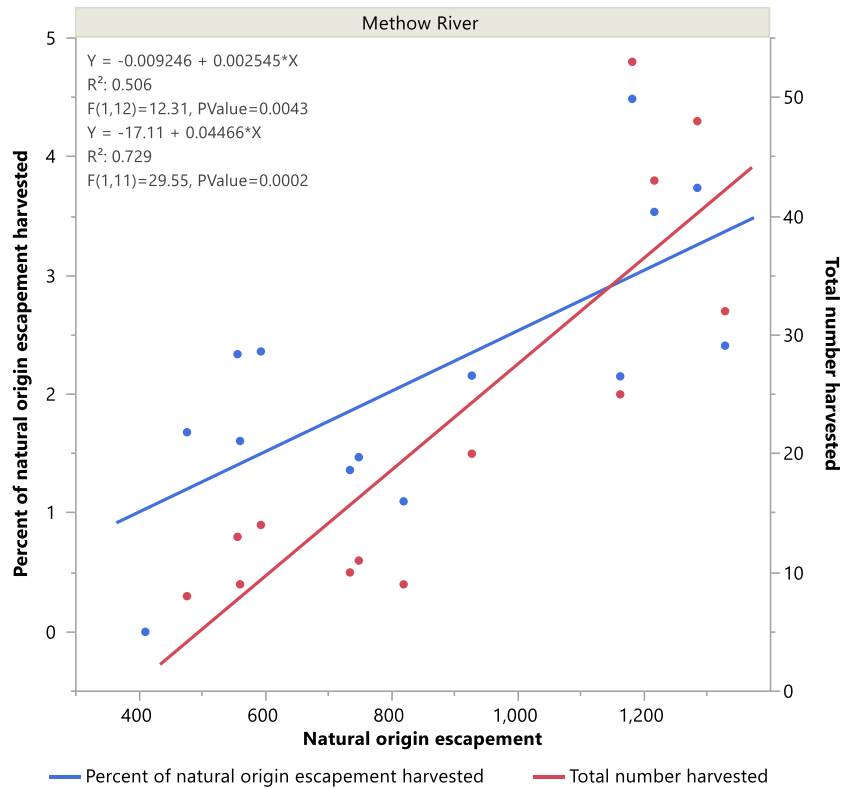
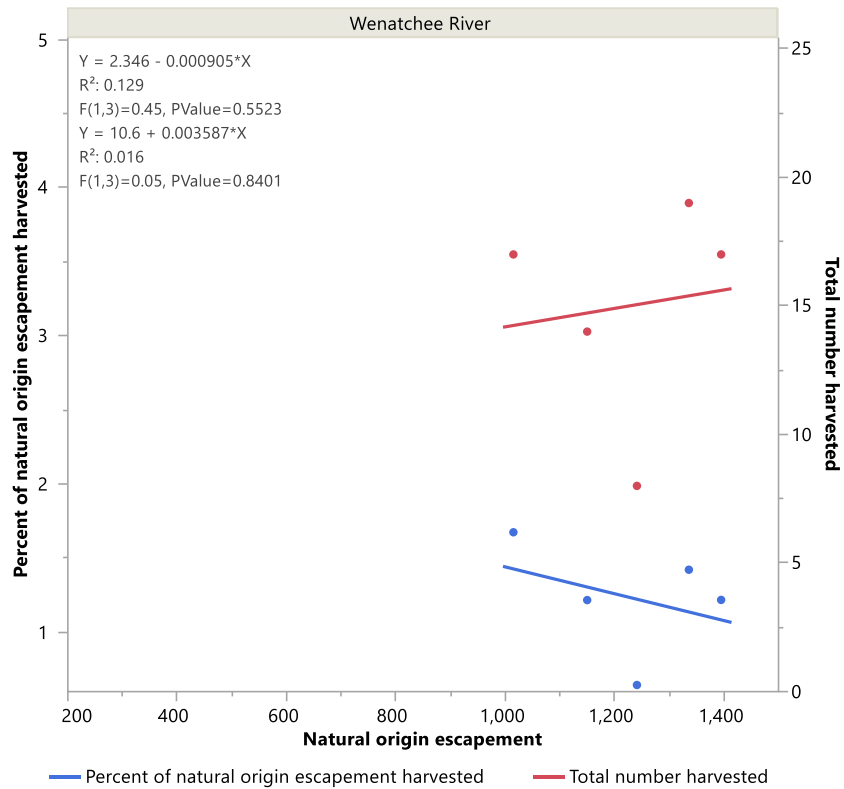


Figure 10. Escapement, total number harvested, and percent of escapement harvested of natural-origin steelhead for the Wenatchee ($\bar{x} = 1.36\%$), Methow ($\bar{x} = 2.17\%$), and Okanogan ($\bar{x} = 2.16\%$), rivers (averages represent returns years 2003-2017 for the Methow and Okanogan rivers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



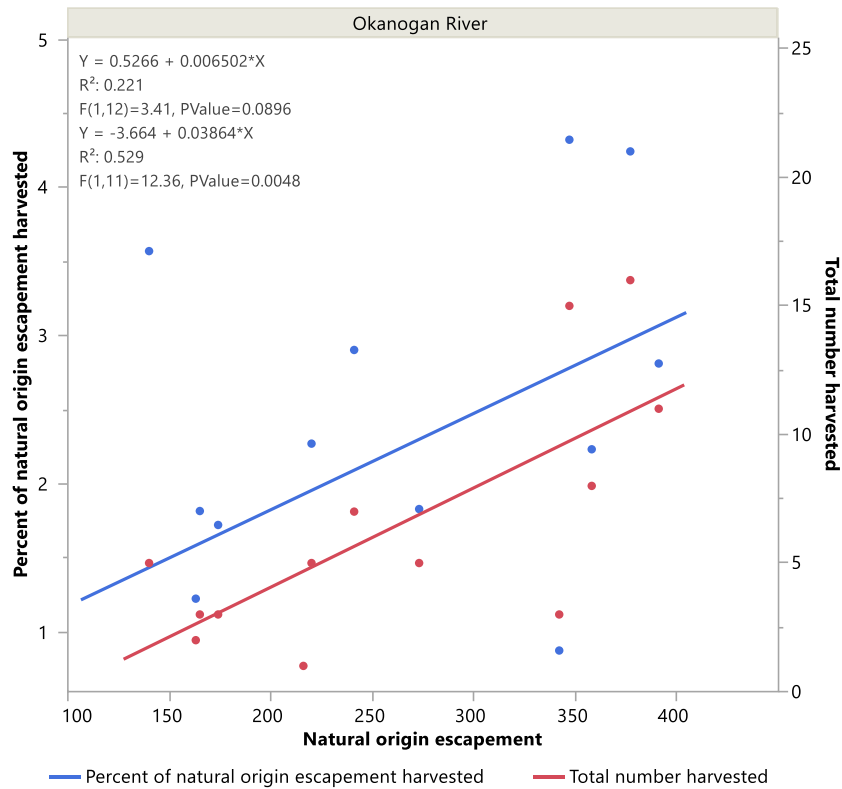


Figure 11. Escapement versus percent of escapement harvested and total number harvested of natural-origin steelhead from the Wenatchee, Methow, and Okanogan rivers.

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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