

**Abundance and Migration Success of Overshoot Steelhead in the Upper Columbia River**

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Abstract: Summer steelhead *Oncorhynchus mykiss* may enter freshwater almost a year before spawning and potentially make long migrations (>1,000 km) to interior headwater habitats. However, in response to sub-optimal freshwater habitat conditions, adult summer steelhead may exhibit complex behaviors during upstream migration in the Columbia River Basin. Steelhead may migrate upstream of their natal tributary, or overshoot, and spend days to several months before subsequently migrating downstream, or fallback, to their natal tributary to spawn. An existing Bayesian patch occupancy model, derived from observations of adult steelhead tagged with passive integrated transponder (PIT) tags to estimate population-specific abundance upstream of the tagging location, was modified to estimate the abundance of overshoot fallbacks. Overshoot steelhead abundance at the tagging location was estimated based on the relationship the number of known overshoot fallbacks and their model-estimated abundance. The annual mean (SD) proportion of overshoot steelhead that successfully migrated downstream of the tagging location (i.e., Priest Rapids Dam) was 0.57 (0.12). The spatial distribution of overshoot steelhead suggested the number of dams negatively affected downstream migration success probability. Improved downstream passage survival for adult steelhead will increase the abundance of those affected populations, while reducing potential genetic introgression of upstream populations (i.e., strays). This is the first study to estimate the abundance of overshoot and fallback steelhead providing the data necessary for scientists to estimate potential conservation benefits of improved downstream survival. The proportion of overshoot steelhead for those affect populations will likely increase in response to climate change related effects (i.e., increasing water temperatures). Studies have consistently shown that surface flow passage routes (e.g., sluiceways and temporary spillway weirs) are very effective in guiding and passing adult steelhead downstream of Columbia River hydroelectric projects suggesting changes in dam operations must occur throughout the migration route to maximize conservation benefits.

Summer steelhead *Oncorhynchus mykiss* in the Columbia River enter freshwater the year prior to spawning. This life history strategy allows for access to spawning habitats that are a greater distance from the ocean, or to areas with only seasonal access (i.e., temporary migration barriers due to low discharge or warm water temperatures), compared to winter steelhead that enter freshwater the same year as spawning. Adult summer steelhead may enter the Columbia River over an eight-month period between March and October (Busby et al. 1996), but peak migration at Bonneville Dam (rkm 234) occurs during August when water temperatures

upstream of Bonneville Dam may be near lethal limits (Richter and Kolmes 2005). The effects of Columbia River water temperatures on survival of adult anadromous salmonids during migration is a concern for fish managers (Keefer et al. 2004). Interior Columbia River summer steelhead populations (i.e., upstream of Bonneville Dam) are thus at greater risk to future climate-change related increases in water temperature (Wade et al. 2013). The physiological effects, both acute and chronic, of elevated water temperatures on salmonids are well studied and include higher metabolic demands, stress, prevalence of disease and death (McCullough 1999). Behavioral effects from elevated water temperatures include delayed migration at hydroelectric dams (Keefer et al. 2004), temporary use of non-natal tributaries (High et al. 2006) and overshooting natal tributaries (Richins and Skalski 2018).

Due to a prolonged period of freshwater entry and residency prior to spawning, summer steelhead may exhibit complex movement patterns as a behavioral thermoregulation response to suboptimal freshwater habitat conditions. Summer steelhead have been shown to temporarily use several non-natal tributaries in the lower Columbia River (i.e., downstream of the confluence with the Snake River) or areas in the Columbia River immediately downstream (i.e., tributary plume) as cool water refuges (High et al. 2006; Keefer et al. 2009; Hess et al. 2016; Keefer et al. 2018). Keefer et al. (2009) found that steelhead passage time through the Bonneville Dam reservoir increased after water temperature exceeded 19 °C, as did their use of cool water refuges. Steelhead may remain in cool water refuges between 1 h and 237 d (High et al. 2006). The spatial extent of non-natal tributary use by steelhead may extend as far upstream as 71 km (Hess et al. 2016). The extent of cool water refuge use varies with Columbia River water temperature and has been reported as high as 66% of all interior Columbia River steelhead and, of those, many steelhead (33%) used more than one tributary (High et al. 2006). Summer

steelhead from the early part of the run (before Aug 25) use cool water refuges at a slightly higher rate (66%) than fish from the later (after Aug 25) part of the run (High et al. 2006). The survival benefits of this behavior are less clear. Keefer et al. (2009) reported that survival of steelhead using cool water refuges was 8% lower overall (11% for hatchery and 5% for wild fish) compared to steelhead that did not use cool water refuges, but lower survival was attributed to higher rates of harvest within the cool water tributaries compared to in the Columbia River.

Summer steelhead from some interior Columbia River populations also may exhibit a complex movement pattern referred to as overshooting. While the use of cool water refuges by summer steelhead as a thermoregulation response typically occurs downstream of natal tributaries, overshooting refers to a behavior that involves steelhead moving upstream of their natal tributary. Richins and Skalski (2018) reported that overshoot probability and Columbia River water temperature near the natal tributary were positively related. To a lesser extent, incomplete or nonsequential homing during the juvenile life stage associated with other conservation actions (i.e., barging smolts through dams during outmigration or hatchery rearing location, respectively) were also found to be important factors, as well as ocean age and adult ladder usage relative to their location of their natal tributary (Richins and Skalski 2018). Overshooting has also been reported in the Columbia River for Chinook Salmon *O. tshawytscha*, but at lower rates than reported for steelhead (Boggs et al. 2004; Keefer et al. 2008a; Eiler et al. 2015; Mann and Snow 2018). Eiler et al. (2015) reported very low rates of overshooting for Chinook Salmon (<1%) in the free-flowing Yukon River, AK. Conversely, Richins and Skalski (2018) reported overshoot rates of adult steelhead as high as 71%, with many populations exhibiting rates > 50%. However, the proportion of overshoot steelhead that successfully

migrate downstream and returned their natal stream, or “overshoot fallback,” is more variable and less understood and ranged from 18% to 75% (Richins and Skalski 2018).

Estimates of overshoot fallback abundance do not account for steelhead that overshoot their natal stream but failed to fallback due to mortality sources both intentional (i.e., harvest) or unintentional (e.g., turbine strikes) that may occur during their downstream movement. Therefore, estimates of spawner abundance and productivity for overshoot populations, based on returns to the natal stream or subbasin, would be negatively biased compared to populations that don’t exhibit overshooting behavior (i.e., no overshoot fallback related mortality). Given the variability in overshoot fallback reported for steelhead populations in the Columbia Basin (Richins and Skalski 2018), the absence of these fish in their natal tributary or presence (i.e., PIT tag detection) in a non-natal tributary may have conservation implications, either demographically, genetically (i.e., introgression), or both. While the apparent mortality or cost of temporarily using downstream non-natal tributaries as cool water refuges can be reduced, in part, through harvest regulations (Keefer et al. 2009), overshoot steelhead exhibit a much broader geographic upstream distribution and are subject to other mortality sources in addition to harvest.

Overshoot steelhead must migrate downstream to return to their natal tributary. Khan et al. (2013) found that downstream migrating adult steelhead greatly prefer surface (e.g., debris sluiceway) over turbine passage routes through dams. However, if the only passage route during non-spill periods is through the turbines (Richins and Skalski 2018), steelhead may experience higher mortality rates (Wertheimer and Evans 2005). If preferred passage routes are not available, steelhead may expend considerable energy searching for passage routes prior to spawning or may simply spawn in the nearest available stream (i.e., stray). Hence, overshoot steelhead may suffer high mortality trying to return to their natal stream during winter months

(i.e., demographic cost to their natal population) or spawn in a non-natal stream and have genetic impacts (i.e., introgression) on upstream populations. Furthermore, if the abundance of overshoot or non-natal steelhead is not known or accounted for, their presence within non-natal populations may mask the true conservation status or viability of those populations. Given the risks associated with overshoot behavior on populations of conservation concern, the objectives of this study were to: (1) estimate the annual abundance of overshoot steelhead that successfully migrated downstream of Priest Rapids Dam prior to spawning (overshoot fallbacks); (2) estimate the annual abundance of overshoot steelhead at Priest Rapids Dam; (3) estimate the annual proportion of overshoot fallback for steelhead that were detected at Priest Rapids Dam; (4) evaluate the effect of downstream dam crossings on fallback success and (5) compare migration patterns and timing of non-overshoot and overshoot steelhead into natal tributaries.

#### <A>Methods

*Study area* – The Upper Columbia River (UCR) steelhead distinct population segment (DPS) is comprised of four steelhead populations and extends upstream from the confluence of the Yakima River to the border with Canada (Figure 1). Steelhead status and trend monitoring has been occurring at Priest Rapids Dam since 1986 (Brown 1995) and is the first location fish can be counted and sampled upstream from the confluence with the Yakima River. Chief Joseph Dam was built without fish ladders, but fish ladders in all downstream dams possess equipment to detect passive integrated transponder (PIT) tags, except Wanapum Dam. The Middle Columbia River (MCR) DPS comprises 17 extant steelhead populations and extends downstream from the Yakima River to the White Salmon River, WA, and Fifteen Mile Creek, OR. The Snake River (SR) DPS includes 24 extant steelhead populations that spawn below all natural and

manmade anadromous fish barriers within the Snake River Basin. Ice Harbor Dam on the Snake River is the first location steelhead entering the SR DPS can be counted during their upstream migration including PIT tag detection.

*PIT tag data collection* – PIT tagging of juvenile steelhead occurs in Columbia River tributaries and hatcheries to estimate smolt abundance, assess juvenile and adult survival, travel time, migration patterns, and to address other research or management questions (e.g., Haeseker et al. 2012). In addition, we systematically sampled adult steelhead at Priest Rapids Dam (PRD), Columbia River rkm 639, during their adult migration in return years 2010 to 2017 (Figure 1, Waterhouse et al. 2020). We collected biological data (length and sex), scale samples, and injected PIT tags into all adult hatchery and wild steelhead at the PRD trap that were not already PIT tagged (i.e., to prevent double tagging) on three days per week from early July through mid-November, with an annual target sample rate of ~15% of all steelhead passing PRD (NMFS 2003). Hatchery steelhead were identified based on the presence of marks (adipose fin removed), tags (coded wire or PIT), or hatchery scale pattern (Bernard and Myers 1996). Adult steelhead PIT tag data were uploaded into the regional PIT Tag Information System database (PSMFC 2015, Tenney et al. 2017). The PTAGIS database (<https://www.ptagis.org>) was subsequently queried to obtain PIT tag detections of adult steelhead PIT tagged at PRD, at mainstem dams on the Snake/Columbia Rivers, and at instream PIT tag detection sites (IPDS). These data were formatted for analysis to estimate adult overshoot fallback and overshoot abundance at PRD as described below.

*Overshoot fallback abundance* – Escapement estimates of the four steelhead populations that comprise the UCR DPS have been estimated using the Bayesian nested patch occupancy model (POM) based on detections of a representative sample of steelhead PIT tagged at PRD beginning

in return year 2010 (Waterhouse et al. 2020). The POM simultaneously estimates the probability of a fish moving along a particular path of the stream network and the probability that a fish is observed at detection sites along that path, essentially a multi-state variation of a spatial Cormack-Jolly-Seber model (Waterhouse et al. 2020, Royle and Kéry 2007).

Observations at each site, as well as detections further upstream, provide the means to estimate detection probabilities at each site (Figure 1). Most IPDS have at least two arrays spanning the river, providing multiple chances to detect a fish passing that site.

For fish  $i$ , whether it has moved past a detection point  $j$  is denoted by a one or a zero ( $z_{i,j} \in (0,1)$ ). The probability of fish  $i$  moving to each of the possible next detection sites along the stream network ( $j+1, j+2, \dots$ ), including the probability of not moving past any of those sites, is modeled using a multinomial distribution with transition probabilities  $\psi_j$ ,

$$z_{i,j+1} \sim \text{MultiNom}(1, \psi_j)$$

and the detection of that fish at each array  $k$  at site  $j$ ,  $y_{i,j,k}$ , is modeled as a Bernoulli distribution with detection probability  $p_{j,k}$ .

$$y_{i,j,k} \sim \text{Bern}(z_{i,j}, p_{j,k})$$

$$p_{j,k} = \Pr(y_{i,j,k} = 1 | z_{i,j} = 1)$$

The overall probability of a fish moving past a detection site is the product of all the sequential downstream transition probabilities along that path. The detection probabilities,  $p$ , were estimated using detections from both hatchery and wild fish but transition probabilities,  $\psi$ , were different for hatchery and wild fish. These overall transition probabilities are multiplied by an estimate of total abundance, by origin, at Priest Rapids Dam, providing estimates of escapement past each detection site. Transition parameters ( $\psi$ ) were given a Dirichlet prior of a vector of ones, and detection parameters ( $p$ ) were given Beta (1,1) priors, all chosen to be as



minimally informative as possible. Further details of the POM can be found in Waterhouse et al. 2020.

Some adult steelhead overshoot their natal stream, get PIT tagged at PRD, fallback, and ascend their presumed natal stream to spawn (downstream of PRD) where they are detected (i.e., overshoot fallbacks). To account for this behavior, the model structure includes PIT tag interrogation sites (site codes in brackets) downstream of Priest Rapids Dam to estimate overshoot fallback abundance (Figure 1). Specifically, overshoot fallback abundances in the MCR DPS were estimated for the Yakima River at rkm 76 (Prosser Dam [PRO]), Walla Walla River at rkm 9 [PRV]), Umatilla River at rkm 5 (Three Mile Falls Dam [TMF]), the John Day River at rkm 35 (McDonald Ferry site [JD1]), and the SR DPS at Ice Harbor Dam at rkm 16 [ICH].

*Overshoot abundance* – The PTAGIS database was queried to obtain a list of wild adult steelhead that were PIT tagged as juveniles in the MCR DPS, detected as adults at PRD from 2010 to 2017 and subsequently detected at other PTAGIS sites in the UCR, MCR, and SR DPSs (Figure 1). These steelhead are referred as “known overshoot” steelhead and were used to estimate overshoot abundance at PRD. Population-specific PIT tag rates of each adult return year are unknown due to the complex rearing strategies of interior Columbia River steelhead juveniles (i.e., multiple age classes of smolts) combined with variability in tagging program effort and catch rates through time. Therefore, we developed a relationship between the number of known wild overshoot fallback steelhead tags (tagged as juveniles) in year  $i$ , ( $t_i$ ), and the POM estimates of overshoot fallback abundance that year ( $F_i$ ). To calculate  $t_i$ , we expanded the number of observed overshoot fallback PIT tags observed at site  $j$  ( $s_{ij}$ ) by the site’s detection probability as estimated by the POM,  $\hat{p}_{ij}$ , and then we summed those expanded estimates across all  $J$  sites.

$$t_i = \sum_{j=1}^J \frac{S_{i,j}}{\hat{p}_{i,j}}$$

To improve the homogeneity of the variances and meet the linear regression assumptions, we natural log-transformed fallback abundance and estimated overshoot tags and then fit a linear model.

$$\ln(F_i) \sim N(\beta_0 + \beta_1 * \ln(t_i), \sigma^2)$$

We then used that linear model to predict the total overshoot abundance that arrived at PRD ( $O_i$ ), based on the number of known overshoot tags that were detected at PRD each year ( $T_i$ ).

$$\ln(O_i) \sim N(\hat{\beta}_0 + \hat{\beta}_1 * \ln(T_i), \hat{\sigma}^2)$$

*Fallback migration success* – Finally, we calculated the proportion of overshoot steelhead that migrated downstream of PRD or their fallback migration success ( $\phi_i$ ) by dividing the estimate of overshoot fallback abundance by the estimate of overshoot abundance at PRD, accounting for uncertainty in the overshoot fallback abundance from the POM. That uncertainty comes from the posteriors of the downstream transition probabilities in the POM, which were all approximately normal in their distribution, so we calculated the variance of their sum,  $\tau^2$ , and used that to propagate uncertainty.

$$R_i \sim N(F_i, \tau^2)$$

$$\phi_i = \frac{R_i}{O_i} \approx \left( \frac{t_i}{T_i} \right)^{\hat{\beta}_1}$$

We implemented the overshoot abundance and fallback migration success as a single model within a Bayesian framework, using R (R Core Team 2019) and JAGS software (Plummer 2019). Beta parameters ( $\beta$ ) had an uninformative prior of a Cauchy distribution with mean of zero and scale of 100, and the standard deviation parameter ( $\sigma$ ) also had a weak prior of a half-

Cauchy with mean of zero and scale of 100, following the recommendation of Gelman et al. (2008). We focused on natural-origin fish, because adipose fin-clipped hatchery steelhead may be harvested and harvest rates both upstream and downstream of Priest Rapids Dam are variable and unknown, making it more problematic to find a relationship between overshoot detections at PRD and overshoot return abundance downstream.

*Dam effects on fallback success* – To evaluate the effect of downstream dam crossings on fallback migration success, defined as being detected downstream of PRD, we grouped known overshoot steelhead based on the PIT tag detection of the furthest upstream dam. Since Wanapum Dam has no PIT tag detection infrastructure, we could only be certain that fish had crossed 1 (Priest Rapids), 3 (Rock Island), 4 (Rocky Reach) or 5 (Wells) dams. Most dams lack the ability to detect adult steelhead moving downstream, except for the juvenile bypass at Rocky Reach Dam which closes August 31. Therefore, we focused on the furthest upstream dam fish were detected during their upstream migration and pooled these data across years due to low sample size. We then fit a logistic regression model using dam number as the independent variable and examined the predicted overshoot fallback success probabilities after crossing one to five dams. We also examined the PTAGIS detection histories of adult steelhead tagged as juveniles in the Yakima River Basin that were detected crossing McNary Dam, the first dam downstream of the Yakima River between 2010 and 2017. Steelhead were pooled across years and based on detection histories, were categorized as non-overshoots, PRD overshoots, Ice Harbor (Snake River) overshoots, or both. Fish detected at Prosser Dam within the Yakima River were categorized as successful migrants. The probability of non-overshoot steelhead observed at Prosser Dam was compared to the predicted value (i.e., 0 dams or y-intercept) from the logistic

regression model for model validation and to better understand the relative survival benefits or costs of steelhead overshooting behavior.

*Overshoot migration timing* – Steelhead exhibiting overshoot behavior must travel longer distances in freshwater compared to non-overshoot steelhead from the same population, which may ultimately influence their migration timing into their natal stream. The relative prevalence of the overshoot behavior and influence of migration timing into their natal tributary was examined using Yakima River steelhead due to its proximity to PRD and high detection probability (0.90) at Prosser Dam. The influence of overshoot and fallback on run timing into their natural tributary was examined at Prosser Dam by using the arrival dates of fish PIT tagged as juveniles in the Yakima basin, and those of fish PIT tagged as adults at Priest Rapids Dam. Arrival day was calculated as days since July 1 of each return year (all years were combined), and the distribution of arrival days between these two groups of fish was compared using a Kolmogorov-Smirnov (KS) test. Mean monthly water temperature data from the lower Yakima River in 2015 (i.e., low water year) were queried from the U.S. Bureau of Reclamation Hydromet station at Kiona, Washington (<https://www.usbr.gov/pn/hydromet/yakima/yakwebarcread.html>). Columbia River water temperatures from the tailrace of Priest Rapids Dam were queried from the Data Access Real time (DART) website ([http://www.cbr.washington.edu/dart/query/river\\_daily](http://www.cbr.washington.edu/dart/query/river_daily)). Tributary water temperatures during a low water year, like those observed in 2015, were used to better represent possible future conditions under climate change. Mean monthly water temperatures in the Yakima and Columbia rivers were used to graphically identify an upper water temperature threshold for tributary migrations. Non-overshoot Yakima steelhead were defined as those PIT tagged adult steelhead that were detected at McNary Dam but not detected at PRD or Ice Harbor

dams. Estimating the proportion of non-overshoot steelhead at Prosser Dam was calculated by dividing the number of non-overshoot steelhead detected at McNary Dam by the number of non-overshoot steelhead detected at Prosser Dam.

## Results

*Overshoot fallback abundance* – Annual overshoot fallback estimates from Priest Rapids Dam, based on adults tagged at PRD, averaged 20% (range 12-31%) and 15% (range 9-22%) of the adjusted Priest Rapids Dam steelhead count for wild and hatchery steelhead, respectively (Table 1). Wild and hatchery steelhead annual overshoot fallback abundance was significantly correlated ( $R^2 = 0.53$ ,  $P < 0.04$ ), suggesting factors influencing abundance affected both wild and hatchery steelhead similarly. The largest group of fallback steelhead was detected in the Snake River at Ice Harbor Dam, followed by the Yakima River at Prosser Dam (Table 2).

*Overshoot abundance* - The estimated annual overshoot fallback abundance of wild steelhead was significantly positively correlated with the annual number of wild known overshoot fallback steelhead ( $R^2 = 0.74$ ;  $P < 0.001$ );

$$\text{Overshoot abundance} = 41.46 * T^{0.99}$$

where  $T$  is the number of known overshoot adult wild steelhead PIT tagged as juveniles detected at Priest Rapids Dam (Table 3). Wild steelhead overshoots comprised an average of 44% (SD = 16%) of the adjusted Priest Rapids Dam count and ranged between 23% and 74%. Wild steelhead counted at PRD originate from one of four extant upstream populations or were overshoots from downstream populations. Hence, we summed the estimated number of wild steelhead overshoots at PRD and the estimated wild steelhead escapement of the four steelhead populations above PRD and compared that value to the total adjusted counts of wild steelhead

that arrived at PRD. The two time-series were highly correlated ( $r = 0.98$ ), with a root mean square error of 430 fish, and a mean relative difference of 3.3%.

*Fallback migration success* – The annual percentage of wild steelhead that overshoot and fell back below PRD were variable (range 34-70%) and averaged 57% (SD = 12%; Table 3).

*Dam effects on fallback success* – The majority of known wild steelhead overshoots (52%) detected at Priest Rapids Dam were not detected at any upstream locations. Of those, 88% were subsequently detected downstream of PRD. The next largest proportion of overshoot wild steelhead (20%) were detected at the farthest upstream dam (Wells Dam), but only 22% of those fish were detected downstream of PRD. A small proportion of known overshoot wild steelhead were detected in tributaries (5.6%), but only 3.2% (N= 8) were detected during the spawning period in the spring. Of those, seven known overshoot steelhead were detected in tributaries upstream of Wells Dam. The logistic model examining the relationship between the dam passage upstream of PRD and overshoot fallback proportions fit the data well (Likelihood ratio test:  $P < 0.0001$ , pseudo  $R^2 = 0.77$ ), suggesting that the number of dams a fish crosses when overshooting was negatively associated with their downstream passage success (Figure 2). Model predictions of overshoot fallback (95% CI) for zero dams or the y-intercept was 0.944 (0.896, 0.971) and comported well with the proportion of non-overshoot Yakima River steelhead (N = 276) at Prosser Dam (0.949) suggesting some level of natural mortality, not attributed to dam passage, was included in the relationship.

*Overshoot migration timing* –Between 2010 and 2017, 327 wild adult steelhead tagged as juveniles in the Yakima River were detected at McNary Dam. Of those, 13% and 3% were detected at Priest Rapids and Ice Harbor dams, respectively. Of those overshoot steelhead, seven steelhead (2% of total) were detected at both Priest Rapids and Ice Harbor dams. The percentage

of overshoot Yakima steelhead at PRD and Ice Harbor Dam that were subsequently detected at Prosser Dam were 78% and 60%, respectively. In general, Yakima steelhead were not observed at Prosser Dam until water temperatures declined and were similar to that of the Columbia River (Figure 3). Few steelhead ( $< 1\%$ ) were detected at Prosser Dam until stream temperatures were below 20 °C. However, the distribution of arrival times for known overshoot steelhead was significantly later compared to all steelhead at Prosser Dam (KS test;  $P < 0.001$ ; Figure 3). Approximately 73% of wild steelhead tagged as juveniles in the Yakima River arrived at Prosser Dam prior to January 1 compared to 50% of overshoot steelhead.

## Discussion

When annual estimates of overshoot abundance were combined with UCR DPS population run escapement estimates, only minor differences (mean = 3.3%) were observed when compared to the adjusted PRD dam count. Not surprisingly, a small proportion of fish could not be accounted for, presumably due to migration or overwintering related mortality prior to entering a tributary. These results suggest that escapement methodologies incorporating dam counts may not represent the status and trend of upstream populations if methodologies do not account for complex migration patterns including overshoots (e.g., Boggs et al. 2004; Buchanan and Skalski 2010; Richins and Skalski 2018; Waterhouse et al. 2020). Estimates of overshoot abundance in this study were based on the relationship between known overshoot fallbacks and fallback abundance estimates. Variability in annual PIT tagging rates of juvenile steelhead from any single population or subbasin required pooling of data across populations, thereby reducing the sample size used in the regression model ( $N = 8$ ). Ideally, similar juvenile PIT tagging rates from all potential overshoot populations would increase the sample size of adult steelhead and

potentially allow for population-specific relationships or simply a larger sample size for greater statistical power. Overshoot and fallback rates for steelhead have been estimated for many populations in the Columbia Basin using PIT tags and a multi-state release-recapture model (Richins and Skalski 2018). In that study, steelhead were tagged as juveniles as part of various research and monitoring projects and assumed to represent the entire population or group of populations. Conversely, steelhead in our study were tagged as adults from throughout the run (i.e., systematic sample) and were representative of the steelhead passing PRD. Richins and Skalski (2018) reported many populations with high rates of overshoot, but both overshoot and fallback rates were highly variable including some wild populations from the MCR DPS (John Day, Yakima, Umatilla and Walla Walla). While comparisons between population- and dam-based estimated rates of overshoot and fallbacks may be difficult to interpret, the high rate of overshoot reported for MCR DPS populations (Richins and Skalski 2018) does comport well with results of our study.

A large component of steelhead migrating upstream of PRD during the study period were from downstream populations. The magnitude, variability, and upstream distribution of overshoot steelhead in the UCR DPS was unknown and not accounted for in historical escapement estimates derived from dam counts (WDFW, unpublished data). Most radio telemetry studies examining overshoot and fallback in the Columbia and Snake rivers were limited in geographic scope to areas downstream of PRD (Boggs et al. 2004; Keefer et al. 2008b). However, English et al. (2003) did report an average of 16.9% of steelhead radio tagged at PRD were last observed downstream of PRD prior to kelting (i.e., potential overshoot fallbacks), but it is unclear if downstream detections were adjusted for detection probability. The spatial distribution of overshoot fallbacks was similar in both our study and English et al. (2003)



with most overshoot fallbacks detected in the Snake River followed by the Yakima River (Table 2). Lack of accounting for fallback and re-ascension at dams can result in biased estimates of fish abundance (Boggs et al. 2004). In this study, PIT tag detection histories were used to adjust ladder counts of steelhead (i.e., adjusted dam count) prior to estimating abundance of upstream populations, overshoot, or fallback. English et al. (2003) reported mean fallback re-ascension rates of radio-tagged steelhead of 3.0% at PRD, similar to the values used in our study (mean = 4.9%, SD = 0.9; WDFW unpublished data). The estimated annual mean (SD) number of wild steelhead overshoot fallbacks at PRD during the study period was 916 (620) or 19.8% (CV=28%) of the adjusted wild steelhead count at PRD. An adult steelhead radio telemetry study, conducted at PRD between 2015 and 2017, reported similar levels of fallback (Fuchs et al. (2021). In that study, radio tag-based estimates of wild steelhead overshoot fallback were slightly higher (mean = 22.1%; SD = 1.8) compared to PIT tag-based model estimates but were based on a smaller sample size. Boggs et al. (2004) reported similar mean overshoot fallback rates for radio-tagged steelhead at McNary and Ice Harbor dams (i.e., nearest downstream dams) of 25.1% and 20.7%, respectively. Estimates of overshoot fallback in our study were based on PIT tag detections at specific locations downstream of PRD prior to the spawning period. Because wild adult steelhead PIT tagged at PRD were from an unknown population, estimating fallback to their natal stream or watershed was not possible in all cases (e.g., Richins and Skalski 2018). Furthermore, based on detection histories of known overshoot fallback steelhead, some steelhead are observed downstream of PRD, but are not successful in homing to their natal stream (e.g., Yakima steelhead PRD overshoot fallback last observed in the Snake River). While some overshoot fallback steelhead may have died, our POM included all possible locations based

on geographic distribution of known overshoot steelhead and accounted for the variability in detection probabilities among sites and years.

Estimated proportion of overshoot fallback for wild steelhead generated for this study (mean = 57%) were like the observed mean proportion of known overshoots (69%, WDFW unpublished data). Potential reasons for disparities in overshoot fallback proportions include intra- and inter-annual variability in the distribution of juveniles that are PIT tagged from downstream populations, and smaller sample size compared to adult steelhead that are PIT tagged at PRD. While the fate of the component of the overshoot steelhead not observed downstream of PRD (annual mean = 43%) is unclear, we can report that only a small proportion of overshoot steelhead were detected in tributaries (i.e., potential strays). Of those known overshoot steelhead that did not successfully fallback, only 16% (N=15) were last observed in tributaries, and only eight known overshoot steelhead (9% of unsuccessful known overshoot steelhead, or 4% of total) were detected during the spring spawning period. While the proportion of fish last observed in tributaries was not adjusted for detection probability, an IPDS was installed in every major and minor spawning stream upstream of Rock Island Dam, with a mean (SD) detection probability of 0.894 (0.132) with a range from 0.505 to 0.999 (Waterhouse et al. 2020). While several potential minor spawning areas were not monitored using IPDSs (Fuchs et al. (2021), we assumed that most unsuccessful overshoot steelhead suffered either natural mortality in the mainstem or downstream passage-related mortality from turbine strikes.

Summer spill programs and juvenile bypasses are shut down for the season in late August or early September because the juvenile outmigration period has ended (UCSRB 2018). Unfortunately, this coincides with the period when overshoot steelhead initiate their downstream migration back to their natal streams (Fuchs et al. 2021). However, surface spill passage routes

are provided until November 15, but only at both Wanapum (i.e., bypass) and Priest Rapids dams (i.e., sluiceway) specifically for adult steelhead (GCPUD 2006). Downstream survival rates of adult salmonids via turbine passage are largely unknown but decrease as fish length increases (Coutant and Whitney 2000). Recent studies at McNary Dam evaluating the survival and downstream passage rates of adult steelhead reported that surface passage routes (i.e., temporary spillway weirs) were most effective during the day (Ham et al. 2021) with higher survival (97.7%) compared to turbine routes (90.7%; Normandeau Associates Inc, 2014) and could explain why overshoot fallback decreased as the number of dams required to pass downstream increased.

Richins and Skalski (2018) reported several factors that were shown to influence overshoot rates (i.e., natal stream water temperature, hatchery rearing location, adult ladder placement, and ocean age). However, a comparison of overshoot fallback proportions of the two basic overshoot pathways (upstream of Priest Rapids or Ice Harbor dams) has not been conducted. Pope et al. (2016) used a multi-state release recapture model to estimate the overshoot fallback rates for Walla Walla River hatchery steelhead. While hatchery steelhead are subject to direct harvest, they reported overshoot return rates for Lower Granite Dam and PRD of 8.3% and 20.2%, respectively. Because Walla Walla River steelhead that make it to Lower Granite Dam must migrate downstream past four dams in the Snake River to return to the Walla Walla River compared to one and five dams in the Upper Columbia, these results are not directly comparable. However, wild overshoot steelhead in the Upper Columbia that migrate past four dams (i.e., equivalent to Lower Granite Dam) have an estimated mean annual proportion of fallback below PRD of 57%. Comparing hatchery and wild overshoot return rates is also problematic due to differential harvest rates, but this comparison does suggest the two primary overshoot pathways

(i.e. past PRD into the UCR DPS and past Ice Harbor into the SR DPS) may have different relationships between overshoot fallback and the number of downstream dams.

While most of the estimated overshoot wild steelhead at Priest Rapids Dam were from the SR DPS (53%), the remainder were from the MCR DPS (47%). The MCR DPS is located downstream of Priest Rapids Dam and Ice Harbor Dam (excluding the Yakima River) and is comprised of four major population groups (MPG) and 20 independent steelhead populations (Figure 1). Steelhead from five sub-basins in the MCR DPS (John Day, Umatilla, Walla Walla, Touchet and Yakima) are routinely observed as overshoots at Priest Rapids and Ice Harbor dams. The composition of wild steelhead overshoots from the MCR DPS detected at Priest Rapids and Ice Harbor dams between 2010 and 2017 were different, but consistent with that reported by Richins and Skalski (2018). The majority of MCR DPS steelhead detected at Priest Rapids Dam were from the Yakima River (53%); whereas steelhead from the Yakima River were the least abundant (6%) of those detected at Ice Harbor Dam (Figure 4). The spatial distribution (i.e., Upper Columbia or Snake River) of overshoot MCR steelhead is consistent with the location (i.e., same side of the river) of their natal population. More importantly, the overall abundance of known overshoot steelhead from the MCR DPS was 507% greater at Ice Harbor Dam (Figure 4). However, because PIT tag detectors were only installed at Little Goose and Lower Monumental dams in 2014, we could not generate a comparable data set. For discussion purposes only, we used a consistent methodology to estimate overshoot patterns and fallback for steelhead returning in 2015. Overshoot fallback patterns in the Snake River were very similar to that in the Upper Columbia River, with the greatest proportion of unsuccessful overshoots last detected at Lower Granite Dam (0.34) and the greatest proportion of successful overshoot fallbacks detected at Ice Harbor Dam (0.12). In 2015, the proportion of overshoot fallback in the Snake River was 0.32

compared to 0.56 in the UCR suggesting approximately 2 out of 3 MCR DPS steelhead that were detected at Ice Harbor Dam did not return to their natal stream. Furthermore, a relatively large proportion of MCR DPS steelhead that were not observed downstream of Ice Harbor Dam were last detected in a spawning stream (0.40) upstream of Ice Harbor Dam. Unlike steelhead spawning areas upstream of Priest Rapids Dam, some major spawning areas (e.g., lower Grande Ronde and lower Salmon rivers), do not have IPDS and fish may have gone undetected and the proportion of overshoot fish in non-natal tributaries in the SR DPS should be considered minimum values. In summary, compared to overshoot steelhead upstream of Priest Rapids Dam, over five times more MCR steelhead overshoot into the Snake River. Of these, almost half as many successfully fallback, and of those unsuccessful steelhead, a large proportion may be spawning (i.e., strays) within the SR DPS. The differences in migration success and magnitude of overshoot steelhead from the MCR DPS should be of great concern for managers. The logistic regression of known overshoot fallback proportions suggests the number of dams requiring downstream passage is an important factor in downstream migration success, but undoubtedly other factors are also important but outside the scope of this study. As migration distance, migration duration, and number of migration obstacles (i.e., dams) increases, fish condition was also likely negatively affected, which likely contributed to lower rates of migration success (Caudill et al. 2007). As a result of an extended migration distance and duration, overshoot steelhead that fallback and arrive at their natal stream may have depleted energy reserves and exhibit greater rates of pre-spawn mortality or lower spawning success (Mann et al. 2009) and are less likely to return as repeat spawners (Keefer et al. 2008c).

## <B>Conservation Implications

Quantifying steelhead overshoot and fallbacks upstream of Priest Rapids Dam assists in defining and prioritizing the issues associated with the downstream movement of pre-spawn steelhead. However, preliminary data suggest that in the Snake River overshoot steelhead are more than five times more abundant and overshoot return rate may only be 50% of those observed in the Upper Columbia River. Researchers in both the Upper Columbia and Snake rivers use a similar patch occupancy model to estimate population abundance upstream of Priest Rapids and Lower Granite dams, respectively (Orme and Kinzer 2018; Waterhouse et al. 2020). An important first step in fully defining the issue of overshoot steelhead in the Columbia-Snake River Basin is to expand the model currently being used at Lower Granite Dam to include more downstream detection sites and perform a similar analysis to estimate overshoot abundance and fallback in the lower Snake River.

Climate change scenarios coupled with observed warming of Columbia River water temperatures (Quinn and Adams 1996; ISAB 2007; Crozier et al. 2008, 2020; Isaak et al. 2018) suggest higher rates of overshoot from a greater number of populations should be expected in the future. As a result of the low proportion of overshoot steelhead that successfully fell back, prolonged migration periods, and potential effects from genetic introgression, steelhead overshooting their natal stream negatively affect population abundance and productivity. Many studies have consistently shown that both overshoot steelhead (Khan et al. 2013) and kelts (Wertheimer and Evans 2005; Wertheimer 2007; Ham et al. 2015; Harnish et al. 2015) prefer surface flow downstream passage routes (i.e., spillway weirs or sluiceways), which also provide higher survival rates. Experiments conducted to evaluate the efficacy of sluiceways (Khan et al. 2013) and temporary spillway weirs (Ham et al. 2015, 2021) operated during non-spill periods (i.e., late fall through winter) found that surface flow passage routes significantly reduced turbine

passage while increasing total steelhead passage. Surface flow passage routes operated during non-spill periods would increase overshoot fallbacks for both MCR and SR DPS steelhead populations. In 2020, limited downstream surface passage routes during non-spills periods at McNary and the four lower Snake River dams were a condition of the Columbia River System Biological Opinion (NOAA Fisheries 2020). Survival standards for steelhead overshoot fallbacks have yet to be identified but should be consistent with upstream migration survival standards. The initial evaluation of these additional protection measures has not been completed as part of a regional adaptive management process. While downstream passage routes reportedly have high project-survival (Ham et al. 2021), the cumulative effect measured at the population scale (i.e., changes in abundance) should be an important consideration for adaptively managing protective measures in the future.

Fuchs et al. (2021) reported that downstream passage at PRD began in early September through mid-December and resumed in early March. Extensive downstream migration studies are resource intensive. Hence, cost-effective long-term monitoring tools would provide the data needed to adaptively manage dam operations. Surface passage routes equipped with PIT tag detection equipment would provide project-specific data such that operations could be optimized to minimize costs. In the interim, existing adult salmonid monitoring programs at Priest Rapids and Lower Granite dams could provide annual estimates of overshoot fallback abundance and serve as a low-cost effectiveness monitoring tool. As river water temperatures continue to increase and more adult salmonids attempt to adapt with complex movement patterns like overshooting, the hydroelectric operations may also need to adapt. Reducing Columbia Basin stream water temperatures notwithstanding, providing effective adult salmon and steelhead

downstream passage routes would provide significant conservation value (e.g., increase spawner abundance and reduce genetic introgression) to most populations in the Columbia Basin.

An extensive monitoring infrastructure exists in the Columbia Basin that provides the data necessary to detect changes in population-specific freshwater movement patterns. Although research has focused on detecting climate-related changes to freshwater fish assemblages (Lynch et al. 2016; Pletterbauer et al. 2014) or changes to migration patterns driven by changes to ocean conditions (Crozier et al. 2011; Lynch et al. 2016), the impacts of climate change on the movement patterns in large freshwater ecosystems with multiple populations like the Columbia River Basin are much less understood. For example, the relatively large number of Snake River steelhead that overshoot into the Upper Columbia or Middle Columbia steelhead that overshoot into the Snake River have both harvest and conservation implications. Given that most fishes are poikilotherms, changes in behavior (e.g., migration) in response to suboptimal habitat conditions are expected. Hence, natural resource managers should reexamine historical harvest paradigms periodically to validate fishery models. Decision-support tools that include population genetic monitoring may be a cost-effective approach that can be applied at multiple spatial scales in freshwater systems lacking a robust monitoring infrastructure to identify climate induced changes in population-specific harvest rates in a timely manner.

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Adjusted Priest										
Rapids Dam			Estimated overshoot fallback abundance							
Run	Count									
Year			Wild				Hatchery			
	Wild	Hatchery	95% CI				95% CI			
			%	Estimate	Lower	Upper	%	Estimate	Lower	Upper
2010	7,295	17,918	22.6	1,652	1,411	1,915	8.6	1,532	1,265	1,765
2011	4,705	15,291	16.0	755	611	901	11.5	1,757	1,546	1,973
2012	3,119	13,201	17.7	552	432	675	14.5	1,909	1,694	2,115
2013	4,954	9,193	21.6	1,068	89	1,214	17.3	1,586	1,393	1,775
2014	6,326	12,277	30.7	1,945	1,764	2,153	22.0	2,705	2,492	2,952
2015	4,560	9,239	19.2	874	747	998	10.9	1,003	871	1,135
2016	1,423	4,765	18.8	267	203	333	20.3	969	852	1,094
2017	1,855	3,634	11.7	217	162	283	13.8	503	419	598

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	Yakima		Snake		Walla Walla		Umatilla		John Day	
Run	PRO		ICH		PRV		TMF		JD1	
Year	(0.90, 0.04)		(0.99, 0.01)		(0.57, 0.09)		(0.75,0.00)		(0.46, 0.13)	
	W	H	W	H	W	H	W	H	W	H
2010	840	56	690	1,397	55	0	33	23	0	22
2011	364	29	363	1,698	21	0	0	0	0	0
2012	181	28	324	1,832	20	14	13	0	0	0
2013	334	32	639	1,433	19	51	19	13	38	19
2014	579	60	1169	2,504	75	27	53	22	43	11
2015	324	20	426	882	57	20	24	0	29	0
2016	89	26	117	685	20	26	12	0	20	0
2017	116	13	65	254	12	9	0	0	21	0
Mean	353	33	474	1,336	35	18	19	7	19	7
%	15.3	1.4	20.6	58.1	1.5	0.8	0.8	0.3	0.8	0.3

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Run Year	Known overshoot fish	Estimated wild steelhead overshoot abundance			Overshoot fallback proportion (# fallbacks/# overshoots)		
		Estimate	95% CI		Estimate	95% CI	
			Lower	Upper		Lower	Upper
2010	53	3,112	1,640	7,578	0.622	0.218	0.977
2011	18	1,289	714	3,367	0.686	0.222	0.985
2012	31	1,614	595	4,727	0.451	0.116	0.919
2013	40	2,262	1,075	6,130	0.578	0.174	0.967
2014	44	3,129	1,917	7,131	0.701	0.275	0.986
2015	35	1,952	908	5,505	0.557	0.156	0.962
2016	21	1,051	334	2,960	0.344	0.089	0.819
2017	6	428	199	1,168	0.646	0.179	0.984
Mean	31	1,855	923	4,820	0.573	0.179	0.950
SD	15	959	603	2,206	0.122	0.060	0.057

1

2

3

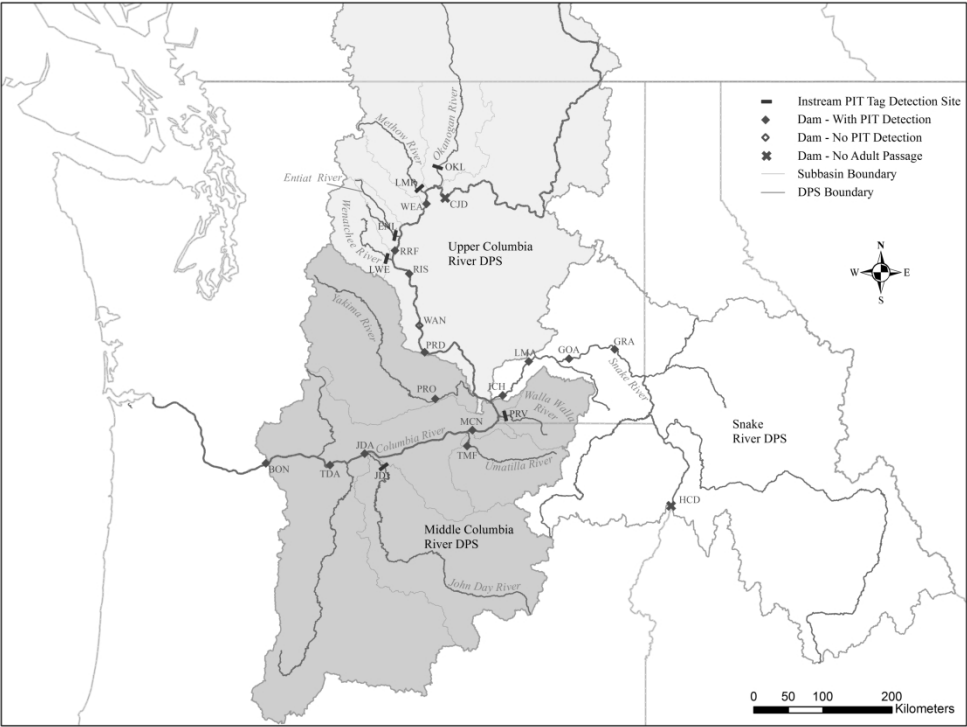


Figure 1. Vicinity map of steelhead distinct population segments (DPS), major rivers and dams, and instream PIT tag detection locations on the Columbia and Snake Rivers. BON = Bonneville Dam, TDA = the Dalles Dam, JDA = John Day Dam, JD1 = Lower John Day River IPDS, TMF = Three Mile Falls Dam, MCN = McNary Dam, PRV = Lower Walla Walla River IPDS, ICH = Ice Harbor Dam, LMA = Lower Monumental Dam, GOA = Little Goose Dam, GRA = Lower Granite Dam, HCD = Hells Canyon Dam, PRO = Prosser Dam, PRD = Priest Rapids Dam, WAN = Wanapum Dam, RIS = Rock Island Dam, LWE = Lower Wenatchee river IPDS, RRF = Rocky Reach Dam, ENL = Lower Entiat River IPDS, WEA = Wells Dam, LMR = Lower Methow River IPDS, OKL = Lower Okanogan River IPDS, CJD = Chief Joseph Dam.

279x215mm (300 x 300 DPI)

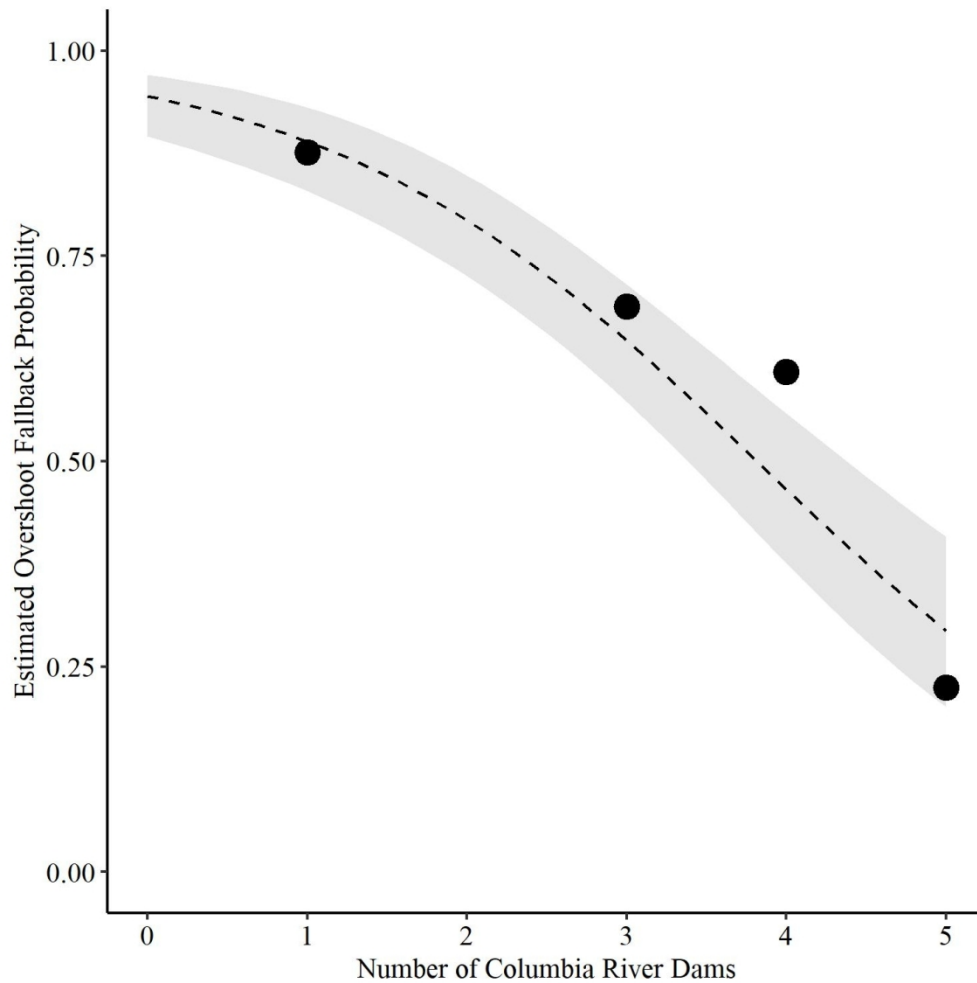


Figure 2. Logistic regression between the number of dams to the furthest upstream detection location for known origin overshoot steelhead detected at Priest Rapids Dam and the overshoot fallback proportion detected downstream of Priest Rapids Dam, 2010-2017.

127x127mm (300 x 300 DPI)

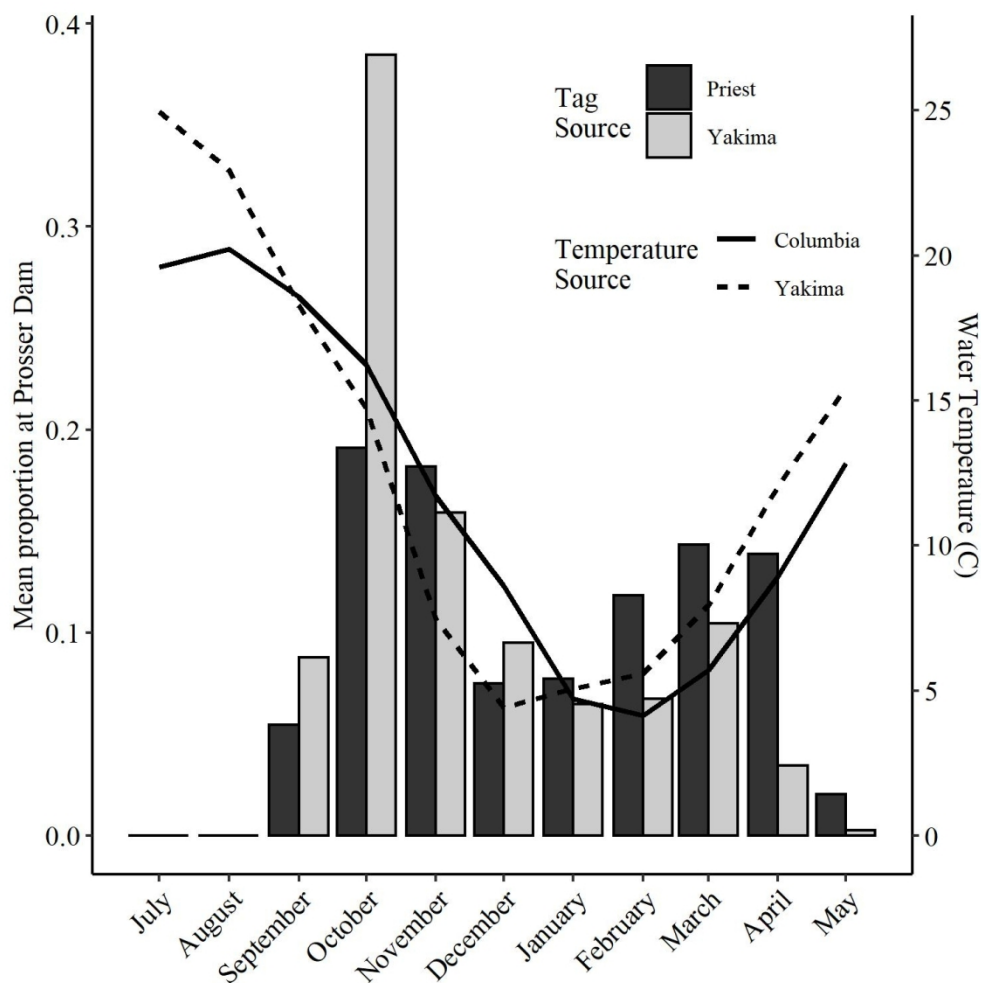


Figure 3. Passage timing of steelhead tagged as juveniles in the Yakima, and fish tagged as adults at Priest who were detected at Prosser Dam in the lower Yakima River, 2010-2017. Mean monthly water temperatures (2015-2016) measured in the lower Yakima River at Kiona (rkm 48) and Columbia River measured at Priest Rapids Dam tailrace.

127x127mm (300 x 300 DPI)

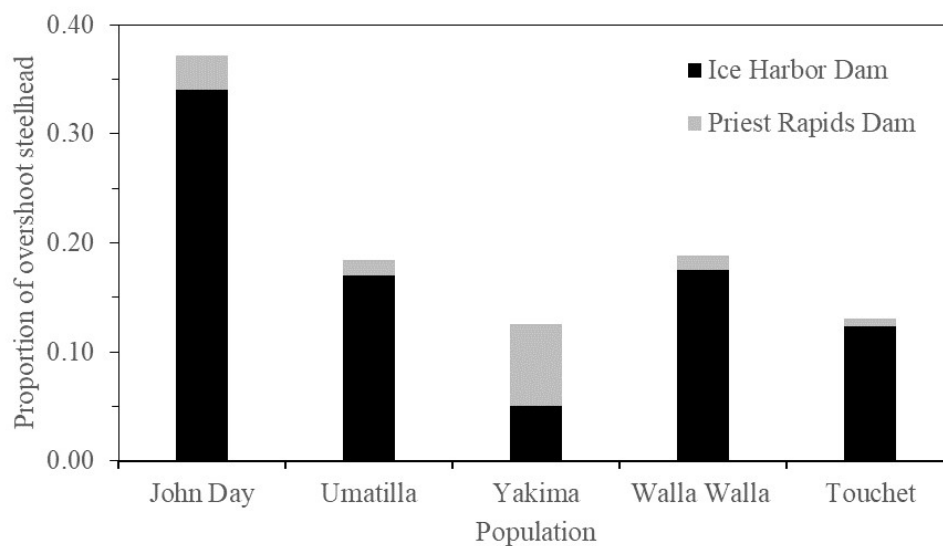


Figure 4. The distribution of overshoot wild steelhead (N = 559) from the Middle Columbia River distinct population segment in the Upper Columbia River (Priest Rapids Dam) and Snake River (Ice Harbor Dam) distinct population segments, 2010-2017.

153x88mm (150 x 150 DPI)