Adult 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, the most downstream dam on the Columbia River located at river kilometer (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 than other steelhead populations because water temperatures are already at near lethal limits (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, and prevalence of disease and death (McCullough 1999). Behavioral effects from elevated water temperatures include delayed migration at hydroelectric dams (Keefer et al. 2004; Siegel et al. 2021), temporary use of non-natal tributaries (High et al. 2006), and overshooting or migrating upstream of 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) 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 that involves steelhead moving upstream of their natal tributary. Richins and Skalski (2018) reported that steelhead overshoot probability and Columbia River water temperature near the natal tributary were positively related. 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; Mann and Snow 2018). Richins and Skalski (2018) reported overshoot percentages of adult steelhead as high as 71%, with many populations exhibiting percentages > 50%. However, the mean annual overshoot fallback probabilities or the probability that overshoot steelhead will successfully migrate downstream and return to their natal stream, hereafter referred to fallback migration success, is more variable, less understood, and ranged from 0.18 to 0.75 (Richins and Skalski 2018). Large variability in population-specific fallback migration success may be attributed to many factors including non-representative or inter-annual variability in tagging, differences in the number of overshoot dams, and overshoot migration patterns, both spatially and temporally. Large variability in fallback migration success also makes it difficult to understand underlying causal mechanisms thereby increasing uncertainty in the implementation of potential adaptive management actions. While less studied in large free-flowing rivers, Eiler et al. (2015) reported low rates of overshooting for Chinook Salmon (<1%) in Yukon River, AK. However, English et al. (2006) compared adult steelhead migration patterns in the Upper Columbia to those in large free-flowing rivers in British Columbia, Cananda. In that study, the proportion of radio-tagged summer steelhead (pooled across years to increase sample size) from the Upper Columbia and British Columbia (Skeena and Nass rivers) tracked to downstream spawning locations (i.e., overshoots) was 0.086 and 0.006, respectively. Based on these studies, overshooting in large natural rivers is an uncommon behavior that is more common, yet highly variable, in the highly regulated Columbia River.

Estimates of overshoot fallback abundance, or the number of steelhead that overshot and successfully migrated downstream to their natal tributary, do not account for steelhead that overshot their natal stream but were unsuccessful 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 populations that exhibit this behavior, 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 low rates of fallback migration success 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 (i.e., all surface passage routes are closed) 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.

Overshoot steelhead have been detected at Priest Rapids Dam (rkm 639), the first dam upstream from the Yakima and Snake rivers, since 2003 (Figure 1), when passive integrated transponder (PIT) detectors in fish ladders became operational. Due to the high variability in abundance and PIT tag rates of overshoot steelhead, the fate of these fish and their contribution to upstream or downstream populations and recreational fisheries was not well understood. Recent advancements in the abundance estimation for populations upstream of Priest Rapids Dam suggested a percentage (~25%) of the steelhead that migrated upstream of Priest Rapids Dam were unaccounted for and were assumed to represent the overshoot component of the total count of steelhead dam at the dam (Waterhouse et al. 2020). Hence, monitoring the status and trends of both overshoot and non-overshoot steelhead at Priest Rapids Dam and their fate was a priority for managers. As water temperatures increase due to climate change, thereby increasing the likelihood of overshooting, understanding the risks associated with this behavior are required for effective management. Given the uncertainty associated with overshooting 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 steelhead that migrated downstream of Priest Rapids Dam to their natal tributary (fallback migration success); (4) evaluate the effect of downstream dam crossings on fallback migration 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 (rkm 877) was built without fish ladders (i.e., end of anadromous distribution), but fish ladders in all downstream dams possess equipment to detect passive integrated transponder (PIT) tags, except Wanapum Dam (rkm 669). The Middle Columbia River (MCR) DPS comprises 17 extant steelhead populations and extends downstream from the Yakima River (rkm 539) to the White Salmon River, WA (rkm 271), and Fifteen Mile Creek, OR (rkm 309). McNary Dam is the last Columbia River dam steelhead encounter before entering the Upper Columbia or Snake rivers. 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 the pelvic girdle for 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). The pelvic girdle was selected as the preferred PIT tag location due to the reported high retention rates (~99%) in other similarly sized adult fish species (Meerbeek 2020). 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 (PTAGIS) 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 approximately 75 sites including 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 (Royle and Kéry 2007, Waterhouse et al. 2020).

Observations at each site, as well as detections further upstream, provided 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 (). The probability of fish *i* moving to each of the possible next detection sites along the stream network (*j*+1, *j*+2, …), including the probability of not moving past any of those sites, is modeled using a multinomial distribution with transition probabilities ,

and the detection of that fish at each array *k* at site *j*, *yi,j,k*, is modeled as a Bernoulli distribution with detection probability *pj,k*.

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, , were estimated using detections from both hatchery and wild fish but transition probabilities, , were different for hatchery and wild fish because hatchery fish were generally returning to their hatchery release sites, while wild fish were returning to their natal stream. These overall transition probabilities were multiplied by an estimate of total abundance, by origin, at Priest Rapids Dam, providing estimates of escapement past each detection site. The estimate of total abundance was generated by discounting the total steelhead counts by an estimate of re-ascension probability based on the proportion of previously PIT-tagged fish observed to ascend Priest Rapids Dam more than once, therefore being counted twice or potentially more times. Transition parameters () 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). Aside from standard mark-recapture assumptions, the POM does assume that each fish is a one-way trip beginning at PRD and ending at their spawning stream. To meet this assumption, detection histories must be examined, and some detections might be dropped for fish that were observed in multiple spawning paths, based on the timing of detections and expert biological opinion.

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 PRD 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*, (*ti*), and the POM estimates of overshoot fallback abundance that year (*Fi*). To calculate *ti*, we expanded the number of observed overshoot fallback PIT tags observed at site *j* (*si,j*) by the site’s detection probability as estimated by the POM, , and then we summed those expanded estimates across all *J* sites.

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.

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

This approach assumes that the overall average juvenile tag rate across all populations downstream of PRD is consistent throughout this time period, or to put it another way that the proportion of returning adults from populations downstream of PRD that were tagged as juveniles is consistent. Fluctuations in the tag rates of individual populations, and the interaction with the variability in how long those fish remain in the ocean before returning to spawn, are part of the overall model variance, .

*Fallback migration success* – Finally, we calculated the proportion of overshoot steelhead that migrated downstream of PRD or their fallback migration success () 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, , and used that to propagate uncertainty in .

We implemented the overshoot abundance and fallback migration success as a single model within a Bayesian framework, using the rjags package (Plummer 2019) with R (R Core Team 2019) and JAGS software (M. Plummer, available at https://sourceforge.net/projects/mcmc-jags/). We chose a Bayesian framework to incorporate all the uncertainty in many of the independent and dependent variables (e.g. , , ). Beta parameters () had an uninformative prior of a Cauchy distribution with mean of zero and scale of 100, and the standard deviation parameter () 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 fallback abundance downstream. Wild steelhead may also have been encountered during sport fisheries which could potentially influence fallback migration success. Sport fishery impacts to wild steelhead upstream of PRD were assessed annually, based on extensive creel surveys using a 5% hooking mortality rate (WDFW, unpublished data). Any indirect hooking mortality or unreported harvest of wild steelhead would be incorporated into our analysis.

*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. To determine the effect of crossing one to five dams on overshoot fallback success probability, we fit a logistic mixed effects model using dam number as the fixed effect variable and allowed the intercept and slope to have random effects by year. As part of model validation, we compared the intercept (the predicted probability of migration success when zero dams were crossed, i.e. no overshooting) with the percentage of PIT tags from fish tagged as juveniles in the Yakima River Basin and detected at McNary Dam, the first dam downstream of the Yakima River, as adults between 2010 and 2017, but not detected at Priest Rapids Dam or Ice Harbor Dam on the Snake River, that were also detected at Prosser Dam within the Yakima River. These tags represent fish displaying a successful non-overshoot behavior.

*Overshoot migration timing* – Steelhead exhibiting overshoot behavior must travel longer distances in freshwater and encounter more dams 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](https://www.usbr.gov/pn/hydromet/yakima/yakwebarcread.html%20)). 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](file:///C:\Users\murdoarm\AppData\Roaming\Microsoft\Word\(http:\www.cbr.washington.edu\dart\query\river_daily)). Tributary water temperatures were not available for the entire study period. Instead, Yakima River water temperatures during a low water year, like those observed in 2015 (i.e., 0.6 C warmer than average at the start of the upstream migration period in July), 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.

Because natural mortality rates are unknown, comparing fallback migration success rates to those of non-overshoot steelhead from the same population provides a more accurate assessment of the risks to steelhead exhibiting the overshooting behavior. 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 non-overshoot steelhead migration success 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.

**<**A>Results

*Overshoot fallback abundance* – During the study period (2010-2017), the annual mean (SD) number of wild steelhead PIT tagged was 664 (281) or an annual mean (SD) proportion of 0.17 (0.05) of the total wild fish. Hatchery steelhead were tagged at the same rate but were more abundant (mean = 1,620; SD = 495). The annual mean (SD) number of adult wild steelhead previously PIT tagged as juveniles from populations downstream of Priest Rapids Dam (i.e., known overshoots) was 31 (15). Annual overshoot fallback estimates from Priest Rapids Dam, based on adults tagged at PRD, averaged 1,135 (range 284-2,355) and 1,656 (range 540-2,879) for wild and hatchery steelhead, respectively, which constituted an average of 25% (range 16-38%) and 16.6% (range 10-24%) of the adjusted Priest Rapids Dam steelhead count for wild and hatchery steelhead (Table 1). Wild and hatchery steelhead annual overshoot fallback abundance was significantly correlated (R2 = 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 (average 456 and 1,321 for wild and hatchery, which was 19.7% and 57% of all fallbacks), followed by the Yakima River at Prosser Dam (average 369 and 34 for wild and hatchery, which was 15.9% and 1.5% of all fallbacks) (Table 2). Excluding hatchery steelhead, steelhead from the Snake and Yakima rivers represented 50% and 40% of all wild steelhead fallbacks, respectively.

*Overshoot abundance* – The log-log regression model between the estimated overshoot fallback abundance of wild steelhead and the estimated number of overshoot fallback PIT tags from PRD fit the data well. For every MCMC draw, including the variation in the dependent and independent variables, as well as the parameters, we calculated the correlation between the observed and predicted values. The mean squared correlation (pseudo-R2) was 0.72. Diagnostic plots suggested that the regression assumptions were met. The fitted model predicted overshoot abundance at PRD, based on the number of known overshoot PIT tags detected at PRD, with the following estimated parameters:

Overshoot abundance = 55.70\**T*0.95

where *T* is the number of known overshoot adult wild steelhead PIT tagged as juveniles detected at Priest Rapids Dam. The estimated mean annual wild steelhead overshoot abundance was 1,856 (SD = 958) and comprised an average of 45% (SD = 16%) of the adjusted Priest Rapids Dam count and ranged between 23% and 75% (Table 3).

Wild steelhead counted at PRD originated 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* = 0.89), with a root mean square error of 448 fish, and a mean relative difference of 9.5%. More simply, including estimates of overshoot abundance from populations downstream of Priest Rapids Dam with our estimates of escapement into the four populations upstream of Priest Rapids Dam provided a more complete accounting of the total number of steelhead passing Priest Rapids Dam (Figure 2).

*Fallback migration success* – The annual percentage of wild steelhead that overshoot and fell back below PRD was variable (range 31-74%) and averaged 59% (SD = 14%; Table 3). Sport fishery impacts on wild steelhead abundance based on the adjusted number of wild fish at PRD and creel survey estimates of catch were low with an annual mean mortality due of 0.97% (SD = 0.67%) consistent with fishery permits (A.R. Murdoch, WDFW, personal communication.).

*Dam effects on fallback success* – From 2010 to 2017, we found 246 known overshoot wild steelhead detected at PRD. The majority of these (52%) were not detected at any upstream locations. Of those 129 tags, 88% were subsequently detected downstream of PRD, demonstrating fallback migration success. The dam with the second largest percentage of known overshoot wild steelhead after PRD was Wells Dam (20%, N = 49), the farthest upstream dam, but only 22% (N = 11) of those fish were detected downstream of PRD. A small percentage of known overshoot wild steelhead were detected in tributaries upstream of PRD (5.6%), but only 3.2% (N= 8) were detected during the spawning period in the spring. Of those known overshoot steelhead detected in tributaries, seven 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 (pseudo marginal R2 = 0.73, pseudo conditional R2 = 0.78), suggesting that the number of dams a fish passed when overshooting was negatively associated with their downstream passage success (Figure 3). Model predictions of overshoot fallback (95% CI) for zero dams or the y-intercept was 0.955 (0.891 – 0.982) and comported well with the proportion of non-overshoot PIT-tagged Yakima River steelhead that crossed McNary Dam (N = 276) and were detected 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 4). 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 4). Approximately 73% of wild steelhead tagged as juveniles in the Yakima River arrived at Prosser Dam prior to January 1 compared to 50% of known overshoot steelhead.

<A>Discussion

The magnitude, variability, and upstream distribution of overshoot steelhead in the UCR DPS was unknown and not fully accounted for in historical escapement estimates derived from dam counts (Ford et al. 2001). However, when the annual estimates of overshoot abundance presented here were combined with UCR DPS population run escapement estimates, only minor differences (mean = 9.5%) 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 dam counts may not represent an index of the spawning population upstream of the dam 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).

A large component of steelhead migrating upstream of PRD during the study period were from downstream populations. 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).

The estimated annual mean (SD) number of wild steelhead overshoot fallbacks at PRD during the study period was 1,135 (729) or 25% (SD = 6.4%) 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 were detected downstream of PRD, but were 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 fallback migration success for wild steelhead, PIT tagged as adults, reported for this study (mean = 59%; SD = 14%) was similar to the fallback migration success of known adult wild steelhead overshoots, tagged as juveniles, (mean = 69%; SD = 9%) during the study period (A.R. Murdoch, WDFW, personal communication). Potential reasons for methodological disparities in fallback migration success percentages include intra- and inter-annual variability in the distribution of juveniles that were PIT tagged from downstream populations, and smaller sample size compared to adult steelhead that were PIT tagged at PRD. Furthermore, 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. While the fate of the component of the overshoot steelhead not observed downstream of PRD (annual mean = 41%) is unclear, we can report that only a small proportion of overshoot steelhead were detected in upstream 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. Although these percentages were not adjusted for detection probability, the mean detection probability of all the IPDS installed in every spawning stream upstream of Rock Island Dam was 0.894 (SD = 0.132) and ranged from 0.505 to 0.999 (Waterhouse et al. 2020), suggesting very few known unsuccessful overshoot steelhead went undetected. While several potential minor spawning areas were not monitored using IPDSs (Fuchs et al. 2021), we assumed that most unsuccessful overshoot steelhead suffered the same rate of mortality in the mainstem as non-overshoot fish or downstream passage-related mortality from turbine strikes, as opposed to successfully spawning in an unmonitored tributary above PRD.

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 fallback migration success decreased as the number of dams required to pass downstream increased.

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 annual 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). Estimates of fallback migration success whether population-based (Richins and Skalski 2108) or dam-based (this study) may be difficult to compare due to differences in overshoot migration routes, dam operations, and the number of dams overshoot fish encounter.

Richins and Skalski (2018) reported several factors that were shown to influence overshoot probabilities (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) had an estimated mean fallback migration success below PRD of 59%. 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 5). 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 over five times greater at Ice Harbor Dam (Figure 5). However, because PIT tag detectors were first 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 those in the Upper Columbia River, with the largest proportion of unsuccessful overshoots last detected at Lower Granite Dam (0.34) and the largest proportion of successful overshoot fallbacks detected at Ice Harbor Dam (0.12). In 2015, the fallback migration success in the Snake River was 0.32 compared to 0.59 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. The differences in fallback 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.

<B>Conservation Implications

Estimating the abundance of steelhead overshoot and fallbacks allows resource managers to quantify the potential increase in spawner abundance for populations exhibiting this behavior, thereby assisting in the prioritization of the issues associated with the downstream movement of pre-spawn steelhead. Overshoot steelhead in the UCR DPS (annual mean = 1,856) comprise on average 45% (SD = 16%) of the adjusted number of steelhead counted at PRD. Of those, an average 59% are estimated to have returned to their natal watersheds suggesting increased fallback migration success is possible. However, preliminary data suggest that overshoot steelhead in the Snake River are over 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 fallback migration success, prolonged migration periods, and potential effects from genetic introgression, steelhead overshooting their natal stream negatively affect population abundance and productivity. Hence, changes in hydroelectric dam operations are likely required to increase fallback migration success. 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). The initial evaluation of these additional protection measures has not been completed as part of a regional adaptive management process.

Survival standards for steelhead overshoot fallbacks have yet to be identified but should be consistent with upstream migration survival standards. While downstream passage routes reportedly have high project-survival (Ham et al. 2021) many overshoot steelhead are required to migrate downstream past more than one hydroelectric project (e.g., John Day or Umatilla steelhead overshooting Wells Dam must pass six dams to reach their natal tributary). Hence, the response variable measured at the population scale (i.e., changes in abundance) should be an important consideration for adaptively managing protective measures intended to increase fallback migration success 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 fallback migration success and serve as a low-cost effectiveness monitoring tool. As river water temperatures continue to increase and more adult salmonids attempt to adapt using 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 consider reexamining 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 periodically 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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