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 migrations 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 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 altered freshwater habitat conditions. Summer steelhead have been shown to temporarily use several non-natal tributaries in the lower Columbia River 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 passage time through the Bonneville Dam reservoir increased after water temperature exceeded 19 °C, as did the 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 magnitude of cool water refuge use varies with Columbia River water temperature and has been reported as high as 66% for 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 relatively to 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 underrepresent the abundance of steelhead that overshot their natal stream due to mortality sources both intentional (i.e., harvest) or unintentional (e.g., turbine strikes) that may occur during their downstream movement. While overshoot fallbacks represent the component of overshoot fish that returned to their natal stream, 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. 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. However, the only passage route during non-spill periods may be through the turbines (Richins and Skalski 2018), which can result in high mortality rates (Wertheimer and Evans 2005). If preferred passage routes are not available, steelhead may expend considerable energy searching 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 steelhead that were detected downstream of Priest Rapids Dam and (4) compare migration patterns and timing of non-overshoot and overshoot steelhead into natal tributaries.

<A>Methods

*Study area*.–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. 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). 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.

*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 that were not previously PIT tagged at the PRD trap three days a week from early July through mid-November, with an annual target sample rate of ~15% of all steelhead passing PRD (NMFS 2003). 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. These data were formatted for analysis to estimate adult overshoot and fallback 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) using detections of steelhead PIT tagged at PRD beginning in return year 2010 (Waterhouse et al. 2020). Some adult steelhead PIT tagged at PRD overshoot their natal stream, fallback, and ascend their presumed natal stream to spawn 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].

We used the POM to estimate overshoot fallback abundance (Waterhouse et al. 2020). The model estimates transition probabilities past various detection points while accounting for imperfect detection at those sites, essentially a multi-state variation of a spatial Cormack-Jolly-Seber model (reference). Detection probabilities are estimated using dams or instream PIT tag detection systems (IPDS) at some sites, as well as detections from IPDSs upstream of a specific site (Figure 1). After each detection point, *j*, (including the initial one at Priest Rapids Dam), the true location of fish *i*, *zi,j+1*, 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 subsequent 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. These overall transition probabilities are multiplied by an estimate of total abundance, by origin, at Priest Rapids Dam, providing estimates of escapement past that detection site.

*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 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 total 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*).

Finally, we calculated the overshoot fallback migration success () by dividing the estimate of total overshoot fallback abundance by the overshoot abundance at PRD, accounting for uncertainty in the overshoot fallback abundance from the POM.

We implemented this model within a Bayesian framework, using R (R Core Team 2019) and JAGS software (Plummer 2019). 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 abundance*.–To evaluate the effect of downstream dam crossings on 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 within the Yakima River (e.g. at Prosser Dam) 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 timing.*–The influence of overshoot and fallback on run timing into their natural tributary was examined at Prosser Dam by expanding steelhead PIT tag detections from Priest Rapids Dam, at a monthly time scale, using an average tag rate of 15% (WDFW, unpublished data). The estimated monthly abundance of overshoot steelhead was compared to non-overshoot steelhead using a Kolmogorov-Smirnov (KS) test. Monthly non-overshoot steelhead abundance was estimated by subtracting estimated overshoot abundance from the total monthly abundance counted at Prosser Dam (<http://www.cbr.washington.edu/dart/query/adult_month_sum>). 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 during a low water year, like those observed in 2015, were used to better represent 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.

**<**A>Results

<B>Abundance of fallback, overshoot, and migration success

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 (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, followed by the Yakima River at Prosser Dam (Table 2). The estimated annual overshoot fallback abundance of wild steelhead was significantly positively related to the annual number of known overshoot fallback fish (R2 = 0.74; *P* < 0.001);

Overshoot abundance = 41.46\**T*0.99

where *T* is the number of known overshoot adult 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 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%. The annual percentage of wild steelhead that overshoot and fell back below PRD were variable (range 35-70%) and averaged 57% (SD = 12%; Table 3).

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, the majority (88%) 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 R2 = 0.77), suggesting that the number of dams a fish crosses when overshooting was negatively associated with their downstream migration 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.

<B>Overshoot migration timing

Steelhead exhibiting overshoot behavior must travel longer distances in freshwater compared to non-overshoot steelhead, 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. 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, a small percentage (14%) were detected at both Priest Rapids and Ice Harbor dams. The proportions of overshoot steelhead at PRD and Ice Harbor Dam that were detected at Prosser Dam were 0.78 and 0.60, 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, based on expanded detections of PRD PIT-tagged steelhead at Prosser Dam, the monthly distribution of overshoot steelhead was significantly later compared to non-overshoot steelhead (KS test; *P* < 0.001; Figure 3). Approximately 73% of non-overshoot steelhead arrived at Prosser Dam prior to January 1 compared to 50% of overshoot steelhead.

<A>Discussion

Mean annual estimates of overshoot wild steelhead at Priest Rapids Dam were 1,855 (SD = 959), or 44% (CV =35%), of the adjusted PRD count and were more variable than estimates of overshoot fallback abundance. When annual estimates of overshoot abundance were combined with 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 greater 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 proprotions 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 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 (Figure 2).

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 return 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 the majority 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). Of which, steelhead from five sub-basins (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 installed at Little Goose and Lower Monumental dams in 2014, we could not generate a comparable data set. For discussion purposes only, we estimated 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 (34%) and the greatest proportion of successful overshoot fallbacks observed at Ice Harbor Dam (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, 40% of the MCR DPS steelhead that were not observed downstream of Ice Harbor Dam were last detected in a spawning stream 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 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 in 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 in order to estimate overshoot abundance and return rates 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, 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, 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 and the initial evaluation of these additional protection measures have not been completed. 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 also be a 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. Unless similar types of studies are conducted periodically at all hydroelectric projects, 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 even more adult salmonids adapt complex movement patterns like overshooting, the Columbia Basin hydroelectric operations must also 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. While much focus has been on detecting changes associated with climate-related changes in ocean conditions on migration patterns (Crozier et al. 2011; Lynch et al. 2016) or freshwater fish assemblages (Lynch et al. 2016; Pletterbauer et al. 2014), much less is understood in large freshwater ecosystems with multiple populations like the Columbia River Basin. 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 has 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.

<A>Acknowledgements

This research was funded by Bonneville Power Administration under Project #2010-034-00. We would like to thank Janet Eckenberg for leading tagging operations at Priest Rapids Dam and Jay Deason, Matt Stilwater, Garret Rains, David Grundy and numerous other technicians for constructing, installing and maintain the IPDS infrastructure upstream of Priest Rapids Dam. Alf Haukenes, Dan Rawding and two anonymous reviewers provided helpful comments on earlier versions of the manuscript. We would also like to thank Grant County PUD for providing access to collect and sample steelhead at Priest Rapids Dam for over 30 years and Chelan County PUD for providing PIT tags for adult steelhead.

<A>References

Boggs, C. T., M. L. Keefer, C. A. Peery, and T. C. Bjornn. 2004. Fallback, reascension, and adjusted fishway escapement estimates for adult Chinook Salmon and steelhead at Columbia and Snake River dams. Transactions of the American Fisheries Society 133:932-949.

Brown, L. G. 1995. Mid-Columbia River summer steelhead stock assessment: A summary of

the Priest Rapids steelhead sampling project 1986-1994 cycles. WA. Dep. Fish Wild.

Progress Report Number AF95-02, 85 p.

Buchanan, R. A., and J. R. Skalski. 2010. Using multistate mark-recapture methods to model adult salmonid migration in an industrialized river. Ecological Modelling 221:582–589.

Busby, P. J., T. C. Wainwright, G. J. Bryant, L, J. Lierheimer, R. S. Waples, F. W. Waknitz, and I. V. Lagomarsino, I. V. 1996. Status review of west coast steelhead from Washington, Idaho, Oregon, and California. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northwest Fisheries Science Center, Coastal Zone and Estuarine Studies Division.

Caudill, C. C., W. R. Daigle, M. L. Keefer, C. T. Boggs, M. A. Jepson, B. J. Burke, R. W. Zabel, T. C. Bjornn, and C. A. Peery. 2007. Slow dam passage in Columbia River salmonids associated with unsuccessful migration: delayed negative effects of passage obstacles or condition-dependent mortality? Canadian Journal of Fisheries and Aquatic Sciences 64:979–995.

Crozier, L. G., A. P. Hendry, P. W. Lawson, T. P. Quinn, N. J. Mantua, J. Battin, R. G. Shaw, and R. B. Huey. 2008. Potential responses to climate change in organisms with complex life histories: evolution and plasticity in Pacific salmon. Evolutionary Applications 1:252–270.

Crozier, L. G., M. D. Scheuerell, and R. W. Zabel. 2011. Using time series analysis to characterize evolutionary and plastic responses to environmental change: a case study of a shift toward earlier migration date in Sockeye Salmon. American Naturalist 178(6):755–773.

Crozier, L. G., J. E. Siegel, L. E. Wiesebron, E. M. Trujillo, B. J. Burke, B. P. Sandford, D. L. Widener. 2020. Snake River sockeye and Chinook salmon in a changing climate: Implications for upstream migration survival during recent extreme and future climates. PLoS ONE 15(9): e0238886. https://doi.org/10.1371/journal.pone.0238886.

Coutant, C. C., and R. R. Whitney. 200. Fish behavior in relation to passage through hydropower turbines: a review. Transactions of the American Fisheries Society 129:351-380.

Eiler, J. H., A. N. Evans, and C. B. Schreck. 2015. Migratory patterns of wild Chinook Salmon Oncorhynchus tshawytscha returning to a large, free flowing river basin. PLoS (Public Library of Science) One [online serial] 10(4):e0123127.

English, K. K., C. Sliwinski, B. Nass, and J. R. Stevenson. 2003. Assessment of adult steelhead migration through the mid-Columbia River using radio-telemetry techniques, 2001-2003. Report for Public Utility District No. 2 of Grant County, Ephrata, Washington, Public Utility District No. 1 of Chelan County, Wenatchee, Washington., and Public Utility District No. 1 of Douglas County, East Wenatchee, Washington.

Fuchs, N. T, C.C. Caudill, A.R. Murdoch, and B.L. Truscott. 2021. Overwintering distribution and postspawn survival of steelhead in the Upper Columbia Basin. North American Journal of Fisheries Management 41 (3):757-774.

GCPUD (Public Utility District of Grant County No.2.) 2006. Priest Rapids Project Salmon and Steelhead Settlement Agreement (SSSA) entered by Grant PUD, USFWS (United States Department of Interior U.S. Fish and Wildlife Service), NOAA Fisheries (National Marine Fisheries Service of the National Oceanic and Atmospheric Administration), WDFW (Washington Department of Fish and Wildlife, CCT (Confederated Tribes of the Colville Reservation) and Yakama Nation.

Haeseker, S. L., J. A. McCann, J. Tuomikoski, and B. Chockley. 2012. Assessing freshwater and marine environmental influences on life-stage specific survival rates of Snake river spring-summer Chinook Salmon and steelhead. Transactions of the American Fisheries Society 141:1221-138.

Ham, K. D., R. P. Mueller, and P. S. Titzler. 2015. Evaluation of adult steelhead passage with TWS spill during the winter of 2014-2015 at McNary Dam. Pacific Northwest National Laboratory, Richland, Washington.

Ham, K.D., P.S. Titzler, R.P. Mueller and R. Harnish. 2021. Evaluation of a surface spill operation to return adult steelhead overshoots downstream of McNary Dam. Final report prepared for the U.S. Army Corps of Engineers, Walla Walla District by Pacific Northwest National Laboratory, Richland, Washington.

Harnish, R. A., A. H. Colotelo, X. Li, K. D. Ham, and Z. Deng. 2015. Factors affecting route selection and survival of steelhead kelts at Snake River dams in 2012 and 2013. Pacific Northwest National Laboratory, Richland, Washington.

Hess, M. A., J. E. Hess, A. P. Matala, R.A. French, C. A. Steele, K. C. Lovtang, and S. R. Narum. 2016. Migrating adult steelhead utilize a thermal refuge during summer periods with high water temperatures. ICES Journal of Marine Sciences 73:2616-2624.

High B., C. A. Peery, and D. H. Bennett. 2006. Temporary staging of Columbia River summer steelhead in cool water areas and its effect on migration rates. Transactions of the American Fisheries Society 135:519 -528.

Isaak D. J., C. H. Luce, D. L. Horan, G. Chandler, S. Wollrab, and N. E.Nagel. 2018. Global warming of salmon and trout rivers in the Northwestern U.S.: road to ruin or path through purgatory? Transactions of the American Fisheries Society 147:566-587.

ISAB (Independent Scientific Advisory Board). 2007. Climate change impacts on Columbia River Basin fish and wildlife, p.136. Northwest Power and Conservation Council, Columbia River Basin Indian Tribes, National Marine Fisheries Service, Portland, Oregon.

Keefer, M. L., C.C. Caudill, C. A. Peery, and C. T. Boggs. 2008a. Non-direct homing behaviors by adult Chinook salmon in a large, multi-stock river system. Journal of Biology 72:27-44.

Keefer, M. L., C. T. Boggs, C. A. Peery, and C. C. Caudill. 2008b. Overwintering distribution, behavior, and survival of adult summer steelhead: variability among Columbia River populations. North American Journal of Fisheries Management, 28(1), 81-96.

Keefer M. L., R. H. Wertheimer, A. F. Evans, C. T. Boggs, C. A. Peery. 2008c. Iteroparity in Columbia River summer-run steelhead (Oncorhynchus mykiss): implications for conservation. Canadian Journal of Fisheries and Aquatic Sciences 65:2592–2605.

Keefer, M. L., T. S. Clabough, M. A. Jepson, E. L. Johnson, C. A. Peery, and C .C Caudill. 2018. Thermal exposure of adult Chinook Salmon and steelhead: diverse behavioral strategies in a large and warming river system. PLOS ONE 13(9), e0204274.

Keefer, M. L., C.A. Peery, T. C. Bjornn, M. A. Jepson, and L. C. Stuehrenberg. 2004. Hydrosystem, dam, and reservoir passage rates of adult Chinook Salmon and steelhead in the Columbia and Snake rivers. Transactions of the American Fisheries Society, 133(6), 1413-1439.

Keefer, M. L., C.A. Peery, and B. High. 2009. Behavioral thermoregulation and associated mortality trade-offs in migrating adult steelhead (*Oncorhynchus mykiss*): variability among sympatric populations. Canadian Journal of Fisheries and Aquatic Sciences, 66(10), 1734-1747.

Khan, F., I. M. Royer., G. E. Johnson, and S. C. Tackley. 2013. Sluiceway operations for adult steelhead downstream passage at The Dalles Dam, Columbia River, USA. North American Journal of Fisheries Management, 33(5), 1013-1023.

Lynch, A. J., B. J. E. Myers, C. Chu, L. A. Eby, J. A. Falke, R. P. Kovach, T. J. Krabbenhoft, T. J. Kwak, J. Lyons, C. P. Paukert, and J. E. Whitney. 2016. Climate change effects on North American inland fish populations and assemblages. Fisheries 41: 346–361.

Mann, R. D., C. A. Peery, A. M. Pinson, C. R. Anderson. 2009. Energy use, migration times, and

spawning success of adult spring–summer Chinook Salmon returning to spawning areas in the South Fork Salmon River in Central Idaho: 2002–2007. Technical Report 2009-4.

Cooperative Fish and Wildlife Research Unit, University of Idaho, Moscow.

Mann, R. D., and C. G. Snow. 2018. Population-specific migration patterns of wild adult summer-run Chinook Salmon passing Wells Dam, Washington. North American Journal of Fisheries Management 38:377-392.

McCullough, D. A. 1999. A review and synthesis of effects of alterations to the water temperature regime on freshwater life stage of salmonids, with special reference to Chinook Salmon, EPA 910-R-99-010. United States Environmental Protection Agency, Seattle, Washington.

NOAA Fisheries. 2020. Endangered Species Act Section 7(a)(2) Biological Opinion and Magnuson-Stevens Fishery Conservation and Management Act Essential Fish Habitat Response. NOAA Fisheries: NMFS Consultation Number: WCRO-2020-00113.

Normandeau Associates, Inc. 2014. Direct Injury and Survival of Adult Steelhead Trout Passing a Turbine and Spillway Weir at McNary Dam. Final report prepared for the U.S. Army Corps of Engineers, Walla Walla District by Normandeau Associates, Inc., Drumore, Pennsylvania.

NMFS (National Marine Fisheries Service). 2003. Biological Opinion and Magnuson-Steve Fishery Conservation Management Act on Issuance of Permit 1395 jointly to WDFW, Chelan PUD, and Douglas PUD, Issuance of Permit 1396 to the USFWS, and Issuance of Permit 1412 to the Confederated Tribes of the Colville Reservation. National Marine Fisheries Service. Seattle, Washington. 87 p.

Orme, R., and R. Kinzer. 2018. Integrated in-stream PIT tag detection system operations and maintenance; PIT tag based adult escapement estimates for spawn years 2016 and 2017. Nez Perce Tribe Department of Fisheries Resources Management, McCall, Idaho.

PSMFC (Pacific States Marine Fisheries Commission). 2015. PTAGIS (Columbia River Basin PIT Tag Information System) [online database]. PSMFC, Portland, Oregon. Available: www.ptagis.org. (February 2019).

Pope, A. C., J. R. Skalski, T. Lockhart, and R. A. Buchanan. 2016. Generation of multistate release-recapture models using a graphic user interface. Animal Biotelemetry 4:23

Pletterbauer, F., A. H. Melcher, T. Ferreira, and S. Schmutz. 2014. Impact of climate change on the structure of fish assemblages in European rivers. Hydrobiologia 744(1):235–254.

Plummer, M. 2019. Rjags: Bayesian Graphical Models using MCMC. Available from <https://CRAN.R-project.org/package=rjags> (accessed August 2020).

Quinn, T. P., and D. J. Adams. 1996. Environmental changes affecting the migratory timing of American shad and sockeye salmon. Ecology 77:1151–1162.

R Core Team. 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria. Available from <http://www.R-project.org> (accessed September 2019).

Richins, S. M. and J. R. Skalski. 2018. Steelhead overshoot and fallback rates in the Columbia-Snake River basin and the influence of hatchery and hydrosystem operations. North American Journal of Fish Management 38:1122-1137.

Richter, A., and S. A. Kolmes. 2005. Maximum temperature limits for Chinook, coho, and chum salmon, and steelhead trout in the Pacific Northwest. Reviews in Fisheries Science, 13(1), 23-49.

Tenney, J., D. Warf, and N. Tancreto. 2017. Columbia Basin PIT Tag Information System, 2016 annual report. Report to Bonneville Power Administration, project 1990-080-00. Pacific States Marine Fish Commission, Portland, Oregon.

UCSRB (Upper Columbia Salmon Recovery Board) 2018. Upper Columbia Integrated Recovery Hydropower Background Summary. Upper Columbia Salmon Recovery Board, Wenatchee, WA. Available from: https://www.ucsrb.org/mdocuments-library/reports/.

Wade, A., T. J. Beechie, E. Fleishman, H. Wu, N. J. Mantua, J. S. Kimball, D. M. Stoms, and J. A. Stanford. 2013. Steelhead vulnerability to climate change in the Pacific Northwest. Journal of Applied Ecology 50(5): 1093–1104. DOI: 10.1111/1365-2664.12137.

Waterhouse, L., J. White, K. See, A. R. Murdoch, and B. X. Semmens. 2019. A Bayesian nested patch occupancy model for estimating the population size form tag data: an application to natal stream steelhead abundance. Ecological Applications doi:10.1002/eap.2202 <https://doi.org/10.1002/eap.2202>.

Wertheimer, R. H. 2007. Evaluation of a surface flow bypass system for steelhead kelt passage at Bonneville Dam, Washington. North American Journal of Fisheries Management 27:21–29.

Wertheimer, R. H., and A. F. Evans. 2005. Downstream passage of steelhead kelts through hydroelectric dams on the lower Snake and Columbia rivers. Transactions of the American Fisheries Society 134:853–865.