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 high 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, physiological stress, higher 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 migration 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 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 (d) 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 the Columbia River.

Summer steelhead from some interior Columbia River populations also may exhibit a complex migration pattern referred to as overshooting. While the use of cool water refuges by summer steelhead as a thermoregulation response occurs downstream of natal tributaries, overshooting refers to a behavior that involves steelhead migrating upstream of their natal tributary for an undetermined time period. 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 (i.e., due to barging during smolt outmigration or improper hatchery practices, respectively) were also found to be important factors, as well as ocean age and adult ladder placement (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; Mann and Snow 2018). Richins and Skalski (2018) reported overshoot rates of known origin adult steelhead as high as 71%, with many populations exhibiting rates > 50%. However, the probability of steelhead returning to their natal stream, or “overshoot fallback,” is more variable and less understood. Overshoot fallback rates (hereafter referred to as overshoot return rates) ranged from 18% to 75% and were positively influenced by the number of days hydroelectric projects spilled water the following March (Richins and Skalski 2018).

Estimates of overshoot fallback abundance underrepresent the abundance of steelhead that overshot their natal stream unless fallback rates are 100% (Richins and Skalski 2018). While overshoot return rates represent the component of overshoot fish that returned to their natal stream, estimates of adult abundance based solely 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 return rates reported for steelhead, failure to return to their natal tributary or presence in a non-natal tributary (i.e., stray) may have serious conservation implications, either demographically, genetically 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 in order to return to their natal tributary, and 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). Khan et al. (2013) found that downstream migrating adult steelhead greatly prefer surface (e.g., sluiceway) over turbine passage routes. 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 conversation status or viability of those populations. Given the risks associated with overshoot behavior on populations of conservation concern, the goals of this study were to: (1) estimate the abundance of overshoot steelhead at Priest Rapids Dam; (2) compare migration patterns and timing of non-overshoot and overshoot steelhead; (3) estimate the overall overshoot return rate for steelhead at Priest Rapids Dam, and (4) examine the relationship between overshoot return rate and downstream migration barriers (i.e., the number of dams passed).

<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). Chief Joseph Dam was built without fish ladders, but fish ladders in all downstream dams also possess equipment to detect passive integrated transponder (PIT) tags, except Wanapum Dam. Steelhead status and trend monitoring for this DPS has been occurring at Priest Rapids Dam since 1986 (Brown 1995). 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.

*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, adult summer steelhead were systematically sampled 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 and scale samples, and injected PIT tags into all adult hatchery and wild steelhead at the PRD trap three days a week from early July through mid- November, with an annual target sample rate of ~15%. 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 return abundance at PRD as described below.

*Overshoot fallback abundance*.–We used a Bayesian nested patch occupancy model (POM) to estimate overshoot return 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. Detection probabilities are estimated using dams or double 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), the true location of fish *i*, *zi,j+1*, is drawn from 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 multiplication of all the subsequent downstream transition probabilities along that path. The detection probabilities, , are estimated using detections from both hatchery and wild fish but transition probabilities, , are 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.

Escapement estimates of the four steelhead populations that comprise the UCR DPS have been estimated using the POM 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 return). To account for this behavior the model structure includes PIT tag interrogation sites downstream of Priest Rapids Dam to estimate overshoot return abundance. Specifically, overshoot return 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].

The PTAGIS database was queried to obtain a list of wild adult steelhead that were PIT tagged as juveniles in the Middle Columbia River (MCR) Distinct Population Segments (DPS), detected as adults at PRD and subsequently detected at other PTAGIS sites in the Upper Columbia River (UCR), MCR, and SR DPSs (Figure 1). These data are referred to as observed known origin steelhead and were used to estimate overshoot and fallback abundance, overshoot return rate, and migration timing of MCR DPS steelhead in the UCR and SR DPSs.

One approach to estimate wild steelhead overshoot abundance at PRD is to use the multistate release-recapture models in Program Brach (Pope et al. 2016; Richins and Skalski 2018) to estimate population-specific proportions of overshoots and then expand by the population-specific juvenile PIT tag rate. However, population-specific tag rates 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 total overshoot return abundance that year (*Fi*). To calculate *ti*, we expanded the number of observed overshoot return tags 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 return survival rate () by dividing the estimate of total overshoot return abundance by the total overshoot abundance at PRD, accounting for uncertainty in the overshoot return 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.

*Overshoot migration success*.–To evaluate the impact of dam crossings on overshoot return success, 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), 3 (Rock Island), 4 (Rocky Reach) or 5 (Wells) dams. Most dams have no way to detect adult fish 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 at during their upstream migration and pooled this 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 return success probabilities after crossing zero 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) from the logistic regression model for model validation and to better understand the relative survival benefits or costs of 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, 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 (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)).

**<**A>Results

<B>Overshoot abundance and migration success

Overshoot fallback estimates from Priest Rapids Dam 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 abundance was significantly related (R2 = 0.53, *P* < 0.04), suggesting factors influencing abundance affected both wild and hatchery steelhead similarly. The largest group of fallback steelhead were observed in the Snake River at Ice Harbor Dam, followed by the Yakima River at Prosser Dam (Table 2). Other overshoot populations in the MCR DPS were less abundant and consistent with that reported by Richins and Skalski (2018). The estimated total overshoot fallback abundance of wild steelhead was significantly related to the number of known overshoot fallback fish (R2 = 0.74; *P* < 0.001). Using this relationship, we estimated the total annual overshoot abundance of wild steelhead at Priest Rapids Dam based on the total number of known overshoots;

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 are overshoots from downstream populations. Hence, we summed the estimated number of overshoots at PRD and the estimated 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%. In addition, overshoot return survival rates of wild steelhead were variable (range 35-70%) and averaged 57% (SD = 12%) (Table 3).

The majority of known wild steelhead overshoots (52%) were last detected at Priest Rapids Dam. 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 observed downstream of PRD. A small proportion of known overshoot wild steelhead were detected in tributaries (5.6%), but only 3.2% (N= 8) were observed during the spawning period in the spring. Of those, the majority (88%) were observed in tributaries upstream of Wells Dam. The logistic model examining the relationship between the number of dams and overshoot return rates 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 is negatively associated with their downstream migration success (Figure 2). Model predictions of overshoot return rates (95% CI) for zero dams was 0.944 (0.896, 0.971) and comported well the observed probability of non-overshoot Yakima River steelhead (N = 276) at Prosser Dam (0.949).

<B>Overshoot migration timing

Steelhead exhibiting overshoot behavior have a longer migration distance 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% were detected at Priest Rapids Dam and 3% at Ice Harbor Dam. Of those overshoot steelhead, a small percentage (14%) were detected at both Priest Rapids and Ice Harbor dams. Yakima steelhead that were not detected at any Upper Columbia or Snake River dam upstream of McNary Dam had the greatest proportion detected at Prosser Dam (94.9%). Overshoot steelhead at PRD and Ice Harbor Dam had overshoot return rates of 78% and 60%, respectively. In general, Yakima steelhead are not observed at Prosser Dam until water temperatures decline and are similar to that of the Columbia River (Figure 3). 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 relative 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 relationships based on a similar number of dams required to fallback. 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 fallbacks 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 does comport well with results of this 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 2018). 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. Overshoot return rates 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 return rates 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 origin 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 gone undetected (i.e., died prior to being detected), our POM included all possible locations, based on geographic distribution of known origin overshoot steelhead, and accounted for the variability in detection probabilities among sites and years.

Estimated overshoot return rates of wild steelhead generated for this study (mean = 57%) were similar to the observed mean overshoot return rate of known overshoots (69%, WDFW unpublished data). Potential reasons for disparities in overshoot return rates 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 (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 2018), 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 2018). Downstream survival rates of adult salmonids via turbine passage are largely unknown but decrease as fish length increases (Coutant and Whitney 2000). This could explain why overshoot return rate decreased as the number of dams increased (Figure 2).

Summer steelhead in the Columbia River Basin may exhibit at least two different behaviors (i.e., utilize cool water refuge downstream of natal tributaries or seek out cool water refuge upstream of their natal tributary) in response to elevated water temperatures but each have potentially different consequences related to both migration delays and success. Keefer et al. (2009) found that steelhead that use temporary cool water refuges in the lower Columbia River during their upstream migration were typically delayed between two weeks and two months, and they found that the lower homing success of wild steelhead (4.5 percentage points) compared to steelhead that did not use cool water refuges was attributed to differential harvest rates. In that study, permanent straying (i.e., spawning in a non-natal stream) could not be differentiated from steelhead that were harvested within the cool water refuges. Conversely, wild steelhead that overshoot their natal stream and migrate upstream of Priest Rapids Dam are not subject to direct harvest but are subject to indirect mortality from recreational fisheries not to exceed 2% (NMFS 2003). Hence, differences in migration success between overshoot and non-overshoot Yakima River steelhead (16.9 percentage points) are more likely not associated with harvest. Furthermore, delays in migration are considerably longer compared to fish using cool water refuges. For example, the average (SD) number days from when Yakima River steelhead were detected at Priest Rapids Dam and subsequently at Prosser Dam was 138 (73). These data suggest that the overshooting behavior of some steelhead populations has greater impacts on population viability (i.e., abundance and productivity) than steelhead that do not overshoot or those that use cool water refugia downstream of their natal population.

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), and the population specific patterns of overshoot from that study are consistent with this study. However, a comparison of migration success of the two basic overshoot pathways (upstream of Priest Rapids or Ice Harbor dams) has not been conducted. Pope et al. (2016) also used a multistate 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 between 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 average downstream return rate of 61%. 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 return rates and the number of 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 only installed at Little Goose and Lower Monumental dams in 2014, for discussion purposes we only examined overshoot patterns and migration success for steelhead returning in 2015. Overshoot return rate 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 overshoot return rate in the Snake River was 32% compared to 56% in the UCR suggesting approximately 2 out 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. In addition, unlike steelhead areas upstream of Priest Rapids Dam, some major spawning areas (e.g., lower Grande Ronde and lower Salmon rivers), and some unknown number of minor spawning areas, do not have IPDS and may have gone undetected. 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 return rates suggests the number of dams is an important factor in downstream migration success, but undoubtedly other factors are also important but outside the scope of the is 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).

The potential effects of genetic introgression of fish from the MCR DPS spawning with fish from the SR DPS is also problematic. This potential level of genetic introgression may explain, in part, the genetic patterns observed by Blankenship et al. (2011). In that study, MCR DPS populations that did not exhibit strong overshooting behavior (i.e., Klickitat and Big White Salmon) were clustered (aggregate 3) from the rest of the DPS (aggregate 4). Conversely, some MCR DPS populations were also clustered together with UCR DPS and SR DPS populations (i.e., potential spawning areas of overshoot steelhead from the MCR DPS), forming the largest cluster (aggregate 5) in the Columbia-Snake River Basin. Khan et al. (2013) suggested that overshoot steelhead may hold for extended periods of time in Columbia River reservoirs because of their preference for surface passage routes over turbines. Hence, lack of a preferred passage route may have contributed to the relatively high proportion of overshoot steelhead detected in upstream tributaries (i.e., potential strays) reported by Richins and Skalski (2018).

<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 relatively low overshoot return rates, 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 high survival rates. Experiments conducted to evaluate the efficacy of sluiceways (Khan et al. 2013) and temporary spillway weirs (Ham et al. 2015) 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.

Previous studies examining steelhead overshoot have also made consistent suggestions to improve overshoot return rates (Khan et al 2013; Richins and Skalski 2018). Surface flow passage routes operated during non-spill periods would increase overshoot return rates for both MCR and SR DPS. Fuchs (2018) reported that downstream passage at PRD began in early September through mid-December and resumed in early March. Furthermore, if surface passage routes were equipped with PIT tag detection equipment, project-specific operations could be refined to minimize operational costs. In the interim, existing monitoring programs at Priest Rapids and Lower Granite dams could provide annual estimates of overshoot return rates and serve as a low-cost effectiveness monitoring tool. Additionally, operation of surface flow passage before and during spill periods through the end of June would also increase the passage efficiency of kelts (Wertheimer and Evans 2005; Wertheimer 2007). As river water temperatures continue to increase and even more adult salmonids adapt complex migration 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 (demographic, genetic or both) to most populations in the Columbia Basin.

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