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

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*Abstract.* – Summer steelhead *Oncorhynchus mykiss* may enter freshwater almost a year before spawning providing opportunity to make long migrations (>1,000 km) to pristine habitats for spawning. However, in response to sub-optimal tributary conditions, adult summer steelhead may exhibit even greater complex behaviors during upstream migration in the Columbia River Basin. Steelhead may migrate upstream of their natal tributary or overshoot from days to several months and subsequently migrate downstream or fallback to their natal tributary to spawn. An existing Bayesian patch occupancy model derived from observations of adult steelhead tagged with passive integrated transponder (PIT) tags to estimate population-specific abundance upstream of the tagging location was modified to estimate the abundance of overshoot fallbacks. Overshoot abundance at the tagging location was estimated based on the number of known overshoot steelhead and the relationship between known fallbacks and their estimated abundance. The annual mean (SD) proportion of overshoot steelhead that successfully migrated downstream of the tagging location (i.e., Priest Rapids Dam) was 0.66 (0.25). The spatial distribution (i.e., number of dams detected upstream of Priest Rapids Dam) of overshoot steelhead suggested the number of dams negatively affected downstream migration success probability. Improved downstream passage survival for adult steelhead will increase the abundance of those affected donor populations (up to 34%), while reducing potential genetic introgression of recipient populations (i.e., overshoot steelhead that spawn in non-natal rivers). This is the first study to estimate the abundance of overshoot and fallback steelhead and can be replicated using existing models in the Snake River Basin. Studies have consistently shown that surface flow passage routes (e.g., sluiceways and temporary spillway weirs) are very effective in guiding and passing adult steelhead downstream of a hydroelectric project. Overshoot rates are expected to increase (i.e., both magnitude and number of populations) in response to climate change and increasing water temperatures. While habitat restoration efforts may produce localized reductions in water temperature, summer steelhead are likely to encounter warmer water temperature in their upstream migration resulting in a growing proportion of some populations overshooting natal watershed. Summer steelhead and to lesser extent other anadromous salmonids have shown their resilience in adapting to these unfavorable migration conditions. However, without significantly increasing the downstream migration success of both pre-spawn (i.e., overshoot) and post-spawn (i.e., kelts) steelhead, greater uncertainty in the efficacy of recovery efforts in other areas (i.e., habitat, hatchery and harvest) may be the consequence.

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 a greater distance from the ocean or areas with only seasonal access (i.e., temporary migrations barriers due to low discharge or high 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 are near lethal limits (Richter and Kolmes 2005). The effects of Columbia River water temperatures on adult anadromous salmonid migration survival 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 cold-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 cold-water refuges. Steelhead may remain in cold 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 as was reported in the Deschutes River (Hess et al. 2016). The magnitude of cold-water refuge use varies with Columbia River water temperature and has been reported as high 66% for interior Columbia River steelhead and many (37%) use more than one tributary (High et al. 2006). Summer steelhead from the early part of the run (before Aug 25) used cold water refuges (66%) at a slightly higher rate than later fish for 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 cold water refuges was 8% lower (11% hatchery and 5% wild) compared to steelhead that did into use cold water refuges, but lower survival was attributed to higher rates of harvest within the cold-water tributaries compared to the Columbia River.

Summer steelhead from some interior Columbia River populations also may exhibit a complex migration pattern referred to 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 a steelhead migrating upstream of the mouth of its natal tributary for an undetermined time period. Overshoot probability was reported as significantly positively related to increasing water temperatures near the natal tributary (i.e., another behavioral thermoregulatory response), but to a lesser extent incomplete or nonsequential homing during the juvenile life stage (i.e., barging during smolt outmigration or improper hatchery practices, respectively) were also found to be factors as well as ocean age and adult ladder placement (Richins and Skalski 2018). This behavior has also been reported in the Columbia River for Chinook Salmon *O. tshawytscha,* but at lower rate than reported for steelhead (Boggs et al. 2004; Keefer et al. 2008a; Mann and Snow 2018). Richins and Skalski (2018) reported that overshoot rates of known origin adult steelhead as high as 71% with many populations exhibited rates > 50%. However, the probability of returning to their natal stream or “overshoot fallback” is more variable and less understood. Overshoot fallback rates were also highly variable and 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 (Richins and Skalski 2018). Estimating overshoot abundance is important because when combined with the abundance of steelhead that did not overshoot their natal tributary it represents the total number of adults that returned to the Columbia River, not including any unaccounted harvest. Therefore, estimates of population abundance and productivity based solely on returns to the natal stream or subbasin may be an underestimate. Given the variability in overshoot fallback 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 temporary using 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 distribution and more importantly the sources of mortality are different. 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 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 donor population) or spawn in a non-natal stream and have genetic impacts on the recipient population. Furthermore, if the abundance of overshoot or non-natal steelhead is not known or accounted for, their presence may mask the true conversation status or viability of recipient 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) describe migration patterns and distribution of steelhead that overshoot Priest Rapids Dam and 3) estimate the overshoot return rate for overshoot steelhead that successfully migrated downstream of Priest Rapids Dam.

**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. Steelhead status and trend monitoring for this DPS has been occurring at Priest Rapids Dam since 1986 (Brown 1995).

*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 sampled at Priest Rapids Dam (PDR) at Columbia River rkm 639 during their adult migration in return years 2010 to 2017 (Figure 1, Waterhouse et al. 2020). We collected biological data, scale samples, and PIT tagged adult hatchery and wild steelhead at the PRD trap using an annual sample rate of ~ 15%. Adult steelhead PIT tag data were uploaded into the regional PIT Tag Information System database (PTAGIS, Tenney et al. 2017). The PTAGIS database (https://www.ptagis.org) was subsequently queried to obtain PIT tag detections at mainstem dams on the Snake/Columbia Rivers and instream PIT tag detection sites from the adults PIT tagged at PRD. 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 double arrays at some sites, as well as detections from sites upstream of a particular 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 particular 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 2011 (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 original model structure was extended to estimate overshoot return abundance at interrogation sites downstream of Priest Rapids Dam. 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 [IHA].

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), MRC, and Snake River (SR) DPSs (Figure 1). These data are referred to as observed known origin steelhead and were used to estimate MCR stray percentages by population detected in the UCR and SR DPSs, overshoot abundance, stray and overshoot return survival, and migration timing.

One approach to estimate wild steelhead overshoot abundance at PDR is to use the methods of Richins and Skalski (2018) to estimate the known percentage of overshoots and 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 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 generate 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 sites.

To improve the homogeneity of the variances and meet the linear regression assumptions, we 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*. – We examined the PTAGIS detection histories of steelhead tagged as juveniles in the Yakima river that were detected crossing McNary dam, the last dam downstream of the Yakima river. Fish detected within the Yakima river (e.g. at Prosser dam) were categorized as successful migrants. To evaluate the impact of dam crossings on overshoot return success, we grouped fish based on the number of dams they were observed to cross, from zero (moved straight from McNary into the Yakima river) up to five (Wells dam). 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. For each group, the overshoot return success rate was calculated as the proportion of successful migrants within each group of fish. For comparison purposes only, because overshoot steelhead that were only detected at Priest Rapids Dam may have also migrated upstream of Wanapum Dam (only 31 km upstream with no PIT tag interrogation), the overshoot return rate was attributed to both dams (i.e., N = 2), while the square root of the two dam overshoot return rate was attributed to Priest Rapids Dam (i.e., N = 1). While this approach may be biased, it does provide some distinction in overshoot returns rates for steelhead that migrated upstream over one or two dams.

*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. Mean monthly water temperature in the lower Yakima River were queried from the U.S, Bureau of Reclamation Hydromet station at Kiona ([https://www.usbr.gov/pn/hydromet/yakima/yakwebarcread.html](https://www.usbr.gov/pn/hydromet/yakima/yakwebarcread.html%20)) and Columbia River from the tailrace of Priest Rapids Dam 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)) in 2015.

**RESULTS**

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 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). Using this relationship, we estimated the total overshoot abundance of wild steelhead at Priest Rapids Dam based on the total number of known overshoots;

Overshoot abundance = 40.71*x*0.99

where *x* is the number of known overshoot adult steelhead PIT tagged as juveniles detected downstream of 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%. We summed the estimated number of overshoots at PRD and the estimates of escapement to the four steelhead populations above PRD and compared that to the total adjusted counts of wild steelhead that arrived at PRD. The two time-series were very similar: highly correlated (*r* = 0.98) with a root mean square error of 430 fish, and a mean relative difference of only 3.3%. In addition, overshoot return survival rates of wild steelhead were variable (range 35-70%) and averaged 57% (SD = 12%) (Table 3).

The plurality of known wild steelhead overshoots (46%) were last detected at Priest Rapids Dam (Figure 2). However, it is likely that some of these fish migrated upstream of Wanapum Dam, but there are no PIT tag detectors in the adult ladders. Conversely, most unsuccessful overshoot steelhead were last detected at Wells Dam (15%). Overall, the proportion of known overshoot steelhead that were detected downstream of Priest Rapids Dam (69%) was similar to the estimated mean conversions rate (66%). A proportion of known overshoot steelhead were last detected in tributaries (16%), primarily upstream of Wells Dam (80%), were typically observed in a tributary upstream of the last dam in which they were detected (93%). A majority of wild steelhead overshoots entered tributaries after January 1 (73%) presumably as part of their spawning migration. A similar trend was observed for overshoot hatchery steelhead where only 14% were in observed in tributaries. Of those, 95% were in a tributary upstream of the last dam in which they were detected and 64% were detected in the spring. Although tributary observations were not adjusted for detection probabilities and should be considered minimum estimates, it is worth noting that 100% of the wild steelhead and 79% of the hatchery steelhead detected in the spring were last detected in known spawning areas.

Individual project conversion rates for the Priest Rapids and Wanapum Projects (i.e., the square root of the Priest/Wanapum conversion rate 0.88) was estimated at 0.94. When fish last observed in a tributary (N = 15) were included, the mean project conversion rate increased from 78% to 86% (Figure 3) and was less variable (CV decreased from 27% to 5%).

The relative prevalence of the overshoot behavior and influence of migration timing into their natal tributary was examined using Yakima River steelhead. Between 2010 and 2017, 327 wild steelhead tagged as juveniles were detected at McNary Dam. Of those, 13% were detected at Priest Rapids Dam and 3% at Ice Harbor Dam consistent with that reported by Richins and Skalski (2018). Of those, a small percentage (2%) were detected at both Priest Rapids and Ice Harbor dams. Yakima steelhead that were not detected at an Upper Columbia or Snake River dam upstream of McNary Dam had the greatest proportion detected at Prosser Dam (95%). Overshoot steelhead at Priest Rapids Dam and Ice Harbor Dam had conversion success rates of 78% and 60%, respectively. Based on detections of steelhead PIT tagged at Priest Rapids Dam at Prosser Dam, overshoot steelhead migrated into the Yakima River between late fall and spring also consistent with that reported by Richins and Skalski (2018). However, based on the estimated number of overshoot steelhead significant differences in migration timing were found when compared to fish that did not overshoot (KS test; *P* < 0.001; Figure 4). While both groups of steelhead initiated their upstream migration once the Yakima River water temperatures were similar to the Columbia River, 50% of overshoot steelhead entered the Yakima Basin prior to January 1 compared to 75% of non-overshoot steelhead.

**DISCUSSION**

The estimated annual mean (SD) number of wild and hatchery steelhead that fell back over Priest Rapids Dam during the study period was 916 (620) and 1,496 (678), respectively. Of steelhead passing Priest Rapids Dam, the mean proportion (CV) of fallbacks was 0.1979 (28%) and 0.1485 (32%) for wild and hatchery steelhead, respectively. An adult steelhead radio telemetry study conducted in 2015 and 2016 reported similar levels of fallback (Fuchs et al. 2020). In that study, radio tag-based estimates of fallback generally estimated higher fallback compared to PIT tag-based model estimates but had higher uncertainty due to a smaller sample size. While these estimates were generated using different tag types, it should be noted that all radio tagged steelhead were also PIT tagged and included in the patch-occupancy model estimates. Mean (SD) annual estimates of overshoot wild and hatchery steelhead at Priest Rapids Dam were 1,385 (685) and 1,860 (816), respectively. Overshoot wild and hatchery steelhead comprised 34% and 19% of the Priest Rapids Dam count and was more variable (wild CV = 47%; hatchery CV = 39%) than estimates of fall back. These data suggest that dam counts may not represent the status and trend of upstream populations and methodologies that use dam counts must account for complex migration patterns (e.g., Buchanan and Skalski 2010; 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 thereby reducing the sample size used in the regression model (N = 8). Ideally, similar PIT tagging rates from all potential overshoot populations would increase the sample size and potentially allow for population-specific relationships or relationships based on a similar number of dams required to fallback. Conversion rates of wild steelhead generated for this study (mean = 66%) were similar to conversion rate based on known overshoots (69%) suggesting that approximately 1 out every 3 overshoot steelhead do not successfully fallback downstream of Priest Rapids Dam. Of those known overshoot steelhead that did not successfully fallback only 16% (N =15) were last observed in tributaries. While the proportion of fish last observed in tributaries was not adjusted for detection probability, an instream PIT tag detection system (IPDS) is 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 are not monitored using IPDSs (Fuchs et al. 2020), we assumed the most unsuccessful overshoot steelhead suffered either natural mortality or were killed during downstream migration from turbine strikes. On August 31, summer spill programs and juvenile bypasses are shut down for the season because the juvenile outmigration period has ended. Unfortunately, this coincides with the period when overshoot steelhead initiate their downstream migration back to their natal streams (Fuchs et al. 2020). Downstream survival rates of adult salmonids via turbine passage are largely unknown but decrease as fish length increases (Coutant and Whitney 2000).

The spatial patterns of known overshoots (i.e., successful versus unsuccessful) upstream of Priest Rapids Dam suggest the number of dams is an important factor. The largest proportion of fallbacks were last observed at Priest Rapids Dam (i.e., one or two dams because Wanapum Dam has no PIT detection) and the largest proportion of overshoot steelhead were last observed at Wells Dam (i.e., five dams). Project specific conversion rates generally declined as fish migrated farther upstream. As migration distance, migration duration, and number of migration obstacles (i.e., dams) increased, fish condition was likely negatively affected which also 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 prespawn mortality or lower spawning success (Mann et al. 2009) and less likely to return as repeat spawners (Keefer et al. 2008b).

Summer steelhead in the Columbia River Basin exhibit at least two different behaviors (i.e., use of cool water refuges and overshooting) in response to elevated water temperatures, but have potentially different consequences related to both migration delays and success. Steelhead that use temporary cold-water refuges in the lower Columbia River during their upstream migration were typically delayed between two weeks and two months, and the higher wild steelhead mortality (4.5 percentage points) was attributed to harvest (Keefer et al. 2009). 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 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 population has greater impacts on population viability (i.e., abundance and productivity) than steelhead that don’t overshoot or those that use cool water refuges.

Overshoot and fallback rates have been estimated for many populations in the Columbia River Basin (Richins and Skalski 2018). While several factors were shown to influence overshoot rates (i.e., natal stream water temperature, hatchery rearing location, adult ladder placement, and ocean age) and many results are consistent with this study, abundance estimates of overshoot and fallback were not reported and a comparison of migration success of the two basic overshoot pathways (upstream of Priest Rapids or Ice harbor dams) was not conducted. While a 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 (except the Yakima) and is comprised of 4 major population groups (MPG) and 20 independent steelhead populations. Of which, steelhead from five subbasins (John Day, Umatilla, Walla Walla, Touchet and Yakima) are routinely observed as overshoots at Priest Rapids and Ice Harbor dams. For comparison purposes only, we assumed the relationship between known overshoots detected at Priest Rapids Dam and estimated abundance is valid for the lower Snake River.

The composition of wild steelhead overshoots from the MCR DPS detected at Priest Rapids and Ice Harbor dams between 2010 and 2017 were different and 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%) but were the least abundant (6%) of those detected at Ice Harbor Dam (Figure 5). More importantly, the overall abundance of known overshoot steelhead from the MCR DPS was 523% greater at Ice Harbor Dam (Figure 6). However, because PIT tag detectors were only installed at Little Goose and Lower Monumental dams in 2014, we only examined overshoot patterns and migration success for steelhead returning in 2015. Overshoot 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%). The conversion rate in the Snake River was 32% compared to 71% in the UCR using the same methodology suggest 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. In addition, unlike the areas upstream of Priest Rapids Dam, some major potential 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 fish upstream of Priest Rapids Dam, over 5 times more MCR steelhead overshoot into the Snake River. Of which, only half as many may successfully fallback and of those unsuccessful steelhead, a large proportion may be spawning 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 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.

**Management Implications**

Quantifying steelhead overshoot and fallbacks upstream of Priest Rapids Dam assists in defining and prioritizing the issues associated with the downstream movement of prespawn steelhead. However, preliminary data suggest that in the Snake River overshoot steelhead are more than 5 times more abundant and conversions 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 conversion 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; Isaak et al. 2018)) suggests higher rates of overshoot from a greater number of populations should be expected in the future. As a result of relatively low conversion rates, prolonged migration periods, potential effects from genetic introgression, steelhead overshooting their natal stream, in response to elevated water temperatures or other factors, 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.

In summary, surface flow downstream passage routes on all 9 Columbia River and 4 lower Snake River hydro-projects should be operated from September 1 through December 15 and from March 1 through April 1 (or the start of spring spill programs) in order to maximize passage efficiency of overshoot fallback steelhead. Lower Columbia River hydro-projects may need to operate downstream surface flow passage routes the entire non-spill period. Additionally, operation of surface flow passage during spills periods through the end of June would also increase the passage efficiency of kelts. Following the completion of a similar analysis in the Snake River, the potential benefit, in terms of population viability, resulting from higher downstream passage efficiency throughout the Columbia-Snake River basin by both pre-spawn and post-spawn steelhead can be estimated using existing models (e.g., population viability or life cycle models). Furthermore, existing monitoring programs at Priest Rapids and Lower Granite dams will provide annual estimates of conversion rates and serve as a low-cost effectiveness monitoring tool. While the recommendations from the study conducted at The Dalles Dam have been implemented (Khan et al 2013), all the steelhead populations exhibiting high rates of overshoot are upstream of The Dalles Dam (Richins and Skalski 2018).

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Table 1. Steelhead abundance (adjusted for ladder fallback) at Priest Rapids Dam and the estimated number of overshoot fallback steelhead using the patch occupancy model, 2010-2017.

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

Table 2. Estimates by subbasin and PTAGIS code of overshoot fallback steelhead downstream of Priest Rapids Dam. (PRO = Prosser Dam; ICH = Ice Harbor Dam; PRV = Pierce RV Park instream array; TMF = Three Mile Falls Dam; JD1 = Lower John Day at McDonald Ferry). Parentheses indicate PIT tag detection probability (mean, mean of SE). W = wild and H = hatchery.

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Run Year | Yakima  PRO  (0.90, 0.04) | | Snake  ICH  (0.99, 0.01) | | Walla Walla  PRV  (0.57, 0.09) | | Umatilla  TMF  (0.75,0.00) | | John Day  JD1  (0.46, 0.13) | |
| W | H | W | H | W | H | W | H | W | H |
| 2010 | 840 | 56 | 690 | 1397 | 55 | 0 | 33 | 23 | 0 | 22 |
| 2011 | 364 | 29 | 363 | 1698 | 21 | 0 | 0 | 0 | 0 | 0 |
| 2012 | 181 | 28 | 324 | 1832 | 20 | 14 | 13 | 0 | 0 | 0 |
| 2013 | 334 | 32 | 639 | 1433 | 19 | 51 | 19 | 13 | 38 | 19 |
| 2014 | 579 | 60 | 1169 | 2504 | 75 | 27 | 53 | 22 | 43 | 11 |
| 2015 | 324 | 20 | 426 | 882 | 57 | 20 | 24 | 0 | 29 | 0 |
| 2016 | 89 | 26 | 117 | 685 | 20 | 26 | 12 | 0 | 20 | 0 |
| 2017 | 116 | 13 | 65 | 254 | 12 | 9 | 0 | 0 | 21 | 0 |
| Mean | 353 | 33 | 474 | 1336 | 35 | 18 | 19 | 7 | 19 | 7 |

Table 3. Estimated abundance of overshoot steelhead at Priest Rapids Dam and the overshoot return rate or proportion of fish observed downstream of Priest Rapids Dam prior to spawning.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Run Year | Estimated wild steelhead overshoot abundance | | |  | Overshoot return rate  (# fallbacks/# of overshoots) | | |
| Estimate | Lower 95% CI | Upper 95% CI |  | Estimate | Lower 95% CI | Upper 95% CI |
| 2010 | 3161 | 1645 | 7725 |  | 0.617 | 0.215 | 0.976 |
| 2011 | 1278 | 712 | 3307 |  | 0.686 | 0.225 | 0.983 |
| 2012 | 1594 | 603 | 4452 |  | 0.450 | 0.122 | 0.916 |
| 2013 | 2254 | 1080 | 5951 |  | 0.579 | 0.175 | 0.968 |
| 2014 | 3112 | 1905 | 7203 |  | 0.703 | 0.270 | 0.990 |
| 2015 | 1945 | 899 | 5282 |  | 0.561 | 0.165 | 0.962 |
| 2016 | 1053 | 329 | 3110 |  | 0.346 | 0.083 | 0.814 |
| 2017 | 426 | 199 | 1230 |  | 0.645 | 0.181 | 0.982 |



Figure 1. Vicinity map of major dams on the Columbia and Snake Rivers.

Figure 2. Relationship between the overshoot return probability and number of dams using the furthest upstream detection. The overshoot probability for zero dams was based on the proportion of Yakima steelhead detected at McNary Dam, but not detected at Priest Rapids or Ice Harbor Dams and subsequently detected in the Yakima River at Prosser Dam. Note since there is no PIT tag interrogation at Wanapum Dam (i.e., second dam) the probability for both Priest Rapids and Wanapum was used and the square root of the value was used for Priest Rapids Dam (i.e., first dam), 2010-2017.

Figure 4. Passage timing of non-overshoot and overshoot steelhead at Prosser Dam in the lower Yakima River, 2010 -2017. Mean monthly lower Yakima River water temperatures measured at Kiona (rkm 48)difference relative to the Columbia River measured at Priest Rapids Dam tailrace in 2015.

Figure 5. The distribution of overshoot wild steelhead (N = 559) from the Middle Columbia Distinct Population Segment, 2010-2017.

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