Definitions

***Overshoot*** is an adult steelhead that is detected upstream of their natal stream (Keefer et al. 2008).

***Overshoot abundance*** is an estimate of the number of steelhead that overshoot their natal stream to a specific location (i.e., Priest Rapids Dam). These fish may return to their natal (i.e., overshoot return abundance) or may not return to their natal stream (i.e., permanent stray abundance including mortalities).

***Overshoot return abundance*** is the number of overshoots that migrate downstream and return ***presumably*** to their natal stream. You described this as fallback abundance as a fish that successfully migrated to their natal stream.

***Overshoot return survival*** is the proportion of overshoots that migrate downstream and return to their natal stream (i.e., overshoot return). You use downstream migration success or conversion rate.

***Direct migrant*** is an adult steelhead that follows a direct migration route to their natal stream (i.e., a Yakima steelhead that is only detected at PRO).

***Dip-in*** is an adult steelhead that temporarily uses an area or stream downstream of their natal stream before continuing their upstream migration to their natal stream (i.e., Yakima steelhead detected in the Snake River).

***Fallback*** is any fish that emigrated upstream past a dam and subsequently emigrated downstream past that dam using any route. Note a fall back is not associated with a downstream location.

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Given the risks associated with adult steelhead overshoot behavior the goals of this study were to 1) estimate the mean stray percentage of MCR steelhead into the UCR and SR DPSs, 2) estimate the overshoot return abundance from adults tagged at Priest Rapids Dam, 3) estimate the overshoot abundance at Priest Rapids Dam 4) examine factors that affect the overshoot return survival from overshoots detected in the above Priest Rapids Dam, and 5) examine tributary migration patterns from adult steelhead exhibiting overshoots and non-overshoot behaviors.

**Methods**

*Data Collection.* – 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.

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). 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.

In a related study, a subset of the PIT tagged steelhead captured at PRD were also radio tagged (Fuchs et al. 2020). The survival of steelhead at PRD tagged in return year 2015 and 2016 was estimated based on radio and PIT tag detections. The last tag observation of wild steelhead that fell back past PRD are presented in Appendix 3 of Fuchs et al. (2000). They found 30/33 steelhead were observed in the SR and MCR DPSs in 2015 and 14/17 in 2015. These data were used to estimate overshoot return survival described below.

*MCR Stray Percentage.* – MCR steelhead have been observed to stray from their natal streams and enter the UCR and SR DPSs. Using known origin MCR adults from juvenile PIT tagging we estimate the proportion from each population that were detected at PRD and IHR Dams. Due to limited sample size we pooled detections across years to estimate these population specific stray percentages.

*Overshoot return 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 from all detections from sites upstream from each 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. These transition probabilities are multiplied by an estimate of total abundance 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].

*Overshoot abundance*. – 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, due to the complex rearing strategies of interior Columbia River steelhead juveniles, the population specific tag rates are unknown (reference). We estimated overshoot abundance at PRD based on linear regression:

where is the combined MCR and SR DPS estimated overshoot return abundance from the POM for year *i*, is the number of known of overshoots that fall back past PRD, α and β are the regression coefficients, and is the unexplained variation. The number of known overshoots that fell back past PRD is based on all the PIT tag juveniles from the MCR and SE DPSs that were detected at PRD (known overshoots) and were subsequently detected downstream of PRD (successful returns). This implies that all fall backs survived to the detection site and detection was 100%. Our review of the POM indicated that for the sites with the 92% of overshoot returns (i.e., IHA, PRO, and TMF) had mean detection probability approached 100% with the remaining mean detection probabilities (i.e., PRV and JD1) above 75% (Table 2). However, it is an unrealistic assumption that overshoot return survival is 100% (Keefer et al. 2008, Fuchs et al. 2020). We used the survival data from Fuchs et al. (2020) to estimate fall back survival from PRD to PIT tag detection sites. Since we could not reject the null hypothesis of no difference in radio tag fall back survival between years ( = 0.18, df = 1, *P* = 0.67), we used the pooled fall back survival (SD) of 0.88 (SD) to adjust observed known PIT overshoot detection at PRD. We did not use the above methodology to develop estimates of hatchery steelhead overshoot abundance at PRD because hatchery steelhead are subject to harvest in steelhead fisheries after being PIT tagged at PRD and there was no information on hatchery harvest rates by DPS in the steelhead fisheries below PRD.

*Factors Influencing Overshoot Returns.* –

Based on known adult returns to PRD from juveniles PIT tagged in their natal streams, we determined the uppermost detection in the UCR. Adults detected above Wells, Rocky Reach, and Rock Island Dams were assigned values of 5, 4, and 3 dams for fish spawning in the McNary pool, respectively. Since there was no PIT tag detection at Wanapum Dam, for adults detected at PRD, we assigned a value of 1.5, which assumes 50% of these fish passed Wanapum Dam. For fish spawning in the John Day pool (e.g., Umatilla and John Day), which is the dam below McNary we added a value of 1 to the dam totals above. Due to the small annual sample size of detections, dam detections were pooled across years. We used logistic regression to estimate the overshoot return survival based on the number of dams.

The influence of overshoot return behavior on run timing at Prosser Dam [PRO] was examined using the monthly counts of known Yakima origin steelhead overshoots detected at PRD and subsequently detected at PRO compared to non-overshoots detected at PRO. The cumulative monthly count of overshoot steelhead was compared to non-overshoot steelhead using a Kolmogorov-Smirnov (KS) test.

All statistical analyses were conducted using R software (R Core Team 2015). In all regression analysis, Likelihood Ratio Tests (LRTs) were used for model selection and goodness of fit (GOF) test were used to assess model fit. Residuals were examined for outliers, and assumptions for linearity, independence, and normality and homogeneity in normal linear regression were assessed using diagnostic plots.

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**METHODS – THIS IS YOUR ORIGINAL VERSION WITH ALFS EDITS**

*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). However, adult steelhead tagged with passive integrated transponder (PIT) tags as juveniles from the Middle Columbia River (MCR) and Snake River (SR) DPSs have been observed annually at Priest Rapids Dam (i.e., overshoots) since PIT tag detectors were installed in the fish ladders in 2003 (Figure 1). To account for overshoots our study area also included the Snake River (SNR) DPS and the upper portion of the Middle Columbia River (MCR) DPS from the John Day to the Yakima rivers. Richins and Skalski (2018) estimated overshoot and fallback rates of selected populations of steelhead throughout Columbia and Snake River basins but did not report estimates of abundance. Because adult steelhead rarely use adult ladders to migrate downstream, dam counts are positively biased as estimates of escapement upstream because some unknown fraction migrate downstream (i.e., fallback) presumably to their natal tributary prior to spawning.

*Fallback abundance*.– Escapement estimates of the four populations that comprise the UCR DPS have been estimated, since 2011, based on adult steelhead tagged with passive integrated transponder (PIT) tags at Priest Rapids Dam (~15% of the run) that were subsequently detected at instream interrogation sites within each population using a multi-state open population model (Waterhouse et al. 2020). Complete PIT tag detection histories for each fish tagged at Priest Rapids Dam (PRD) were queried from the PIT Tag Information System (PTAGIS) database operated by the Pacific States Marine Fisheries Commission (PSMFC 2015). The model estimates movement rates past various detection points while accounting for imperfect detection at those sites. Detection probabilities are estimated through the use of double arrays at some sites, as well as detections from sites upstream of a particular point. When combined with an estimate of total abundance at Priest Rapids Dam, it translates those movement estimates into escapement estimates. Because some steelhead overshoot Priest Rapids Dam, fallback, and ascend their natal stream to spawn, where their PIT tags are detected, the model structure includes some interrogation sites downstream of Priest Rapids Dam. A majority of downstream sites (PTAGIS site code in brackets) are in the MCR DPS including 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]), and the John Day River at rkm 35 (McDonald Ferry site [JD1]). The abundance of steelhead that passed Priest Rapids Dam and fell back to the SR DPS was estimated at Ice Harbor Dam at rkm 16 [IHA]. Relationships between hatchery and wild steelhead fallback abundance were examined using linear regression by comparing the model estimate of fallback abundance (i.e., PRD PIT tagged adults) with the number of known fallbacks (i.e., PIT tagged as juveniles downstream of PRD) detected as adults at Priest Rapids and subsequently downstream of PRD.

*Overshoot abundance*. – Richins and Skalski (2018) used adult steelhead tagged as juveniles in the natal stream to estimate rates of overshoot and successful fallback. They reported that fallback rates were unrelated to overshoot rates and ranged from 7.7% to 93.4%. Hence, fallback abundance estimates underrepresent the abundance of steelhead that overshot their natal stream.

Estimating overshoot abundance is important because when combined with the abundance of steelhead that did not overshoot their natal tributary represents the total number of adults that returned at least as far as the Columbia River. Therefore, estimates of population abundance and productivity based solely on returns to the natal stream or subbasin may be an underestimate. The relationship between the abundance of fallbacks estimated from the patch occupancy model (i.e., based on steelhead tagged as adults at Priest Rapids) and the number of steelhead adults tagged as juveniles that were observed at Priest Rapids Dam and subsequently downstream of Priest Rapid Dam (i.e., successful downstream migration) was examined using a linear regression through the origin. Hatchery steelhead were not included in this relationship because harvest rates both upstream and downstream of Priest Rapids Dam are variable and unknown. We did not estimate an intercept because not only was it not statistically significant (p = 0.50) but a no-intercept model is more realistic biologically. Using that relationship, the abundance of steelhead that overshoot their natal stream and migrated past Priest Rapids Dam was estimated using the total number of known overshoots (tagged as juveniles) observed at Priest Rapids Dam. The fallback-overshoot ratio or conversion rate was calculated annually and incorporated uncertainty from both estimates of fallback and overshoot using the delta method (Doob, 1935). All statistical analyses were conducted using R software (R Core Team 2015).

*Overshoot migration success and timing*. – Adult steelhead tagged as juveniles in their natal tributary downstream of Priest Rapids Dam are known overshoot steelhead. Complete detection histories for each fish between 2010 and 2017 were queried from the PTAGIS database in order to examine migration patterns. PIT tag detections during downstream migration are limited upstream of Priest Rapids Dam to the juvenile bypass Rocky Reach Dam and closes August 31. Due to the limited spatial and temporal extent of downstream detections, the last dam fish were detected during their upstream migration was used and pooled across years due to low sample sizes. Known overshoots at each dam were categorized as successful downstream migrant if subsequently observed downstream of Priest Rapid Dam (i.e., before spawning, but not as kelts). Hydro-project specific conversion rates were estimated by dividing by the number of known overshoots by the number of known fallbacks detected downstream of the hydro-project. Because overshoot steelhead that were last detected at Priest Rapids Dam may have also migrated upstream of Wanapum Dam (i.e., joint conversion rate), the conversion rate for each project (i.e., Priest Rapids and Wanapum) was calculated by taking the square root of the observed conversion rate of Priest Rapids/Wanapum Project ().

As a consequence of exhibiting an overshoot behavior, steelhead must migrate further, expend greater amounts of energy and may be in poorer condition when entering their natal tributary. For example, steelhead tagged at Priest Rapids Dam and subsequently detected at Prosser Dam in the lower Yakima River must migrate a minimum of 200 km (100 km each way) more than fish that entered the Yakima River directly. 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))