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ARTICLE

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 and potentially make long migrations (>1,000 km) to interior headwater habitats. However, in response to suboptimal freshwater habitat conditions (e.g., warmer water temperatures), adult summer steelhead may exhibit complex behaviors during upstream migration in the Columbia River basin. Steelhead may migrate upstream of their natal tributary (hereafter, referred to as "overshoot") and spend days to several months before subsequently migrating downstream (hereafter, referred to as "fallback") to their natal tributary to spawn. An expansion of an existing Bayesian patch occupancy model, derived from observations of adult steelhead that were PIT-tagged to estimate population-specific abundance upstream of the tagging location, incorporated downstream detection locations to estimate the abundance of overshoot fallbacks. Overshoot steelhead abundance at the tagging location was estimated based on the relationship between the number of known overshoot fallbacks (i.e., the number of steelhead that overshot and successfully migrated downstream to their natal tributary) and their model-estimated abundance. During the study period (2010–2017), the annual mean proportion of overshoot steelhead that successfully migrated downstream of the tagging location (Priest Rapids Dam) was 0.59 (SD = 0.14). The number of dams encountered by overshoot steelhead during their downstream migration was negatively correlated with their downstream migration success probability. Improved downstream passage survival for adult steelhead will increase the abundance of affected populations while reducing potential genetic introgression of upstream populations (i.e., strays). This is the first study to estimate the abundance of overshoot and fallback steelhead, providing the data necessary for scientists to estimate potential conservation benefits of improved downstream survival. For example, surface flow passage routes (e.g., sluiceways and temporary spillway weirs) are very effective in guiding and passing adult steelhead downstream of Columbia River hydroelectric projects and data from this assessment show that changes in dam operations throughout the downstream migration period may maximize conservation benefits.

Adult summer steelhead *Oncorhynchus mykiss* in the Columbia River enter freshwater during the year prior to spawning. This life history strategy allows for access to spawning habitats that are a greater distance from the ocean or to areas with only seasonal access (i.e., temporary migration barriers due to low discharge or warm water temperatures), compared to winter steelhead that enter freshwater during the same year as spawning. Adult summer steelhead may enter the Columbia River over an 8-month period between March and October (Busby et al. 1996), but peak migration at Bonneville Dam, the downstream-most dam on the Columbia River (located at river kilometer [rkm] 234), occurs during August when water temperatures upstream of Bonneville Dam may be near lethal limits (Richter and Kolmes 2005). The effects of Columbia River water temperatures on survival of adult anadromous salmonids during migration are a concern for fish managers (Keefer et al. 2004). Interior Columbia River summer steelhead

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populations (i.e., upstream of Bonneville Dam) are thus at a greater risk from future climate change-related increases in water temperature than other steelhead populations because water temperatures are already near lethal limits (Wade et al. 2013). The physiological effects, both acute and chronic, of elevated water temperatures on salmonids are well studied and include higher metabolic demands, stress, and prevalence of disease and death (McCullough 1999). Behavioral effects from elevated water temperatures include delayed migration at hydroelectric dams (Keefer et al. 2004; Siegel et al. 2021), temporary use of nonnatal tributaries (High et al. 2006), and overshooting or migrating upstream of natal tributaries (Richins and Skalski 2018).

Due to a prolonged period of freshwater entry and residency prior to spawning, summer steelhead may exhibit complex movement patterns as a behavioral thermoregulation response to suboptimal freshwater habitat conditions. Summer steelhead have been shown to temporarily use several nonnatal tributaries in the lower Columbia River (i.e., downstream of the confluence with the Snake River [SR]) or areas in the Columbia River immediately downstream (i.e., tributary plume) as coolwater refuges (High et al. 2006; Keefer et al. 2009, 2018; Hess et al. 2016). Keefer et al. (2009) reported that survival of steelhead using coolwater refuges was 8% lower overall (11% for hatchery fish and 5% for wild fish) compared to steelhead that did not use coolwater refuges, but lower survival was attributed to higher rates of harvest within the coolwater tributaries compared to harvest in the Columbia River.

Summer steelhead from some interior Columbia River populations also may exhibit a complex movement pattern referred to as “overshooting,” which involves steelhead moving upstream of their natal tributary. Richins and Skalski (2018) reported that the steelhead overshoot probability and Columbia River water temperature near the natal tributary were positively related. Overshooting has also been reported for Chinook Salmon *O. tshawytscha* in the Columbia River but at lower rates than reported for steelhead (Boggs et al. 2004; Keefer et al. 2008b; Mann and Snow 2018). Richins and Skalski (2018) reported overshoot percentages of adult steelhead as high as 71%, with many populations exhibiting percentages greater than 50%. However, the mean annual overshoot fallback probability, or the probability that overshoot steelhead will successfully migrate downstream and return to their natal stream (hereafter, “fallback migration success”), is more variable and less understood, ranging from 0.18 to 0.75 (Richins and Skalski 2018). Large variability in population-specific fallback migration success may be attributed to many factors, including nonrepresentative or interannual variability in tagging, differences in the number of overshoot dams, and differences in overshoot migration patterns, both spatially and temporally. Large variability in fallback migration success also makes it difficult to understand the underlying causal mechanisms, thereby increasing uncertainty in the implementation of potential adaptive management actions. Although overshoot rates are less studied in large, free-flowing rivers, Eiler et al. (2015) reported low rates of overshooting for Chinook Salmon (<1%) in the Yukon River, Alaska. However, English et al. (2006) compared adult steelhead migration patterns in the upper Columbia River (UCR) to those in large, free-flowing rivers in British Columbia, Canada. In that study, the proportions of radio-tagged summer steelhead (pooled across years to increase sample size) from the UCR and British Columbia (Skeena and Nass rivers) tracked to downstream spawning locations (i.e., overshoots) were 0.086 and 0.006, respectively. Based on these studies, overshooting in large, natural rivers is an uncommon behavior that is more common—yet highly variable—in the highly regulated Columbia River.

Estimates of overshoot fallback abundance, or the number of steelhead that overshoot and successfully migrate downstream to their natal tributary, do not account for steelhead that overshoot their natal stream but are unsuccessful due to mortality sources, both intentional (i.e., harvest) and unintentional (e.g., turbine strikes), that may occur during their downstream movement. Therefore, estimates of adult abundance and productivity for populations that exhibit this behavior, based on returns to the natal stream or subbasin, would be negatively biased compared to populations that do not exhibit overshooting behavior (i.e., no overshoot fallback-related mortality). Given the low rates of fallback migration success reported for steelhead populations in the Columbia River basin (Richins and Skalski 2018), the absence of these fish in their natal tributary or the presence (i.e., PIT tag detection) of these fish in a nonnatal tributary may have conservation implications demographically, genetically (i.e., introgression), or both. While the apparent mortality or cost of temporarily using downstream nonnatal tributaries as coolwater refuges can be reduced, in part, through harvest regulations (Keefer et al. 2009), overshoot steelhead exhibit a much broader geographic upstream distribution and are subject to other mortality sources in addition to harvest.

Overshoot steelhead must migrate downstream to return to their natal tributary. Khan et al. (2013) found that downstream-migrating adult steelhead greatly prefer surface (e.g., debris sluiceway) over turbine passage routes through dams. However, if the only passage route during nonspill periods (i.e., all surface passage routes are closed) is through the turbines (Richins and Skalski 2018), steelhead may experience higher mortality rates (Wertheimer and Evans 2005). If preferred passage routes are not available, steelhead may expend considerable energy in searching for passage routes prior to spawning or may simply spawn in the nearest available stream (i.e., stray). Hence, overshoot steelhead may suffer high mortality in trying to return to their natal stream during winter months (i.e., demographic cost to their natal population) or they may spawn in a nonnatal stream and have genetic impacts (i.e., introgression) on upstream populations. Furthermore, if the abundance of overshoot or nonnatal steelhead is not known or accounted for, their presence within nonnatal populations may mask the true conservation status or viability of those populations.

Overshoot steelhead have been detected at Priest Rapids Dam (PRD; rkm 639), the first dam upstream from the Yakima River and SR, since 2003 (Figure 1), when PIT detectors in fish ladders became operational. Due to the high variability in abundance and PIT tag rates of overshoot steelhead, the fate of these fish and their contribution to upstream or downstream populations and recreational fisheries were not well understood. Recent advancements in the abundance estimation for populations upstream of PRD suggested that a percentage (~25%) of the steelhead that migrated upstream of PRD were unaccounted for, and they were assumed to represent the overshoot component of the total count of steelhead at the dam (Waterhouse et al. 2020). Hence, monitoring the status and trends of both overshoot and non-overshoot steelhead at PRD and their fate was a priority for managers. As water temperatures increase due to climate change, thereby increasing the likelihood of overshooting, understanding the risks associated with this behavior is required for effective management.

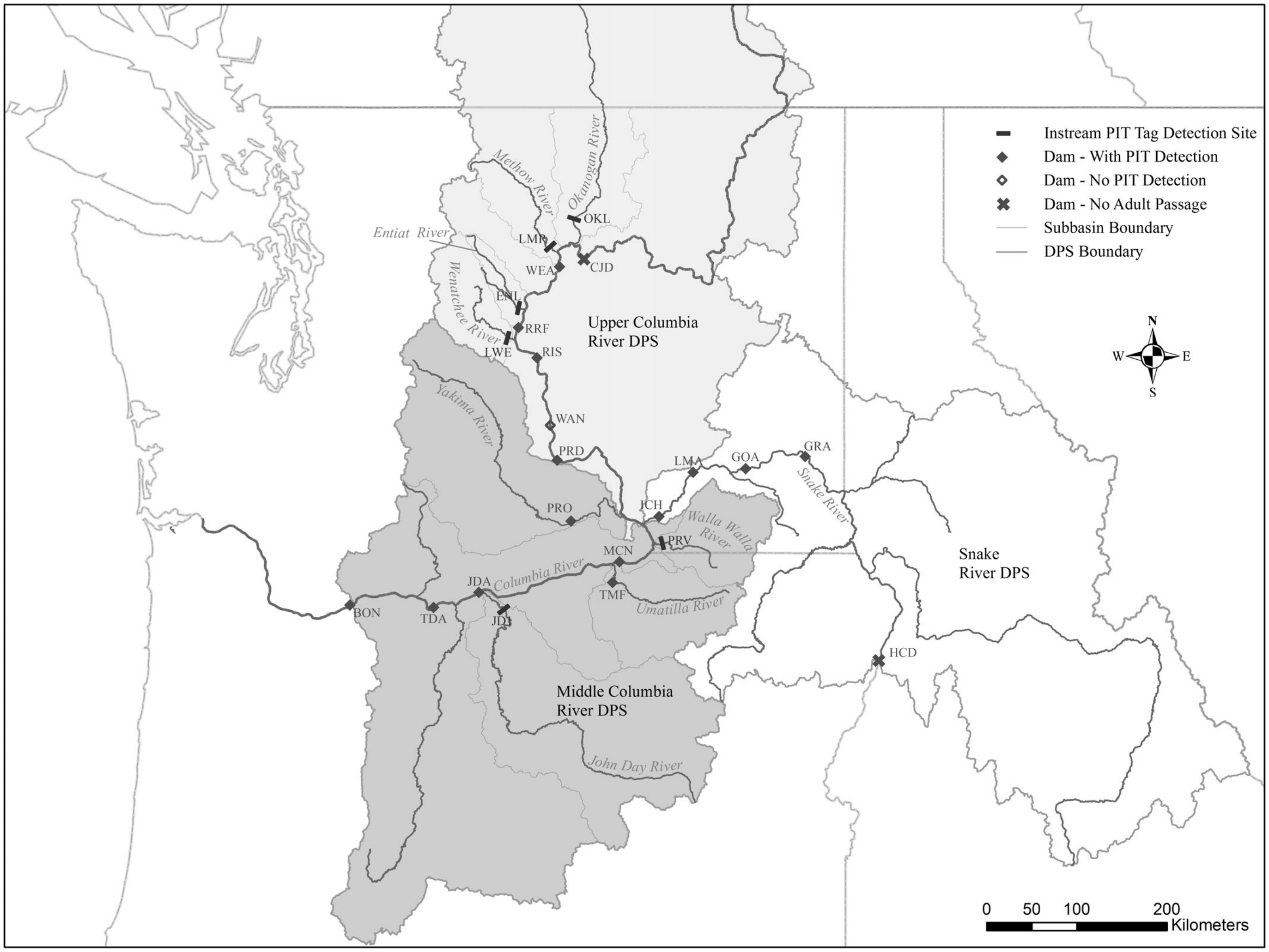

FIGURE 1. Vicinity map of steelhead distinct population segments (DPSs), major rivers and dams, and instream PIT tag detection locations on the Columbia and Snake rivers (BON = Bonneville Dam; TDA = The Dalles Dam; JDA = John Day Dam; JD1 = lower John Day River instream PIT tag detection site [IPDS]; TMF = Three Mile Falls Dam; MCN = McNary Dam; PRV = lower Walla Walla River IPDS; ICH = Ice Harbor Dam; LMA = Lower Monumental Dam; GOA = Little Goose Dam; GRA = Lower Granite Dam; HCD = Hells Canyon Dam; PRO = Prosser Dam; PRD = Priest Rapids Dam; WAN = Wanapum Dam; RIS = Rock Island Dam; LWE = lower Wenatchee River IPDS; RRF = Rocky Reach Dam; ENL = lower Entiat River IPDS; WEA = Wells Dam; LMR = lower Methow River IPDS; OKL = lower Okanogan River IPDS; CJD = Chief Joseph Dam).

Given the uncertainty associated with overshooting behavior in populations of conservation concern, the objectives of this study were to (1) estimate the annual abundance of overshoot steelhead that successfully migrated downstream of PRD prior to spawning (overshoot fallbacks); (2) estimate the annual abundance of overshoot steelhead at PRD; (3) estimate the annual proportion of overshoot steelhead that migrated downstream of PRD to their natal tributary (fallback migration success); (4) evaluate the effect of downstream dam passage on fallback migration success; and (5) compare migration patterns and timing of non-overshoot and overshoot steelhead into natal tributaries.

METHODS

Study area.— The UCR distinct population segment (DPS) of steelhead is comprised of four populations and extends upstream from the confluence of the Yakima River to the border with Canada (Figure 1). Steelhead status and trend monitoring has been occurring at PRD since 1986 (Brown 1995), and this dam is the first location at which fish can be counted and sampled upstream from the confluence with the Yakima River. Chief Joseph Dam (rkm 877) was built without fish ladders (i.e., end of anadromous distribution), but fish ladders in all downstream dams possess equipment to detect PIT tags, with the exception of Wanapum Dam (rkm 669). The middle Columbia River (MCR) DPS comprises 17 extant steelhead populations and extends downstream from the Yakima River (rkm 539) to the White Salmon River, Washington (rkm 271), and Fifteen Mile Creek, Oregon (rkm 309). McNary Dam is the last Columbia River dam encountered by steelhead before they enter the UCR or SR. The SR DPS includes 24 extant steelhead populations that spawn below all natural and manmade anadromous fish barriers within the SR basin. Ice Harbor Dam (ICH) on the SR is the first location at which steelhead entering the SR DPS can be counted (including PIT tag detection) during their upstream migration.

Passive integrated transponder tag data collection.— The PIT tagging of juvenile steelhead occurs in Columbia River tributaries and hatcheries to estimate smolt abundance; assess juvenile and adult survival, travel time, and migration patterns; and address other research or management questions (e.g., Haeseker et al. 2012). In addition, we systematically sampled steelhead at PRD during their adult migration in return years 2010–2017 (Figure 1; Waterhouse et al. 2020). We collected biological data (length and sex) and scale samples, and PIT tags were injected into the pelvic girdle for all adult hatchery and wild steelhead at the PRD trap that were not already PIT-tagged (i.e., to prevent double tagging) on 3 d/week from early July through mid-November, with an annual target sample rate of approximately 15% of all steelhead passing PRD (NMFS 2003). The pelvic girdle was selected as the preferred PIT tag location due to the reported high retention rates (~99%) in similarly sized adult fish of other species (Meerbeek 2020). Hatchery steelhead were identified based on the presence of marks (adipose fin removed), tags (coded wire or PIT), or hatchery scale pattern (Bernard and Myers 1996). Adult steelhead PIT tag data were uploaded into the regional PIT Tag Information System (PTAGIS) database (PSMFC 2015; Tenney et al. 2017). The PTAGIS database (https://www.ptagis.org) was subsequently queried to obtain PIT tag detections of adult steelhead (i.e., those PIT-tagged at PRD) at approximately 75 sites, including main-stem dams on the SR and the Columbia River and at instream PIT tag detection sites (IPDSs). These data were formatted for analysis to estimate adult overshoot fallback and overshoot abundance at PRD as described below.

Overshoot fallback abundance.— Escapement estimates of the four steelhead populations that comprise the UCR DPS have been generated using the Bayesian nested patch occupancy model (POM) based on detections of a representative sample of steelhead that were PIT-tagged at PRD beginning in return year 2010 (Waterhouse et al. 2020). The POM simultaneously estimates the probability of a fish moving along a particular path of the stream network and the probability that a fish is observed at detection sites along that path, essentially a multi-state variation of a spatial Cormack–Jolly–Seber model (Royle and Kery 2007; Waterhouse et al. 2020).

Observations at each site as well as detections further upstream provided the means to estimate detection probabilities at each site. Most IPDSs have at least two arrays spanning the river, providing multiple chances to detect a fish passing that site.

For fish i, whether it has moved past a detection point j is denoted by a one or a zero ($z_{i,j} \in [0, 1]$). The probability of fish i moving to each of the possible next detection sites along the stream network ($j+1$, $j+2$, …), including the probability of not moving past any of those sites, is modeled using a multinomial distribution with transition probabilities ψ_j,

$$z_{i,j+1} \sim Multinom\left(1, \psi_j\right),$$

and the detection of that fish at each array k at site j ($y_{i,j,k}$) is modeled as a Bernoulli distribution with detection probability $p_{j,k}$:

$$y_{i,j,k} \sim Bern\left(z_{i,j}, p_{j,k}\right).$$

The overall probability of a fish moving past a detection site is the product of all sequential downstream transition probabilities along that path. The detection probabilities p were estimated using detections from both hatchery and wild fish, but transition probabilities ψ were different for hatchery and wild fish because hatchery fish were generally returning to their hatchery release sites, while wild fish were returning to their natal stream. These overall transition probabilities were multiplied by an estimate of total abundance, by origin, at PRD, providing estimates of escapement past each detection site. The estimate of total abundance was generated by discounting the total steelhead counts by an estimate of re-ascension probability based on the proportion of previously PIT-tagged fish that were observed to ascend PRD more than once, therefore being counted twice or potentially more times. Transition parameters (ψ) were given a Dirichlet prior of a vector of ones, and detection parameters (p) were given Beta(1, 1) priors, all chosen to be as minimally informative as possible. Further details of the POM can be found in Waterhouse et al. (2020). Aside from standard mark–recapture assumptions, the POM does assume that each fish undertakes a one-way trip beginning at PRD and ending at their spawning stream. To meet this assumption, detection histories must be examined and some detections might be dropped for fish that were observed in multiple spawning paths based on the timing of detections and expert biological opinion.

Some adult steelhead overshoot their natal stream, are PIT-tagged at PRD, fall back, and ascend their presumed natal stream to spawn (downstream of PRD), where they are detected (i.e., overshoot fallbacks). To account for this behavior, the model structure includes PIT tag interrogation sites downstream of PRD to estimate overshoot fallback abundance (Figure 1). Specifically, overshoot fallback abundances in the MCR DPS were estimated for the Yakima River at rkm 76 (Prosser Dam [PRO]), the Walla Walla River at rkm 9 (Pierce RV Park instream array [PRV]), the Umatilla River at rkm 5 (Three Mile Falls Dam [TMF]), and the John Day River at rkm 35 (McDonald Ferry site [JD1]), and overshoot fallback abundances in the SR DPS were estimated at ICH at rkm 16.

Overshoot abundance.— The PTAGIS database was queried to obtain a list of wild adult steelhead that were PIT-tagged as juveniles in the MCR DPS, detected as adults at PRD from 2010 to 2017, and subsequently detected at other PTAGIS sites in the UCR, MCR, and SR DPSs (Figure 1). These steelhead are referred to as "known overshoot" steelhead and were used to estimate overshoot abundance at PRD. Population-specific PIT tag rates of each adult return year are unknown due to the complex rearing strategies of interior Columbia River steelhead juveniles (i.e., multiple age-classes of smolts) combined with variability in tagging program effort and catch rates through time. Therefore, we developed a relationship between the number of known wild overshoot fallback steelhead tags (fish tagged as juveniles) in year i (t_i) and the POM estimates of overshoot fallback abundance in that year (F_i). To calculate t_i, we expanded the number of overshoot fallback PIT tags observed at site j ($s_{i,j}$) by the site's detection probability as estimated by the POM ($\widehat{p_{i,j}}$) and then we summed those expanded estimates across all J sites:

$$t_i = \sum_{j=1}^{J} \frac{s_{i,j}}{\widehat{p_{i,j}}}.$$

To improve homogeneity of variances and meet the linear regression assumptions, we natural log-transformed fallback abundance and estimated overshoot tags and then fit a linear model:

$$\ln(F_i) \sim N\left[\beta_0 + \beta_1 \cdot \ln(t_i), \sigma^2\right].$$

Next, we used that linear model to predict the total overshoot abundance that arrived at PRD (O_i) based on the number of known overshoot tags that were detected at PRD each year (T_i):

$$\ln(O_i) \sim N\left[\hat{\beta_0} + \hat{\beta_1} \cdot \ln(T_i), \hat{\sigma^2}\right].$$

This approach assumes that the overall average juvenile tag rate across all populations downstream of PRD is consistent throughout this time period—in other words, the proportion of returning adults from populations downstream of PRD that were tagged as juveniles is assumed to be consistent. Fluctuations in the tag rates of individual populations and the interaction with the variability in how long those fish remain in the ocean before returning to spawn are part of the overall model variance σ^2.

Fallback migration success.— Finally, we calculated the proportion of overshoot steelhead that migrated downstream of PRD, or their fallback migration success (ϕ_i), by dividing the estimate of overshoot fallback abundance (R_i) by the estimate of overshoot abundance at PRD, accounting for uncertainty in the overshoot fallback abundance from the POM. That uncertainty comes from the posteriors of the downstream transition probabilities in the POM, which were all approximately normal in their distribution, so we calculated the variance of their sum (τ^2) and used that to propagate uncertainty in R_i:

$$\phi_i = \frac{R_i}{O_i} \approx \left(\frac{t_i}{T_i}\right)^{\hat{\beta_1}},$$

$$R_i \sim N\left(F_i, \tau^2\right).$$

We implemented the overshoot abundance and fallback migration success as a single model within a Bayesian framework using the rjags package (Plummer 2019) with R (R Core Team 2019) and JAGS software (M. Plummer, University of Warwick, Coventry, UK; available at https://sourceforge.net/projects/mcmc-jags/). We chose a Bayesian framework to incorporate all of the uncertainty in many of the independent and dependent variables (e.g., $p_{i,j}$, t_i, and F_i). Beta parameters (β) had an uninformative prior of a Cauchy distribution with mean of zero and scale of 100, and the SD parameter (σ) also had a weak prior of a half-Cauchy with mean of zero and scale of 100, following the recommendation of Gelman et al. (2008).

We focused on natural-origin fish because adipose fin-clipped hatchery steelhead may be harvested and harvest rates both upstream and downstream of PRD are variable and unknown, making it more problematic to find a relationship between overshoot detections at PRD and overshoot fallback abundance downstream. Wild steelhead may also have been encountered during sport fisheries, which could potentially influence fallback migration success. Sport fishery impacts to wild steelhead upstream of PRD were assessed annually based on extensive creel surveys using a 5% hooking mortality rate (Washington Department of Fish and Wildlife, unpublished data). Any indirect hooking mortality or unreported harvest of wild steelhead would be incorporated into our analysis.

Dam effects on fallback success.— To evaluate the effect of downstream dam crossings on fallback migration success, defined as being detected downstream of PRD, we grouped known overshoot steelhead based on the PIT tag detection of the furthest upstream dam. Since Wanapum Dam has no PIT tag detection infrastructure, we could only be certain that fish had crossed one (PRD), three (Rock Island), four (Rocky Reach), or five (Wells) dams. Most dams lack the ability to detect adult steelhead moving downstream, except for the juvenile bypass at Rocky Reach Dam, which closes on August 31. Therefore, we focused on the furthest upstream dam at which fish were detected during their upstream migration. To determine the effect of crossing one to five dams on overshoot fallback success probability, we fit a logistic mixed-effects model using the number of dam crossings as the fixed effect variable and allowed the intercept and slope to have random effects by year. As part of model validation, we compared the intercept (the predicted probability of migration success when zero dams were crossed; i.e., no overshooting) with the percentage of PIT tags from fish tagged as juveniles in the Yakima River basin and detected at McNary Dam (the first dam downstream of the Yakima River) as adults between 2010 and 2017—but not detected at PRD or ICH on the SR—that were also detected at PRO on the Yakima River. These tags represent fish displaying a successful non-overshoot behavior.

Overshoot migration timing.— Steelhead exhibiting overshoot behavior must travel longer distances in freshwater and encounter more dams compared to non-overshoot steelhead from the same population, which may ultimately influence their migration timing into their natal stream. The relative prevalence of the overshoot behavior and the influence of migration timing into the natal tributary were examined using Yakima River steelhead due to the river's proximity to PRD and the high detection probability (0.90) at PRO. The influence of overshoot and fallback on run timing into their natural tributary was examined at PRO by using the arrival dates of fish that were PIT-tagged as juveniles in the Yakima River basin and the arrival dates of fish that were PIT-tagged as adults at PRD. Arrival day was calculated as days since July 1 of each return year (all years were combined), and the distribution of arrival days between these two groups of fish was compared using a Kolmogorov–Smirnov test. Mean monthly water temperature data from the lower Yakima River in 2015 (i.e., a 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). Columbia River water temperatures from the tailrace of PRD were queried from the Data Access in Real Time Web site (http://www.cbr.washington.edu/dart/query/river_daily). Tributary water temperatures were not available for the entire study period. Instead, Yakima River water temperatures during a low water year, like the temperatures observed in 2015 (i.e., 0.6°C warmer than average at the start of the upstream migration period in July), were used to better represent possible future conditions under climate change. Mean monthly water temperatures in the Yakima and Columbia rivers were used to graphically identify an upper water temperature threshold for tributary migrations.

Because natural mortality rates are unknown, comparing fallback migration success rates to those of non-overshoot steelhead from the same population provides a more accurate assessment of the risks to steelhead exhibiting the overshooting behavior. Non-overshoot Yakima River steelhead were defined as those PIT-tagged adults that were detected at McNary Dam but not detected at PRD or ICH. Estimating non-overshoot steelhead migration success at PRO was calculated by dividing the number of non-overshoot steelhead detected at McNary Dam by the number of non-overshoot steelhead detected at PRO.

RESULTS

Overshoot Fallback Abundance

During the study period (2010–2017), the annual mean number of wild steelhead that were PIT-tagged was 664 (SD = 281), or an annual mean proportion of 0.17 (SD = 0.05) of the total wild fish. Hatchery steelhead were tagged at the same rate but were more abundant (mean = 1,620; SD = 495). The annual mean number of adult wild steelhead that were previously PIT-tagged as juveniles from populations downstream of PRD (i.e., known overshoots) was 31 (SD = 15). Annual overshoot fallback estimates from PRD, based on adults tagged at PRD, averaged 1,135 (range = 284–2,355) for wild steelhead and 1,656 (range = 540–2,879) for hatchery steelhead, which constituted an average of 25% (range = 16–38%) and 16.6% (range = 10–24%) of the adjusted PRD count for wild and hatchery steelhead, respectively (Table 1). Wild and hatchery steelhead annual overshoot fallback abundance was significantly correlated ($R^2 = 0.53$, $P < 0.04$), suggesting that factors influencing abundance affected both wild and hatchery steelhead similarly. The largest group of fallback steelhead was detected in the SR at ICH (average = 456 and 1,321 for wild and hatchery fish, respectively, representing 19.7% and 57% of all fallbacks), followed by the Yakima River at PRO (average = 369 and 34 for wild and hatchery fish, representing 15.9% and 1.5% of all fallbacks; Table 2). Excluding hatchery fish, steelhead from the SR and the Yakima River represented 50% and 40%, respectively, of all wild steelhead fallbacks.

Overshoot Abundance

The log–log regression model between the estimated overshoot fallback abundance of wild steelhead and the estimated number of overshoot fallback PIT tags from PRD fit the data well. For every Markov chain–Monte Carlo draw, including the variation in the dependent and independent variables as well as the β parameters, we calculated the correlation between the observed and predicted values. The mean pseudo-R^2 was 0.72. Diagnostic plots suggested that the regression assumptions were met. The fitted model predicted overshoot abundance at PRD based on the number of known overshoot PIT tags detected at PRD, with the following estimated parameters:

$$\text{Overshoot abundance} = 55.70 \cdot T^{0.95},$$

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

Wild steelhead counted at PRD originated from one of four extant upstream populations or were overshoots from downstream populations. Hence, we summed the estimated number of wild steelhead overshoots at PRD and the estimated wild steelhead escapement of the four steelhead populations above PRD and compared that value to the total adjusted counts of wild steelhead that arrived at PRD. The two time series were highly correlated ($r = 0.89$), with a root mean square error of 448 fish and a mean relative difference of 9.5%. More simply, including the estimates of overshoot abundance from populations downstream of PRD with our estimates of escapement into the four populations upstream of PRD provided a more complete accounting of the total number of steelhead passing PRD (Figure 2).

Fallback Migration Success

The annual percentage of wild steelhead that overshot and fell back below PRD was variable (range = 31–74%) and averaged 59% (SD = 14%; Table 3). Sport fishery impacts on wild steelhead abundance based on the adjusted number of wild fish at PRD and creel survey estimates of

TABLE 1. Steelhead abundance (adjusted for ladder reascension) at Priest Rapids Dam (PRD) and the number of overshoot fallback steelhead estimated by using the patch occupancy model, 2010–2017 (LCL = lower 95% confidence limit; UCL = upper 95% confidence limit).

	Adjusted PRD count		Estimated overshoot fallback abundance							
			Wild				Hatchery			
Run year	Wild	Hatchery	%	Estimate	LCL	UCL	%	Estimate	LCL	UCL
2010	7,257	17,938	26.3	1,911	1,570	2,295	9.8	1,755	1,475	2,022
2011	4,672	15,115	20.6	963	799	1,137	12.8	1,931	1,696	2,141
2012	3,065	13,008	23.8	730	580	866	16.8	2,180	1,957	2,399
2013	4,864	9,027	28.1	1,367	1,161	1,580	19.5	1,757	1,522	1,988
2014	6,232	12,088	37.8	2,355	2,104	2,608	23.8	2,879	2,644	3,105
2015	4,675	8,949	24.6	1,150	995	1,320	13.2	1,179	1,053	1,338
2016	1,404	4,709	23.0	323	249	400	21.8	1,027	896	1,151
2017	1,817	3,573	15.6	284	217	351	15.1	540	456	635
Mean	4,248	10,551	25.0	1,135	959	1,320	16.6	1,656	1,462	1,847
SD	2,040	4,950	6.4	729	649	820	4.8	730	676	778

TABLE 2. Estimated abundance of overshoot fallback steelhead (W = wild; H = hatchery) downstream of Priest Rapids Dam, by subbasin and PIT Tag Information System location code (PRO = Prosser Dam; ICH = Ice Harbor Dam; PRV = Pierce RV Park instream array; TMF = Three Mile Falls Dam; JD1 = lower John Day River instream array at McDonald Ferry). Values in parentheses indicate PIT tag detection probability (mean, SE) estimated from the patch occupancy model. Percent (%) in the bottom row represents the percentage of all fallback steelhead based on the mean value.

	Yakima River, PRO (0.81, 0.08)		Snake River, ICH (0.98, 0.01)		Walla Walla River, PRV (0.54, 0.10)		Umatilla River, TMF (0.62, 0.00)		John Day River, JD1 (0.35, 0.11)	
Run year	W	H	W	H	W	H	W	H	W	H
2010	929	53	675	1,429	45	0	33	23	0	23
2011	401	36	351	1,683	22	0	0	0	0	0
2012	214	33	316	1,815	21	14	0	0	0	0
2013	348	38	626	1,371	19	51	18	13	140	87
2014	537	57	1,088	2,451	69	21	48	21	115	35
2015	311	16	411	880	58	20	20	0	58	0
2016	91	29	123	681	21	21	8	0	30	18
2017	122	14	61	259	9	0	0	0	28	0
Mean	369	34	456	1,321	33	16	16	7	46	20
%	15.9	1.5	19.7	57.0	1.4	0.7	0.7	0.3	2.0	0.9

TABLE 3. Number of known overshoot steelhead detected at Priest Rapids Dam (PRD), estimated abundance of overshoot steelhead at PRD, and the corresponding fallback migration success (number of fallbacks/number of overshoots), or the proportion of overshoot fallbacks detected downstream of PRD prior to spawning (LCL = lower 95% confidence limit; UCL = upper 95% confidence limit).

		Estimated wild steelhead overshoot abundance			Fallback migration success		
Run year	Known overshoot fish	Estimate	LCL	UCL	Estimate	LCL	UCL
2010	53	3,048	1,842	8,243	0.626	0.227	0.976
2011	18	1,326	904	4,101	0.729	0.231	0.987
2012	31	1,574	779	5,458	0.464	0.130	0.933
2013	40	2,277	1,363	7,223	0.600	0.190	0.976
2014	44	3,182	2,300	7,970	0.743	0.295	0.988
2015	35	1,960	1,161	6,513	0.588	0.178	0.971
2016	21	1,051	392	3,697	0.308	0.086	0.837
2017	6	426	266	1,732	0.667	0.162	0.983
Mean	31	1,856	1,126	5,617	0.591	0.187	0.956
SD	15	958	697	2,297	0.144	0.065	0.051

catch were low, with an annual mean mortality of 0.97% (SD = 0.67%), consistent with fishery permits (A. R. Murdoch, personal observation).

Dam Effects on Fallback Success

From 2010 to 2017, we found 246 known overshoot wild steelhead that were detected at PRD. The majority of these (129 fish; 52%) were not detected at any upstream locations. Of those 129 tags, 88% were subsequently detected downstream of PRD, demonstrating fallback migration success. The dam with the second-largest percentage of known overshoot wild steelhead after PRD was Wells Dam (20%; N = 49), the farthest upstream dam, but only 22% (N = 11) of those fish were detected downstream of PRD. A small percentage of known overshoot wild steelhead were detected in tributaries upstream of PRD (5.6%), but only 3.2% (N = 8) were detected during the spawning period in the spring. Of those known overshoot steelhead that were detected in tributaries, seven individuals were detected in tributaries upstream of Wells Dam. The logistic model examining the relationship between the dam passage upstream of PRD and overshoot fallback proportions fit the data well (marginal pseudo-$R^2 = 0.73$; conditional pseudo-$R^2 = 0.78$), suggesting that the number of dams passed by a fish when overshooting was negatively associated with their downstream passage success (Figure 3). The model prediction of

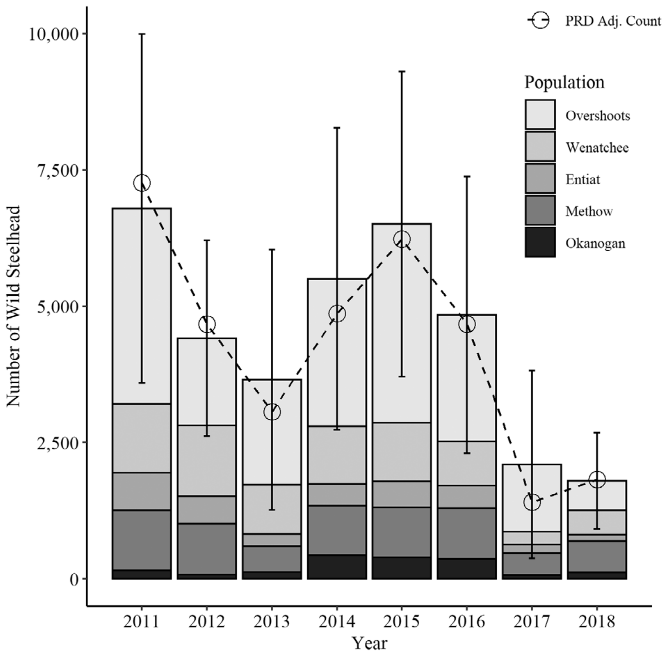

FIGURE 2. Comparison between adjusted dam counts at Priest Rapids Dam (PRD; circles) and summed estimates of the four upper Columbia River steelhead populations plus estimates of steelhead overshoots at PRD. Whiskers represent 95% confidence intervals of those sums, of which 98% is due to uncertainty in overshoot estimates.

overshoot fallback for zero dams, or the *y*-intercept, was 0.955 (95% CI = 0.891–0.982) and comported well with the proportion of non-overshoot PIT-tagged Yakima River steelhead that passed McNary Dam ($N = 276$) and were detected at PRO (0.949), suggesting that some level of natural mortality not attributed to dam passage was included in the relationship.

Overshoot Migration Timing

Between 2010 and 2017, 327 wild adult steelhead that were tagged as juveniles in the Yakima River were detected at McNary Dam. Of those, 13% and 3% were detected at PRD and ICH, respectively. Of those overshoot steelhead, seven fish (2% of total) were detected at both PRD and ICH. The percentages of overshoot Yakima River steelhead at PRD and ICH that were subsequently detected at PRO were 78% and 60%, respectively. In general, Yakima River steelhead were not observed at PRO until water temperatures declined and were like those of the Columbia River (Figure 4). Few steelhead (<1%) were detected at PRO until stream temperatures were below 20°C. However, the distribution of arrival times for known overshoot steelhead was significantly later compared to all steelhead at PRO (Kolmogorov–Smirnov test: $P < 0.001$; Figure 4). Approximately 73% of wild steelhead that were tagged as juveniles in the Yakima River arrived at PRO prior to January 1, compared to 50% of known overshoot steelhead.

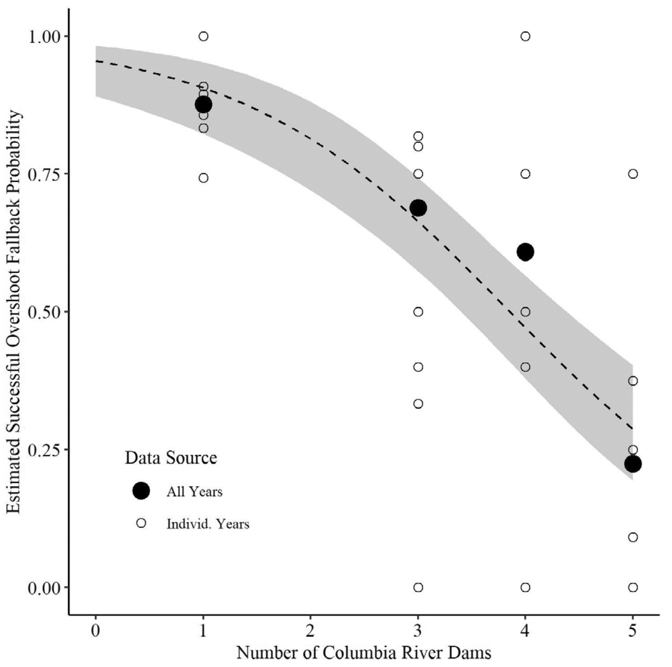

FIGURE 3. Points depicting the percentage of successful known overshoot steelhead detected at Priest Rapids Dam that were detected downstream of Priest Rapids Dam, 2010–2017. Solid circles represent the percentages across all years, while open circles represent percentages in individual years. The dashed line and gray area depict the predicted probability of success and 95% confidence interval from a logistic mixed-effects model based only on the fixed effect of the number of dams.

DISCUSSION

The magnitude, variability, and upstream distribution of overshoot steelhead in the UCR DPS were unknown and not fully accounted for in historical escapement estimates derived from dam counts (Ford et al. 2001). However, when the annual estimates of overshoot abundance presented here were combined with UCR DPS population run escapement estimates, only minor differences (mean = 9.5%) were observed when compared to the adjusted PRD count. Not surprisingly, a small proportion of fish could not be accounted for, presumably due to migration- or overwintering-related mortality prior to entering a tributary. These results suggest that dam counts may not represent an index of the spawning population upstream of the dam if methodologies do not account for complex migration patterns, including overshoots (e.g., Boggs et al. 2004; Buchanan and Skalski 2010; Richins and Skalski 2018; Waterhouse et al. 2020).

A large component of steelhead migrating upstream of PRD during the study period was from downstream populations. Most radiotelemetry studies examining overshoot and fallback in the Columbia River and the SR were limited in geographic scope to areas downstream of PRD (Boggs et al. 2004; Keefer et al. 2008a). However, English

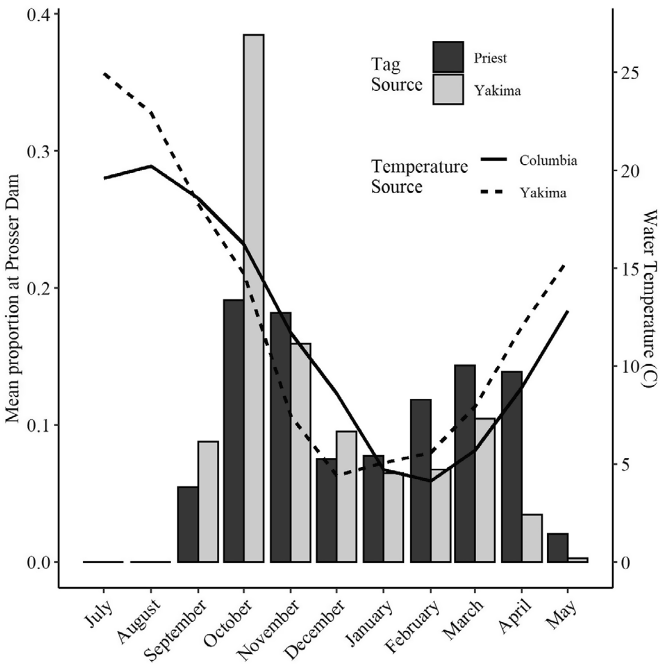

FIGURE 4. Passage timing of steelhead tagged as juveniles in the Yakima River and fish tagged as adults at Priest Rapids Dam that were detected at Prosser Dam in the lower Yakima River, 2010–2017. Mean monthly water temperatures (2015–2016) measured in the lower Yakima River at Kiona (river kilometer 48) and in the Columbia River at the Priest Rapids Dam tailrace are also shown.

et al. (2003) did report that 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 whether downstream detections were adjusted for detection probability. The spatial distribution of overshoot fallbacks was similar in both our study and the English et al. (2003) study, with most overshoot fallbacks detected in the SR, followed by the Yakima River (Table 2).

The estimated annual mean number of wild steelhead overshoot fallbacks at PRD during the study period was 1,135 (SD = 729), or 25% (SD = 6.4%) of the adjusted wild steelhead count at PRD. A radiotelemetry study of adult steelhead, which was conducted at PRD between 2015 and 2017, reported similar levels of fallback (Fuchs et al. 2021). In that study, radio tag-based estimates of wild steelhead overshoot fallback were slightly higher (mean = 22.1%; SD = 1.8%) than PIT tag-based model estimates but were based on a smaller sample size. Boggs et al. (2004) reported similar mean overshoot fallback rates of 25.1% and 20.7% for radio-tagged steelhead at McNary Dam and ICH (i.e., nearest downstream dams), respectively. Estimates of overshoot fallback in our study were based on PIT tag detections at specific locations downstream of PRD prior to the spawning period. Because wild adult steelhead that were PIT-tagged at PRD were from an unknown population, estimating fallback to their natal stream or watershed was not possible in all cases (e.g., Richins and Skalski 2018). Furthermore, based on detection histories of known overshoot fallback steelhead, some steelhead were detected downstream of PRD but were not successful in homing to their natal stream (e.g., a Yakima River steelhead PRD overshoot fallback that was last observed in the SR). While some overshoot fallback steelhead may have died, our POM included all possible locations based on geographic distribution of known overshoot steelhead and accounted for the variability in detection probabilities among sites and years.

Estimated fallback migration success reported here for wild steelhead that were PIT-tagged as adults (mean = 59%; SD = 14%) was similar to the fallback migration success of known adult wild steelhead overshoots that were tagged as juveniles (mean = 69%; SD = 9%) during the study period (Murdoch, personal observation). Potential reasons for methodological disparities in fallback migration success percentages include intra- and interannual variability in the distribution of juveniles that were PIT-tagged from downstream populations and a smaller sample size compared to adult steelhead that were PIT-tagged at PRD. Furthermore, estimates of overshoot abundance in this study were based on the relationship between known overshoot fallbacks and fallback abundance estimates. Variability in annual PIT tagging rates of juvenile steelhead from any single population or subbasin required pooling of data across populations, thereby reducing the sample size used in the regression model ($N = 8$). Ideally, similar juvenile PIT tagging rates from all potential overshoot populations would increase the sample size of adult steelhead and potentially allow for population-specific relationships or simply a larger sample size for greater statistical power. Although the fate of the overshoot steelhead component not observed downstream of PRD (annual mean = 41%) is unclear, we can report that only a small proportion of overshoot steelhead were detected in upstream tributaries (i.e., potential strays). Of those known overshoot steelhead that did not successfully fall back, only 16% ($N = 15$) were last observed in tributaries and only eight known overshoot steelhead (9% of unsuccessful known overshoot steelhead, or 4% of the total) were detected during the spring spawning period. Although these percentages were not adjusted for detection probability, the mean detection probability for all IPDSs installed in every spawning stream upstream of Rock Island Dam was 0.894 (SD = 0.132) and ranged from 0.505 to 0.999 (Waterhouse et al. 2020), suggesting that very few known unsuccessful overshoot steelhead went undetected. While several potential minor spawning areas were not monitored using IPDSs (Fuchs et al. 2021), we assumed that most of the unsuccessful overshoot steelhead suffered the same rate of mortality in the main stem as non-overshoot fish or downstream passage-related mortality from turbine strikes, as opposed to successfully spawning in an unmonitored tributary above PRD.

Summer spill programs and juvenile bypasses are shut down for the season in late August or early September because the juvenile out-migration period has ended (UCSRB 2018). Unfortunately, this coincides with the period when overshoot steelhead initiate their downstream migration back to their natal streams (Fuchs et al. 2021). However, surface spill passage routes are provided until November 15, but only at both Wanapum Dam (i.e., bypass) and PRD (i.e., sluiceway), specifically for adult steelhead (GCPUD 2006). Downstream survival rates of adult salmonids via turbine passage are largely unknown but decrease as fish length increases (Coutant and Whitney 2000). Recent studies at McNary Dam evaluating the survival and downstream passage rates of adult steelhead reported that surface passage routes (i.e., temporary spillway weirs) were most effective during the day (Ham et al. 2021), with higher survival (97.7%) compared to turbine routes (90.7%; Normandeau Associates 2014), which could explain why fallback migration success decreased as the number of dams required to pass downstream increased.

Overshoot and fallback rates for steelhead have been estimated for many populations in the Columbia River 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 were assumed to represent the entire population or group of populations. Conversely, steelhead in our study were tagged as adults from throughout the annual run (i.e., systematic sample) and were representative of the steelhead passing PRD. Richins and Skalski (2018) reported many populations with high rates of overshoot, but both overshoot and fallback rates were highly variable, including in some wild populations from the MCR DPS (John Day, Yakima, Umatilla, and Walla Walla rivers). Estimates of fallback migration success, whether population based (Richins and Skalski 2018) or dam based (this study), may be difficult to compare due to differences in overshoot migration routes, dam operations, and the number of dams encountered by overshoot fish.

Richins and Skalski (2018) reported several factors that were shown to influence overshoot probabilities (i.e., natal stream water temperature, hatchery rearing location, adult ladder placement, and ocean age). However, a comparison of overshoot fallback proportions of the two basic overshoot pathways (upstream of PRD or ICH) has not been conducted. Pope et al. (2016) used a multi-state release–recapture model to estimate the overshoot fallback rates for Walla Walla River hatchery steelhead. While hatchery steelhead are subject to direct harvest, Pope et al. (2016) reported overshoot return rates of 8.3% and 20.2% for Lower Granite Dam and PRD, respectively. Because Walla Walla River steelhead that make it to Lower Granite Dam must migrate downstream past four dams in the SR to return to the Walla Walla River compared to between one and five dams in the UCR, these results are not directly comparable. However, wild overshoot steelhead in the UCR that migrated past four dams (i.e., equivalent to Lower Granite Dam) had an estimated mean fallback migration success below PRD of 59%. Comparing hatchery and wild overshoot return rates is also problematic due to differential harvest rates, but this comparison does suggest that the two primary overshoot pathways (i.e., past PRD into the UCR DPS and past ICH into the SR DPS) may have different relationships between overshoot fallback and the number of downstream dams.

Most of the estimated overshoot wild steelhead at PRD were from the SR DPS (53%), whereas the remainder were from the MCR DPS (47%). The MCR DPS is located downstream of PRD and ICH (excluding the Yakima River) and is comprised of four major population groups and 20 independent steelhead populations (Figure 1). Steelhead from five subbasins in the MCR DPS (John Day, Umatilla, Walla Walla, Touchet, and Yakima rivers) are routinely observed as overshoots at PRD and ICH. The composition of wild steelhead overshoots from the MCR DPS detected at PRD and ICH between 2010 and 2017 differed, but the composition was consistent with that reported by Richins and Skalski (2018). The majority of MCR DPS steelhead detected at PRD were from the Yakima River (53%), whereas steelhead from the Yakima River were the least abundant (6%) of those detected at ICH (Figure 5). The spatial distribution (i.e., UCR or SR) of overshoot MCR steelhead is consistent with the location (i.e., same side of the river) of their natal population.

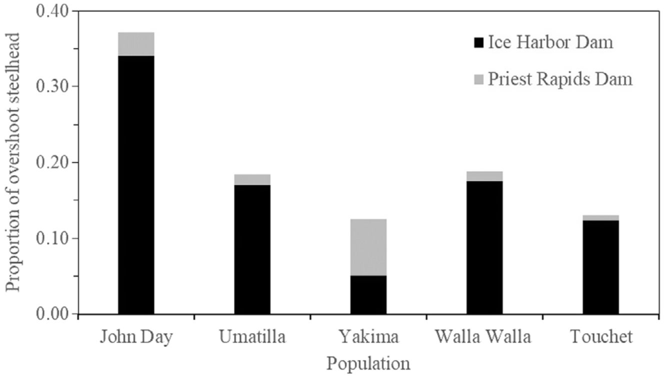

FIGURE 5. Distribution of overshoot wild steelhead ($N = 559$) from the middle Columbia River distinct population segment (DPS) that were detected in the upper Columbia River DPS (Priest Rapids Dam) and the Snake River DPS (Ice Harbor Dam), 2010–2017.

More importantly, the overall abundance of known overshoot steelhead from the MCR DPS was over five times greater at ICH (Figure 5). However, because PIT tag detectors were first installed at Little Goose and Lower Monumental dams in 2014, we could not generate a comparable data set. For discussion purposes only, we used a consistent methodology to estimate overshoot patterns and fallback for steelhead returning in 2015. Overshoot fallback patterns in the SR were very similar to those in the UCR, with the largest proportion of unsuccessful overshoots last detected at Lower Granite Dam (0.34) and the largest proportion of successful overshoot fallbacks detected at ICH (0.12). In 2015, the fallback migration success in the SR was 0.32 compared to 0.59 in the UCR, suggesting that approximately two out of three MCR DPS steelhead that were detected at ICH did not return to their natal stream. Furthermore, a relatively large proportion of MCR DPS steelhead that were not observed downstream of ICH were last detected in a spawning stream (0.40) upstream of ICH. Unlike steelhead spawning areas upstream of PRD, some major spawning areas (e.g., lower Grande Ronde River and lower Salmon River) do not have IPDSs, and fish may have gone undetected; therefore, the proportions of overshoot fish in nonnatal tributaries within the SR DPS should be considered minimum values. The differences in fallback migration success and the magnitude of overshoot steelhead from the MCR DPS should be of great concern for managers. The logistic regression of known overshoot fallback proportions suggests that the number of dams requiring downstream passage is an important factor in downstream migration success; undoubtedly, other factors are also important but are outside the scope of this study.

Conservation Implications

Estimating the abundance of overshoot steelhead and fallbacks allows resource managers to quantify the potential increase in spawner abundance for populations exhibiting this behavior, thereby assisting in the prioritization of issues associated with the downstream movement of pre-spawn steelhead. Overshoot steelhead in the UCR DPS (annual mean = 1,856) comprised on average 45% (SD = 16%) of the adjusted number of steelhead counted at PRD. Of those, 59% on average were estimated to have returned to their natal watersheds, indicating that increased fallback migration success is possible. However, preliminary data suggest that overshoot steelhead in the SR are over five times more abundant and the overshoot return rate may only be 50% of that observed in the UCR. Researchers in both the UCR and the SR use a similar POM to estimate population abundance upstream of PRD and Lower Granite Dam, respectively (Orme and Kinzer 2018; Waterhouse et al. 2020). An important first step in fully defining the issue of overshoot steelhead in the Columbia–SR basin is to expand the model currently being used at Lower Granite Dam to include more downstream detection sites and perform a similar analysis to estimate overshoot abundance and fallback in the lower SR.

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 that higher rates of overshoot from a greater number of populations should be expected in the future. As a result of the low fallback migration success, prolonged migration periods, and potential effects from genetic introgression, steelhead that overshoot their natal stream negatively affect population abundance and productivity. Hence, changes in hydroelectric dam operations are likely required to increase fallback migration success. Many studies have consistently shown that both overshoot steelhead (Khan et al. 2013) and kelts (Wertheimer and Evans 2005; Wertheimer 2007; Ham et al. 2015; Harnish et al. 2015) prefer surface flow downstream passage routes (i.e., spillway weirs or sluiceways), which also provide higher survival rates. Experiments conducted to evaluate the efficacy of sluiceways (Khan et al. 2013) and temporary spillway weirs (Ham et al. 2015, 2021) operated during nonspill periods (i.e., late fall through winter) found that surface flow passage routes significantly reduced turbine passage while increasing total steelhead passage. Surface flow passage routes operated during nonspill periods would increase overshoot fallbacks for steelhead populations in both the MCR and SR DPSs. In 2020, limited downstream surface passage routes during nonspill periods at McNary Dam and the four lower SR dams were a condition of the Columbia River System biological opinion (NMFS 2020). The initial evaluation of these additional protection measures as part of a regional adaptive management process has not been completed.

Survival standards for steelhead overshoot fallbacks have yet to be identified but should be consistent with upstream migration survival standards. While downstream passage routes reportedly have high project survival (Ham et al. 2021), many overshoot steelhead are required to migrate downstream past more than one hydroelectric project (e.g., John Day or Umatilla River steelhead overshooting Wells Dam must pass six dams to reach their natal tributary). Hence, the response variable measured at the population scale (i.e., changes in abundance) should be an important consideration for adaptively managing protective measures that are intended to increase fallback migration success in the future.

Fuchs et al. (2021) reported that downstream passage at PRD began in early September through mid-December and resumed in early March. Extensive downstream migration studies are resource intensive. Hence, cost-effective long-term monitoring tools would provide the data needed to adaptively manage dam operations. Surface passage routes equipped with PIT tag detection equipment would provide project-specific data such that operations could be optimized to minimize costs. In the interim, existing adult salmonid monitoring programs at PRD and Lower Granite Dam could provide annual estimates of fallback migration success and serve as a low-cost effectiveness monitoring tool. As river water temperatures continue to increase and more adult salmonids attempt to adapt by using complex movement patterns like overshooting, hydroelectric operations may also need to adapt. Reductions in Columbia River basin stream water temperatures notwithstanding, providing effective downstream passage routes for adult salmon and steelhead would yield significant conservation value (e.g., by increasing spawner abundance and reducing genetic introgression) to most populations in the Columbia River basin.

An extensive monitoring infrastructure exists in the Columbia River basin that provides the data necessary to detect changes in population-specific freshwater movement patterns. Although research has focused on detecting climate-related changes to freshwater fish assemblages (Pletterbauer et al. 2014; Lynch et al. 2016) or changes to migration patterns driven by alterations in ocean conditions (Crozier et al. 2011; Lynch et al. 2016), the impacts of climate change on the movement patterns in large freshwater ecosystems with multiple populations like the Columbia River basin are much less understood. For example, the relatively large numbers of (1) SR steelhead that overshoot into the UCR and (2) MCR steelhead that overshoot into the SR have both harvest and conservation implications. Given that most fishes are poikilotherms, changes in behavior (e.g., migration) in response to suboptimal habitat conditions are expected. Hence, natural resource managers should consider reexamining historical harvest paradigms periodically to validate fishery models. Decision support tools that include population genetic monitoring may be a cost-effective approach that can be applied periodically at multiple spatial scales in freshwater systems lacking a robust monitoring infrastructure to identify climate-induced changes in population-specific harvest rates in a timely manner.

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