# Overwintering Distribution and Post-Spawn Survival of Steelhead in the Upper Columbia River Basin

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# *Running Head: Overwintering Distribution and Post-Spawn Survival of Steelhead in the Upper Columbia River*

# [A]Abstract

Adult summer-run steelhead (*Oncorhynchus mykiss*) overwinter in freshwater for several months prior to spawning and thus monitoring distribution and survival is important for management and conservation. Monitoring is particularly true in populations such as the upper Columbia River with hatchery-origin components valued by anglers, natural origin components of conservation concern, and temporary strays from downstream populations. We used radio- and PIT telemetry to monitor behavior, distribution and survival in adult Upper Columbia River steelhead during fall, overwintering, spawning and post-spawn periods with a focus on use of mainstem versus four major tributaries.  Adult steelhead (N = 807) were tagged at Priest Rapids Dam in 2015 and 2016.  One fifth (20%) of steelhead fell back below Priest Rapids Dam and did not reascend.  A slight majority of tagged steelhead that overwintered upstream of Priest Rapids Dam did so in main-stem reservoirs (54%; N = 548).  Overwintering in the main-stem Columbia River was more likely for later-arriving steelhead and was concentrated in the most upstream reservoir.  Tributary use during winter was highest in the Wenatchee (26%; 2016) and Methow (18%; 2015) rivers while no steelhead overwintered in the Entiat River.  Harvest of hatchery-origin steelhead was 18% in 2015 and was near zero in 2016 when the fishery was suspended due to low adult returns. After accounting for reported harvest, annual overwinter survival did not differ between main-stem and tributary habitats and relatively low adjusted survival of hatchery-origin steelhead in 2015 suggested unreported harvest.  In contrast to low iteroparity rates (<3%), the majority of post-spawn steelhead (56.5%) exited tributaries as kelts and kelt survival to Bonneville Dam was 65% in 2016 and 23% in 2017.  Collectively, the results highlight the importance of understanding patterns of habitat use and mortality for steelhead populations when managers are faced with balancing harvest and conservation goals.

**[A]Introduction**

Steelhead (anadromous *Oncorhynchus mykiss*) are highly valued by anglers and exhibit a high degree of behavioral and life history diversity relative to most other *Oncorhynchus* spp. ‘Summer-run’ or ‘summer’ steelhead exhibit two life history traits potentially affecting survival and population productivity: a stream-maturing life history (i.e., upstream migration in the summer or fall before sexual maturation, freshwater ‘overwintering’, and spring spawning) and iteroparity. Upper Columbia summer steelhead undertake among the longest of freshwater migrations (Busby et al. 1996) and are currently listed as threatened under the United States Endangered Species Act (ESA) (NOAA 2016). Consequently, overwinter distribution, survival and factors in freshwater affecting iteroparity rate are of interest to resource managers. Additionally, Upper Columbia River steelhead support popular recreational fisheries, supported in part by hatchery programs intended to mitigate for impacts from hydroelectric dams in the Columbia River basin (Waples 1991), creating a need for knowledge of the distribution, survival and interactions with fisheries for both hatchery-origin and natural-origin subpopulations. For example, estimating the proportion of hatchery-origin and natural-origin steelhead returning to Upper Columbia River tributaries is necessary to monitor the status and trends of natural-origin steelhead and proportion of hatchery-origin steelhead (pHOS) returning to each tributary population (Stelle 2016). Maintaining and/or increasing iteroparity rates is an important additional component of steelhead ESA recovery planning.

Freshwater overwintering behavior in stream-maturing steelhead has been hypothesized as one of a suite of traits allowing migration to spawning habitats that would otherwise be inaccessible because of flow and/or temperature conditions (Robards and Quinn 2002; Trudel et al. 2004). Notably, both radio-tag and passive integrated transponder (PIT) tag monitoring has revealed complex behaviors in migrating adult steelhead, including tributary overshoot and fallback, use of main-stem mainstem rather than tributary habitats during winter (e.g., Keefer et al. 2008a; Richins and Skalski 2018), and complex movements near natal reaches, including temporary and permanent straying (Keefer and Caudill 2014; Pearsons and O’Connor 2020). Overwintering mortality (including pre-spawn mortality) has been attributed to a variety of mechanisms (Keefer et al. 2008a; Bowerman et al. 2016), including spatial and temporal overlap of hatchery- and natural-origin subpopulations with fisheries (Feeken et al. 2019). Given the possible range of behaviors and potential sources of mortality prior to spawning, determining patterns of overwintering distribution and survival for summer steelhead populations is an important first step toward effective management and conservation.

In contrast to most other Pacific salmonids, iteroparity in steelhead is common and can increase individual fitness and population productivity (Fleming 1998; Fleming and Reynolds 2003; Wilbur and Rudolf 2006). The rate of iteroparity is negatively correlated with migration distance in steelhead (Copeland et al. 2019). For instance, iteroparity rates decline from 10-20% in coastal populations (e.g., Meehan and Bjornn 1991; Busby et al. 1996) to 2.9-9.0% for lower Columbia River steelhead (Keefer et al. 2008b) to 0.5-2.0% in Snake River populations which migrate upstream more than 700 km through eight hydro-electric projects (Keefer et al. 2018; Copeland et al. 2019). Survival during post-spawn migration to marine habitats (‘kelt migration’) is thus an important factor that may constrain iteroparity rate if kelt survival during outmigration is low, as has been reported for Snake River kelts (e.g. 13-20% survival through the lower Snake and Columbia rivers; Keefer et al. 2017).

Our goal was to quantify migration behaviors, seasonal habitat-use, and survival for adult steelhead in the Upper Columbia basin to inform management and conservation efforts. Few adult migration studies have been conducted focusing on steelhead in the Upper Columbia River with the exception of those focused on upstream main-stem dam passage and migration rates (English et al. 2001; English et al. 2006; Keefer et al. 2008b). Notably, the Upper Columbia Distinct Population Segment (DPS) is comprised of four distinct tributary populations (Wenatchee, Entiat, Methow, and Okanogan) which may vary in behavior, survival rates and hatchery contribution. Currently, monitoring in Upper Columbia River basin by Washington Department of Fish and Wildlife (WDFW) relies on tributary-specific escapement estimates generated using a (PIT) tag-based mark-resighting patch occupancy model (Waterhouse et al. 2020). However, survival in the Columbia River and tributaries prior to spawning (i.e., overwinter) or during post-spawn outmigration (i.e., kelting) is largely unknown because poor PIT tag detection rates during downstream kelt migrations at instream detector sites and hydroelectric dams make survival estimation challenging.

The specific objectives of this study were to: (1) monitor the pre-spawning distribution and tributary entry timing of steelhead in main-stem Upper Columbia River above Priest Rapids Dam and spawning tributary habitats; (2) estimate survival before, during, and after the spawning period in both the main-stem Upper Columbia River and tributaries, and; (3) monitor post-spawn (kelting) movements from tributaries and estimate downstream migration survival. Quantifying fallback was an important ancillary objective of our study because fallback at Priest Rapids Dam can inflate estimates of escapement to the study area (e.g., Boggs et al. 2004). We hypothesized that a portion of steelhead entering the upper Columbia River are ‘overshoot’ temporary strays that would return downstream, that tributary entry timing and overwinter habitat selection would be associated with arrival timing and tributary environmental conditions, that hatchery-origin survival would be lower during periods with active fisheries, that overwinter survival rates would be higher in main-stem than tributary habitats (Keefer et al. 2008a), and that post-spawn steelhead would commonly exit tributaries but kelt survival to the ocean would be low (e.g., Wertheimer et al. 2005; Keefer et al. 2018).

# [A]Methods

[B]Collection and tagging of steelhead

Summer steelhead returning to the Upper Columbia River were collected and radio-tagged at the Off-Ladder Adult Fish Trap (OLAFT) facility at Priest Rapids Dam from July 6 through November 10, 2015 and between July 6 and November 2, 2016. Sampling occurred three days per week during daylight hours (0800 to 1600 hours) with 1:6 steelhead selected for radio-tagging in 2015 and a 1:3 tag ratio in 2016 without respect to origin (i.e., both natural-origin and hatchery-origin steelhead received tags; Truscott et al. 2015; 2016). All sampled steelhead received a PIT tag in both years (Truscott et al. 2016). Fish were anesthetized using tricaine methanesulfonate (MS-222) at a concentration of 50 mg/L in a 378 L sampling tank, measured (FL, nearest cm), and visual markings (hatchery- or natural-origin) were recorded, and each steelhead was scanned for a previously implanted PIT tag prior to tagging. Hatchery-origin steelhead were identified by the presence of adipose or pelvic fin clips, Floy tags, and/or coded wire tags. Unmarked and non-coded wire tagged adults were presumed to be of natural-origin. Scales were taken above the lateral line between the dorsal and adipose fins (Bernard and Myers 1996). Steelhead lacking a PIT tag were injected with a 12 mm PIT tag into the pelvic girdle (Gibbons and Andrews 2004) and sex was determined using an ultrasound device (Martin et al. 1983). Radio-tagged steelhead received an intragastrically implanted 3-volt coded transmitter (model MCFT2-3A, 16 mm x 46 mm at 10 g in air, 52-week battery life, Lotek Wireless, Newmarket, Ontario) that included an angler reward label ($50 US). Once tagged, all steelhead were given adequate time to recover in a holding tank that allowed volitional return to the fish ladder at Priest Rapids Dam.

[B]Fishing mortality

A recreational steelhead fishery for adipose-clipped (hatchery-origin) steelhead occurred from October 15th, 2015 through March 9th, 2016 upstream of Priest Rapids Dam and included use of a single barbless hook. During this period, downstream sections of the Columbia and Snake rivers were also open to fishing. We used tag returns to quantify known harvest by season and habitat. Unreported harvest upstream of Priest Rapids Dam was estimated as the difference between creel survey harvest rates and the proportion of radio-tags returned by anglers. WDFW creel surveys estimated 8,210 anglers fished for 32,153 hours and caught 3,202 steelhead during the 2015 season (WDFW 2016). We calculated an estimate of mortality from catch-and-release angling for the radio-tagged sample in each year. The capture rate estimated from creel data (WDFW 2016) was multiplied by the number of natural-origin radio-tagged fish available for harvest to estimate landings and this value was multiplied by an assumed rate of catch-and-release mortality rate of 5% (NMFS 2003).

[B]Fixed telemetry sites and mobile tracking

A total of 28 fixed site radio telemetry receivers were installed and maintained throughout the Upper Columbia River basin between July 2015 and June 2017 with a maximum of 25 fixed sites operating at any given time throughout the study (Figure 1; Supplement 1). Fixed sites in the lower reaches of tributaries (henceforth ‘lower tributary fixed sites’) were installed at or near the mouth of tributaries and within 20 m of lower tributary instream PIT tag arrays. Each lower tributary fixed site was outfitted with two receivers (each with 1 antenna) to provide monitoring redundancy and information on movement direction of steelhead (upstream or downstream as indicated by last detection at that site). Additionally, two fixed sites were located near Chief Joseph Hatchery, which is a commonly used overwintering area for steelhead returning to the Upper Columbia River that overshoot their natal tributaries (English et al. 2003). Tributary fixed sites were outfitted with 4-6 element Yagi antennas with typical detection range of 150 - 300 m (minimum 100 m). Receivers were downloaded a minimum of once per month and as frequently as multiple times per week. Monitoring was limited at Rocky Reach and Wells dams to PIT tag antenna arrays in fishways. Monitoring duration and locations were consistent at lower tributary fixed sites and differed slightly between years at some other locations (Supplement 1). Mobile tracking was conducted to augment fixed site monitoring in reservoirs and tributaries (Wenatchee, Entiat, Methow, and Okanogan) and refine fate classification. Mobile tracking took place via truck, raft, and jet boat from November-May 2015-2016 and 2016-2017.

[B]Data analysis

We compiled a database with fish traits measured at tagging (i.e., origin, sex, and fork length), detections from PIT tag interrogation sites, fixed sites, and mobile tracking records, and angler harvest locations for returned tags. PIT detection data were downloaded from the Pacific States Marine Fisheries Commission PIT tag Information System database (PTAGIS; [www.ptagis.org](http://www.ptagis.org)). Individual steelhead movement histories were reviewed for errors and telemetry records were used to score behaviors and to classify individual steelhead fates. Key parameters included fallback behavior below Priest Rapids Dam, tributary entry, mortality estimates, overwinter distribution and survival, survival to spawn, and post-spawn movements, including kelting behaviors. Prior to analyses, we tested whether the distribution of passage date (i.e., tagging date) differed between PIT only and PIT plus radio-tag samples within each sampling year using Kolmogorov-Smirnov (K-S) tests (Smirnov 1939). We identified three periods for analyses: fall, overwintering, and spawn/kelting periods. We defined the onset of winter as 1 January using the criteria of Keefer et al. (2008a) and March 15 as the onset of the spawning period using Keefer (2008b) and Hillman et al. (2016).

[B]Fallback out of the Upper Columbia Basin

Fallback by radio-tagged steelhead was identified by one or more detections at sites upstream of Priest Rapids Dam followed by detection at a PIT tag array downstream of Priest Rapids Dam (e.g., Snake River), detection at the Priest Rapids Dam tailrace fixed site, mobile tracking detection below Priest Rapids Dam, or by reported harvest or collection at hatcheries downstream of Priest Rapids Dam. Steelhead with downstream movement records below Priest Rapids Dam that also included presence in a tributary during the spawning period were classified as kelts rather than fallbacks. We tested whether the distribution of passage date at Priest Rapids Dam differed among tagged steelhead that ultimately fell back below Priest Rapids Dam vs. those that overwintered in the Upper Columbia River using K-S tests. We excluded steelhead fallbacks from most analyses to emphasize patterns within steelhead remaining in the Upper Columbia River basin during the spawning period.

[B]Tributary entry and fixed site detection probabilities

Entry timing and detection probabilities at fixed sites were estimated using detections at lower tributary fixed sites and detections at in-stream PIT arrays, mobile tracking detections, and additional fixed sites located upstream. Detection efficiencies () of lower tributary fixed site locations (*i*) were calculated for the four major Upper Columbia River tributaries for fall and spring monitoring periods. was calculated as:

Where is the total number of fish detected at lower tributary fixed site *i* and is the total number of fish known to have entered the tributary at all upstream sites including in-stream PIT arrays , mobile tracking detections, and additional upstream fixed sites. Upper and lower 95% confidence interval limits were estimated as described in Newcombe (1998):

√{p(1 – p)/n}

Fish known to have shed radio transmitters, and fish that were reported harvested below tributary fixed sites were censored from the analyses.

Steelhead classified as unknown fate likely included steelhead that regurgitated their radio-tag without further PIT detection, as well as mortality, a concern in any radio-tagging study.  We examined telemetry records for evidence of shed tags and identified potential shed tags if those steelhead were: 1) detected at PIT arrays but not radio-telemetry sites at more than one location and date; 2) reported as collected at hatcheries without radio-tags present; and/or 3) PIT detections that occurred after a radio-tag was returned.  Fish meeting these criteria were not censored from the analysis and were assigned a fate given detection histories. We denoted unknown fates as ‘mortalities’ and note this category may have included fish with the following fates: (1) died as a result of tagging at Priest Rapids Dam; (2) undetected fallback below Priest Rapids Dam; (3) shed radio-tags; (4) unreported harvest; and/or (5) natural mortality. We defined ‘non-harvest mortality’ as mortality that could not be assigned to known fishery take.

[B]Overwintering location and survival-to-spawning

Overwintering locations (Columbia River main-stem or tributary) were assigned based on the location where a tagged fish was detected most frequently during winter. A steelhead was considered to have survived the overwintering period in a reservoir if detected after March 15: (1) > 0.5 km from a overwintering location determined by mobile-tracking; (2) passing a dam; (3) passing any PIT array (instream or at dams); or (4) at any radio-telemetry fixed site. Unadjusted overwinter survival, i.e., survival-to-spawning, was estimated using the number of steelhead classified as live at the onset of spawning/kelting (15 March) divided by the number classified live at the beginning of winter (1 January). Steelhead were classified as having survived to the spawning period in a tributary if detection histories indicated they survived until 15 March and were present in the tributary a majority of the winter period. Steelhead that overwintered in the Upper Columbia and fallbacks detected after January 1 were included as overwinter survivors. Estimates of survival-to-spawning represent minimum estimates because some surviving steelhead may have gone undetected during winter and/or spawning periods at radio-telemetry fixed sites, PIT tag arrays, or during mobile tracking. Steelhead assigned a spawning fate of ‘other survivors’ where those detected in smaller Columbia River tributaries. Steelhead detected moving after March 15th but that were never detected in tributaries were assigned a fate of ‘unknown tributary survivors’. Uncertainty in the classification of individual steelhead fates using telemetry date can bias estimates of behavior and survival, an important consideration because the primary goals of the study were to identify overwintering distribution and to estimate survival rates. Consequently, we first considered the influence of uncertainty in fate classification by comparing survival estimates under the following three scenarios: (1) survival excluding (censoring) unknown tributary survivors; (2) survival including unknown tributary steelhead as spawners (best-case survival); and (3) survival including unknown tributary steelhead as presumed mortalities (worst-case survival). We used logistic regression analysis to determine if there was a relationship between use of overwintering habitat (tributary vs. main-stem) and arrival date at Priest Rapids Dam.

[B]Distribution of spawning steelhead

Spawning distribution was assessed at the tributary level and focused on the major Upper Columbia basin tributaries (Entiat, Methow, Okanogan, and Wenatchee rivers) and also included monitoring at minor tributaries (Supplement 1). Foster Creek, located in Wells Dam reservoir near Chief Joseph Dam, was the only minor tributary to the Columbia River that was not outfitted with a radio-telemetry site but was monitored by PIT array. Potential unmonitored spawning sites included the lower Chelan River, Chelan Hatchery outfall (Beebee Springs), Wells Dam tailrace outfall (Rocky Reach Pool), Eastbank Hatchery outfall (Rock Island Pool), and Crab Creek (Priest Rapids Pool). Spawning in the Columbia River is also possible but has never been rigorously evaluated. Very limited spawning is also possible in small tributaries flowing into Wanapum and Rock Island reservoirs (Baldwin 2007). We used Chi-square tests to test for interannual differences in proportion of hatchery- vs. natural-origin steelhead fall mortalities, overwintering survivors, survival-to-spawning estimates, and tributary-specific pHOS.

[B]Post-spawn survival rates

Steelhead were classified as kelts if they were detected moving downstream (PIT tag or radio-tag) at monitoring sites located near the mouth of each subbasin on or after March 15. Spawning-to-kelt survival was estimated by dividing the number of kelts by the number of spawners in each tributary. Kelt migration survival through the Columbia River was estimated using PIT tags for fish detected at Bonneville Dam because radio-telemetry monitoring only extended downstream as far as Priest Rapids Dam. At Bonneville Dam, detection of PIT-tagged kelts was possible at the Bonneville corner collector (BCC) or the juvenile bypass facility (B2J); spillways were not monitored for downstream movement. Therefore, PIT tag detection probability of kelts at Bonneville Dam during outmigration was estimated from iteroparous adults observed at Bonneville Dam in subsequent years (e.g., 2017 kelt outmigrants returning to spawn in fall 2017 or 2018). We assumed Columbia River steelhead kelts, *S,* that were successfully detected outmigrating at Bonneville Dam were a binomially distributed subset of the totalnumber of fish, *T,* that re-ascended the dam on repeat spawning attempts (either in the same year or the following year as consecutive or skip-spawners, respectively), and this likelihood was used to estimate Bonneville Dam detection probability *p,* for each kelt outmigration year *y*:

*Sy ~* binomial (*Ty* , *py*)

We estimated these detection probabilities in a Bayesian framework using JAGS (Plummer 2003) using detections from a sample of adult steelhead tagged only with PIT tags to avoid potential radio-tagging effects on kelt survival. Kelt detection probabilities were given independent uninformative priors using a beta distribution with shape parameters equal to 0.001. We ran a total of 50,000 MCMC simulations on four chains, of which the first 10,000 were discarded as burn-in, and of the remaining iterations, one in forty was retained. Convergence was assessed using the Rhat statistic (Brooks and Gelman 1997; Gelman and Rubin 1992) and based on the number of effective iterations, which was confirmed to be equal to 4,000.

# [A]Results

[B]Steelhead tagging and fallback

A total of 400 and 407 adult summer steelhead were radio-tagged at the Priest Rapids Dam OLAFT facility in 2015 and 2016, respectively (Supplement 2). Run timing within both years peaked later than the ten-year average, and steelhead were under-sampled during the second half of the run in 2015 (Figure 2). Hatchery-origin steelhead comprised nearly three quarters of the total tagged (72.5% hatchery-origin, 27.5% natural-origin). The distribution of tagging dates did not differ between PIT and radio-tagged steelhead in either year (Kolmogorov-Smirnov test, 2015: *D* = 0.057, df = 138, *P* = 0.978; 2016 *D* = 0.137, df = 138, *P* = 0.149). Over the course of the study, fixed site detection probabilities were greater than 85% for nearly all tributaries with the exception of the Okanogan River in the spring and fall of 2016 (Supplement 3). A total of 25 radio-tagged fish had detection histories indicating they had shed radio-tags across the two years (~3.1% of total), a rate similar to that observed in steelhead in the Snake and Lower Columbia rivers (~4.0%; Keefer et al. 2004).

Across both years, 20% of tagged fish were recorded falling back over Priest Rapids Dam (2015: *n* =71 [18%]; 2016: *n =* 94 [23%]; fallback locations provided in Supplement 4). Fallbacks were predominately detected during fall months (Figure 3; 87% of fallback in 2015 and 72% in 2016). The proportion of radio-tagged steelhead fallbacks among hatchery-origin and natural-origin steelhead was similar to the proportion of the total tagged steelhead (fallbacks: 70% hatchery-origin, *n =* 115; 30% natural-origin, *n* = 50; *X2* = 0.53; *P =* 0.466). Steelhead arriving to Priest Rapids Dam earlier in the season were more likely to fallback than later in the season in 2015 (two-sample Kolmogrov-Smirnov test; *D* = 0.18, *P* = 0.02), but not in 2016 (*D* = 0.09, *P* = 0.54).

[B]Harvest rate

Reported harvest from the Upper Columbia River was higher in the 2015 sample than 2016 sample (Table 1) because the steelhead fishery was suspended in 2016-2017. Reported harvest in 2015 hatchery-origin tagged steelhead was similar between the Upper Columbia River (18.0%; 42/233) and among tagged steelhead that fell back below Priest Rapids Dam (19.7%; 14/71). More tagged steelhead were harvested in tributaries (65%; 28/43) than in main-stem reservoirs in 2015 (35%; 15/43), though proportion of harvest between habitat types was not significantly different (exact binomial test *P* = 0.066). The largest proportion of tagged steelhead harvested in tributaries were reported from the Methow River (75% of tributary harvest; 49% [21/43] of total harvest). Reported harvest in hatchery-origin steelhead in 2015 was concentrated in the fall (93%; 40/43 in fall vs. 7%; 3/43 in winter). Reported harvest rate in 2016 was an order of magnitude lower than 2015 and was reported only below Priest Rapids Dam (6/407 = 1.5%). In total, 74 (19% of 2015 tagged steelhead) and 47 (11.5% of 2016 tagged steelhead) radio-tags were returned from fisheries, collection locations, and other sources (Table 1).

[B]Tributary entry timing

A majority of steelhead remaining above Priest Dam moved into tributaries during fall in both 2015 (73%; *n*= 177) and 2016 (73%; *n* = 180), though not all steelhead remained in tributaries during winter (Figure 4). The pattern of fall entry was consistent across tributaries except for the Entiat River, where only 20% (2015) and 39% (2016) of entry events were in fall. Notably, none of the steelhead that entered the Entiat River in the fall were detected overwintering there. Within tributary, a similar percentage of hatchery- and natural-origin steelhead entered during fall vs. winter in both years (Supplement 5). A small percentage (~5%) of tagged steelhead remaining above Priests Rapids Dam were detected entering an Upper Columbia tributary other than their final spawning tributary, i.e., were temporary strays.

[B] Non-harvest mortality in fall

Fall non-harvest mortality was less than 10% in both years (9.2% in 2015; 9.1% in 2016). Mortality was concentrated in reservoirs, with the majority assigned to Upper Columbia River reservoirs (76% and 81% of fall non-harvest mortality within reservoirs in 2015 and 2016, respectively; Table 2) and the Methow River (68% of non-harvest fall mortalities within tributaries). Hatchery-origin steelhead remaining above Priest Rapids Dam were more commonly classified as non-harvest mortalities than natural-origin steelhead during fall 2015 (*n* = 32; 17% of total hatchery-origin steelhead vs. *n* = 5; 5% of total natural-origin: = 6.63, df = 1, *P* < 0.01). However, rates between natural-origin and hatchery-origin steelhead were not different in fall 2016 (n = 27; 10% of total hatchery-origin steelhead vs. *n* = 10; 13% of total natural-origin; = 0.17, df = 1, *P* = 0.68). We estimated a total of 2 tagged steelhead were indirect harvest mortalities and 7 steelhead were harvested and not reported based on comparison of creel data and assumed rates of post-hooking mortality (Supplement2).

[B]Overwintering distribution, survival and movement

Similar numbers of tagged steelhead overwintered in the upper Columbia River main-stem compared to tributaries during both study years (~54%; Table 3). Steelhead arriving at Priest Rapids Dam earlier in the run season had a higher probability of overwintering in tributaries, though median arrival dates differed by less than a week between the two groups (logistic regression; *z* = 2.7, df = 521, *P* < 0.01; Aug 26 and 28th, median tag date of tributary vs. main-stem in 2015, Sept 12 and 16th, median tag date of tributary vs. main-stem in 2016). Use of reservoirs was concentrated in the upper half of the impounded system (Wells and Rocky Reach dam reservoirs) in both years. The proportion of steelhead that survived to spawn and overwintered in the same tributary differed among locations and years, declining in the Methow and Okanogan rivers, but increasing in the Wenatchee River. Hatchery-origin steelhead were the majority of overwintering steelhead in every location with the exceptions of the Wenatchee River (both years) and Rocky Reach Dam reservoir (2016; Table 3).

Overall, reported harvest was low in winter and overwinter survival above Priest Rapids Dam after accounting for harvest and fall mortality was 83.2% and did not differ among tributary or main-stem habitats or by steelhead origin (Table 3). Overwinter survival did not significantly differ for steelhead occupying main-stem Columbia River reservoirs (78%, n= 296) compared to tributary habitats ( = 0.86, df = 1, *P* = 0.35). Overwinter survival in hatchery-origin steelhead (74% and 85% in 2015 and 2016, respectively) was lower but not significantly different from survival for natural-origin steelhead (90% and 89%; *n* = 548, = 0.55, df = 1, *P* = 0.46).

Radio-tagged steelhead that successfully overwintered in the main-stem Columbia River exhibited three primary movement behaviors during the overwinter period: 1) tributary entry (52% of main-stem overwintering survivors; *n* = 121); 2) fallback out of the Upper Columbia River basin (35% of fallbacks; *n* = 34); or 3) movement within the Columbia River without detection in a tributary (44%; *n* = 43; see Table 4; ‘other survivors’).

[B]Survival-to-spawning

The mean total survival-to-spawning rate of hatchery- and natural-origin steelhead remaining above Priest Rapids Dam was 0.693 (CI = 0.649, 0.737) across both years (Table 4). Total mean annual steelhead survival-to-spawning under scenario (1, censoring unknown tributary survivors) was 0.68 and 0.70 for the 2015 and 2016 run-years, respectively. By including unknown tributary steelhead as survivors (scenario 2) or conversely as mortalities (scenario 3), rates were 0.69 and 0.73 (best-case), and 0.67 and 0.62 (worst-case) for 2015 and 2016, respectively. The potential for biases related to detection efficiency was small because annual survival estimates adjusted for detection efficiency were 0.68 and 0.70, falling within the ranges of the 2nd and 3rd scenarios.

Notably, steelhead survival was reduced by harvest in 2015 by 18%, resulting in a relatively large difference in survival-to-spawn between hatchery- and natural-origin groups. Survival in hatchery-origin steelhead increased somewhat in 2016, but declined in natural-origin steelhead, and the difference in rates between hatchery- and natural-origin steelhead was reduced (Table 4). Consequently, the increased relative survival in hatchery-origin steelhead in 2016 was associated with increased pHOS across the four major tributaries between years, from ~1:1 hatchery- to natural-origin steelhead in 2015 (50.9% hatchery-origin, *n* = 165 spawners, Table 4) to ~2:1 in 2016 (68.7%; *n* = 144, = 9.410, df = 1, *P* < 0.01). Similarly, among steelhead that survived overwintering but could not be assigned to a tributary, the total number of hatchery-origin steelhead increased four-fold between years (2015: 15/21 unassigned spawners [pHOS = 0.71]; 2016: 62/76 [pHOS = 0.82], respectively; see Table 4), though the frequencies between years were not significantly different in the smaller sample ( = 1.392, df = 1, *P* < 0. 238). Among tributary populations, hatchery-origin steelhead were more abundant in the Methow and Okanogan rivers during both monitored years. Total counts per tributary differ slightly from overwintering survival estimates (Table 3) given that 11 steelhead overwintered in a tributary other than their spawning tributary. Adjusting total tributary entry by detection efficiencies of the lower tributary fixed sites increased the estimated total entry from 309 to 321 (see Table 4; ‘Det. Efficiency’).

[B]Post-spawn movement and survival

A total of 174 steelhead were classified as kelts based on downstream movements (~56% of steelhead surviving-to-spawning in tributaries), providing a minimum estimate of the number of steelhead surviving to post-spawn status. Kelting rates among tributaries generally followed the distribution of steelhead that survived to spawn (Table 5). Few radio-tagged steelhead were detected on PIT antennas at Bonneville Dam: 14 steelhead (9 females and 2 males natural-origin and 3 hatchery-origin females; 15.2% of kelts) tagged in 2015 and a single natural-origin male kelt tagged in 2016 were detected at Bonneville Dam (1.2% of kelts). The PIT-tag only sample was used to estimate repeat spawning rate and revealed 112 (2015) and 45 (2016) steelhead passing Bonneville Dam upstream on a second spawning migration. Natural-origin kelts detected at Bonneville Dam spawned in the Wenatchee and Entiat rivers (45% and 36%, respectively), but were rare from the Methow River (8%), and absent from the Okanogan River (0%). Median kelt PIT tag detection probabilities at Bonneville Dam calculated from repeat spawners for the two years were 33.1% (2015; 95% credible interval = 24.5 - 42.2%) and 15.1% (2016; 95% C.I. = 6.7 - 27.3%). The adjusted natural-origin steelhead kelt downstream migration survival rate (95% credible interval) was 65.1% (51.2%, 88.1%) and 22.9% (12.6%, 51.7%) for the 2015 and 2016 run-years, respectively. Hatchery-origin kelt downstream migration survival (95% credible interval) was 22.1% (17.2%, 29.9%) for the 2015 sample. No hatchery-origin kelts tagged in 2016 were detected during downstream migration. This may be due to low detection probabilities and a low survival rate assuming the relative difference in observed in 2015-2016 between hatchery- and natural-origin steelhead was similar in 2016-2017.

# [A]Discussion

Understanding patterns of distribution and survival during pre- and post-spawning periods is critical for effective management and conservation of steelhead populations. This is especially true for summer-run populations, which spend up to a year in freshwater as adults and for regions such as the Upper Columbia River with multiple tributary populations that may be demographically and genetically distinct, but which share main-stem river corridors during migration and overwintering. The key findings of this study include: 1) approximately one-fifth of steelhead entering the Upper Columbia River were fallbacks, i.e., migrated downstream out of the basin prior to spawning; 2) broad patterns of fate were similar between years (Figure 5), but differences in recreational harvest and other factors between years resulted in a complex pattern of survival within hatchery- and natural-origin steelhead; 3) overwinter use of main-stem habitats was more likely for later-arriving steelhead; 4) estimated survival rates during winter were similar between main-stem and tributary habitats, but steelhead were not evenly distributed within habitat type; and 5) post-spawn and kelt survival were higher than implied by the low iteroparity rate of the population. Survival estimates fell within a relatively narrow range across a broad array of assumptions concerning uncertainty in fate classification and detection efficiency, and the true overall survival rate was very likely at or near 0.69 in both years. These findings were broadly consistent with our initial hypotheses, with the exception of the observed lack of survival differences between habitat types, some harvest effects, and higher than expected kelt survival in one year.

[B]Fallback

While not the directly related to our primary goal, we found approximately 1 in 5 steelhead of the total radio-tagged sample were fallbacks below Priest Rapids Dam. Presumably many of these steelhead represented overshoots from downstream populations, though the mechanisms causing both overshoot and fallback remain uncertain. Fallback behavior is associated with a complex set of factors including local hydraulic cues (Reischel et al. 2003), origin and migration history (Keefer et al. 2008c; Bond et al. 2017; Richins and Skalski 2018; Tattam and Ruzycki 2020), and seasonal environmental conditions during route-finding (e.g., Keefer et al. 2006). Fallback occurred primarily in fall and was more frequent in early arriving steelhead during 2015. The seasonal decline in fallback probability may have been related to reduced activity later in the season, differences in run timing between Upper Columbia River steelhead and overshooting steelhead from downstream populations, and/or steelhead seeking coldwater refuges downstream, though the latter seems unlikely as a major factor given the lack of cool tributary inputs downstream of Priest Rapids Dam. The relatively late distribution of tagging in 2016 compared to the run may have limited our ability to detect an association between fallback and timing in that year. Regardless of mechanisms, the large number of fallbacks can inflate escapement estimates if not accounted for (Boggs et al. 2004). The high rate of fallback at Priest Rapids Dam, including overshoot fallback, also highlights the need for benign downstream passage routes for adults given the potential for increased mortality associated with fallback (e.g., Keefer et al. 2005; 2008c).

Fallback behaviors are associated with higher straying rates, and while we were unable to estimate straying because natal origin of sampled adults was unknown, a recent analyses from natural-origin steelhead PIT-tagged as juveniles in the same system revealed more frequent straying within the Upper Columbia basin to sites upstream of natal sites (Pearsons and O’Connor 2020), though there was some uncertainty in distinguishing overshoot/temporary straying from permanent strays due to the challenge of detecting downstream movements with PIT tags. Ideally, future studies would be able to distinguish overshoot fallback, temporary straying and permanent straying from successful homing and spawning by establishing natal origin of adults at the time of tagging using PIT tags implanted in juveniles at natal sites or genetic approaches (e.g., using parentage-based tagging; Keefer et al. 2018).

[B]Harvest and survival in fall

Legal harvest in the Upper Columbia River was restricted to the first year of the study, providing an unexpected opportunity to compare rates between years in addition to planned comparisons between tributary and main-stem habitats. The WDFW 2015 creel survey estimated 1,588 of 8,696 hatchery-origin steelhead were harvested (18.3%), a rate very similar to that from our radio-tag sample (18.0%), suggesting the $50 US tag reward was effective in motivating anglers to return radio-tags. The majority of basin-wide harvest (above Priest Rapids Dam) was concentrated during fall months (93% of total reported harvest). Point estimates of harvest in tributaries were nearly twice those in the main-stem habitats, though this difference was not statistically significant (65% vs. 35% of harvest in tributaries; *P* = 0.066). Examination of non-harvest mortality across years suggested the potential that unreported harvest and/or indirect fishing mortality contributed to mortality of hatchery-origin steelhead in 2015. Specifically, estimated non-harvest mortality during fall in hatchery-origin steelhead declined from 17% to 10% between the 2015 and 2016, whereas rates for natural-origin steelhead increased from 5% to 13% between years. Additionally, while most harvest was in fall, the trend in overwinter survival in hatchery- vs. natural-origin steelhead between years paralleled this pattern, though the differences were not significant. Overall, tagging and creel estimates were closely aligned and the telemetry data were useful for evaluating potential effects of unreported harvest and indirect mortality.

[B]Tributary entry timing, overwinter distribution, and survival-to-spawning

The timing of freshwater entry by summer steelhead has been associated with overwinter habitat use within the Snake River basin (Keefer et al. 2008a, 2013) whereby arriving earlier in the migration season were more likely to overwinter in a spawning tributary than in a Snake River reservoir. We found a similar pattern in the Upper Columbia River, though steelhead detected entering tributaries prior to the January 1 overwintering period were not always detected residing within tributaries throughout the overwintering period and the difference in timing between the groups in this study were relatively small (2-4 day difference in median tag date). Tributary exit behavior was observed primarily in the Entiat River and also was common in the three other major tributaries (mean = 30%, range = 11-43% of spawners per tributary). The apparent rejection of the Entiat River in winter by steelhead suggests environmental factors there such as ice formation and/or predators (e.g., river otters) differ from other tributaries.

Overwinter survival trended lower in main-stem compared to tributary habitats, but was not significantly different and the relatively large samples size used here implies the differences were relatively small if undetectable. Regardless, the pattern superficially contrasts with those observed for overwintering survival of steelhead in the lower Columbia and Snake river reservoirs (Keefer et al. 2008a), where steelhead that overwintered in reservoirs survived at a higher rate (82%) compared to steelhead reaching tributaries in fall (maximum overwinter survival = 62%). However, differences in scale of monitoring preclude direct comparison of rates between studies. For instance, higher relative survival rates observed by Keefer et al. (2008a, 2013) in main-stem overwintering vs. tributary habitats were due in part to the fact that overwintering steelhead survived fall fisheries by definition and because mortality was not directly estimated in Snake River tributaries. Thus, although the Upper Columbia River and Snake River basins are broadly similar inland rivers with dams and tributaries and lower fishing mortality in winter, direct comparison of seasonal and habitat-specific estimates of overwinter survival or survival-to-spawning is not possible at this time. Future comparisons between the systems using similarly configured monitoring arrays could provide useful insights to the relationships among life history traits, spatial configuration of main-stem and tributary habitats and patterns of natural and fishery-related mortality.

[B]Post-spawn survival and kelting rate

A majority of steelhead survived the spawning period and exited tributaries as kelts. Survival during the spawning period and downstream kelt survival to Bonneville Dam in our small sample (0.23-0.65) was higher than has been reported recently for Snake River steelhead (0.14-0.17 annual survival during the spawning period and 0.13-0.20 annual kelt downstream survival to Bonneville Dam; Keefer et al. 2018) and higher than in land-locked Atlantic Salmon attempting to pass a similar number of dams (0.00; Nyqvist et al. 2016). Direct comparisons to Snake River steelhead kelt survival are also complicated by differences in monitoring arrays because survival during the overwinter and spawning periods could not be partitioned in the Snake River study (Keefer et al. 2018) and because all Snake River steelhead kelts pass eight dams and reservoirs during downstream migration before re-entering the ocean whereas the number of dams varies by tributary among Upper Columbia River steelhead populations.

The higher downstream kelt survival for Upper Columbia River reported here may be related to lower mortality during passage at Upper Columbia River dams, differences in traits such as post-spawn sex ratio or average kelt condition (Buelow and Moffit 2015; Harnish et al. 2015; Penney and Moffit 2014), interannual differences in environmental conditions such as flow in the lower Columbia River between the two studies, and/or the fact that some Upper Columbia River steelhead pass fewer total dams. Similar to other studies, more kelts were female than male for every tributary population in both years (except the Entiat River in 2017). Female bias in kelts has been reported in other steelhead populations and other species such as Atlantic Salmon and differential energetic demands on the sexes during spawning is thought to contribute to the pattern (Niemelä et al. 2000; Keefer et al. 2008b; Marston et al. 2012; Nyqvist et al. 2016; Copeland et al. 2019). We were unable to assess condition of post-spawn steelhead, which has previously been associated with kelt survival (e.g., Harnish et al. 2015) and it is plausible that annual differences in average condition of post-spawn steelhead contributed to the variation in kelt survival rate. Differences in kelt survival rates among species, sexes, and systems may be related to differences in energetic requirements among systems, methodology, passage routes at dams, and/or environmental conditions during outmigration. Regardless, the rates observed for Upper Columbia River steelhead suggest relatively high survival to tributary exit may be possible under some conditions.

While iteroparity rates in interior summer steelhead were likely always lower than coastal populations (Clemens 2015; Copeland et al. 2019), iteroparity rate for steelhead has been identified as an element in recovery planning in the Columbia and Snake rivers (NMFS 2003; English et al. 2006; Keefer et al. 2008b) because iteroparity contributes to population productivity and diversity. Recent analyses of iteroparity patterns in Atlantic Salmon at the continental scale identified high variation of iteroparity rate within and among populations and decadal trends suggesting increased iteroparity was associated with release from a mortality factor (ocean fishing; Bordeleau et al. 2020). Notably, duration of freshwater residency during spawning is also associated with migration distance whereby coastal populations are often ocean-maturing with both shorter freshwater spawning durations and lower energetic costs of reaching spawning grounds. Thus, freshwater habitat use, behavior, and duration may jointly influence survival and iteroparity rate beyond the energetics effects of migration distance alone (e.g., Jenkins et al. 2018; Copeland et al. 2019). Collectively, these studies highlight the connections between post-spawn kelting rate, kelt migration survival and iteroparity rate, and also highlight the potential benefits of benign downstream winter passage routes and/or programs such as the kelt reconditioning implemented in the Columbia River basin (Hatch et al. 2013) for increasing the effective iteroparity rate in populations of conservation concern.

[A]Management implications

Recreational steelhead fisheries in the Upper Columbia River are used as a conservation tool to manage the abundance of excess hatchery-origin steelhead on the spawning grounds as part of broader hydropower mitigation goals of the hatchery program (NMFS 2017). During the study period, steelhead radio-tagged in 2015 were subjected to a recreational fishery upstream of Priest Rapids Dam while steelhead radio-tagged in 2016 were not. Hatchery-origin steelhead harvested in the first year comprised 18% of the available steelhead, a value influenced in part by early closure of the Methow River fishery (historically the most productive) once the target harvest for pHOS management had been reached. We found little evidence that harvest strongly affected natural-origin steelhead survival and conclude that unreported harvest was likely not major factors in driving total overwinter mortality, and that fishing interacted with other factors affecting interannual mortality rates to influence pHOS.

Notably, understanding population-specific migration patterns to tributaries could be used to manage fisheries to meet goals for angler opportunity while minimizing impacts on natural-origin steelhead in mixed-population systems. For example, Entiat River steelhead comprise the smallest population in the Upper Columbia DPS, does not have a hatchery component and overwinters entirely in the Columbia River. Assuming the consistent behavior of steelhead observed in the two years of this study are representative, managers can estimate population-specific impacts and institute localized closures (i.e., Rocky Reach pool) when estimated allowable impacts to natural-origin Entiat steelhead have been reached. Future analyses of the influence of winter thermal conditions may be also useful for elucidating habitat selection by steelhead in the Upper Columbia River and in other systems. Such population, season, and location-specific information may be especially important because recent analyses by Pearsons and O’Connor (2020) indicate straying among tributaries of the Upper Columbia River basin is relatively rare, and thus populations are likely largely demographically independent (e.g., some populations such as the Entiat may not be greatly subsidized by strays). Similar consideration of winter distribution among populations may be important because we found uneven spatial distribution of steelhead during winter, although we note annual overwintering rates varied from 0.11 to 0.43 among the three other major tributaries in the Upper Columbia River basin and thus planning would need to integrate such interannual variation in overwinter distribution. Better understanding of migration and overwintering location of hatchery-origin steelhead in similar systems obtained using active-telemetry technologies could provide for more harvest opportunity, reduce hatchery-origin steelhead on the spawning grounds, pHOS and interactions between hatchery- and natural-origin steelhead on spawning grounds, and minimize any indirect fishing mortality in natural-origin steelhead using targeted fisheries in individual reservoirs and tributaries.

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Figure 1**.**  Location of dams (black rectangles), fixed site radio-telemetry antennas (green triangles), and lower tributary PIT arrays (red dots), and Columbia River Hatcheries (yellow squares) in the Upper Columbia River basin. The study area encompasses the waters between Priest Rapids and Chief Joseph dams and tributaries. All fixed site names and description locations are provided in Supplement 1.

Figure 2. Summer Steelhead count passage over Priest Rapids Dam in 2015 (top) and 2016 (bottom). Ten year average annual passage (black line) and radio-tagged steelhead counts are provided (blue bars).

Figure 3. Cumulative proportion of steelhead detected as fallbacks below Priest Rapids Dam by detection date. Fallback detections are split between fallback detection date (unbroken lines) and tag date (broken lines) each year.

Figure 4. Cumulative proportion of radio-tagged steelhead entry and exit by tributary population for steelhead released and monitored in 2015-2017. Tributary entry (solid lines) and kelting outmigration timing (dashed lines) by date of steelhead assigned fates as putative spawners. 1-Jan overwintering onset date (solid black line) and 15-March kelting onset date (dashed black line), separate the different stages and directions of migration.

Figure 5. Proportion of radio-tagged steelhead assigned to each fate by year. Fate assignments are indicated by color, and total tagged steelhead sample sizes are provided. Harvested and collected proportions indicate those that occurred above Priest Rapids Dam.

Table 1. Number of returned tags by tag year, origin and type of return.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Fate | Hatchery | Natural | Total |  | Hatchery | Natural | Total |
| 2015 | | |  | 2016 | | |
| Reported harvest above Priest Rapids Dam | 42 | 1 | 43 |  | 0 | 0 | 0 |
| Reported harvest below Priest River Dam | 8 | 0 | 8 |  | 6 | 0 | 6 |
| Caught and released | 1 | 4 | 5 |  | 3 | 0 | 3 |
| Found on riverbank | 0 | 1 | 1 |  | 3 | 0 | 3 |
| Collected at hatcheries | 10 | 1 | 11 |  | 32 | 3 | 35 |
| **Total** | **67** | **7** | **74** |  | **44** | **3** | **47** |

Table 2. Annual distribution of radio-tagged steelhead mortality by mainstem reach and tributary during fall, defined as last detected prior to January 1.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Location | 2015 Fall Mortalities | | | | 2016 Fall Mortalities | | | |
| Count | | Percent by Origin | | Count | | Percent by Origin | |
| H | W | H | W | H | W | H | W |
|  | *Columbia River* | | | | | | | |
| Priest | 6 | 3 | (67) | (33) | 7 | 2 | (78) | (22) |
| Wanapum | 2 | 1 | (67) | (33) | 1 | - | (100) | - |
| Rock Island | 5 | - | (100) | - | 5 | 2 | (71) | (29) |
| Rocky Reach | - | - | - | - | 2 | - | (100) | - |
| Wells | 10 | 1 | (91) | (09) | 7 | 4 | (64) | (36) |
| Total | 23 | 5 | (82) | (18) | 22 | 8 | (73) | (27) |
|  | *Tributary* | | | | | | | |
| Entiat | - | - | - | - | - | - | - | - |
| Methow | 9 | - | (100) | - | 1 | 1 | (50) | (50) |
| Okanogan | - | - | - | - | 1 | - | (100) | - |
| Wenatchee | - | - | - | - | 3 | 1 | (75) | (25) |
| Total | 9 | - | (100) | - | 5 | 2 | (71) | (29) |

Table 3. Annual counts and percentages of radio-tagged steelhead alive at start of winter (1 Jan, ‘OW steelhead’) and steelhead classified as successfully overwintering (‘Survived’ 1 January – 15 March) by location and origin (hatchery-origin [H] or natural-origin [N]).

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Location | 2015 | | | | | | | | | | 2016 | | | | | | | | | | |
| OW Fish | | | | Survived | | | Percent survived | | | OW Fish | | | | Survived | | | Percent survived | | | |
| H | N | T | % | H | N | T | H | N | T | H | N | T | % | H | N | T | H | N | T | Total |
|  | *Columbia River* | | | | | | | | | | | | | | | | | | | | |
| Priest | 9 | 6 | 15 | (6) | 6 | 3 | 9 | (67) | (50) | (60) | 8 | 3 | 11 | (4) | 7 | 3 | 10 | (88) | (100) | (91) | 19 (73) |
| Wanapum | 5 | 3 | 8 | (3) | 1 | 3 | 4 | (20) | (100) | (50) | 10 | - | 10 | (3) | 2 | - | 2 | (20) | - | (20) | 6 (33) |
| Rock Island | 3 | 5 | 8 | (3) | 2 | 3 | 5 | (67) | (60) | (63) | 4 | 7 | 11 | (4) | 1 | 6 | 7 | (25) | (86) | (64) | 12 (63) |
| Rocky Reach | 13 | 13 | 26 | (10) | 7 | 12 | 19 | (54) | (92) | (73) | 24 | 15 | 39 | (13) | 21 | 14 | 35 | (88) | (93) | (90) | 54 (83) |
| Wells | 53 | 23 | 76 | (31) | 41 | 21 | 62 | (77) | (91) | (82) | 81 | 11 | 92 | (31) | 68 | 11 | 79 | (84) | (100) | (86) | 141 (84) |
| Total | 83 | 50 | 133 | (54) | 57 | 42 | 99 | (69) | (84) | (74) | 127 | 36 | 163 | (54) | 99 | 34 | 133 | (78) | (94) | (82) | 232 (78) |
|  | *Tributary* | | | | | | | | | | | | | | | | | | | | |
| Entiat | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Methow | 26 | 16 | 42 | (17) | 21 | 16 | 37 | (81) | (100) | (88) | 64 | 13 | 77 | (26) | 60 | 12 | 72 | (94) | (92) | (94) | 109 (92) |
| Okanogan | 19 | 9 | 28 | (11) | 15 | 8 | 23 | (79) | (89) | (82) | 39 | 5 | 44 | (15) | 36 | 4 | 40 | (92) | (80) | (91) | 63 (88) |
| Wenatchee | 20 | 25 | 45 | (18) | 16 | 24 | 40 | (80) | (96) | (89) | 4 | 12 | 16 | (05) | 3 | 9 | 12 | (75) | (75) | (75) | 52 (85) |
| Total | 65 | 50 | 115 | (46) | 52 | 48 | 100 | (80) | (96) | (87) | 107 | 30 | 137 | (46) | 99 | 25 | 124 | (93) | (83) | (91) | 224 (89) |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Total | 148 | 100 | 248 | (100) | 109 | 90 | 199 | (74) | (90) | (80) | 234 | 66 | 300 | (100) | 198 | 59 | 257 | (85) | (89) | (86) | 456 (83) |

Table 4. Counts of steelhead remaining above Priest Rapids Dam surviving the spawning period (15 March) by fate and location. Counts of survivors detected entering unmonitored tributaries (via PIT array) and counts of steelhead assigned to tributaries using detection efficiency estimates are provided.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Location | 2015 | | | 2016 | | | All |
| H | N | Total | H | N | Total |
|  | *Survived-to-spawning* | | | | | |  |
| Entiat | 3 | 14 | 17 | 4 | 15 | 19 | 36 |
| Methow | 32 | 25 | 57 | 53 | 13 | 66 | 123 |
| Okanogan | 25 | 14 | 39 | 32 | 4 | 36 | 75 |
| Wenatchee | 24 | 28 | 52 | 10 | 13 | 23 | 75 |
| Other Survivors | 7 | 6 | 13 | 34 | 7 | 41 | 54 |
| Unknown Tributary | 8 | 0 | 8 | 31 | 4 | 35 | 43 |
| Unadjusted Survivors | 105 | 90 | 195 | 166 | 57 | 223 | 418 |
| Adjusted for Det Efficiency | 111 | 93 | 204 | 168 | 58 | 226 | 430 |
|  | *Mortalities* | | | | | |  |
| Fall Mortalities | 32 | 5 | 37 | 27 | 10 | 37 | 74 |
| Overwintering Mortalities | 39 | 10 | 49 | 36 | 7 | 43 | 92 |
| Total Mortalities | 71 | 15 | 86 | 63 | 17 | 80 | 166 |
|  |  |  |  |  |  |  |  |
| *Survival probabilities* | | | | | | | |
| Minimum Survival Probability | 0.58 | 0.86 | 0.68 | 0.68 | 0.76 | 0.70 | 0.69 |
| Survival prob Censoring Unk Tributary | 0.60 | 0.86 | 0.70 | 0.73 | 0.77 | 0.74 | 0.72 |
| Survival Adjusted for Detection Efficiency | 0.61 | 0.86 | 0.70 | 0.73 | 0.77 | 0.74 | 0.72 |

Table 5. Number and percent of adult steelhead detected exiting tributaries after spawning by sex and origin. The count and percentage of the tributary putative spawners (n = 165 and 144 in 2016 and 2017, respectively) by tributary and year are also provided.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Tributary | Hatchery | | Natural | | Sex (percent) | | Exiting % of  Spawners | |
|
| F | M | F | M | F | M | Count | % |
| *2015 Sample, Post-Spawn 2016* | | | | | | | | |
| Entiat | 0 | 0 | 6 | 5 | (55) | (45) | 11 | (65) |
| Methow | 6 | 4 | 9 | 2 | (71) | (29) | 21 | (37) |
| Okanogan | 9 | 4 | 7 | 1 | (76) | (24) | 21 | (54) |
| Wenatchee | 12 | 6 | 14 | 7 | (67) | (33) | 39 | (75) |
| Total | 27 | 14 | 36 | 15 | (69) | (31) | 92 | (56) |
| *2016 Sample, Post-Spawn 2017* | | | | | | | | |
| Entiat | 0 | 3 | 6 | 7 | (38) | (62) | 16 | (84) |
| Methow | 27 | 0 | 6 | 1 | (97) | (3) | 34 | (52) |
| Okanogan | 15 | 1 | 2 | 0 | (94) | (6) | 18 | (50) |
| Wenatchee | 3 | 4 | 6 | 1 | (64) | (36) | 14 | (61) |
| Total | 45 | 8 | 20 | 9 | (79) | (21) | 82 | (57) |

*Supplement 1*.Fixed site radio-telemetry receivers deployed in the Upper Columbia River basin in 2015-17. Sites, river kilometer (RKM) distances from the Columbia River estuary, installation dates, and working duration are provided.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Fixed Antenna Site | Site code | RKM | Install Date | Days in Operation | Days With Outages |
| Priest Rapids Dam Tailrace | 1PR | 635.4 | 07/30/15 | 554 | 15 |
| Priest Rapids Dam Forebay 1 (right bank) | 2PR | 639 | 07/16/15 | 560 | 28 |
| Priest Rapids Dam Forebay 2 (left bank) | 3PR | 639.1 | 07/16/15 | 568 | 98 |
| Priest Rapids Ladder Exit | 4PR\* | 639.1 | 07/16/15 | 238 | 78 |
| Wanapum Dam Tailrace | 1WP | 668.2 | 08/13/15 | 542 | 95 |
| Rock Island Dam Tailrace | 1RI | 728.5 | 07/23/15 | 660 | 10 |
| Rock Island Dam Forebay 1 (right) | 2RI | 730 | 07/24/15 | 659 | 57 |
| Rock Island Dam Forebay 2 (center) | 3RI | 730 | 08/04/16 | 648 | 96 |
| Rock Island Dam Forebay 3 (left) | 4RI | 730 | 08/17/15 | 635 | 27 |
| Lower Wenatchee River Fixed site 1 | 1LW | 756.7 | 07/17/15 | 641 | 17 |
| Lower Wenatchee River Fixed site 2 | 2LW | 756.7 | 07/17/15 | 641 | 21 |
| Middle Wenatchee at Icicle Bridge | MWN | 796.1 | 06/18/15 | 605 | 84 |
| Lower Entiat River Fixed site 1 | 1EN | 780 | 06/15/15 | 667 | 12 |
| Lower Entiat River Fixed site 2 | 2EN | 780 | 06/15/15 | 667 | 12 |
| Entiat River Array at Ardenvoir | ENT | 795.6 | 06/15/15 | 667 | 60 |
| Lower Methow River Fixed site 1 | 1ME | 845.5 | 06/17/15 | 647 | 96 |
| Lower Methow River Fixed site 2 | 2ME | 845.5 | 06/17/15 | 647 | 72 |
| Upper Methow in Winthrop | MET | 921.7 | 07/28/15 | 599 | 61 |
| Chewuch in Winthrop | CHE | 921.7 | 07/28/15 | 599 | 57 |
| Lower Okanogan Fixed site 1 | 1OK | 883.3 | 07/27/15 | 623 | 93 |
| Lower Okanogan Fixed site 2 | 2OK | 883.3 | 07/27/15 | 623 | 97 |
| Below Ihot Island | IHI | 977 | 06/17/15 | 667 | 26 |
| Similkameen River | SIM | 984.2 | 06/17/15 | 667 | 49 |
| Chief Joseph Hatchery | 1CJ\* | 871 | 06/19/15 | 228 | 108 |
| Chief Joseph Hatchery | 2CJ | 871 | 06/19/15 | 629 | 116 |
| Twisp River Smolt Trap | 1TP\* | 911 | 03/14/16 | 89 | 5 |
| Twisp River Weir (Downstream) | 2TP | 921.9 | 03/14/16 | 147 | 64 |
| Twisp River Weir (Upstream) | 3TP | 922.1 | 03/14/16 | 99 | 32 |

\*sites were active during 2015 run year only.

*Supplement 2.* Final fates of the 2015 Priest Rapids Dam radio-tagged summer Steelhead sample. Fates are split between steelhead that were detected falling back below Priest Rapids, steelhead detected remaining above Priest Rapids, and steelhead whose ultimate fates were more difficult to determine given fewer detections and presumed mortalities. Total counts of steelhead by rearing origin and proportions are provided.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Location | 2016 Final Fate | | | | | | 2017 Final Fate | | | | | | Total | |
| Hatchery | | Natural | | Total | | Hatchery | | Natural | | Total | |
| N | % | N | % | N | % | N | % | N | % | N | % | N | % |
| Last Detected Below Priest Rapids Dam | | | | | | | | | | | | | | |
| Harvested/Collected | 18 | 0 | 0 | 0 | 18 | 5 | 6 | 100 | 0 | 0 | 6 | 1 | 24 | 3 |
| Detected in Snake or Lower Columbia | 20 | 41 | 29 | 59 | 49 | 12 | 71 | 82 | 16 | 18 | 87 | 21 | 136 | 17 |
| Kelt Lower Columbia Tributary | 0 | 0 | 4 | 100 | 4 | 1 | 0 | 0 | 1 | 100 | 1 | <1 | 5 | 1 |
| Total | 38 | 54 | 33 | 46 | 71 | 18 | 77 | 82 | 17 | 18 | 94 | 23 | 165 | 20 |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Last Detected Above Priest Rapids Dam | | | | | | | | | | | | | | |
| Reported Harvested/Collected in Columbia River | 16 | 100 | 0 | 0 | 16 | 4 | 10 | 100 | 0 | 0 | 10 | 2 | 26 | 3 |
| Reported Harvested/Collected in Tributary | 34 | 93 | 2 | 7 | 36 | 8 | 22 | 88 | 3 | 12 | 25 | 6 | 55 | 7 |
| Estimated Indirect Hooking Mortalities | 0 | 0 | 2 | 100 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | <1 |
| Estimated Unreported Harvest | 7 | 100 | 0 | 0 | 7 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 1 |
| Total Upper Columbia Harvest Fates | 57 | 93 | 4 | 7 | 61 | 14 | 32 | 91 | 3 | 9 | 35 | 9 | 90 | 11 |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Fates of Tributary Survivors to Spawn | | | | | | | | | | | | | | |
| Survivors to Spawn\* | 43 | 62 | 30 | 38 | 73 | 20 | 64 | 80 | 16 | 20 | 80 | 20 | 159 | 20 |
| Kelts | 37 | 49 | 39 | 51 | 76 | 19 | 53 | 65 | 29 | 35 | 82 | 20 | 158 | 20 |
| Kelts (Detected at Bonneville) | 4 | 25 | 12 | 75 | 16 | 4 | 0 | 0 | 1 | 100 | 1 | <1 | 17 | 2 |
| Total Tributary Putative Spawners | 84 | 53 | 81 | 47 | 165 | 43 | 117 | 72 | 46 | 28 | 163 | 40 | 334 | 41 |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Upper Columbia Tagged Steelhead Presumed Mortalities | | | | | | | | | | | | | | |
| Presumed Fall Mortalities | 32 | 86 | 5 | 14 | 37 | 9 | 27 | 73 | 10 | 27 | 37 | 9 | 74 | 9 |
| Presumed Overwinter Mortalities | 39 | 80 | 10 | 20 | 49 | 12 | 36 | 84 | 7 | 16 | 43 | 11 | 92 | 11 |
| Total Presumed Mortalities | 71 | 83 | 15 | 17 | 86 | 22 | 63 | 79 | 17 | 21 | 80 | 20 | 166 | 21 |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Overwinter Survivors Not Detected in Tributaries | | | | | | | | | | | | | | |
| Columbia River | 12 | 86 | 2 | 14 | 14 | 4 | 32 | 91 | 3 | 9 | 35 | 9 | 49 | 6 |
| Kelted Survivors (Detected at Bonneville) | 2 | 67 | 1 | 33 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | <1 |
| Total Survivors | 14 | 82 | 3 | 18 | 17 | 4 | 32 | 91 | 3 | 9 | 35 | 9 | 52 | 6 |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Total Upper Columbia Fates | 226 | 69 | 103 | 31 | 329 | 82 | 244 | 78 | 69 | 22 | 313 | 77 | 642 | 80 |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Total Tagged | 264 | 66 | 136 | 34 | 400 | 100 | 321 | 79 | 86 | 21 | 407 | 100 | 807 | 100 |

*Supplement 3.* Lower tributary radio-telemetry array observed steelhead detections, detections probabilities, confidence intervals, predicted non detected and total counts of tributary entry.

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Location | Year | Season | Observed | | | Detection Probability | | | Predicted | |
| H | W | T | Estimate | Upper 95% CI | Lower 95% CI | Non-Detected | Total Entry |
| Entiat | 2015 | Fall | 0 | 0 | 0 | 1 | 1 | 0.541 | 0 | 0 |
|  | 2016 | Spring | 3 | 14 | 17 | 0.933 | 0.998 | 0.681 | 1 | 18 |
|  | 2016 | Fall | 0 | 0 | 0 | 1 | 1 | 0.398 | 0 | 0 |
|  | 2017 | Spring | 3 | 15 | 18 | 0.941 | 0.999 | 0.713 | 1 | 19 |
|  |  |  |  |  |  |  |  |  |  |  |
| Methow | 2015 | Fall | 26 | 16 | 42 | 0.941 | 0.984 | 0.856 | 3 | 45 |
|  | 2016 | Spring | 15 | 9 | 24 | 0.958 | 0.999 | 0.789 | 1 | 25 |
|  | 2016 | Fall | 37 | 9 | 46 | 0.961 | 0.992 | 0.89 | 2 | 48 |
|  | 2017 | Spring | 16 | 4 | 20 | 0.951 | 0.994 | 0.835 | 1 | 21 |
|  |  |  |  |  |  |  |  |  |  |  |
| Okanogan | 2015 | Fall | 19 | 9 | 28 | 0.857 | 0.97 | 0.637 | 5 | 33 |
|  | 2016 | Spring | 10 | 6 | 16 | 0.696 | 0.868 | 0.471 | 7 | 23 |
|  | 2016 | Fall | 28 | 4 | 32 | 0.706 | 0.849 | 0.525 | 14 | 46 |
|  | 2017 | Spring | 4 | 0 | 4 | 0.947 | 0.999 | 0.74 | 0 | 4 |
|  |  |  |  |  |  |  |  |  |  |  |
| Wenatchee | 2015 | Fall | 20 | 25 | 45 | 0.851 | 0.938 | 0.717 | 8 | 53 |
|  | 2016 | Spring | 8 | 4 | 12 | 0.9 | 0.997 | 0.555 | 1 | 13 |
|  | 2016 | Fall | 4 | 9 | 13 | 0.885 | 0.976 | 0.698 | 2 | 15 |
|  | 2017 | Spring | 6 | 4 | 10 | 0.909 | 0.998 | 0.587 | 1 | 11 |

*Supplement 4*. Frequency of final location for radio-tagged summer Steelhead observed falling back below Priest River Dam. Locations are split between fallbacks returning to the Snake River and tributaries, Middle Columbia River tributary and other fallback locations. Counts of fallback steelhead by rearing origins (H or N) and totals (T) are provided.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Region | River/Other | H | N | T | H | N | T | All |
| 2015 Run Fallbacks | | | 2016 Run Fallbacks | | |
| Middle Columbia | |  |  |  |  |  |  |  |
|  | John Day River | 0 | 2 | 2 | 1 | 0 | 1 | 3 |
|  | Umatilla River | 0 | 2 | 2 | 0 | 0 | 0 | 2 |
|  | Walla Walla River | 0 | 0 | 0 | 1 | 1 | 2 | 2 |
|  | Yakima River | 0 | 12 | 12 | 2 | 6 | 8 | 20 |
|  | Columbia River - Hanford Reach | 8 | 3 | 11 | 11 | 3 | 14 | 25 |
|  | Columbia River - McNary Dam | 0 | 0 | 0 | 1 | 0 | 1 | 1 |
|  | Columbia River - Priest Hatchery | 0 | 0 | 0 | 1 | 0 | 1 | 1 |
|  | Columbia River - Ringold Hatchery | 1 | 0 | 1 | 9 | 0 | 9 | 10 |
|  | *Total* | 9 | 19 | 28 | 26 | 10 | 36 | 64 |
| Snake River | |  |  |  |  |  |  |  |
|  | Asotin Creek | 0 | 1 | 1 | 0 | 0 | 0 | 1 |
|  | Joseph Creek | 0 | 1 | 1 | 1 | 0 | 1 | 2 |
|  | Salmon River | 4 | 2 | 6 | 3 | 0 | 3 | 9 |
|  | Grande Ronde River | 4 | 0 | 4 | 0 | 0 | 0 | 4 |
|  | Tucannon River | 1 | 1 | 2 | 3 | 0 | 3 | 5 |
|  | Snake River | 20 | 9 | 29 | 44 | 7 | 51 | 80 |
|  | *Total* | 29 | 14 | 43 | 51 | 7 | 58 | 101 |
|  |  |  |  |  |  |  |  |  |
| *Grand Total* | | 38 | 33 | 71 | 77 | 17 | 94 | 165 |

*Supplement 5.* The number and percent of steelhead detected entering a tributary before and after 1-January, 2016 (upper) 2017 (lower).

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Tributary | Entry Before 1-Jan 2016 | | | | | | Entry After 1-Jan 2016 | | | | | | Grand Total |
| Hatchery | | Natural | | Total | | Hatchery | | Natural | | Total | |
| Entiat | 1 | 25.0% | 6 | 42.9% | 7 | 38.9% | 3 | 75.0% | 8 | 57.1% | 11 | 61.1% | 18 |
| Methow | 65 | 84.4% | 23 | 85.2% | 88 | 84.6% | 12 | 15.6% | 4 | 14.8% | 16 | 15.4% | 104 |
| Okanogan | 25 | 62.5% | 9 | 64.3% | 34 | 63.0% | 15 | 37.5% | 5 | 35.7% | 20 | 37.0% | 54 |
| Wenatchee | 22 | 73.3% | 26 | 83.9% | 48 | 78.7% | 8 | 26.7% | 5 | 16.1% | 13 | 21.3% | 61 |
| Foster Ck. | 0 | 0.0% | 0 | 0.0% | 0 | 0.0% | 4 | 100.0% | 0 | 0.0% | 4 | 100.0% | 4 |
| Total | 113 | 72.9% | 64 | 74.4% | 177 | 73.4% | 42 | 27.1% | 22 | 25.6% | 64 | 26.6% | 241 |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Tributary | Entry Before 1-Jan 2017 | | | | | | Entry After 1-Jan 2017 | | | | | | Grand Total |
| Hatchery | | Natural | | Total | | Hatchery | | Natural | | Total | |
| Entiat | 1 | 20.0% | 3 | 20.0% | 4 | 20.0% | 4 | 80.0% | 12 | 80.0% | 16 | 80.0% | 20 |
| Methow | 93 | 79.5% | 22 | 84.6% | 115 | 80.4% | 24 | 20.5% | 4 | 15.4% | 28 | 19.6% | 143 |
| Okanogan | 37 | 82.2% | 5 | 83.3% | 42 | 82.4% | 8 | 17.8% | 1 | 16.7% | 9 | 17.6% | 51 |
| Wenatchee | 7 | 53.8% | 12 | 92.3% | 19 | 73.1% | 6 | 46.2% | 1 | 7.7% | 7 | 26.9% | 26 |
| Foster Ck. | 0 | 0.0% | 0 | 0.0% | 0 | 0.0% | 6 | 100.0% | 0 | 0.0% | 6 | 100.0% | 6 |
| Total | 138 | 74.2% | 42 | 70.0% | 180 | 73.2% | 48 | 25.8% | 18 | 30.0% | 66 | 26.8% | 246 |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Sum Total | 251 | 73.6% | 106 | 72.6% | 357 | 73.3% | 90 | 26.4% | 40 | 27.4% | 130 | 26.7% | 487 |