Technical Report 2015-15

OVERWINTERING DISTRIBUTION AND FALLBACK BEHAVIOR BY ADULT RADIO-TAGGED STEELHEAD IN THE FEDERAL COLUMBIA RIVER POWER SYSTEM, MIGRATION YEARS 2013-2014 AND 2014-2015

A Report for Study Code ADS-P-13-2

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Executive Summary

Our primary objectives in this two-year study were to: 1) estimate the percentages of adult summer steelhead (*Oncorhynchus mykiss*) that overwintered in the Federal Columbia River Power System (FCRPS); 2) summarize the spatial distribution of FCRPS-overwintering fish; 3) evaluate the timing, location, and routes of wintertime fallback events at FCRPS dams; 4) estimate overwintering steelhead survival to tributaries; and 5) summarize the downstream movements and FCRPS survival of post-spawn steelhead kelts.

We collected and radio-tagged 789 (2013) and 799 (2014) adult steelhead at Bonneville Dam and used radiotelemetry and PIT tags to monitor their behaviors and distribution. Each annual sample was split into two study groups: an early-run group that was collected from June through August, and a late-run group that was collected in September and October. The samples were weighted for late-run fish because they were more likely to overwinter in the FCRPS and because the late-run, 'B-group' steelhead are a management and conservation priority. A substantial portion of the run in late summer could not be sampled due to high temperatures in both years. Tissue samples were collected for all steelhead, and parentage-based tagging (PBT) and genetic stock identification (GSI) was used to help assign fish to tributary populations.

Overwintering estimates – The probability of FCRPS overwintering substantially increased as steelhead migration date at Bonneville Dam increased. We estimated that 5.8-7.7% of early-run steelhead and 21.8-27.4% of the late-run steelhead at least partially overwintered in the lower Columbia and lower Snake River portions of the FCRPS. Overwintering estimates were higher at 8.7-12.2% for the early group and 29.9-37.8% for the late group after we censored fish that were reported as harvested and that were unaccounted for in the FCRPS (many were presumably harvested but not reported to us). The genetic data indicated that majorities of the late-run samples were from the Clearwater River basin whereas early-run groups originated from a more geographically diverse set of locations. Population-specific overwintering estimates generally aligned with the aggregated estimates for early- and late-run groups.

FCRPS distribution – In both years, some steelhead at least partially overwintered in each of the monitored FCRPS reservoirs. The highest proportions of overwintering steelhead were in the Lower Granite reservoir in December, January, and February, reflecting the preponderance of Snake River – and especially Clearwater River – steelhead in the radio-tagged samples. Other FCRPS areas with relatively high overwintering abundance included The Little Goose to Lower Granite reach and the McNary reservoir reach. There was a general upstream movement by steelhead through the winter period and some overwintering steelhead exited the FCRPS into tributaries in each month. Large majorities of the overwintering fish in each reach had entered tributaries by 1 April. Population-specific distributions indicated that Clearwater River steelhead overwintered primarily in Snake River reservoirs while steelhead with genetic assignments to other tributaries (including other Snake River tributaries) were distributed more equally among FCRPS reaches, with relatively more fish in the lower Columbia River reaches.

Winter fallback – Fallback by pre-spawn steelhead occurred at almost all dams during the late fall and winter study period. Events were most frequent at The Dalles and McNary dams, and there was a nadir in fallback activity in January at most dams in both study years. There was

considerable evidence that some winter fallback events were associated with natal tributary overshoot behavior, particularly by John Day River steelhead at McNary Dam but also by Tucannon River fish (Little Goose and Lower Granite dams), Walla Walla River fish (Ice Harbor and Lower Monumental dams), and fish from Bonneville reservoir tributaries (The Dalles and John Day dams).

Winter and early spring radiotelemetry monitoring was used at The Dalles, John Day, and McNary dams to help infer fallback routes. Many steelhead were detected in dam forebays for days to weeks before falling back. We were most confident assigning routes to fallback events that were through ice and trash sluiceways at The Dalles (8.3-21.1% of events) and McNary (4.8-12.0%) dams and through the adult fish ladders (4.2-9.5%). Several events were likely via the navigation locks (2.1-5.7%, all dams) which were monitored in 2014 only. The percentage of fallback events that appeared to occur via spillways and powerhouses was highly variable. Estimates through spillways ranged from ~5-71% (all dams, both years) and were ~9-21% via powerhouses (all dams, 2014 only); there was more uncertainty regarding use of powerhouse routes in 2013 when the navigation locks were unmonitored. In 2014-2015, a temporary spillway weir (TSW) was operated experimentally at McNary Dam to test whether surface flow would facilitate steelhead fallback. Results were inconclusive from the small number of radio-tagged steelhead that were exposed to the experiment, in part because the operational experiment could not be fully implemented.

Survival and distribution – Steelhead that at least partially overwintered in the FCRPS survived to tributaries at high rates (91-92%) in the two study years. These survival rates were far higher than for the steelhead that did not overwinter in the FCRPS (56-58% survival), though rates are not directly comparable because overwintering was conditional on surviving the summer and fall fisheries. Several factors likely contributed to the higher survival for the overwintering group, including that they had survived the summer and fall fisheries and that many overwintered in an FCRPS reservoir close to their natal tributary confluence.

The final pre-spawn detection locations (i.e., the most upstream locations) for all radio-tagged steelhead included ~26% at Columbia River main stem sites, ~10% at lower Snake River dams or reservoirs, ~14-16% in Columbia River tributaries other than the Snake River, and ~49-50% in Snake River tributaries (we note again that late-run Snake River stocks were oversampled and a portion of the run was not sampled due to high temperatures). The most frequent final location in both 2013 and 2014 was the Clearwater River (29-30% of total samples). The Salmon River had 8-9%, the Snake River upstream from the Lower Granite reservoir had 7-11%, and the John Day and Deschutes rivers had 4-5% each. The final pre-spawn locations for the FCRPS overwintering groups were much different from the total samples: ~81% were in Snake River tributaries (primarily Clearwater River), ~10-11% were in Columbia River tributaries, and just ~2-6% and 3-6% were in the main stem Columbia and main stem Snake rivers, respectively.

Kelts – Of the steelhead that entered tributaries and were not reported as harvested in tributary fisheries or recaptured at hatcheries, 17% (2013-2014) and 25% (2014-2015) had springtime behaviors that indicated that they initiated downstream kelt migrations and entered the FCRPS. Most (77-87%) of the identified kelts were from Snake River tributaries. A total of

511 kelt dam fallback events were detected or inferred from downstream monitoring, with 38% of the events at lower Columbia River dams and 62% at Snake River dams. The earliest fallback events by post-spawn kelts were in late March or early April at most dams and events were most frequent from mid-April to mid-May.

Migration mortality for kelts appeared to be quite high, especially for populations with long migration distances. Survival of Snake River kelts was 35-44% from Lower Granite Dam to Ice Harbor Dam and was 12-26% from Lower Granite Dam to Bonneville Dam. Among the Snake River kelt groups, survival to Bonneville Dam was 17% (fin-clipped), 22% (unclipped), 26% (male), 19% (female), 10% (Clearwater River), 33% (Salmon River), and 30% (other Snake River tributaries). There were 18 kelts from the John Day River and their survival to Bonneville Dam was 83%; kelt sample sizes were ≤3 for other Columbia River tributaries.

Introduction

Returning adult Columbia and Snake River summer steelhead (*Oncorhynchus mykiss*) often have complex, multi-stage homing migrations (Busby et al. 1996; Robards and Quinn 2002; Keefer et al. 2008a, 2009) followed by rapid post-spawn 'kelt' migrations (Evans et al. 2004; Wertheimer and Evans 2005; Colotelo et al. 2013). Their extended freshwater migration and residency periods, as well as use of habitats outside of their direct migration route, create a variety of concerns for management of the Federal Columbia River Power System (FCRPS), including a potential need for surface-flow (i.e., non-turbine) downstream passage routes at dams during traditional non-spill periods. This is especially a concern in winter and spring when many adult steelhead are present in the FCRPS and can be overwintering (holding by pre-spawn fish), migrating upstream (post-overwintering pre-spawn fish), or moving downstream (post-spawn kelts and pre-spawn adults that 'overshoot' their natal tributary).

In previous radiotelemetry studies, approximately ~12% (*annual range* = 7-20%) of the summer steelhead that passed Bonneville Dam and subsequently reached spawning tributaries overwintered in the FCRPS (Keefer et al. 2008a). Most overwintering steelhead slow or stop migration in response to falling water temperatures in late fall and then resume upstream movement in February-April as rivers warm and discharge increases, and in response to maturation cues. Because the onset of overwintering behavior appears to be primarily temperature related, steelhead with later migration timing, including the two-ocean 'B-group' fish that originate in the Clearwater and Salmon Rivers (Brannon et al. 2004), are more likely to overwinter than early summer migrants. For example, more than 40% of the steelhead released in October in a previous six-year summary overwintered in the FCRPS (Keefer et al. 2008a).

Some overwintering fish move upstream and downstream past dams, and the downstream 'fallback' behavior is a management concern because of associated enumeration errors, and injury and mortality risks (Boggs et al. 2004; Keefer et al. 2005; Wertheimer 2007). Risks appear to be elevated for both pre- and post-spawn (i.e., kelt) steelhead in winter and spring when surface-flow routes are limited at the dams and fish are more likely to pass through turbines as a consequence (Colotelo et al. 2013; Khan et al. 2013; Rayamajhi et al. 2013). Winter- and spring-time use of surface-flow passage routes by pre-spawn steelhead and kelts has been evaluated at Bonneville, The Dalles, and McNary dams (Wertheimer 2007; Ham et al. 2012; Khan et al. 2013). Results from these tagging and hydroacoustic studies and from direct mortality and injury research using balloon-tagged adults indicate that provision of surface-flow fallback routes likely provides a survival benefit for adult steelhead relative to fallback through turbines. Notably, considerable uncertainty remains regarding the most effective locations and times to provide non-turbine passage routes.

This report summarizes results from two summer steelhead migration years (2013-2014 and 2014-2015). Adults were collected, genetically sampled, and double-tagged (radio and PIT tags) at Bonneville Dam and monitored as they moved through the Columbia and Snake rivers and entered spawning tributaries. Summaries of upstream migration, including reach survival, were reported in Keefer et al. (2015). Study objectives addressed in this report include:

1) estimate the proportion of radio-tagged steelhead that at least partially overwintered in the FCRPS;

2) summarize the geographic distribution of radio-tagged steelhead that overwintered in the FCRPS;

3) evaluate the timing, location, and routes of downstream movements (i.e., fallback) at FCRPS dams during the winter, with an emphasis on The Dalles, John Day, and McNary dams;

4) summarize migration distribution and survival of overwintering steelhead; and

5) summarize the downstream movements and survival of post-spawn kelts.

Methods

Steelhead collection and tagging at Bonneville Dam

We collected and intragastrically radio-tagged adult summer steelhead at the Adult Fish Facility (AFF), located adjacent to the Washington-shore ladder using protocols used in previous years (e.g., Keefer et al. 2008a). In contrast to previous radiotelemetry studies at Bonneville Dam, we did not tag steelhead strictly in proportion to the 2013 or 2014 runs. The target sample design called for 50% run-of-river tagging across the run (~400 steelhead), with supplemental tagging in September and October, also in proportion to the run (~400 steelhead). There were two reasons for the disproportionate sampling: (1) a portion of the sample was targeted at later-timed migrants to increase the proportion of overwintering fish in the sample for distribution and fallback evaluations (intentional); and (2) extended water temperature shutdowns of the AFF prevented the scheduled tagging in most of August and early September (unintentional), further skewing the sample towards late migrants beyond the intended design.

On the days when steelhead were tagged, fish were selected in the order that they entered the AFF trap. We did not select for any particular size class or group but we did select *against* fish that had PIT tags from juvenile projects (i.e., 'known-origin' fish were excluded) due to concerns about handling effects on research outcomes for other projects. Selection against known-origin fish meant that the samples were not fully representative of the steelhead runs at large.

Fish receiving a radio transmitter (3-volt, MCFT2-3A; Lotek Wireless Inc.) were anesthetized in a ~18 mL/L solution of eugenol (AQUI-S-20E, Aquatactics, Inc., Kirkland, WA). All were also tagged with a full duplex PIT-tag inserted to the abdominal cavity as a secondary tag that allowed identification of transmitter loss and provided additional detection data at sites not monitored with radio antennas. A small fin clip was collected for genetic analyses (see below) and fish trait data were collected (i.e., size, fin clips, injuries, etc.). After recovery from anesthesia, radio-tagged steelhead were transported by truck in oxygenated river water and released ~ 8 km downstream from Bonneville Dam from sites on both sides of the river.

Radiotelemetry and PIT-tag monitoring

We used an extensive array of fixed-site radio receivers at dams, in reservoirs, and in major tributaries to monitor tagged steelhead (Tables 1 and 2). Radio receivers with Yagi aerial

Table 1. Radiotelemetry monitoring sites in the Columbia River in 2013-2015. Some receivers monitored multiple areas of some dams (e.g., the forebay and a fishway) so there is slight inflation of receiver counts although the number of receivers and antenna types monitoring any area is accurate.

Site	Antenna type	# Receivers
Bonneville Dam Tailrace	Aerial	2
Bonneville Dam Fishways	Aerial	6
Bonneville Dam Fishways	Underwater	11
Bonneville Reservoir – Bridge of the Gods	Aerial	1
Bonneville Tributary – Wind River Mouth	Aerial	1
Bonneville Reservoir – Viento State Park	Aerial	1
Bonneville Reservoir – Cook-Underwood Rd	Aerial	1
Bonneville Tributary – Little White Salmon River Mouth	Aerial	1
Bonneville Tributary – White Salmon River	Aerial	2
Bonneville Tributary – Hood River Mouth	Aerial	1
Bonneville Reservoir – Chamberlain Lake Rest Area	Aerial	1
Bonneville Reservoir – Memaloose Rest Area State Park	Aerial	1
Bonneville Tributary – Klickitat River Mouth	Aerial	1
The Dalles Dam Tailrace[1]	Aerial	2-4
The Dalles Navigation Lock[1,4]	Aerial	2
The Dalles Dam Fishways	Underwater	8
The Dalles Ice and trash sluiceway[1]	Aerial	1
The Dalles Forebay[1]	Aerial	3
The Dalles Reservoir – Celilo Park	Aerial	1
The Dalles Reservoir – Wishram-Celilo	Aerial	1
The Dalles Tributary – Deschutes River Mouth	Aerial	1
The Dalles Tributary – Deschutes River Sherars Falls	Aerial	1
John Day Dam Tailrace[2]	Aerial	2-5
John Day Navigation Lock[2,4]	Aerial	1
John Day Navigation Lock[2,4]	Underwater	1
John Day Dam Fishways	Underwater	6
John Day Dam Juvenile Bypass[4]	Aerial	1
John Day Forebay[2]	Aerial	3
John Day Tributary – John Day River Mouth	Aerial	1
McNary Dam Tailrace[3]	Aerial	2-6
McNary Navigation Lock[4]	Aerial	1
McNary Navigation Lock[4]	Underwater	1
McNary Dam Fishways	Underwater	7
McNary Ice and trash sluiceway[3]	Underwater	1
McNary Forebay[3]	Aerial	3
Priest Rapids Dam Fishways	Underwater	2

[1] Overwintering monitoring sites installed 11 Dec (2013) and 29 Sep-1 Oct (2014)
[2] Overwintering monitoring sites installed 16 Dec (2013) and 13-14 Oct (2014)
[3] Overwintering monitoring sites installed 5 Dec (2013) and 15-28 Oct (2014)
[4] Sites added for winter 2014-2015

Table 2. Radiotelemetry monitoring sites in the Snake River in 2013-2015. Some receivers monitored multiple areas of some dams (e.g., the forebay and a fishway) so there some redundancy in receiver counts, however the number of receivers and antenna types monitoring any area is accurate.

Site	Antenna type	# Receivers
Ice Harbor Dam Tailrace	Aerial	2
Ice Harbor Dam Fishways *(1 receiver added in 2014)*	Underwater	7
Ice Harbor Dam Forebay[1]	Aerial	2
Lower Monumental Dam Tailrace	Aerial	2
Lower Monumental Dam Fishways	Underwater	6
Lower Monumental Forebay[2]	Aerial	2
Lower Monumental Tributary – Tucannon River	Aerial	1
Little Goose Dam Tailrace	Aerial	2
Little Goose Dam Fishways	Underwater	6
Little Goose Dam Forebay[3]	Aerials	2
Lower Granite Dam Tailrace	Aerial	2
Lower Granite Dam Fishways	Underwater	6
Lower Granite Dam Forebay[4]	Aerial	2
Lower Granite Tributary – Clearwater River near Potlatch Mill	Aerial	1
Lower Granite Tributary – Snake River upstream of Three Mile Island	Aerial	1

[1-4] Overwintering monitoring sites in 2014-2015 only, installed 27 Jan (Ice Harbor), 29 Jan (Lower Monumental), 4 Nov (Little Goose), and 5 Nov (Lower Granite)

antennas were used to monitor dam tailraces, reservoirs, and tributaries. At dams, most antennas were underwater coaxial cable antennas, though a few sites also had aerial Yagis, including forebay monitoring sites at The Dalles, John Day, and McNary dams that were installed in early December 2013 and in October 2014 to monitor forebay residency and fallback by overwintering steelhead. Similar antennas were installed to monitor winter behaviors at the lower Snake River dams, but in 2014-2015 only. Underwater antennas at dams were used to monitor fishway openings, collection channels, transition areas, ladders, ice and trash sluiceways (The Dalles and McNary only) and top-of-ladder exit areas. Fish detection efficiencies on these arrays have historically been >95% at most sites, and antenna redundancy in most fishways increased dam-wide detection efficiency to near 100% for upstream migrants. Downstream migrants (i.e., pre- or post-spawn steelhead that fell back) passed fewer antennas and had considerably lower probability of detection.

We supplemented the radiotelemetry histories using PIT-tag detections inside dam fishways (Bonneville, The Dalles, McNary, Ice Harbor, Lower Monumental, Little Goose, Lower Granite, and upper Columbia River dams), in juvenile bypass systems, inside tributaries, and at fish collection facilities. The PIT detection data were downloaded from the Pacific States Marine Fisheries Commission PIT Tag Information System database (PTAGIS). PIT detections were also used to identify passage by steelhead that lost transmitters or that had transmitters that were not working. Both radio and PIT data were used to assess overwintering and pre-spawn distribution among tributaries, and to assign final detection locations.

Genetic stock assignment

Genetic samples were processed by the Hagerman Genetics Laboratory (Hagerman, ID) and were analyzed using two methods: parentage-based tagging (PBT) and genetic stock identification (GSI). Both methods were used on all fish (i.e., fin-clipped and unclipped). The PBT assignments rely on genetic data from adult broodstock collected at Snake River hatcheries starting in ~2008. The PBT method used single nucleotide polymorphisms (SNPs) to identify the parents of many hatchery-origin steelhead that were collected and radio-tagged in this study (for a full description of genetic procedures see Steele et al. (2013) and Matala et al. (2014)). The accuracy level for these assignments approaches 100% and is geographically and temporally precise (i.e., brood year and location can be identified). A total of 11 hatchery steelhead populations (Table 3) were represented in the radio-tagged samples.

Table 3. Genetic stock identification (GSI) reporting groups (top) and parentage-based tagging (PBT) hatcheries that were identified in genetic analyses of radio-tagged steelhead in 2013-2014. The PBT assignments were for hatchery steelhead only (primarily from the Snake River basin) whereas hatchery and wild fish had GSI assignments.

GSI Reporting Group	**Reporting Group Description**
02_LOWCOL	Lower Columbia
03_SKAMAN	Skamania
04_WILLAM	Willamette River
06_KLICKR	Klickitat River
07_MGILCS	*Mixed: Deschutes, mid-Columbia, lower Snake, lower Clearwater, Grande Ronde, Imnaha, lower Salmon*
08_YAKIMA	Yakima River
09_UPPCOL	Upper Columbia River: *mix of Wenatchee, Methow, Entiat, Okanogan*
10_SFCLWR	South Fork Clearwater River
11_UPCLWR	Upper Clearwater River
12_SFSALM	South Fork Salmon River
13_MFSALM	Middle Fork Salmon River
14_UPSALM	Upper Salmon River

PBT Source Hatchery	**River Basin**	**GSI Reporting Group**
Idaho Power/IDFG, Pahsimeroi F.H.	Upper Salmon River	14_UPSALM
Idaho Power/IDFG, Oxbow F.H.	Upper Snake River	14_UPSALM
LSRCP/IDFG Sawtooth (EFSR)	Upper Salmon River	14_UPSALM
LSRCP/IDFG Sawtooth (IDFG & SBT[1])	Upper Salmon River	14_UPSALM
LSRCP/IDFG Sawtooth (USB/Squaw)	Salmon River[2]	10_SFCLWR
LSRCP/IDFG/USFWS Dworshak/C.W.	Clearwater River	10_SFCLWR
LSRCP/ODFT - Little Sheep Cr. F.H.	Imnaha River	07_MGILCS
LSRCP/ODFW-Wallowa F.H.	Grand Ronde River	07_MGILCS
LSRCP/WDFW-L.F. (G.R. Cottonwood)	Grand Ronde River	07_MGILCS
LSRCP/WDFW-L.F. (Touchet)	Walla Walla River	07_MGILCS
LSRCP/WDFW-Lyons Ferry	Snake River	07_MGILCS

[1] Shoshone-Bannock tribal outplant
[2] Original source: Clearwater River

The GSI method used an extensive baseline of genetic data (microsatellites) to assign individual fish to stock-based reporting groups (e.g., Seeb et al. 2007; Anderson et al. 2008; Hess et al. 2011, 2015). In contrast to PBT, GSI was used for both hatchery- and wild-origin fish but differentiation among genetically-similar stocks was somewhat limited and geographic precision was therefore reduced relative to PBT. GSI assignments were probability-based (i.e., a fish could have a 67% probability of belonging to reporting group A and a 33% probability of belonging to reporting group B); we summarized the GSI data using the highest probability for each fish, including PBT information when available (a 'compiled' estimate). A total of 12 steelhead GSI reporting groups (Table 3) were represented in the radio-tagged samples. An additional genetic marker was used to identify steelhead sex with a reported assignment accuracy of >95% (J. Hess, *personal communication*).

Results

Sample summary

We collected and radio-tagged 789 steelhead at Bonneville Dam in 2013, including an 'early' group of 169 fish and a 'late' group of 620 fish (Figure 1). The early group was 0.2% of the 70,431 steelhead counted at the dam during the 22 June to 3 August tagging interval (i.e., there were ~417 untagged steelhead for each radio-tagged steelhead). The late group was 3.4% of 18,110 steelhead counted at the dam from 22 September to 15 October (~29 untagged for each tagged steelhead). The total sample of 789 was ~0.3% of the 226,464 steelhead counted during the full tagging period (22 June through 15 October; ~287 untagged for each tagged steelhead).

The sample was 799 steelhead in 2014, including an 'early' group of 208 fish and a 'late' group of 591 fish (Figure 1). The early group was 0.3% of the 77,061 steelhead counted at the dam during the 10 June to 27 July tagging interval (~370 untagged steelhead for each radio-tagged steelhead). The late group was 0.6% of 92,049 steelhead counted at the dam from 5 September to 15 October (~176 untagged for each tagged steelhead). The total sample of 799 was ~0.3% of the 312,523 steelhead counted during the full tagging period (10 June through 15 October; ~391 untagged for each tagged steelhead).

The size distributions and composition of fin-clipped (known hatchery origin) and unclipped (presumed wild origin) steelhead differed among tagging groups. In the early-run samples, 35-39% of the radio-tagged steelhead had fin clips and 61-65% was unclipped. The late-run samples were 68-80% fin-clipped and 20-32% unclipped. Steelhead in the early samples were smaller on average (annual *means* = 59.4-66.2 cm, SD = 6.1-6.4 cm) than those in the late-run samples (*means* = 71.0-75.4 cm, SD = 9.4-10.5 cm), consistent with a higher proportion of 2- and 3-ocean B-group steelhead later in the runs.

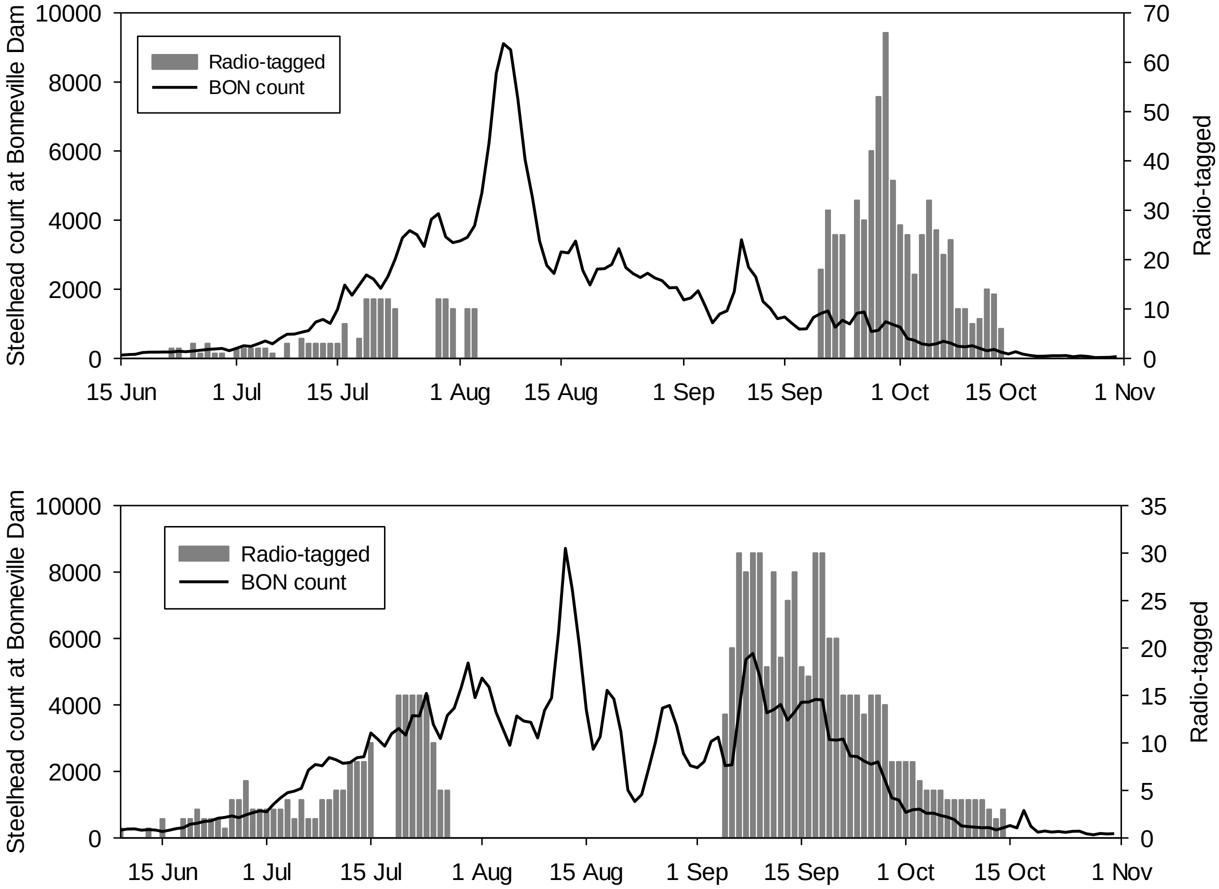

Figure 1. The numbers of adult steelhead that were radio-tagged and released downstream from Bonneville Dam in 2013 (top, *n* = 789) and 2014 (bottom, *n* = 799) in relation to the daily counts of steelhead at the dam.

Genetic assignments

PBT assignments to hatcheries were possible for 64% (2013) and 59% (2014) of the radio-tagged steelhead (Table 4). Proportionately fewer early-run fish (23-27%) than late-run fish (74-90%) were assigned to a PBT hatchery in each year. The most abundant origin group – by far – was from the Dworshak / Clearwater hatchery group, at 64% of the PBT-assigned steelhead in 2013 and 66% of the 2014 sample. Other PBT hatcheries with relatively high numbers of radio-tagged fish included the Pahsimeroi (12-15% of the samples), Sawtooth (IDFG & SBT) (10-14%), Lyons Ferry (6-7%), and Wallowa (4-9%) groups (Table 4). We note that 13.5% (2013) and 19.0% (2014) of the PBT-assigned steelhead did not have fin clips despite hatchery parents.

The PBT-assigned fish could be assigned a likely ocean age (i.e., 1, 2 or 3 years in the Pacific) because their parental brood year was known. Both the early- and late-run steelhead samples included a mix of 1- and 2-ocean individuals, and the late-run group also included a few 3-ocean fish (Figure 2).

Table 4. Parentage-based tagging (PBT) genetic assignments for all steelhead radio-tagged at Bonneville Dam in 2013-2014, with the percentages that were in early- and late-timed groups, that likely had 1-, 2-, and 3-ocean life history types, and that were male or female.

			Timing (%)		Age (%)			Sex (%)	
PBT Hatchery	Year	*n*	Early	Late	1	2	3	M	F
Pahsimeroi	2013	58	24	76	69	31	-	53	47
	2014	47	26	74	77	23	-	64	36
Oxbow	2013	9	11	89	78	22	-	44	56
	2014	24	10	14	4	96	-	21[1]	75[1]
Sawtooth (EFSR)	2013	6	-	100	100	-	-	83	17
	2014	6	-	100	-	100	-	50	50
Sawtooth (IDFG & SBT)	2013	45	9	91	69	31	-	40	60
	2014	32	16	84	66	34	-	53[1]	44[1]
Sawtooth (USB/Squaw)	2013	2	-	100	-	100	-	50	50
	2014	6	-	100	-	100	-	-	100
Dworshak/C.W.	2013	323	-	100	27	71	2	58	42
	2014	310	-	100	1	98	1	33[1]	67[1]
Little Sheep Cr. F.H.	2013	2	-	100	100	-	-	100	-
	2014	3	-	100	67	33	-	67	33
Wallowa F.H.	2013	29	7	93	72	28	-	52	48
	2014	13	8	92	38	62	-	62	38
Lyons Ferry (Cottonwood)	2013	9	22	78	78	22	-	44	56
	2014	6	50	50	-	100	-	-	
Lyons Ferry (Touchet)	2013	-	-	-	-	-	-	-	-
	2014	1	100	-	-	100	-	100	-
Lyons Ferry	2013	20	100	-	85	15	-	35	65
	2014	21	67	33	57	43	-	33	67
Total assigned	2013	503	9	91	43	55	2	55	45
	2014	469	10	90	17	83	<1	37	63

[1] 1 fish not assigned

Table 5. Genetic stock identification (GSI) assignments for all steelhead radio-tagged at Bonneville Dam in 2013-2014, with the percentages of early- and late-timed fish and males and females.

GSI group	*n*	Early	Late	M	F	*n*	Early	Late	M	F
02_LOWCOL	-	-	-	-	-	1	-	100	100	-
03_SKAMAN	7	100	-	29	71	14	93	7	21	79
04_WILLAM	1	-	100	100	-	1	100	-	-	100
06_KLICKR	1	100	1	-	100	13	77	-	38	62
07_MGILCS	198	55	45	45	55	189	64	36	28	72
08_YAKIMA	4	75	25	50	50	4	75	25	-	100
09_UPPCOL	15	73	27	27	73	15	53	47	27	73
10_SFCLWR	351	-	100	57	43	352	-	100	33	67
11_UPCLWR	17	-	100	65	35	31	3	97	26	74
12_SFSALM	4	-	100	50	50	9	11	89	44	56
13_MFSALM	2	50	50	-	100	7	-	100	29	71
14_UPSALM	157	23	77	51	49	143	31	69	50	48
Total assigned	757	22	78	52	48	779	26	74	34	65
Total -tagged	*789*	*21*	*79*			*799*	*26*	*74*		

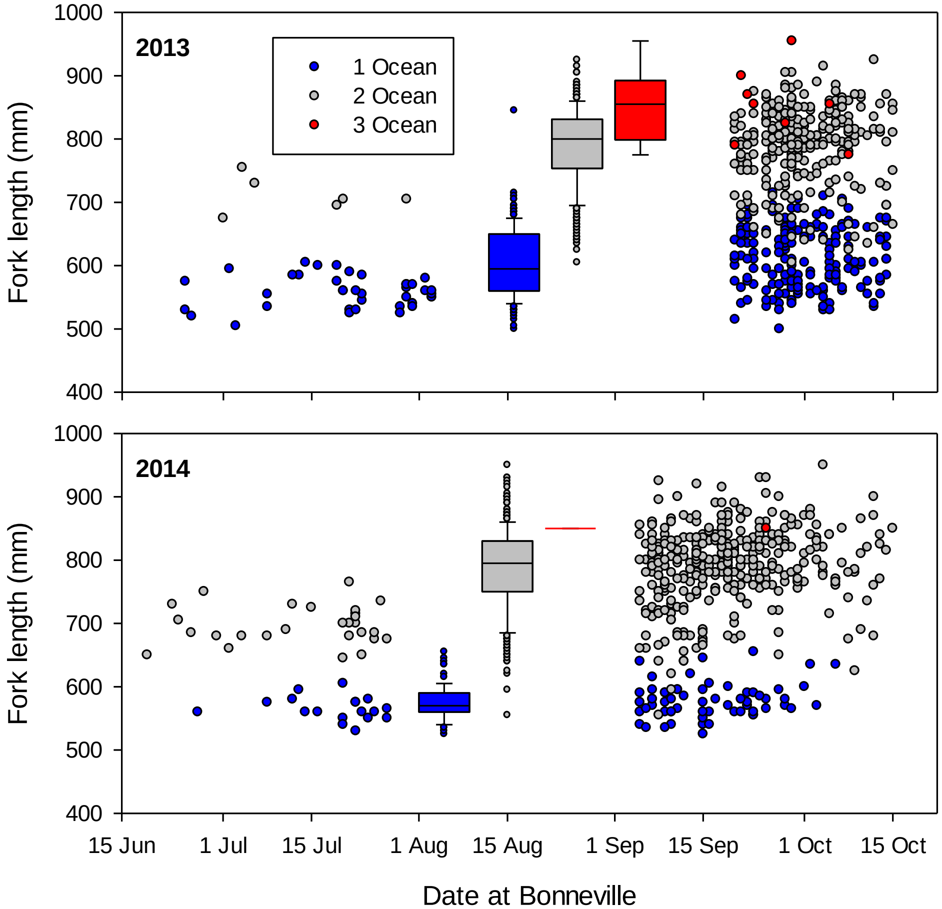

Figure 2. Relationship between the dates that steelhead were collected and radio-tagged at Bonneville Dam and their fork length and ocean age, as determined from parentage-based tagging genetic assignments to specific brood years. Open circles are for individual fish and box plots show fork length distributions (median, quartile, 10th and 90th percentiles, and all outliers) by presumed ocean age. Note 1 possible misclassified 2-ocean fish in 2013.

Probability-based GSI assignments were possible for 96% (2013) and 99% (2014) of the radio-tagged samples (Table 5). The largest numbers of fish were assigned to the SFCLWR reporting group, which exclusively included late-run fish and made up 45-46% of the radio-tagged samples in both years. The next-most abundant reporting groups were the mixed-stock MGILCS (24-26%) and UPSALM (18-21%) groups. Smaller numbers were assigned to the UPCLWR (2-4%) and UPPCOL (2%) groups, and generally <1% of the fish assigned to other GSI reporting groups in each year.

Upstream migration timing

In both years, the sample weighting towards late migrants at Bonneville Dam was evident in the timing distributions of radio-tagged fish as they passed upstream dams (examples in Figures

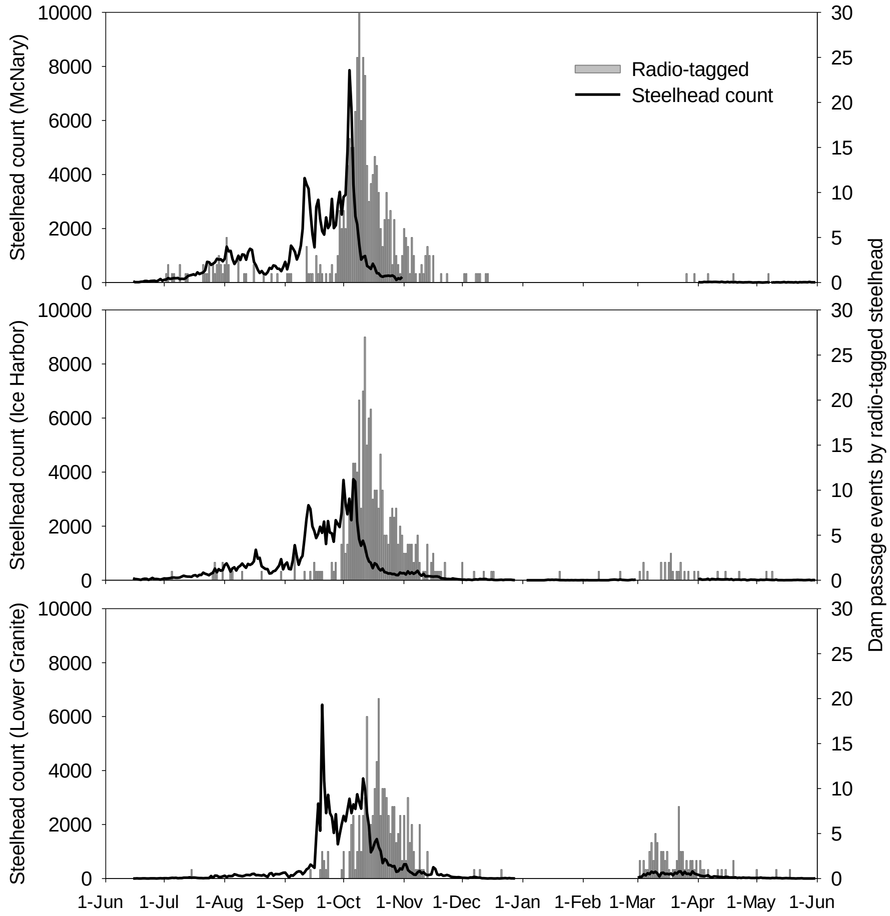

Figure 3. Migration timing of radio-tagged steelhead relative to the run-at-large in 2013-2014. Bars show numbers of radio-tagged steelhead detected on radiotelemetry antennas as they passed McNary (top), Ice Harbor (middle), and Lower Granite (bottom) dams and lines show steelhead counts at the dams. Some radio-tagged fish were not detected passing, including ~8% at McNary Dam, 4% at Ice Harbor Dam, and 14% at Lower Granite Dam, mostly due to antenna outages or lost transmitters. These fish are not shown.

3 and 4). Majorities of the tagged fish passed after the peak steelhead migration dates at all lower Columbia and lower Snake River dams. Upstream dam passage events were detected in all months at most dams, though proportionately more springtime passage events were at the Snake River dams.

Overwintering estimates: all fish

Determining whether steelhead overwintered in the FCRPS is a somewhat subjective task because the behavior varies among fish and among locations. We followed the criteria in Keefer et al. (2008a), where overwintering was assigned to: (1) steelhead that moved upstream past at

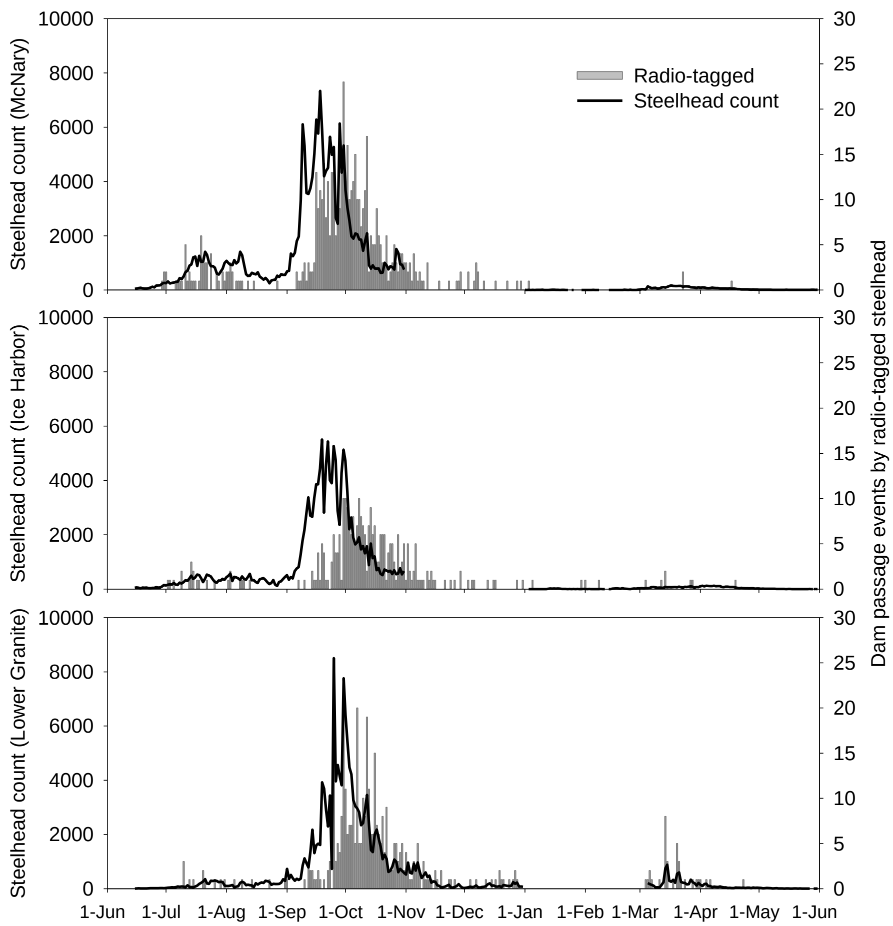

Figure 4. Migration timing of radio-tagged steelhead relative to the run-at-large in 2014-2015. Bars show numbers of radio-tagged steelhead detected on radiotelemetry antennas as they passed McNary (top), Ice Harbor (middle), and Lower Granite (bottom) dams and lines show steelhead counts at the dams. Some radio-tagged fish were not detected passing, including ~3% at McNary Dam, 35% at Ice Harbor Dam, and 8% at Lower Granite Dam, mostly due to antenna outages or lost transmitters. These fish are not shown.

least one FCRPS dam on or after 1 January (based on radio or PIT detections); and (2) steelhead that first exited a FCRPS reservoir into a monitored spawning tributary after 1 January.

We estimated overwintering percentages in two ways (Table 6). The first was the number of overwintering steelhead divided by the number that were radio-tagged and released. This was likely an underestimate of the behavior because overwintering required a longer period of exposure to fisheries by definition and some fish (i.e., those that were harvested) never had the opportunity to overwinter, but it is a useful estimate for extrapolating overwintering estimates from steelhead counts at Bonneville Dam. The second estimate excluded *a priori* the steelhead that were voluntarily reported harvested in the FCRPS in the reward program and those that were ‘unaccounted for’ in the FCRPS. The latter group included all fish that were last detected in

Table 6. Numbers of radio-tagged steelhead released in 2013 and 2014 that met the 1 January criteria for at least partial overwintering in the FCRPS and the estimated overwintering percentages for the full sample and the 'early' and 'late' release groups. The two sets of estimates included all of the released steelhead (likely underestimates) and the subset that excluded those that were reported harvested or were unaccounted for in the FCRPS.

		All released fish included			Harvested, unaccounted fish excluded		
Release group	Year	*n*	Overwinter	%	*n*	Overwinter	%
All fish[1]	2013	789	183	23.2%	511	168	32.9%
All fish[1]	2014	799	141	17.6%	521	129	24.8%
Early group	2013	169	13	7.7%	98	12	12.2%
Early group	2014	208	12	5.8%	126	11	8.7%
Late group	2013	620	170	27.4%	413	156	37.8%
Late group	2014	591	129	21.8%	395	118	29.9%

[1] non-representative sample: skewed toward late-run steelhead

reservoirs or at FCRPS dams with no evidence of tributary entry. Censoring these fish could produce an unbiased estimate of the true probability of overwintering if the probability of harvest before 1 January was similar for overwintering and non-overwintering groups. Actual fates of unaccounted for fish likely included a mix of harvest that was not reported to us, prespawn mortality, undetected tributary entry, and perhaps some main stem spawners. The censoring of steelhead that were reported as harvested and those that were unaccounted for in the main stem slightly reduced the number of overwintering fish (i.e., the number in the numerator) and more substantially reduced the number in the denominator and consequently likely produced slight overestimates of overwintering percentage, though we cannot be certain. In combination, the two overwintering estimation methods likely capture the true FCRPS overwintering percentages.

In 2013, we estimated that 173 steelhead retained radio transmitters and at least partially overwintered in the FCRPS and another 10 fish likely overwintered but lost or had non-functioning transmitters (based on PIT tag detections). Estimated 2013 overwintering percentages were 7.7% (13 of 169 released) for the early release group and 27.4% (170 of 620 released) for the late release group with all fish included (Table 6). The predicted probability of overwintering was strongly, positively associated with 2013 release date below Bonneville Dam (logistic regression $\chi^2 = 30.3$, $P < 0.001$; Figure 5). When steelhead that were reported harvested and those that were unaccounted for in the FCRPS were censored, the 2013 overwintering estimates were 12.2% (early) and 37.8% (late). The release date effect was similar for the reduced sample as for the full sample (logistic regression, $\chi^2 = 24.7$, $P < 0.001$).

In 2014, we estimated that 133 steelhead retained transmitters and at least partially overwintered in the FCRPS and another 8 likely overwintered based solely on PIT tag detections (Table 6). Overwintering percentages were 5.8% for the early release group and 21.8% for the late release group. The predicted probability of overwintering was strongly positively associated with release date (logistic regression $\chi^2 = 40.9$, $P < 0.001$). Modeled probabilities in 2014 were remarkably similar to those in 2013 (Figure 5). Note that the 2014 model included more dates in June and early September than the 2013 model due to tagging differences. After excluding the censored groups, the 2014 overwintering estimates were 8.7% (early) and 29.9% (late) (Table 6).

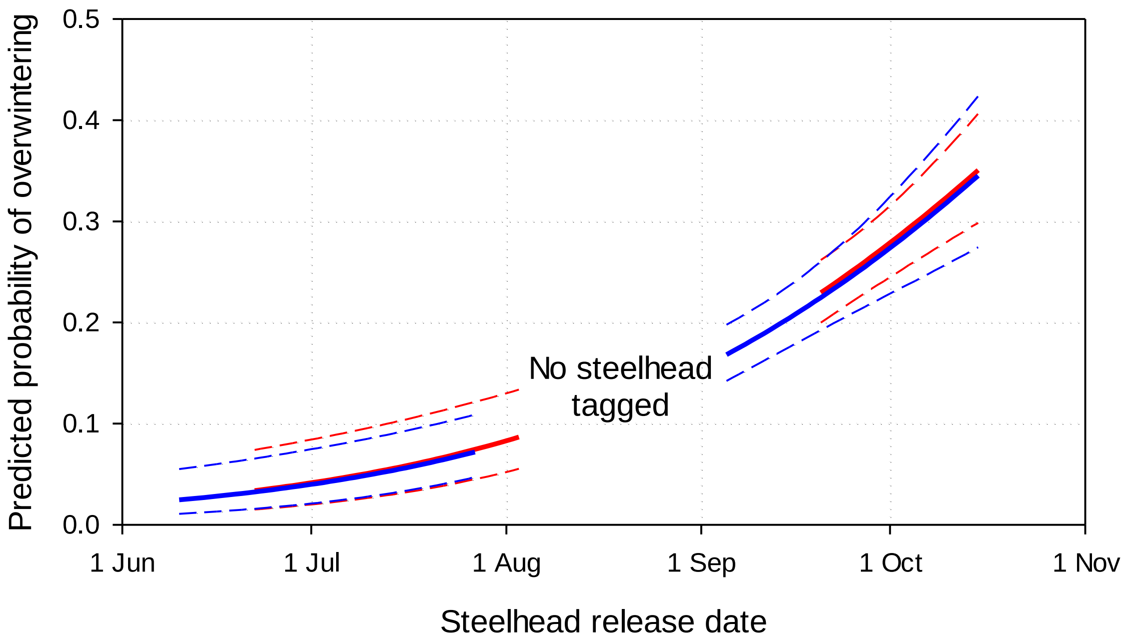

Figure 5. Predicted probabilities (and 95% confidence intervals) that radio-tagged steelhead would overwinter in the FCRPS in relation to release date at Bonneville Dam in 2013 (red) and 2014 (blue). Probabilities were generated using a logistic regression model with all tagged steelhead included.

Table 7. Numbers of radio-tagged steelhead in the early and late 2013 and 2014 samples that were assigned to PBT hatcheries and that met the 1 January criteria for at least partial overwintering in the FCRPS. The estimated overwintering percentages (in parentheses) were calculated for all released fish and are likely underestimates.

	2013 Early		2013 Late		2014 Early		2014 Late	
PBT Hatchery	PBT (*n*)	Overwinter *n* (%)	PBT (*n*)	Overwinter *n* (%)	PBT (*n*)	Overwinter *n* (%)	PBT (*n*)	Overwinter *n* (%)
Pahsimeroi	14	-	44	10 (22.7)	12	-	35	3 (8.6)
Oxbow	1	-	8	2 (25.0)	10	-	14	1 (7.1)
Sawtooth (EFSR)			6	2 (33.3)			6	1 (16.7)
Sawtooth (IDFG & SBT)	4	-	41	3 (7.3)	5	-	27	-
Sawtooth (USB/Squaw)			2	-			6	-
Dworshak/C.W.			323	108 (33.4)			310	96 (31.0)
Little Sheep Cr. F.H.			2	-			3	-
Wallowa F.H.	2	-	27	5 (18.5)	1	-	12	-
Lyons Ferry (Cottonwood)	2	1 (50.0)	7	1 (14.3)	3	-	3	-
Lyons Ferry (Touchet)					1	-		
Lyons Ferry	20	-			14	-	7	-
Total assigned	43	1 (2.3)	460	131 (28.5)	46	0 (0.0)	423	101 (23.9)
Total radio-tagged[1]	169	13 (7.7)	620	170 (27.4)	208	12 (5.8)	592	131 (22.1)
Unassigned[1]	*126*	*12 (9.6)*	*160*	*39 (24.4)*	*162*	*12 (7.4)*	*169*	*30 (17.8)*

Overwintering estimates: PBT- and GSI-assigned populations

Most PBT-assigned steelhead from the early run hatchery groups had no FCRPS overwintering fish, though sample sizes in the early run were small (*n* = 1-20 fish per PBT hatchery group) (Table 7). Aggregated across hatcheries (*n* = 43-46 early-run steelhead per year) the FCRPS overwintering estimates were 2.3% (2013) and 0.0% (2014) with all PBT-assigned fish released as the denominators.

Overwintering estimates for the aggregate late-run, PBT-assigned steelhead were 28.5% (2013) and 23.9% (2014) with all released fish as the denominator (Table 7). Sample sizes were relatively larger for the late-run than the early-run groups and in 2013 four late-run hatchery groups had ≥10 steelhead. Overwintering estimates were 33.4% (Dworshak, *n* =323), 22.7% (Pahsimeroi, *n* = 44), 18.5% (Wallowa, *n* = 27), and 7.3% (Sawtooth IDFG & SBT, *n* = 41). Five late-run groups had ≥10 steelhead in 2014 and overwintering estimates were 31.0% (Dworshak, *n* =310), 8.6% (Pahsimeroi, *n* = 35), and 7.1% (Oxbow, *n* = 14); no FCRPS overwintering fish were identified in the 2014 Sawtooth IDFG & SBT (*n* = 27) or Wallowa (*n* = 12) groups (Table 7).

Large majorities of the early- and late-run samples were assigned to GSI reporting groups and FCRPS overwintering estimates for the GSI aggregates were therefore very similar to the estimates for all radio-tagged steelhead released (Table 8). Three GSI reporting groups had ≥10

Table 8. Numbers of radio-tagged steelhead in the early and late 2013 and 2014 samples that were assigned to GSI reporting groups and that met the 1 January criteria for at least partial overwintering in the FCRPS. The estimated overwintering percentages (in parentheses) were calculated for all released fish and are likely underestimates.

	2013 Early		2013 Late		2014 Early		2014 Late	
GSI group	GSI (*n*)	Overwinter *n* (%)	GSI (*n*)	Overwinter *n* (%)	GSI (*n*)	Overwinter *n* (%)	GSI (*n*)	Overwinter *n* (%)
02_LOWCOL							1	-
03_SKAMAN	7	-			13	-	1	-
04_WILLAM			1	-	1	-		
06_KLICKR	1	-			10	-	3	-
07_MGILCS	106	12 (11.3)	92	19 (20.6)	121	11 (9.1)	68	7 (10.3)
08_YAKIMA	3	-	1	-	3	-	1	-
09_UPPCOL	11	-	4	-	8	-	7	-
10_SFCLWR			351	116 (33.0)			352	103 (29.3)
11_UPCLWR			17	7 (41.2)	1	-	30	10 (33.3)
12_SFSALM			4	1 (25.0)	1	-	8	1 (12.5)
13_MFSALM	1	-	1	-			7	-
14_UPSALM	36	1 (2.8)	121	18 (14.9)	45	1 (2.2)	98	5 (5.1)
Total assigned	165	13 (7.9)	592	161 (27.2)	203	12 (5.9)	576	126 (21.9)
Total tagged	169	13 (7.7)	620	170 (27.4)	208	12 (5.8)	592	131 (22.1)
Unassigned	*4*		*28*	*9 (32.1)*	*5*		*16*	*5 (31.2)*

steelhead in the early run in each year. Overwintering estimates were 9.1-11.3% for the mixed-origin MGILCS group (*n* = 106-121) and 2.2-2.8% for the UPSALM group (*n* = 36-45); no other early-run reporting groups had FCRPS overwintering fish. In the late run, four reporting groups had ≥10 steelhead in both years. Overwintering estimates were 10.3-20.6% for the MGILCS group (*n* = 68-92), 29.3-33.0% for the SFCLWR group (*n* = 351-352), 33.3-41.2% for the UPCLWR group (*n* = 17-30), and 5.1-14.9% for the UPSALM group (*n* = 98-121) (Table 8).

Overwintering locations: all fish

We used the radiotelemetry and PIT detections to estimate where overwintering steelhead were located on the first of each month from December through April (Tables 9 and 10, Figure 6). In both years, the highest proportions of FCRPS overwintering steelhead were in the Lower Granite reservoir reach, with 31-34% (2013 sample) and 45-53% (2014) of all overwintering steelhead located there on 1 December, 1 January, and 1 February. On 1 March, the highest proportions were in the Little Goose to Lower Granite Reach (29-36%) and on 1 April the highest proportions were in the Little Goose-Lower Granite reach in 2013 (22%) and the Lower Monumental-Little Goose reach in 2014 (30%) (Tables 9 and 10). The overwintering concentration in the Little Goose and Lower Granite reservoirs reflects the abundance of Clearwater River steelhead in the samples.

In each month, some overwintering fish exited the FCRPS into tributaries (Figure 6). The largest movement into tributaries was in March, presumably in response to environmental (i.e., river warming, increased discharge and increased day length) and reproductive cues. In both years there were changes in the relative abundance of overwintering steelhead among reaches from month to month, as fish moved upstream and downstream in the main stem Columbia and Snake rivers and exited the FCRPS into tributaries (Tables 9 and 10). In general, there was net upstream movement through the winter study period. Lastly, some steelhead that eventually returned to Snake River sites partially overwintered in the Deschutes and John Day rivers prior to upstream movement in spring, a 'temporary straying' behavior that was consistent with results in previous radiotelemetry studies.

Overwintering locations: PBT- and GSI-assigned populations

In the two study years, the FCRPS overwintering fish included 92-100 steelhead with PBT assignments to the Dworshak/Clearwater hatchery group (Tables 11 and 12); other assignment groups had sample sizes <= 10. As with the full samples, the Dworshak steelhead were concentrated in the Lower Granite reservoir (42-62%) and in the Little Goose-Lower Granite reach (14-18%) on 1 January. From one to nine (1-9%) of the overwintering Dworshak fish were located in each of the other dam-to-dam reaches on this date, and some fish were located in the Deschutes and John Day rivers as well. In contrast with the Dworshak samples, steelhead with PBT assignments to other Snake River hatcheries (Pahsimeroi, Sawtooth, Oxbow, Wallowa, Cottonwood) were distributed more equally among reaches, with proportionately more fish in the lower Columbia River reaches. However, samples sizes for these hatcheries were relatively small, with 2-10 steelhead per PBT hatchery group in 2013 and only 1-2 per group in 2014 (Tables 11 and 12).

The overwintering locations for the GSI reporting groups paralleled those for the PBT samples (Tables 13 and 14). On 1 January, steelhead from the Clearwater River reporting groups (SFCLWR and UPCLWR) were concentrated in the Lower Granite reservoir (41-62%) and Little Goose-Lower Granite reach (14-19%), with another 1-9% in each of the reaches further downstream. By comparison, overwintering fish from the Salmon River reporting groups (SFSALM and UPSALM) were distributed more evenly among reaches, with less concentration in the Little Goose and Lower Granite reservoirs. The mixed-origin MGILCS overwintering fish were also distributed across multiple FCRPS reaches, and the highest percentages on 1 January were 29-39% in the McNary reservoir reach. Similar percentages of the overwintering MGILCS group were in the combined lower Snake River reaches in both study years (35-36%) (Tables 13 and 14).

Table 9. Number (percent) of overwintering steelhead by river reach on the first of each month from December 2013 to April 2014. Fish that lost transmitters or had non-functioning transmitters were excluded because their locations were less clear.

	Date				
Overwintering site	1-Dec	1-Jan	1-Feb	1-Mar	1-Apr
n	173	168	152	118	23
Below Bonneville	7 (4.0)	8 (4.8)	6 (3.9)	4 (3.4)	3 (13.0)
Bonneville-The Dalles	4 (2.3)	6 (3.6)	4 (2.6)	2 (1.7)	3 (13.0)
The Dalles-John Day	12 (6.9)	11 (6.5)	11 (7.2)	12 (10.2)	-
Deschutes River	11 (6.4)	4 (2.4)	3 (2.0)	-	-
John Day-McNary	6 (3.5)	6 (3.6)	4 (2.6)	9 (7.6)	2 (8.7)
John Day River	5 (2.9)	7 (4.2)	8 (5.3)	3 (2.5)	-
McNary pool	21 (12.1)	18 (10.7)	16 (10.5)	16 (13.6)	2 (8.7)
>Priest Rapids	2 (1.2)	2 (1.2)	2 (1.3)	-	2 (8.7)
Ice Harbor-Lower Monumental	12 (6.9)	12 (7.1)	11 (7.2)	13 (11.0)	-
Lower Monumental-Little Goose	4 (2.3)	7 (4.2)	6 (3.9)	6 (5.1)	3 (13.0)
Little-Goose-Lower Granite	30 (17.3)	31 (18.5)	34 (22.4)	34 (28.8)	5 (21.7)
Lower Granite pool	59 (34.1)	56 (33.3)	47 (30.9)	19 (16.1)	3 (13.0)

Table 10. Number (percent) of overwintering steelhead by river reach on the first of each month from December 2014 to April 2015. Fish that lost transmitters or had non-functioning transmitters were excluded because their locations were less clear.

	Date				
Overwintering site	1-Dec	1-Jan	1-Feb	1-Mar	1-Apr
n	133	133	106	56	10
Below Bonneville	-	-	-	-	-
Bonneville-The Dalles	2 (1.5)	3 (2.3)	2 (1.9)	2 (3.6)	1 (10.0)
The Dalles-John Day	10 (7.5)	5 (3.8)	5 (4.7)	2 (3.6)	1 (10.0)
Deschutes River	4 (3.0)	-	-	1 (1.8)	-
John Day-McNary	3 (2.3)	8 (6.0)	5 (4.7)	5 (8.9)	-
John Day River	4 (3.0)	1 (0.8)	1 (0.9)	-	-
McNary pool	9 (6.8)	12 (9.0)	9 (8.5)	5 (8.9)	-
>Priest Rapids	1 (0.8)	1 (0.8)	1 (0.9)	1 (1.8)	1 (10.0)
Ice Harbor-Lower Monumental	11 (8.3)	12 (9.0)	15 (14.2)	7 (12.5)	1 (10.0)
Lower Monumental-Little Goose	5 (3.8)	4 (3.0)	4 (3.8)	8 (14.3)	3 (30.0)
Little-Goose-Lower Granite	22 (16.5)	16 (12.0)	16 (15.1)	20 (35.7)	1 (10.0)
Lower Granite pool	62 (46.6)	71 (53.4)	48 (45.3)	5 (8.9)	2 (20.0)

Table 11. Number (percent) of overwintering PBT-assigned steelhead by river reach on 1 January 2014 (collected and radio-tagged in 2013). Fish that lost transmitters or had non-functioning transmitters were excluded because their locations were less clear.

	Location on 1 January				
Overwintering site	Dworshak	Pahsimeroi	Sawtooth[1]	Oxbow/Wallowa	Cottonwood
n	100	10	5	6	2
Below Bonneville		3 (30.0)	1 (20.0)	2 (33.3)	
Bonneville-The Dalles	4 (4.0)	1 (10.0)	1 (20.0)		
The Dalles-John Day	9 (9.0)				
Deschutes River	3 (3.0)	1 (10.0)		1 (16.7)	
John Day-McNary	3 (3.0)		1 (20.0)		
John Day River	3 (3.0)				
McNary pool	5 (5.0)	1 (10.0)	1 (20.0)	1 (16.7)	1 (50.0)
>Priest Rapids				1 (16.7)	
Ice Harbor-Lower Monumental	7 (7.0)	1 (10.0)			
Lower Monumental-Little Goose	6 (6.0)	1 (10.0)			
Little-Goose-Lower Granite	18 (18.0)	2 (20.0)	1 (20.0)	1 (16.7)	
Lower Granite pool	42 (42.0)				1 (50.0)

[1] all Sawtooth PBT groups (see Table 3)

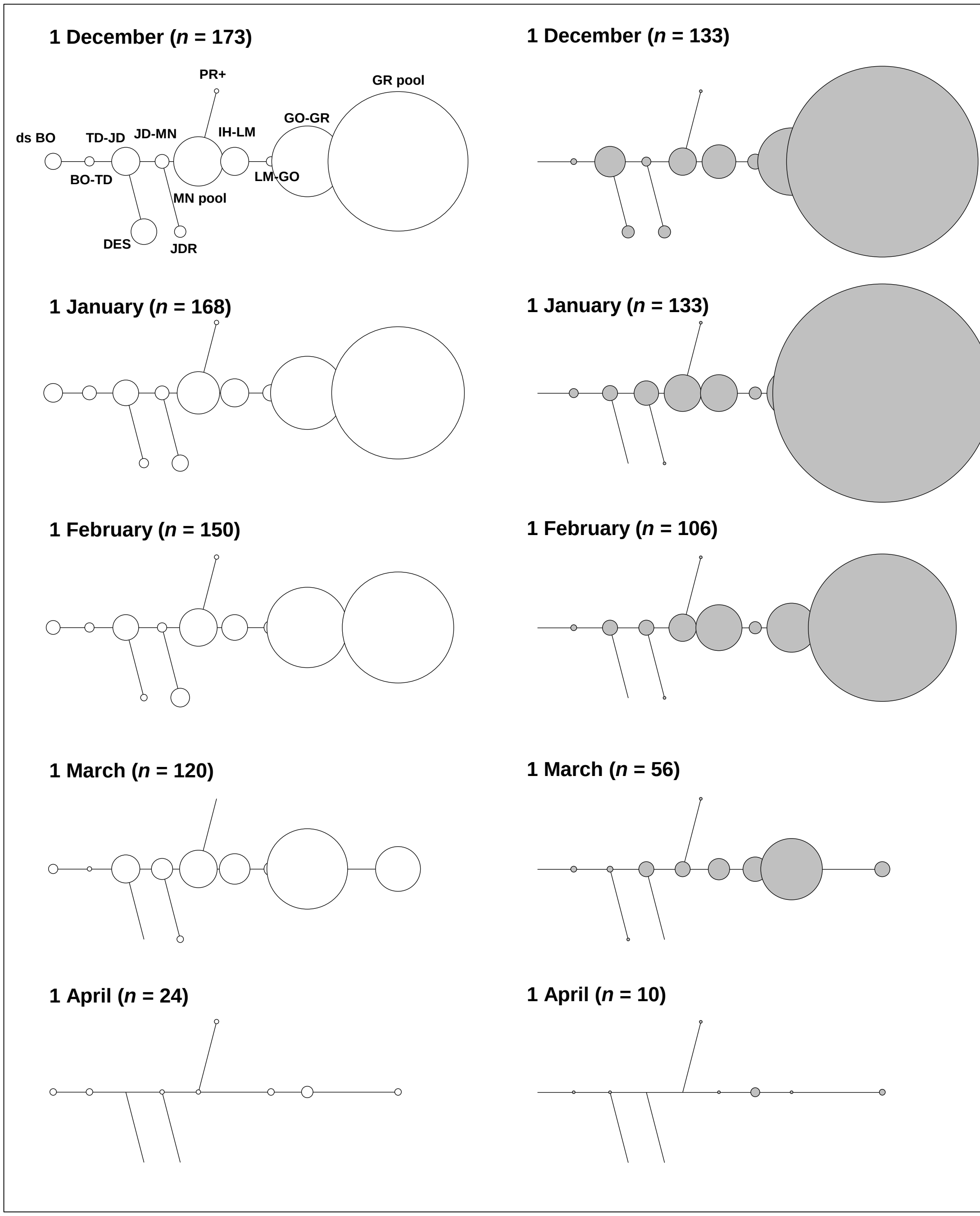

Figure 6. Estimated locations where overwintering radio-tagged steelhead were in the FCRPS on the first of each month from December 2013 to April 2014 (left) and from December 2014 to April 2015 (right). Fish in the Deschutes and John Day rivers eventually migrated to other tributaries and so were included here. Circle size is scaled relative to the overwintering fish with radio functioning transmitters (*n* = 173 in 2013 and *n* = 133 in 2014).

Table 12. Number (percent) of overwintering PBT-assigned steelhead by river reach on 1 January 2015 (collected and radio-tagged in 2014). Fish that lost transmitters or had non-functioning transmitters were excluded because their locations were less clear.

	Location on 1 January			
Overwintering site	Dworshak	Pahsimeroi	Sawtooth-EFSR	Oxbow
n	92	2	1	1
Below Bonneville				
Bonneville-The Dalles	2 (2.2)	1 (50.0)		
The Dalles-John Day	2 (2.2			
Deschutes River				
John Day-McNary	4 (4.3)			
John Day River				
McNary pool	6 (6.5)			
>Priest Rapids		1 (50.0)		
Ice Harbor-Lower Monumental	7 (7.6)		1 (100)	
Lower Monumental-Little Goose	1 (1.1)			1 (100)
Little-Goose-Lower Granite	13 (14.1)			
Lower Granite pool	57 (62.0)			

Table 13. Number (percent) of overwintering GSI-assigned steelhead by river reach on 1 January 2014 (collected and radio-tagged in 2013). Fish that lost transmitters or had non-functioning transmitters were excluded because their locations were less clear.

	Location on 1 January				
Overwintering site	MGILCS	SFCLWR	UPCLWR	SFSALM	UPSALM
n	28	107	6	1	17
Below Bonneville	2 (7.1)				5 (29.4)
Bonneville-The Dalles		4 (3.7)			2 (11.8)
The Dalles-John Day	1 (3.6)	10 (9.3)			
Deschutes River		3 (2.8)			2 (11.8)
John Day-McNary		4 (3.7)			1 (5.9)
John Day River	2 (7.1)	4 (3.7)			1 (5.9)
McNary pool	11 (39.3)	5 (4.7)	1 (16.7)		1 (5.9)
>Priest Rapids	2 (7.1)				
Ice Harbor-Lower Monumental	1 (3.6)	7 (6.5)	1 (16.7)		1 (5.9)
Lower Monumental-Little Goose		6 (5.6)			1 (5.9)
Little-Goose-Lower Granite	4 (14.3)	20 (18.7)	2 (33.3)	1 (100)	3 (17.6)
Lower Granite pool	5 (17.9)	44 (41.1)	2 (33.3)		

Table 14. Number (percent) of overwintering GSI-assigned steelhead by river reach on 1 January 2015 (collected and radio-tagged in 2014). Fish that lost transmitters or had non-functioning transmitters were excluded because their locations were less clear.

	Location on 1 January				
Overwintering site	MGILCS	SFCLWR	UPCLWR	SFSALM	UPSALM
n	17	98	8	-	5
Below Bonneville					
Bonneville-The Dalles	1 (5.9)	2 (2.0)			
The Dalles-John Day	2 (11.8)	2 (2.0)			1 (20.0)
Deschutes River					
John Day-McNary	2 (11.8)	4 (4.1)			2 (40.0)
John Day River		1 (1.0)			
McNary pool	5 (29.4)	6 (6.1)	1 (12.5)		
>Priest Rapids	1 (5.9)				
Ice Harbor-Lower Monumental	3 (17.6)	7 (7.1)	1 (12.5)		1 (20.0)
Lower Monumental-Little Goose	1 (5.9)	1 (1.0)	1 (12.5)		1 (20.0)
Little-Goose-Lower Granite		14 (14.3)			
Lower Granite pool	2 (11.8)	61 (62.2)	5 (62.5)		

Final distribution of radio-tagged steelhead: all fish

Excluding post-spawn kelt movements, about 36% (282 of 789 released in 2013; 289 of 799 released in 2014) of radio-tagged steelhead were last recorded in the main stem Columbia or Snake FCRPS (Table 3). Of these ‘main stem’ fish, 51 in 2013 (6.5% of 789) and 102 in 2014 (12.8% of 799) were self-reported as harvested in recreational or tribal fisheries in the transmitter reward program. Another 210 (26.6%) of the 2013 sample and 216 (27.0%) of the 2014 sample was last detected in a reservoir or at a dam in the Columbia River downstream from Priest Rapids Dam or in the Snake River downstream from the Clearwater River / Snake River confluence. This group had unknown fate (i.e., was ‘unaccounted for’). A portion of the unaccounted for steelhead was presumed harvested (with no transmitter returns); others were presumed mortalities or entered tributaries undetected. The few remaining fish in the main stem group either had apparent lost transmitters or were last detected upstream from Priest Rapids Dam where monitoring was limited to PIT antennas.

Steelhead were last recorded in a variety of Columbia River tributaries (n = 123, 15.6% of 789 released in 2013; n = 108, 13.5% of 799 released in 2014) and in the Snake River and its tributaries (n = 384, 48.7% in 2013 and n = 402, 50.3% in 2014; Table 15). The most abundant single tributary group in both 2013 and 2014 was in the Clearwater River (n = 233 and 234, respectively; 29-30%). The Salmon River had 60-69 (8-9%) fish and the Snake River upstream from the Lower Granite reservoir had 58-86 (7-11%). Many steelhead last detected in the Snake River upstream from Lower Granite reservoir presumably overwintered in the Hells Canyon reach prior to dying, being harvested, or entering unmonitored tributaries in spring. The large proportion of the sample in the Snake River basin was not surprising given the relative oversampling of late migrant steelhead at Bonneville Dam. The largest tributary groups outside the Snake River basin were last detected in the John Day (n = 36-41, ~5%) and Deschutes (n = 28-33, ~4%) rivers.

Final distribution of radio-tagged steelhead: all overwintering fish

The final pre-kelt detection (i.e., most upstream) locations for the FCRPS-overwintering steelhead were much different from the final locations of the total radio-tagged samples (compare Tables 15 and 16). A much smaller percentage of the overwintering fish were last detected in the main stem Columbia River (2.1-5.5%) compared with the full samples (~26% each year). This was driven, in part, by the fact that the overwintering group survived the summer and fall fisheries; it also reflected the Snake River origin and late migration timing of a majority of the overwintering group. Proportionately fewer overwintering fish were also last detected in the impounded main stem Snake River (3.3-6.4%) compared with the full samples (~10% each year).

As noted previously, a majority of the overwintering steelhead eventually entered the Clearwater River, and in total ~81% of the overwintering sample in both study years entered Snake River tributaries or the Snake River upstream from Lower Granite reservoir (Table 16). For comparison, 49-50% of the full samples were last recorded at Snake River tributaries or above Lower Granite reservoir (Table 15). The percentage of FCRPS-overwintering steelhead last detected in other Columbia River tributaries (10-11%) was slightly lower than the percentages for the full samples (14-16%).

In 2013, survival to tributaries (including the Snake River upstream from Lower Granite reservoir) was 91.3% for 183 FCRPS overwintering steelhead and was 56.1% for 606 steelhead that did not overwinter (Pearson's $\chi^2 = 75.6$, $P < 0.0001$), though this difference is confounded by the requirement of adults to survive to 1 Jan to be classified as overwintering, i.e., to have survived the summer and fall fishery. The pattern was very similar in 2014, when survival to tributaries was 91.5% for 141 overwintering steelhead and 57.9% for 658 non-overwintering steelhead ($\chi^2 = 56.7$, $P < 0.0001$). Results did not substantively change when all steelhead that passed Priest Rapids Dam were treated as successful (i.e., reached a tributary).

Table 15. Last pre-spawn detection sites for steelhead radio-tagged at Bonneville Dam in 2013 and 2014. Sites determined from radiotelemetry antennas, PIT antennas at dams and in tributaries, and self-reported transmitter returns from fisheries, hatcheries and traps. Post-spawn kelt detections were excluded from this summary.

	2013		2014			2013		2014	
Last detection site	*n*	%	*n*	%	Last detection site	*n*	%	*n*	%
Columbia River main stem	**204**	**25.9%**	**209**	**26.2%**	**Snake River main stem**	**78**	**9.9%**	**80**	**10.0%**
Downstream Bonneville	[1]13	1.6%	17	2.1%	Downstream Ice Harbor	-	0.0%	6	0.8%
Bonneville Dam	41	5.2%	47	5.9%	Ice Harbor Dam	15	1.9%	6	0.8%
Bonneville pool	66	8.4%	63	7.9%	Ice Harbor pool	7	0.9%	6	0.8%
The Dalles Dam	19	2.4%	5	0.6%	Lower Monumental Dam	6	0.8%	1	0.1%
The Dalles pool	6	0.8%	16	2.0%	Lower Monumental pool	2	0.3%	11	1.4%
John Day Dam	18	2.3%	18	2.3%	Little Goose Dam	14	1.8%	1	0.1%
John Day pool	5	0.6%	16	2.0%	Little Goose pool	2	0.3%	4	0.5%
McNary Dam	19	2.4%	10	1.3%	Lower Granite Dam	27	3.4%	37	4.6%
McNary pool	9	1.1%	7	0.9%	Lower Granite pool	5	0.6%	8	1.0%
Priest Rapids Dam	1	0.1%	1	0.1%					
Rock Island Dam	-	0.0%	2	0.3%					
Rocky Reach Dam	1	0.1%	1	0.1%					
Wells Dam	6	0.8%	6	0.8%					
Columbia River tributaries	**123**	**15.6%**	**108**	**13.5%**	**Snake River tributaries**	**384**	**48.7%**	**402**	**50.3%**
Wind River	-	0.0%	5	0.6%	Lyons Ferry	1	0.1%	-	0.0%
Little White Salmon River	5	0.6%	-	0.5%	Tucannon River	5	0.6%	3	0.4%
White Salmon River	1	0.1%	4	0.1%	Clearwater River	233	29.5%	234	29.3%
Hood River	1	0.1%	1	0.1%	Snake > Lower Granite pool	58	7.4%	86	10.8%
Klickitat River	9	1.1%	12	1.5%	Grande Ronde River	13	1.6%	16	2.0%
Fifteen Mile Creek	-	0.0%	1	0.1%	Salmon River	69	8.7%	60	7.5%
Deschutes River	33	4.2%	28	3.5%	Imnaha River	5	0.6%	3	0.4%
John Day River	41	5.2%	36	4.5%					
Rock Creek	3	0.4%	-	0.0%					
Umatilla River	4	0.5%	3	0.4%					
Walla Walla River	5	0.6%	2	0.3%					
Yakima River	4	0.5%	4	0.5%					
Priest Rapids Hatchery	1	0.1%	-	0.0%					
Wenatchee River	6	0.8%	3	0.4%					
Entiat River	3	0.4%	2	0.3%					
Methow River	4	0.5%	7	0.9%					
Okanogan River	3	0.4%	-	0.0%					

[1] 12 near release site, 1 in Willamette River

Table 16. Last pre-spawn detection sites for steelhead radio-tagged at Bonneville Dam in 2013 (n = 183) and 2014 (n = 141) that at least partially overwintered in the FCRPS. Sites determined from radiotelemetry antennas, PIT antennas at dams and in tributaries, and self-reported transmitter returns from fisheries, hatcheries and traps. Post-spawn kelt detections were excluded from this summary.

	2013		2014			2013		2014	
Last detection site	*n*	%	*n*	%	Last detection site	*n*	%	*n*	%
Columbia River main stem	**10**	**5.5%**	**3**	**2.1%**	**Snake River main stem**	**6**	**3.3%**	**9**	**6.4%**
Downstream Bonneville			1	0.7%	Downstream Ice Harbor				
Bonneville Dam	5	2.7%			Ice Harbor Dam			2	1.4%
Bonneville pool	2	1.1%			Ice Harbor pool				
The Dalles Dam	2	1.1%			Lower Monumental Dam				
The Dalles pool					Lower Monumental pool				
John Day Dam					Little Goose Dam				
John Day pool			1	0.7%	Little Goose pool				
McNary Dam			1	0.7%	Lower Granite Dam	6	3.3%	7	5.0%
McNary pool					Lower Granite pool				
Priest Rapids Dam									
Rock Island Dam									
Rocky Reach Dam									
Wells Dam	1	0.5%							
Columbia River tributaries	**19**	**10.4%**	**15**	**10.6%**	**Snake River tributaries**	**148**	**80.9%**	**114**	**80.9%**
Wind River					Lyons Ferry				
Little White Salmon River					Tucannon River	3	1.6%	1	0.7%
White Salmon River	1	0.5%			Clearwater River	122	66.7%	103	73.0%
Hood River	1	0.5%			Snake > Lower Granite pool	16	8.7%	7	5.0%
Klickitat River	1	0.5%	2		Grande Ronde River	2	1.1%	1	0.7%
Fifteen Mile Creek					Salmon River	4	2.2%	1	0.7%
Deschutes River			1	0.7%	Imnaha River	1	0.5%	1	0.7%
John Day River	16	8.7%	11	7.8%					
Rock Creek									
Umatilla River									
Walla Walla River									
Yakima River									
Priest Rapids Hatchery									
Wenatchee River									
Entiat River									
Methow River			1	0.7%					
Okanogan River									

[1] 12 near release site, 1 in Willamette River

Fallback at dams: all fish

In 2013, a total of 525 steelhead fallback events were identified at lower Columbia and lower Snake River dams. Of the 525 events, 506 had sufficient information to infer fallback dates (Figure 7). This was likely a minimum estimate because we think it was more likely for a steelhead to fall back with no corroborating radio or PIT-tag detections than it was to mistakenly assign a fallback event to a fish that did not fall back. The total with dates included 271 events (54% of 506) that were considered pre-spawn fallbacks, 194 (38%) that were considered post-spawn (i.e., kelt) fallbacks based on steelhead detection at appropriate times inside tributaries, and 41 (8%) that were uncertain with regards to steelhead reproductive status. In 2014, 509 fallback events were identified and 446 had sufficient date information, including 189 (42% of 446) pre-spawn events, 251 (56%), kelt events, and 6 (1%) events by fish with uncertain reproductive status (Figure 8). The events with insufficient data to infer date were primarily for post-spawn kelts.

Pre-spawn fallback percentages for early-run steelhead were quite variable across dams and – to a lesser degree – between years (Table 17). Fallback percentages were relatively low at Bonneville (1.8-4.0%) and The Dalles (2.3-4.9%) dams, were intermediate at John Day Dam

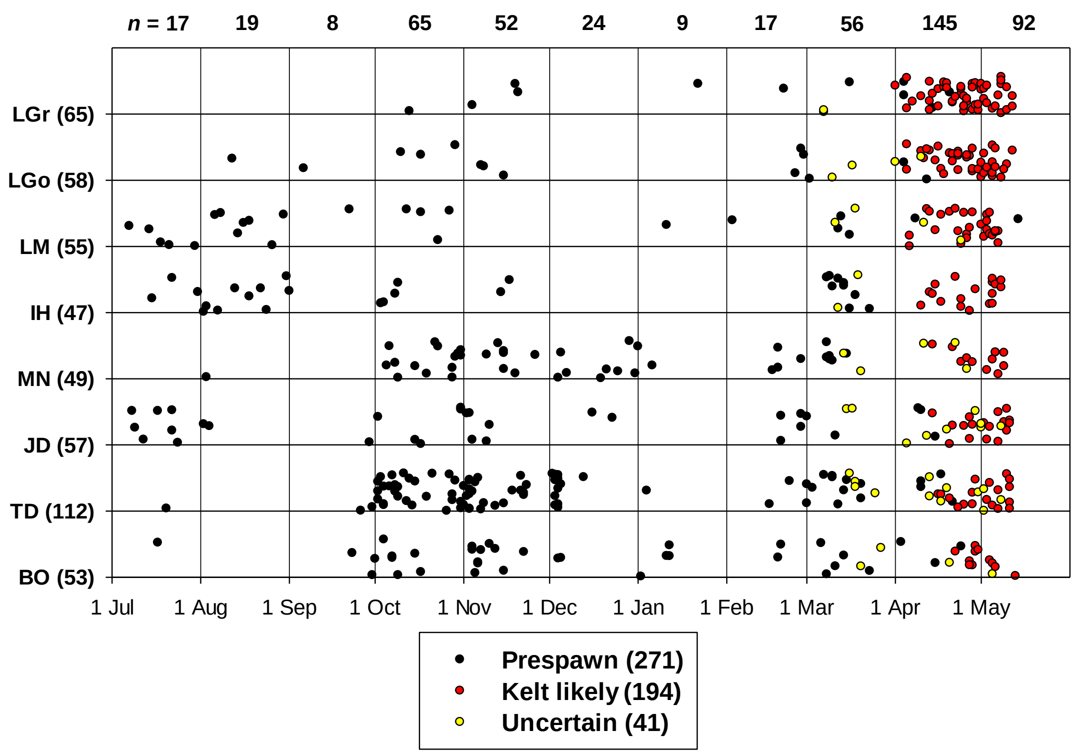

Figure 7. Estimated dates that steelhead radio-tagged in 2013 fell back at dams in 2013-2014. Fallback events are color coded to represent likely steelhead reproductive status at the time of fallback and slightly jittered on the y-axis for each dam to better display the data. Two fallback events at Priest Rapids Dam and two Bonneville events in June and those with insufficient timing information are not shown.

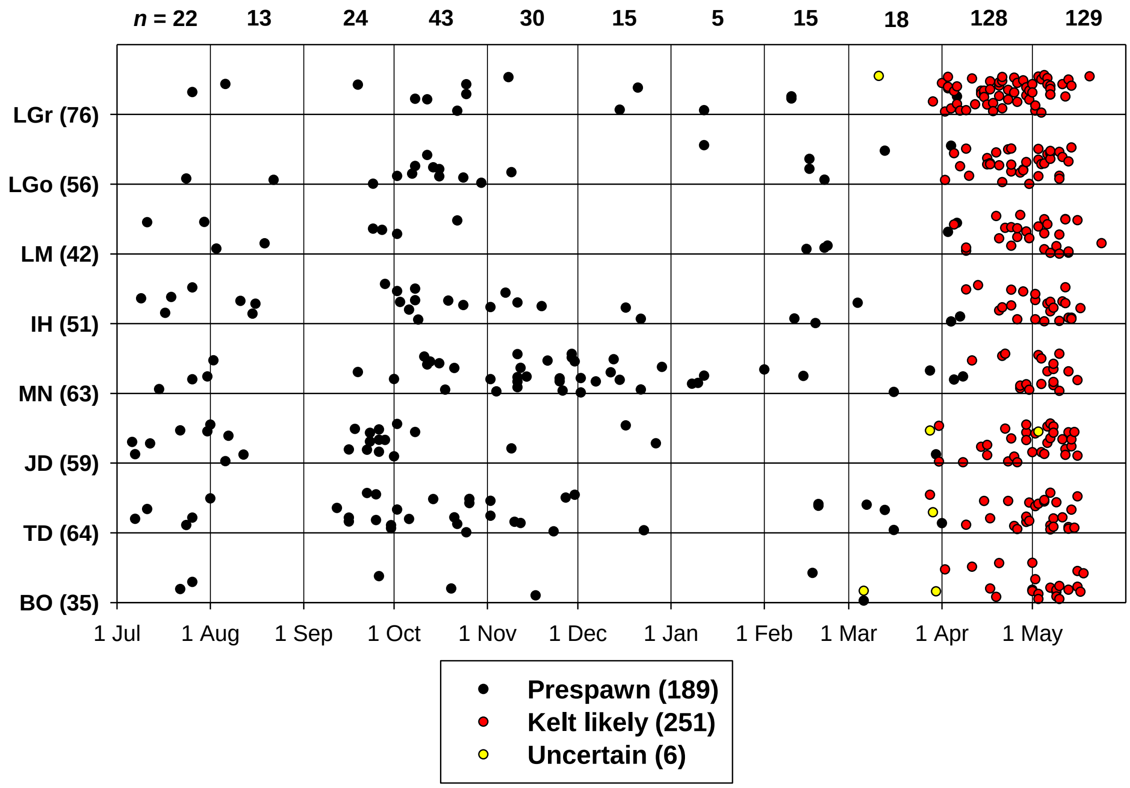

Figure 8. Estimated dates that steelhead radio-tagged in 2014 fell back at dams in 2014-2015. Fallback events are color coded to represent likely steelhead reproductive status at the time of fallback and randomly jittered on the y-axis for each dam to better display the data. Four Bonneville events in June and those with insufficient timing information are not shown.

(7.2-8.2%), at Lower Monumental Dam in 2014 (6.1%), and at Lower Granite Dam in 2013 (9.1%). Fallback percentages were highest at McNary (17.0-21.8%) and Little Goose (14.1-15.2%) dams, at Lower Monumental Dam in 2013 (27.3%), and at Lower Granite Dam in 2014 (14.5%). There was considerable evidence that the high fallback percentage and rate at McNary Dam was associated with tributary overshoot behavior. Many steelhead that fell back at McNary Dam were subsequently detected in the John Day River, including 9 of 15 (60%) in 2013 and 19 of 24 (79%) in 2014; others were detected on PIT antennas in the Umatilla River (there was no radio antenna in the Umatilla River). Overshoot fallbacks by early- and late-run steelhead were also identified for some Tucannon River fish (Little Goose and Lower Granite dams) and Walla Walla fish (Ice Harbor and Lower Monumental dams). Similarly, some Klickitat, White Salmon, and Hood River steelhead had likely overshoot fallback events at The Dalles and John Day dams.

Pre-spawn fallback percentages for late-run steelhead were between 1.4% and 5.1% at all dams in both years with a single exception: 10.7% fell back at The Dalles Dam in 2013 (Table 17). Fallback rates were higher than percentages by up to 4.3%, with the largest difference at The Dalles Dam in 2013 where 13 steelhead fell back twice and five fell back three times. There was evidence of tributary overshoot fallback by late-run steelhead at McNary Dam, with 7 of 23 (30%, 2013) and 3 of 18 (17%, 2014) subsequently detected in the John Day River.

Table 17. Fallback percentages (unique fish that fell back / unique fish that passed dam) and fallback rates (total fallback events / unique fish that passed dam) of radio-tagged steelhead at Bonneville, The Dalles, John Day, and McNary dams in 2013-2014 and 2014-2015. Fallback events that occurred after spawning (i.e., by kelts) were not included.

Run	Dam	Tag year	Passed dam[1]	Unique FB fish	Total FB events	Fallback %	Fallback rate
Early	Bonneville	2013	164	3	3	1.8%	1.8%
		2014	201	8	8	4.0%	4.0%
	The Dalles	2013	131	3	3	2.3%	2.3%
		2014	144	7	9	4.9%	6.3%
	John Day	2013	110	9	11	8.2%	10.0%
		2014	125	9	10	7.2%	8.0%
	McNary	2013	88	15	15	17.0%	17.0%
		2014	110	24	26	21.8%	23.6%
	Ice Harbor	2013	45	9	14	20.0%	31.1%
		2014	74	11	13	14.9%	17.6%
	L. Monumental	2013	44	12	16	27.3%	36.4%
		2014	66	4	6	6.1%	9.1%
	Little Goose	2013	33	5	5	15.2%	15.2%
		2014	64	9	9	14.1%	14.1%
	Lower Granite	2013	33	3	3	9.1%	9.1%
		2014	62	9	10	14.5%	16.1%
Late	Bonneville	2013	579	26	35	4.5%	6.0%
		2014	576	2	3	0.3%	0.5%
	The Dalles	2013	525	56	79	10.7%	15.0%
		2014	502	18	26	3.6%	5.2%
	John Day	2013	474	18	20	3.8%	4.2%
		2014	455	14	15	3.1%	3.3%
	McNary	2013	451	23	27	5.1%	6.0%
		2014	417	18	18	4.3%	4.3%
	Ice Harbor	2013	405	13	13	3.2%	3.2%
		2014	390	13	14	3.3%	3.6%
	L. Monumental	2013	387	8	8	2.1%	2.1%
		2014	378	7	7	1.9%	1.9%
	Little Goose	2013	369	9	9	2.4%	2.4%
		2014	369	10	10	2.7%	2.7%
	Lower. Granite	2013	365	9	9	2.5%	2.5%
		2014	365	5	5	1.4%	1.4%

[1] only includes fish that retained radio transmitters

Pre-spawn fallbacks estimated to have occurred during limited or no-spill months included 8-21 events in September, 36-65 in October, 25-52 in November, 14-24 in December, 5-9 in January, 12-17 in February, and 16-56 in March (Figures 7 and 8). These events were generally most frequent at The Dalles and McNary dams. Note that relatively few radio-tagged fish were migrating in August and September, resulting in likely underestimation of fallback frequency for those months. There were also brief periods of spill during the fall-winter period, particularly at McNary Dam (see Figures 9 and 10).

Post-spawn fallbacks by kelts were concentrated in April and May (Figures 7 and 8). These events were most common at Lower Granite Dam, and were progressively less frequent at subsequent downstream dams (also see Table 22).

The relationship between pre-spawn fallback and survival to tributaries varied widely among dams and across seasons, in part because fallback fish sample sizes were often small (Table 18). Across all dates, average survival to tributaries for pre-spawn steelhead that fell back was 33% (fell back at Bonneville), 60% (The Dalles), 62% (John Day), 76% (McNary), 69% (Ice Harbor), 58% (Lower Monumental), 71% (Little Goose), and 64% (Lower Granite). Of the steelhead that fell back in summer (15 June to 31 August), 50% (2013) and 67% (2014) survived to tributaries. Of those that fell back in September or October, 55% (2013) and 67% (2014) survived, and of those that fell back from November through March, 56% (2013) and 61% (2014) survived to tributaries (Table 18). Note that there was very limited monitoring downstream from Bonneville Dam.

Table 18. Numbers of radio-tagged steelhead that fell back at dams in 2013-2014 and 2014-2015 prior to spawning (i.e., no known or suspected kelt fallback events included) and the percent of events that were eventually followed by tributary entry (% Trib).

	Tag	15 Jun – 31 Aug		1 Sep – 31 Oct		1 Nov – 31 Mar		All dates[1]	
Dam	year	*n*	% Trib	*n*	% Trib	*n*	% Trib	*n*	% Trib
Bonneville	2013	3	33%	9	22%	23	39%	38	39%
	2014	6	33%	2	0%	3	33%	11	27%
The Dalles	2013	1	100%	29	52%	48	50%	82	54%
	2014	5	60%	16	69%	13	62%	35	66%
John Day	2013	9	67%	6	67%	13	46%	31	61%
	2014	9	89%	12	42%	4	75%	27	63%
McNary	2013	1	100%	14	64%	27	70%	42	69%
	2014	4	75%	8	88%	30	80%	44	82%
Ice Harbor	2013	11	55%	5	80%	11	82%	27	70%
	2014	7	43%	9	89%	11	64%	27	67%
L. Monumental	2013	12	33%	5	40%	5	40%	24	38%
	2014	4	75%	4	100%	5	60%	13	77%
Little Goose	2013	1	0%	4	75%	5	40%	13	77%
	2014	2	100%	10	70%	6	33%	20	65%
Lower Granite	2013	1	0%	1	100%	7	71%	13	85%
	2014	1	100%	6	50%	6	17%	14	43%
Any dam	2013	38	50%	73	55%	141	56%	271	58%
	2014	39	67%	67	67%	74	61%	191	66%

[1] includes some presumed pre-spawn events in April and May

Fallback routes during winter monitoring

Additional radio antennas were installed in December of 2013 and October of 2014 at The Dalles, John Day, and McNary dams to help estimate late fall and winter-time fallback routes at these sites. During the winter monitoring period in 2013-2014, 50 fallback events were identified: 19 at The Dalles Dam, 10 at John Day Dam, and 21 at McNary Dam (Table 18, Figure 9). The period was slightly longer in fall and winter 2014-2015, and 48 (The Dalles), 35 (John Day), and 50 (McNary) events were identified (Table 19, Figure 10).

It was difficult to confidently assign fallback routes using primarily aerial radio antenna data, particularly the events that occurred via deep water routes like the powerhouses. We were most confident assigning routes to fallback events that were through ice and trash sluiceways at The Dalles (8.3-21.1% of events) and McNary (4.8-12.0%) dams and through the adult fish ladders at The Dalles (4.2-5.3%) and McNary 9.5% in 2013) dams; these sites were monitored using underwater coaxial antennas. We were also relatively confident assigning fallback events that were via the navigation locks, which were monitored with narrow-coverage aerial antennas in 2014 only (2.1-5.7%, all dams) (Table 19).

The annual percentage of fallback events that appeared to occur via spillways (i.e., 'possible spillway') was highly variable between years (Table 19). Estimates ranged from 5.2-33.3% of events at The Dalles Dam, from 10.0-71.4% at John Day Dam, and from 33.3-38.0% at McNary Dam. In 2013, when the navigation locks were not monitored, estimates of 'possible' fallback via either the powerhouse or navigation lock were 47.4% (The Dalles), 60.0% (John Day), and 38.1% (McNary); these events were primarily during no-spill conditions. Estimates of 'possible' fallback via powerhouses in 2014 were 20.8% (The Dalles), 8.6% (John Day), and 12.0% (McNary) during no-spill periods.

Table 19. Estimated fallback (FB) routes of overwintering steelhead at The Dalles, John Day, and McNary dams during forebay radiotelemetry monitoring[1] in winter 2013-2014 and 2014-2015. Aerial radiotelemetry coverage in the forebay was not definitive for assigning fallback route, particularly via the spillways, powerhouses (PH), and navigation locks (navlock). Underwater or shielded radiotelemetry antennas in the ice and trash sluiceways and adult fish ladders allowed for a higher confidence and "likely" route assignment to these locations. Steelhead that fell back with no forebay radiotelemetry detections did not receive a route assignment. No fish in these groups were detected on juvenile bypass (JBS) PIT tag antennas. FB (*n*) is the number of fallback events.

			Estimated fallback route (%)						
Dam	Year	FB *n*	Possible spillway	Possible PH / navlock	Likely ice/trash[2]	Likely ladder	Likely navlock	No radio detection	Post-FB % in tributary
The Dalles	2013	19	1 (5.2)	9 (47.4)	4 (21.1)	1 (5.3)	-	4 (21.1)	68%
	2014	48	16 (33.3)	10 (20.8)	4 (8.3)	2 (4.2)	1 (2.1)	15 (31.3)	81%
John Day	2013	10	1 (10.0)	6 (60.0)	-	-	-	3 (30.0)	50%
	2014	35	25 (71.4)	3 (8.6)	-	-	2 (5.7)	5 (14.3)	94%
McNary	2013	21	7 (33.3)	8 (38.1)	1[3] (4.8)	2 (9.5)	-	3 (14.3)	71%
	2014	50	19 (38.0)	6 (12.0)	6 (12.0)	-	2 (4.0)	17 (34.0)	88%

[1] Start dates in 2013 were 11 Dec (The Dalles), 16 Dec (John Day), and 5 Dec (McNary); end dates were 1 April. Start dates in 2014 were 1 Oct (The Dalles), 14 Oct (John Day), and 28 Oct (McNary); end dates were 13 May, 14 May, and 27 May, respectively in 2015.
[2] McNary ice / trash sluiceway was dewatered for part of the winter study period
[3] event recorded on 19 December 2013 was possible false positive; dewatering status uncertain

Notable percentages of the fallback events did not have any radiotelemetry records at the respective dams to help assign fallback route (Table 19). This category comprised 21.1-31.3% of events at The Dalles Dam, 14.3-30.0% of those at John Day Dam, and 14.3-34.0% of those at McNary Dam; these could have been undetected movements through monitored routes or movements via powerhouses in either year or via the unmonitored navigation locks in 2013. We also note that juvenile bypass systems (JBS) were not operated at John Day or McNary dams during most of the overwintering period and no JBS detections of the overwintering fallback fish were recorded.

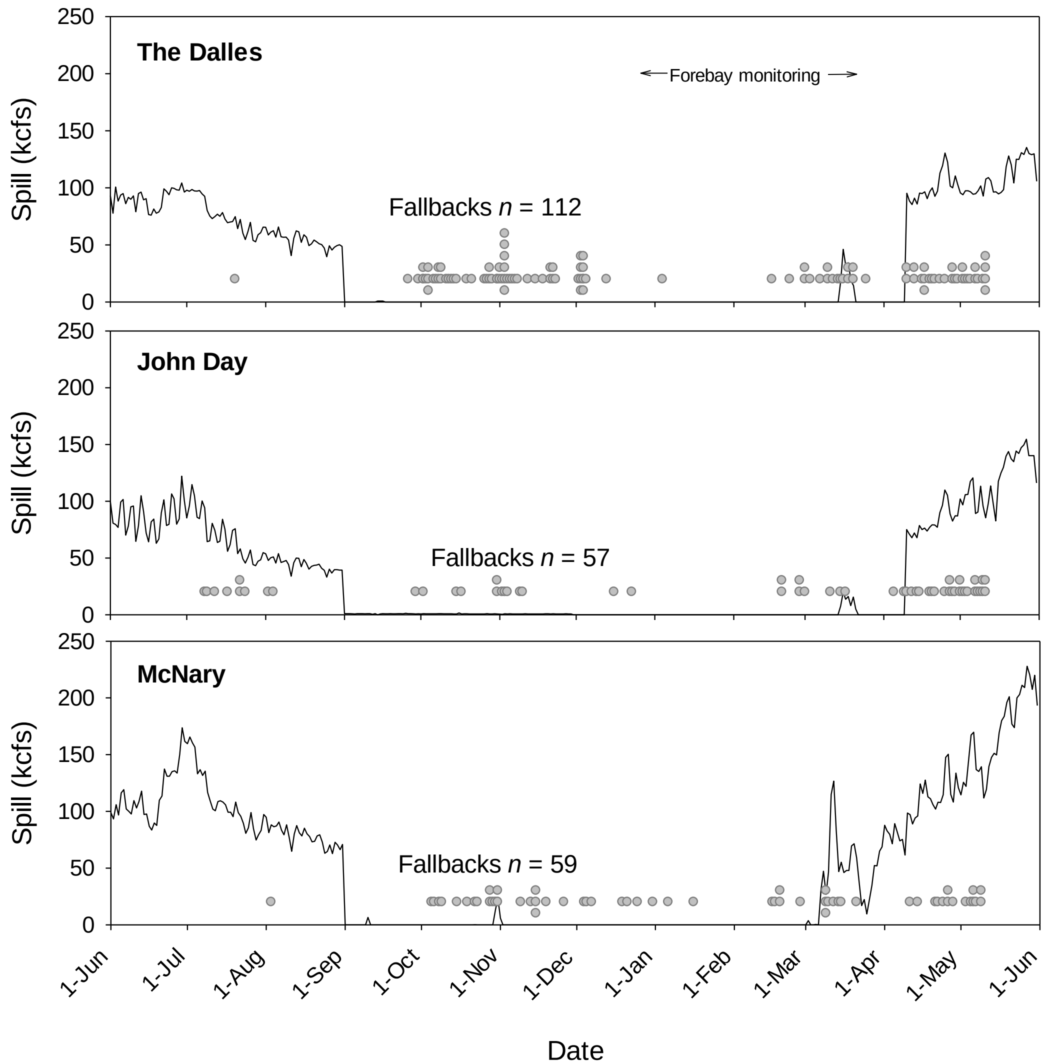

Figure 9. Estimated radio-tagged steelhead fallback dates at The Dalles, John Day, and McNary dams in relation to spill in 2013-2014. Dotted vertical lines show dates that additional radio antennas were deployed in the forebays and tailraces to monitor winter fallback and estimate fallback routes.

Forebay residency prior to winter fallback

Detections on the forebay antennas at The Dalles, John Day, and McNary dams suggested that some overwintering steelhead spent extended periods (days to months) in the forebays prior to falling back, while others moved in and out of the range of forebay antennas prior to falling back (Figures 11 and 12). It was not possible to differentiate steelhead movement upstream out of a forebay from movement within the forebay into deeper water beyond the range of radio detection.

There were notable differences in the detection histories of steelhead in the forebay across the three monitored dams. At The Dalles Dam, most pre-spawn steelhead that fell back during

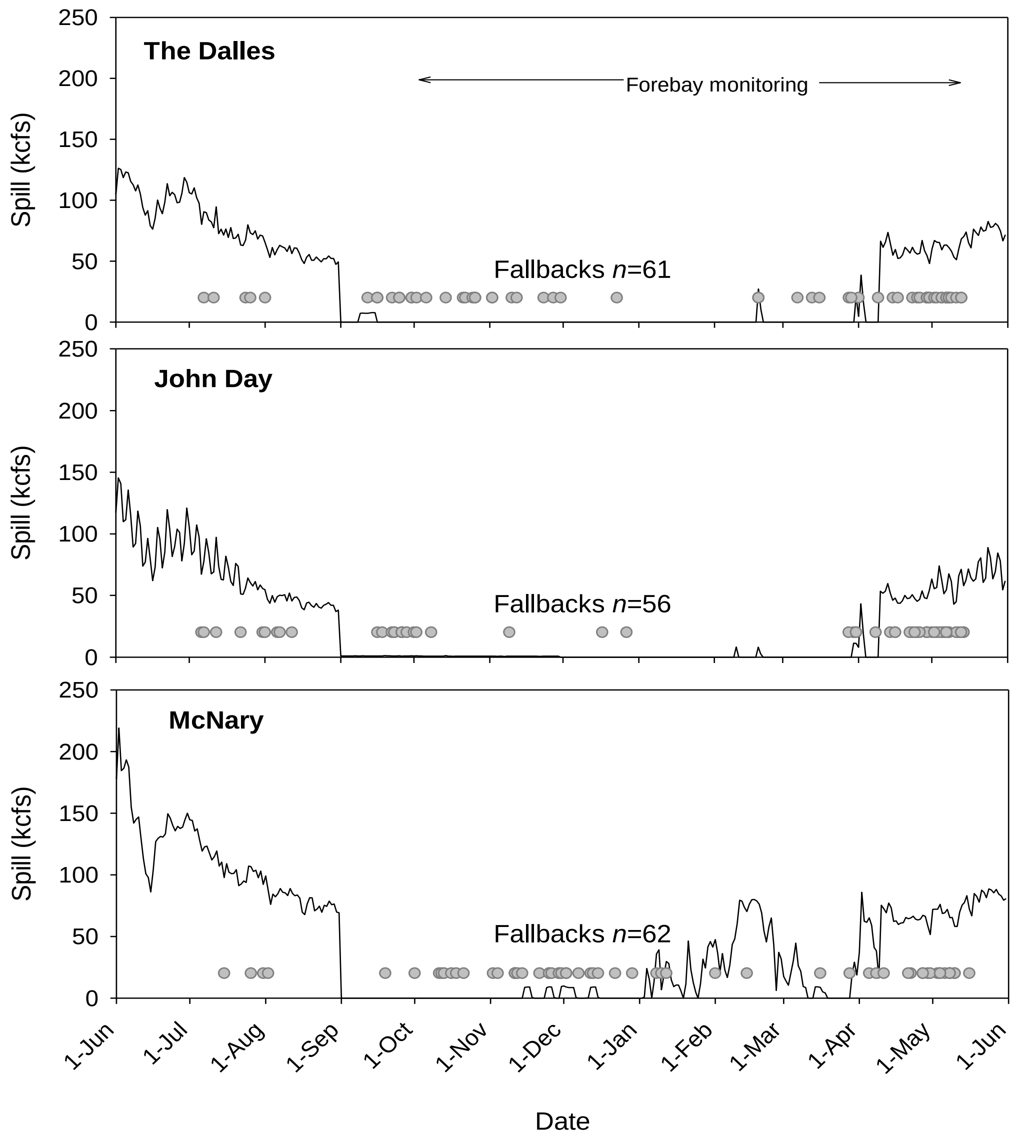

Figure 10. Estimated radio-tagged steelhead fallback dates at The Dalles, John Day, and McNary dams in relation to spill in 2014-2015. Dotted vertical lines show dates that additional radio antennas were deployed in the forebays and tailraces to monitor winter fallback and estimate fallback routes.

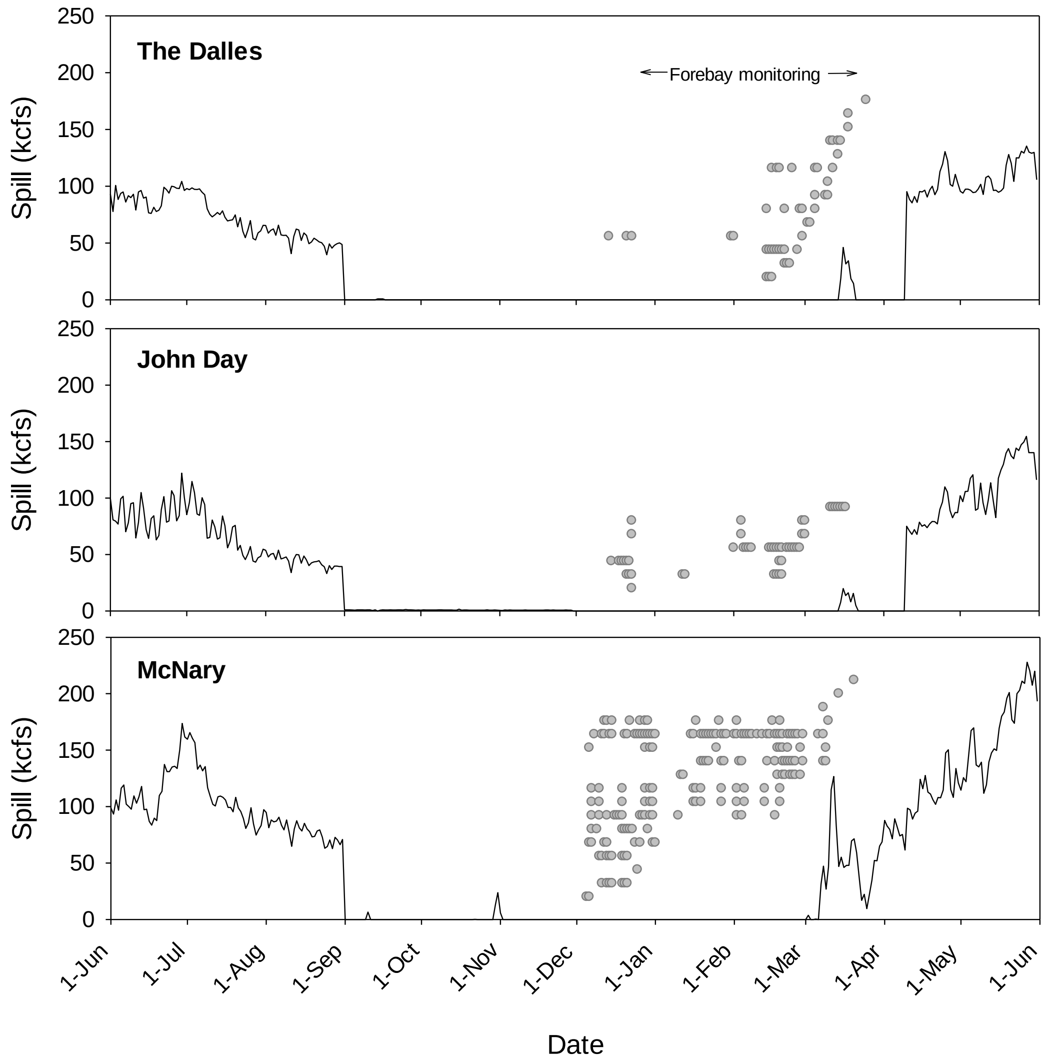

Figure 11. Unique dates that radio-tagged steelhead were detected on antennas used to monitor the forebays of The Dalles, John Day, and McNary dams in 2013-2014. Graph only includes steelhead that fell back at the dam during the winter monitoring period. Each row of circles represents an individual steelhead. Note that not all overwintering fish that fell back were detected on forebay antennas.

the winter monitoring period were detected for 1-4 d before falling back in both years, while a few fish were detected over several weeks, mostly in 2013 (Figure 11). A few steelhead were present for a week or more in the John Day forebay in 2013, whereas most were detected only briefly in 2014. In both years there were considerably more fish detected in the McNary forebay, and many fish were detected over multiple weeks. In 2013, many of the winter fallback events at McNary Dam appeared to occur when spill was initiated in March, suggesting that some fish (potentially including tributary overshoot fish) may have been waiting for the opportunity to move downstream via surface routes (Figure 11). Alternatively, the initiation of spill may have coincided with other cues initiating directed movements (temperature, photoperiod, etc.). As noted previously, some spill occurred at McNary Dam in all months in 2014. Proportionately fewer overwintering steelhead were detected for extended periods from January-March 2014, perhaps because spill was frequently occurring during this period (Figure 12).

In 2014, the forebay monitoring continued into May at all three dams (Figure 12). In contrast to the pre-spawn fish, almost all kelts that fell back encountered spill and almost all moved quickly downstream past McNary, John Day, and/or The Dalles dams. Few kelts were detected on forebay antennas on more than one date.

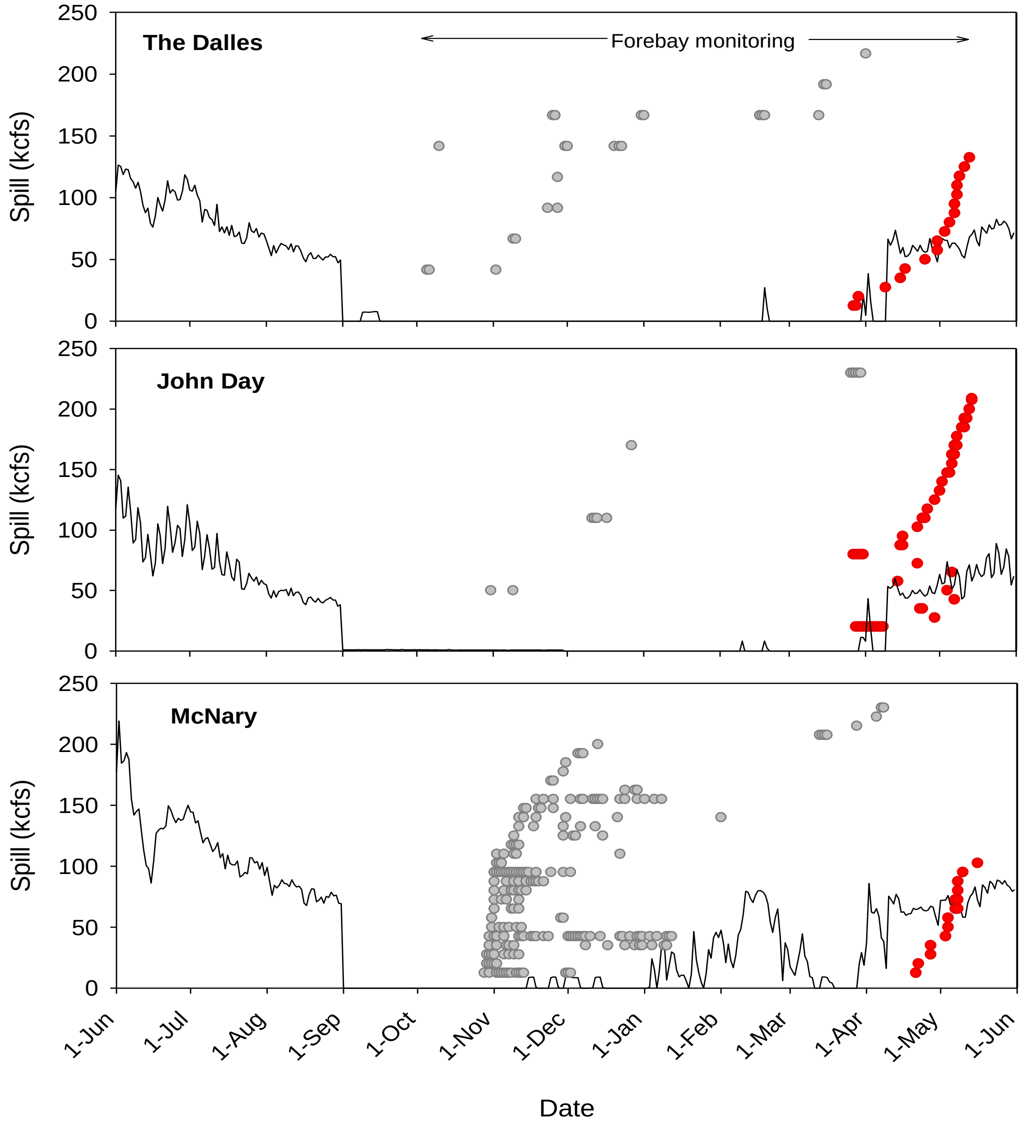

Figure 12. Unique dates that radio-tagged steelhead were detected on antennas used to monitor the forebays of The Dalles, John Day, and McNary dams in 2014-2015. Graph only includes steelhead that fell back at the dam during the winter monitoring period. Each row of circles represents an individual steelhead (gray circles=overwinter fish; red circles=kelts). Note that not all overwintering fish that fell back were detected on forebay antennas.

McNary temporary spillway weir (TSW) spill test in 2014-2015

A spill test in the winter of 2014 (11 November-14 December) and spring of 2105 (15 February-16 March) was implemented at McNary dam to estimate passage efficiency of adult steelhead passing the temporary spillway weir (TSW). Treatments of TSW spill consisted of three day "on" and "off" blocks. The experiment was implemented as planned in the Nov-Dec schedule (Figure 13) but high flow through spill bays disrupted the treatments during the Feb-Mar period (Figure 14).

A small number of radio-tagged steelhead were detected during the TSW experiment and many fish encountered both TSW treatments in the test that was conducted from 11 November to14 December. During the no-spill treatment blocks, 17 unique radio-tagged steelhead were detected in the McNary Dam forebay (Table 20). Of the 17, 4 (24%) fell back. During the TSW treatment blocks with spill, 17 unique steelhead were detected holding in the forebay and 7 (41%) fell back. There was no statistical difference in fallback percentage between the two treatments (Pearson's $\chi^2 = 1.2$, $P = 0.271$). Furthermore, there was some uncertainty regarding fallback times for three events: two that were assigned to the no-spill treatment and one assigned to the with-spill treatment. If these events were misclassified with respect to treatment, the difference between treatments may have changed.

As noted above, the test conducted from 15 February to 16 March was compromised by spill operations that conflicted with the TSW operations (Figure 14). In addition, few radio-tagged steelhead fell back at McNary Dam during this period and consequently no statistical analysis was conducted.

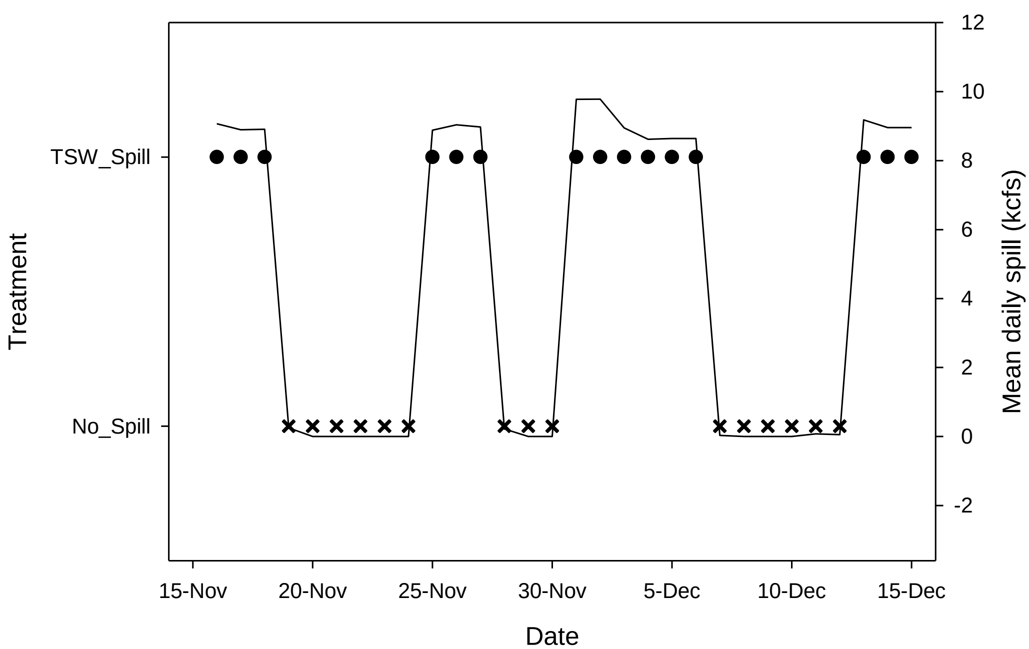

Figure 13. Winter spill test treatment blocks (symbols) and mean daily spill (lines) at McNary Dam from 15 November to 15 December 2014.

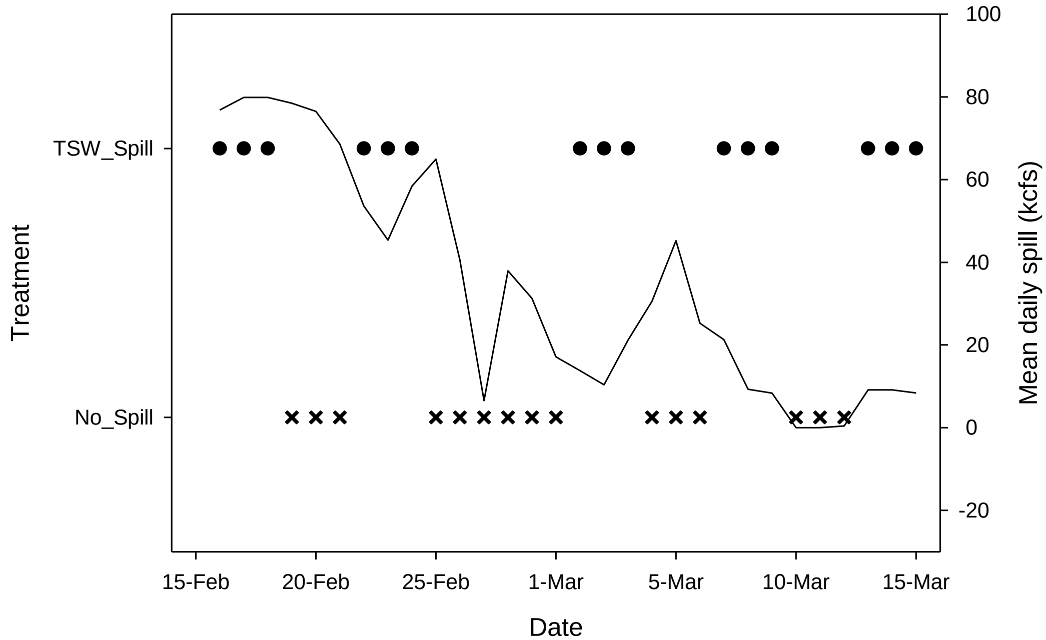

Figure 14. Spring spill test treatment blocks (symbols) and mean daily spill at McNary Dam from 15 February to 15 March 2015.

Detection of kelts in the FCRPS

Collecting data on kelt migration was not a planned study objective, but the 315-day radio transmitters, seasonally extended radiotelemetry monitoring effort and existing PIT antennas provided an opportunity to evaluate kelt behaviors and survival. The full adult migration histories provide relatively unique information, especially for the 'B-group' steelhead.

For the following summaries, we considered a steelhead a post-spawn kelt if it met three criteria: 1) it was detected in a spawning tributary; 2) it remained in a tributary until the typical spring-time spawning period; and 3) it was detected at an FCRPS dam or in a reservoir during or after the typical spawning period. Fish that exited tributaries in spring and then moved upstream in the FCRPS were not considered kelts. The FCRPS re-entry criterion was used because there are clear management implications for fish that attempt downstream migration through the hydrosystem versus those that do not survive to exit a spawning tributary.

In 2013-2014, 61 steelhead met the kelt criteria, including 53 from the Snake River basin and 8 from other Columbia River tributaries (Table 21). Twelve of the kelts were from the early run (7.1% of 169 released) and 49 were from the late run (7.9% of 620 released). In 2014-2015, 96 steelhead were identified as kelts, including 74 from the Snake River basin and 22 from other Columbia River tributaries (Table 21). Twenty-seven of the kelts were from the early run (13.0% of 208 released) and 78 were from the late run (13.2% of 591 released).

Table 20. McNary Dam TSW spill treatment dates in 2014-2105, the numbers of radio-tagged steelhead that were detected in the forebay, and the numbers that fell back.

Date	Treatment	Number of steelhead detected in forebay	Number that fell back	Percent that fell back	Spill (kcfs)
11/18/2014	No_Spill	6	0	0	0.25
11/19/2014	No_Spill	4	0	0	0
11/20/2014	No_Spill	4	0	0	0
11/21/2014	No_Spill	4	1	25	0
11/22/2014	No_Spill	2	0	0	0
11/23/2014	No_Spill	3	0	0	0
11/29/2014	No_Spill	4	2[1]	50	0
12/6/2014	No_Spill	5	0	0	0.03
12/7/2014	No_Spill	4	1	25	0
12/8/2014	No_Spill	3	0	0	0
12/9/2014	No_Spill	2	0	0	0
12/10/2014	No_Spill	2	0	0	0.07
12/11/2014	No_Spill	3	0	0	0.05
	Total	46	4	9	
	Unique fish	**17**	**4**	**24**	
11/15/2014	TSW_Spill	1	0	0	9.07
11/16/2014	TSW_Spill	2	0	0	8.89
11/17/2014	TSW_Spill	4	0	0	8.91
11/24/2014	TSW_Spill	2	0	0	8.88
11/25/2014	TSW_Spill	4	2	50	9.04
11/30/2014	TSW_Spill	3	1	33	9.78
12/1/2014	TSW_Spill	2	0	0	9.78
12/2/2014	TSW_Spill	3	2[2]	66	8.95
12/3/2014	TSW_Spill	2	0	0	8.62
12/4/2014	TSW_Spill	3	0	0	8.64
12/5/2014	TSW_Spill	3	0	0	8.64
12/12/2014	TSW_Spill	4	1	25	9.18
12/13/2014	TSW_Spill	3	1	33	8.96
12/14/2014	TSW_Spill	2	0	0	8.96
	Total	38	7	18	
	Unique fish	**17**	**7**	**41**	

[1] exact date of fallback events uncertain
[2] exact date of one of the fallback events is uncertain

In the two study years, 507 (2013-2014) and 510 (2014-2015) steelhead entered Columbia and Snake River tributaries, and 356 and 379 were 'potential' kelts (i.e., they entered tributaries but were not reported as harvested or as recovered at hatcheries) (Table 21). Using the potential kelts as the denominators, percent kelt estimates were 17.1% (2013-2014) and 25.3% (2014-2015) with all tributaries combined. Estimates were 20.8% and 26.0%, for all Snake River tributaries and were 7.9% (2013-2014) and 23.4% (2014-2015) for the non-Snake River tributaries, respectively.

Table 21. Numbers of radio-tagged steelhead that were detected in tributaries, the numbers that were potentially kelts (i.e., fish recovered at hatcheries and harvested in fisheries excluded), and the numbers and percentages that were detected at FCRPS dams or in reservoirs as likely kelts.

	2013				2014			
Tributary	Entered tributary	Potential kelts	Kelts	% Kelt	Entered tributary	Potential kelts	Kelts	% Kelt
Columbia River tributaries	**123**	**101**	**8**	**7.9**	**108**	**94**	**22**	**23.4**
Wind River					5	4	-	
Little White Salmon River	5	4	-					
White Salmon River	1	1	-		4	4	-	
Hood River	1	1	-		1	1	-	
Klickitat River	9	7	-		12	12	3	25.0
Fifteen Mile Creek					1	1	-	
Deschutes River	33	16	1	6.3	28	20	2	10.0
John Day River	41	41	5	12.2	36	36	13	36.1
Rock Creek	3	2	1	50.0				
Umatilla River	4	4	-		3	3	1	33.3
Walla Walla River	5	5	1	20.0	2	0	-	
Yakima River	4	4	-		4	4	3	75.0
Priest Rapids Hatchery	1	0	-					
Wenatchee River	6	5	-		3	2	-	
Entiat River	3	3	-		2	2	-	
Methow River	4	4	-		7	5	-	
Okanogan River	3	3	-					
Snake River tributaries	**384**	**255**	**53**	**20.8**	**402**	**285**	**74**	**26.0**
Lyons Ferry	1	0	-					
Tucannon River	5	5	1	20.0	3	3	-	
Clearwater River	233	157	33	21.0	234	167	38	22.8
Snake > Lower Granite pool	58	51	7	13.7	86	71	17	23.9
Grande Ronde River	13	6	4	66.7	16	12	4	33.3
Salmon River	69	32	6	18.8	60	30	15	50.0
Imnaha River	5	4	2	50.0	3	2	-	
All tributaries	**507**	**356**	**61**	**17.1**	**510**	**379**	**96**	**25.3**

Kelt estimates for individual tributary groups varied widely among sites (Table 21), likely due to a variety of factors including tributary fishery effort, sample demographics (e.g., wild versus hatchery origin, age, etc.), and the proximity and efficiency of monitoring arrays used to detect kelts. Of the tributaries with >10 potential kelts, kelt estimates in 2013-2014 were 6.3% (Deschutes), 12.2% (John Day), 21.0% (Clearwater), 13.7% (Snake above Lower Granite reservoir), and 18.8% (Salmon River). Estimates in 2014-2015 were 25.0% (Klickitat), 10.0% (Deschutes), 36.1% (John Day), 22.8% (Clearwater), 23.9% (Snake above Lower Granite reservoir), 33.3% (Grande Ronde), and 50.0% (Salmon).

Kelt fallback at FCRPS dams

In the 2013-2014 sample, we identified 198 likely post-spawn fallback events by kelts that were assigned to tributaries using telemetry records, including 61 events at lower Columbia River dams and 137 events at Snake River dams (Table 22). In the 2014-2015 sample, there were 134 likely kelt fallback events at lower Columbia River dams and 179 at Snake River dams, for a total of 313 events. In contrast to Figures 7 and 8, which show only fallback events for which we were reasonably confident about dates, the totals in Table 22 include fallback events with unknown date that were inferred from downstream radio or PIT detections. Table 22 also does not include fallback events for steelhead with uncertain reproductive status.

Given the relative abundance of late-run and Snake River kelts in the samples, it was not surprising that the largest numbers of fallback events were at Lower Granite and Little Goose dams in both study years (Table 22). There were proportionately more kelt fallback events at the lower Columbia River dams in 2015 than in 2014, reflecting the larger proportion of kelts from the Yakima, Klickitat, Deschutes, and John Day rivers in 2015 (Table 21).

Based on fallback detection dates, Snake River kelts passed from Lower Granite Dam to Ice Harbor Dam in an average of 6.9 d (*median* = 7 d), which was ~22 river kilometers (rkm) per day. Those that survived to Bonneville Dam passed from Lower Granite Dam to Bonneville in an average of 14.5 d (*median* = 15 d), or ~31 rkm/d. Times from McNary Dam to The Dalles Dam averaged 4.5 d (*median* = 5 d), or ~32 rkm/d.

Table 22. Numbers of fallback events by kelts at each FCRPS dam, by kelt origin tributary in 2013-2014 and 2014-2015. Includes fallback events that were not detected at radio or PIT antennas but that were inferred from detections at downstream sites. (Note: some kelts entered reservoirs but were not detected falling back at any dams.)

	2013-2014								2014-2015							
	BO	TD	JD	MN	IH	LM	GO	GR	BO	TD	JD	MN	IH	LM	GO	GR
Klickitat River									1							
Deschutes River									1	1						
John Day River	5	5	5						9	10	12					
Umatilla River											1					
Walla Walla R.	1	1	1	1												
Yakima River									1	3	3	3				
Tucannon River		1	1	1	1	1										
Clearwater River	2	6	6	7	11	19	24	32	5	7	7	7	11	14	18	34
Snake > GR pool	2	4	4	4	6	6	8	9	5	7	7	8	10	12	12	16
Grande Ronde R.							3	3	2	2	2	2	2	2	2	4
Salmon River	1	1	1	1	1	2	4	6	6	7	7	8	8	8	11	15
Imnaha River								1								
Total	**11**	**18**	**18**	**14**	**19**	**28**	**39**	**51**	**30**	**37**	**39**	**28**	**31**	**36**	**43**	**69**

Kelt survival in the FCRPS

A total of 122 kelts from the Snake River upstream from Lower Granite Dam were detected falling back at one or more FCRPS dams during outmigration. The total included 52 kelts in 2013 and 70 in 2014, 54 had fin clips and 68 were unclipped, and the genetic tests indicated that 23 were male and 97 were female (2 were not sex assigned). Origin tributaries included the Clearwater River with 68 kelts (56% of 122), the mixed-origin group detected in the Snake River upstream from Lower Granite reservoir (*n* = 23, 19%), the Salmon River (*n* = 21, 17%), and 10 (8%) from the Grande Ronde or Imnaha rivers.

There was high apparent mortality for most kelt groups in the lower Snake River (Figure 15). Based on radio- and PIT-tag detections only (i.e., no statistical modeling), cumulative survival from Lower Granite Dam to Ice Harbor Dam was: 0.346 (2013), 0.443 (2014), 0.389 (fin-clipped), 0.412 (unclipped), 0.435 (male), 0.392 (female), 0.652 (kelts from the Snake above LGR reservoir), 0.309

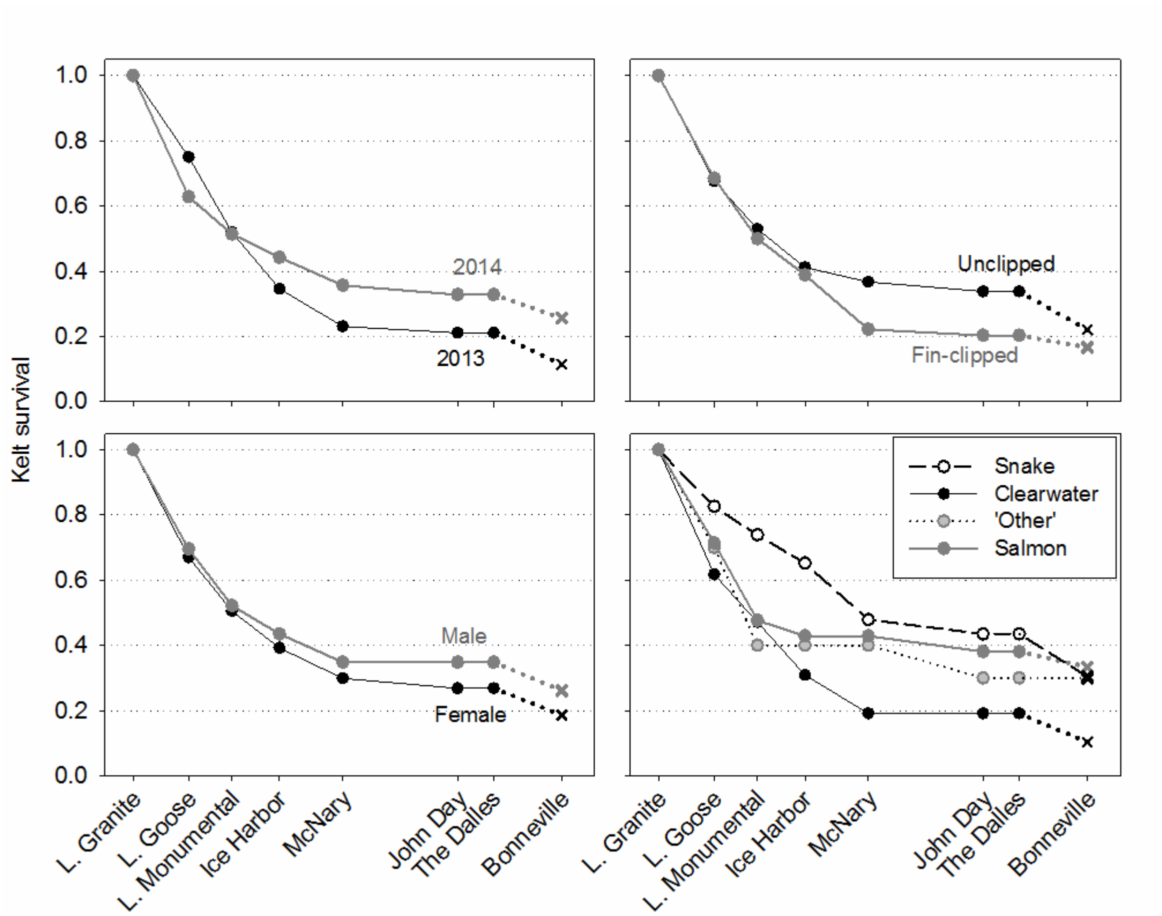

Figure 15. Cumulative survival plots for steelhead kelts that exited tributaries upstream from Lower Granite reservoir and were detected at one or more FCRPS dams during outmigration. Dam passage events were inferred from radiotelemetry and PIT-tag detections. Survival estimates are minimums for all groups because some fish may have passed undetected. Passage at Bonneville Dam had the most uncertainty because there was very limited radio or PIT monitoring effort downstream.

(Clearwater), 0.429 (Salmon), and 0.400 (Grande Ronde and Imnaha combined into 'other' category). Cumulative survival to Bonneville Dam for these Snake River groups was: 0.115 (2013), 0.257 (2014), 0.167 (fin-clipped), 0.221 (unclipped), 0.261 (male), 0.186 (female), 0.304 (Snake > LGR reservoir), 0.103 (Clearwater), 0.333 (Salmon), and 0.300 ('other').

Kelt sample sizes were much smaller from most other tributaries. The largest group was 18 kelts from the John Day River, for which cumulative survival to Bonneville Dam was 0.833. There were three kelts each from the Klickitat, Deschutes, and Yakima River and cumulative survival to Bonneville was: 0.667 (Klickitat), 0.333 (Deschutes), and 0.333 (Yakima). Single kelts were identified from Rock Creek, and the Umatilla, Walla Walla, and Tucannon rivers; only the Walla Walla River kelt was detected at Bonneville Dam.

Discussion

Steelhead overwintering estimates in the FCRPS

The probability that a radio-tagged steelhead would at least partially overwinter in the FCRPS steadily increased with migration date at Bonneville Dam, consistent with past studies (Keefer et al. 2008a). Less than 5% of the steelhead that were collected and radio-tagged in June subsequently overwintered in reservoirs versus more than 30% of those collected in October. Of all the fish released, we estimate that 6-8% early-run fish and 22-27% of late-run fish at least partially overwintered in the FCRPS. Overwintering estimates were higher for the sub-samples that survived to tributaries, at 9-12% for early-run fish and 30-38% for late-run fish. The latter estimates were consistent with the ~6% (May-August) and ~30% (September-October) estimates reported for radio-tagged steelhead that were collected throughout the summer steelhead migrations in 1996-1997 and 2000-2003 (Keefer et al. 2008a). In both studies, the strong positive relationship between migration timing at Bonneville Dam and the likelihood of FCRPS overwintering indicates that environmental cues like water temperature, river discharge, or photoperiod reliably cue the behavior and/or result from stock-specific differences in return timing and upstream migration behavior.

In the current study, radio-tagged steelhead were not sampled in proportion to the overall runs due to temperature-related handling restrictions at Bonneville Dam in late summer and the decision to oversample late-run fish. The restriction and the study design made it somewhat difficult to estimate the total proportion of steelhead that overwintered in the FCRPS, particularly because no fish were radio-tagged in late summer in either year. However, we think that the logistic regression relationships shown in Figure 5 provide a reasonable basis for estimating overwintering probability throughout the runs, including the time when no steelhead were radio-tagged. To generate estimates of total numbers of overwintering steelhead, we multiplied the predicted probability of FCRPS overwintering for each date (from the logistic regression models) by the daily numbers of steelhead counted during the radio-tagging intervals at Bonneville Dam:

from 10 June to 15 October (2013) and from 15 June to 15 October (2014). The resulting estimates were ~27,300 FCRPS overwintering steelhead in 2013-2014 and ~43,100 steelhead in 2014-2015. When we restricted the calculations to the blocks of dates that steelhead were radio-tagged within year (see Figures 1 and 5), total FCRPS overwintering estimates dropped to ~9,700 in 2013-2014 and ~26,100 in 2014-2015. The latter estimates should be considered absolute minima and require the implausible assumption that no steelhead that passed Bonneville Dam during the periods without tagging subsequently overwintered. Also note that all estimates do not account for overwintering that occurred in reservoirs upstream from Priest Rapids Dam as we did not monitor that region; they also do not account for any overwintering fish that passed Bonneville Dam before or after the radio-tagging period.

The genetic data provided an opportunity to estimate some hatchery- and reporting group-specific FCRPS overwintering estimates independent from assignments made using migration histories. The largest PBT-assigned samples were for late-run Clearwater River hatchery steelhead whose overwintering estimates closely matched estimates for the aggregate late-run samples. There were smaller sample sizes for other PBT hatchery groups and these samples generally had more variable overwintering estimates. Some of the among-group differences in overwintering can likely be attributed to population-based differences in run timing (e.g., Keefer et al. 2008a, 2009) and also to sample size constraints. Overwintering estimates for the GSI reporting groups were generally consistent with estimates for the telemetry-based assignment totals for early- and late-run samples. The late-run SFCLWR reporting group was by far the largest GSI group in each year, and the 29-33% FCRPS overwintering estimates were very similar to those for the aggregate late runs.

FCRPS distribution of overwintering steelhead

The observed distribution of overwintering steelhead in the FCRPS was strongly influenced by the oversampling of late-run fish. The preponderance of steelhead from the Snake River basin and especially from the Clearwater River in both years likely skewed the overwintering distribution towards the Snake River reservoirs. Large numbers of Clearwater River steelhead at least partially overwintered in the Lower Granite or Little Goose reservoirs, the closest FCRPS sites to the Clearwater–Snake River confluence. This behavior was very consistent with what was reported for Clearwater River steelhead in the 1996-1997 and 2000-2003 studies (Keefer et al. 2008a). Despite the sample-related effects on distribution, some steelhead from each of the primary Snake River tributary populations overwintered in lower Columbia River reaches as well as in the Deschutes and John Day rivers. Steelhead from the Salmon River basin were among the most widely distributed during the overwintering period. This was also consistent with previous results and may reflect the wide range of migration dates for the several steelhead tributary populations and life history types within the Salmon River metapopulation.

Steelhead from tributaries outside the Snake River basin tended to overwinter in FCRPS reservoirs near their natal river confluence. However, some fish overwintered upstream from their natal sites (i.e., they ‘overshot’ their home stream). This behavior was most commonly identified for fish last detected in the John Day River, many of which overwintered in the reach upstream from McNary Dam. We note, however, that there was some uncertainty regarding the origin of some radio-tagged steelhead that entered the John Day River. Most were genetically assigned to the mixed-stock MGILCS reporting group which includes the John Day River, but several fish were assigned to Snake River GSI groups (UPSALM, SFCLWR) and a few had PBT hatchery assignments (e.g., Dworshak, Pahsimeroi, Cottonwood). Some steelhead assigned to the John Day River were therefore likely permanent strays rather than overshoot fish, including Snake River steelhead barged as juveniles (Keefer et al. 2008c).

Timing and location of fallback at dams

Some radio-tagged steelhead fell back at each of the monitored FCRPS dams in each month of each study year. We note that the distributions of pre- and post-spawn fallback events among dams were likely skewed towards the Snake River projects given our sampling design. Nonetheless, the fallback results broadly align with previous reports of pre-spawn steelhead moving downstream during the late fall and winter (Keefer et al. 2008a; Ham et al. 2012; Khan et al. 2013) as well as of widespread downstream movement by kelts in the spring (Wertheimer 2007; Evans et al. 2004; Keefer et al. 2008b; Colotelo et al. 2013; Rayamajhi et al. 2013). The temporal and spatial distribution of pre- and post-spawn fallback events by steelhead highlight the need for downstream passage routes at the FCRPS dams that are less hazardous than routes through powerhouses.

At the three dams where fallback route monitoring was prioritized (The Dalles, John Day, McNary), steelhead fallback events occurred via a variety of routes and occurred during periods with and without surface spill routes. During the winter monitoring period, small percentages (<10%) of the pre-spawn fallback events appeared to be via adult fishways and navigation locks. Slightly more (~5-21%) were via ice and trash sluiceways at The Dalles and McNary dams. The remaining events were via the spillway or through powerhouses and we had varying levels of confidence associated with assigning individual fallback events to each of these routes. Without monitoring the turbine intake areas (historically done with diver-mounted underwater antennas in telemetry studies), we had to infer turbine passage for events by subtraction. Events were assigned to ‘possible powerhouse’ when steelhead did not appear to encounter surface spill and were not detected using other monitored routes (adult fishway, ice and trash sluiceway, navigation lock, juvenile bypass system). This route assignment approach was imprecise, but was required given the limitations of the monitoring array and the use of radiotelemetry as opposed to acoustic telemetry. The approach provides minimum estimates for monitored routes and may have overestimated passage through the powerhouse as missed detections at monitored routes were assigned to powerhouse passage. Overall, the results generally indicated that steelhead passed via the spillways when they were operated and that some passed through powerhouses at each dam.

Lastly, data from the forebay monitoring antennas at The Dalles, John Day, and McNary dams suggested that some pre-spawn steelhead held position in or near the forebays for extended periods. Several of these steelhead eventually fell back during periods of surface spill, though it was impossible to determine cause and effect or to assess whether fallback events were volitional or non-volitional via any route. The TSW spill experiment at McNary Dam was designed and implemented for a separate steelhead study (reported separately by the Pacific Northwest

National Laboratory), and we used the spill treatment opportunistically to assess behaviors by radio-tagged steelhead. Our evaluation was limited by the small numbers of tagged steelhead that encountered the treatments and by the few that fell back during the test period. Only 17 fish were exposed to each of the experimental treatments in the fall and fallback percentages did not statistically differ by treatment. We do, however, recommend continued experimental assessments of surface route operations for overwintering steelhead as these types of tests can provide important information on route selection and efficacy. In particular, future tests should aim to evaluate the potential for seasonal differences in directed movement behaviors because it is plausible that the motivation to pass downstream by adult steelhead increases as spring approaches, particularly for adults having overshot their natal tributaries.

Fallback at dams has been associated with reduced adult steelhead survival in a variety of studies (e.g., Keefer et al. 2005, 2008c; Keefer and Peery 2007; Normandeau Associates 2014). Estimating fallback effects on survival of tagged adults has typically relied on indirect assessments such as comparing the final detection locations of fish that did and did not fall back at a site. In the current study, we found that pre-spawn steelhead that fell back at any monitored dam in September or October survived to tributaries at rates of 55% (2013) and 67% (2014). Those that fell back at any dam from November through March survived at comparable rates: 56% (2013) and 61% (2014). For comparison, overall survival to tributaries for all overwintering fish (including those that fell back) was estimated to be 91-92% each year. The much lower survival to tributaries for fallback fish indicate a significant mortality cost associated with fallback events. It is also possible, of course, that some steelhead in poor condition fell back at dams because they were unable to complete migration (i.e., cause and effect could not be determined because almost no unsuccessful steelhead were recovered).

Survival to tributaries of overwintering steelhead

As noted above, steelhead that overwintered in the FCRPS survived to tributaries at high rates: 91-92% each year. These estimates were higher than the 82% survival for overwintering steelhead reported by Keefer et al. (2008b) aggregated across the 1996-1997 and 2000-2003 study years. Higher survival in the current study likely reflects, at least in part, the oversampling of late-run migrants. On average, late-run steelhead are exposed to lower fishery effort in the lower Columbia River reservoirs than early-run fish, both because the fishery intensity declines seasonally and because late migrants are exposed to all fisheries for a shorter duration. The late-run group also has relatively limited temporary use of non-natal tributaries, where fishery risks can be elevated (High et al. 2006; Keefer et al. 2009). Additionally, many of the Clearwater River steelhead that overwintered did so in the Lower Granite reservoir in close proximity to the Clearwater-Snake River confluence requiring limited movement to enter the natal tributary. These fish may have been at somewhat lower risk than the samples in previous radiotelemetry research, which included a more diverse mix of populations, many of which overwintered at lower Columbia River sites where there are active winter fisheries; many steelhead overwintering in lower Columbia River reservoirs also had to migrate long distances in the FCRPS after resuming migration in spring.

Kelt behavior and survival

Collecting data on kelt outmigration was not a planned study objective, but the data provide relatively unique information, especially for the late-run 'B-group' steelhead. Radio-tagged kelts – primarily from the Clearwater River – entered the FCRPS from late March through mid-May, with peak abundance in April at most dams. This emigration timing meant that many kelts encountered surface-flow passage routes (spill bays, spillway weirs, the Bonneville Corner Collector, etc.) at the dams and we think that a majority of kelts likely passed these routes. Smaller proportions presumably passed through turbines, and some were detected in juvenile bypass systems. Kelt use of surface routes when available would be consistent with the previous telemetry study results from Wertheimer and Evans (2005), Rayamajhi et al. (2013), and Colotelo et al. (2013, 2014). The observed difference in survival between steelhead that fell back and those that did not prior to spawning implies downstream movement past dams by kelts is associated with a survival cost and that cost almost certainly differs by route used.

Radio-tagged kelts in our study were typically detected on the dam forebay antennas on only one date, indicating that most moved quickly past the dams. Colotelo et al. (2013, 2014) also reported that Snake River kelts had brief forebay residency, with median times of less than two hours at all monitored sites. We estimated that Snake River kelts passed through the lower Snake River in about seven days, on average, which translates to rates of ~22 rkm/d, and then they moved more rapidly (>30 rkm/d) through the lower Columbia River reaches. These estimates were similar to those reported by Wertheimer and Evans (2005) and slightly slower than the rates reported by Colotelo et al. (2014), though the start and end points differed slightly among studies, making direct comparisons difficult.

It is important to note that there were several other important methodological and sampling differences between the current study and the Wertheimer and Evans (2005) and Colotelo et al. (2013, 2014) studies. First, none of the kelts in our study were collected at the FCRPS dams during outmigration, whereas all of those in the Wertheimer and Evans study and a majority in the Colotelo et al. (2013, 2014) studies were collected from the juvenile bypass systems at dams. Second, the samples in the earlier studies likely included kelts from a broader variety of sites and included more early-run, 'A-group' steelhead whereas our samples were weighted for larger, late-run fish. Third, the Colotelo studies only tagged kelts in fair or good physical condition, whereas we could not assess condition in our samples. These differences among studies mean that comparisons among results should be made cautiously, and this applies to the survival data in particular as we expect that larger kelts and those in poor condition would have lower outmigration survival (Keefer et al. 2008b).

With the above caveats, we estimated that cumulative survival of radio-tagged kelts from Lower Granite Dam to Bonneville Dam was ~12% for the aggregated 2013-2014 Snake River group and ~26% for the aggregated 2014-2015 group. These estimates were generally lower than those reported by Colotelo et al. (2013-2014), whose survival estimates were from Little Goose Dam to Bonneville Dam and ranged from ~40% for mixed-origin Snake River kelts tagged in spring 2013 to ~50% for a similar sample tagged in spring 2012. Our estimates were higher than, or similar to, those reported by Wertheimer and Evans (2005), who estimated survival of 4.1-15.6% from Lower Granite Dam to the Bonneville Dam tailrace. Both our study and the previous studies indicated considerable variability in kelt survival among origin groups, with generally lower survival for Clearwater River fish. Similarly, our study and the Wertheimer and Evans (2005) study indicated much higher survival to Bonneville Dam for kelts from tributaries downstream from the Snake River (our study, small *n*) and those collected at John Day or McNary dams (Wertheimer and Evans 2005).

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Appendix A. Supplementary material on genetic data.

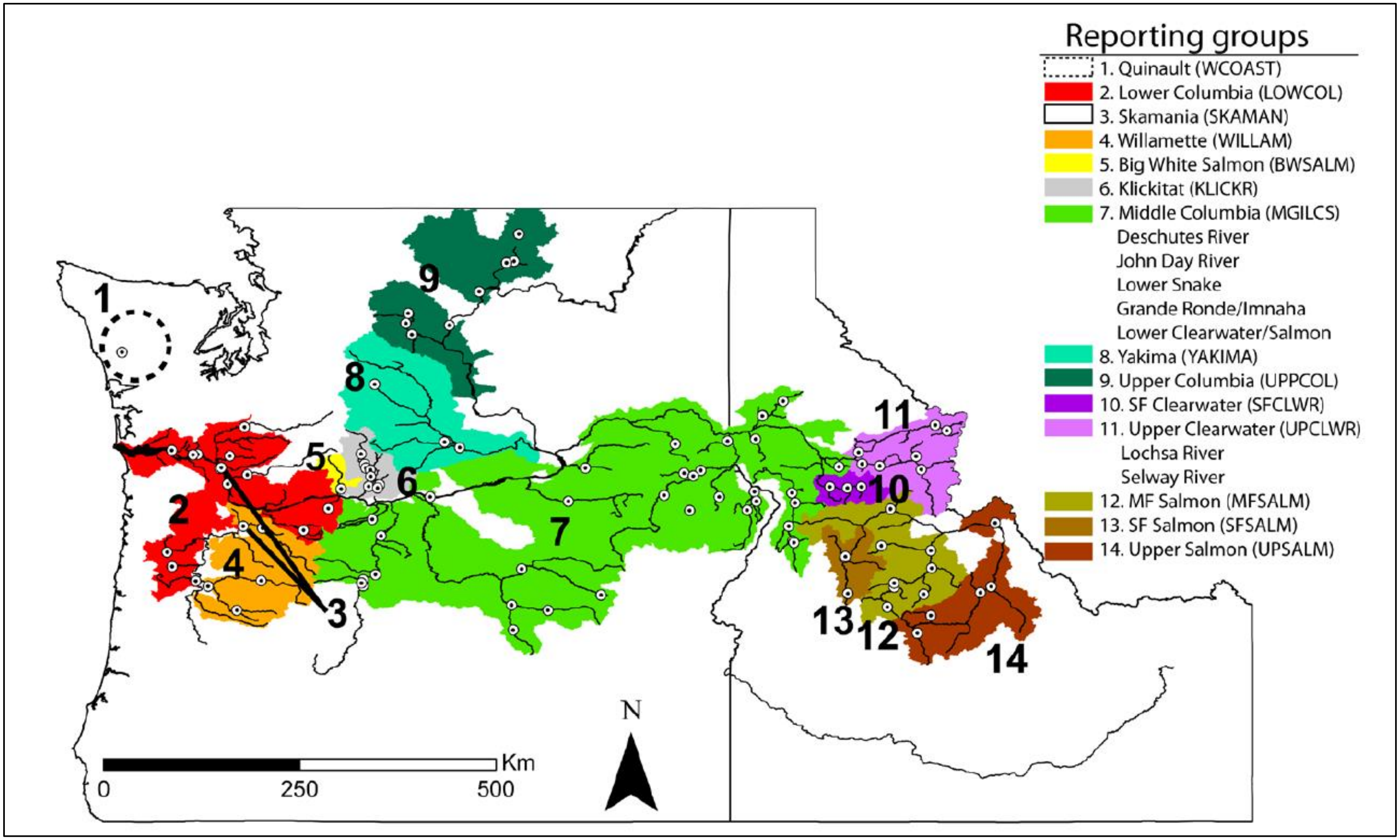

Figure A1. Map of reporting groups used in genetic stock identification (GSI). Source: Hess et al. (2015): 2013 Annual Report: Genetic assessment of Columbia River stocks. Report... Columbia River Inter-Tribal Fish Commission.

Source references for the microsatellites used in genetic stock identification (GSI) and the single nucleotide polymorphisms (SNPs) used in parentage-based tagging (PBT) genetic analyses:

1) Chinook salmon microsatellites: Seeb, L. W. and 19 coauthors. 2007. Development of a standardized DNA database for Chinook salmon. Fisheries 32(11):540-552.

Table 1. Microsatellite loci standardized for Chinook salmon. Reference, curator agency, and observed number of alleles are given for baseline Version 1.1.

2) Chinook salmon SNPs: Narum, S., N. Campbell, A. Matala, and J. Hess. 2010. Genetic assessment of Columbia River stocks, 2009 Annual Report. Columbia River Inter-Tribal Fish Commission, Portland, OR.

Appendix 1. Chinook salmon descriptive statistics from analysis of the Chinook salmon SNP baseline of 52 collections. Column heading are: (n) sample size with complete genotype, (A) mean number of observed alleles , (He)_ Expected Heterozygostiy, (Ho) Observed Heterozygosity, (Fis) Fixation Index, (Fst(mean)) among-collection variation per locus, and (%p) percentage of polymorphic loci. Values in bold identify number of significant HWE deviations.

3) Steelhead microsatellites: Blankenship, S. M. and 12 coauthors. 2011. Major lineages and metapopulations in Columbia River *Oncorhynchus mykiss* are structured by dynamic landscape features and environments. Transactions of the American Fisheries Society 140:665-684.

4) Steelhead SNPs: Matala, A. P., M. W. Ackerman, M. R. Campbell, and S. R. Narum. 2014. Relative contributions of neutral and non-neutral genetic differentiation to inform conservation of steelhead trout across highly variable landscapes. Evolutionary Applications 7(6):682-701.

Table S2. List of 191 SNP markers assayed for O. mykiss in the Columbia River Basin. The minor allele frequency (MAF), locus-specific F_{ST}*, and observed heterozygosity (*H_o*) are the mean values among all populations, with respect to lineage-of-origin.*