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Distribution and Movement of Steelhead and Anglers in the Clearwater River, Idaho

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Abstract

Steelhead Oncorhynchus mykiss is a species that is of high economic value that supports popular sport fisheries across the Pacific Northwest. The Clearwater River in Idaho provides a trophy steelhead fishery, and it is home to both wild- and hatchery-origin steelhead. To manage the fishery effectively, information is needed about the spatial and temporal overlap of wild and hatchery steelhead in the Clearwater River, as well as the activity of anglers. We conducted a radiotelemetry study to describe the distribution of steelhead and their final fate in the Clearwater River, and creel surveys were used to describe the distribution of anglers. In total, 289 wild (Potlatch River and Lochsa River) and hatchery (from Dworshak National Fish Hatchery and South Fork Clearwater River) steelhead were radio-tagged at Lower Granite Dam, 51 river kilometers (rkm) downstream from the mouth of the Clearwater River. Fish were monitored upon their entry into the Clearwater River by using mobile tracking surveys (boat and vehicle) and stationary antennas. The majority of wild and hatchery steelhead arrived in the Clearwater River in the fall with the exception of those from the Lochsa River, which arrived in the fall and following spring. Average daily movement of the fish was minimal (range = 0.3-4.7 km/d) and dependent on water temperature and flow. The fates of wild and hatchery steelhead varied. Fish returned to spawning grounds, were harvested by anglers (hatchery fish only), or had unknown fates. Both wild and hatchery steelhead returned at high rates to their natal tributaries and release locations. No straying was observed in either group; however, occasions when steelhead have overshot their natal tributaries and release locations were documented. Spatial and temporal overlap of the distributions of wild and hatchery steelhead was minimal. The distribution of anglers overlapped with that of hatchery steelhead in the fall, winter, and spring. The distributional overlap of anglers and wild steelhead was minimal and largely occurred in September in the lower Clearwater River. This suggests that the Clearwater River has a highly compartmentalized fishery and that current fishing regulations in the Clearwater River are providing for a diversity of angling opportunities while conserving wild

*Corresponding author: stacey.feeken@idfg.idaho.gov Received February 27, 2019; accepted July 26, 2019 steelhead and offering harvest of hatchery fish. The results from this study have important implications for the conservation and management of wild and hatchery steelhead.

Steelhead Oncorhynchus mykiss is the anadromous form of Rainbow Trout, and this species has a native distribution that includes portions of North America and Asia. In North America, steelhead have historically been distributed throughout coastal drainages from Alaska to the Baja Peninsula of Mexico and inland through the Fraser, Columbia, and Snake River basins (MacCrimmon 1971). The current distribution of steelhead extends from Port Heiden, Alaska, to southern California, and steelhead remain in the Columbia and Snake River basins (Behnke 2002). Steelhead populations in the Pacific Northwest have experienced declines in their distribution and abundance in many systems. Although a number of factors have contributed to the decline of steelhead, the primary factors associated with their poor conservation status include changes to ocean conditions (Smith et al. 2000; Robards and Quinn 2002), water development (e.g., the construction of hydroelectric dams), and land use activities (e.g., timber harvest, mining, and urbanization; Chapman 1986; Nehlsen et al. 1991; Moyle 1994; Congleton et al. 2000). Currently, steelhead populations are federally listed under the Endangered Species Act (ESA) as endangered and threatened in parts of California, and they are listed as threatened in portions of Idaho, Oregon, and Washington (U.S. Office of the Federal Register 1997).

Although wild steelhead are listed under the ESA, steelhead are a popular sportfish throughout their distribution. A prime example of a popular steelhead fishery is the Clearwater River, Idaho, where steelhead are valued economically, recreationally, and culturally (Gilbreath et al. 1976; Nehlsen et al. 1991). Recreational fisheries for steelhead have increased in popularity since the 1940s (Sheppard 1972). The Clearwater River provides a trophy steelhead fishery, attracting anglers from around the world (NPCC 2003). The steelhead fishing season extends from July through April and covers hundreds of kilometers of rivers and streams.

Steelhead in the Clearwater River are considered summer run (i.e., fish that pass over Bonneville Dam [Figure 1] between April 1 and October 31 in a sexually immature state; Sheppard 1972; Copeland et al. 2017), and they are separated into five wild populations (lower Clearwater River, South Fork Clearwater River [SFCR], Lolo Creek, Selway River, and Lochsa River populations) and one hatchery stock (from Dworshak National Fish Hatchery [DNFH]; Copeland et al. 2015) with multiple release locations (i.e., the main-stem Clearwater River and SFCR). Since steelhead are listed as threatened under the ESA, wild steelhead cannot be harvested by recreational anglers (U.S. Office of the Federal Register 1997). The fishery (including both wild- and hatchery-origin steelhead) in the Clearwater River is supported by the production of hatchery steelhead, identified by a clipped adipose fin, that provide angling and harvest opportunities for recreational and tribal fisheries (Waples et al. 1993; McCormick et al. 2012, 2015).

The Idaho Department of Fish and Game (IDFG) is pursuing a long-term goal of conserving Idaho's steelhead runs to provide benefits for all users. Achieving this goal requires an in-depth understanding of how steelhead populations function relative to the fishery. The Clearwater River steelhead fishery is highly valued by anglers, so it is essential that fishery managers sustain an economically important fishery while also conserving extant wild steelhead populations (Nelson et al. 2005). Previous studies in the Snake River basin (which includes the Clearwater River) have used run reconstruction models to provide the information on steelhead that is necessary for effective fisheries management (e.g., abundance, spatial distribution of spawning fish; Copeland et al. 2015; Stark et al. 2018). In Idaho, harvest and angling effort data have been collected through on-site angler surveys (i.e., creel surveys) as well as off-site angler surveys (i.e., mail, telephone, and internet surveys; Simpson and Bjornn 1965; Lindland et al. 1976; McCormick et al. 2015). The information that is derived from run reconstruction efforts and various angler surveys has provided estimates for the total number of wild and hatchery steelhead that return to the Clearwater River, escaping to their natal tributaries. However, these estimates contain substantial uncertainty (Copeland et al. 2015). In particular, run reconstruction efforts estimate escapement by river reach by assuming that all of the stocks return to their natal tributary or point of release, the movement of all of the stocks in a reach is simultaneous, and the stocks are exposed to fishery-related mortality in proportion to their relative abundance. The actual movement and distribution of wild and hatchery steelhead in the Clearwater River is poorly understood. Additionally, little is known about rates of overshooting (i.e., fish that pass their natal stream before returning to it; Keefer and Caudill 2013) and straying (i.e., fish that do not return to their natal stream; Quinn 1993).

Gathering information on steelhead populations and angler use is crucial for effectively managing the fishery.



FIGURE 1. Location of the fixed telemetry stations in the main-stem Clearwater River, Middle Fork Clearwater River, and at the mouth of primary tributaries (open circles). The fixed stations ran continuously and were in operation from September 2016 to June 2017 and September 2017 to June 2018. The locations of Bonneville Dam (BON) and Lower Granite Dam (LGD) are indicated by solid circles, and Dworshak National Fish Hatchery is represented by a solid triangle.

Information on the spatial and temporal distributions of wild and hatchery steelhead and anglers may influence management decisions that direct angling effort towards hatchery fish and away from wild fish that are of conservation concern (Johnson and Kucera 1985; Nelson et al. 2005). Such data may also provide insight as to how the location of juvenile release may influence the distribution and final fates of hatchery steelhead in the Clearwater River. Therefore, additional information is needed to better understand steelhead movement dynamics and angler use in the system.

The objectives of this research were to describe (1) the distribution and movement of wild- and hatchery-origin steelhead, (2) the distribution of anglers, and (3) the fate of steelhead in the Clearwater River. Radiotelemetry was used to evaluate the movement of steelhead. Relocations of radio-tagged fish provided information on their spatial distributions that was used to generate populationspecific estimates of movement and residence time. Radiotracking also provided insight on stock-specific differences in migratory patterns between wild- and hatchery-origin steelhead. Additionally, information on straying, homing, and kelting for wild and hatchery steelhead was obtained. Angler counts identified the locations of fishing effort. The results of this study identified the spatial distributions of steelhead and anglers, which will aid in ongoing management and conservation efforts.

Study Area

The Clearwater River watershed encompasses 25,000 km² in north-central Idaho (Munn and Brusven 2003; Figure 1). The major watersheds of the Clearwater River include the North Fork Clearwater River (NFCR), SFCR, Lochsa River, and Selway River (Figure 1). The Clearwater River originates in the Bitterroot Mountains on the Idaho-Montana border (NPCC 2003). The Lochsa and Selway rivers converge to become the Middle Fork Clearwater River (MFCR). The MFCR meets the SFCR, which forms the Clearwater River at roughly river kilometer (rkm) 75 (measuring from the mouth of the Clearwater River; Mallet 1974). Downstream, the NFCR meets the Clearwater River. The Clearwater River merges with the Snake River at the Washington-Idaho border, which later merges with the upper Columbia River in Franklin County, Washington (Munn and Brusven 2003). The Clearwater River, including the MFCR, is approximately 157 rkm in length.

The Clearwater River recreational steelhead fishery is open from July 1 to April 30 and is restricted to the area downstream of where Clear Creek meets the MFCR (rkm ~125). From the mouth of the Clearwater River upstream to Memorial Bridge of U.S. Highway 12 (rkm ~3) at Lewiston, Idaho, the river is open on July 1 to catch-andrelease fishing and then open to harvest of hatchery fish from August 1 through April 30. From Memorial Bridge upstream to Clear Creek (the mouth of Clear Creek is about 3.7 rkm upstream of the mouth of the SFCR), the river is open to catch-and-release angling from July 1 to October 14, and from October 15 to April 30, it is open to harvest. Regulations (e.g., length restrictions, bag limits) vary by year and are set based on the projected abundance of hatchery steelhead that return to the Clearwater River.

METHODS

Data collection.—The natal origins of steelhead in the Clearwater River were identified by using passive integrated transponder (PIT) tags. Wild juvenile steelhead were captured in the Clearwater River watershed from 2013 to 2016 by using rotary screw traps in the Potlatch River, Lochsa River, and Fish Creek (a tributary of the Lochsa River). At each location, PIT tags were inserted into the body cavity of juveniles that were migrating downstream (Marvin 2012). Hatchery smolts were PIT-tagged before they were released into the Clearwater River or SFCR.

Adult steelhead from the Clearwater River were radiotagged at Lower Granite Dam, 51 rkm downstream from the mouth of the Clearwater River (Figure 1). The adults were sorted by known destination at Lower Granite Dam by using the separation by code system for preselected PIT tag codes (McCutcheon et al. 1994; Harmon 2003). The fish were radio-tagged across two spawn years (SY) between July 2016 and June 2017 (hereafter referred to as "SY2017") and July 2017 and June 2018 (hereafter referred to as "SY2018"). Radio tags were allocated to steelhead across the run to ensure that fish that arrived at various times at Lower Granite Dam were represented. Postrun investigations confirmed that the distribution of when the fish were radio-tagged was similar to the distribution of the different tagging groups that had crossed over Lower Granite Dam. Specifically, adult steelhead that migrated upstream were detected by PIT tag arrays at hydroelectric facilities in the Columbia and Snake rivers. The PIT-tagged adults were monitored via the Columbia Basin PIT Tag Information System (Pacific States Marine Fisheries Commission 2016) and the Columbia River Data Access in Real Time system (Townsend et al. 1997; Marvin 2012; Columbia Basin Research 2016). The targeted natal origins or release locations included the Potlatch River, NFCR, SFCR, Lochsa River, and their tributaries.

The radio tag groups consisted of wild steelhead from the Potlatch River (hereafter referred to as "Potlatch steelhead"), wild steelhead from the Lochsa River (hereafter referred to as "Lochsa steelhead"), hatchery Dworshak steelhead, and hatchery SFCR steelhead. Steelhead from the Potlatch and Lochsa rivers are of high conservation interest for the recovery of Clearwater River steelhead. Steelhead from the SFCR and DNFH are the two hatchery groups in the Clearwater River basin with the largest numbers of smolt releases. Steelhead from the SFCR were further divided into two subgroups for radio-tagging: general production and local brood. "General production" fish were produced from adult hatchery steelhead that had returned to DNFH where they were spawned and their progeny were reared at DNFH and later released as smolts in SFCR. "Local brood" were fish from SFCR that were caught in the SFCR and transported to DNFH where they were spawned. Their progeny were reared at DNFH and Clearwater Fish Hatchery (directly across the NFCR from DNFH), and they were then released as smolts in the SFCR. Additional general production fish from DNFH were released as smolts in the main-stem Clearwater River near DNFH and at the mouth of the NFCR.

The steelhead were radio-tagged with Model MCFT2-3A radio tags (Lotek Wireless, Inc., Newmarket, Ontario). Tags were 16×46 mm, weighed 16 g, and did not exceed 1.7% of the fish's body weight (Mellas and Haynes 1985). The transmitters were programmed (165.200 MHz and 164.260 MHz) with a continuous burst interval, emitting a signal every 5 to 6 s. The longevity of the transmitters was approximately 320 d. Fish that were radiotagged were anesthetized prior to the insertion of the transmitters. Transmitters were gastrically implanted (Mellas and Haynes 1985) by dipping the radio tags into glycerin to facilitate the ease of insertion down the esophagus into the stomach. A surgical rubber band was placed on each transmitter to increase transmitter retention (Keefer et al. 2004). Fish that measured under 600 mm (FL) were excluded from the study to reduce tag loss and fish mortality (Ramstad and Woody 2003). The fish that were radio-tagged were immediately released at the tagging facility to move upstream of Lower Granite Dam.

After the tagging commenced, the radiotelemetry surveys were conducted. Radio-tagged steelhead were relocated by using a combination of 12 fixed telemetry stations (hereafter referred to as "fixed stations"; Figure 1). The locations of fixed stations were selected based on the following criteria: accessibility, areas of low noise (e.g., those that are away from power lines), and current or future fishery management areas. Model SRX-400A, Model SRX-600, and Model SRX-800D receivers (Lotek Wireless, Inc.) were used at the fixed stations. A single directional Yagi antenna (Lotek Wireless, Inc.) was positioned at each fixed station with a direct line of sight towards the river and away from objects that might hinder signal reception (e.g., radio towers; McCleave et al. 1978; Lee et al. 1985). The fixed stations were powered by a 12-volt battery. The receivers switched from 164.260

MHz to 165.200 MHz at 7-s intervals. Fixed stations continuously tracked fish from August through June during SY2017 and SY2018. During the tracking periods, data downloads and battery changes occurred on a weekly basis.

Mobile radio-tracking of steelhead was conducted by vehicle and drift boat during both spawn years. The main-stem Clearwater River and MFCR were divided into eight sampling reaches (Table 1). Mobile tracking by vehicle was conducted once per week in reaches 1-8. Additionally, the NFCR from the mouth to Dworshak Dam was tracked during the vehicle surveys. Mobile tracking was also conducted from a drift boat to obtain more accurate steelhead locations. During the boat tracking sessions, a directional Yagi antenna and an SRX800-M/MD-Series receiver were used. The receiver switched from 164.260 MHz to 165.200 MHz at 7-s intervals. Sampling reaches 1-7 were surveyed by drift boat once per month during SY2017 and SY2018. Sampling reach 8 and the NFCR were not surveyed by drift boat due to the lack of boat access. The mobile tracking methods that were used entailed homing in on the tagged fish by monitoring the signal strength and adjusting the gain on the receiver (McCleave et al. 1978; Eiler 2012).

In the spring, telemetry surveys as well as PIT tag arrays were used to locate steelhead in the Clearwater River basin. Additional surveys included several flights in spring 2017 (flight surveys were not conducted in 2018 due to the weather conditions) and mobile tracking (i.e., vehicle tracking) in various tributaries throughout the Clearwater River basin that were outside of the study area. Also, PIT tag arrays that were located in tributaries (e.g., SFCR, Lapwai Creek, Lolo Creek, and Lochsa River) that were inside and outside of the study area were used to assist in relocating steelhead.

The ability to detect radio-tagged steelhead at various depths and distances in the Clearwater River was estimated. The achievable detection distance was dependent on the water conditions (e.g., water discharge flow); radiotagged steelhead could be detected up to 20 m away in 14m deep water and up to 116 m away in 1-m deep water. The majority of the Clearwater River is shallower than 14 m with a few exceptions (e.g., Big Eddy, ~26 m deep). Trials similar to those of Simpkins and Hubert (1998) were conducted to evaluate the location error when relocating the radio tags. The location error was 1.6 m (SE ± 0.1) at a distance of 116 m from the antenna to the radio tag and decreased to 1.1 m (SE ± 0.1) at 50 m. Beacon tags were deployed in the water directly across the river from each fixed station. Beacon tags had burst intervals that were programmed for every 8 h to confirm that the fixed stations were operating.

Anglers on the Clearwater River, NFCR, and MFCR were surveyed by IDFG personnel throughout the fishing season by using a roving-roving survey (i.e., a mobile survey of an incomplete trip interview; Pollock et al. 1997). Roving creel surveys were conducted every Saturday and Sunday and on two randomly selected weekdays. The creel clerks surveyed and georeferenced boat and shore anglers from sampling reaches 1–5 on weekdays; all of the sampling reaches (1–8) were surveyed on weekends (Table 1). A systematic random design was used to select the count times for the angler count surveys. The initial count time was randomly selected, and subsequent count times were established at 3-h intervals for a total of three counts per day. One of the three angler count times was randomly selected for collecting the georeference locations of the

Sampling			Coordinates (°)				
reach	Telemetry section	rkm	Latitude	Longitude	Latitude	Longitude	
1	Mouth of Clearwater River–Clearwater Paper Mill	0–7	46.42616	-117.03178	46.43227	-116.96540	
2	Clearwater Paper Mill–Spalding Railroad Bridge	7–22	46.43227	-116.96540	46.45675	-116.79112	
3	Spalding Railroad Bridge–Nez Perce Tribal Hatchery	22–36	46.45675	-116.79112	46.51468	-116.65758	
4	Nez Perce Tribal Hatchery–Peck, Idaho	36-56	46.51468	-116.65758	46.49888	-116.43965	
5	Peck, Idaho-Orofino Bridge	56-72	46.49888	-116.43965	46.47400	-116.25185	
6	Orofino Bridge–Kamiah Park	72-108	46.47400	-116.25185	46.23018	-116.01933	
7	Kamiah Park-Clear Creek	108-124	46.23018	-116.01933	46.13350	-115.95000	
8	Clear Creek-mouth of Lochsa River	124–157	46.13350	-115.95000	46.14365	-115.59749	

TABLE 1. Sampling reaches in the Clearwater River and Middle Fork Clearwater River. The boundaries of the sampling reaches were defined by fixed telemetry stations.

anglers. The starting location and terminus of the angler georeference surveys were randomly selected. During each survey, the creel clerk would either start at the mouth of the Clearwater River, travel upriver, and end at the Orofino Bridge (the NFCR was included in the survey) or travel downstream from Orofino Bridge to the mouth of the Clearwater River (including the NFCR). During weekend surveys, the creel clerks would either travel from Orofino Bridge upriver towards Clear Creek or downriver from Clear Creek to Orofino Bridge.

Data analysis.— The detection efficiency of each fixed station was estimated across both years of the study and an average was taken for each fixed station. In SY2017 and SY2018, the number of unique radio-tagged steelhead that were detected at each fixed station varied (mean \pm SD; SY2017, 86 \pm 59; SY2018, 53 \pm 40). The detection efficiency for each fixed station was estimated by the number of unique radio-tagged steelhead that were detected at upstream fixed stations. Detection efficiency was generally high but varied from 0.46 to 1.00 (mean \pm SD; 0.81 \pm 0.05) in SY2017 and from 0.59 to 1.00 (0.87 \pm 0.06) in SY2018.

The arrival of radio-tagged steelhead in the Clearwater River was determined by the first fixed station in Lewiston, Idaho, or it was obtained from mobile tracking downstream of the first fixed station to the mouth of the Clearwater River (Figure 1; Table 1). The steelhead relocations that were collected via mobile tracking efforts were mapped with ArcGIS (ESRI, Redlands, California) for each fish. The distance between each relocation (in order by date) was calculated, and the direction of the movement (i.e., upstream or downstream) was noted. The distance between two consecutive relocations was divided by the number of days between those relocations to estimate the average minimum km/d that a fish moved (excluding the fish that were detected in the NFCR) by month. Movement of fish was evaluated with consideration of the context of water temperature and discharge in the Clearwater River. Data for water temperature and river discharge were gathered from the U.S. Geological Survey National Water Information System (station numbers: 13337000, 13340000, 13341050, 13341570, 13342500, and 13338500).

Kernel density estimators were used for the spatial-scale comparison of the distributions. The river kilometer of each relocation for individual steelhead or angler locations was defined using ArcGIS. When assigning river kilometers to the steelhead relocations that were collected via mobile tracking, fish in the NFCR were placed at the mouth of the NFCR because steelhead tend to move in and out of the NFCR. River kilometers were also assigned to boat and shore anglers, and their locations were collected from angler georeferences. The proportional use of the main-stem Clearwater River by wild and hatchery steelhead and anglers was estimated by using a kernel density estimator (Vokoun 2003). The density estimate was derived from detections of radio-tagged fish along the main-stem Clearwater River via mobile tracking. Peaks in the distribution represented the locations that were used most frequently by the fish. The univariate kernel density estimator was defined as

$$\hat{f}(x) = \frac{1}{nh} \sum_{i=1}^{n} K\left(\frac{x - X_i}{h}\right),$$

where K(x) was the Gaussian kernel function, h was the bandwidth, and X_i was a random sample of sample size n(Vokoun 2003; Vokoun and Rabeni 2005). A Sheather– Jones plug-in model was used to select the bandwidth (Jones et al. 1996). The kernel density function was estimated for wild steelhead (i.e., Potlatch and Lochsa), hatchery steelhead (i.e., DNFH and SFCR), and anglers (i.e., data for boat and shore anglers were combined) in the fall (September–November), winter (December–February), and spring (March–May) by using the base package in R statistical software (R Development Core Team, 2017).

The mean weekly abundance of wild and hatchery steelhead that were radio-tagged and anglers within a given sampling reach was summarized from September through April for SY2017 and SY2018. The data for the relocations of individual steelhead were used to estimate which sampling reach each fish had occupied on a weekly basis during its time in the Clearwater River. For instance, if an individual steelhead was detected in reach 1 during the first week of September and was not relocated again until the last week of October in reach 3, the fish was placed in reach 1 for every week leading up to the last week of October. The locations were grouped as wild (from Lochsa or Potlatch) or hatchery (from DNFH or SFCR) steelhead. For each sampling reach, a mean weekly abundance of wild and hatchery steelhead and anglers was summarized by month. Additionally, both spawn years were combined and the Pearson correlation coefficient (r) was used to evaluate the correlation between angler abundance and wild and hatchery steelhead abundances using the base package in R statistical software (Higgins 2004; R Development Core Team 2017).

The proportion of steelhead that had returned to their natal tributaries or release locations (return rates) was detected at fixed stations that were located at the mouths of tributaries and the PIT tag arrays in the tributaries. The return rates were estimated by radio tag group by dividing the number of steelhead that were detected at each terminal location by the number of radio-tagged steelhead that were detected in the Clearwater River. Additionally, the fate of the fish was also described. Fate was defined as the final destination in the Clearwater River of the radio-tagged steelhead. Fate of fish was estimated from detections that were compiled from the mobile tracking surveys and fixed stations. The fate of an individual steelhead was classified as a return to its natal tributary or release site (i.e., Potlatch River, NFCR, SFCR, or Lochsa River), a return to a nonnatal tributary or nonrelease site, angler harvest, possible harvest, DNFH trap, dead or shed, and unknown. A fish was classified as harvested when an angler reported the harvest of a radiotagged fish. A fish was classified as a "possible harvest" when the radiotelemetry data suggested that the radio tag was no longer in the fish. For example, a radio tag that was detected multiple times per day moving up or down the river at the rate of a vehicle or boat was considered a possible harvest. Steelhead that were classified as "DNFH trap" were collected for use as broodstock at DNFH, and "dead or shed" were radio tags that remained in one location until the end of the study. Steelhead that were assigned a fate of "unknown" were fish that had last been detected in the main-stem Clearwater River and never relocated.

The fixed stations and mobile tracking efforts provided insight as to the proportion of radio-tagged steelhead that demonstrated kelting behavior. A kelt was defined as a postspawn steelhead that was detected migrating downstream (Wertheimer and Evans 2005) in the spring and moving out of the Clearwater River into the Snake River. The proportion of radio-tagged steelhead from each of the four radio tag groups that were included in the study that displayed kelting behavior was calculated. Moreover, the data for kelting behavior were used to better understand the fates of steelhead in the study area.

RESULTS

In the two study years, we captured and radio-tagged 289 steelhead at Lower Granite Dam. In SY2017, 38 wild and 150 hatchery steelhead were tagged from August 25, 2016, to June 5, 2017 (Table 2). During SY2018, 18 wild and 93 hatchery steelhead were tagged from September 10, 2017 to April 19, 2018. The total length of the radio-tagged fish during SY2017 varied from 650 to 880 mm (mean \pm SD; 788.4 \pm 49.7 mm) and from 600 to 920 mm in SY2018 (732.9 \pm 78.5 mm; Table 2).

The arrival timing of wild and hatchery steelhead into the Clearwater River varied by radio tag group, but it generally remained consistent across years (Figure 2). In

TABLE 2. The number of steelhead by radio tag group that were radio-tagged at Lower Granite Dam and the number of steelhead that were detected in the Clearwater River during spawn year 2017 (July 2016–June 2017) and spawn year 2018 (July 2017–June 2018). The minimum, maximum, and mean (\pm SD) fork length for each radio tag group are included.

	Lower Granite	Clearwater	Fork length (mm)				
Radio tag group	Dam	River	Minimum	Maximum	Mean	SD	
	Spawn	year 2017					
Wild	-	-					
Potlatch	15	14	650	760	702	46	
Lochsa	23	19	690	830	759	39	
Hatchery							
Dworshak National Fish Hatchery	60	58	710	880	808	40	
South Fork							
General production	40	36	720	850	782	35	
Local brood	40	38	660	870	805	45	
Total	178	165					
	Spawn	year 2018					
Wild							
Potlatch	8	7	600	810	660	87	
Lochsa	10	9	600	710	658	46	
Hatchery							
Dworshak National Fish Hatchery	43	42	620	920	728	76	
South Fork							
General production	14	13	670	850	800	57	
Local brood	36	30	640	860	746	69	
Total	111	101					

total, 266 (92%) of the radio-tagged steelhead were detected in the Clearwater River (Table 2). During SY2017, 93% of the Potlatch steelhead, 97% of the DNFH steelhead, and 92% of the SFCR steelhead entered the Clearwater River in the fall. During SY2018, 100% of the Potlatch fish, 98% of the DNFH fish, and 91% of the SFCR fish were in the Clearwater River by the end of the fall. Interestingly, in SY2017 roughly 32% of the Lochsa steelhead entered in the fall, 10% in the winter, and 47% in the following spring; 11% were not detected until they had reached the Lochsa River (having been detected in the Lochsa River at PIT tag antennas, the radio tag likely had malfunctioned or had been shed by the fish). The majority of the Lochsa fish that entered in the spring overwintered downriver of Lower Granite Dam. In SY2018, approximately 56% of the Lochsa steelhead entered in the fall and 33% entered in the spring; 11% were not detected until they were in the Lochsa River. The entrance timing of the local brood steelhead into the Clearwater River was similar to that of the general production steelhead (i.e., SFCR steelhead).

Movement data from all of the groups of radio-tagged steelhead that were in the Clearwater River were combined to obtain a general understanding of the movement rates, which varied across seasons and spawn years (Figure 3). Additionally, movement was evaluated with consideration of the context of discharge and temperature. In SY2017, mean movement was 3.6 km/d (SE = 0.5 km/d) in the fall, 0.8 km/d (SE = 0.3) in the winter, and 4.7 km/d (SE = 1.9) in the spring. Similar movement patterns were



FIGURE 2. The cumulative distribution of steelhead by radio tag group

(i.e., Potlatch River, Lochsa River, Dworshak, and South Fork

Clearwater River) that entered the Clearwater River from August 2016

through June 2017 of spawn year 2017 (SY2017: July 2016-June 2017)

and August 2017 through June 2018 of spawn year 2018 (SY2018: July

2017-June 2018).

FIGURE 3. Minimum movement rates of radio-tagged steelhead (wild and hatchery) by month in the main-stem Clearwater River and Middle Fork Clearwater River in spawn year 2017 (SY2017: July 2016–June 2017) and in spawn year 2018 (SY2018: July 2017–June 2018). Positive values (above the solid black line) indicated upstream movements, whereas negative values (below the solid black line) indicated downstream movements. The boxplots are shown with medians, first and third quartiles, and outliers (black points). Numbers above months represent the number of individual radio-tagged steelhead that were relocated during each month.



observed in SY2018, with the highest movement rates in the fall $(3.2 \pm 0.4 \text{ km/d})$, followed by winter $(1.1 \pm 0.4 \text{ km/d})$ and spring $(0.3 \pm 0.1 \text{ km/d})$. Differences in discharge and temperature were observed in winter for SY2017 and SY2018. In the winter of SY2017, discharge flows and water temperature in the Clearwater River were lower (mean \pm SD; $303 \pm 127 \text{ m}^3/\text{s}$; $3.4 \pm 0.6^{\circ}\text{C}$) than were flows and temperature in the winter of SY2018 (490 $\pm 168 \text{ m}^3/\text{s}$; $4.3 \pm 0.4^{\circ}\text{C}$).

Wild steelhead were primarily distributed in the lower Clearwater River (downstream of the NFCR confluence) across seasons (Figure 4). However, the Lochsa steelhead were distributed throughout the entire Clearwater River in the spring. In the fall, the extent of use by Potlatch steelhead in both spawn years was from the mouth of the Clearwater River upstream to DNFH and the NFCR confluence at rkm 64. By winter, the Potlatch steelhead had moved out of the area near the mouth of the Clearwater River and were distributed between rkm 20 and 64. As spring approached, the Potlatch steelhead migrated downriver and resided between rkm 0 and 24. The Lochsa steelhead displayed similar patterns of use in the Clearwater River. In the fall and winter, Lochsa fish were primarily detected in the lower Clearwater River from rkm 0 to 110 in SY2017 and rkm 10 to 64 in SY2018. In SY2018, there was a peak in the kernel density estimate near the NFCR for Lochsa steelhead, but this represented a single individual. By spring, additional



FIGURE 4. Kernel density estimates for detections of radio-tagged wild steelhead (Potlatch River and Lochsa River), hatchery steelhead (Dworshak and South Fork Clearwater River), and anglers (boat and shore) in the main-stem Clearwater River, Idaho, in spawn year 2017 (July 2016–June 2017; solid) and spawn year 2018 (July 2017–June 2018; dashed lines). The seasons include fall (September–November), winter (December–February), and spring (March–May). The number of fish that were detected by year and season for spawn year 2017 and spawn year 2018 are included. The arrows along the *x*-axis represent where the Potlatch River (PO), North Fork Clearwater River (NF), South Fork Clearwater River (SF), and Lochsa River (LO) meet the main-stem Clearwater River.

0.08

Fall

South Fork

Fall





FIGURE 4. Continued

Lochsa steelhead entered the Clearwater River, which was demonstrated by the peak in the kernel density estimate between rkm 0 and 24, and Lochsa steelhead generally moved rapidly upriver to the Lochsa River (Figure 4).

Dworshak

0.08

The distribution of hatchery steelhead in the Clearwater River varied by season, but the patterns were consistent across spawn years (Figure 4). In the fall and winter, the distribution of DNFH fish varied from rkm 0 to 115 during SY2017 and from rkm 0 to 110 during SY2018. However, the highest proportion of DNFH steelhead were concentrated near DNFH at rkm 64. During the spring of SY2017 and SY2018, all but two DNFH fish congregated near DNFH; these two fish were detected downstream near rkm 28. The spatial and temporal distributions of the local brood and general production steelhead in the Clearwater River were similar. Therefore, the distributions for the local brood and general production fish were combined under SFCR for the purpose of describing the distributions. The SFCR steelhead occupied a large extent of the Clearwater River during the fall and winter of both spawn years, with a distribution from the mouth of the Clearwater River up to rkm 140 (Figure 4). In the winter of both spawn years, a few SFCR fish were located near the mouth of the Clearwater River. As spring approached, the SFCR steelhead that had remained in the main-stem Clearwater River in both spawn years were found between rkm 10 and 120, with a high concentration of fish near DNFH.

Both boat and shore anglers were primarily concentrated near DNFH across all of the seasons (September– June) and spawn years (Figure 4). In the fall, anglers fished between rkm 0-130, but the majority of the anglers were observed in the lower Clearwater River, with an emphasis near DNFH. We observed some overlap between wild steelhead, hatchery steelhead, and anglers in the fall. By mid to late fall, winter, and into spring, the angler distributions overlapped with the distributions for the hatchery steelhead that were near DNFH and there was little to no overlap in the distributions for anglers and wild steelhead.

The mean weekly abundance of the radio-tagged wild and hatchery steelhead and anglers varied spatially and temporally (Figure 5). The numbers of anglers and wild steelhead were highly correlated in September (r = 0.88),



FIGURE 5. Pearson correlation coefficients of the weekly mean abundance per month of wild steelhead and anglers and hatchery steelhead and anglers across eight sampling reaches in the Clearwater River. Pearson correlation coefficients were averaged per month across spawn year 2017 (July 2016–June 2017) and spawn year 2018 (July 2017–June 2018).

but the association was weak thereafter $(r \le 0.14)$. In contrast, the numbers of anglers and hatchery steelhead were highly related throughout the year $(r \ge 0.64)$, suggesting that anglers were focused on harvesting hatchery steelhead.

Return rates and timing of wild steelhead to their natal tributaries and the fates of fish varied by group (Table 3). Seventy-nine percent of the radio-tagged Potlatch steelhead in the Clearwater River during SY2017 returned to the Potlatch River from February to April. The remaining Potlatch steelhead were categorized as unknowns. During SY2018, 43% of the Potlatch fish returned to the Potlatch River between January and April and the remaining fish had fates of dead or shed (14%) and unknown (43%; Table 3). During SY2017, 84% of the Lochsa steelhead returned to the Lochsa River between March and June and the remaining 16% had unknown fates. During SY2018, 89% of Lochsa fish made it to the Lochsa River between March and May, and 11% were categorized as unknown.

Return rates and timing of the hatchery steelhead to their release locations and the fates of fish also varied by radio tag group. During SY2017, 72% of the DNFH steelhead returned to the NFCR between September and March and 93% returned to the same location between September and February during SY2018. A large percentage of DNFH steelhead returned to the NFCR, but their release location (near the mouth of NFCR) was not their final fate. The DNFH fish that returned to the

TABLE 3. Proportion of steelhead by radio tag group that were detected in the Clearwater River and were classified into different fates for spawn year 2017 (July 2016–June 2017) and spawn year 2018 (July 2017–June 2018). Fates include natal tributary or release location, nonnatal tributary, angler harvest, possible harvest, Dworshak National Fish Hatchery (DNFH) trap, dead or shed, or unknown.

Radio tag group	Natal tributary or release location	Nonnatal tributary or nonrelease location	Angler harvest	Possible harvest	DNFH trap	Dead or shed	Unknown
		Spawn year 2017					
Wild		x v					
Potlatch	0.79	0.00	0.00	0.00	0.00	0.00	0.21
Lochsa	0.84	0.00	0.00	0.00	0.00	0.00	0.16
Hatchery							
DNFH	0.45	0.00	0.12	0.19	0.07	0.05	0.12
South Fork							
General production	0.58	0.14	0.08	0.03	0.03	0.00	0.14
Local brood	0.74	0.05	0.05	0.05	0.00	0.05	0.06
		Spawn year 2018					
Wild							
Potlatch	0.43	0.00	0.00	0.00	0.00	0.14	0.43
Lochsa	0.89	0.00	0.00	0.00	0.00	0.00	0.11
Hatchery							
DNFH	0.24	0.00	0.19	0.19	0.26	0.05	0.07
South Fork							
General production	0.69	0.08	0.00	0.00	0.00	0.00	0.23
Local brood	0.67	0.07	0.07	0.03	0.00	0.03	0.13

NFCR cannot migrate upstream because the river is blocked by Dworshak Dam. Therefore, these fish tended to linger at the confluence of the NFCR and Clearwater River where they are vulnerable to broodstock trapping and harvesting. A higher proportion of DNFH steelhead returned to their release location in SY2017 than in SY2018 because DNFH increased their trapping rates (i.e., the amount of time the trap was open to allow steelhead to move into the hatchery) in SY2018 (Table 3). The fates for the remaining DNFH steelhead were harvested, possibly harvested, died or shed their tag, or their fate was unknown. The fates in the Clearwater River of SFCR fish varied between the general production and local brood groups. In SY2017, 58% of general production steelhead returned to the SFCR and 74% of local brood returned to the SFCR. In SY2018, the general production and local brood steelhead had similar return rates (68%) to the SFCR (Table 3). During both spawn years, roughly 10-20% of the local brood and general production steelhead entered the SFCR between October and November. The remaining fish from SY2017 primarily moved into the SFCR between February and April and between January and February in SY2018. In both spawn years, a small proportion of the general production and local brood SFCR steelhead remained in the NFCR. In SY2017, one general production SFCR steelhead entered the DNFH trap. During the two study years, kelting behavior was detected for 50-64% of the Potlatch steelhead, 42-44% of the Lochsa steelhead, 14-18% of the DNFH fish, and 27% of the SFCR steelhead.

Although straying was not observed for either wild or hatchery steelhead in the Clearwater River basin, some of them temporarily overshot their natal tributary or release location. The data that were collected from the fixed stations and mobile tracking surveys documented that Potlatch. DNFH. and SFCR steelhead overshot their natal or release locations in both spawn years. Instances where Lochsa steelhead overshot their tributaries in the Lochsa River were not observed because the single monitoring site in the Lochsa River prevented the detection of overshooting. In both spawn years, radio-tagged Potlatch steelhead (36–43%) overshot the Potlatch River up to 41 rkm (mean \pm SD; SY2017: 15.0 \pm 11.7 rkm; SY2018: 18.5 \pm 11.1 rkm). The DNFH steelhead (19-31%) overshot their release location near the mouth of the NFCR up to 49 rkm (SY2017: 14.9 ± 12.9 rkm; SY2018: 23.3 ± 19.9 rkm). As for the SFCR steelhead, 11% and 7% of the fish overshot the SFCR in SY2017 and SY2018, respectively, with fish relocated as far as 4 rkm $(3.5 \pm 0.1 \text{ rkm})$ upriver.

DISCUSSION

The migration timing of wild and hatchery steelhead into rivers is highly variable among systems and among different groups within populations (Copeland et al. 2017). The migration timing of steelhead into freshwater systems is dependent on water temperature, discharge, and photoperiod (Robards and Quinn 2002; Keefer et al. 2008), and the differences among populations are largely genetic (Hess et al. 2016). Previous research conducted by Keefer et al. (2008) suggested that hatchery steelhead from the Clearwater River migrated through the Columbia and Snake rivers later than wild steelhead from the Clearwater River. The authors also estimated that approximately 53% of Clearwater River steelhead overwintered in Lower Granite Reservoir, and an additional 25% overwintered in the lower Columbia River. Unlike Keefer et al. (2008), we found that the majority of wild and hatchery steelhead arrived in the Clearwater River around the same general period in the fall (i.e., September to November). The exception was that about half of the Lochsa steelhead arrived in the Clearwater River in the fall and the other half arrived the following spring.

Once fish had entered the Clearwater River, their movement varied by season. The movement rates for the fish averaged from 0.3 to 4.7 km/d depending on the season and spawn year, and it was much lower than what has been reported in other systems. For instance, steelhead in the Dean and Fisher channels, British Columbia, were detected moving upstream and downstream with an average travel time of 17.2 km/d in the late spring and early summer (Ruggerone et al. 1990). Haynes et al. (1986) observed high movement rates (12.0 km/d) for steelhead in the Great Lakes during the spring, as did English et al. (2006) for steelhead in the mid-Columbia River (20.0 km/d) and Skeena River, British Columbia (12.0–16.0 km/d). However, it is important to note that differences in the movement rates of steelhead across systems could be attributable to the size of the river and the distance to spawning grounds (i.e., fish in the Clearwater River were near their final destinations). Also, it is important to mention that the movement rates observed in the Clearwater River were likely biased downward because individual fish were not continuously tracked over a 24-h period and not all of the fish were detected on each mobile tracking event. Furthermore, the rates for steelhead movements in the Clearwater River were lowest in the winter of SY2017 and in the spring of SY2018. The dissimilar patterns were likely the result of differences in water temperature and discharge. Previous research that was conducted in the Columbia River showed that steelhead movements were low in the winter and increased in the spring with the onset of warming water temperatures (Keefer et al. 2008). Similar results of increased movement with warming waters have been reported for other anadromous salmonids (e.g., Chinook Salmon Oncorhynchus tshawytscha and Coho Salmon O. kisutch; Dittman and Quinn 1996; Caudill et al. 2007; Quinn et al. 2016). The discharge and

water temperature in the Clearwater River during the winter of SY2017 were lower than flows and temperature in the winter of SY2018. Therefore, steelhead started to display increased movements earlier in the year in SY2018 than in SY2017.

Knowledge of the distributions of wild and hatchery steelhead is important because overlap could increase ecological interactions and may warrant changes in fisheries management (Mackey et al. 2001). The spatial and temporal overlap of wild and hatchery steelhead populations in the Clearwater River was minimal-occurring in very few locations during a short period. Wild Potlatch and Lochsa steelhead primarily used the lower Clearwater River in the fall and winter. Hatchery steelhead were also found in the lower Clearwater River in the early fall, but the majority of these fish had moved upriver towards the NFCR and SFCR by late fall and early winter. Unfortunately, few studies have published information on the overlap of populations of wild and hatchery steelhead. Using radiotelemetry to investigate the spatial distributions of wild- and hatchery-origin steelhead, Mackey et al. (2001) conducted a study in Forks Creek, Washington, and reported substantial overlap among the populations. Nelson et al. (2005) used radiotelemetry to describe the distribution of prespawning wild and hatchery steelhead in the Vedder-Chilliwack River, British Columbia. They found considerable overlap in the spatial distributions of wild and hatchery steelhead. Differences among the studies are likely attributable to variations in the distances between wild steelhead spawning grounds and the release locations for hatchery fish, which ultimately influences the spatial distributions. In our study, the hatchery stocking locations and the wild steelhead spawning grounds were not in close spatial proximity (they were ~37-96 rkm apart). Nevertheless, the distributional overlap between wild and hatchery steelhead in the Clearwater River was minimal and it occurred for a short period in the early fall.

An understanding of angler distribution in relation to wild and hatchery steelhead distributions is critical for fisheries management. We are unaware of any studies that have evaluated the relationship between angler and steelhead distributions. Consequently, our understanding of angler dynamics in steelhead fisheries is limited. In the Clearwater River, steelhead and angler distributions overlapped during both years, but the extent and location of overlap varied by season. An important finding from this study was that little overlap was observed between wild steelhead and anglers. Some minimal overlap of anglers and wild (i.e., Potlatch and Lochsa) steelhead occurred during the late summer and early fall in the lower Clearwater River, but by mid-October (when harvest is allowed throughout the river), anglers concentrated most of their effort in and around the NFCR and SFCR. A change in the distribution of anglers was undoubtedly a response to

the distribution of hatchery steelhead, given that angler distributions mirrored those of hatchery fish throughout the fall, winter, and spring of both spawn years. Moreover, the majority of angling effort was focused near the mouth of the NFCR and DNFH where hatchery fish congregate. Not only are densities of steelhead high near the NFCR, but anglers recognize that steelhead that are returning to the NFCR and DNFH are hatchery fish and thus available for harvest. Although information on angler distributions is lacking for other steelhead fisheries, studies conducted in other fisheries have suggested that anglers focus effort in the areas with high fish abundance (Post et al. 2008; Askey et al. 2013; Melstrom et al. 2017). For instance, Hunt (2005) identified general attributes that influenced an angler's selection of a fishing site, which included quality of fishing locations (e.g., those with large quantities of fish). Similarly, Post and Parkinson (2012) suggested that anglers allocate effort in locations that have high fish densities in British Columbia. Likewise, Pitman et al. (2019) stated that a higher abundance of steelhead was associated with increased angling effort in the Skeena River watershed, British Columbia.

Whether or not steelhead congregate in a specific location, summer-run steelhead overwinter in freshwater, such as the Clearwater River, before moving to tributaries to spawn (Busby et al. 1996; Robards and Quinn 2002). Information about the timing of escapement (i.e., the movement of fish out of the Clearwater River steelhead fishery) of steelhead to their natal tributaries and release locations is useful for estimating the proportion of fish that remain in a fishery. Previous research conducted in the Clearwater River has suggested that hatchery steelhead (i.e., from the DNFH) were not detected at DNFH and the NFCR until early March (Pettit 1977). Byrne et al. (1992) reported that hatchery steelhead returned to their release location six weeks earlier than did wild steelhead in the Clearwater River. In our study, the timing of escapement was relatively consistent across spawn years but varied among steelhead groups. Slight differences in the timing of steelhead escapement across years were likely related to differences in water temperature and discharge (Bjornn and Reiser 1991; Robards and Quinn 2002). Wild and hatchery steelhead were observed returning to their natal tributaries and release locations at high rates, but the timing varied among groups. For instance, DNFH steelhead returned to the NFCR and DNFH from fall through winter and were vulnerable to the Clearwater River steelhead fishery until it closed. The majority of SFCR steelhead were detected moving into the SFCR in late winter and early spring, but a small group of fish escaped the main-stem Clearwater River fishery in the fall. Furthermore, wild steelhead were less likely to spend as much time in the Clearwater River fishery as the hatchery steelhead. The majority of Potlatch steelhead moved out of the Clearwater River before spring when the fishery closed. Lochsa steelhead were detected migrating through the Clearwater River and into the Lochsa River starting in April and continuing through June when the Clearwater River steelhead fishery was closed.

In the Clearwater River, the final fate of the fish varied widely among the tagging groups and the data for the fates of the wild and hatchery steelhead provided insight on the distributions of the fish and hatchery effectiveness (e.g., supporting a sustainable fishery). Previous research has assessed the fates of radio-tagged fish to better understand in-river survival and the distribution of fishes (Keefer et al. 2004, 2017; English et al. 2005; Nelson et al. 2005). Keefer et al. (2005) evaluated the fate of radio-tagged steelhead in the Columbia and Snake rivers and found that the majority of steelhead escaped to spawning grounds. The remaining fish were reported as being classified either as harvested by anglers or as unknown. The primary limitation to our study was the inability to relocate all of the radio-tagged steelhead and provide a final fate. Unfortunately, given the size of the Clearwater River basin, relocating all of the steelhead during every tracking event was not possible without additional telemetry equipment and personnel. Nevertheless, most of the wild steelhead in our study returned to their natal tributary and the remaining fish were classified as unknowns, with the exception of a few fish that were categorized as dead or shed tag. Some of the wild steelhead with unknown fates (particularly Potlatch steelhead in SY2018) were last detected in the main-stem Clearwater River while they were making a downstream, postspawn migration; however, they did not return to their natal tributary. Most of the hatchery steelhead returned to their release location, and the remaining fish fell into the other six fate categories. Angler harvests of steelhead from the SFCR were likely low because among the local brood and general production populations there were supplemental (adipose fin intact) steelhead. Steelhead that were classified with an unknown fate could have been harvested (recreational or tribal) and not reported, had transmitters that malfunctioned, or strayed and were never relocated. In the Clearwater River, unknown hatchery fish were likely harvested but not reported since both recreational and tribal anglers (tribal fisheries can harvest hatchery and wild steelhead) were common in the areas where the most steelhead were last relocated.

The fate of local brood and general production steelhead is of particular interest with regard to hatchery effectiveness. In the Clearwater River, SFCR hatchery steelhead (i.e., the local brood and general production steelhead) were more likely to home to release sites than to their rearing location. Slaney et al. (1993) studied hatchery-raised steelhead in the Chilliwack River, British Columbia, and found that homing was most influenced by rearing location. Nelson et al. (2005) evaluated the behavior and survival of wild- and hatchery-origin steelhead in Vedder-Chilliwack River, British Columbia, and observed a considerable amount of hatchery steelhead returning to the hatchery rather than to their release locations. The return of hatchery steelhead to their release or rearing locations is likely influenced by the spatial proximity of the two locations such that if the two locations are relatively close to one another then steelhead are likely to return to their rearing locations (Slaney et al. 1993; Dittman and Quinn 1996; Nelson et al. 2005). Also, the amount of time that hatchery smolts spend in the river prior to emigrating to the ocean influences their ability to home to their release site (Keefer and Caudill 2013). Furthermore, local brood and general production populations of steelhead were highly successful in homing to the SFCR, which is ideal for maintaining a steelhead fishery in the SFCR.

Natal homing and nonnatal straving of salmonids has been well studied, and most studies have shown that behaviors are highly variable among populations and hatchery groups (Quinn 1993; Dittman et al. 2010; Westley et al. 2013). Schroeder et al. (2011) studied steelhead in 16 rivers along the Oregon coast and found that steelhead strayed. Similar results were found among salmonids in southeast Vancouver Island, British Columbia (Labelle 1992), and in the Clackamas River, Oregon (Kostow et al. 2003). In the Clearwater River, straying of radiotagged wild and hatchery steelhead was not detected, despite extensive mobile tracking of tributaries, flight surveys, and tracking via PIT tag antenna arrays. Overshooting natal tributaries or release locations is quite common in summer steelhead populations. Richins and Skalski (2018) evaluated eight populations of steelhead in the Columbia and Snake River basins and found that some fish overshot their natal tributaries up to 120 rkm. Boggs et al. (2004) observed that $\sim 30\%$ of the steelhead passing over Columbia and Snake River dams eventually fell back and returned to downriver tributaries or hatcheries (i.e., overshoot fallbacks). The wild and hatchery steelhead in our study were estimated to have overshot their natal tributaries or release locations anywhere from 4 to 49 rkm.

Management Implications

The results from this study have important implications for the conservation and management of wild and hatchery steelhead. We evaluated the return rates of steelhead to their natal tributaries and release locations, which ultimately provided information about hatchery effectiveness. During SY2017, very few radio-tagged DNFH steelhead were collected at the DNFH trap and used for broodstock even though a large proportion of these fish returned to the NFCR and the DNFH. Our observations prompted hatchery managers to increase trapping rates in SY2018 and confirmed the need for the hatchery to collect a higher proportion of fish for brood stock. Consequently, more radio-tagged DNFH steelhead were collected at the DNFH trap in SY2018 than in SY2017. Additionally, local brood and general production steelhead returned to the SFCR at high rates. The return of hatchery steelhead to the SFCR is ideal for providing opportunities for anglers to harvest steelhead throughout the main-stem Clearwater River and the SFCR. Future management could use either local brood or general production steelhead for hatchery stocking in the SFCR.

Due to the diversity of life history strategies (e.g., migration timing, distribution) of wild and hatchery steelhead in the Clearwater River, the management of steelhead is complex. Steelhead cannot be categorized into a single group that is descriptive of their typical timing into the Clearwater River or the spatial and temporal distributions of wild and hatchery fish. In fact, differences in the timing, distribution, and movement among wild populations and hatchery groups were common. The spatial and temporal distributions of steelhead in the Clearwater River suggest that there is very little overlap between wild and hatchery steelhead. This observation will increase the ability of fishery managers to further direct angling effort away from wild fish and towards hatchery steelhead. The findings from our study indicate that as hatchery steelhead enter the Clearwater River, anglers tend to follow the fish as they move upriver towards their release locations. As such, anglers focus their efforts on hatchery steelhead that concentrate in large numbers near the NFCR and DNFH. This suggests that the Clearwater River has a highly compartmentalized fishery. Further observations have revealed that wild steelhead, once in the Clearwater River, return at very high rates to their natal tributaries and straying is minimal for both wild and hatchery steelhead. The information that was collected during this study suggests that current fishing regulations in the Clearwater River are providing for a diversity of angling opportunities while conserving wild steelhead and offering opportunities to harvest hatchery fish. Based on the current results, future management and conservation efforts for steelhead may consider the population-specific behaviors and distributions of both wild and hatchery steelhead when implementing fishing regulations.

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REFERENCES

- Askey, P. J., E. A. Parkinson, and J. R. Post. 2013. Linking fish and angler dynamics to assess stocking strategies for hatchery-dependent, open-access recreational fisheries. North American Journal of Fisheries Management 33:557–568.
- Behnke, R. J. 2002. Trout and salmon of North America. Free Press, New York.
- Bjornn, T. C., and D. W. Reiser. 1991. Habitat requirements of salmonids in streams. Pages 83–138 in W. R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society, Special Publication 19, Bethesda, Maryland.
- Boggs, C. T., M. L. Keefer, C. A. Peery, and T. C. Bjornn. 2004. Fallback, reascension, and adjusted fishway escapement estimates for adult Chinook Salmon and steelhead at the Columbia and Snake River dams. Transactions of the American Fisheries Society 133:932–949.
- Busby, P. J., T. C. Wainwright, E. J. Bryant, L. J. Lierheimer, R. S. Waples, F. W. Waknitz, and I. A. Lagomarsino. 1996. Status review update for West Coast steelhead from Washington, Idaho, Oregon, and California. NOAA Technical Memorandum NMFS-NWFSC-27.
- Byrne, A., T. C. Bjornn, and J. D. McIntyre. 1992. Modeling the response of native steelhead to hatchery supplementation programs in an Idaho River. North American Journal of Fisheries Management 12:62–78.
- Caudill, C. C., W. R. Daigle, M. L. Keefer, C. T. Boggs, M. A. Jepson, B. J. Burke, R. W. Zabel, T. C. Bjornn, and C. A. Peery. 2007. Slow dam passage in adult Columbia River salmonids associated with unsuccessful migration: delayed negative effects of passage obstacles or condition-dependent mortality? Canadian Journal of Fisheries and Aquatic Sciences 64:979–995.
- Chapman, D. W. 1986. Salmon and steelhead abundance in the Columbia River in the nineteenth century. North American Journal of Fisheries Management 115:662–670.
- Columbia Basin Research. 2016. Columbia and Snake rivers hydroelectric project information [online database]. University of Washington School of Aquatic and Fishery Sciences, Seattle. Available: www.cbr. washington.edu. (September 2019).
- Congleton, J. L., W. J. Lavoie, C. B. Schreck, and L. E. Davis. 2000. Stress indices in migrating juvenile Chinook Salmon and steelhead of

wild and hatchery origin before and after barge transportation. Transactions of the American Fisheries Society 129:946–961.

- Copeland, T., M. W. Ackerman, K. K. Wright, and A. Byrne. 2017. Life history diversity of Snake River steelhead populations between and within management categories. North American Journal of Fisheries Management 37:395–404.
- Copeland, T., J. D. Bumgarner, A. Byrne, P. Cleary, L. Denny, J. L. Hebdon, C. A. Peery, S. Rosenberger, E. R. Sedell, G. E. Shippentower, C. Warren, and S. P. Yundt. 2015. Reconstruction of the 2012/2013 steelhead spawning run into the Snake River basin. Report to the Bonneville Power Administration, Portland, Oregon
- Dittman, A. H., D. May, D. A. Larsen, M. L. Moser, M. Johnston, and D. Fast. 2010. Homing and spawning site selection by supplemented hatchery- and natural-origin Yakima River spring Chinook Salmon. Transactions of the American Fisheries Society 139:1014–1028.
- Dittman, A. H., and T. P. Quinn. 1996. Homing in Pacific salmon: mechanisms and ecological basis. Journal of Experimental Biology 199:83–91.
- Eiler, J. H. 2012. Tracking aquatic animals with radio telemetry. Pages 163–188 *in* N. S. Adams, J. W. Beeman, and J. H. Eiler, editors. Telemetry techniques: a user guide for fisheries research. American Fisheries Society, Bethesda, Maryland.
- English, K. K., W. R. Koski, C. Sliwinski, A. Blakley, A. Cass, and J. C. Woodey. 2005. Migration timing and river survival of late-run Fraser River Sockeye Salmon estimated using radiotelemetry techniques. Transactions of the American Fisheries Society 134:1342–1365.
- English, K. K., D. Robichaud, C. Sliwinski, R. F. Alexander, W. R. Koski, T. C. Nelson, B. L. Nass, S. A. Bickford, S. Hammond, and T. R. Mosey. 2006. Comparison of adult steelhead migrations in the mid-Columbia hydrosystem and in large naturally flowing British Columbia rivers. Transactions of the American Fisheries Society 135:739–754.
- Gilbreath, L. G., L. R. Basham, and E. Slatick. 1976. Distribution, age, and size of tagged adult steelhead trout in the Snake River drainage. Marine Fisheries Review 39:14–18.
- Harmon, J. R. 2003. A trap for handling adult anadromous salmonids at Lower Granite Dam on the Snake River, Washington. North American Journal of Fisheries Management 23:989–992.
- Haynes, J. M., D. C. Nettles, K. M. Parnell, M. P. Voiland, R. A. Olson, and J. D. Winter. 1986. Movements of rainbow steelhead trout (*Salmo* gairdneri) in Lake Ontario and a hypothesis for the influence of spring thermal structure. Journal of Great Lakes Research 12:304–313.
- Hess, J. E., J. S. Zendt, A. R. Matala, and S. R. Narum. 2016. Genetic basis of adult migration timing in anadromous steelhead discovered through multivariate association testing. Proceedings of the Royal Society Biological Sciences 283:20153064.
- Higgins, J. J. 2004. Tests for trends and associations. Pages 145–194 in C. Crockett and A. Day, editors. Introduction to modern nonparametric statistics. Brooks/Cole, Cengage Learning, Belmont, California.
- Hunt, L. M. 2005. Recreational fishing site choice models: insights and future opportunities. Human Dimensions of Wildlife 10:153–172.
- Johnson, J. H., and P. A. Kucera. 1985. Summer–autumn habitat utilization of subyearling steelhead trout in tributaries of the Clearwater River, Idaho. Canadian Journal of Zoology 63:2283–2290.
- Jones, M. C., J. S. Marron, and S. J. Sheather. 1996. A brief summary of bandwidth selection for density estimation. Journal of the American Statistical Association 91:401–407.
- Keefer, M. L., C. T. Boggs, C. A. Peery, and C. C. Caudill. 2008. Overwintering distribution, behavior, and survival of adult summer steelhead: variability among Columbia River populations. North American Journal of Fisheries Management 28:81–96.
- Keefer, M. L., and C. C. Caudill. 2013. Homing and straying by anadromous salmonids: a review of mechanisms and rates. Reviews in Fish Biology and Fisheries 24:333–368.

- Keefer, M. L., M. A. Jepson, T. S. Clabough, E. L. Johnson, S. R. Narum, J. E. Hess, and C. C. Caudill. 2017. Sea-to-sea survival of late-run adult steelhead (*Oncorhynchus mykiss*) from the Columbia and Snake rivers. Canadian Journal of Fisheries and Aquatic Sciences 75:331–341.
- Keefer, M. L., C. A. Peery, W. R. Daigle, M. A. Jepson, S. R. Lee, C. T. Boggs, K. R. Tolotti, and B. J. Burke. 2005. Escapement, harvest, and unknown loss of radio-tagged adult salmonids in the Columbia River–Snake River hydrosystem. Canadian Journal of Fisheries and Aquatic Sciences 62:930–949.
- Keefer, M. L., C. A. Peery, R. R. Ringe, and T. C. Bjornn. 2004. Regurgitation rates of intragastric radio transmitters by adult Chinook Salmon and steelhead during the upstream migration in the Columbia and Snake rivers. North American Journal of Fisheries Management 24:47–54.
- Kostow, K. E., A. R. Marshall, and S. R. Phelps. 2003. Naturally spawning hatchery steelhead contribute to smolt production but experience low reproductive success. Transactions of the American Fisheries Society 132:780–790.
- Labelle, M. 1992. Straying patterns of Coho Salmon (Oncorhynchus kisutch) stock from southeast Vancouver Island, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 49:1843–1855.
- Lee, J. E., G. C. White, R. A. Garrott, R. M. Bartmann, and A. W. Alldredge. 1985. Accessing accuracy of a radiotelemetry system for estimating animal locations. Journal of Wildlife Management 49:658– 663.
- Lindland, R., S. Pettit, and M. Renigold. 1976. Annual survey of salmon and steelhead sport fishery harvest in Idaho. Idaho Department of Fish and Game, Federal Aid in Fish Restoration, Project F-18-R-22, Boise.
- MacCrimmon, H. R. 1971. World distribution of Rainbow Trout (Salmo gairdneri). Journal of the Fisheries Board of Canada 28:663– 704.
- Mackey, G., J. E. McLean, and T. P. Quinn. 2001. Comparisons of run timing, spatial distribution, and length of wild and newly established hatchery populations of steelhead in Forks Creek, Washington. North American Journal of Fisheries Management 21:717–724.
- Mallet, J. 1974. Inventory of salmon and steelhead resources, habitat, use and demands. Idaho Department of Fish and Game, Federal Aid in Fish Restoration, Project F-58-R-1, Boise.
- Marvin, D. P. 2012. The success of the Columbia Basin passive integrated transponder (PIT) tag information system. American Fisheries Society, Symposium 76, Bethesda, Maryland.
- McCleave, J. D., J. H. Power, and S. A. Rommel Jr. 1978. Use of radio telemetry for studying upriver migration of adult Atlantic Salmon (*Salmo salar*). Journal of Fish Biology 12:549–558.
- McCormick, J. L., M. C. Quist, and D. J. Schill. 2012. Effect of survey design and catch rate estimation on total catch estimates in Chinook Salmon fisheries. North American Journal of Fisheries Management 32:1090–1101.
- McCormick, J. L., D. Whitney, M. C. Quist, and D. J. Schill. 2015. Evaluation of angler reporting accuracy in an off-site survey to estimate statewide steelhead harvest. Fisheries Management and Ecology 22:134–142.
- McCutcheon, C. S., E. F. Prentice, and D. L. Park. 1994. Passive monitoring of migrating adult steelhead with PIT tags. North American Journal of Fisheries Management 14:220–223.
- Mellas, E. J., and J. M. Haynes. 1985. Swimming performance and behavior of Rainbow Trout (*Salmo gairdneri*) and White Perch (*Morone americana*): effects of attaching telemetry transmitters. Canadian Journal of Fisheries and Aquatic Sciences 42:488–493.
- Melstrom, R. T., D. H. Jayasekera, T. A. Boyer, and C. Jager. 2017. Scale heterogeneity in recreationists' decision making: evidence from a site choice model of sport fishing. Journal of Outdoor Recreation and Tourism 18:81–87.

- Moyle, P. B. 1994. The decline of anadromous fishes in California. Conservation Biology 8:869–870.
- Munn, M. D., and M. A. Brusven. 2003. The influence of Dworshak Dam on epilithic community metabolism in the Clearwater River, U.S.A. Hydrobiologia 513:121–127.
- Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16(2):4–21.
- Nelson, T. C., M. L. Rosenau, and N. T. Johnston. 2005. Behavior and survival of wild and hatchery-origin winter steelhead spawners caught and released in a recreational fishery. North American Journal of Fisheries Management 25:931–943.
- NPCC (Northwest Power and Conservation Council). 2003. Clearwater subbasin plan. NPCC, Portland, Oregon.
- Pacific States Marine Fisheries Commission. 2016. PTAGIS (Columbia Basin PIT Tag Information System) [online database]. Pacific States Marine Fisheries Commission, Portland, Oregon. Available: www.pta gis.org. (September 2019).
- Pettit, S. W. 1977. Comparative reproductive success of caught-andreleased and unplayed hatchery female steelhead trout (*Salmo gairdneri*) from the Clearwater River, Idaho. Transactions of the American Fisheries Society 106:431–435.
- Pitman, K. J., S. M. Wilson, E. Sweeney-Bergen, P. Hirshfield, M. C. Beere, and J. W. Moore. 2019. Linking anglers, fish, and management in a catch-and-release- steelhead trout fishery. Canadian Journal of Fisheries and Aquatic Sciences 76:1060–1072.
- Pollock, K. H., J. M. Hoenig, C. M. Jones, D. S. Robson, and C. J. Greene. 1997. Catch rate estimation for roving and access point surveys. North American Journal of Fisheries Management 17: 11–19.
- Post, J. R., and E. A. Parkinson. 2012. Temporal and spatial patterns of angler effort across lake districts and policy options to sustain recreational fisheries. Canadian Journal of Fisheries and Aquatic Sciences 69:321–329.
- Post, J. R., L. Pearson, E. A. Parkinson, and T. Van Kooten. 2008. Angler numerical response across landscapes and the collapse of freshwater fisheries. Ecological Applications 18:1038–1049.
- Quinn, T. P. 1993. A review of homing and straying of wild and hatchery-produced salmon. Fisheries Research 18:29–44.
- Quinn, T. P., P. McGinnity, and T. E. Reed. 2016. The paradox of "premature migration" by adult anadromous salmonid fishes: pattern and hypotheses. Canadian Journal of Fisheries and Aquatic Sciences 73:1015–1030.
- R Development Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: http://www.Rproject.org/. (September 2019).
- Ramstad, K. M., and C. A. Woody. 2003. Radio tag retention and tagrelated mortality among adult Sockeye Salmon. North American Journal of Fisheries Management 23:978–982.
- Richins, S. M., and J. R. Skalski. 2018. Steelhead overshoot and fallback rates in the Columbia/Snake River basin and the influence of hatchery and hydrosystem operations. North American Journal of Fisheries Management 38:1122–1137.
- Robards, M. D., and T. P. Quinn. 2002. The migratory timing of adult summer-run steelhead in the Columbia River over six decades of environmental change. Transactions of the American Fisheries Society 131:523–536.

- Ruggerone, G. T., T. P. Quinn, I. A. McGregor, and T. D. Wilkinson. 1990. Horizontal and vertical movements of adult steelhead trout, *Oncorhynchus mykiss*, in the Dean and Fisher channels, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 47:1963–1969.
- Schroeder, K. R., R. B. Lindsay, and K. R. Kenaston. 2011. Origin and straying of hatchery winter steelhead in Oregon coastal rivers. Transactions of the American Fisheries Society 130:431–441.
- Sheppard, D. 1972. The present status of the steelhead trout stocks along the Pacific coast. Pages 519–556 in D. H. Rosenberg, editor. A review of the oceanography and renewable resources of the Northern Gulf of Alaska. University of Alaska, Fairbanks.
- Simpkins, D. G., and W. A. Hubert. 1998. A technique for estimating the accuracy of fish locations identified by radiotelemetry. Journal of Freshwater Ecology 13:263–268.
- Simpson, J. C., and T. C. Bjornn. 1965. Methods used to estimate salmon and steelhead harvest in Idaho. Proceedings of the Annual Conference of the Western Association of State Game and Fish Commissioners 89:1–21.
- Slaney, P. A., L. Berg, and A. F. Tautz. 1993. Returns of hatchery steelhead relative to site of release below an upper-river hatchery. North American Journal of Fisheries Management 13:558–566.
- Smith, B. D., B. R. Ward, and D. W. Welch. 2000. Trends in wild adult steelhead (*Oncorhynchus mykiss*) abundance in British Columbia as indexed by angler success. Canadian Journal of Fisheries and Aquatic Sciences 57:255–270.
- Stark, E. J., A. Byrne, P. J. Cleary, J. Ebel, T. Miller, D. Nemeth, S. Rosenberger, E. R. Sedell, and C. Warren. 2018. Snake River basin 2015–2016 steelhead run reconstruction. Report to Bonneville Power Administration, Portland, Oregon.
- Townsend, R. L., D. Y. Asuda, and J. R. Skalski. 1997. Evaluation of the 1996 predictions of the run-timing of wild migrant spring/summer yearling Chinook in the Snake River basin using program realtime. University of Washington, Seattle.
- U.S. Office of the Federal Register. 1997. Endangered and threatened wildlife and plants; listing of several evolutionary significant units of West Coast steelhead, final rule. Federal Register 62:159(August 18, 1997):43937–43954.
- Vokoun, J. C. 2003. Kernel density estimates of linear home ranges for stream fishes: advantages and data requirements. North American Journal of Fisheries Management 23:1020–1029.
- Vokoun, J. C., and C. F. Rabeni. 2005. Home range and space use patterns of Flathead Catfish during the summer-fall period in two Missouri streams. Transactions of the American Fisheries Society 134:509–517.
- Waples, R. S., O. W. Johnson, P. B. Aebersold, C. K. Shiflett, D. M. VanDoornik, D. J. Teel, and A. E. Cook. 1993. A genetic monitoring and evaluation program for supplemented populations of salmon and steelhead in the Snake River basin. National Oceanic and Atmospheric Administration, Seattle.
- Wertheimer, R. H., and A. F. Evans. 2005. Downstream passage of steelhead kelts through hydroelectric dams on the lower Snake and Columbia rivers. Transactions of the American Fisheries Society 134:853–865.
- Westley, P. A. H., T. P. Quinn, and A. H. Dittman. 2013. Rates of straying by hatchery-produced Pacific salmon (*Oncorhynchus* spp.) and steelhead (*Oncorhynchus mykiss*) differ among species, life history types, and populations. Canadian Journal of Fisheries and Aquatic Sciences 70:735–746.