Evaluating the Migration and Spawning Behaviors of Upper Columbia Summer Steelhead Using Radio Telemetry and Accelerometer Biotelemetry

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Authorization to Submit Thesis

Authorization to Submit thesis of Nate Fuchs, submitted for the degree of Master of Science with a Major in Natural Resources and titled "Evaluating the Migration and Spawning Behaviors of Upper Columbia Summer Steelhead Using Radio Telemetry and Accelerometer Biotelemetry" has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

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Abstract

Understanding population migration trends is of importance to fisheries managers especially for populations listed under the Endangered Species Act. In recent years passive integrated transponder tags (PIT) have been increasingly used to monitor tributary escapement of adult summer Steelhead (*Oncorhynchus mykiss*) returning to the Upper Columbia River, but do not fully characterize behavior and survival. We evaluated the migration, overwintering distribution, and survival of Upper Columbia using radio telemetry. Additionally we monitored post spawn exit from spawning tributaries ("kelting" rate). We also analyzed the efficacy of newly developed, gastrically implanted acceleration sensing tags applied with the primary aim of detecting spawning behaviors. Using video observations, we collected movement data from telemetered steelhead within an enclosure. We developed criteria for analyzing acceleration data to infer the behaviors of tagged steelhead, released *at-liberty* in the natural environment. Monitoring of *at-liberty* steelhead revealed spawning behaviors similar to those observed among enclosure steelhead.

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Dedication

I would like to dedicate this work to my wife Marlene and my son Caleb who was born during the time this research was taking place. I hope he can one day learn from me in the way that I have already learned so much from him. Without the sacrifices made possible by my wife, this thesis would not exist. She is the true author of this work.

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Chapter 1: General Introduction to Upper Columbia Summer Steelhead

Pacific Steelhead (*Oncorhynchus mykiss*) provide important economic, recreational, and societal benefits. Consequently, declines in many steelhead populations have raised concerns among fisheries managers (Busby et al., 1996). The existence of man-made hydroelectric barriers resulting in passage difficulties (Caudill et al., 2007; Keefer et al. 2004), loss of habitat (Nehlsen et al., 1991), overharvest, altered selective pressures (Robards & Quinn, 2002), reduction in fitness related to hatchery genetic introgression (Araki et al., 2007; Christie et al., 2014; Waples, 1991), and environmental variation related to climate changes are among factors implicated in the declines (Farrell et al 2008; Quinn & Adams 1996; Ruckelhaus et al., 2002; Ruesch et al., 2012; Wenger et al., 2011). Many steelhead populations are listed under the Endangered Species Act (ESA), including the Upper Columbia Steelhead Evolutionary Significant Unit (ESU), which is the focus of this thesis. Recovery planning and implementation under the ESA requires research on the migration, distribution, overwintering and spawning behaviors, and estimation of escapement to tributaries.

Steelhead populations or runs in the Pacific Northwest initiate upstream migration from marine habitats in summer or winter (hereafter, summer and winter Steelhead). Winter Steelhead reside in the ocean before entering freshwater during winter months (December – March), while summer Steelhead enter freshwater during summer months. Summer Steelhead overwinter in freshwater at or near spawning sites or may complete migrations to spawning grounds in the spring after overwintering in downstream river reaches (Shapovalov & Taft, 1954). Winter Steelhead populations generally spawn in coastal streams, while summer Steelhead populations are generally found further inland, east of the Cascade Crest in the Columbia Basin (Behnke, 1992). Steelhead returning to the Upper Columbia River have a summer run life history, with entry to the Columbia River during summer prior to full sexual maturation, a prolonged period of dormancy through winter in spawning tributaries or in main stem habitats, followed by a final migration to spawning grounds (Jepson et al., 2013; Keefer et al., 2008a; Keefer et al., 2017).

Whereas most Pacific salmon species are semelparous and die after spawning, steelhead exhibit an iteroparous (repeat spawning) life history where they return to the ocean after spawning and may repeat the process in future years (Dodson, 1997; Keefer et al., 2008b). This life history strategy is thought to minimize the chance of reproductive failure, associated with unfavorable environmental factors or limited access to conspecific mates by spreading the risk over multiple breeding seasons and maximize an individual fishes lifetime reproductive success (Seamons & Quinn, 2010; Wilbur & Rudolf, 2006). Steelhead that survive and initiate an outmigration after spawning are referred to as kelts. Summer Steelhead typically exhibit a reduced frequency of kelting (or low kelting rate), compared to coastal winter Steelhead, thought to be the result of the lengthy migration distance and limited energetic reserves commonly associated with summer Steelhead (Keefer et al., 2008b; Leider et al., 1986). Survival during downstream migration is also low for kelts in the impounded Columbia River system (Keefer et al., 2014; Keefer et al., 2017). Nonetheless, monitoring the rate of iteroparity in steelhead from the basin is the first step toward establishing baseline estimates (Stelle, 2016).

The Upper Columbia basin encompasses the hydrologic drainage above the Yakima-Columbia River confluence (~560 rkm from estuary). The headwaters of the Upper Columbia basin extend from the crest of the Cascade Mountain range (north-central Washington State, USA) along the west, to Osoyoos Lake to the north (British Columbia Province, Canada). Historically Pacific Salmon (*Oncorhynchus spp.*) migrated much further upstream than present, and currently, anadromous migrations in the Columbia River end at Chief Joseph Dam (~870 rkm). Upper Columbia River Steelhead are currently listed as threatened under the ESA, a status reaffirmed in 2011 (NMFS, 2003). Four primary tributaries of the Upper Columbia River remain accessible to anadromous fishes

(Wenatchee, Entiat, Methow, and Okanogan Rivers), each with its own federally recognized sub population (Ford et al., 2011). Low abundance of natural-origin spawners and poor returning adult escapement were among the reasons for listing (Ford et al., 2011; Good et al., 2005). Currently, there are six artificial propagation programs releasing hatchery reared juvenile steelhead at different locations throughout the basin. Juveniles released from hatchery must pass between four and nine hydroelectric dams before arrive at the Columbia River estuary. Adult steelhead returning to the Methow and Okanogan Rivers ascend a total of 9 major hydroelectric dams before accessing their natal spawning tributaries. Adult escapement to the Upper Columbia River is monitored at main-stem dams, beginning with Priest Rapids Dam. Tributary escapement monitoring is currently conducted by Washington Department of Fish and Wildlife using an array of more than thirty in-stream passive integrated transponder (PIT) arrays. PIT arrays detections are used to estimate escapement abundance, aid in estimation of juvenile recruitment per spawner (A. Murdoch, Personal communication, March 2018), and in maintaining target proportion hatchery-origin spawner (PHOS) ratios required for each population under recovery planning (Stelle, 2016).

Relatively few radio telemetry studies involving steelhead have been conducted in the Upper Columbia River basin. English et al. (2006) compared migration times among steelhead populations with and without dams. Fallback and dam passage rates, and kelt rate estimates were also reported by the research group (English et al., 2001; English et al., 2003). However, these studies were conducted prior to development of the in-stream PIT array network and did not address overwintering distribution and survival for Upper Columbia steelhead. Tributary escapement is currently estimated using a PIT-based patch occupancy model, but tributary specific escapement estimates require validation by alternate means. Upper Columbia Steelhead overwintering habitat use, mortalities, migration and survival post-wintering are also poorly described.

Redd counts are commonly used to verify salmonid escapement and population trends (Maxell, 1999; Beland, 1996) and can provide an index of effective population size and to infer spawning success (Rieman & McIntyre, 1996; Rieman & Myers, 1997; Gallagher & Gallagher, 2005). However, Upper Columbia Summer Steelhead spawn during high flow spring months (March-early June), resulting in poor visibility and uncertainty with regards to redd count estimates. Steelhead enter tributaries during spring or prior to overwintering (fall) and females select a site, with suitable substrate for oviposition. Female salmon create a redd by tailing against the substrate to dig a wide depression in the stream bed which ranges in size from 2.4 to 11.2 m^2 (Orcutt et al., 1968). Salmonid redds are easily visible under ideal visibility conditions because they contrast with the surrounding substrate. Biotelemetry methods that aid in quantifying the timing and distribution of spawning and redd construction with relying on direct observation could improve estimates of spawning success and recruitment to tributary populations.

My thesis has two primary objectives aimed at increasing our understanding of steelhead migration, distribution, escapement to spawning grounds, and behavior on spawning grounds. The first was to monitor steelhead migration from Priest Rapids Dam through the Upper Columbia basin to overwintering locations, estimate survival, and estimate escapement to and from (kelting) tributaries using radio telemetry techniques. The second objective was to develop a method to quantify spawning behavior of fishes using a newly developed intragastrically implanted accelerometer tag. We used video observations of behavior and telemetry records to demonstrate that acceleration records can be used to infer spawning and other behaviors from the magnitude, frequency, and variation in acceleration of tagged steelhead.

Thesis Structure

The thesis is comprised of three chapters including this introductory chapter. The second chapter evaluates the migration of Upper Columbia Summer Steelhead, monitoring the overwintering distribution and survival, and escapement to spawning tributaries. Chapter two is intended for submission to the *North American Journal of Fisheries Management.* The third chapter develops a framework for analyzing acceleration records from biotelemetry tags by evaluating the effectiveness of newly developed intragastrically implanted accelerometer tags to detect steelhead spawning behaviors. Chapter three is intended for submission to *Methods in Ecology and Evolution*.

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Chapter 2: Evaluating the Migration Behaviors of Upper Columbia Summer Steelhead Using Radio Telemetry

Abstract

Monitoring migrating adult anadromous fish species is essential for determining run sizes, harvest quotas, and reach-specific survival. Estimating survival of returning adult summer-run Steelhead (*Oncorhynchus mykiss*) is particularly important as these fish display a distinctive life history strategy in which they overwinter for several months in freshwater prior to a final migration to spawning grounds in spring. Upper Columbia River Steelhead overwinter in both the main-stem river and spawning tributaries. A key metric is the proportion of hatchery and natural origin adult steelhead returning to tributaries, currently estimated using a PIT tag-based patch occupancy model. We conducted a radio telemetry study to track migration behaviors, distribution, and survival of adult summer Steelhead in the Upper Columbia basin with the goal of characterizing behavior, distribution and survival during overwintering, spawning and post-spawn periods, and to generate independent tributary escapement estimates to compare to PIT-derived estimates. A total of 807 steelhead were tagged with both intragastrically implanted coded radio transmitters and passive integrated transponder (PIT) tags and released at Priest Rapids Dam during 2015 and 2016. During both years, 165 tagged fish (~20% of total tagged sample) were detected falling back below Priest Rapids Dam without reascension. A total of 548 tagged fish were detected overwintering in the Upper Columbia basin with 296 in main-stem reaches (54%) and 252 in tributaries (46%). The majority of main-stem overwintering occurred relatively high in the impounded system above Wells Dam across both study years (56%-57%), while the highest percentage of tributary overwintering fish were detected in the Wenatchee River (39%) in 2015 and the Methow River (56%) in 2016. Annual

main-stem overwinter survival was 74% to 82% and was lower than survival in tributaries (87%-91%), a pattern that contrasts with steelhead overwintering in the impounded lower Snake River. Total estimated survival from release at Priest Rapids Dam to spawn for radio-tagged steelhead was 70% to 74% in 2016 and 2017, respectively. Post-spawn kelt outmigration, defined as fish detected leaving tributaries, indicated 56% of steelhead surviving to the spawning period attempted downstream migration as kelts. Of these, 63 and 65 were female (68% and 80% of steelhead surviving to the spawning period in 2016 and 2017, respectively). A combined total of 17 kelts were ultimately detected a Bonneville Dam by PIT arrays where detection is incomplete, indicating a minimum downstream kelt survival rate of 10%. Overall, the results highlight how different overwintering behaviors affect adult steelhead distribution and survival prior to spawning, which in turn may affect tributary-specific escapement and production. More broadly, contrasting patterns of mortality between the Upper Columbia and Snake Rivers suggest landscape patterns of river networks may affect steelhead overwinter site selection behaviors and mortality risk.

Introduction

Understanding the migration behaviors of anadromous fishes is crucial for fisheries management, especially for those listed under the Endangered Species Act (ESA). Anadromous fish species have complex migratory behaviors, out-migrating to the ocean only to return to their freshwater basin of origin and spawn after a period of years. These migrations are cued by environmental stimuli that vary among the life histories of the species and populations of interest (Quinn & Adams, 1996).

Many Pacific Salmonid populations (*Oncorhynchus spp.*) are currently depressed in abundance (Gustafson et al., 2007; Nehlsen et al., 1991). A range of negative anthropogenic factors have been implicated in contributing to these declines (Busby et al., 1996; Ruckelshaus et al., 2002) including difficulties in navigating man-made hydroelectric barriers (Keefer et al., 2004; Keefer et al., 2017), the loss of genetic diversity and subsequent reduction in fitness brought about by natural and hatchery origin genetic introgression (Araki et al., 2008; Chilcote, 2003; Christie et al., 2014; Quinn, 1993), harvest rates and selection pressures (Heino & Godoe, 2002; Ratner & Lande, 2001), habitat loss (Pess et al., 2002; Paulsen & Fisher, 2001), and climate impacts to marine and freshwater life history stages (Cooney & Brodeur, 1998; Quinn & Adams, 1996). Future climate and landscape changes will likely alter migratory behavior and survival in salmonids, illustrating the importance of establishing baseline understanding of the timing, distribution, and survival of migratory populations (Beamish & Bouillon, 1993; Farrell et al., 2008; Ruesch et al., 2012).

Anadromous Steelhead (*Oncorhynchus mykiss*) populations along the North American west coast exhibit complex life histories split most commonly between Winter (coastal, *O. mykiss irideus*) and Summer (interior/redband, *O. mykiss gairdneri*) lineages, associated with their seasonal entry timing into freshwater systems and the distance they must travel in order to reach natal spawning tributaries (Busby et al., 1996; Withler, 1966). Summer Steelhead returning to the Columbia River display particularly complex migrations with entry to freshwater in later summer and early fall, dormant holding during winter (overwintering) in spawning tributaries, main-stem rivers, and major river dam reservoirs, followed by a post wintering migration to spawning grounds (Jepson et al., 2013; Keefer et al., 2008a; Keefer et al., 2009). Steelhead can display highly variable migratory behaviors, and instances of straying, fallback, and re-ascension over dams and into/out of tributaries are common (Boggs et al., 2004; Keefer et al., 2004). These behaviors may effect individual survival and fitness for steelhead moving through impounded river systems, where individual fish may pass as many as eight (Snake River) or nine major dams (Upper Columbia River) before reaching spawning grounds (English et al., 2006; Caudill et al., 2007).

Upper Columbia Summer Steelhead undertake among the longest of freshwater migrations (Busby et al., 1996) and are currently listed as threatened under the ESA, a status reaffirmed in 2011 (NMFS, 2003). Low abundance of natural origin spawners and poor returning adult escapement were among the reasons for listing (Ford et al., 2011; Good et al., 2005). Like many other declining salmon populations, Upper Columbia River Steelhead artificial propagation programs have been used to boost return spawner abundance to mitigate for natural origin fish declines associated with migration passage difficulties and habitat loss (Waples, 1991). Estimating the proportion of hatchery and natural origin fish returning to Upper Columbia tributaries is necessary to monitor and maintain established annual Proportional hatchery origin spawner (PHOS) escapement goals to each tributary population (Stelle, 2016). Currently, escapement to tributaries is estimated for steelhead using a PIT tag-based mark-re-sight patch occupancy model, but model rates have not been validated. Similarly, survival in the Columbia River and tributaries prior to spawning or during post-spawn out-migrating (kelting) is largely unknown because these parameters are challenging to estimate with PIT technology.

Overwintering holding behavior has been hypothesized as an adaptation allowing migrations to spawning habitats that would otherwise be inaccessible during spring high flow events or low temperature regimes (Robards & Quinn, 2002; Trudel et al., 2004). Instances of overwintering mortality (including pre-spawn mortality) are commonly observed among steelhead prior to spawning and a variety of mechanisms causing this mortality have been proposed (Keefer et al., 2008a; Bowerman et al., 2016). Thus, determining spatio-temporal patterns in overwintering locations and survival are the first steps in identifying and mitigating for mortality factors.

Notably, PIT-tag records have revealed overwintering and prespawning behavior to be complex. However, identifying specific behaviors and assigning fish to specific spawning populations post overwintering can be difficult based on PIT records, given existing PIT detectors, the variability in overwintering locations, and fallback and straying behaviors (Keefer et al., 2008a). Radio telemetry methods afford researchers a more comprehensive spatial understanding of migratory timing, periodic holding behaviors, and dam passage frequencies (i.e., fallback, overshoot, etc.) than are otherwise possible with the use of passive integrated transponder (PIT) tags alone.

In contrast to most other Pacific salmonids, iteroparity (repeat spawning) in steelhead is commonly documented throughout their range, and is thought to increase the lifetime fitness of an individual fish, and can increase population productivity (Fleming, 1998; Fleming & Reynolds, 2003; Wilbur & Rudolf, 2006). Prior research conducted on Snake River and Lower Columbia River Steelhead estimated iteroparity rates of 0.5 to 1.2% and 2.9 to 9.0%, respectively (Keefer et al., 2008b). More recent research suggests current full-cycle freshwater sea-to-seas survival rates for Snake River Steelhead to be 0.01 to 0.02% (Keefer et al., 2017) excluding post-spawn marine survival, consistent with the general observation that iteroparity rates of interior population are typically lower than coastal populations. Maintaining and/or increasing iteroparity rates are an important component of steelhead ESA recovery planning. Surprisingly few telemetry studies have been conducted focusing on steelhead in the Upper Columbia River, aside from those intended to identify upstream main-stem dam passage and migration rates (English et al., 2001; English et al., 2006; Keefer et al., 2008b).

The overall aim of this research was to quantify migration behaviors, seasonal habitat use and survival for adult Upper Columbia Steelhead to address key information needs for harvest, hatchery, and ESA recovery planning and management. The specific objectives of this study were to: 1) to validate tributary PIT array based escapement estimates using radio telemetry tags and methods; 2) estimate the proportion of hatchery and wild steelhead within each tributary population; 3) monitor the migration, distribution, and overwinter survival by rearing origin of tagged steelhead in both tributary and Columbia River habitats; 4) identify overwinter holding habitats and behavior; and 5) monitor post-spawn and kelting movements and down-stream survival in the Upper Columbia River basin.

Methods

PIT and Radio-Tagging

Summer Steelhead were collected and radio-tagged at the Off Ladder Adult Fish Trap (OLAFT) facility at Priest Rapids Dam from 6-July through 10-November 2015 and between 6-July and 2-November in 2016 by WDFW personnel. Sampling occurred three days per week during daylight hours (8:00 AM to 5:00 PM). Fish entered the OLAFT volitionally, where they were sorted from non-target species though a series of hydraulic diversions. Once positively identified, steelhead were immediately directed into a sampling tank. Radio-tagged fish were tagged in proportion to the run at a rate of one out of six fish in 2015 regardless of origin (i.e., both wild run and hatchery fish received tags). The steelhead return in 2016 was approximately 33% of historic ten year average Priest Rapids return escapement, and consequently the tag rate was increased from one in six to as high as one in every three fish to achieve the target sample size. Steelhead not previously PIT tagged were injected with a 12 mm PIT tag into the pelvic girdle (Gibbons & Andrews, 2004) and fish sex was determined using an ultrasound device (Martin et al., 1983). As sampling rates differed between both years of tagging we used a Kolmogorov-Smirnov (K-S) test to determine if there was a significant difference in the passage date (i.e., tagging date) distribution of fish that were PIT tagged vs those that were radio-tagged and released at Priest Rapids Dam for each sampling year (Smirnov, 1939). Fish were anesthetized using tricaine-S methanosulfate (MS-222) at a concentration of 50 mg/L in a 100 gallon sampling tank (378 L). Once fish were sedated, measurements of length (cm), and visual markings (hatchery or wild) were recorded and handled fish were scanned for a PIT tag. Each steelhead received an intragastrically implanted 3-volt coded transmitter (model MCFT2-3A, Lotek Wireless, Newmarket, Ontario) that included a label with reward information ($50 US) with which anglers could report the location and date of tagged fish recaptures. The manufacturer reported radio tag life was 52 weeks and tag size was 16 mm x 46 mm at 10 grams weight in air. The radio tag antenna was bent around the jaw allowing it to trail alongside the body. Known hatchery origin fish were determined by the presence of adipose or pelvic fin clips, floy tags, and/or coded wire tags. Unmarked adults were presumed to be of natural origin. Scales were taken to confirm rearing origin estimated from adipose fin clips using scale pattern analysis (Bernard & Myers, 1996). Scales were taken above the lateral-line between the dorsal and adipose fins. Once tagged, all fish were released into an approximately 20m long holding tank adjacent to the fish ladder, where tagged fish could recover and volitionally return to the fish ladder at Priest Rapids Dam and resume upstream migration.

Fixed Telemetry Sites

A total of 28 fixed site receivers were installed and distributed throughout the Upper Columbia River basin between July-2015 to June-2017 with a maximum of 25 fixed sites operating at any given time throughout the entire season (Figure 2.1). Upper Columbia tributary fixed sites were deemed priority sites for meeting the objectives of this study and thus each tributary mouth was outfitted with two fixed site receivers to minimize the chances of missing detections should one receiver fail, and to attempt to infer movement direction of radio-tagged steelhead. The upper tributaries were also outfitted with one or two fixed sites (depending on tributary width) to allow estimation of detection efficiency of tributary mouth sites, by detecting fish missed initially at the lower fixed sites. Two fixed sites were located near Chief Joseph Hatchery, which is a commonly used overwintering area for steelhead returning to the Upper Columbia that overshoot tributaries prior to later entry. Receivers were downloaded a minimum of once per month, and heavily used sites were downloaded weekly or multiple times per week. Most sites were outfitted with four element yagi antennas, with the exception of sites located at Rock Island (1-4RI), Wanapum (1WP), and Priest Rapids Dams (1-4PR) that were outfitted with six element antennas. Fixed sites located at Chief Joseph Hatchery were also outfitted with six element antennas (1CJ and 2CJ). Monitoring was limited to PIT tag arrays at Rocky Reach and Wells Dams, which typically have high upstream PIT array detection efficiencies. Not all sites were monitored continuously during both years of the study. The Twisp River sites (1TP, 2TP, and 3TP) were not installed until 14-March 2016, although mobile tracking was conducted prior to installation. Lower river main-stem dam fixed site receivers (at Priest Rapids and Wanapum Dams) were removed in March 2016 to augment the Twisp River detection sites and subsequently returned to the dams prior to July 2016 tagging. Fixed sites 4PR, 1CJ, and 1TP were removed prior to the 2016 tagging as these sites were deemed redundant after the 2015 tagging season (Table 2.1).

Mobile Tracking

Mobile tracking augmented the fixed site detections used to estimate detection efficiency, and was used to evaluate overwinter survival and migration behavior into tributaries. Mobile monitoring took place via truck, raft, and jet boat from November-2015 through May-2016 for the 2015 return year (hereafter ‘run year’), and from November-2016 through May-2017 for the 2016 run year. Over the course of the study, mobile tracking was conducted by University of Idaho, Colville Confederated Tribes, and Washington Department of Fish and Wildlife (Methow and

Wenatchee offices) personnel. Mobile tracking by truck was the most commonly used method throughout the study with major river tributaries (i.e., Wenatchee) and smaller order tributaries surveyed at least once a month in the early season, and multiple times per month during spawning months (March-May 2016 and 2017). A total of 135 truck and raft based mobile tracking events occurred between 13-November 2015 and 20-May 2016 (2015 run year), and 81 truck and raft mobile tracking events occurred from 22-November to 30-May 2017 (2016 run year). Days spent mobile tracking tributaries were variable given differing tributary lengths and the proximity of the road to tributaries (relative ease of receiving detections). Each major Upper Columbia tributary was tracked a minimum of once per month starting January 2016 and was repeated again in January 2017. Boat tracking was exclusively used in monitoring the main-stem Columbia River between all dam reserviors from Priest Rapids Dam to Chief Joseph Dam (~875 river kilometers from the Columbia River Estuary), with a total of 24 boat tracking days occurring between 2-Febuary and 14-April 2016 (2015 run year), and 26 boat tracking days occurring between 26-January and 22-May 2017 (2016 run year). Each reach between main-stem dams was similarly tracked once per month starting in February 2016, one boat tracking day constituted approximately 6 hours of continuous tracking time. Tracking also took place downstream of Priest Rapids Dam to Ice Harbor Dam on the Snake River (rkm 538). Mobile tracking by raft was conducted primarily in tributaries where road access near the river was poor, or when a high degree of accuracy in determining fish location was necessary, and took place most commonly in Upper Wenatchee and Methow Rivers.

Data Analysis

After fish were tagged and released, a database was compiled that included fish traits measured at tagging, detections from radio telemetry fixed sites, PIT tag detections, and mobile tracking records. PIT detection data was downloaded from the Pacific States Marine Fisheries

Commission PIT Tag Information System database (PTAGIS; www.ptagis.org) and used to supplement radio telemetry fish detection histories. All data sets included location and date relational data, from which we were able to create general migration histories for each fish. Telemetry records were compiled and used to score and quantify several behaviors and metrics as described below, and to classify individual steelhead fates. Key parameters included fallback behavior below Priest Rapids, tributary entry, mortalities estimates, overwinter distribution and survival, survival to spawn, and post-spawn movements including kelting behaviors. In order to synthesize detection histories to address the specific objectives previously outlined, several smaller datasets were also generated (i.e., tributary PIT array detections for escapement estimate validation). Additional data used for analysis included 2015-16 Upper Columbia harvest creel estimates (WDFW, unpublished data) and return tag angler harvest locations.

Upper Columbia Fallbacks

Radio-tagged steelhead fallbacks were identified by one or more detections at sites upstream of Priest Rapids Dam followed by detection at an out of basin PIT tag array downstream (e.g., Snake River), detection at the lower Priest Rapids Dam radio telemetry fixed site (1PR), mobile tracking detection below Priest Rapids Dam down to Ringold Hatchery, or if they were reported harvested or collected at hatcheries downstream of Priest Rapids Dam.

Tributary Entry Detections

Detection events at tributary fixed sites were classified as either tributary entries occurring during the fall upriver migration (detections pre 1-Jan) or those that occurred after overwintering (post 1-Jan). The total number of steelhead detected entering a tributary differed from the number of steelhead assigned as spawning in that tributary in some cases because: 1) fish detected in a tributary were sometimes later detected falling back out of the Upper Columbia River system; 2) fish were detected in a tributary, detected back downstream and then in an alternate tributary; and 3) fish were detected entering a tributary, then moved back downstream, overwintered in the main-stem Columbia and then returned to the original tributary in spring. All steelhead detected entering a tributary were used for estimation of fixed site detection efficiencies regardless of final spawning location to maximize sample size for detection efficiency calculations. Fish with multiple tributary detections served to bolster the number of total unique fish detections and hence were included in detection efficiency calculations.

Tributary Fixed Site Detection Efficiencies

In order to estimate tributary escapement and detection efficiencies of lower tributary radio telemetry fixed site arrays, the total number of unique fish detections at each tributary were complied. Detections at in-stream PIT arrays, mobile tracking detections, and additional radio telemetry fixed sites located midway up tributaries were also quantified to determine the number of fish that entered a tributary undetected by radio telemetry fixed sites. Lower tributary radio telemetry fixed sites were installed at or near the mouth of tributaries and within ± 20m of lower tributary instream PIT tag arrays.

Detection efficiencies (DE_i) of lower tributary radio telemetry fixed site arrays locations (*i*) during upstream migration were calculated for the four major Upper Columbia River tributaries separately for fall and spring monitoring periods. DE_i was calculated as the total number of fish detected by lower tributary radio telemetry fixed sites (LF_i) then dividing by the sum total number of fish known to have entered the tributary (TF_i) using detections at all upstream sites including, in-stream PIT arrays (PIT_i), mobile tracking detections (Mob_i), and additional upstream fixed site radio telemetry arrays (UF_i).

$$DE_i = \frac{LF_i}{TF_i} = \frac{LF_i}{PIT_i + Mob_i + UF_i}$$

Upper and lower bound 95% confidence interval limits were estimated as described in Newcombe (1998). Fish known to have shed radio transmitters, and fish that were reported harvested in a tributary below tributary fixed sites were censored from the analyses.

Comparison of Origin Composition by Tributary Using PIT and Radio Tags

We calculated minimum estimates of tributary entry for radio-tagged steelhead and estimated the total entry rates by adjusting for seasonal detection efficiency. The number of radio-tagged fish, grouped by season and origin, was divided by the respective seasonal tributary specific detection efficiency. The sum of the seasonal estimates (i.e., total of unique hatchery and wild steelhead) was used to estimate the proportion of hatchery and wild steelhead that entered each year. Chi-square tests (X^2) were used to test for significant differences in the proportion of hatchery and wild fish estimated using PIT tag arrays and proportions generated using radio telemetry fixed sites after adjusting for detection efficiency (adjusted). Steelhead proportions (by rearing origin) escaping to lower tributary PIT array locations were provided by Washington Department of Fish and Wildlife, using a PIT tag-based patch occupancy model (WDFW, unpublished data).

Unknown Fates, Fall Monitoring Period

Telemetry records were used to identify overwintering holding and classify fates. Previous research conducted by Keefer et al. (2008a) determined 1-Jan to be a reasonable date for the onset of the overwintering period for Lower Columbia and Snake River Summer Steelhead because movements among locations were rare. We used the same date in tributary entry timing detections because the majority of fish had reached their overwintering locations by this date, where they were repeatedly detected “holding” in the same location throughout the wintering period and on into the spring spawning season. A subset of the tagged fish were last detected prior to 1-Jan and subsequently never detected further in either main-stem pools or tributaries anywhere within the system, or by any detection method (radio telemetry, PIT array, or mobile tracking). These fish with unknown final fate were classified as fall natural mortalities, but we note this subset may have included the following fates: 1) harvested and unreported; 2) indirect harvest mortalities; 3) died as a result of handling or tagging; 4) fallback below Priest Rapids Dam and not detected further; and 5) shed tags and were never detected further. The approach is conservative because it provides an upper limit on mortality/lowest limit on survival; we evaluate the potential magnitude of subcomponents of the unknown/mortality class and the effects on estimated rates in the Discussion.

We also estimated seasonal survival by estimating mortality for several sources. We accounted for unreported harvest based on creel survey harvest rates (available for 2015 tagged sample only) and the proportion of radio tags returned by anglers. These fate categories were estimated with the aim of distinguishing between natural mortality ('Mortalities Prior to Wintering') and other forms of mortalities that occurred prior to 1-Jan. We assigned unknown fish with last records in the fall to these categories as nearly all reported steelhead harvest occurred prior to 1-Jan 2016. Expansion of harvest to locations of unreported fish harvest were estimated using the overall harvest rate distribution provided by Washington Department of Fish and Wildlife creel data (WDFW, unpublished data).

Overwintering Locations, Mortalities, and Survival

Overwintering locations (Columbia River main-stem or tributary) were assigned based on the location where a tagged fish was detected with most frequency after 1-Jan but before the spawning period onset of 15-March. We used 15-March as the spawning period onset based on similar research conducted in the Snake River where sampling of post-spawn kelts occurred during mid-

March (Keefer et al., 2008b). Overwintering locations within the Columbia River were split between Upper Columbia River dam reservoirs and tributaries. Overwintering fates were assigned by evaluating the detection history of tagged fish overwintering within the main-stem Upper Columbia River and in tributaries. Steelhead were considered to have survived the overwintering period if detected: 1) having moved greater than 0.5 km from their overwintering location at any time after 1-Jan; 2) passing a dam; 3) at any PIT array (instream or at dams); or 4) at any radio telemetry fixed site. We note overwintering mortalities may have included other fate categories as noted above for fall mortalities and hence mortality estimates may be overestimates.

Spawning Locations

Spawning locations were assessed at the tributary level given that steelhead spawning has been documented in all four of the major Upper Columbia basin tributaries including the Entiat, Methow, Okanogan, and Wenatchee Rivers. We defined the spawning onset date to be 15-March (2016 and 2017, respectively) as many fish had entered tributaries or were detected having made movements prior to this date. This date is consistent with the known onset of spawning for summer Steelhead, and steelhead redd presence has been documented on or very near this date (WDFW, personal communication), and was observed occasionally while conducting mobile tracking. Foster Creek located in Wells Pool near Chief Joseph Dam was the only minor tributary to the Columbia River that was not outfitted with a radio telemetry site, but was monitored by PIT array. Unmonitored potential spawning sites include the lower Chelan River, Chelan Hatchery outfall, Wells Dam tailrace outfall (Rocky Reach Pool), Eastbank Hatchery outfall (Rock Island Pool), and Crab Creek (Priest Pool). Spawning in the Columbia River is also possible but has never been rigorously documented. Very limited spawning is also possible in the small tributaries flowing into Wanapum Dam and Rock Island Dam reservoirs (Baldwin, 2007).

Overwintering Survival and Survival to Spawning Period

Radio-tagged steelhead overwintering survival was estimated as 1-mortality given survival to the beginning of winter (1-Jan). Overwintering survival was calculated separately for fish overwintering in Columbia River dam reservoirs and for those that overwintered in tributaries. Mortalities were determined using individual fish detection histories and should be considered upper-bound estimates, as determination of survival was dependent on fish being detected by radio telemetry fixed sites, PIT tag arrays, and mobile tracking detections. Fish were classified as having survived to the spawning period ('Tributary Survival to Spawn') if detection histories indicated they had survived the overwintering period or were detected entering tributaries at some point after 1-Jan ('Spring Tributary Entry Fish'). Steelhead classified as reported harvest and fallbacks below Priest Rapids Dam prior to 1-Jan were not included in survival rate estimates. Steelhead that overwintered in the Upper Columbia and fallbacks detected after 1-Jan were included as overwinter survivors. Survivors detected moving post-wintering with unknown spawning locations were included in survival to spawn estimates given that many of these were detected in major tributaries and it is likely a subset of these fish entered tributaries undetected.

Kelting Rates and Kelt Survival to Bonneville Dam

General migration detection histories were used to classify individual fish detected in tributaries as kelts if the adult fish was subsequently detected moving down river and ultimately detected arriving at the mouth of their returning tributary (by in-stream PIT array or fixed site) on or after 15 -March. March 15 was selected based on similar work conducted in the Lower Columbia-Snake River basins (Keefer et al. 2008b). The minimum kelt survival rate through the Lower Columbia River was estimated from fish detected to or downstream of Bonneville Dam. All kelts detected at Bonneville Dam were detected by the Bonneville corner collector (BCC), the juvenile bypass facility

(B2J), or by the estuary towed array (TWX); spillways were not monitored for downstream movement. Steelhead kelt detection efficiency at Bonneville Dam will not be available until summer/fall of 2018 when kelts return to spawn.

Results

PIT and Radio-Tagging

A total of 400 and 407 adult summer Steelhead were radio-tagged at the Priest Rapids Dam OLAFT facility in 2015 and 2016, respectively. The sampling periods ranged from 6-July 2015 and 10-November in 2015 and 6-July 2016 through 2-November 2016. A total of 13,766 and 5,927 fish were counted at Priest Rapids Dam during the sample periods (2015 and 2016, respectively); tagged fish constituted 2.91% of the run passing during the sample period in 2015, and 6.87% in 2016 (http://www.cbr.washington.edu/dart/query/adult_daily). The distributions of radio-tagged steelhead and the total steelhead passage over Priest Rapids Dam were variable among both sampling years (Figure 2.2, 2015 run year; Figure 2.3, 2016 run year). Of the total fish tagged in 2015, 264 were of hatchery origin and 136 were of wild origin, comprising 66% and 34% of the total fish tagged, respectively (Table 2.2). A total of 321 hatchery and 86 wild fish were tagged in 2016, comprising 79% and 21% of the total tagged fish, respectively. Results of the Kolmogrov-Smirnov (K-S) Test indicated no significant difference in the distribution timing of fish tagged by PIT and radio telemetry tags in either year of sampling (P = 0.978 for 2015 return, P = 0.149 for 2016 return).

Summary of Distribution and Fates of Radio-Tagged Sample

All fish radio-tagged and released at Priest Rapids Dam in 2015 were assigned a final fate based on individual detection histories, and were split between those detected above Priest Rapids

Dam in the Upper Columbia and below (i.e. Fallbacks). A total of 642 radio-tagged steelhead had detection histories and final detections suggesting they remained above Priest Rapids Dam within the Upper Columbia after release (329 in 2015, and 313 in 2016, respectively; Tables 2.3 and 2.4; Figure 2.4). Of these, a total of 166 were presumed mortalities ('unknowns') based on last detections, and split between pre-wintering and overwintering groups (86 in 2015, and 80 in 2016). 334 radio-tagged steelhead (41% of the total sample) were presumed to have survived overwintering and were detected moving during spawning months in Upper Columbia River tributaries (171 in 2016, and 163 in 2017), of these 174 were detected kelting from their respective tributaries (92 in 2016, and 82 in 2017) with 17 ultimately detected at Bonneville Dam. An additional subset of Upper Columbia radio-tagged steelhead were never detected entering a tributary but were presumed to have survived based on movement detections within the Upper Columbia main-stem during the spawning period (17 in 2016, and 35 in 2017). During both years steelhead were monitored, a total of 114 were reported harvested, collected at hatcheries, or estimated as harvested and unreported, the majority of which occurred above Priest Rapids Dam in the Upper Columbia (55 in 2015, and 35 in 2016). The remaining 165 steelhead were detected below Priest Rapids Dam and assigned a fate as fallbacks (Figure 2.5). Below, we provide details on behavior, survival and distribution during the fall migration, overwintering, spawning and post-spawn periods.

Upper Columbia River Radio-Tagged Steelhead Fallbacks

A total of 71 fish (18% tagged in 2015) and 94 fish (23% tagged in 2016) at Priest Rapids Dam were detected falling back below Priest Rapids Dam without re-ascension (Table 2.5). Combined for both years of this study, fallbacks represent (20%) of the total tagged fish released at Priest Rapids Dam ($n_{tagged}=807$). A majority of fallbacks were last detected or reported in the Snake River basin and tributaries in both 2015 (61%) and 2016 (62%) run years. The remaining 28 fish (39%) in 2015 and 36 fish (38%) in 2016 were detected or reported in the Middle Columbia River, tributaries, or at hatcheries below Priest Rapids Dam.

Tributary Return Timing

Among steelhead remaining above Priest Rapids Dam that were recorded in a tributary, a majority moved into tributaries prior to 1-January in both years (overall proportions 2015: 73%, n = 241; 2016: 73%, n = 246) with the exception of the Entiat River (20-39% annual entry prior to 1-Jan). Percentages of seasonal tributary entry were similar between hatchery and wild samples in both years (Table 2.6). A small percentage (~5%) of tagged fish were detected entering an Upper Columbia tributary other than their final return tributary detection, i.e., they were apparent temporary strays and were assigned based on their final tributary entry. Foster Creek was monitored by PIT tag array, and mobile tracked in 2016, where the small sample suggested similar entry rates after 1-Jan.

Fish Harvest and Collection Locations in 2015-2016

In total, 70 (17% of the 2015 tagged sample) and 47 (11.5% of 2016 tagged sample) radio tags were returned (Table 2.7). The reported harvest rate for the 2015 run year was lower in the Upper Columbia River (18.0%; 42/233) for radio-tagged adipose clipped steelhead (n=233), compared to the reported harvest rate among steelhead that fellback below Priest Rapids Dam (19.7%; 14/71). The majority of fates assigned to steelhead with returned tags in 2015 were the result of harvest (81%; Table 2.8), while steelhead fates assigned to returned tags in 2016 were most commonly the result of collection at hatcheries (74%) due to the suspension of the steelhead fishery for the 2016 run year in the Upper Columbia River (Table 2.9).

A total of 64 radio tags were returned by anglers or collected at hatcheries or weirs during the 2015 run season, not including 4 fish caught and released and 1 tag found on the bank of the Methow River, as well as 1 additional tag pulled from a fish in the Umatilla River that was released. The majority of tagged fish harvested in Upper Columbia tributaries were harvested from the Methow River, where 20 hatchery fish and 1 wild fish were reported harvested by anglers. Radio tags were returned by anglers, hatchery staff, various departmental employees, and private-citizens.

Adjusting for Unreported Harvest of Radio-Tagged Fish 2015

The minimum harvest rates obtained from reported harvest were compared to estimates accounting for unreported harvest. The reported harvest rate in the radio-tagged sample for the 2015 run year (18.0%) was lower than the estimate obtained by WDFW during a creel survey (20.1% from 1,588 reported harvest of an estimated 7,907 adipose-clipped hatchery steelhead available for legal harvest; WDFW, unpublished data). We therefore estimated an overall adjusted harvest rate assuming the WDFW rate (i.e., 233 * 0.201 = 47 total harvest) and tributary-specific rates. This adjustment was not applied to the 2016 run year given the restricted fishing effort. An additional two hatchery origin radio-tagged fish were detected at private residences but were not reported and represent the only tags with last known detections repeatedly detected out of water. As only 44% of the anglers that reported harvesting radio-tagged steelhead reside in the Upper Columbia basin (based on addresses submitted by anglers) it is plausible that not all unreported radio tags were be detected during surveys.

Fish Harvest and Collection Locations in 2016-2017

The 2016 Upper Columbia River Steelhead fishery was suspended given the low adult escapement to the basin for that year. With the exception of 1 fish harvested in the Upper Columba River (tribal harvest) the 5 remaining reported harvested fish were harvested at locations below

Priest Rapids Dam (1 in Hanford Reach, 4 in Snake River and tributaries) (Tables 2.8 and 2.9). A total of 41 radio tags were returned by anglers or collected at hatcheries or weirs during the 2016 run season. With the exception of 1 fish harvested in the Upper Columba River (tribal harvest) the 5 remaining reported harvested fish were harvested at locations below Priest Rapids Dam.

Mortalities Prior to Wintering Period

The majority of steelhead assigned as fall mortalities had final detections in main-stem Upper Columbia reservoirs (75% and 81% for 2015 and 2016, respectively) while tributary fall mortalities were most commonly last detected in the Methow River (68% of total tributary assigned fall mortalities). A total of 37 radio-tagged fish (both years, independently) last detected prior to 1-Jan were classified as fall mortalities and constitute 9.2% and 9.1% of the total tagged samples for 2015 and 2016, respectively (Table 2.10). Hatchery fish were more commonly detected as mortalities during both years and constituted 86% and 72% of the total fall mortalities (2015 and 2016, respectively).

Overwintering Distribution

A large majority of radio-tagged steelhead were detected alive at the beginning of the overwintering period (85.3%, 548 of the 642 steelhead remaining above Priest Rapids Dam). A greater proportion of fish overwintered in the Columbia River than tributaries (133 and 163, vs 115 and 137, main-stem and tributary overwintering steelhead) representing ~54% of the total overwintering fish during each consecutive year (2016 and 2017, respectively). Wells Dam reservoir had the highest percent (31%) of total overwintering fish across all monitored locations during both years. Methow River overwintering fish represented 17% and 26% of the total tributary overwintering fish (2016 and 2017, respectively) and represented the majority of the total tributary overwintering fish in 2017, but not 2016. Conversely, Wenatchee River overwintering fish represented 18% of total fish in 2016, but only 5% in 2017 (Table 2.11). No fish were consistently observed overwintering in the Entiat River in either year, although some were detected entering prior to 1-Jan. Hatchery origin fish made up the majority of overwintering fish in every location with the exceptions of the Wenatchee River (both years) and Rocky Reach reservoir (2016).

Overwintering Mortality

Estimated overwinter mortality was 16.8% (92 overwintering fish of the total 548 combined overwintering fish; 19.7% and 14.3% for 2015 and 2016 run years, respectively; Table 2.12). Seventy percent of overwinter mortalities were last detected in main-stem Upper Columbia reservoirs rather than tributary overwintering locations (both years). Hatchery origin fish made up the majority of overwintering mortalities (~80% and 84%) in both years (2016 and 2017, respectively). Wells Dam reservoir had the highest proportion of mortalities of any one location (0.29 and 0.30) across both years of the study (2016 and 2017, respectively).

Overwintering Survivors

Of the total 548 radio-tagged steelhead 456 made movements indicating of survival after the overwintering holding period, and represented 80% and ~86% of the total overwintering steelhead in the 2015 and 2016 run years, respectively (199 during winter 2016, and 257 during winter 2017). Of 296 total main-stem overwintering fish 232 were observed having survived overwintering (78%), while of 252 tributary overwintering fish 88% (n=224) were detected having survived within the tributaries. Hatchery origin fish exhibited lower overwintering survival (73% and 85%) versus wild fish (90% and 89%) throughout the Upper Columbia basin and between years (2016 and 2017, respectively). Hatchery fish overwintering in reservoirs had lower survival rates (69% and 78%) versus wild fish (84% and 94%) across both years (2016 and 2017, respectively). Tributary overwintering survival of hatchery fish was lower than wild fish in 2016 (80% vs 96%) but not in 2017

(92% vs 83% hatchery and wild, respectively). Total counts and proportions of fish having survived overwintering by location and rearing origin in 2016 and 2017 are provided in Appendix 1 (see Supplemental Data chapter 2).

Spring Tributary Entry of Steelhead Overwintering in the Main-Stem

Radio-tagged steelhead observed to have overwintered in the main-stem Columbia River and survive to the beginning of the spawning period exhibited three primary behaviors: 1) detected entering a tributary; 2) detected falling back out of the Upper Columbia River basin; or 3) detected moving within the Columbia River but not detected entering a tributary. A total of 121 steelhead overwintering in the main-stem Columbia were detected entering tributaries after the overwintering period (52% of main-stem overwintering survivors). These values differ from those previously reported for entry timing because mobile tracking detections were included in survival and distribution estimation, but timing was estimated solely from fixed-site radio telemetry and PIT detections. An additional 109 steelhead were observed moving after the wintering period but were not detected entering Upper Columbia River tributaries (‘Additional survivors’; Table 2.13). Of this subset, 34 were classified as fallbacks below Priest Rapids Dam (31%) after the overwintering onset date. Twelve were detected entering Foster Creek (Wells Dam reservoir; detected by PIT array), and 8 were detected entering Beebee Springs Hatchery outflow channel (Rocky Reach reservoir; detected via mobile tracking; in 2017 exclusively).

Survival to Tributaries and Spawning Period

The overall probability of movement into a spawning tributary and survival to the onset of spawning by steelhead that were not harvested, collected for broodstock, surplused, or fell back over Priest Rapids Dam prior to 1-Jan was 0.72 among those surviving to 1-Jan for the Upper Columbia basin radio-tagged steelhead across both years of this study (Table 2.14). A total of 311 (57% of overwinter survivors, and ~39% of the total radio-tagged sample) steelhead were observed in tributaries having survived overwintering or having entered tributaries from the Columbia River after 1-Jan. Hatchery origin fish survival probability was lower (0.60 and 0.73, for 2016 and 2017, respectively) than wild origin fish (0.86 and 0.77, for 2016 and 2017, respectively).

Total counts per tributary differ slightly from overwintering survival estimates given that 5 and 6 (2016 and 2017, respectively) fish overwintered in a tributary other than their ultimate return tributary (see *Appendix 1*). Six of these fish overwintered in the Methow River and then 3 fell back to the Wenatchee River (2 in 2016 and 1 in 2017, respectively), 2 to the Okanogan River (1 each year), and one fish to the Entiat (2017). Five steelhead overwintered in the Okanogan River and fell back to the Methow River (2 in 2016 and 3 in 2017). Fish collected at hatcheries in the Methow River (2 in 2016, and 25 in 2017, respectively) were not included as putative spawners.

Adjusting observed frequencies for non-detection using detection probabilities generated for tributary radio telemetry fixed sites resulted in 9 and 3 (2016 and 2017, respectively) main-stem survivors with unknown tributary assignments were estimated to have entered tributaries (i.e., Adjusted; Table 2.13). The remaining 43 (8 in 2016 and 35 in 2017, constituting 39% of the remaining main-stem overwintering survivors) steelhead were detected moving in the main-stem after overwintering but were never detected entering an Upper Columbia tributary by any method.

Tributary Fixed Site Detection Efficiencies

Radio telemetry fixed site detection probabilities were greater than 85% for nearly all tributaries with the exception of the Okanogan River in the spring and fall of 2016. The mean detection efficiency for all tributaries over the course of this study was 0.88 and 0.90 (2016 and 2017, respectively). The Entiat River lower radio telemetry fixed site array detection efficiency was 1.0 in fall when all fish that entered were detected and 0.933 in spring. This site had the smallest sample size (*n* = 21, in both years), resulting in the largest confidence intervals. The Methow River had the largest sample size and the least variable detection efficiency between seasons and across both years. The Okanogan River lower RT fixed site displayed the highest temporal variation in detection probability decreasing from 0.86 to 0.70 in 2016 (fall and spring, respectively) then increasing from 0.71 to 0.95 in 2017 (fall and spring, respectively). The primary factors decreasing detection efficiency were radio telemetry fixed site power outages, damaged or windblown antennas, and spring flooding events. Detection efficiency estimates for all tributaries, across season, and years, and counts of unique fish detections for lower tributary fixed site arrays (Lower) and all other upper tributary detection sites (Upstream) are provided (Table 2.15).

Tributary Entry Detections and Predicted Tributary Escapement

We estimated the number of steelhead reaching tributaries each season and year by adjusting the observed frequencies for undetected entry using estimated detection efficiencies. Overall, the adjusted escapement rate across all tributaries, seasons, and years was 112% of the unadjusted value (1/0.89). Spring escapement rates were slightly more variable than fall rates across all tributaries and years (110-113% for fall, and 106-115% for spring). The Okanogan River had the greatest number of predicted undetected tributary entries because its detection probability was the most variable between seasons and years monitored (range 0-14 undetected entries). Conversely, the Entiat River had only 2 fish estimated to have entered the tributary undetected, one per year (spring 2016 and 2017, respectively). Total counts of observed numbers of tributary detected radio-tagged fish by origin, tributary detection probability estimates, estimated counts of undetected fish, and totals are provided (Table 2.16).

Tributary Return Fish Origin Composition

The expected hatchery and wild Steelhead proportions based on the PIT based patch occupancy model were similar to the observed proportions detected using radio telemetry. Chi-square test results indicated that there was no significant difference in predicted and observed hatchery and natural origin tributary compositions for any of the major tributaries steelhead populations in either year (Table 2.17).

Kelting Rate and Bonneville Dam Detections

A total of 174 fish were classified as kelts based on downstream movements (~56% of survivors to tributaries), providing a minimum estimate of the number of steelhead surviving to post-spawn status (kelts). This total included two kelts collected for reconditioning at Rock Island Dam by Yakama Nation Fisheries staff in spring 2016. Of kelts, 63 and 65 were female indicating a 68% (n=63) and 80% (n=65) female kelt majority in 2016 and 2017 kelts, respectively (Figures 2.18 and 2.19). Survival to PIT detection at Bonneville was low, with only 16 tagged steelhead (12 females, 4 males) detected at Bonneville Dam in 2016. Only 1 male kelt was detected at Bonneville Dam in 2017. The kelt migration survival (16/92 = 0.17) in 2016 and (1/82 = 0.01) in 2017 are minimum values given that kelt detection efficiency at Bonneville Dam was likely low, particularly in 2017 which had higher than average river discharge. An additional three tagged fish were detected at or below Bonneville Dam in 2016 with unknown return tributaries (part of the 'Unknown Spawn Location' survivors group, Table 2.13). Presuming these adults spawned upstream of Priest Rapids Dam produces a slightly higher survival rate through the kelt migration (19/92 = 0.21) for that year. An additional 5 steelhead detected as fallbacks below Priest Rapids Dam were detected at Bonneville Dam. Approximately 9.6% and 1.0% (2016 and 2017, respectively) of the total Upper Columbia 'Tributary Putative Spawners' group were detected at or below Bonneville Dam. We note the reported proportions are unadjusted for the female sex-bias in tagging rate and thus likely overestimate overall survival to kelting assuming females exhibited higher survival to kelting than males (Keefer et al. 2017).

Discussion

Understanding steelhead migratory movement and behaviors is essential to facilitate proper management and conservation of the Upper Columbia population, currently listed as threatened under the Endangered Species Act. We tagged and monitored the overwintering distribution of adult steelhead using radio telemetry throughout the basin and estimated survival and return to major tributaries. Upper Columbia Steelhead escapement to Priest Rapids Dam differed substantially between study years. Approximately 1 in 5 steelhead of the total radio-tagged sample were detected as fallbacks below Priest Rapids Dam at any time after release. The majority of radio-tagged fish were detected overwintering with the Upper Columbia River basin and post-overwintering survival to tributaries was high. Overwinter survival rates were higher in tributaries than main-stem (reservoir) habitats, a pattern that contrasts with similar research conducted for steelhead in the Snake River basin. The absence of an Upper Columbia River Steelhead fishery during the second year provided opportunity to compare pre-wintering survival to a year with a more typical fishery. A majority of steelhead detected in tributaries during the spawning season were also detected kelting, although detections at Bonneville Dam were low.

Detection Efficiencies and PIT array Validation

Successful detection of telemetered fish is an underlying assumption of biotelemetry studies, though perfect detection is rarely achieved, and estimates of detection efficiency can be used to adjust raw rates. Estimated detection efficiency of radio telemetry fixed sites differed between sites, seasons, and years and adjustment for detection efficiency suggested modestly higher escapement than raw estimates because detection efficiencies were generally high (>85%). The Okanogan River lower tributary fixed site radio telemetry array had the most variability across all sites do in part to frequent power outages (Fall 2016) and heavy flooding that occurred in spring of 2016. In contrast, the Entiat River had the highest seasonal detection efficiencies, including two seasons where all fish entering the tributary were detected (Fall of 2015 and 2016, respectively). Detection efficiency at tributaries is likely affected in part by the morphology, water depth, and geographic characteristics of the tributary location at which the fixed site was located, as well as equipment outages. Differences in river gradient, channelization, and annual flow regime dynamics may explain to some degree detection efficiency variation between tributaries and seasons.

Steelhead classified as unknowns/mortalities likely included steelhead that regurgitated the radio tag without further PIT detection, as well as mortality, a concern in any radio-tagging study. We examined telemetry records for evidence of shed tags and identified potential shed tags if those steelhead were: 1) detected at PIT arrays but not radio telemetry sites at more than one location and date; 2) reported as collected at hatcheries without radio tags present; and/or 3) plausible PIT detections occurred after a radio tag was returned. A total of 25 radio-tagged fish met one or more of these criteria across the two years (~3.1% of total), a rate similar to that observed in steelhead in the Snake and Lower Columbia Rivers (~4.0%; Keefer et al., 2004).

Independent validation of the proportion of hatchery fish entering each tributary estimated using PIT tags was a primary objective of the radio telemetry study because the PIT-based models are currently used to estimate escapement to tributaries, estimate the proportion of hatchery origin spawners (pHOS), and provide an estimate of spawner productivity. The proportion of hatchery and wild steelhead entering a tributary detected by radio telemetry arrays was not significantly different than the predicted proportion by origin generated using a patch occupancy model (WDFW, unpublished data), and hence no evidence of significant bias was found. Validation of the PIT-based patch occupancy model was necessary before the formal adoption of this method for future estimation of steelhead tributary-specific abundance, detection efficiency, and pHOS using PIT-based monitoring. The comparison presented here supports the future use of the PIT-based approach.

Overwintering Distribution and Survival

Uncertainty in the classification of individual fates could bias survival estimates. Consequently, we considered the influence of uncertainty in fate classifications on estimating survival rates by comparing survival estimates under the following three scenarios: 1) survival excluding (censoring) unknown tributary spawners; 2) survival including unknown tributary spawners as spawners (best-case survival); and 3) survival including unknown tributary spawners as presumed mortalities (worst-case survival). By excluding unknown tributary steelhead (i.e., scenario 1) total mean steelhead survival probability for both years was 0.69 and 0.70 (2016 and 2017, respectively). By including unknown tributary fish as survivors or conversely as mortalities (scenarios 2 and 3) the total mean probability of survival for each year was 0.70 and 0.80 (best-case), and 0.67 and 0.68 (worst-case) for 2016 and 2017, respectively. Our base survival estimates adjusted for detection efficiency were ~0.70 and ~0.74, falling within the ranges of the 2^{nd} and 3^{rd} scenarios. Thus, survival estimates fell within a relatively narrow range across a broad array of assumptions concerning uncertainty in fate classification, and the true survival rate was very likely at or near 0.70 in both years.

The survival to the overwintering period differed among years, in part, because there was no sport fishing season for hatchery fish tagged in 2016. Consistent with the lower harvest, proportionately more hatchery fish were detected overwintering and surviving to spawn in spring

2017 compared to 2016. We would expect the proportion of hatchery fish overwintering mortalities to be greater in 2015 than 2016 given that unreported harvest and indirect angler mortalities would inflate mortality assignments as a result of the fishery. However, the expectation was not supported because the point estimate of mortality rate in overwintering hatchery steelhead (available for legal harvest) was actually higher in the year without a fishery (80% of total mortalities in 2015, and 84% in 2016). This finding implies the true unreported harvest rate was likely not a major factor in driving total overwinter mortality.

Steelhead detected entering tributaries prior to the 1-Jan overwintering period were not always detected residing within tributaries throughout the wintering period, rather a substantial proportion (82/296; 28%) of main-stem overwintering fish had entered tributaries before being detected overwintering in the main-stem. This behavior may represent habitat sampling and selection behavior, with preference for overwintering habitats outside some tributaries. Notably, this behavior was observed exclusively for steelhead detected entering the Entiat River (Figure 2.6 and 2.7). The exit behavior from the Entiat may be attributed to the fact that much of the river has been observed freezing (surface ice, to include the lower river) and may not provide desirable overwintering habitat. The majority of research focusing on steelhead migration survival in relation to temperature has focused on upper temperature threshold limits and determining thermal refugia in relation to high use harvest areas (Keefer et al., 2009; Richter & Kolmes, 2005). Future temperature monitoring could elucidate whether overwinter distribution is related to minimum temperatures, diel or seasonal variation in temperature, or is primarily related to other factors such as water depth that may provide reduced exposure to natural predators (e.g. otters).

Overwintering mortality was greater in Upper Columbia Dam reservoirs than tributaries in both years of this study. This finding contrasts with the pattern observed for overwintering survival in Steelhead in the Snake River reservoirs (Keefer et al., 2008a), where higher proportions of fish survived that overwintered in the Hydrosytem vs tributaries. Although, the Upper Columbia River and Snake River basins are broadly similar inland rivers with dams and tributaries, fishing effort in the Snake River was concentrated in tributaries prior to wintering (Keefer et al., 2008a). Harvest in the Upper Columbia in fall/winter of 2015-2016 was also concentrated in tributaries with approximately 60% and 40% of reported harvest in tributaries and reservoirs, respectively, with the majority of tributary harvest occurring in the lower Methow River (WDFW, unpublished creel data). However, the overwintering distribution and total mortalities in the main-stem Columbia River were similar in a year with (2015) and without (2016) an active winter fishery, suggesting differences between reservoirs and tributary harvest-related mortality was not the sole cause of overwintering mortality. We also estimated seasonal survival by estimating mortality for several sources. Additional factors contributing to the difference in mortality between habitat types within the Snake River, may include the fact that few spawning tributaries empty into Snake River reservoirs, suggesting differences in overwinter behavior and distribution within reservoirs between Snake and Upper Columbia River systems may influence vulnerability among the two habitat types. Alternatively, the contrast in relative mortality between the Columbia and Snake systems may be related in part to seasonal run timing because the probability of overwintering in a reservoir increased for later arriving steelhead in the Snake (Keefer et al., 2008a), but seasonal association between migration date and overwinter location was not observed in this study. Future research could focus on comparing survival between main-stem and tributary habitats at the population and/or at the macro habitat scale (e.g. pool, riffle, etc.). The contrast also suggests the potential that the proximity of spawning tributaries to deep, main-stem overwintering sites (e.g., reservoirs) may influence steelhead winter distribution at the macroscale, although this hypothesis requires further study.

Main-stem reservoir overwinter survivors with unknown spawning locations were more frequently observed during the 2016 monitoring year than 2015 (Table 2.13). As the majority of these fish were of hatchery origin (39/43 = 91%), it is possible many returned to hatcheries located in reservoirs (i.e., East bank Hatchery, Wells Dam Hatchery, and Chief Joe Hatchery) but were never detected at hatchery PIT arrays. Survivors with unknown spawning locations were included in survival estimates given that many of these were detected briefly (≤1 day) in major tributaries and it is possible a subset of these fish entered tributaries and spawned below lower tributary radio telemetry arrays. It is equally likely that some of these fish spawned in as yet unmonitored tributaries (i.e., Crab Creek, Chelan Falls, etc.) or may have spawned on the banks of reservoirs. Baldwin et al. (2007) conducted steelhead spawning ground surveys on numerous small order tributaries between Priest Rapids and Rocky Reach Dam reservoirs and found spawning steelhead present. Future efforts focused on monitoring steelhead returning to hatcheries and small order main-stem tributaries may be warranted.

Kelting Rate and Bonneville Dam Detections

Post spawning kelting rates to the main-stem Upper Columbia were similar for both monitored years of the study (~55% and ~57% for 2016 and 2017 out migrating years). Fish were assigned as kelts if they were detected leaving their presumed spawning tributary or if they were detected by any radio telemetry fixed sites located at Rock Island or Priest Rapids Dams. Proportionately more kelts were female than male for every tributary population, other than the Entiat (2016), during both years of monitoring, a finding largely consistent with other research regarding sex ratios in kelts, and thought to be the result the differential energetic demands on the sexes undertaken during spawning (Keefer et al., 2008b; Marston et al., 2012; Niemelä et al., 2000).

Estimated downstream migration success to Bonneville was lower in 2017 than 2016 where a single fish leaving Upper Columbia tributaries was detected at Bonneville, versus 16 detected in 2016. Given that radio telemetry monitoring during downstream migration ended at Priest Rapids

Dam, monitoring further downstream was restricted to PIT tag arrays in juvenile bypass systems and by the Bonneville Corner Collector and estuary towed arrays. Flows during the kelt outmigration period were ~28% higher in 2017 than the ten year mean (https://waterdata.usgs.gov/nwis/) and it is likely that downstream passage detection efficiency at Bonneville Dam was reduced in that year as kelts may have passed via unmonitored spillways at a higher rate than PIT array monitored routes. Research conducted on kelt downstream passage at the Dallas Dam indicated high rates of passage success whereby <90% of kelts passed via non-turbine routes, suggesting high passage survival (Khan et al., 2010; Khan et al., 2013). Downstream kelt outmigration survival from the Snake River has been estimated as high as 0.13-0.20 (Keefer et al., 2017).

Proportionately more fish assigned as kelts were of hatchery origin in 2017 while 2016 kelting origin composition had a wild majority. The higher proportion of wild-origin kelts in 2016, a year with a winter fishery, is consistent with previous observations of reduced kelt outmigration success in hatchery-origin fish and for older (salt age 2) fish (Keefer & Caudill, 2014; Keefer at al., 2017) in the Snake and Lower Columbia River basins, where reduced hatchery kelt survival was largely attributed to harvest and broodstock collection. As the 2016 Upper Columbia River tagged sample was comprised of proportionally more hatchery and salt age 2 fish than the previous 2015 tagged sample, this may account in some degree to the limited number of kelts detected at Bonneville in 2017, though inter-annual differences in main-stem detection efficiency likely contributed to numbers detected at Bonneville and downstream.

Considering the great distance associated with migrating to and kelting from the Upper Columbia basin, it is not surprising that so few fish survive to post spawning kelting status. While iteroparity rates in interior summer Steelhead were likely always low, other research focusing on the Snake and Lower Columbia River (English et al., 2006; Keefer et al., 2008b) highlights the need for benign downstream winter passage routes.

The findings provided here indicate returning adult steelhead migration behaviors in the Upper Columbia River are complex and that behaviors are associated with survival and variation in life history traits such as kelting. The continued use of PIT tag array technology and methods appears to be an adequate method for monitoring and estimating escapement at the tributary population level. A better understanding of the mechanisms driving overwintering mortality and the potential for overwintering habitat preference may aid in the recovery of the currently threatened population.

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Tables

Table 2.1. Listed fixed site radio telemetry receivers deployed in the Upper Columbia River basin in 2015-17. Sites, river kilometer (RKM) distances from the Columbia River estuary, installation dates, and working duration is provided.

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

*sites were active during 2015 run year only.

Table 2.2. Origin and estimated sex frequencies of adult summer Steelhead radio-tagged at Priest Rapids Dam 2015 (*n* = 400) and 2016 (*n* = 407). Proportions of males and females by origin are provided.

Sex	Number of Steelhead			Proportion	
	Hatchery	Wild	Total	Hatchery	Wild
		2015			
Male	103	54	157	0.656	0.344
Female	161	82	243	0.663	0.337
Total	264	136	400	0.660	0.340
		2016			
Male	75	30	105	0.714	0.286
Female	246	56	302	0.815	0.185
Total	321	86	407	0.789	0.211
		Total			
Male	178	84	262	0.679	0.321
Female	407	138	545	0.747	0.253
Grand Total	585	222	807	0.725	0.275

Table 2.3. Final fates of the 2015 Priest Rapids Dam radio-tagged summer Steelhead sample. Fates are split between fish that were detected falling back below Priest Rapids, fish detected remaining above Priest Rapids, and fish whose ultimate fates were more difficult to determine given fewer detections and suspected mortalities. Total counts of fish by rearing origin and proportions are provided.

Radio-Tagged Steelhead Fate	Number of Fish			Proportion		
	H	W	Total	H	W	Total
Last Detected Below Priest Rapids Dam						
Harvested/Collected	18	0	18	1.000	0.000	0.045
Detected in Snake or Lower Columbia	20	29	49	0.408	0.592	0.123
Kelt Lower Columbia Tributary	0	4	4	0.000	1.000	0.010
Total	38	33	71	0.535	0.465	0.178
Last Detected Above Priest Rapids Dam						
Reported Harvested/Collected in Columbia River	16	0	16	1.000	0.000	0.040
Reported Harvested/Collected in Tributary	28	2	30	0.933	0.067	0.075
Estimated Indirect Hooking Mortalities	0	2	2	0.000	1.000	0.005
Estimated Unreported Harvest	7	0	7	1.000	0.000	0.018
Total Upper Columbia Harvest Fates	51	4	55	0.927	0.073	0.138
Fates of Tributary Survivors to Spawn						
Survivors to Spawn*	49	30	79	0.620	0.380	0.198
Kelts	37	39	76	0.487	0.513	0.190
Kelts (Detected at Bonneville)	4	12	16	0.250	0.750	0.040
Total Tributary Putative Spawners	90	81	171	0.526	0.474	0.428
Upper Columbia Tagged Fish Presumed Mortalities						
Presumed Fall Mortalities	32	5	37	0.865	0.135	0.093
Presumed Overwinter Mortalities	39	10	49	0.796	0.204	0.123
Total Presumed Mortalities	71	15	86	0.826	0.174	0.215
Overwinter Survivors Not Detected in Tributaries						
Columbia River	12	2	14	0.857	0.143	0.035
Kelted Survivors (Detected at Bonneville)	2	1	3	0.667	0.333	0.008
Total Survivors	14	3	17	0.824	0.176	0.043
Total Upper Columbia Tagged Fish Fates	226	103	329	0.687	0.313	0.823
Grand Total Radio-Tagged Fish	264	136	400	0.660	0.340	1.000

*Includes fish detected in Foster Creek, and estimated tributary entry fish.

Table 2.4. Final fates of the 2016 Priest Rapids Dam radio-tagged summer Steelhead sample. Fates are split between fish that were detected falling back below Priest Rapids, fish detected remaining above Priest Rapids, and fish whose ultimate fates were more difficult to determine given fewer detections and suspected mortalities. Total counts of fish by rearing origin and proportions are provided.

Radio-Tagged Steelhead Fate	Number of Fish			Proportion		
	H	W	Total	H	W	Total
Last Detected Below Priest Rapids Dam						
Harvested/Collected	6	0	6	1.000	0.000	0.015
Detected in Snake or Lower Columbia	71	16	87	0.816	0.184	0.214
Kelt Lower Columbia Tributary	0	1	1	0.000	1.000	0.002
Total	77	17	94	0.819	0.181	0.231
Last Detected Above Priest Rapids Dam						
Reported Harvested/Collected in Columbia River	10	0	10	1.000	0.000	0.025
Reported Harvested/Collected in Tributary	22	3	25	0.880	0.120	0.061
Estimated Indirect Hooking Mortalities	0	0	0	0.000	0.000	0.000
Estimated Unreported Harvest	0	0	0	0.000	0.000	0.000
Total Upper Columbia Harvest Fates	32	3	35	0.914	0.086	0.086
Fates of Tributary Survivors to Spawn						
Survivors to Spawn*	64	16	80	0.800	0.200	0.197
Kelts	53	29	82	0.646	0.354	0.201
Kelts (Detected at Bonneville)	0	1	1	0.000	1.000	0.002
Total Tributary Putative Spawners	117	46	163	0.718	0.282	0.400
Upper Columbia Tagged Fish Presumed Mortalities						
Presumed Fall Mortalities	27	10	37	0.730	0.270	0.091
Presumed Overwinter Mortalities	36	7	43	0.837	0.163	0.106
Total Presumed Mortalities	63	17	80	0.788	0.213	0.197
Overwinter Survivors Not Detected in Tributaries						
Columbia River	32	3	35	0.914	0.086	0.086
Kelted Survivors (Detected at Bonneville)	0	0	0	0.000	0.000	0.000
Total Survivors	32	3	35	0.914	0.086	0.086
Total Upper Columbia Fates	244	69	313	0.780	0.220	0.769
Total Tagged Fish	321	86	407	0.789	0.211	1.000

*Includes Fish detected in Foster Creek, Beebee Springs, and estimated tributary entry fish.

Table 2.5. Frequency of final location for radio-tagged summer Steelhead observed falling back below Priest River Dam. Locations are split between fallbacks returning to the Snake River and tributaries, Middle Columbia River tributary and other fallback locations. Counts of fallback fish rearing origins (H and W) and totals (T) are provided.

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

Table 2.6. The number and proportion (in parenthesis) of steelhead detected entering a tributary before and after 1-January, 2016 (upper) 2017 (lower).

Tributary	Detection Before 1-Jan 2016						Detection After 1-Jan 2016						Grand Total
	Hatchery		Wild		Total		Hatchery		Wild		Total		
Entiat	1	(0.25)	6	(0.43)	7	(0.39)	3	(0.75)	8	(0.57)	11	(0.61)	18
Methow	65	(0.84)	23	(0.85)	88	(0.85)	12	(0.16)	4	(0.15)	16	(0.15)	104
Okanogan	25	(0.63)	9	(0.64)	34	(0.63)	15	(0.38)	5	(0.36)	20	(0.37)	54
Wenatchee	22	(0.73)	26	(0.84)	48	(0.79)	8	(0.27)	5	(0.16)	13	(0.21)	61
Foster Ck.	0	(0.00)	0	(0.00)	0	(0.00)	4	(1.00)	0	(0.00)	4	(1.00)	4
Total	113	(0.73)	64	(0.74)	177	(0.73)	42	(0.27)	22	(0.26)	64	(0.27)	241

Tributary	Entry Before 1-Jan 2017						Entry After 1-Jan 2017						Grand Total
	Hatchery		Wild		Total		Hatchery		Wild		Total		
Entiat	1	(0.20)	3	(0.20)	4	(0.20)	4	(0.80)	12	(0.80)	16	(0.80)	20
Methow	93	(0.79)	22	(0.85)	115	(0.80)	24	(0.21)	4	(0.15)	28	(0.20)	143
Okanogan	37	(0.82)	5	(0.83)	42	(0.82)	8	(0.18)	1	(0.17)	9	(0.18)	51
Wenatchee	7	(0.54)	12	(0.92)	19	(0.73)	6	(0.46)	1	(0.08)	7	(0.27)	26
Foster Ck.	0	(0.00)	0	(0.00)	0	(0.00)	6	(1.00)	0	(0.00)	6	(1.00)	6
Total	138	(0.74)	42	(0.70)	180	(0.75)	48	(0.26)	18	(0.30)	66	(0.27)	246
Sum Total	251	(0.74)	106	(0.73)	357	(0.74)	90	(0.26)	40	(0.27)	130	(0.27)	487

Table 2.7. Number of returned tags by origin and type of return.

Fate of Tagged Fish	Hatchery	Wild	Total	Hatchery	Wild	Total
	2015 Run Year			*2016 Run Year*		
Reported Harvested	56	1	57	6	0	6
Caught and released	1	4	5	3	0	3
Found on river bank	0	1	0	3	0	3
Collected at hatcheries	6	1	7	32	3	35
Total	63	7	70	44	3	47

Table 2.8. Reported harvested radio-tagged steelhead locations by origin and run year. Harvest rate given as percent of total radio-tagged fish by above and below Priest Rapids Dam in 2015-16 is indicated (in parenthesis).

Location	Reported Harvest					
	2015 Run Year			2016 Run Year		
	Hatchery	Wild	Total	Hatchery	Wild	Total
	Upstream of Priest Rapids Dam					
Entiat	1 (>1)	0 (0)	1 (>1)	0	0	0
Methow	20 (6.1)	1 (>1)	21 (6.4)	0	0	0
Okanogan	6 (1.8)	0 (0)	6 (1.8)	0	0	0
Wenatchee	0 (0)	0 (0)	0 (0)	0	0	0
Columbia River	15 (4.6)	0 (0)	15 (4.6)	1	0	1
Total	42 (12.8)	1 (>1)	43 (13.0)	1	0	1
	Downstream of Priest Rapids Dam					
Columbia River	6 (8.5)	0 (0)	6 (8.5)	1	0	1
Snake River Basin	8 (11.2)	0 (0)	8 (11.2)	4	0	4
Total	14 (19.7)	0 (0)	14 (19.7)	5	0	5
Grand Total	56 (14.0)	1 (>1)	57 (14.3)	6	0	6

Table 2.9. Radio-Tagged steelhead reported collection and found tag locations. Counts provided are based on information reported by hatchery departmental staff and private residents.

Location	Collected/Found Tags 2015			Collected/Found Tags 2016		
	Hatchery	Wild	Total	Hatchery	Wild	Total
			Upstream of Priest Rapids Dam			
Entiat	0	0	0	0	0	0
Methow	1	1	2	22	3	25
Okanogan	0	0	0	0	0	0
Wenatchee	0	0	0	0	0	0
Columbia River	1	0	1	9	0	9
Total	2	1	3	31	3	34
			Downstream of Priest Rapids Dam			
Columbia River	1	0	1	1	0	1
Snake River Basin	3	0	3	0	0	0
Total	4	0	4	1	0	1
Grand Total	6	1	7	32	3	35

Table 2.10. Locations of radio-tagged steelhead last detected prior to 1-Jan in the Upper Columbia River and tributaries across both tagging years by origin.

Location	Hatchery	Wild	Total	Hatchery	Wild	Total	All
	Columbia River Reach 2015			*Columbia River Reach 2016*			
Priest	6	3	9	7	2	9	18
Wanapum	2	1	3	1	0	1	4
Rock Island	5	0	5	5	2	7	12
Rocky Reach	0	0	0	2	0	2	2
Wells	10	1	11	7	4	11	22
Total	23	5	28	22	8	30	58
	Tributary 2015			*Tributary 2016*			
Entiat	0	0	0	0	0	0	0
Methow	9	0	9	1	1	2	11
Okanogan	0	0	0	1	0	1	1
Wenatchee	0	0	0	3	1	4	4
Total	9	0	9	5	2	7	16
Grand Total	32	5	37	27	10	37	74

Table 2.11. Counts of radio-tagged fish by overwintering distribution within Upper Columbia River reservoirs and tributaries in 2016. Total counts by overwintering location and proportions of fish by rearing origin (H and W, hatchery and wild respectively) and totals (T) by location are given.

Location	2016 Overwintering Steelhead						2017 Overwintering Steelhead						Total	
	Hatchery		Wild		Total		Hatchery		Wild		Total			
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
							Columbia River Reach							
Priest	9	60	6	40	15	6	8	73	3	27	11	4	26	5
Wanapum	5	63	3	38	8	3	10	100	0	0	10	3	18	3
Rock Island	3	38	5	63	8	3	4	36	7	64	11	4	19	3
Rocky Reach	13	50	13	50	26	10	24	62	15	38	39	13	65	12
Wells	53	70	23	30	76	31	81	88	11	12	92	31	168	31
Total	83	62	50	38	133	54	127	78	36	22	163	54	296	54
							Tributary							
Entiat	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Methow	26	62	16	38	42	17	64	83	13	17	77	26	119	22
Okanogan	19	68	9	32	28	11	39	89	5	11	44	15	72	13
Wenatchee	20	44	25	56	45	18	4	25	12	75	16	5	61	11
Total	65	57	50	44	115	46	107	78	30	22	137	46	252	46
Grand Total	148	60	100	40	248	100	234	78	66	22	300	100	548	100

Table 2.12. Overwintering radio-tagged steelhead mortalities by last detection location post 1-January. Counts, proportions of total overwintering fish, and total mortalities by rearing origin (H, W, and T indicate hatchery, wild and total, respectively) and the proportion of total (All) mortalities are given.

Location	Overwinter 2016			Proportion			Overwinter 2017			Proportion			Total	
	H	W	T	H	W	T	H	W	T	H	W	T	All	Prop
Columbia River Reach														
Priest	3	3	6	0.20	0.20	0.40	1	0	1	0.09	0.00	0.09	7	0.08
Wanapum	4	0	4	0.50	0.00	0.50	8	0	8	0.80	0.00	0.80	12	0.13
Rock Island	1	2	3	0.13	0.25	0.38	3	1	4	0.27	0.09	0.36	7	0.08
Rocky Reach	6	1	7	0.23	0.04	0.27	3	1	4	0.08	0.03	0.10	11	0.12
Wells	12	2	14	0.16	0.03	0.18	13	0	13	0.14	0.00	0.14	27	0.29
Total	26	8	34	0.20	0.06	0.26	28	2	30	0.17	0.01	0.18	64	0.70
Tributary														
Entiat	0	0	0	0.00	0.00	0.00	0	0	0	0.00	0.00	0.00	0	0.00
Methow	5	0	5	0.12	0.00	0.12	4	1	5	0.05	0.01	0.06	10	0.11
Okanogan	4	1	5	0.14	0.04	0.18	3	1	4	0.07	0.02	0.09	9	0.10
Wenatchee	4	1	5	0.09	0.02	0.11	1	3	4	0.06	0.19	0.25	9	0.10
Total	13	2	15	0.11	0.02	0.13	8	5	13	0.06	0.04	0.09	28	0.30
Grand Total	39	10	49	0.16	0.04	0.20	36	7	43	0.12	0.02	0.14	92	1.00

Table 2.13. The number and origin of radio-tagged fish that were detected entering tributaries after 1-Jan 2016 and 2017. Estimated numbers of fish were based on spring 2016 and 2017 tributary detection probabilities. Fish detected in Foster Creek, Beebee Springs, fallbacks after overwintering, and unknown return tributary fish are included.

Location	2016 Survivors			2017 Survivors			All
	Hatchery	Wild	Total	Hatchery	Wild	Total	
				Raw Detected			
Entiat	3	14	17	3	15	18	*35*
Methow	15	9	24	16	4	20	*44*
Okanogan	10	6	16	4	0	4	*20*
Wenatchee	8	4	12	6	4	10	*22*
Total	36	33	69	29	23	52	*121*
				Adjusted From Detection Efficiency			
Entiat	0	1	1	0	1	1	*2*
Methow	1	0	1	1	0	1	*2*
Okanogan	4	2	6	0	0	0	*6*
Wenatchee	1	0	1	1	0	1	*2*
Total	6	3	9	2	1	3	*12*
				Other Detected Survivors			
Foster Creek	3	1	4	8	0	8	*12*
Beebee Springs	0	0	0	8	0	8	*8*
Unknown Spawn Location	8	0	8	31	4	35	*43*
Below Priest	4	5	9	18	7	25	*34*
Total	15	6	21	65	11	76	*97*
Grand Total	57	42	99	96	35	131	*230*

Table 2.14. Final counts of Upper Columbia radio-tagged steelhead survivors to tributaries, total survivors, and total mortalities (fall and overwintering). Survival probabilities indicated are derived as the proportion of total survivors from the total combined mortalities.

Location	2016 Spawners			2017 Spawners			All
	Hatchery	Wild	Total	Hatchery	Wild	Total	
				Tributary Putative Spawners			
Entiat	3	14	17	4	15	19	36
Methow	36	25	61	53	13	66	125
Okanogan	25	14	39	32	4	36	75
Wenatchee	24	28	52	10	13	23	75
Total	87	80	167	99	45	144	311
				Other Detected Survivors and Adjusted From DE			
Columbia River	21	9	30	67	12	79	109
Grand Total Survivors	108	89	197	166	57	223	420
				Mortalities			
Fall Mortalities	32	5	37	27	10	37	74
Overwintering Mortalities	39	10	49	36	7	43	92
Grand Total Mortalities	71	15	86	63	17	80	166
Survival Probability	0.60	0.86	0.70	0.73	0.77	0.74	0.72

Table 2.15 Detection efficiency estimates for major tributaries using radio telemetry fixed sites (Lower), and all detections within the tributary upstream of the lower site (Upstream).

Location	Lower	Upstream	Estimated Efficiency	Lower	Upstream	Estimated Efficiency	Lower	Upstream	Estimated Efficiency
		Fall 2015			*Spring 2016*			*Total*	
Entiat	6	6	1.000	14	15	0.933	20	21	0.952
Methow	64	68	0.941	23	24	0.958	87	92	0.946
Okanogan	18	21	0.857	16	23	0.696	34	44	0.773
Wenatchee	40	47	0.851	9	10	0.900	49	57	0.860
Total	128	142	0.912	62	72	0.872	190	214	0.883
		Fall 2016			*Spring 2017*			*Total*	
Entiat	4	4	1.000	16	17	0.941	20	21	0.952
Methow	74	77	0.961	39	41	0.951	113	118	0.958
Okanogan	24	34	0.706	18	19	0.947	42	53	0.792
Wenatchee	23	26	0.885	10	11	0.909	33	37	0.892
Total	125	141	0.888	83	88	0.937	208	229	0.899
Grand Total	253	283	0.900	145	160	0.905	398	443	0.891

Table 2.16 Observed numbers of fish detected entering tributaries at lower tributary fixed site radio telemetry arrays (lower) and all upstream sites (RT, PIT, mobile tracking) across seasons and between years. Detection probability estimates and upper and lower confidence intervals (95%) are given. Predicted numbers of non-detected (ND) and the total number of tributary entry fish are also provided.

Location	Year	Season	Observed			Detection Probability			Predicted	
			H	W	T	Estimate	Upper 95% CI	Lower 95% CI	ND	Total Entry
Entiat	2015	Fall	0	0	0	1.000	1.000	0.541	0	0
	2016	Spring	3	14	17	0.933	0.998	0.681	1	18
	2016	Fall	0	0	0	1.000	1.000	0.398	0	0
	2017	Spring	3	15	18	0.941	0.999	0.713	1	19
Methow	2015	Fall	26	16	42	0.941	0.984	0.856	3	45
	2016	Spring	15	9	24	0.958	0.999	0.789	1	25
	2016	Fall	37	9	46	0.961	0.992	0.890	2	48
	2017	Spring	16	4	20	0.951	0.994	0.835	1	21
Okanogan	2015	Fall	19	9	28	0.857	0.970	0.637	5	33
	2016	Spring	10	6	16	0.696	0.868	0.471	7	23
	2016	Fall	28	4	32	0.706	0.849	0.525	14	46
	2017	Spring	4	0	4	0.947	0.999	0.740	0	4
Wenatchee	2015	Fall	20	25	45	0.851	0.938	0.717	8	53
	2016	Spring	8	4	12	0.900	0.997	0.555	1	13
	2016	Fall	4	9	13	0.885	0.976	0.698	2	15
	2017	Spring	6	4	10	0.909	0.998	0.587	1	11

Table 2.17 Proportions of hatchery and wild steelhead detected entering major tributaries after adjusting radio telemetry frequencies for detection efficiency. Chi-square test statistics and P-Values (0.05) are provided.

Tributary Population	PIT Tag Arrays		Radio Telemetry (adjusted)			
	H	W	H	W	$\mathbf{X^2}$	*P*-Value
2016						
Entiat	0.093	0.907	0.167	0.833	1.098	0.295
Methow	0.637	0.363	0.629	0.371	0.022	0.881
Okanogan	0.750	0.250	0.643	0.357	3.429	0.064
Wenatchee	0.481	0.519	0.500	0.500	0.103	0.749
2017						
Entiat	0.289	0.711	0.158	0.842	1.599	0.206
Methow	0.714	0.286	0.812	0.188	3.189	0.074
Okanogan	0.885	0.115	0.880	0.120	0.008	0.930
Wenatchee	0.520	0.480	0.462	0.538	0.247	0.556

Table 2.18. Number of downstream migrating kelts detected and proportions calculated from return tributary surviving radio-tagged fish detections, and the total 2015 tagged sample. Counts of fish are divided between those assigned as part of the kelting rate group (upper table) and those that were detected at or below Bonneville Dam (lower table). Counts of tagged fish sex (F and M, female and male, respectively) separated between rearing origins and totals (T) and proportions are provided.

Tributary	Hatchery			Wild			Total	Proportion Tributary Survivors *n*=167		
	F	M	All	F	M	All		F	M	All
Downstream Detected Kelts										
Entiat	0	0	0	6	5	11	11	0.036	0.030	0.066
Methow	6	4	10	9	2	11	21	0.090	0.036	0.126
Okanogan	9	4	13	7	1	8	21	0.096	0.030	0.126
Wenatchee	12	6	18	14	7	21	39	0.156	0.078	0.234
Total	27	14	41	36	15	51	92	0.377	0.174	0.551
Kelts Detected at Bonneville										
Entiat	0	0	0	3	1	4	4	0.018	0.006	0.024
Methow	0	0	0	2	0	2	2	0.012	0.000	0.012
Okanogan	2	0	2	0	0	0	2	0.012	0.000	0.012
Wenatchee	1	1	2	4	2	6	8	0.030	0.018	0.048
Total	3	1	4	9	3	12	16	0.072	0.024	0.096

Table 2.19 Number of downstream migrating kelts detected and proportions calculated from return tributary surviving radio-tagged fish detections, and the total 2016 tagged sample. Counts of fish are divided between those assigned as part of the kelting rate group (upper table) and those that were detected at or below Bonneville Dam (lower table). Counts of tagged fish sex (F and M, female and male, respectively) separated between rearing origins and totals (T) and proportions are provided.

Tributary	Hatchery			Wild			Total	Proportion Tributary Survivors *n*=144		
	F	M	All	F	M	All		F	M	All
Downstream Detected Kelts										
Entiat	0	3	3	6	7	13	16	0.042	0.069	0.111
Methow	27	0	27	6	1	7	34	0.229	0.007	0.236
Okanogan	15	1	16	2	0	2	18	0.118	0.007	0.125
Wenatchee	3	4	7	6	1	7	14	0.063	0.035	0.097
Total	45	8	53	20	9	29	82	0.451	0.118	0.569
Kelts Detected at Bonneville										
Entiat	0	0	0	0	1	1	1	0.000	0.007	0.007
Methow	0	0	0	0	0	0	0	0.000	0.000	0.000
Okanogan	0	0	0	0	0	0	0	0.000	0.000	0.000
Wenatchee	0	0	0	0	0	0	0	0.000	0.000	0.000
Total	0	0	0	0	1	1	1	0.000	0.007	0.007

Figures

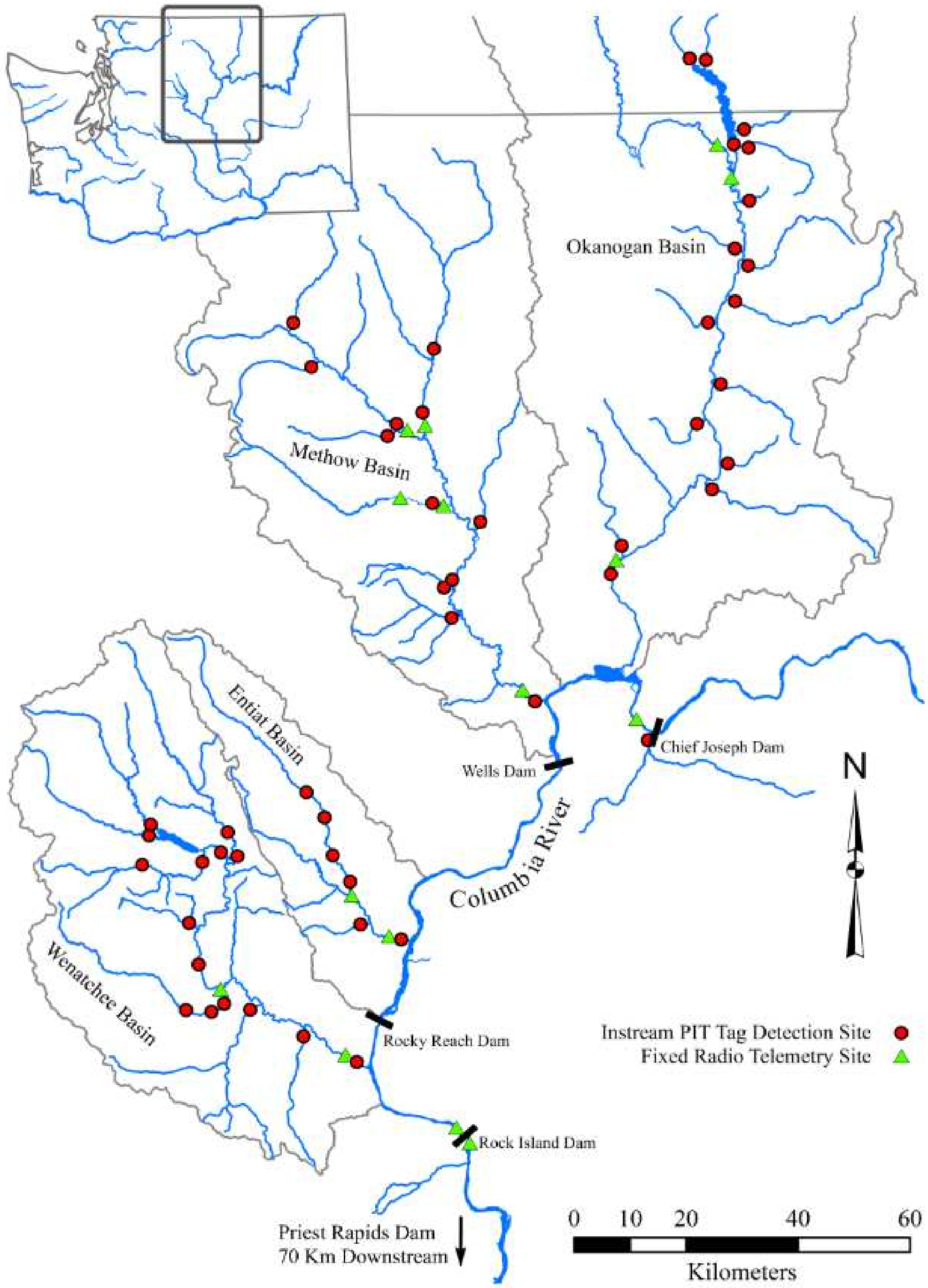

Figure 2.1**.** Location of dams (black rectangles), fixed site radio telemetry antennas (green triangles), and lower tributary PIT arrays (red dots) in the Upper Columbia River basin. The study area encompasses the waters between Priest Rapids Dam and Chief Joseph Dam and tributaries. All fixed site names and description locations are provided in Table 2.1.

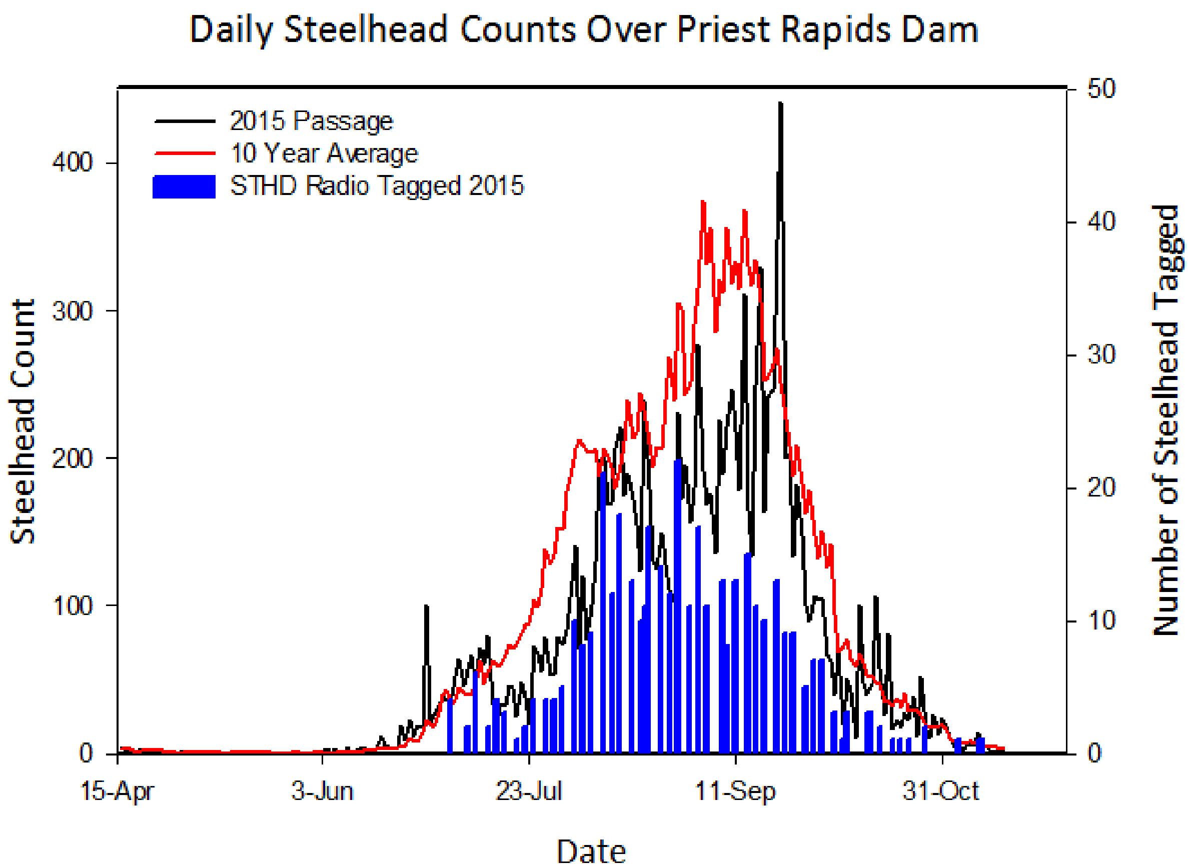

Figure 2.2. Summer Steelhead count passage over Priest Rapids Dam in 2015 and average annual passage for the previous ten years are given by count date. Daily counts of summer Steelhead radio-tagged from 6-July through 10-November 2015 are also indicated (blue bars) and radio-tagged fish counts are represented along the right y-axis.

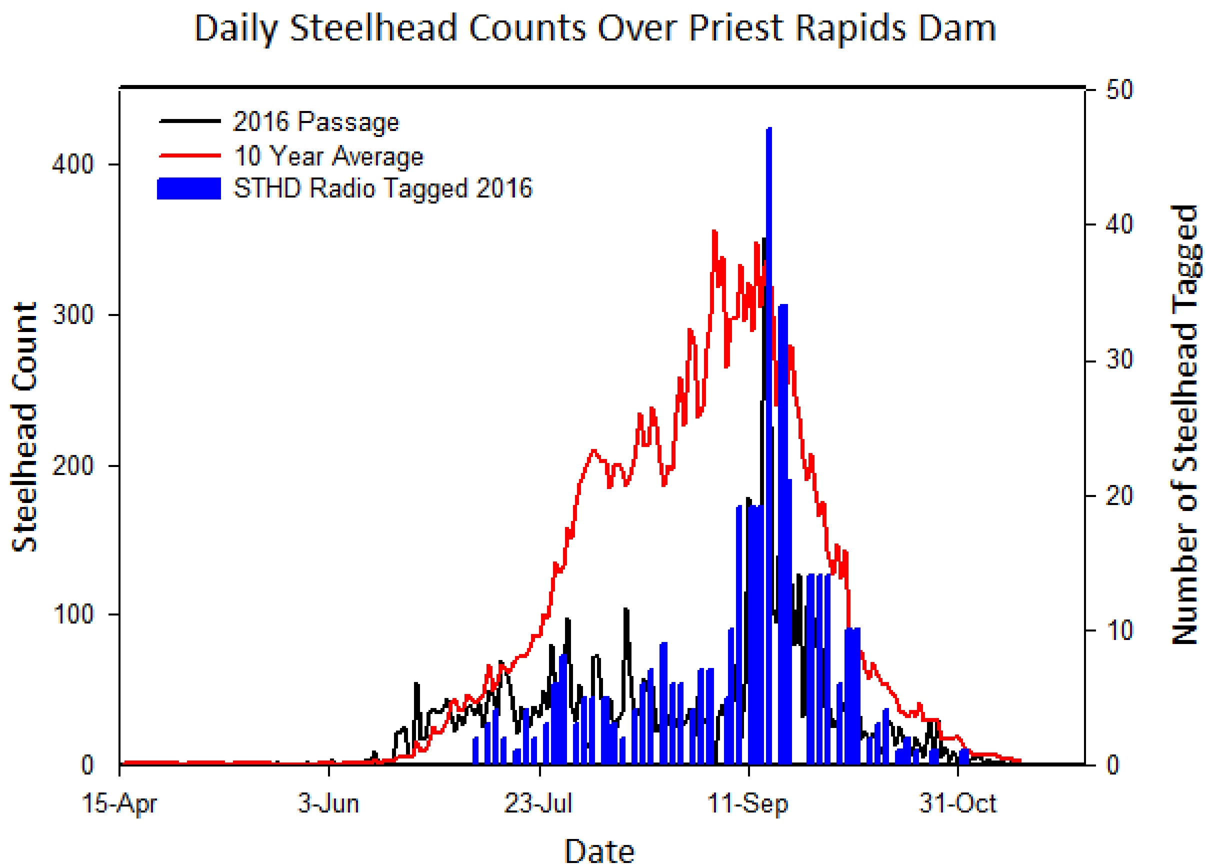

Figure 2.3. Summer Steelhead count passage over Priest Rapids Dam in 2016 and average annual passage for the previous ten years are given by count date. Daily counts of summer Steelhead radio-tagged from 6-July through 2-November 2016 are also indicated (blue bars) and radio-tagged fish counts are represented along the right y-axis.

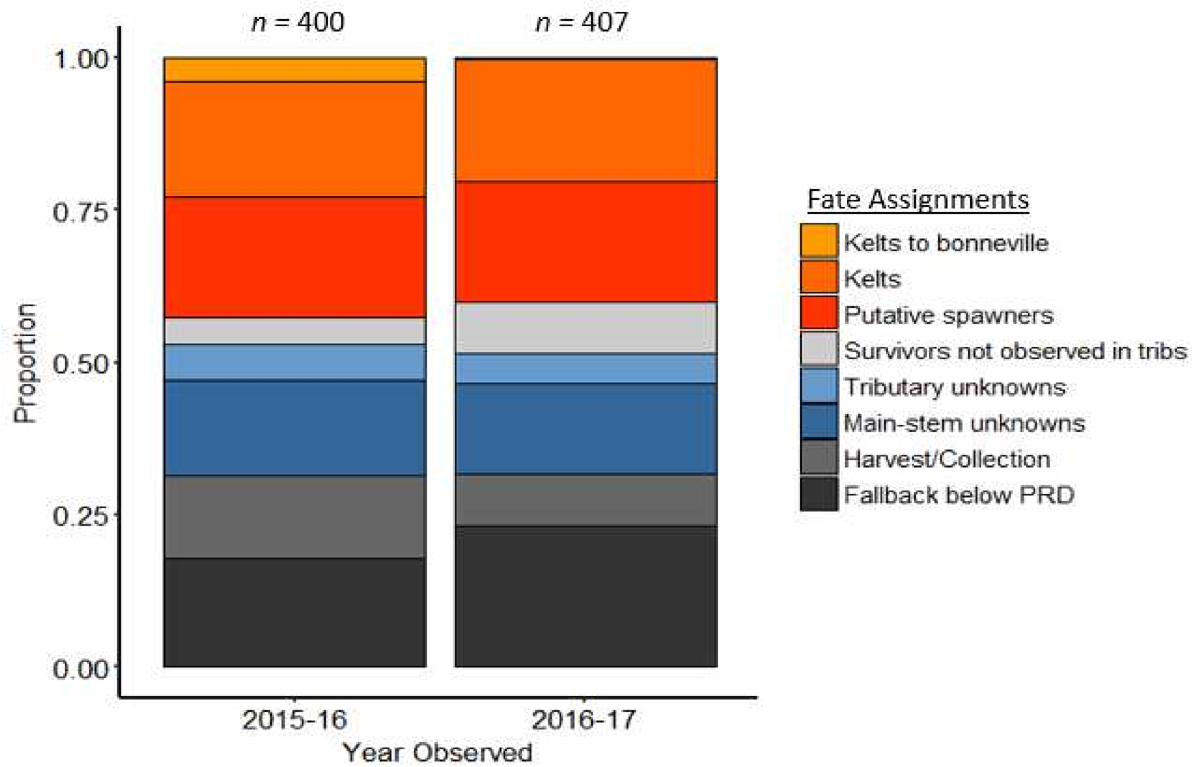

Figure 2.4. Proportion of radio-tagged steelhead assigned to each fate for both years fish were monitored. Fate assignments are indicated by color, and total tagged steelhead sample sizes are provided. Harvested and collected proportions indicate those that occurred above Priest Rapids Dam.

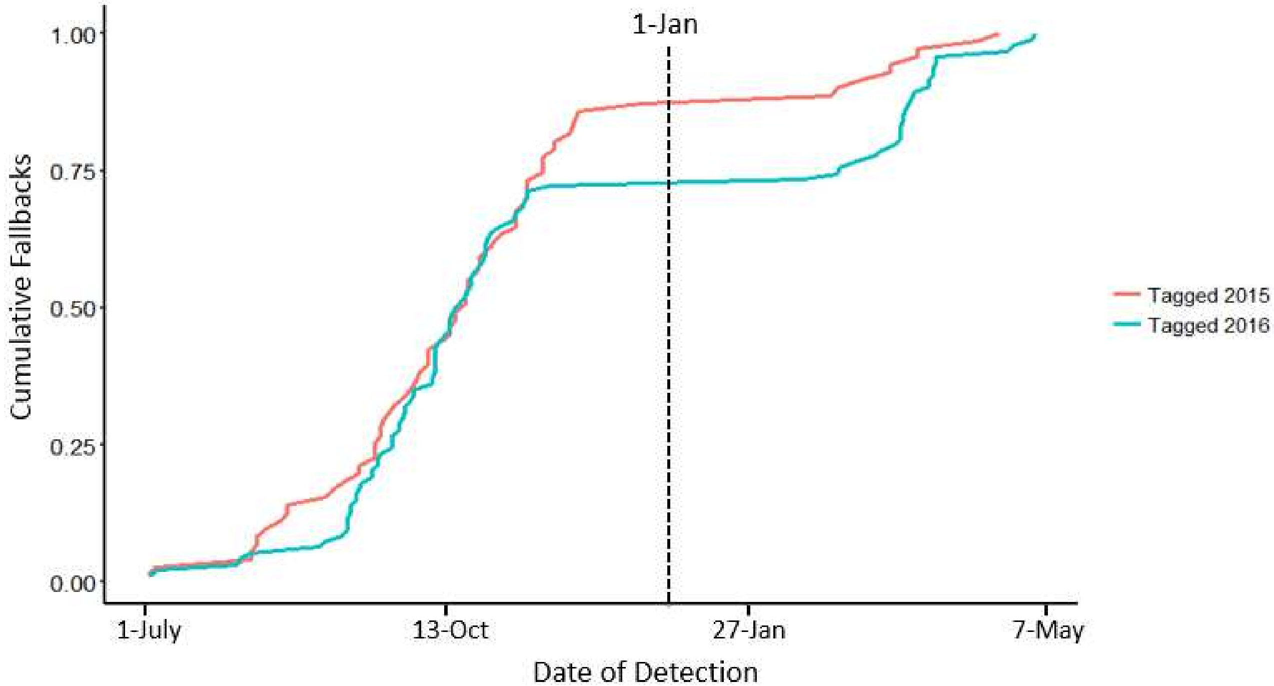

Figure 2.5. Cumulative proportion of radio-tagged steelhead detected as fallbacks below Priest Rapids Dam by detection date. Fallback detections are split between 2015 (red line) and 2016 (blue line) radio-tagged and released sample groups. The 1-Jan overwintering onset date (dashed line) is indicated.

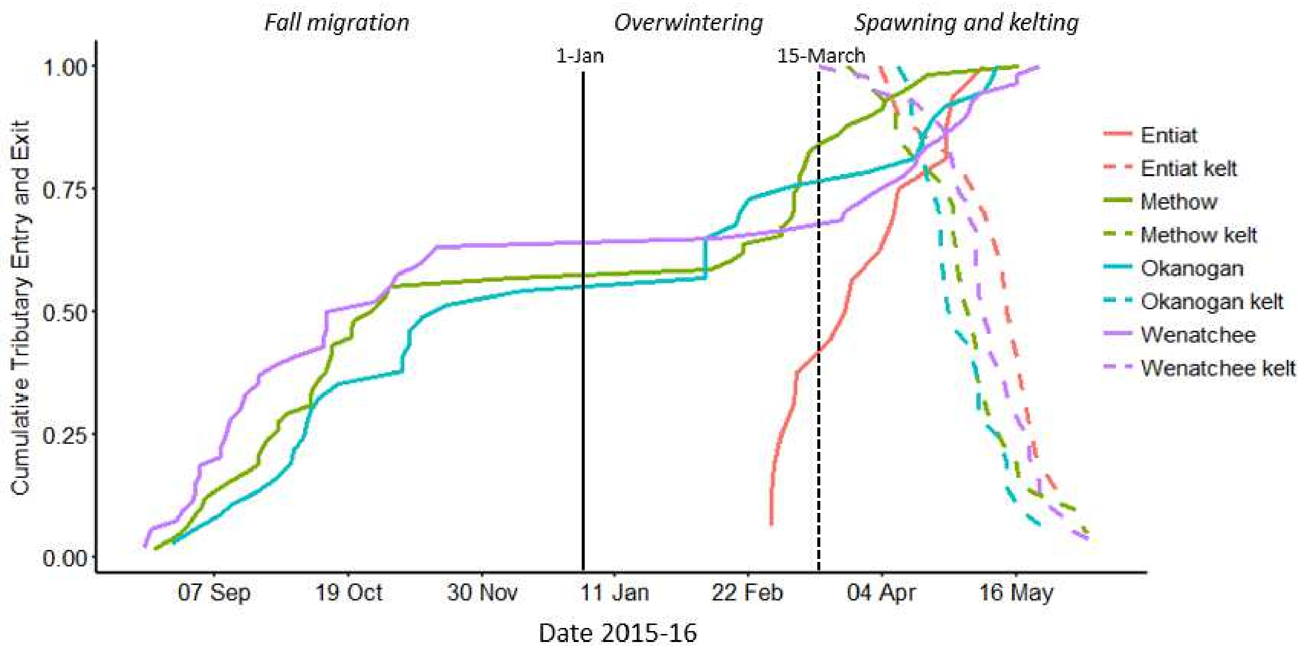

Figure 2.6. Cumulative proportion of radio-tagged steelhead entry and exit by tributary population for steelhead released and monitored in 2015. Tributary entry (solid lines) and kelting outmigration timing (dashed lines) by date of steelhead assigned fates as putative spawners. The 1-Jan overwintering onset date (solid black line) and 15-March kelting onset date (dashed black line), separating the fall migration, overwintering, and spawning/kelting periods are indicated.

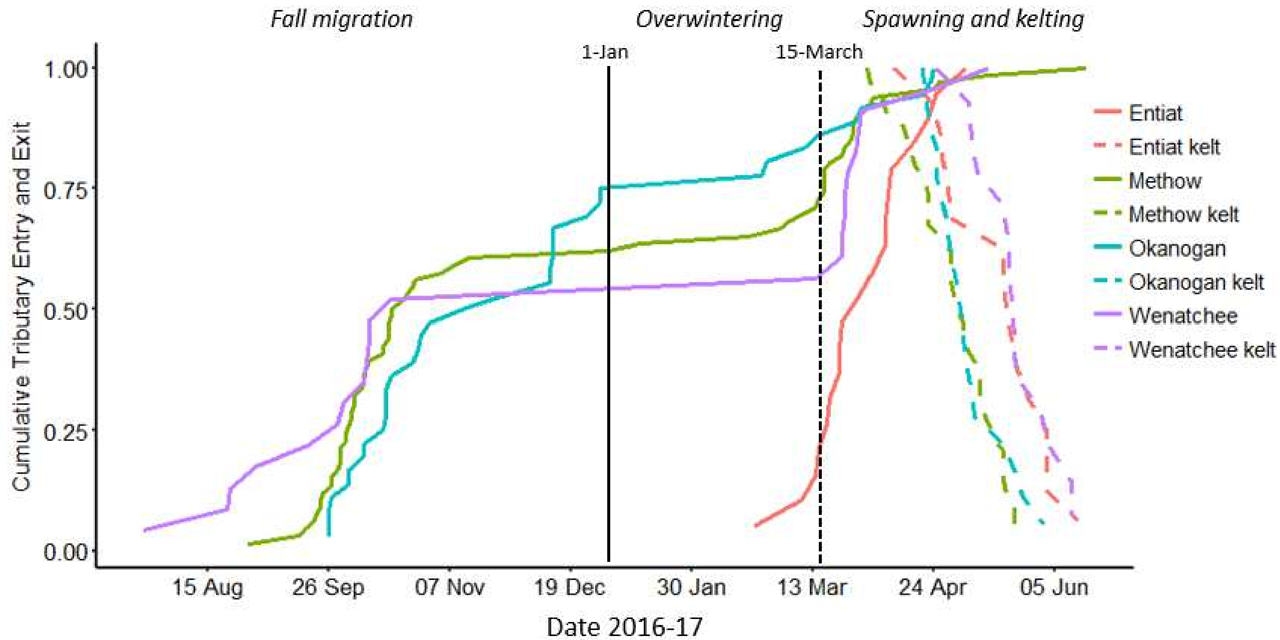

Figure 2.7. Cumulative proportion of radio-tagged steelhead entry and exit by tributary population for steelhead released and monitored in 2016. Tributary entry (solid lines) and kelting outmigration timing (dashed lines) by date of steelhead assigned fates as putative spawners. The 1-Jan overwintering onset date (solid black line) and 15-March kelting onset date (dashed black line), separating the fall migration, overwintering, and spawning/kelting periods are indicated.

Chapter 3: A Framework for Classifying and Inferring Behavioral Data from Accelerometer Biotelemetry Developed With Spawning Behaviors of Steelhead Trout

Summary

1. The ability to observe animal movement and behaviors can be essential for the proper management and protection of species, especially for ESA listed species or those in decline. Movement sensing technologies that utilize accelerometers are useful in detection of behaviors that are otherwise difficult to observe visually under field conditions, and may enhance the ability to quantify behaviors at the population scale.

2. We monitored Summer Steelhead spawning behaviors within a semi-natural channelized enclosure using accelerometer telemetry tags while simultaneously observing behaviors with underwater cameras. Behavioral assignments from visual observations were compared to acceleration histories to develop assignment criteria for identifying a key behavior (oviposition events) in Steelhead solely from acceleration data. Behavioral events independently classified using acceleration data and unviewed video were compared and 97% of holding behaviors, 93% of digging behaviors, and 86% of oviposition/covering behaviors were correctly assigned.

3. We then applied the method to *at-liberty* Steelhead in spawning tributaries. Acceleration records revealed putative spawning in *at-liberty* female Steelhead, and time budgets for *at-liberty* Steelhead were largely similar to those of Steelhead monitored within enclosures.

4. The use of movement sensing tags and similar classification approaches offer a method for monitoring movement in a broad array of aquatic and terrestrial taxa, and may be especially useful for establishing activity and habitat-use relationships where direct observation of behavior is limited.

Introduction

The movement behaviors of animals are intimately linked to individual fitness at multiple scales. Therefore, attaining information on the movement behaviors is critical to understanding limiting life history stages, environmental factors, and population trends that may affect species of ecological and management interest. Collecting data on species moving at night or in visually limited environments has been particularly challenging. Newly developed technologies have continued to facilitate improvements in many fields of fisheries research including optics (Graham et al., 2004), acoustic cameras (Martignac et al., 2015; Mueller et al., 2006), the use of passive integrated transponder (PIT) tags (Roussel et al., 2000), and accelerometer tag technology for tracking movements and behaviors (Broell et al., 2016; Moser et al., 2017; Thiem et al., 2015; Watanabe et al., 2013). Development of commercially available accelerometer tags will provide the opportunity to detail behaviors *in situ* for many species. A growing body of research has already begun applying new acceleration sensing technologies and quantifying associated movements with the aim of better understanding habitat preference and foraging behavior in many species (Laich et al., 2008; Wakefield et al., 2009; Wang et al., 2015). Determining the relationship between specific behaviors and time series of acceleration data is a key step in implementing accelerometer tag technology in field studies of *at-liberty* animals. Here, we describe a general framework for the classification and validation of accelerometer data, using spawning behaviors of Steelhead (*Oncorhynchus mykiss*) and prototype commercial accelerometer tags as a case study. The approach uses video observations to identify behaviors and classify acceleration data based on maximum acceleration and the frequency and variability of acceleration events. A subset of video data was then used to assess the accuracy of the behavioral classification (female spawning) scored from accelerometer data (Figure 3.1) and identify limitations in classifying behaviors from acceleration records. We then quantified individual time budgets and key behaviors (female spawning and redd digging [nest building; Esteve, 2005]) in tagged *at-liberty* steelhead.

Fitness is closely tied to spawning behaviors in anadromous salmonids (*Oncorhynchus spp.*) because adults use energetic stores obtained in the ocean for upstream migration and spawning. Further, most Pacific salmon species are semelparous and die after spawning. Steelhead (anadromous Rainbow Trout, *O. mykiss*) exhibit an iteroparous (repeat spawning) life history where they may spawn in future years after returning to marine habitats (Dodson, 1997; Keefer et al., 2008b). Iteroparity is relatively common in coastal steelhead populations. In contrast, interior summer-run steelhead enter freshwater in late summer (July-Sept), overwinter in freshwater before spawning during spring months (March-May), and exhibit low rates of iteroparity (>5% [Keefer et al., 2008b; Keefer et al., 2017; Leider et al., 1986]). Consequently, migration success (reaching spawning grounds), holding success (survival during the overwintering period), and spawning success (successful redd building and egg deposition) by adult females are important life history parameters of management and conservation concern.

In recent years, gastrically implanted radio telemetry tags have been increasingly used to monitor fish behavior in anadromous fishes which do not feed during the breeding migration, including those protected under the Endangered Species Act (ESA). Gastrically implanted tags afford researchers the ability to detect and monitor movements with relatively low failure/regurgitation rates, while also minimizing risk of mortality to the tagged species (Keefer et al., 2004b; Ramstad &

Woody, 2003; Corbett et al. 2012; Naughton et al., 2017). Studies have evaluated behaviors, including population migration timing and passage success (Keefer et al., 2004a; Boggs et al., 2004; Keefer et al., 2013 [Diel behaviors]), and to estimate survival (Cooke et al., 2006; Keefer et al., 2008a) at relatively large (100 m-1000 km) scales.

Extensive research has been conducted on the reproductive behavior of salmonid species, and behaviors are broadly similar between and among species (Esteve, 2005; Fleming, 1998; Quinn, 1999). Anadromous salmonid (*Oncorhynchus spp*.) reproduction takes place after returning from the ocean to freshwater where the female selects a site in the natal stream to dig a redd and deposit eggs. Field studies over more than 80 years have described specific spawning behaviors (i.e., digging, covering, oviposition; Needham & Taft, 1934; Orcutt, 1968; Shapavolov & Taft, 1934; Tautz & Groot, 1975), which are consistent among steelhead populations. Adult female steelhead select a redd site location with preferred flow conditions and suitable substrate, then commence periodic digging, vigorously beating their tails against the substrate. Once the redd dimensions have been constructed the female begins “probing” the substrate with her anal fin and creates small pockets in which to deposit eggs. Males position themselves along-side the female frequently “quivering” (hereafter “coaxing”) and releases milt in synchrony with the female as she deposits eggs. Immediately following oviposition the female hastily covers her eggs in the stream substrate with frequent and rapid tailbeats. Additional digging/oviposition events occur until the female has released all her eggs.

While there is a rich literature detailing salmonid spawning behaviors, quantifying spawning behavior is challenging for steelhead in many rivers given springtime spawning conditions. Spawn timing typically coincides with seasonally variable environmental conditions including elevated flows, high turbidity, and low visibility associated with spring snowmelt and terrestrial runoff. Fisheries managers often rely on redd counts to estimate spawning escapement, and spawning success at the population level (Gallagher & Gallagher, 2005; Zimmerman & Reeves, 2000), but lack of visibility, potential interpopulation differences in redd digging and oviposition behavior, and limited redd life duration introduce a large degree of uncertainty when estimating the number of successful spawners.

Accelerometry provides instrumentation to address such issues. Tsuda et al. (2006) was successful in detecting spawning behaviors through the use of archival acceleration data-loggers attached to the backs of chum Salmon (*Oncorhynchus keta*) that monitored the amplitude of surge and swaying acceleration of spawning fish on a 2 dimensional axis. Data were accessible only after loggers were recovered after the monitored fish had spawned and subsequently died. Recent development of accelerometer transmitters provides the opportunity to quantify behavior without recovery of the tag, which is not always possible.

Here a sample of steelhead were isolated in a spawning enclosure and behaviors were video recorded while acceleration histories were remotely monitored. A second sample of tagged individuals were released into the natural environment and were monitored during late migration and spawning. By comparing observed spawning behaviors to telemetry records transmitted by the accelerometer tags, we demonstrate a combination of acceleration magnitude, frequency and variability can be used to identify and quantify some (but not all) behaviors using currently available technology for fish tagged and released into the natural environment.

Method Development

Step 1: Tagging Animals for Direct Observation

Accelerometer Tags

Steelhead movement and spawning behavior was monitored using prototypes of a commercial 3-volt coded transmitter tags (model MCFT3-3A, Lotek Wireless, Newmarket, Ontario, 16mm X 58mm, 20 grams in air, manufacturer reported tag life 90 - 120 days). The tags were designed to transmit an integrated acceleration value, based on the measured maximum differential acceleration in any of three axis, with a maximum 1.5 gravity (g) acceleration, 0.03 g resolution, and 4 sec transmission intervals ('burst interval', BI). Transmitted programmed sampling interval (PSI) values were converted to g based on manufacturer specifications. Tags were activated and tested prior to being implanted in fish in order to ensure burst timing collisions between multiple tags would be minimized. Telemetry data from tags was collected from monitoring receivers positioned at the spawning enclosure using Lotek SRX800 Receivers.

Study Site, Collection and Tagging

We tagged and observed spawning by steelhead using optical video (Step 2) under semi-natural conditions. Monitoring took place at Winthrop National Fish Hatchery (WNFH) located on the Methow River in north-central Washington State (USA). The Methow River is a major tributary to the Upper Columbia River basin. Steelhead returning to (WNFH) must traverse nine major hydro-electric dams and travel approximately 924 rkm from the Columbia River estuary. All steelhead used for Steps 1-4 behavioral observations were of hatchery-origin and were collected by USFWS personnel to reduce hatchery genetics on the spawning grounds. Fish were held at the hatchery until mature. Four females and four males were released in two sample spawning groups of two males and two females respectively (Table 3.1). Males and females were tagged exclusively on two different frequencies in order to minimize the collision of transmissions on a given frequency.

Tagged fish received an intragastrically implanted accelerometer 3-volt coded transmitter activity sensor tag (model MCFT3-3A, Lotek Wireless, Newmarket, Ontario), as well as Passive Integrated Transponder (PIT) tags implanted ventrally between the pelvic fins. A ~1 cm slice of surgical rubber tubing was attached around the accelerometer tag prior to gastric implantation consistent with other radio telemetry tagging research with the aim of reducing regurgitation rates (Keefer et al., 2004b; Thorstad et al., 2013). After tagging, fish were allowed to recover before being released into the enclosure. Fish were anesthetized, tagged, and released by USFWS Mid-Columbia Fish & Wildlife Conservation Office staff.

Step 2: Direct Observation of Bio-telemetered Animals

Enclosure Experiment and Video Monitoring

A temporary enclosure constructed of stainless steel weir panels was positioned in an irrigation diversion channel located at WNFH (Figure 3.2). The channel flows parallel to the Methow River providing water to the hatchery facility and is partially flow controlled. The enclosure was installed upstream of an impassable fish barrier that is integral to WNFH fish collection operations. The enclosure measured approximately 12 meters in length and 2 to 4 meters in width with the maximum width located roughly halfway between the culvert and downstream weir panels. The enclosure was installed and positioned with weir panels on the downstream end of a section approximately 2 m wide (Figure 3.3). The upstream weir panel was located just above two 0.7 m diameter culverts, preventing fish from escaping upstream but also providing cover for released fish within the culverts or under the culvert outflow. Spawning gravel was present throughout the enclosure, ranging in size from gravel to bolder (1 cm to 100 cm), the depth within the enclosure ranged from 0.5 to 1.0 meters depending on the local daily precipitation and temperature (snow melt). Anadromous steelhead have been observed spawning naturally in the outflow channel during a previous year when the barrier structure failed (M. Humling, personal communication, March 2017).

Fish movements and behaviors were monitored and recorded using 4 SPECO underwater cameras (Global Equipment Company Inc., Port Washington, New York) while acceleration data were recorded by receivers present on site. The first sample group was monitored by video from 26-April – 28 April 2017 and thereafter by telemetry receiver until 1-May 2017. Females F1 and F2 and males M1 and M2 were monitored during this experiment. The second sample group was released and monitored from 3-May to 5-May 2017 until a high flow event resulted in poor visibility (beginning 4-May) and two fish (M4 male and F4 female) escaped the enclosure moving upstream and out of view of the positioned cameras. The latter fish were not evaluated for behavior in the enclosure but were considered *at-large* after escape on the evening of 4-May 2017 (Step 5).

STEP 3a: Identification of Behaviors Using Underwater Video

Behaviors of female and male steelhead were identified and cataloged using a combination of preliminary review of video observations and existing literature (Esteve, 2005; Needham & Taft, 1934; Orcutt et al., 1968; Shapovalov & Taft, 1954). Female steelhead behaviors included holding, lateral movement, burst movement, digging, and aggression. Digging was the primary observed female spawning behavior and was further subdivided among redd construction (digging), oviposition, and covering following oviposition. Male behaviors were similar to those of females aside from an absence of digging/covering, and the addition of coaxing (quivering) behavior observed when males were present alongside a female on a redd. After classifying behaviors from optical video, acceleration records were aligned and compiled for the preliminary sample (Figure 3.4).

Behavioral observations and acceleration data relevant to methods development are reported in the section below while general behavioral patterns are presented in the Results.

Holding

Holding behaviors were categorized by a fish remaining in place in the water column or moving very gradually in any direction but never traveling further than approximately one body length distance during a single burst index duration. Holding behaviors were most frequently observed when fish were hiding or resting away from a redd, and immediately before and after digging. Telemetry burst index rates rarely exceeded 0.3 g, and long duration holding periods were common (Figure 3.4a).

Digging

Digging behaviors were assigned when a female was observed rolling onto one side and beating her tail rapidly against the stream substrate dislodging rocks and gravel for a span of 1 to 2.5 seconds (*mean* = 1.9). Two to seven tail beats were observed during each digging event, carrying the female upstream. Immediately following digging, the female would resume an upright position and reoccupy her original location on the redd by swimming downstream in a loop pattern (“lateral movement/looping”) or allowing the current to carry her downstream. A single digging event occurred typically within the span of a single tag burst index, but occasionally carrying over to a second (Figure 3.4b). Observed digging behaviors averaged 1.26 g (range: 0.8 -1.5 g).

Oviposition and Covering

At the onset of oviposition, females pitched upward and angled their tail downward into the substrate. Females were then observed releasing eggs with a male (or males) positioned adjacent, releasing milt. At the time eggs (and milt) were released all the participating fish opened their mouths wide while their bodies quiver slightly for a duration of one to two burst durations (~6 seconds). Acceleration during oviposition was low (mean = 0.24 g, range 0.06 to 0.42 g).

Oviposition events were immediately followed by covering events, visually similar to the digging events previously described, but with increased frequency (4-5 events per minute). The duration of covering events following oviposition typically lasted between 2 to 6 minutes and averaged 14 consecutive covering events (Figure 3.4c). Covering behavior also differed from redd construction digging events whereby the duration of a single covering event rarely exceeded 1.5 seconds (*mean* = 1.2 s) and was followed by a low acceleration interval of approximately 30 sec to several minutes. Brief holding (3-6 s) and lateral movements were common between each covering event as the female would reposition herself following each covering movement. Oviposition was detectible in telemetry records from the frequent high amplitude covering events. Telemetry outputs detected while covering was observed averaged 1.15 g and ranged from 0.7 g to 1.5 g.

Lateral movements

Lateral behaviors occurred when a fish was observed moving in any direction but returned to its original position within the time span of a single burst index (4 seconds). These behaviors were particularly common when a female was observed holding on a redd and moving side-to-side between specific digging events. In some cases, the female would swim in a rounded loop back to her original position immediately following digging (‘looping’); these movements were included in the lateral movement category. Lateral movements were common among males when they were within close proximity to a female (Figure 3.4d). Maximum acceleration during lateral movements was low to moderate and averaged 0.27 g (range: 0.15 g - 0.5 g).

Aggression

Aggression among fish within the spawning enclosure occurred between fish of the same sex and attacks were usually observed between larger sized fish, directed toward smaller sized ones (Figure 3.4e). Typically, the largest male in the enclosure would repeatedly attack a smaller male, which would in turn attack untagged precocial juvenile male steelhead (not excluded from entering the enclosure through the weir panels). Aggressive chasing behaviors by dominant males and fleeing by subordinate males were commonly observed in an apparent attempt to exclude access to females. Aggressive movements were most often short duration (<1 BI) but were occasionally sustained for up to ~ 16 to 20 seconds (4-5 bursts). Aggression between females was also observed, but less frequently than among males. Acceleration during aggression events averaged 0.51 g (range: 0.21 to 1.5 g).

Burst Movements

Burst movements were rapid swimming events that resulted in movement of at least one body length during one BI. Burst movements were typically longitudinal (up/downstream). Burst movements were typically less than one BI in duration (Figure 3.4f). Telemetry data burst movement outputs averaged 0.3 g and ranged from 0.15 to 0.75 g with occasional bursts reaching the maximum tag threshold of 1.5 g.

Coaxing

Male coaxing events occurred when a male positioned alongside a female and ran its nose along the length of the females dorsal or ventral sides surfaces then, remaining stationary, rapidly undulated while parallel to the female for 1 to 2 seconds with moderate detected acceleration (Figure 3.4g). All males within both enclosure treatments were observed displaying coaxing behaviors along-side females. Coaxing behaviors where observed with most frequency leading up to an observed oviposition event, after which males would typically hold position behind the female until covering events had ceased, and holding and digging behaviors had resumed. Telemetry detections observed by coaxing males averaged 0.37 g and ranged from 0.15 g to 0.8 g.

Out of View

Fish exiting the camera field of views were assigned as 'out of view' when off all cameras within the enclosure. This was commonly the case following a significant burst or lateral movement, or during aggressive interactions. Out of view assignments were very common during the first 1 hour following the release of fish into the enclosure as they would typically spend several hours hiding/resting under the culvert out-flow within the enclosure. Out-of-view periods were excluded from analyses in Steps 3b-4.

STEP 3b: Alignment of Video and Biotelemetry Time Series

Randomly selected 10-15 minute blocks from each clock-hour of daytime video were selected for review for each steelhead and each block was manually reviewed to assign behavior to start and end times for behaviors for the entire block. Behavioral events were then aligned to the time series of acceleration telemetry data using time stamps, with each BI record assigned to a behavioral class using video data. Observations were limited to daylight hours (~6:00am to 8:00pm) due to limited visibility from dusk to dawn.

Daytime observations of the six enclosure monitored fish revealed steelhead spent the majority of time holding (*mean* = 63%; Figure 3.5), while other movement oriented behaviors combined (burst movement, lateral movement and aggression) encompassed a mean ~7% of the total observed behavior. Spawning related behaviors (digging, oviposition/covering, and coaxing) made up only ~6% of observed behaviors and the remaining 25% of time was spent out of view. All assigned behavior tag detection strength ranges were compiled for comparison for both males and females tagged for observations within the enclosure (Figure 3.6).

STEP 3c: Development of Criteria for Classification of Accelerometer Records

Once criteria for scoring behaviors were established and aligned to acceleration records, we examined the distributions of acceleration records to identify thresholds and decision rules for identifying behaviors based on the amplitude, frequency, and variability of acceleration records (Figure 3.7). A subset of the telemetry records were reserved and used to assign behaviors using acceleration criteria prior to observing video records in order to compare the success of assigning a given behavior to telemetry records (Step 4).

Notably, sets of behavior were largely distinct based on the magnitude of acceleration alone (Figure 3.7). The mean holding behavior telemetry detection strength averaged 0.09 g for all fish, with a mean of 0.08 g and 0.10 g for males and females, respectively (Table 3.2). A threshold of $\leq$ 0.21 g successfully classified 96% of acceleration records as holding events observed by video. Acceleration records of 0.0 g (no movement) were common (4.0% of holding behavior detections), though durations of no movement greater than 3 consecutive BIs were exceedingly rare (0.02% of total time).

The vast majority of digging and covering behaviors were associated with acceleration records exceeding the 0.9 g. Of the total 422 observed digging detections approximately 88% registered at or above the 0.9 g threshold, of these 41% registered at the maximum BI output (1.5 g). The mean detection strengths were ~1.27 g across all observed and detected digging events. Of the 76 observed covering events 93% were observed at or above 0.9 g, with mean detection strength of

1.14 g. A small minority of aggression (10%) and burst/lateral events (6%) were associated with accelerations above the 0.9 g threshold. Male coaxing behavior was observed registering over the 0.9 g threshold in only 1.5% of observed and detected instances.

While high magnitude acceleration events (>0.9 g) were associated with several behaviors, oviposition and covering could be reliably separated from digging/burst plus movement/aggression events. Immediately following oviposition, covering events were recognizable by consistent detections above 0.9 g at low frequency (*mean* ~5 events/min) over the course of approximately 2 to 7 minutes, whereas digging events were associated with longer intervals between >0.9 g acceleration events (e.g. compare Figure 3.4b with 3.4c). Overall, the combined criteria distinguished among three classes: holding, oviposition/covering, and digging/burst movement/aggression (Figure 3.7).

STEP 4: Validation of Accelerometer Assignments using Video Observations

A random subset of video observations were reserved when identifying behaviors and establishing classification criteria for acceleration values to evaluate the accuracy of the acceleration-based assignments. Only female behaviors were validated as detection of spawning behaviors was the primary objective of this study. Validation of predicted behaviors assigned to tag burst detections indicated >92% of digging and holding events were correctly classified (Table 3.3). Burst and lateral movement behaviors were correctly assigned less consistently (48% and 45%, respectively). Oviposition events were detectable by the frequent and rapid covering events that immediately followed egg deposition, and were correctly assigned in ~86% of the events identified from accelerometer records (N= 7).

STEP 5: Biotelemetry of At-Liberty Steelhead

Steelhead were tagged, released, and monitored in the Twisp and Wenatchee Rivers in north/central Washington State, both rivers are tributaries of the Upper Columbia River. A total of 3 fish were tagged and released at Twisp River weir (~75 km up the Methow River) in April-May of 2016 (2 females and 1 male) and 6 fish were tagged at Tumwater Dam (~45 km up the Wenatchee River) in April-May of 2017 (4 females and 2 males). Sample sizes were limited as steelhead returns to the Upper Columbia River basin were less than the annual 10 year mean during both study years. All tagged fish released into the Wenatchee and Twisp Rivers were of presumed natural rearing origin given the absence of markings and fin clips at the time fish were handled. Steelhead were tagged with an accelerometer tag and a PIT-tag using identical methods for steelhead sampled for the enclosure observations. Tags used for *at-liberty* steelhead transmitted differential acceleration at a sampling interval of 3, 3.5, or 4 seconds, depending on the specific tag. The 0.5 second offset among tags was used to reduce the potential for continuous interference by two tags transmitting simultaneously on the same frequency. Fish were anesthetized, tagged, and released by Washington Department of Fish and Wildlife (WDFW).

Once tagged fish were allowed to recover in holding tanks located at Twisp River weir (Twisp River, 2016) and Tumwater Dam (Wenatchee River, 2017) for 20-30 minutes before release into their respective rivers. Upon release fish were allowed to continue migrating to spawning grounds and mobile monitoring took place daily, tracking tagged fish's movement until they had left the system, or were classified as regurgitated tag/dead based on continuous zero g acceleration records. After release, fish were monitored to a presumed spawning location (i.e., at a riffle, or were detected at historic known spawning site) and a temporary fixed site receiver (SRX-800, Lotek Wireless, Newmarket, Ontario) was installed and equipped with a battery and antenna after 24 hours holding in a location. Once installed, a fixed site was visited daily and fish presence, antenna placement, and battery life were verified until the fish was detected leaving its location. Monitoring continued as the steelhead moved downstream out of the system or relocated to another spawning reach. Tracking and fixed site relocation continued until all tagged fish had either left the system or were presumed dead or to have shed their tags.

STEP 6: Quantify Behavior of At-liberty Steelhead using Classification

Data Analysis

Telemetry data was collected from monitoring receivers positioned both in the field and at the spawning enclosure. *At-liberty* steelhead acceleration records were classified (Step 3c) and *at-liberty* steelhead time budgets were compiled from the time series and compared to those obtained for steelhead in the enclosures, with the exception that digging/burst movement/aggression were aggregated for *at-liberty* steelhead.

Results

Quantification of Spawning Behavior in Enclosures

All tagged females in each group that remained within the enclosure were observed exhibiting spawning behaviors on video (digging, oviposition and covering). Both females in the first group were observed digging on the first day post-release. Female F3 in the second sample group was not observed digging until the second day. Digging behavior was episodic in nature lasting for several hours followed by several hours of apparent inactivity (based on telemetry records and visual observations). Female F2 was first observed ovipositing and covering during the evening of the first day of release, while Females F1 and F3 were not observed ovipositing until the morning of second day in the enclosure.

With the obvious exception of one female and one male that escaped the spawning enclosure (M4 and F4) all other video monitored tagged fish were observed exhibiting the behaviors described previously (Figure 3.5). Total counts of all observed behavioral events and proportions of total by sex are provided for each steelhead (see Supplemental Data Chapter 3). The most commonly observed behavior was holding, accounting for an average 63.9% (female) and 62.9% (male) of observed behaviors. The mean proportion of observed burst movements where likewise similar for both females and males (2.9% and 2.7%, respectively) while lateral movements where slightly more common among males than females (4.3% and 3.2%, respectively). Spawning behaviors (digging, oviposition/covering) accounted for only an average 3.7% of female behavior. Behaviors assigned as out-of-view made up a total of 25% of observations. Notably, 94% of out-of-view observations registered at or below the 0.21 g holding threshold, suggesting holding was the dominant behavior during those periods.

Aggressive behaviors were more commonly observed by males than females (1.8% and 0.2% male and female, respectively). Although aggressive behaviors did not make up a large proportion of any individual steelhead time budget, aggressive behaviors were the highest accelerations recorded for males over the duration of the enclosure observations. The total mean acceleration magnitude detected for aggressive behaviors was 0.55 g, and aggression was more frequently observed by male fish, mean acceleration was slightly higher for females than males (0.60 g and 0.52 g, respectively). Male-to-male aggression was observed on every day fish were observed within the enclosure and among both enclosure groups. One female (F3) was never observed displaying aggression.

A combined total of 498 digging and covering events by females were observed and were relatively invariant. Mean individual dig duration ranged from 1.68 to 1.87 seconds, while mean individual covering duration ranged from 1.14 to 1.25 seconds. Digging events longer than the tag burst rate (4 seconds) were not observed and thus all events were limited to 1 or 2 BI. Oviposition events were indistinguishable from holding events (*mean* of 0.24 g), but oviposition could easily be identified indirectly by the frequent covering events following oviposition (Figure 3.4c). Covering events occurred approximately every 8 to 12 seconds after oviposition, and continued for a mean of 3:26 (min:seconds) and ranged from 1:43 to 6:19 (min:seconds). The mean number of covering events observed following oviposition was 14 and ranged between 9 and 24.

Behavior of At-Liberty Steelhead

A total of 11 tagged and released steelhead were monitored for *at-liberty* analysis of behaviors (Table 3.4). The sample includes 3 steelhead released from Twisp River weir (2016), 6 released from Tumwater Dam (2017), and 2 that escaped the spawning enclosure and were monitored exclusively by fixed site telemetry array. In total, 7 *at-liberty* released steelhead (5 females and 2 males) had suitable detection histories for inferring behaviors. *At-liberty* males were difficult to monitor continuously, because they rarely remained at any one location for longer than a single day.

One female (I24) released into the Twisp River was tracked moving upstream from the Twisp River weir release site and entered Little Bridge Creek (tributary of the Twisp River ~3 rkm upstream of the weir) five days after release. After a holding period of 4 days, detections consistent with sporadic digging events took place. At least 6 oviposition/covering events were detected through the following five days, after which time she was detected moving downstream out of the Twisp River (e.g. of oviposition/covering; Figure 3.8). Female (I22) tagged and released at Tumwater Dam was detected digging 20 km above the release site in the Upper Wenatchee River. A total of 11 consecutive days of detections were recorded, during which time at least 5 events consistent with enclosure oviposition/covering behaviors were observed. I22 was observed holding on a redd, and briefly observed digging. The enclosure escaped female (I30) was detected ovipositing 4 days after escape, and remained ~150m above the enclosure for a total of 9 days.

An additional female released at Tumwater (I25) was detected digging ~2 km above the release site, although rapid covering detections were not recorded, it is possible these were missed as only 6 days of episodic and non-continuous detections were recorded. I25 was eventually recaptured at Tumwater Dam 6 days after it was tagged, whereby it was recorded as having decreased in mass (WDFW, personal communication). She was released again and detected moving downstream out of the Wenatchee River, indicating it had likely spawned, but telemetry records indicating oviposition/covering were inconclusive given inconsistent and non-continuous telemetry detections. Records from I25 were included in subsequent analyses (Table 3.5).

Four of the tagged fish were presumed to have died or shed their tags (I16, I21, I28, and I32) within one week of monitoring after release. In each of these instances tag detections were not continuous through time, but limited in monitoring duration, given that the daily movements of the fish resulted in acceleration magnitudes of repeating series of 0.0 g bursts, indicating little or no movement without change. One fish tagged in the Wenatchee River was detected falling back below Tumwater Dam before being detected in a spawning tributary (via PIT-tag antennas) without further detection (I27), while another was detected moving downstream out of the monitored area after entering an unmonitored tributary for 12 days (I26).

Acceleration records implied *at-liberty* steelhead spent the majority of their time holding (Figure 3.9). The mean proportion holding for all *at-liberty* steelhead was 94.6% and was slightly higher proportion in females (96.5%) than males (89.9%). *At-liberty* males mean proportion 1.7% and 8.5% of the total inferred behaviors, burst movement, aggression (≥0.90 g) and burst/lateral movement (0.21 g – 0.90 g), respectively. *At-liberty* females were detected exhibiting behaviors other than holding in just ~3.5% of mean detections. The three steelhead, exhibiting oviposition/covering detections had nearly identical time budget behavioral proportions (~97% holding, ~1.5% burst/lateral movements, ~1.5% digging, oviposition/covering) compared to the two that were not detected ovipositing.

Time budgets for enclosure and *at-liberty* steelhead were similar within sex and there were not large differences in activity of *at-liberty* and enclosure steelhead during daylight hours (06:00 - 20:00) vs. at night (~20:00 – 06:00; Figure 3.9; Table 3.6). Low sample size precluded statistical tests of differences between groups.

Discussion

A growing body of research has been conducted using accelerometer tags for monitoring of animal behaviors, but to date, most studies have used externally attached tags intended to monitor movements for a limited duration following capture (Broell et al., 2016), and many require recapture of archiving tags (Lowe et al., 1998; Thiem et al., 2015). Intragastrically implanted accelerometer telemetry tag studies exist but thus far have been limited to studies of large-bodied species (Moser et al., 2017; Whitney et al., 2007) suited to tags with greater battery capacity and transmission ranges. Other studies have been conducted with the goal of quantifying or modeling energy expenditure both in laboratory and wild settings using accelerometers (Wilson et al., 2013). We inferred spawning of *at-liberty* female steelhead and develop time budgets remotely, using intragastrically implanted radio telemetry accelerometer tags. Similar to other systems, environmental conditions during tagging prevented direct observation of behavior and the large spatial extent and high velocity of rivers would have precluded recovery of archival tags. To the best of our knowledge this may be the first use of accelerometer tags in fish that both transmitted acceleration data and that were non-surgically inserted. Regardless of tag type, a key step in quantifying behaviors using acceleration data is establishing criteria to classify telemetry records that robustly allow inference of behaviors in field setting when actual behaviors cannot be directly observed or when it would be impractical or impossible to do so.

A key element of the study was the direct observation of individuals carrying tags prior to releasing *at-liberty* individuals. Our spawning enclosure experiments allowed observation of spawning behaviors/success at close proximity. Salmonid spawning experiments have been conducted in order to compare intraspecies mate selection and competitive exclusion behaviors (Schroder, 1981), measure spawning success of adult spawning fish (De Gaudemar et al., 2000), and anadromous/non-anadromous life history reproductive strategies (Hutchings and Myers 1985; McMillan et al. 2007). An important assumption when observing salmonid spawning in a semi-natural (instream enclosure) or laboratory setting is that observed behaviors are representative of those in the natural environment. It is possible that acceleration records of *at-liberty* steelhead included behaviors not observed in the enclosures or behaviors that were misclassified because *at-large* individuals had a wider behavioral repertoire. For example, fish monitored within enclosures were not subject to any form of predation whereas steelhead released in the natural environment may have exhibited predator avoidance behaviors. However, the similarity between time budgets observed for enclosed and *at-liberty* monitored steelhead, distinctiveness of key behaviors (e.g., covering), and similarity in behavior of enclosed steelhead compared to *in situ* observations of other salmonids during spawning (Newcombe & Hartman, 1980; Esteve, 2005) suggest any such bias to be minimal. Nonetheless, future studies should carefully design enclosure observations to minimize the potential for artifacts and minimize the potential for misclassification of key behaviors.

Tag effects are a concern in any telemetry study, and the accelerometer tags provided evidence of short-term changes in behavior post-release. Enclosure bound fish were released after tagging but may have been displaying heightened stress responses in that hours of inactivity were rarely recorded on the first day of release and only for a 2 to 3 hour duration. The act of remaining confined in the enclosure may have brought about an increased level of activity (as a stress response) not displayed by the *at-liberty* released steelhead. For this reason, the first day of telemetry records were omitted from the enclosure fish activity to *at-liberty* time budget comparison. However, tagging effects are common among tag and release/radio telemetry studies, and the accelerometer tags used here can be applied to help identify post-release behaviors and the duration of short term handling/tagging effects that would otherwise remain undetected, and heretofore, largely unquantified.

The classification developed here demonstrates the importance of both the magnitude of acceleration and temporal variance in acceleration for identifying behaviors. For example, oviposition/covering was recognizable given low frequency high magnitude detections over an extended time period while behaviors with similar acceleration, especially digging, occurred as short duration, high magnitude events. Future application of multivariate time series analyses or machine learning could further enhance the discriminatory power and accuracy of behavioral classifications based on acceleration time series data.

We were not able to distinguish among all observed behaviors using available acceleration data. The accelerometer tags used in this study were programed to report an integrated acceleration value, based on the measured maximum differential acceleration in any of the three axes (x, y, z) during 4 sec transmission intervals (BI). Current archival tags can record 3 axis and future tags will likely transmit acceleration for each axis separately, increasing potential for discrimination. For example, qualitative laboratory testing revealed that rotating the tag 90° with moderate speed, mimicking the roll associated with a female digging, would result in a burst reading reaching the maximum magnitude in >50% of trials. Thus, we hypothesize that spawning behaviors would be more easily distinguishable from aggression events given that redd building involves acceleration in all three axes as fish roll onto their sides, beat their tails against the substrate and burst upstream, whereas aggression events rarely involve rolling of the body. Similarly, changes in pitch would likely allow detection of oviposition in female steelhead and identify feeding events in a wide variety of fish taxa that tip up or down during feeding.

Two observed behaviors were not included in our classification because they could not be discriminated from holding (probing), or were rarely observed (gulping). Probing is a common behavior associated with female steelhead redd construction (Esteve, 2005; Tautz & Groot, 1975). The female will lower her tail and position the anal fin between substrate cobbles for up to ten seconds, preparing a pocket in which to deposit eggs. Probing was observed frequently among spawning females within the enclosure but observed magnitude of maximum acceleration (*mean* = 0.16 g) was indistinguishable from holding behavior (0.21 g lower threshold) and thus this behavior was not assigned.

Steelhead rapidly surfacing and gulping air were observed during the enclosure spawning observations. Four of the six enclosure observed steelhead (males and females) were observed briefly rising to the surface, gulping air, and returning to their original location while air bubbles passed through their gills. The behavior was rare and did not seem to be affiliated with any other spawning or movement related observed behaviors, nor did it result in an activity magnitude greater than 0.5 g (*mean* = 0.24 g). Air gulping has been observed commonly among salmonids as a buoyancy compensation method or alternatively it has been reported as a "comfort" behavior (Esteve, 2005; Schroder, 1981). Both behaviors (probing and gulping) would potentially be recognizable in three-axis acceleration records because both involve briefly pitching the head up.

Selection of design criteria for telemetry studies often requires trade-offs, particularly in the on-going effort to produce smaller tags. Consideration of key behaviors and acceleration forces during the design stage should help inform tag selection and specifications. For example, key behaviors may be readily identified with a single axis accelerometer, allowing smaller tag size, increased battery life or increased BI time duration. Increases in the number of transmitted data types (e.g., 1- vs. 3-axis data streams) reduces the number of individual tag codes that can be programmed on a single frequency. Orientation of accelerometer(s) within the tag and tag placement on the animal will also affect the resulting acceleration data and classification criteria.

Spawning Behaviors

Behavioral assignment accuracy of acceleration records was high in most cases, but not error-free. Digging behavior was detected using telemetry and was correctly assigned for 93% of events independently identified by video observation. The duration of events and BI accounted for some of the variability in digging events (0.27-1.5 g). Tags reported maximum acceleration every 4 seconds and some digging events were recorded across two separate bursts. The result was typically, one high magnitude detected burst followed by a second burst of lesser magnitude (or reversed in order) that in some cases did not register higher than the 0.9 g threshold. This would also account for why a higher proportion of enclosure observed covering events (93% of total covering vs 89% of total digging) than digging events, were recorded above threshold, as covering events were more limited in duration (~1.8 versus 1.2 seconds for digging and covering, respectively). There were also instances where digging events were observed in video but telemetry detections were recorded by the receiver as noise (no acceleration 'code 999'). The presence of noise resulting in 'bad' detections is a common problem in any radio telemetry study but can be minimized by reducing the number of tags detected at any one time (tagging and monitoring different frequencies) and by placing receivers in locations with less proximity to noise emitting devices such as powerlines, generators, power tools, etc. As the enclosure was located on hatchery grounds it is difficult to quantify the extent to which detections were caused by surrounding noise. Digging behavior performed by males was not observed during this study, although it has been observed in Rainbow Trout (steelhead non-anadromous life history) and other *Oncorhynchus spp.* (Esteve, 2005; Schroeder, 1981).

All enclosure females were observed ovipositing at least twice in each enclosure sample. Instances of observed oviposition were fairly uncommon and may be attributed in part to the fact that steelhead are believed to continue spawning after dark and during times of high turbidity (Needham & Taft 1934). We were unable to directly observe spawning behaviors in video after dusk in this study. We did confirm digging and oviposition under high turbidity conditions. Female F3 was observed digging during a period of high turbidity, but only because the fish was digging within 0.5m of a camera positioned adjacent to her redd. It is possible that oviposition occurred more commonly than was observed visually, although no putative oviposition events were identified in telemetry records after dusk for enclosure steelhead. Interestingly, only a single oviposition/covering event was detected occurring after dusk (between 08:00 pm and 06:00 am), among all *at-liberty* steelhead. Both enclosure and *at-liberty* females time series recorded long periods of comparative inactivity (prolonged holding) that would last for hours (Figure 3.8), and differences in activity cycles among individuals may have been intrinsic or related to differences in experienced external stimuli.

Several apparent oviposition events by females in the enclosure video were not followed by covering and may represent an example of a false spawning event. In these instances the female and male positioned adjacent to one another, with mouths opened in gape behavior while the male was observed to release milt on one occasion, but was not followed by the characteristic female covering behaviors easily detectible by the biotelemetry tags. This behavior has been observed among other salmonids and is thought to take place when a female does not receive enough stimuli to release eggs in the seconds leading up to oviposition (Esteve, 2005; Fleming, 1996; Jones & Ball, 1954).

In all but a single oviposition event, one or two tagged males were present releasing milt along-side females at the time of oviposition. In the one instance where tagged males were absent and actively courting an alternate female, several precocious steelhead parr were present positioning themselves on the ventral and posterior sides of the female and released milt when oviposition took place. Similar behavior has been reported in spawning steelhead and other salmonids when dominant anadromous males are absent when a female is ready for oviposition (Fleming, 1996; McMillan et al., 2007; Myers & Hutchings, 1987).

Instances of female steelhead and Atlantic Salmon (*Salmo salar*) constructing more than one redd have been previously reported in spawning enclosure experiments and in the wild (Reingold, 1965; Berejikian et al., 2005; De Gaudemar et al., 2000; Kuligowski et al., 2005). This behavior was not observed among the females monitored within the enclosure during this study, although multiple instances of oviposition per female were observed but were always observed occurring within the circumference of their initial constructed redd. Acceleration data records alone cannot be used to infer the presence of multiple redds being constructed without a precise location, but it does allow for the inference of a given females spawning success. Redd counts are commonly used to estimate salmonid escapement and recruitment (Riemam & Myers 1997; Beland, 1996) but the presence of test digs (false redds; Crisp & Carling, 1989) and detection error (missed redds) may introduce considerable bias in estimates (Dunham et al., 2001; Gallagher & Gallagher, 2005). The approach used here could be used to improve accuracy by quantifying the number of oviposition/redds per female and assist in distinguishing test digs from true redds.

At-Liberty Tagged Steelhead

The spatial distribution of tagged animals will affect the ability to track movements and quantify behavior in natural settings. In this study, *at-liberty* steelhead were challenging to monitor while migrating, and unfortunately some time series data sets were either to limited in duration, or were inconsistent in detection frequency at short time scales (i.e., minute to minute) to be usable in this analysis. The large extent of steelhead migration presented a challenge, partially overcome by PIT monitoring that narrowed the whereabouts to individual tributaries and selecting tag/release locations near to spawning grounds, but was exacerbated by the size and number of tributaries accessible to steelhead. Once tagged steelhead were released, they were tracked daily until they reached spawning grounds where they typically remained for 7 days or more, during which time detections were recorded continuously via temporary fixed site array. Male *at-liberty* steelhead rarely remained within 500m reaches for longer than a single day, substantially reducing our ability to collect sufficient time series to classify behaviors in two of the four males. While a larger sample is required for robust inferences, spatial and acceleration records from the two *at-liberty* males indicate higher activity levels. This finding is consistent with enclosure observations and past research, suggesting that male fitness is limited by access to the number of females during spawning, that males increase access to females by ranging over a larger territory than females during spawning, and that aggressive interactions among males are common (Esteve, 2005; Foote, 1990; Kuligowski et al., 2005).

Time budgets were generally similar between enclosure and *at-liberty* steelhead. *At-liberty* detected female steelhead were more commonly detected making movements at and above the upper threshold (0.90 g) during daylight hours than night (mean 74% recorded during day vs 26% after dark) versus the females monitored within enclosures were nearly ~64% of upper threshold detections occurred during the day and ~36% at night. If upper threshold detections related to spawning (digging, covering) were occurring evenly over 24 hours per day and with 14 hours of daylight the expected proportions would result in ~60% and ~40% of upper threshold detections occurring during the day and at night, respectively. These proportions more closely mirror those detected among enclosure females, and although the differences found here are not vastly different, it does suggest accelerometer monitoring was successful during day (with video) and night (without video) and can be applied to animals that display diel behaviors of interest.

Future Considerations

On-going advances in telemetry technology will continue to improve the sophistication and reduce the size of telemetry tags, opening future research potential. In our study, we add to a growing number of studies revealing accelerometers can be used to quantify specific behaviors. This case study combined remote accelerometer telemetry with tags that did not require surgical procedures. Future applications of gastric accelerometer tags in anadromous fishes could include 1) monitoring for differences in spawning behavior and success between hatchery and natural-origin adults; 2) detection of spawning behaviors in high turbidity and poor visibility habitats (i.e., glacial melt fed streams); 3) evaluating energy costs and swimming performance thresholds affecting passage success at migration obstacles, including fishways.

Monitoring and evaluating the behaviors of other species using similar acceleration sensory tags should be of interest to animal researchers. Accelerometer telemetry using a similar framework to that used here could quantify behavior in habitats where direct observation of animals *in situ* is limited or impossible, including in nocturnal species, aquatic species living in turbid waters, or terrestrial species inhabiting thick vegetation. Regardless of habitat, the technology will allow rapid quantification of behaviors in great detail and sample sizes to permit population-level inferences. For example, foraging behavior research, commonly associated with head movements would benefit greatly from the application of movement sensory tags (Kokubun et al., 2011; Laich et al., 2008). Similarly, habitat association studies pertaining to trophic interactions and ecosystem functioning have been conducted and could be further quantified with similar technology to that utilized here (Jessop et al., 2013; Wakefield et al., 2009). Coupling interindividual mating activities with pedigree analysis research may provide important insights to the links between mating behavior, individual fitness and sexual selection for traits measured at the time of tagging. Use of tags to identify timing and habitats of key behaviors such as mating or spawning may be especially helpful in the management of invasive or nuisance species by pinpointing areas for control effort.

Regardless of future application, we advocate the direct observation of telemetered animals to establish criteria for the recognition of key behaviors prior to inferences about behavior of *at-liberty* animals monitored via accelerometer biotelemetry.

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Tables

Table 3.1. Body size, sample observation start date, duration, and social status of steelhead tagged and monitored in the spawning enclosure.

Fish No.	Sex	Fork Length (cm)	Release Date	Video Recording Duration (h)	Status within Enclosure Group
F1	Female	70	28-Apr-17	38	Subordinate Female
F2	Female	74	28-Apr-17	38	Dominant Female
F3	Female	68	3-May-17	24	Subordinate Female
M1	Male	74	28-Apr-17	38	Dominant Male
M2	Male	55	28-Apr-17	38	Subordinate Male
M3	Male	61	3-May-17	24	Subordinate Male

Table 3.2. Mean maximum acceleration (g) by individual steelhead during enclosure observations. Behaviors were identified using video observations.

	Mean Tag Burst Output of Assigned Behaviors (g)								
Fish No.	Holding	Burst Movement	Lateral Movement	Digging	Oviposition	Covering	Coaxing	Aggression	Out of View
					Females				
F1	0.06	0.46	0.24	1.26	0.18	1.20	-	0.55	0.13
F2	0.12	0.33	0.25	1.25	0.32	1.15	-	0.55	0.12
F3	0.13	0.38	0.30	1.34	0.19	1.01	-	-	0.16
Mean	0.10	0.37	0.27	1.27	0.24	1.14	-	0.55	0.13
					Males				
M1	0.08	0.30	0.24	-	-	-	0.40	0.37	0.10
M2	0.09	0.39	0.30	-	-	-	0.36	0.54	0.12
M3	0.07	0.39	0.26	-	-	-	0.32	0.64	0.14
Mean	0.08	0.36	0.27	-	-	-	0.37	0.51	0.12
Mean Total	0.09	0.37	0.27	1.27	0.24	1.14	0.37	0.51	0.12

Table 3.3. Counts and proportions (in parenthesis) of predicted assigned behaviors and observed assigned behaviors using acceleration criteria prior to being assigned using video observations. Counts and proportions correctly assigned are indicated in bold.

		Observed Behavior					
		Digging	Holding	Burst Moves	Lat Moves	Oviposition /Covering	Total
Predicted Behavior	Digging	**264 (0.93)**	0	14 (0.05)	7 (0.02)	0	285
	Holding	1 (<0.01)	**2089 (0.97)**	15 (<0.01)	58 (0.02)	0	2163
	Burst Moves	8 (0.05)	39 (0.22)	**83 (0.48)**	43 (0.25)	0	173
	Lat Moves	2 (0.01)	64 (0.32)	44 (0.22)	**91 (0.45)**	0	201
	Oviposition /Covering	0	0	1 (0.14)	0	**6 (0.86)**	7

Table 3.4. Size, sex, release locations and dates, approximate detection durations and presumed fates after release for *at-liberty* steelhead.

Tag ID	Sex	FKL (cm)	Release Site	Release Date	Days	Presumed behaviors and fates
I16	Ma	74	Twisp	3-May-16	6	Active 3 days, shed tag/mortality
I19	Fe	60	Twisp	29-Apr-16	9	Fallback below weir, active
I24	Fe	61	Twisp	2-May-16	10	Detected Spawning, kelted
I26	Fe	72	Tumwater	15-Apr-17	>2	Entered unmonitored tributary, kelted
I27	Ma	73	Tumwater	17-Apr-17	>1	Fallback below dam
I21	Fe	77	Tumwater	20-Apr-17	>1	Shed tag/mortality, 1 day after release
I22	Fe	77	Tumwater	20-Apr-17	11	Detected Spawning, and kelting, redd observed
I28	Ma	76	Tumwater	20-Apr-17	>2	Entered unmonitored tributary, shed tag mortality
I25	Fe	79	Tumwater	11-May-17	6	Detected digging, fallback below dam
I30(F4)	Fe	72	Enclosure	3-May-17	8	Detected Spawning, kelted
I32(M4)	Ma	75	Enclosure	3-May-17	5	Active 3 days, shed tag/mortality

Table 3.5. Counts of acceleration records by behaviors assigned using acceleration criteria for female *at-liberty* steelhead. Counts of presumed holding events are given in thousands.

	Counts of Detected Presumed Behavior			
Female ID	Ovipostion/covering	Detections< 0.90g	Diggings	Holding (x1000)
I24	6	1072	777	87
I22	5	1984	1437	155
I19	0	115	83	22
I25	~1	351	254	34
I30	3	939	680	141

Table 3.6. Proportions of total detection magnitude registering as high (≥0.90 g), moderate (<0.90 g to >0.21 g), and low (≤0.21 g). Detections are split between those detected from 6:00 am to 8:00 pm (day) and all others (night). Enclosure and *at-liberty* steelhead magnitude of detection proportions are provided.

			Enclosure Steelhead				
		Day			Night		
ID	Sex	High	Moderate	Low	High	Moderate	Low
M1	Male	0.006	0.056	0.939	0.004	0.029	0.967
M2	Male	0.009	0.108	0.883	0.007	0.085	0.908
M3	Male	0.005	0.035	0.960	0.002	0.014	0.984
Mean		*0.006*	*0.066*	*0.927*	*0.004*	*0.043*	*0.953*
F1	Female	0.033	0.026	0.941	0.030	0.044	0.926
F2	Female	0.029	0.033	0.938	0.018	0.020	0.961
F3	Female	0.017	0.019	0.964	0.016	0.025	0.959
Mean		*0.026*	*0.026*	*0.948*	*0.021*	*0.030*	*0.949*
			At-Liberty Released Steelhead				
I16	Male	0.034	0.147	0.819	0.028	0.089	0.883
I32	Male	0.003	0.057	0.940	0.003	0.045	0.952
Mean		*0.018*	*0.102*	*0.880*	*0.016*	*0.067*	*0.917*
I24	Female	0.018	0.014	0.968	0.003	0.006	0.991
I22	Female	0.016	0.025	0.959	0.007	0.008	0.985
I19	Female	0.006	0.063	0.931	0.004	0.050	0.946
I25	Female	0.014	0.030	0.956	0.012	0.021	0.967
I30	Female	0.019	0.016	0.964	0.007	0.011	0.982
Mean		*0.015*	*0.030*	*0.956*	*0.007*	*0.019*	*0.974*

Figures

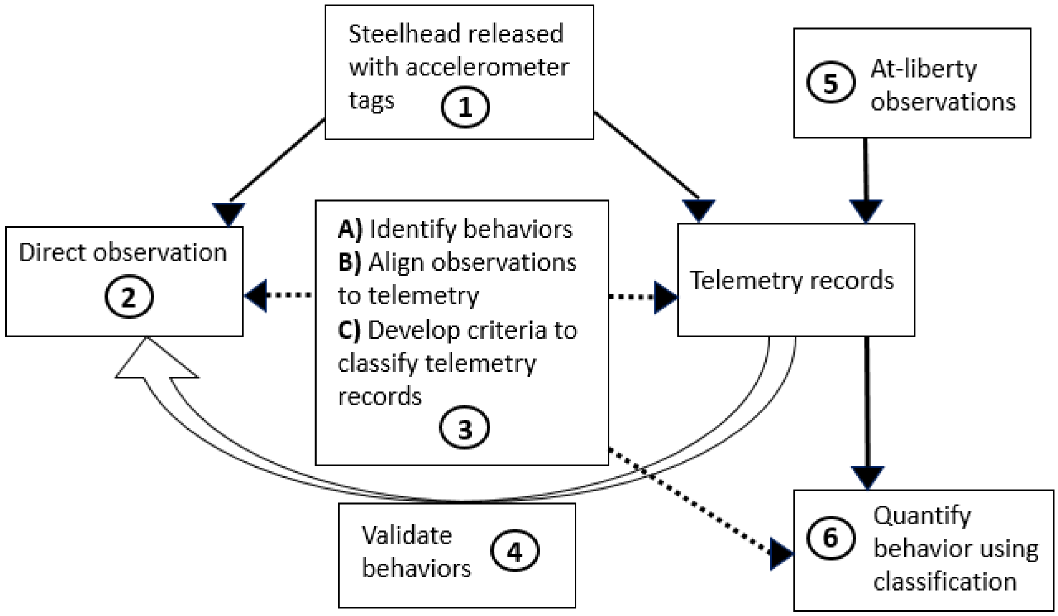

Figure 3.1. Overview of study design, using six steps: 1) tag and release steelhead with accelerometer tags for observation within an enclosed monitoring space; 2) simultaneously record behaviors via underwater video camera and monitor acceleration; 3) identify behaviors from video observations, align observed behaviors to accelerometer time series, and establish criteria for classifying acceleration records using the amplitude, frequency, and variability of the acceleration time series; 4) comparison of video- and telemetry-classified behaviors using independent subsets of the data; 5) tag, release, and monitor a sample of *at-liberty* steelhead, and; 6) classify acceleration histories to quantify key behaviors.

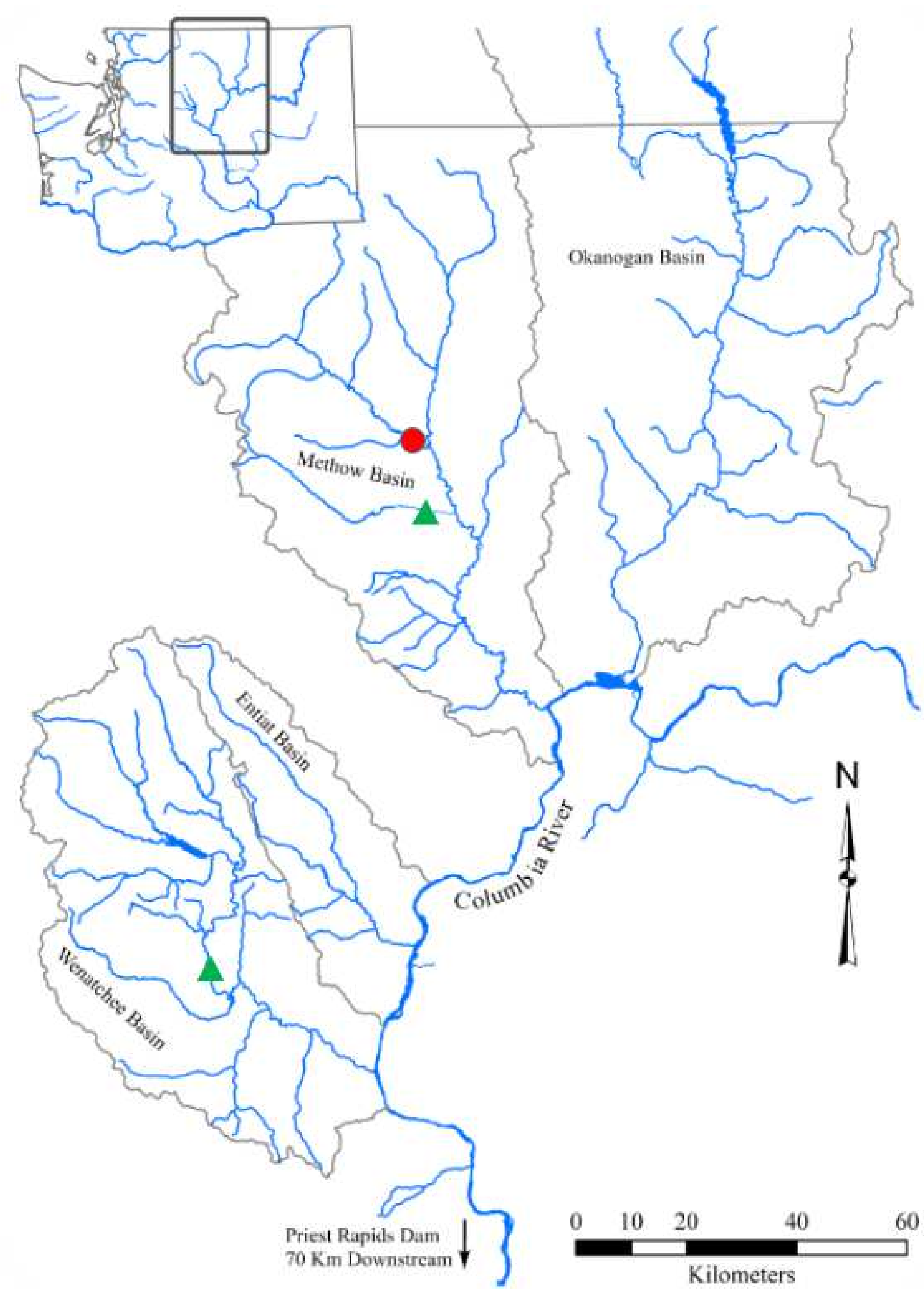

Figure 3.2. Upper Columbia River basin study site locations. The enclosure experiment took place at Winthrop National Fish Hatchery spring creek acclimation site (red dot). Tagged fish release sites Tumwater dam on the Wenatchee River and Twisp River weir in the Methow River basin (green triangles).

Figure 3.3. Spawning enclosure at Winthrop National Fish Hatchery, facing downstream.

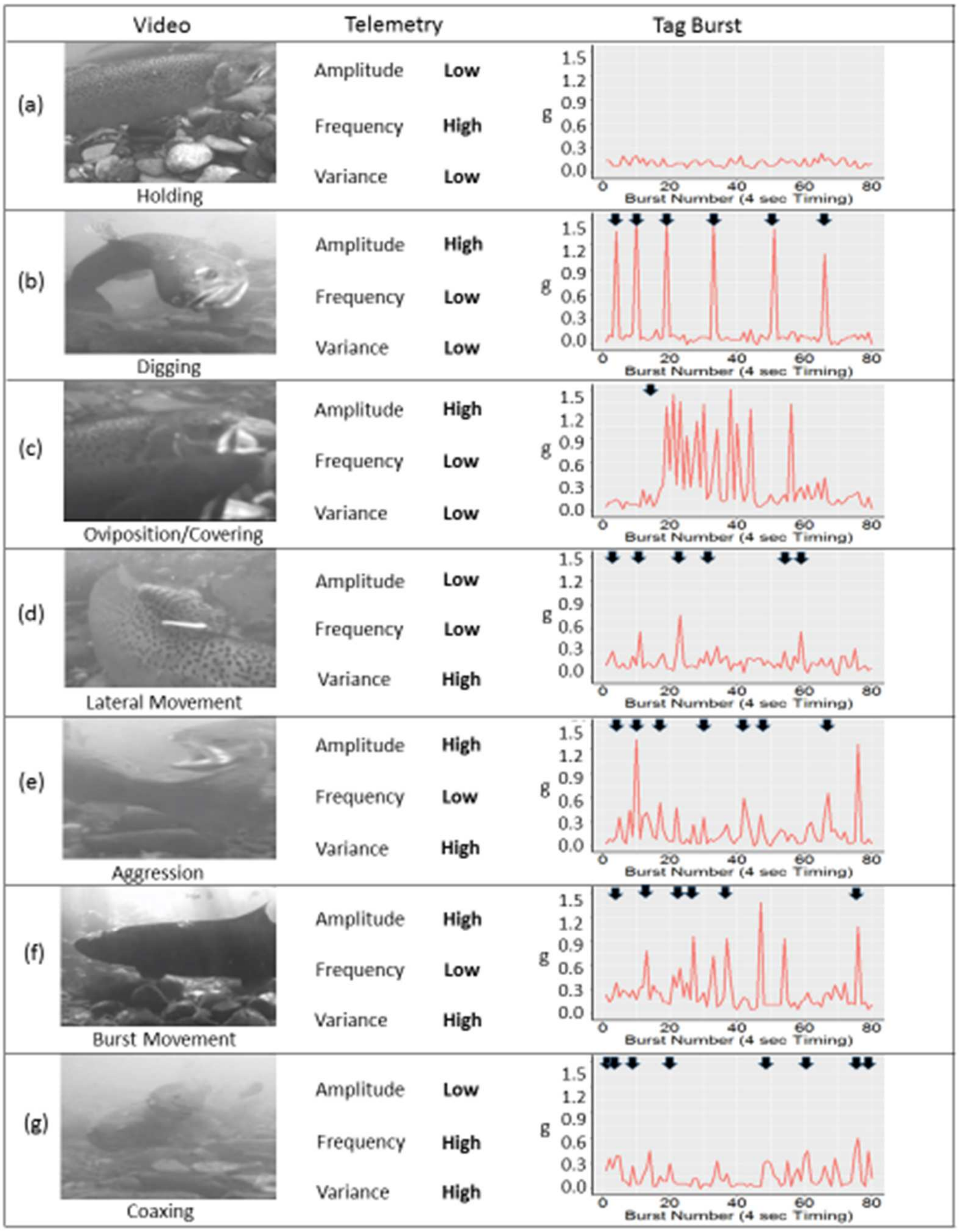

Figure 3.4. Observed spawning/movement behaviors and radio telemetry profiles of steelhead tagged and monitored in spawning enclosure experiment. Tag burst outputs represent raw programed sampling interval (PSI) detections over approximately 5 minute time period. Instances of behaviors were observed at the timing indicated (black arrows).

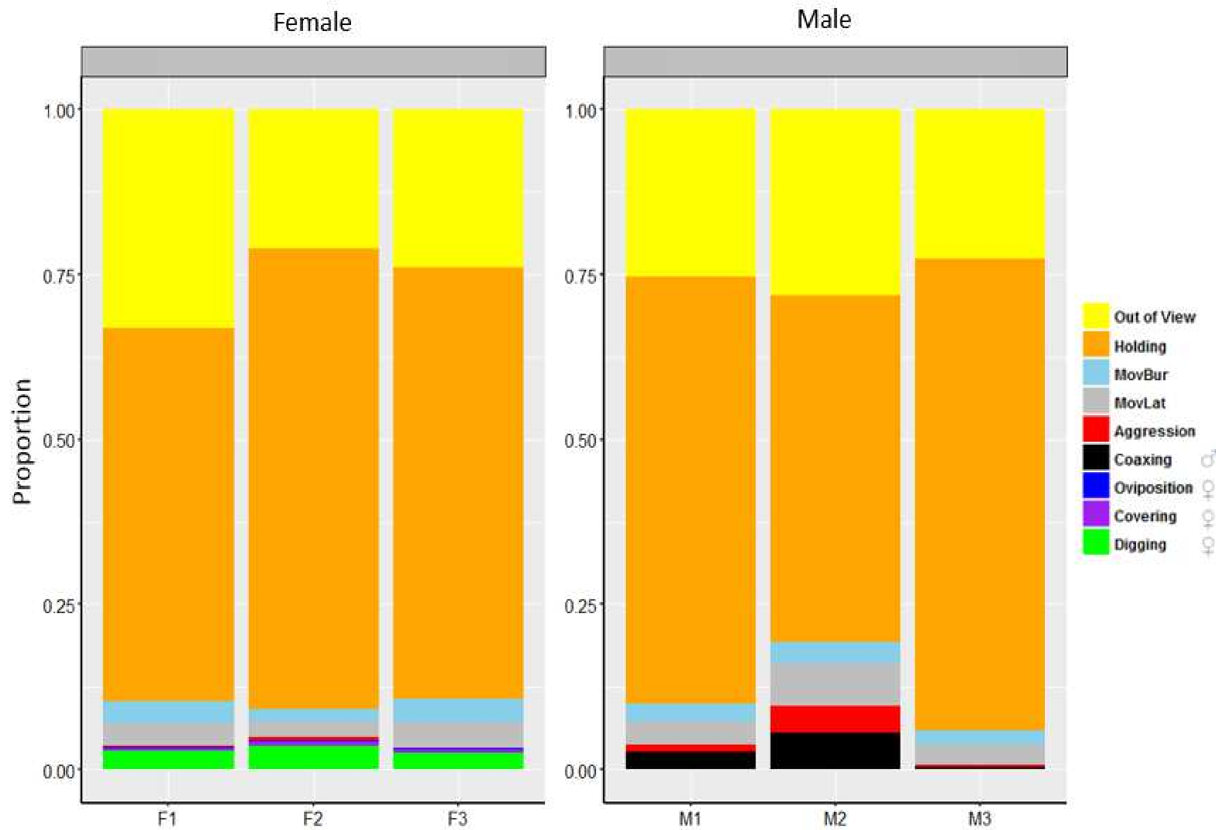

Figure 3.5. Proportional of time tagged fish were observed displaying each behavior, during video monitoring. Coaxing behavior observations (red) pertain to males only, Oviposition (dark blue), covering (violet), and digging (green) were exclusive to females only.

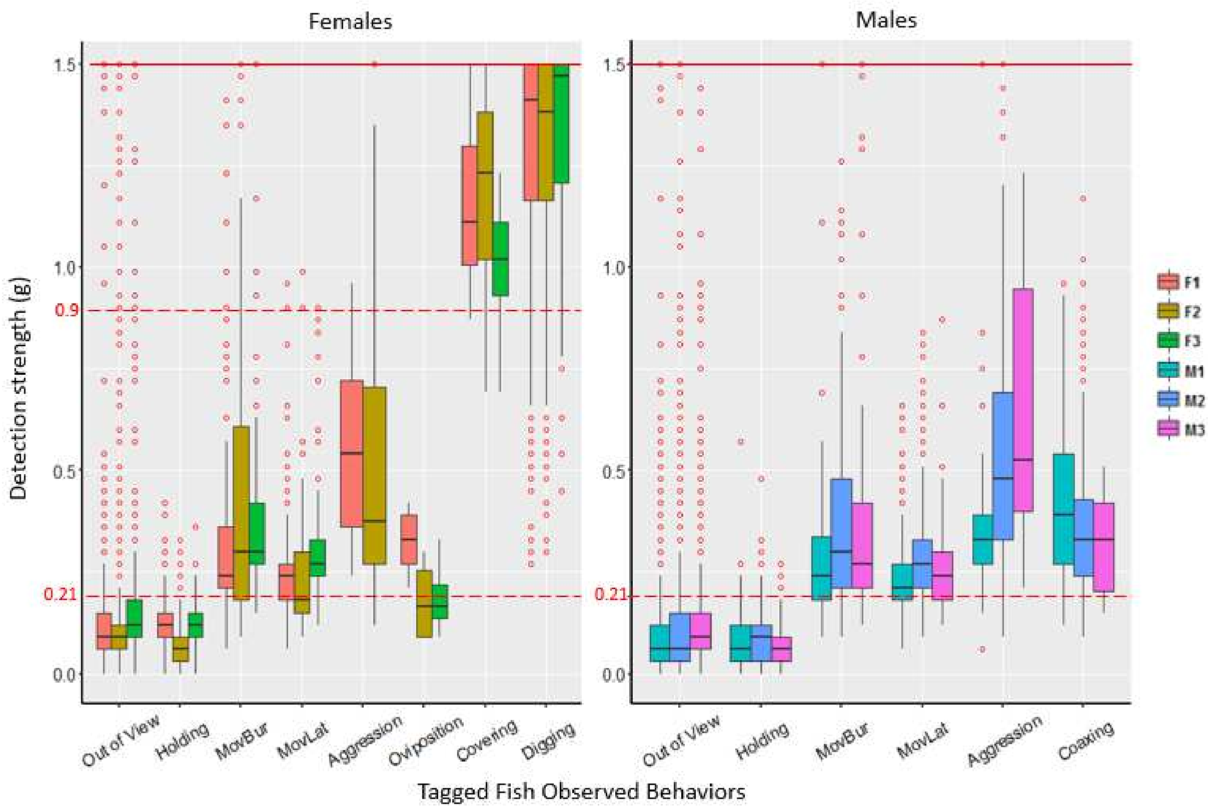

Figure 3.6. Range of detection strengths assigned to observed behaviors of all fish within the spawning enclosure separated by sex. Upper threshold burst index (maximum) is indicated (1.5 g), the spawning detection threshold (digging and covering) and holding threshold are indicated (0.9 g and 0.21 g respectively).

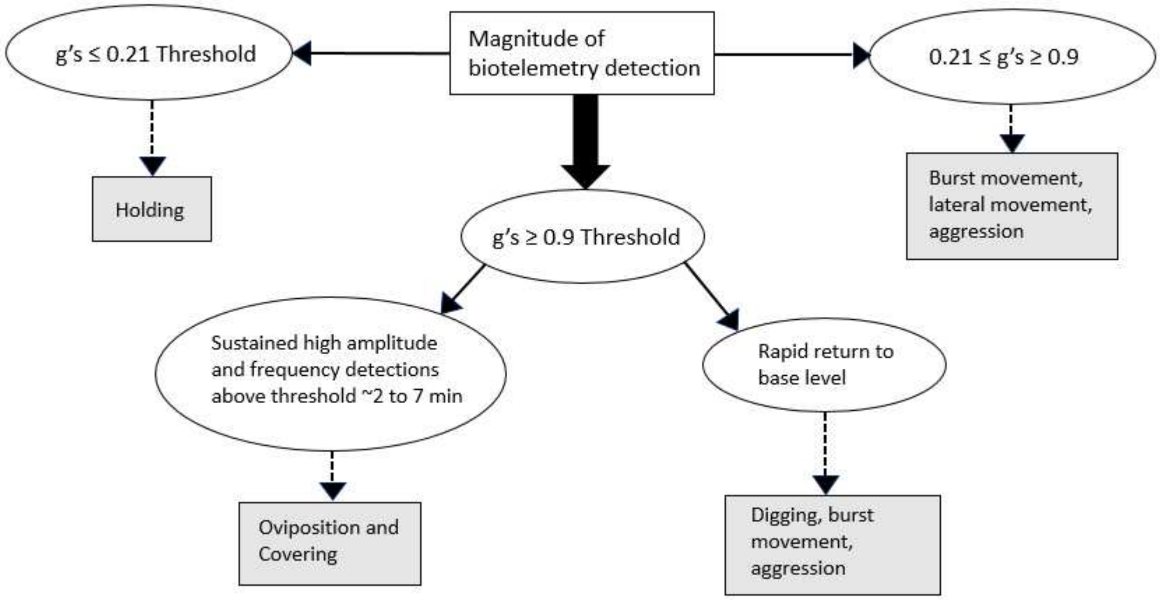

Figure 3.7. Stepwise criteria for assigning behaviors to acceleration records; criteria could not discriminate among all behaviors identified in visual observations.

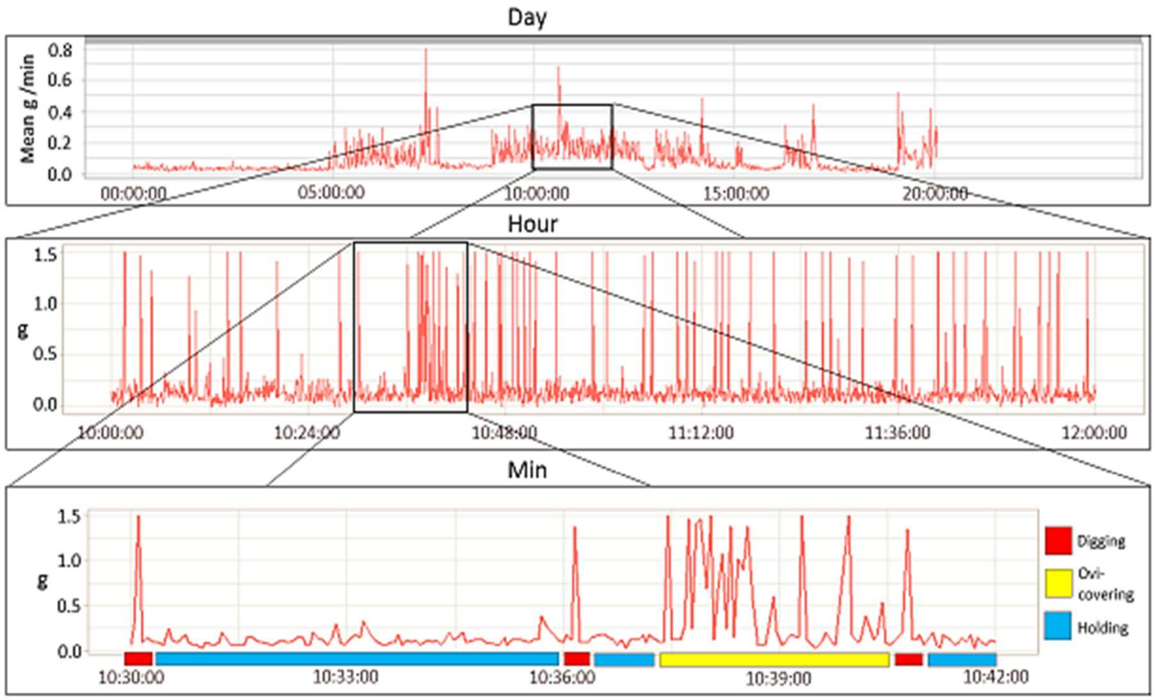

Figure 3.8. Example time series of acceleration for an *at-liberty* steelhead, including an inferred oviposition event. Mean acceleration (g's) per minute over a single day of detections (top bar), a two hour detection time series (middle bar), and 12 minute time series (bottom bar, showing all records). Inferred behaviors digging (red), oviposition/covering (yellow), and holding (blue) are indicated by bottom colored bar.

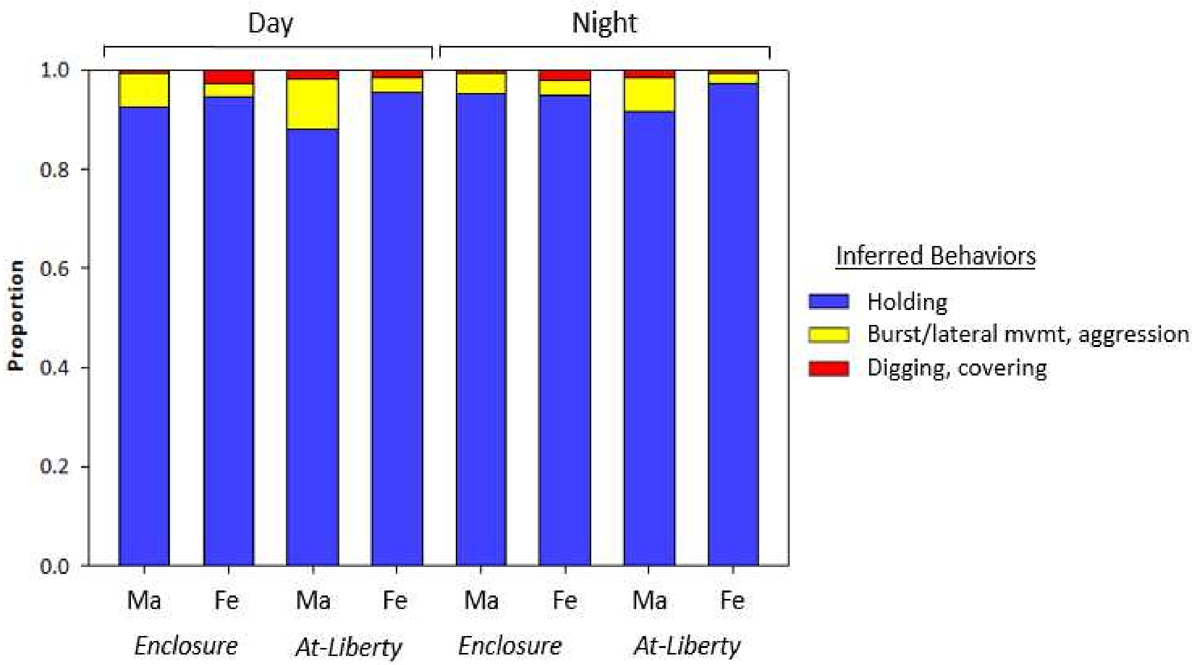

Figure 3.9. Relative time budget for inferred behaviors comparing enclosure and *at-liberty* steelhead. Detections are split by sex, monitoring group (enclosure/*at-liberty*), and by the time of day detections took place. Behaviors were classified using criteria in Figure 3.7. Male behaviors shown in red represent detection strengths above 0.90 g threshold and correspond to burst movement and aggressive behaviors.

Appendix 1: Steelhead Overwintering Counts 2016-17

Supplemental Data chapter 2. Counts, rearing origins and locations of tagged steelhead detected surviving the overwintering period in 2016; proportions based on the total number of overwintering fish at each location. Values in the parenthesis represent the number of fish present at the onset of overwintering.

Location	Number of Fish			Proportion Survived		
	Hatchery	Wild	Total	Hatchery	Wild	Total
			Columbia River Reach			
Priest	6 (9)	3 (6)	9 (15)	0.667	0.500	0.600
Wanapum	1 (5)	3 (3)	4 (8)	0.200	1.000	0.500
Rock Island	2 (3)	3 (5)	5 (8)	0.667	0.600	0.625
Rocky Reach	7 (13)	12 (13)	19 (26)	0.538	0.923	0.731
Wells	41 (53)	21 (23)	62 (76)	0.774	0.913	0.816
Total	57 (83)	42 (50)	99 (133)	0.689	0.840	0.744
			Tributary			
Entiat	0 (0)	0 (0)	0 (0)	0.000	0.000	0.000
Methow	21 (26)	16 (16)	37 (42)	0.808	1.000	0.881
Okanogan	15 (19)	8 (9)	23 (28)	0.789	0.889	0.821
Wenatchee	16 (20)	24 (25)	40 (45)	0.800	0.960	0.889
Total	52 (65)	48 (50)	100 (115)	0.800	0.960	0.870
Grand Total	109 (148)	90 (100)	199 (248)	0.736	0.900	0.802

Supplemental Data chapter 2. Counts, rearing origins and locations of tagged steelhead detected surviving the overwintering period in 2017. Proportions based on the total number of overwintering fish at each location. Values in the parenthesis represent the number of fish present at the onset of overwintering.

Location	Number of Fish			Proportion Survived		
	Hatchery	Wild	Total	Hatchery	Wild	Total
			Columbia River Reach			
Priest	7 (8)	3 (3)	10 (11)	0.875	1.000	0.909
Wanapum	2 (10)	0 (0)	2 (10)	0.200	0.000	0.200
Rock Island	1 (4)	6 (7)	7 (11)	0.250	0.857	0.636
Rocky Reach	21 (24)	14 (15)	35 (39)	0.875	0.933	0.897
Wells	68 (81)	11 (11)	79 (92)	0.840	1.000	0.859
Total	99 (127)	34 (36)	133 (163)	0.780	0.944	0.816
			Tributary			
Entiat	0 (0)	0 (0)	0 (0)	0.000	0.000	0.000
Methow	60 (64)	12 (13)	72 (77)	0.938	0.923	0.935
Okanogan	36 (39)	4 (5)	40 (44)	0.923	0.800	0.909
Wenatchee	3 (4)	9 (12)	13 (16)	0.750	0.750	0.765
Total	99 (107)	25 (30)	124 (137)	0.925	0.833	0.905
Grand Total	198 (234)	59 (66)	257 (300)	0.846	0.894	0.857

Appendix 2: Assigned Observed Behavioral Counts and Proportions

Supplemental Data chapter 3. Counts of video assigned behaviors for all fish monitored within enclosure.

	Frequency of Assigned Behaviors								
Fish No.	Holding	MovBur	MovLat	Digging	Oviposition	Covering	Coaxing	Aggression	Out of View
					Females				
F1	2963	179	178	156	5	16	-	9	1731
F2	3488	92	124	176	4	41	-	24	1055
F3	2275	124	134	90	4	19	-	0	833
Mean	2909	132	145	141	4	25	-	11	1206
					Males				
M1	2959	120	163	-	-	-	124	51	1157
M2	2398	149	289	-	-	-	260	184	1288
M3	2511	77	110	-	-	-	12	10	792
Mean	2623	115	187	-	-	-	132	82	1079
Grand Total	16594	741	998	422	13	76	396	278	6856

Supplemental Data chapter 3. Proportions of total video-assigned behaviors for all fish monitored within enclosure groups.

	Proportion of Assigned Behaviors								
Fish No.	Holding	Burst Moves	Lateral Moves	Digging	Oviposi-tion	Covering	Coaxing	Aggression	Out of View
					Females				
F1	0.566	0.034	0.034	0.030	0.001	0.003	-	0.002	0.331
F2	0.697	0.018	0.025	0.035	0.001	0.008	-	0.005	0.211
F3	0.654	0.036	0.039	0.026	0.001	0.005	-	0.000	0.239
Mean	0.639	0.029	0.032	0.030	0.001	0.006	-	0.002	0.260
					Males				
M1	0.647	0.026	0.036	-	-	-	0.027	0.011	0.253
M2	0.525	0.033	0.063	-	-	-	0.057	0.040	0.282
M3	0.715	0.022	0.031	-	-	-	0.003	0.003	0.226
Mean	0.629	0.027	0.043	-	-	-	0.029	0.018	0.253
Mean Total	0.634	0.028	0.038	0.030	0.001	0.006	0.029	0.010	0.257