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Bull Trout and Westslope Cutthroat Trout movement in a dam tailrace.

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Abstract

Populations of Bull Trout *Salvelinus confluentus* and Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi* in the Pend Oreille Basin have declined, partly due to fragmentation caused by hydropower dams. This study aimed to analyze the movements and behavior of these species downstream of Albeni Falls Dam over two years to inform fishway design. Radiotracking investigations were conducted to monitor 10 adult Bull Trout and 17 adult Westslope Cutthroat Trout from September 2008 to July 2010. Macro and micro detection zones were delineated to study fine- and large-scale movements in the tailrace. Macro zones included the spillway and powerhouse tailrace areas. Micro zones were nested within macro zones to identify regions close to the dam where fishway structures could be built. Both Bull Trout and Westslope Cutthroat Trout exhibited high mobility in the dam tailrace, transitioning between macro detection zones. Seasonal variations influenced their distribution patterns. During the spring freshet migration season, both species were primarily detected at the left powerhouse micro zone. In sedentary periods (fall/winter and summer), fish actively swam throughout the tailrace, displaying search behavior. These behavior observations suggest that potential fishway entrances located near dam concrete would be effective: the area near the left powerhouse was identified as the optimal construction location. This study highlights the feasibility of designing fish passage structures to mitigate population fragmentation and support species recovery.

Introduction

Healthy fish populations are largely determined by the quality of their aquatic habitats. Migratory fish are especially susceptible to changes within systems because they require distinct habitats during different life stages (Bonneau and Scarnecchia 1998). In riverine ecosystems, dams can block or delay upstream fish migration, which can lead to the decline or extinction of species by inhibiting their ability to spawn in natal habitat (Gray and Haynes 1980; Cada and Sale 1993). Several studies have addressed the negative effects of dams on salmonid populations in the Pacific Northwest U.S.A. (e.g., Raymond 1969, 1979; Kareiva et al. 2000; Hatten et al. 2009). Habitat loss and fragmentation are primary reasons many salmonids in the Pacific Northwest are at risk of local and regional extinction. Impassable dams have led to the extirpation of salmonid stocks that are unable to reach spawning grounds (Beamish and Northcote 1989; Nehlsen et al. 1991), providing evidence that movement between habitats is critical to buffer populations against local extinction.

Bull Trout *Salvelinus confluentus* and Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi* are native stream-dwelling fish in the Columbia River Basin of the contiguous northwest United States. Their populations have declined in abundance throughout their historical range, mainly due to habitat destruction and fragmentation (Rieman et al. 1997; Shepard et al. 2005). Bull Trout have been listed as a threatened species under the Endangered Species Act since 1998 (ESA 1973; U.S. Fish and Wildlife Service USFWS, 1998). Some local populations are extinct, and some are remnants isolated in declining patches of suitable habitat (Rieman and McIntyre 1993). Westslope Cutthroat Trout are also listed as a Species of Special Concern in parts of their native range, including Montana and British Columbia.

Within the Pend Oreille Basin of northern Idaho and northeastern Washington, factors contributing to the decline of fish populations include poor agricultural land-use activities, logging, mining, loss of spawning and rearing habitat, and inappropriate fisheries management practices (USFWS 2002a, 2002b; Kiser et al. 2010). Although these factors undoubtedly contributed to a decrease in fish abundance, the construction of Albeni Falls Dam (AFD) between 1951 and 1955 immediately impacted Bull Trout populations in the Pend Oreille Basin by blocking a major migration route between Lake Pend Oreille and a majority of the Pend Oreille River and its tributaries (DuPont et al. 2007). Impassable dams have long-term effects on population dynamics of Bull Trout by precluding migration and gene flow between populations (Neraas and Spruell 2001). Bull Trout and Westslope Cutthroat Trout have both fluvial and adfluvial life histories (Behnke 1992; Jakober et al. 1998) and are consequently known to migrate between Lake Pend Oreille and the Pend Oreille River and its tributaries (Scholz et al. 2005). Fish from natal tributaries upstream of AFD that either become entrained or volitionally pass downstream of the dam are unable to return to spawn in these tributaries; additional information on Bull Trout migration patterns specific to the Pend Oreille Basin can be found in DuPont et al. (2007). Moreover, similar upper incipient lethal temperatures of both species ($\sim 24^{\circ}\text{C}$, Bear et al. 2007) make them particularly susceptible to blockage by AFD, which is a barrier to thermal refuge of Lake Pend Oreille in summer when the mainstream Pend Oreille River downstream of AFD typically exceeds 24°C . Other habitat requirements that are similar between both species, but have been degraded because of dam construction, include the need for high structural diversity and low levels of sediment, chemical pollution and non-native fish (Montana Bull Trout Scientific Group, 1998; USFWS 1999).

Fisheries managers, researchers, and hydroelectric dam operators have explored the use of fish passage to recover populations of Bull Trout and Westslope Cutthroat Trout (Duff 1996; Odeh 1999; Neraas and Spruell 2001). Where passage has been provided, radio-tracking studies revealed long migration patterns of Bull Trout that successfully allow them to complete their life cycle (BioAnalysts, Inc. 2002; Bahr and Shrimpton 2004; Starcevich et al. 2012). Recovery of Bull Trout and Westslope Cutthroat Trout in the Pend Oreille Basin may ultimately require connectivity between the Pend Oreille River and Lake Pend Oreille through AFD (USFWS 2000). The U.S. Fish and Wildlife Service stated that: “effective passage solutions will be able to pass both downstream-origin and upstream-origin Bull Trout at all life stages over the dam as well as provide passage for adult Bull Trout that are returning to spawn in tributaries downstream of the dam” (Miller 2008). Thus, data on fish movements at AFD are necessary to determine potential fish passage structure locations that are compatible with their behavior.

Several considerations must be made when determining a proper fish passage structure, including the type of structure (e.g., fish passes, bypass channels, lifts, locks, or collection and transportation), the location of the structure, as well as the knowledge of the fish behavior and hydraulic conditions (Williams et al. 2012). Generally, the location of fish passage entrances and attractant flows are considered the most critical factors when designing an effective fish passage system for anadromous salmonids (Larinier 2001). Failure of anadromous salmonids to use fish passage systems is largely attributed to insufficient attractant flow, an inappropriate entrance location, or hydraulic conditions within the passage system that are unsuitable for the target species (Larinier 2001). However, biological factors of anadromous fish such as their thermal tolerance and migratory behavior positively influence attraction and passage efficiency (Bunt et al. 2012).

Attraction and passage at fishways have been shown to be successful for non-anadromous fish similar to Bull Trout and Westslope Cutthroat Trout (Forty et al. 2016, Hodge et al 2017).

Based on a lack of information on Bull Trout and Westslope Cutthroat Trout behavior when encountering dams or other migration barriers, this study was designed to accomplish two primary objectives: 1) quantify spatial distributions of Bull Trout and Westslope Cutthroat Trout in the AFD tailrace by season and 2) examine the relationship between fish location and flow in the AFD powerhouse tailrace, including turbine-discharge configurations and an experimental flow release from a sluice. The results of this study provide insight into how Bull Trout and Westslope Cutthroat Trout behave in the tailrace of a hydroelectric dam, as well as allow a better understanding of the effects of dam discharge as a fish attractant (or deterrent). This information will be useful to fisheries managers and engineers in designing passage structures that are congruent with species-specific biology and behavior patterns.

Methods

Study site

The Pend Oreille River in northern Idaho and northeastern Washington flows northwest from Lake Pend Oreille to British Columbia, Canada, where it joins the Columbia River (Figure 1). Cabinet Gorge Dam on the Clark Fork River, which flows into Lake Pend Oreille, and Box Canyon Dam on the Pend Oreille River impound the river system upstream and downstream of AFD, respectively. The study was conducted at AFD, which is located on the Pend Oreille River approximately 44 km below the outlet of Lake Pend Oreille.

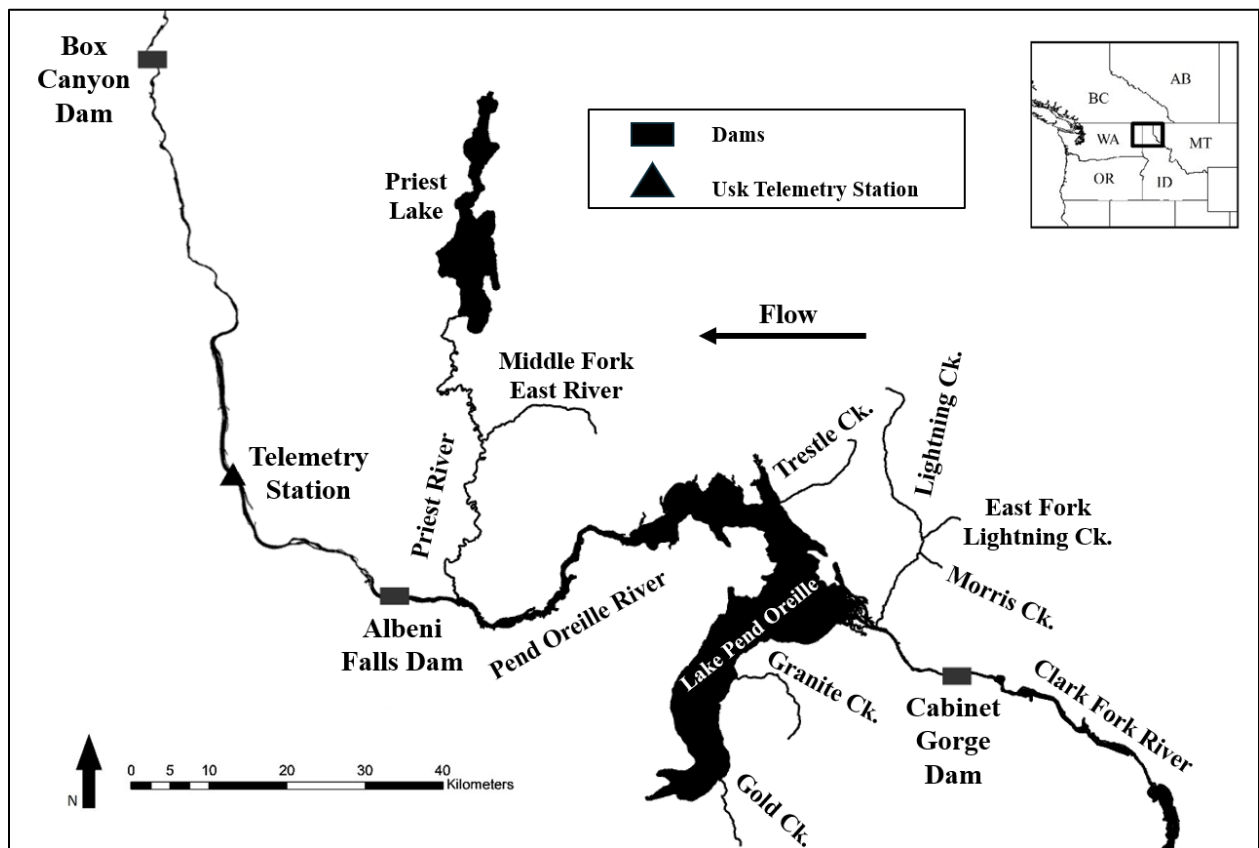


Figure 1. Pend Oreille River Basin of northern Idaho and northeastern Washington. Three radio telemetry monitoring stations were located at Albeni Falls Dam, and one station was located downstream on the Pend Oreille River near Usk, Washington. Ck. = Creek.

Fish capture and transmitter implantation

Bull Trout used in the study were captured from a 3 km section of the Pend Oreille River downstream of AFD and at sites in Lake Pend Oreille, where the Idaho Department of Fish and Game has contracted with commercial gill net fishermen to remove nonindigenous Lake Trout and Bull Trout are bycatch. Westslope Cutthroat Trout were all captured within the 3 km section of the Pend Oreille River downstream of AFD.

Captured fish included 10 adult Bull Trout (mean length \pm SD = 445 \pm 121 mm; mean weight \pm SD = 953 \pm 784 g) and 17 adult Westslope Cutthroat Trout (mean length \pm SD = 384 \pm 32 mm; mean weight \pm SD = 566 \pm 91 g). These fish were implanted with transmitters from 2008 to 2010 (Table 1) and released downstream of AFD between October 2008 and May 2010. All Westslope Cutthroat Trout and 40% of Bull Trout (n = 4) were captured using electrofishing in the Pend Oreille River downstream of AFD. The remaining Bull Trout were captured in Lake Pend Oreille. Natal tributaries of Bull Trout were assigned through genetic analysis: nonlethal fin clips were taken from individuals in the basin and DNA was extracted to create a baseline dataset for population assignment. Samples were grouped based on the tributary of collection, and a nonspatial Bayesian clustering analysis was performed in BAPS v. 5.3 (DeHaan et al. 2011). Leave-one-out assignment tests were conducted on identified clusters, and the log of odds (LOD) ratio calculated between the first and second most likely tributary genetic group of origin was utilized to evaluate confidence in assignments (DeHaan et al., 2011). Bull Trout included in this study were determined as having originated from populations that spawn in tributaries of Lake Pend Oreille or the Pend Oreille River upstream of AFD (Table 1), and were assumed to have a propensity to return to these tributaries, thus it was assumed that study fish would display migratory behavior at AFD as they attempted to return to their natal streams.

Table 1. Characteristics of Bull Trout and Westslope Cutthroat Trout tagged in the Pend Oreille River (Idaho) from 2008 to 2010.

Species	Capture location	Release day	Transmitter life (days)	Fork length (mm)	Weight (g)	Genetic origin	Fate	Fish used for analyses
BT	Pend Oreille River	6/24/2008	663	535	1535	Lightning Creek	Not detected	
BT	Pend Oreille River	7/22/2008	441	285	200	Middle Fork East River	Presumed dead	
BT	Lake Pend Oreille	10/21/2008	449	392	502	Granite Creek	Detected	X
BT	Lake Pend Oreille	4/16/2009	449	443	785	Gold Creek	Not detected	
BT	Lake Pend Oreille	4/22/2009	449	538	1265	Gold Creek	Detected	X
BT	Lake Pend Oreille	4/23/2009	449	485	917	Granite Creek	Detected	X
BT	Lake Pend Oreille	4/23/2009	441	301	243	Trestle Creek	Detected	X
BT	Lake Pend Oreille	4/28/2009	449	318	303	Granite Creek	Presumed dead	
BT	Pend Oreille River	5/11/2009	663	657	2787	East Fork Lightning Creek	Detected	X
BT	Pend Oreille River	6/11/2009	663	493	991	Morris Creek	Detected	X
WCT	Pend Oreille River	10/21/2008	449	340	418	NA	Not detected	
WCT	Pend Oreille River	10/21/2008	449	345	463	NA	Detected	X
WCT	Pend Oreille River	11/4/2008	449	423	568	NA	Detected	X
WCT	Pend Oreille River	3/31/2010	NA	381	545	NA	Detected	X
WCT	Pend Oreille River	3/31/2010	NA	393	555	NA	Detected	X
WCT	Pend Oreille River	3/31/2010	NA	345	427	NA	Detected	X
WCT	Pend Oreille River	3/31/2010	NA	395	624	NA	Detected	X

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WCT	Pend Oreille River	4/5/2010	NA	400	562	NA	Detected	X
WCT	Pend Oreille River	4/5/2010	NA	401	689	NA	Detected	X
WCT	Pend Oreille River	4/5/2010	NA	385	510	NA	Detected	X
WCT	Pend Oreille River	4/5/2010	NA	428	777	NA	Detected	X
WCT	Pend Oreille River	4/5/2010	NA	402	578	NA	Detected	X
WCT	Pend Oreille River	4/6/2010	NA	395	567	NA	Detected	X
WCT	Pend Oreille River	4/6/2010	NA	420	630	NA	Detected	X
WCT	Pend Oreille River	5/6/2010	NA	363	542	NA	Detected	X
WCT	Pend Oreille River	6/7/2010	353	313	NA	NA	Detected	X
WCT	Pend Oreille River	6/14/2010	NA	395	593	NA	Detected	X

Weekly electrofishing surveys were conducted during both daytime and nighttime hours. When a fish was captured during electrofishing, it was implanted with a transmitter using methods described in Paluch et al. (2009). To increase Bull Trout sample size, one Bull Trout in fall 2008 and five Bull Trout in spring 2009 were captured as by-catch from the commercial lake trout removal program in Lake Pend Oreille, implanted with transmitters, and relocated 2 km downstream of AFD. No Bull Trout were added to the study in 2010 due to a collection permit requirement to move Bull Trout caught downstream of the dam to the upstream side of the dam (i.e., to allow Bull Trout access to their genetically determined natal tributary). All fish were released immediately after recovering from surgery. During the study, five Bull Trout died and one was permanently lost to the study due to entrainment at Box Canyon Dam. Four of the Bull

Trout mortalities occurred in July and August when water temperatures of the Pend Oreille River varied from 18.3°C to 24.4°C, which are lethal temperatures for Bull Trout (Selong et al. 2001). Six Westslope Cutthroat Trout also died by the end of the study: three due to unknown causes.

Radio transmitters were implanted into each fish without exceeding the 2% tag to body weight ratio recommended by Winter (1996). Combination acoustic and radio transmitters (CARTs), Models CART16_1 and CART16_2s with expected lifetimes of 663 and 904 d, respectively, were implanted into the largest fish. Radio-frequency-only transmitters, Models NTC-6-2, and SR-11-18 with expected lifetimes of 441 and 449 d, respectively, were implanted into smaller fish. Radio-only tags had a 5-s ping rate and CART tags had a 5-s ping rate which alternated between radio and acoustic signals. The transmitting frequency of all tags was 151.890 MHz.

Monitoring stations and mobile tracking

Four radio telemetry monitoring stations were installed and configured in summer and fall 2008 and used to detect fish in the study area from September 2008 through July 2010 (Figure 2). Three telemetry stations were installed at AFD, and one station was installed 29 km downstream on the Pend Oreille River near Usk, Washington to detect fish leaving the primary study area and entering Box Canyon Reservoir (Figure 1). Receivers (Models SRX400 or SRX600, Lotek Wireless Inc., Newmarket, Ontario, Canada) and corresponding electronic equipment (e.g., antenna switch boxes, AC/DC converters, solar panels), herein termed “stations”, were housed in waterproof plastic or steel toolboxes. Five, six-element aerial Yagi antennas delineated the two macro detection zones (i.e., spillway and powerhouse) and the two micro detection zones within the spillway tailrace macro zone; underwater balanced loop-vee antennas delineated the two micro

detection zones within the powerhouse macro zone (Figure 2). Detailed information on the specifications and performance of balanced loop-vee antennas as compared to other underwater radio antennas can be found in Gingerich et al. (2012). One six-element Yagi antenna was used to detect transmitters across the width of the Pend Oreille River at Usk.

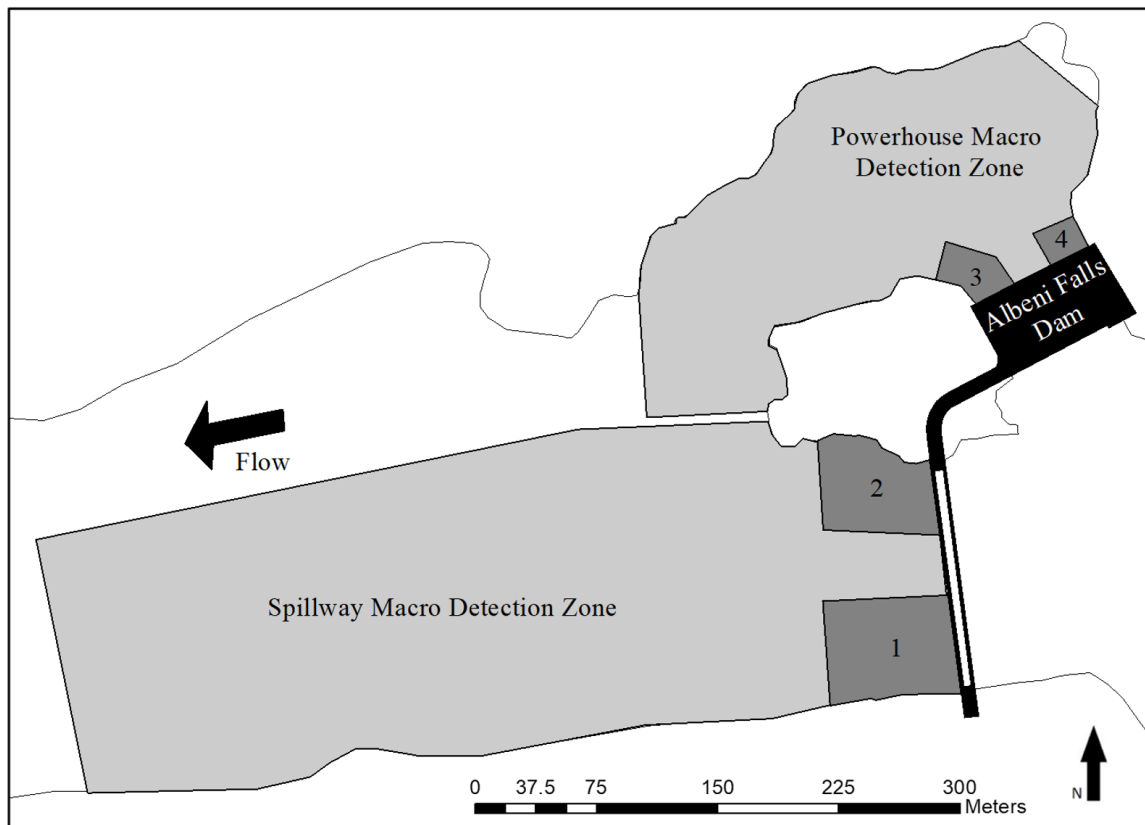


Figure 2. Locations of the spillway and powerhouse and detection range of the macro detection zones (light grey) and micro detection zones (dark grey). Micro detections zones are numbered from 1 to 4: left spillway (1), right spillway (2), left powerhouse (3), and right powerhouse (4).

Monitoring stations were tested to ensure functionality and to configure detection zones for macro and micro spatial scales (Figure 2). The reception range of all receivers and antennas at AFD, combined, covered the tailrace from the dam concrete to about 600 m downstream. Monitoring stations at AFD were configured to differentiate fish locations between the powerhouse macro detection zone (3.80 ha) and spillway macro detection zone (9.79 ha; Figure 2). Micro detection zones nested within macro detection zones were located immediately

downstream and adjacent to the dam concrete at the left (0.49 ha) and right (0.38 ha) sides of the spillway and left (0.11 ha) and right (0.06 ha) sides of the powerhouse (labels 1–4, respectively, in Figure 2). The macro and micro detection zones were configured to be non-overlapping, and micro detection zones were chosen based on potential areas for construction of a fish passage structure (Pizzimenti and Rainey 2009). Beacon transmitters were installed at each station and transmitted a signal once every 5 s for a 1-min period each hour; beacon receptions were verified to validate detection efficiency of each monitoring station throughout the study.

The Pend Oreille River from AFD downstream to the town of Usk, Washington, was mobile-tracked monthly via plane, vehicle, or boat to determine the fate of study fish that strayed from the AFD tailrace. A handheld, three-element Yagi antenna was affixed to the plane, vehicle, or boat and used to detect study fish in combination with a Lotek telemetry receiver. Study fish were considered dead if the transmitter was physically recovered or if the transmitter was located repeatedly in the same area (i.e., did not move more than a few meters) for several weeks.

Data collection and management

Data from telemetry monitoring stations were downloaded approximately once every two weeks and internal receiver clocks were synchronized to an atomic clock to ensure accuracy of detection-data timestamps among stations. Data collected during mobile tracking were used in conjunction with monitoring station data to determine detection histories for individual study fish.

Detection data collected from 22 October 2008 to 19 August 2010 were queried by detection signal strength to include detections within each of the macro and micro detection zones. Detection data filtered by the six detection zones were then summarized into macro or micro zone detection “events” to describe the movement behavior of each fish. Macro detection events were expressed

as residence time in units of days; an individual event began when a fish entered a macro detection zone and ended when a fish left the zone, determined by the fish being detected in another macro detection zone, or if the fish was not detected for 180 min. Subsequent detection in another macro detection zone or the same macro detection zone following non-detection for 180 min began a new detection event. Macro zone detection events required a minimum of 20 consecutive transmitter detections to be considered a valid event to minimize the potential for spurious, false-positive detections to affect macro event calculations. Micro detection events were expressed as a sum of individual transmitter detections and began when a fish was first detected in a micro detection zone. The micro zone detection event then ended when the fish was detected in another micro detection zone or if the fish was not detected in the same micro zone for a 10-min period following the previous detection. Subsequent detection in another micro detection zone or the same micro zone following non-detection for 10 min began a new micro zone detection event. Micro detection events required only one transmitter detection to be considered valid because of the high signal strength required (i.e., Power > 175). Macro and micro zone detection events were then summarized by individual fish and reported as proportional data. Individual fish were considered to be the sampling unit.

Dam operations data were combined with fish behavioral data to analyze potential interactions between operations and fish behavior. Bulk discharge data were collected from the U.S. Army Corps of Engineers (USACE) data query site for AFD (USACE 2016) and turbine-specific operations data were provided by AFD operations staff from the Corps' Generic Data Acquisition and Control System (GDACS) at AFD. As shown in Figure 2, turbine 1 is located at river left (at micro detection zone #3), turbine 2 is located mid-channel (between micro zone #3 and #4), and turbine 3 is located at river right (at micro zone #4). Seasons used for behavioral

analyses were defined based on differences in flow and water temperature (Figure 3), and the life history of Bull Trout and Westslope Cutthroat Trout: the spring season (1 May to 30 June) was the period of increasing flow and temperature, when Bull Trout and Westslope Cutthroat Trout are known to actively migrate; the summer season (1 July to 30 August) was considered the period after peak flow with relatively high water temperatures; and the fall/winter season (1 September to 30 April) corresponded to decreasing water temperature and relatively stable flows.

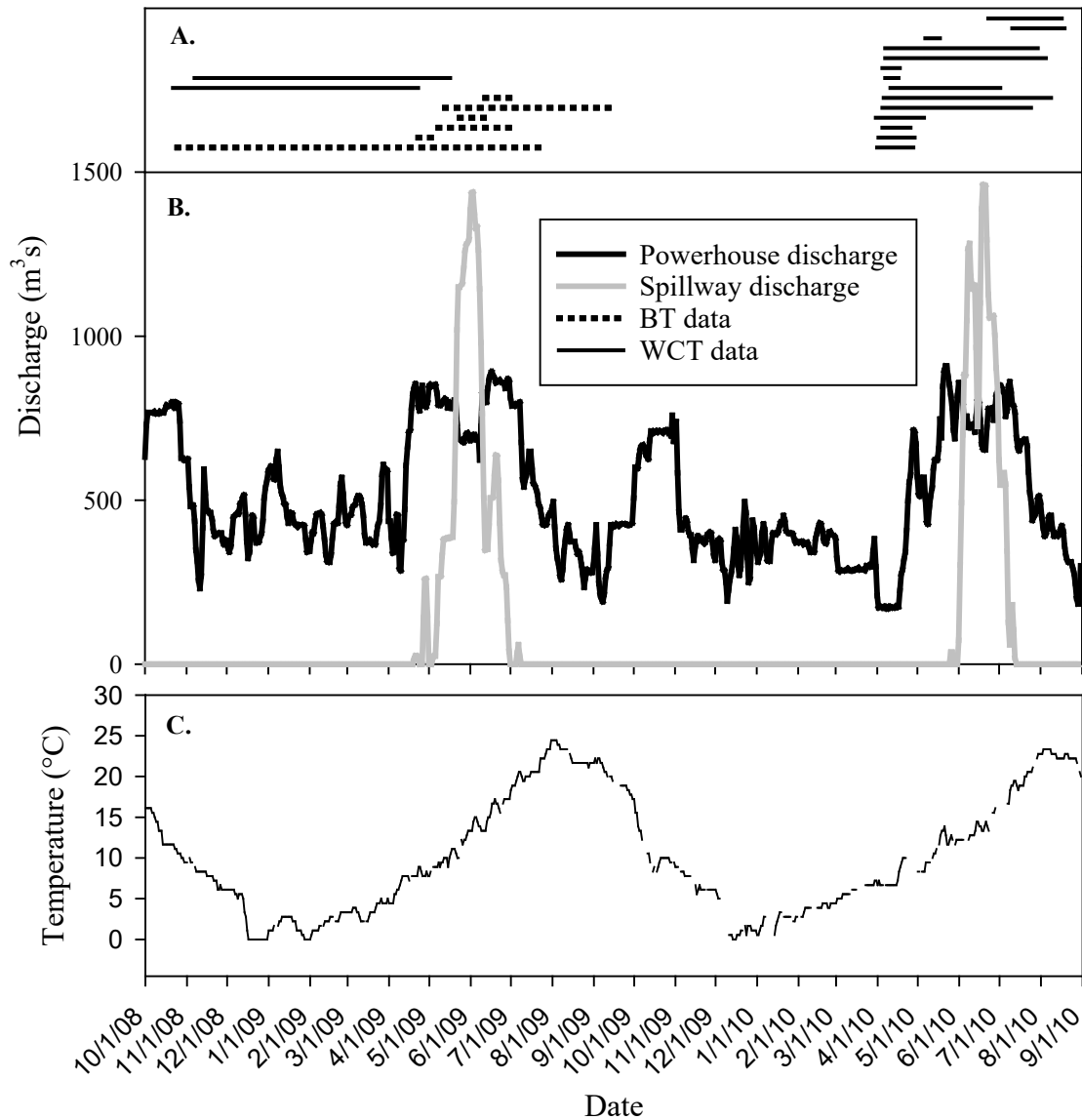


Figure 3. First to last detection of Bull Trout (BT; dotted lines) and Westslope Cutthroat Trout (WCT; solid lines) (A; each line represents the detection history of one individual, $n=22$), flow discharge at the powerhouse and spillway (B), and Pend Oreille River temperature (C) at Albeni Falls Dam from September 2008 through August 2010.

A manipulative discharge experiment was also conducted at the left powerhouse micro detection zone to determine if Bull Trout and Westslope Cutthroat Trout could be attracted by flow to this specific area of the powerhouse tailrace. For this experiment, $0.11 m^3$ of flow was released

through a sluice that routed water from the forebay and discharged it to the upstream portion of the left powerhouse micro zone. Sluice discharge treatments occurred from 15 June to 12 October 2009. Treatments alternated between “on” and “off” discharge for 3.25 and 3.58 days, respectively, for a total of 17 replicates.

Analysis

All statistical analyses were performed using the JMP statistical software package (SAS Institute, Cary, NC, USA) or the FishTel software package (version 1.4, Rogers and White 2007). Lengths of individual macro zone detection events were summed to calculate residence times within each macro zone, which were compared to seasonal behavioral data. One-way chi-square log-likelihood tests and Manly selection ratios (Manly et al. 2002) with 95% simultaneous Bonferroni confidence intervals were calculated using FishTel to analyze habitat selection of Bull Trout and Westslope Cutthroat Trout in relation to seasons and dam operating conditions. Habitat availability was calculated as the two-dimensional area (in m²) for both the powerhouse and spillway macro detection zones. To calculate the availability of turbine-operation configurations for selection analyses, the proportion of time that each operation was occurring during the period from 22 October 2008 through 19 August 2010 was used, which corresponded to the first and last dates of fish detection events. Although some expected values used for chi-square analyses were less than the common recommendation of 5, chi-square tests are robust to smaller expected values (Roscoe and Byars 1971; Lawal and Upton 1984). We checked the assumptions of all statistical tests before running analyses and set significance at $\alpha = 0.05$.

Results

Fish detection and movement

Of the 10 Bull Trout and 17 Westslope Cutthroat Trout tagged for the study, 60% ($n = 6$) and 94% ($n = 16$) were detected on multiple days at AFD, respectively, and provided behavioral data to be used for analyses (Figure 3A). Most study fish detection data occurred during the spring freshet in 2009 and 2010. In addition to detections at AFD, four Bull Trout were also detected moving downstream between the dam and the telemetry station at Usk, Washington. These large-scale movements occurred during spring and early summer (not shown in figures).

Five Bull Trout and 12 Westslope Cutthroat Trout were first detected in the spillway macro zone. Four Bull Trout were detected in the left spillway micro zone whereas 10 Westslope Cutthroat Trout were detected in the right powerhouse micro zone. Median time from release to first detection at a macro zone was 2.75 d (range = 0.26 – 30.95 d) for Bull Trout and 0.95 d (range = 0.11 – 33.24 d) for Westslope Cutthroat Trout, and the time to first macro zone detection did not differ by species (Median test, $P = 0.3496$). Following first detection in a macro zone, Bull Trout and Westslope Cutthroat Trout took a median of 3.5 hrs (range = 0.04 – 15.5 hrs) and 2.2 hrs (range = 0.1 – 223.6 hrs), respectively, until first detection at a micro detection zone, which also did not differ by species (Median test, $P = 0.9035$).

Bull Trout and Westslope Cutthroat Trout repeatedly transitioned between detection zones throughout the study period. Bull Trout and Westslope Cutthroat Trout transitioned between macro detection zones an average of 67 (SD = 71) and 58 (SD = 40) times, respectively, which did not differ by species (two-sided t -test, $P = 0.7155$). Mean transitions between micro detection zones were 432 (SD = 476.8) for Bull Trout and 370 (SD = 382.3) for Westslope Cutthroat Trout, which also did not differ between species (two-sided t -test, $P = 0.7847$).

Seasonal distribution in macro detection zones

Both species resided within both the spillway and powerhouse macro detection zones and residence time varied by species and season (Figures 4 and 5). Proportionally, Bull Trout median residence time in the spillway macro zone was 0.85 in fall/winter, 0.58 in spring, and 0.36 in summer (Figure 4); median proportion of residence time in the powerhouse macro zone was the complement (i.e., 0.15, 0.42, and 0.64, respectively). The proportion of median residence time of Westslope Cutthroat Trout in the spillway macro zone was 0.30 in fall/winter, 0.20 in spring, and 0.79 in summer (Figure 4); median residence time in the powerhouse zone was the complement (i.e., 0.70, 0.80, and 0.21, respectively).

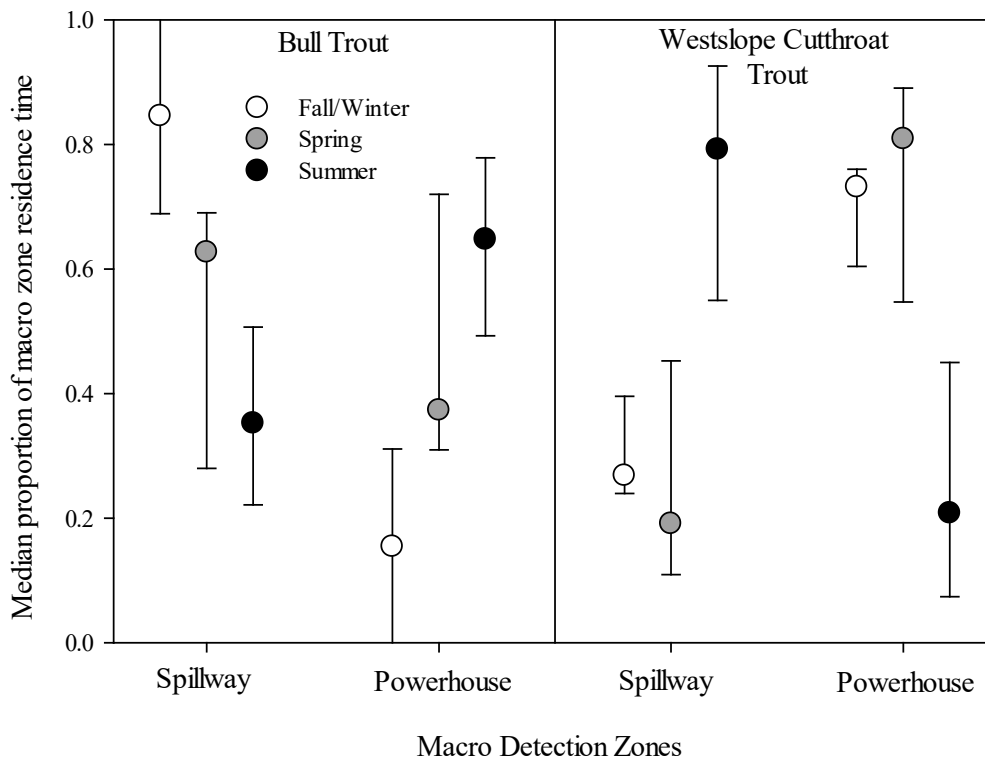


Figure 4. Median proportion of residence time by macro detection zone for Bull Trout (left panel) and Westslope Cutthroat Trout (right panel) in the Albeni Falls Dam tailrace. Colors of symbols denote season and error bars are two standard errors of the mean.

Bull Trout and Westslope Cutthroat Trout did not use macro zones in proportion to their availability (i.e., area in m²) across seasons (Bull Trout: $\chi^2 = 1250.87$, $df = 36$, $P < 0.0001$; Westslope Cutthroat Trout: $\chi^2 = 3337.60$, $df = 65$, $P < 0.0001$; Figure 5A, C). Bull Trout avoided the powerhouse macro zones in the fall/winter and the spillway macro zones in summer but selected the powerhouse macro zones during both the spring and summer seasons (Figure 5A). All other macro zone and season combinations were selected by Bull Trout in proportion to their availability. Westslope Cutthroat Trout did not select the spillway macro zone in fall/winter and spring and selected the powerhouse macro zone in these two seasons (Figure 5C). Westslope Cutthroat Trout selected both macro zones in proportion to their availability during summer.

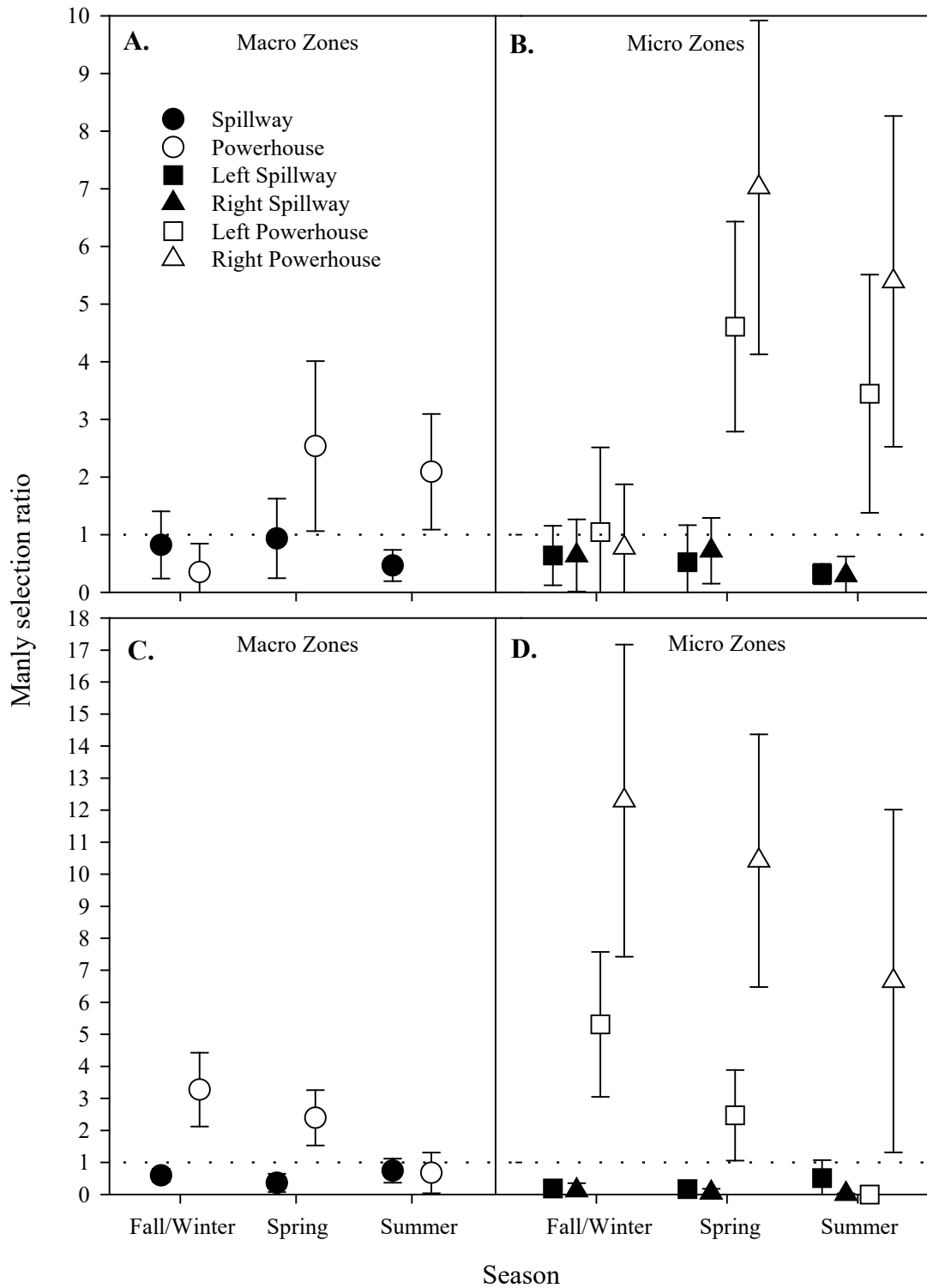


Figure 5. Seasonal selection of macro and micro detection zone areas downstream of Albeni Falls Dam for Bull Trout (A, B) and Westslope Cutthroat Trout (C, D). Manly selection ratios greater than 1 indicate positive selection, values overlapping 1 indicate selection in proportion to availability, and values less than one indicate negative selection (avoidance). Error bars are 95% Bonferroni confidence intervals.

Seasonal distribution in micro detection zones

Bull Trout and Westslope Cutthroat Trout did not use micro detection zones in proportion to availability (i.e., area in m²) across seasons (Bull Trout: $\chi^2 = 2180.78$, $df = 66$, $P < 0.0001$; Westslope Cutthroat Trout: $\chi^2 = 10458.86$, $df = 156$, $P < 0.0001$; Figure 5B, D). Bull Trout positively selected both powerhouse micro zones during spring and summer, avoided both spillway micro zones during summer, and used all other micro zone and season combinations in proportion to availability (Figure 5B). Westslope Cutthroat Trout positively selected both powerhouse micro zones in fall/winter and spring, positively selected only the right powerhouse micro zone in summer and avoided both spillway micro zones in all three seasons except for the left spillway micro zone in summer, which was selected in proportion to availability (Figure 5D).

During the fall/winter season, the median proportion of Bull Trout detection events at micro zones differed across the face of the dam, with more events observed at the left spillway micro zone and fewer events observed at the right powerhouse micro zone (Figure 6A). In contrast, during the spring and summer, the median proportions of Bull Trout detection events in micro zones shifted, with fewer events recorded at the spillway micro zones and more events recorded at the powerhouse micro zones, suggesting that Bull Trout may have used different areas of the tailrace depending on the season. For Westslope Cutthroat Trout, the median proportion of detection events at micro zones was consistently greatest at the right powerhouse across all seasons (Figure 6B).

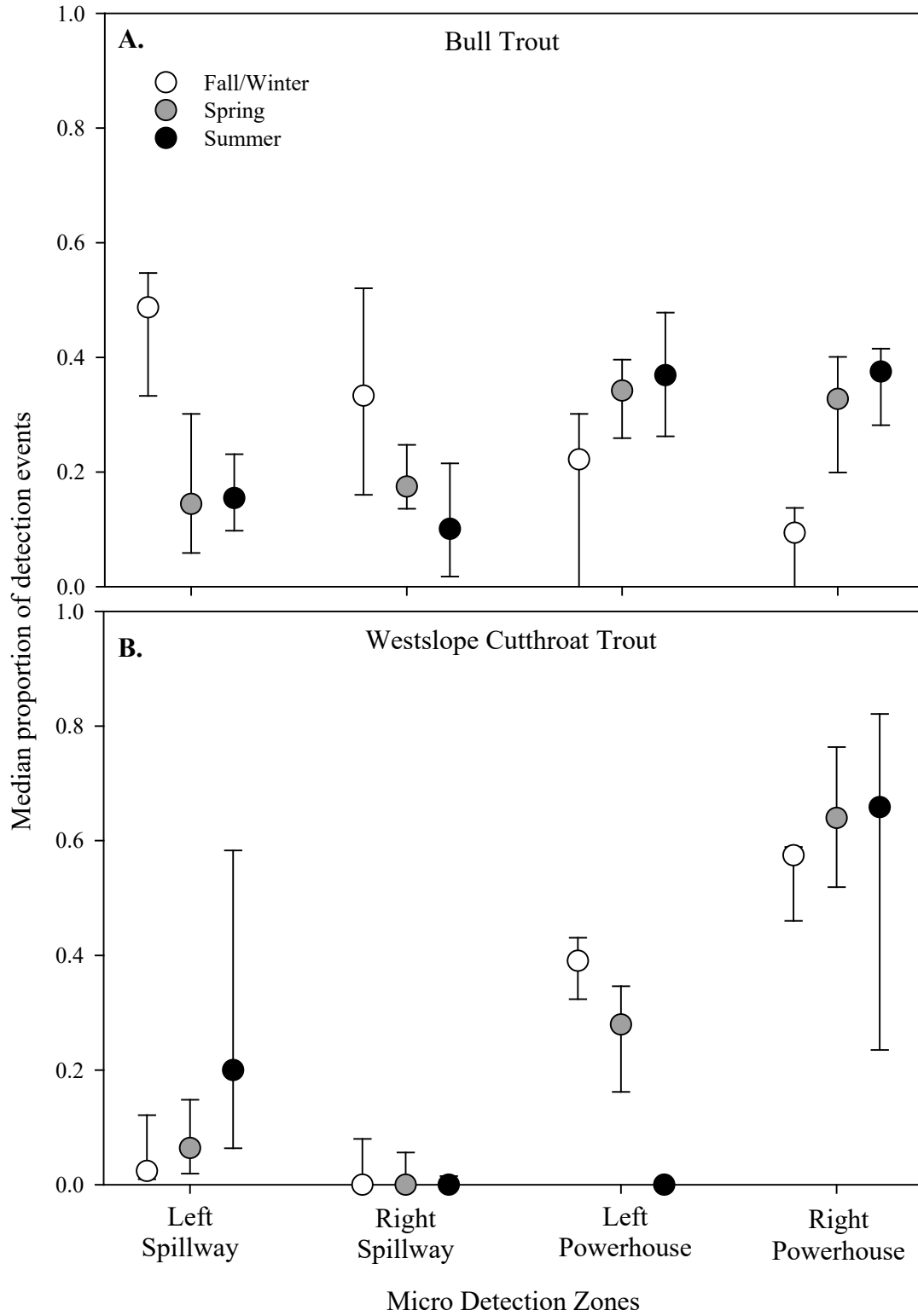


Figure 6. Median proportion of detection events of Bull Trout (A) and Westslope Cutthroat Trout (B) at the four micro detection zones in the spillway and powerhouse tailrace of Albeni Falls Dam. Colors of symbols denote season and error bars are two standard errors of the mean.

Fish behavior related to dam operations

All eight of the possible turbine-discharge scenarios occurred during the study period and use of the left and right powerhouse micro zones during discharge scenarios differed by species (Figure 7). The most common turbine configuration was the operation of all three turbines simultaneously (proportion = 0.68) whereas turbine-2 only (proportion = 1×10^{-4}) and the no turbines operating (proportion = 6×10^{-5}) occurred very infrequently (Figure 7). Nearly all Bull Trout detections at the powerhouse micro zones occurred when all turbines were operating and a few detections occurred when turbines 1 and 2 were operating, and when turbines 1 and 3 were operating (Figure 7). Westslope Cutthroat Trout use of micro zones was more evenly distributed during the various turbine operations, but most use occurred during all turbines, turbine 1 only, turbines 2 and 3, and turbines 1 and 3 operations (Figure 7).

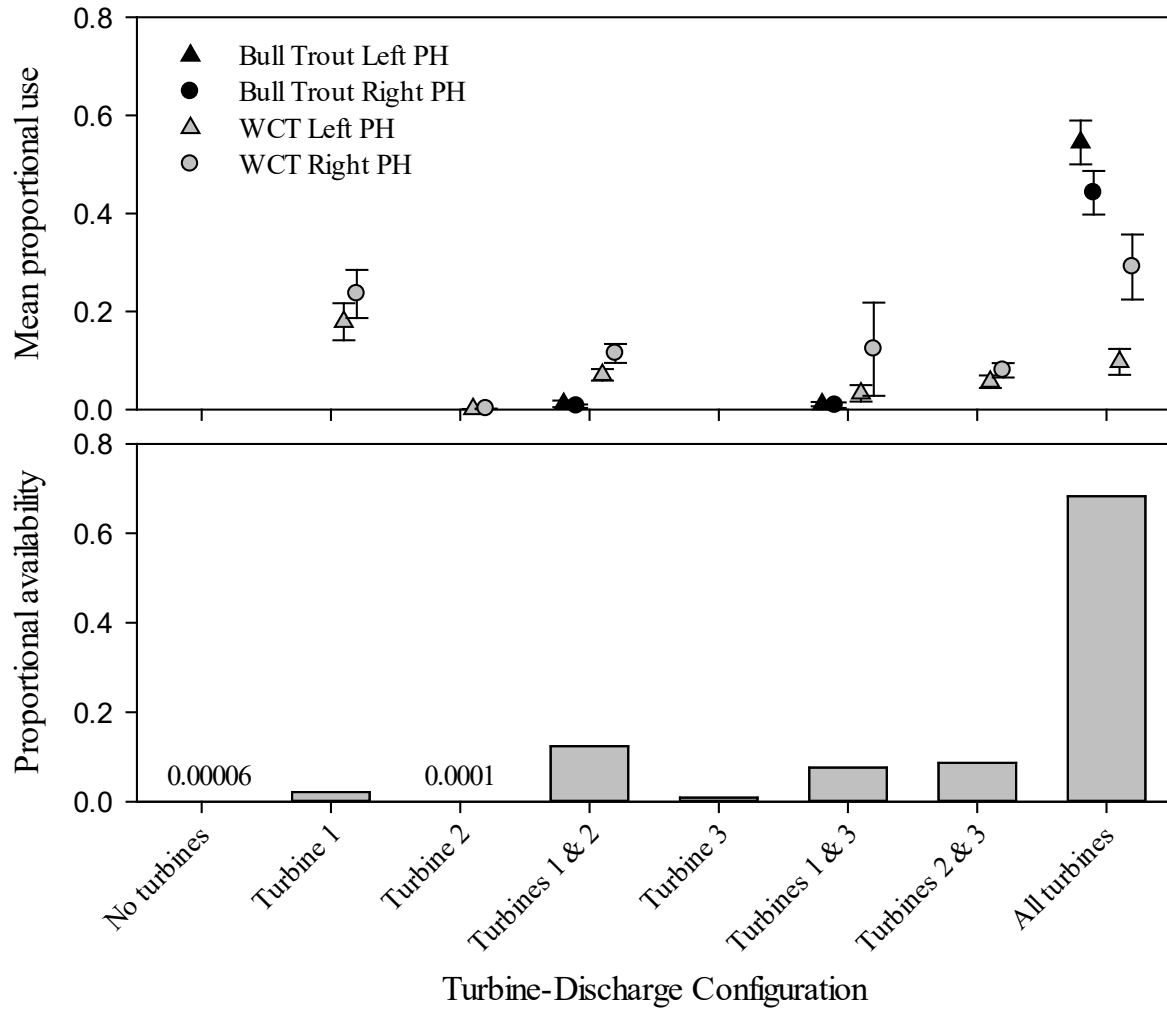


Figure 7. Proportional availability of the eight turbine-discharge configurations at Albeni Falls Dam (bottom panel) and mean proportional use (top panel) of each configuration for Bull Trout (black symbols) and Westslope Cutthroat Trout (grey symbols) at the left powerhouse (Left PH; triangle symbols) and right powerhouse (Right PH; circle symbols) micro detection zones from 1 October 2008 through 31 December 2010. One standard error of the mean is shown.

Bull Trout did not use the turbine-discharge scenarios in proportion to availability at either of the powerhouse micro zones (left powerhouse: $\chi^2 = 735.31$, $df = 42$, $P < 0.0001$; right powerhouse: $\chi^2 = 706.69$, $df = 42$, $P < 0.0001$; Figure 8). Similarly, Westslope Cutthroat Trout did not use the turbine-discharge scenarios in proportion to availability (left powerhouse: $\chi^2 = 5806.14$, $df = 112$, $P < 0.0001$; right powerhouse: $\chi^2 = 6781.63$, $df = 112$, $P < 0.0001$).

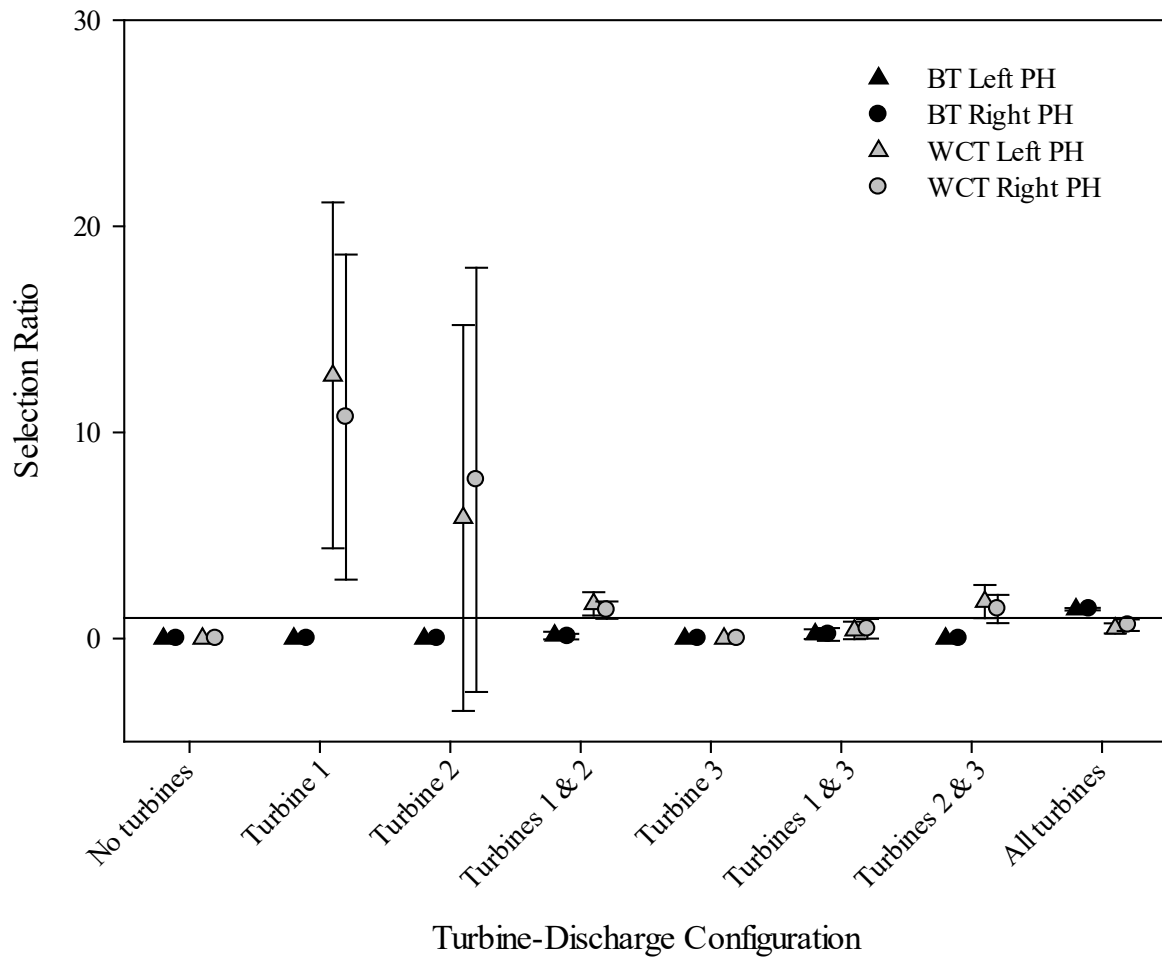


Figure 8. Selection of powerhouse micro zones by Bull Trout (BT) and Westslope Cutthroat Trout (WCT) during turbine-discharge configurations at Albeni Falls Dam from 1 October 2008 through 31 December 2010. Manly selection ratios greater than 1 indicate positive selection, values overlapping 1 indicate selection in proportion to availability, and values less than one indicate negative selection (avoidance). Error bars are 95% Bonferroni confidence intervals.

Discussion

The multiple detections of Bull Trout and Westslope Cutthroat Trout at the micro detection zones adjacent to the dam concrete and the several transitions of the fish between macro detection zones indicate that both species were highly mobile in the AFD tailrace. Our study suggests that both species would likely encounter a fish passage structure near the dam concrete if one was available.

Both species were detected at all four micro detection zones adjacent to the dam structure indicating that Bull Trout and Westslope Cutthroat Trout can approach all areas of the dam (hydrology did not prohibit their movements) where a fish passage entrance structure may be located. However, fish distribution was variable among the micro detection zones. Both species were detected more at the powerhouse micro zones than at the spillway micro zones although the powerhouse zones were spatially smaller. One reason for this behavior may have been higher discharge in powerhouse zones. Also, we observed several transitions of the fish in the micro zones and short residence times in one micro zone, likely indicating a searching behavior similar to fish-seeking movements in a dam tailrace by Larinier et al. (2003).

Fish detections in the micro zones varied by species and seasons. In fall/winter and spring, when they are assumed to migrate to spawning areas (Behnke 1992), Westslope Cutthroat Trout were detected in the powerhouse micro zones. Following peak discharge and as flows decreased following spring, Westslope Cutthroat Trout were detected mostly in the spillway. Muhlfeld et al. (2009) also observed migration of Westslope Cutthroat Trout towards spawning sites in the Flathead River system (Montana) as flows increased during spring. However, unlike what we observed at AFD, Muhlfeld et al. (2009) observed greater migration distances as flows decreased.

In spring and summer, Bull Trout were detected several times transitioning between the powerhouse and spillway micro detection zones. As suggested by Geist et al. (2004), these transitions could be a searching behavior for a passage route at AFD to find cold water refugia. In Idaho, adult Bull Trout migrated about 84 km from the Middle Fork East River (Figure 1) after spawning to overwintering areas in Lake Pend Oreille or the Pend Oreille River and remained relatively sedentary (i.e., moved less than 5 km) during winter (DuPont et al. 2007). Following winter, Bull Trout migrated back to spawning grounds in the Middle Fork East River (DuPont et

al. 2007). Muhlfeld et al. (2003) also observed relatively short diel movements of subadult Bull Trout during the winter in the Flathead River (Montana). In spring, Bull Trout exhibited longer downstream migrations as river discharge increased (Muhlfeld and Marotz 2005). If AFD did not entrain and block Bull Trout from completing their seasonal migration, it is suspected that they would return to Lake Pend Oreille during the winter and/or summer, similar to the Middle Fork East River population (Scholz et al. 2005).

Distribution of both Bull Trout and Westslope Cutthroat Trout also varied by season in the macro detection zones. Both species were detected in the portion of the tailrace (i.e., powerhouse or spillway) where discharge was occurring during the spring freshet and summer. During the spring freshet when both the powerhouse and spillway were discharging, Bull Trout were located approximately equally in both tailrace macro zones. In summer and fall when only the powerhouse was discharging, Bull Trout spent a greater amount of time in the powerhouse macro zone; winter locations were almost solely in the spillway macro zone, but this is likely due to the low activity level of Bull Trout. These observations were similar to those by Bonneau and Scarnecchia (1998) who observed Bull Trout inhabited areas of lower velocity during winter. Other studies also observed limited winter movement by Bull Trout (Swanberg 1997; Starcevich et al. 2012). Westslope Cutthroat Trout also spent most of their time in the powerhouse macro zone during summer and fall when discharge was through the powerhouse only; however, during the winter, Westslope Cutthroat Trout were located approximately equally in both macro detection zones.

Bull Trout and Westslope Cutthroat Trout migrated downstream of AFD during spring and early summer, possibly searching for an alternative route of passage past the dam, seeking thermal refuge, or searching for their spawning tributary. Prior to mid-June 2009, water temperatures were less than the Bull Trout-preferred maximum temperature, 15°C (McPhail and Baxter 1996), so it

is unlikely that Bull Trout were seeking thermal refuge at that time. Because there are no extant populations of Bull Trout in tributaries downstream of AFD, these fish did not discover other spawning locales, and most returned to the dam numerous times, likely seeking passage. Following mid-June, water temperatures in the Pend Oreille River exceeded 15°C, and movement downstream likely continued because fish were searching for thermal refuge.

Prior to this study, it was hypothesized by USACE fisheries and hydrology staff that the various turbine-discharge configurations might create turbulence that would inhibit Bull Trout and Westslope Cutthroat Trout from getting close enough to the dam concrete to discover a fish passage structure entrance. However, results from our study suggest that turbine operations did not limit fish entry into the powerhouse tailrace. During both years of the study, Bull Trout and Westslope Cutthroat Trout were detected in both the left and right micro zones of the powerhouse tailrace during most turbine discharge configurations. Particularly, Bull Trout positively selected the ‘all turbines’ discharge configuration whereas Westslope Cutthroat Trout positively selected the ‘turbine 1 only’ discharge. Overall, the different turbine discharge configurations did not appear to adversely affect fish behavior in relation to potential passage structure areas.

Based on Bull Trout and Westslope Cutthroat Trout movement patterns observed in our study; it is likely that both species would come within the vicinity of a passage structure at AFD. Several studies showed that when passage is provided, Bull Trout tend to use it and return to home streams (DeHaan et al. 2013, Ringel et al. 2014, Scholz et al. 2005). However, to guide fish into the entrance structure, previous research has shown attractants are often required (e.g., flow, rest structures, guides into passage) (Larinier 2001, Scholz et al. 2005, Williams et al. 2012). Because of the difference in life cycle between anadromous salmonids and Bull Trout and Westslope Cutthroat Trout, attractants may differ. Adult salmonids in general display complex movement

patterns when encountering dams and spend significant periods of time in dam tailraces searching for passage routes. Atlantic Salmon (*Salmo salar*) returning to spawn in the Tuloma River, Russia, explored the entire tailrace of a hydroelectric dam to seek passage, including both the spillway and powerhouse tailraces that were located about 2 km apart (Karppinen et al. 2002). However, a fish passage structure entrance near the powerhouse was used little by migrating salmon, and fish that entered the structure often returned to the tailrace without passing the dam. Researchers attributed the infrequent use of the fish ladder to weak flow through the structure. In the Gave de Pau River in France, radio-tagged Atlantic Salmon spent most of their time at a pool located 500–1200 m downstream of the dam and only a small percentage entered the structure during the first year (Larinier et al. 2003). An attractant flow was tested the second year, which increased the number of fish passing upstream to 87% that year (Larinier et al. 2003).

The main limitation of our study was the small size of fish tagged. This was mainly due to Bull Trout and Westslope Cutthroat Trout being rare as they are classified as endangered species. Difficulties in catching fish in deep water below the dam by electrofishing were also encountered. Although the number of fish tagged in our study was low, the results can assist fisheries managers in determining potential locations for a fish passage structure at AFD that is congruent with fish behavior. The left side of the powerhouse is considered to be one of the most suitable construction locations for an upstream fish passage facility because the powerhouse is the most-upstream discharge location and is a logistically suitable location for construction. Behavioral data suggested that Bull Trout approached the left powerhouse numerous times during all seasons of the year except in winter and were detected at the left powerhouse repeatedly during the spring migration season. Westslope Cutthroat Trout were detected also at the left powerhouse during the fall/winter and spring freshet; however, no summer behavioral data were collected

because fish moved downstream, away from the dam. The ability of Bull Trout and Westslope Cutthroat Trout to swim throughout the entire tailrace was first documented in fall 2008 and was verified for spring and early summer 2009 and 2010. This ability suggests that Bull Trout and Westslope Cutthroat Trout, regardless of where they first approach the dam, eventually swim throughout the entire downstream part of the dam within meters of the dam concrete where an adult fishway entrance may be constructed.

Based on the results of this study, a temporary fish passage structure was installed at the left side of the AFD powerhouse in spring 2016 and operated intermittently through spring 2017. The structure initially (in 2016 and 2017) consisted of a floating pontoon structure with a Denil fishway leading to a trap box located on the pontoon, with a finger weir at the entrance to the trap box. Although Bull Trout were located frequently near the trap entrance (unpublished data from 2016 study), no Bull Trout entered the temporary structure and no other species have been captured in the trap.

In March of 2018, the Denil ladder section was replaced with a submerged orifice entrance structure that had interchangeable orifice 'plates' allowing for tests of varying dimensions. The pool was sized to fit within the existing pontoon frame with a finger weir. No fish of any species was collected in the pool between 2018 and October 2019, leading to the cessation of trap and haul. The trap was permanently removed from the dam in November 2019; only seasonal electrofishing near the dam and downstream coldwater refugia has been used to pass fish since. Consequently, ongoing discussions with regional fisheries managers and the USACE at AFD are working to design and install a fish passage structure at AFD to enable fish migration; however, full funding of the structure is pending as of fall 2025.

The presence of a fish passage mechanism at AFD is necessary to reconnect the historical migration routes of Bull Trout and Westslope Cutthroat Trout in the Pend Oreille system. In addition to those species, other fishes important to recreational fisheries of Lake Pend Oreille will also likely benefit from the implementation of fish passage (e.g., Rainbow Trout and Kokanee). Hydropower dams will continue to alter waterways in the world and consequent effects on migratory fish can be expected to remain until their ability to migrate is restored. These effects can be largely mitigated by successful fish passage systems devised with a thorough understanding of fish movement and behavior.

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Conflicts of Interest

None declared.

Data Availability

Shared data are not available. Data are not publicly available nor in a format suitable for transferrable use.

Ethics Statement

This research meets the ethical guidelines and legal requirements of the United States of America, primarily through review and approval of animal handling guidelines as approved by the Institutional Animal Care and Use Committee (IACUC) of Eastern Washington University (EWU). Although this study occurred prior to the forming of an IACUC at EWU, this project used the same methods as those approved under EWU IACUC Protocol "Bull Trout-IACUC 2012-04-02."

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