SUBADULT BULL TROUT OUT-MIGRATION IN THE THOMPSON RIVER DRAINAGE, MONTANA

by

Jeffrey Robert Glaid

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DEDICATION

To my grandfather, Michael G. Kosala, who gave me my first fishing rod at age five and spent the rest of his life fostering my love of fish and science.

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ABSTRACT

Bull Trout populations in the Thompson River drainage have declined over the past century. Declines have been attributed to habitat fragmentation, habitat degradation, and non-native species. Out-migration characteristics (e.g., temporal and spatial origins, abiotic cues, and movement) of subadult Bull Trout (100 – 300 mm TL) were evaluated throughout the drainage to increase our understanding of local populations and better inform conservation efforts. In autumn 2014, 53 subadult Bull Trout were tagged with passive integrated transponder (PIT) tags; 29 were also surgically implanted with acoustic transmitters. Minimal Bull Trout out-migration ($N = 7$) was observed in 2014. In summer 2015, 566 subadult Bull Trout were PIT-tagged in the Fishtrap Creek and West Fork Thompson River drainages (Thompson River tributaries). Stream-width PIT antennas were used to monitor out-migration at the confluences of the Thompson River tributaries and at the mouth of the Thompson River. Out-migrating Bull Trout ($N = 135$) were sampled using directional weir traps at the tributary confluences, PIT-tagged, and implanted with acoustic- ($N = 29$) or radio-tags ($N = 14$) in autumn 2015. From July through December 2015, 10.1% of all PIT-tagged Bull Trout out-migrated from the Thompson River tributaries (11.4% of fish in the Fishtrap Creek drainage [$N = 420$] and 6.2% of fish in West Fork Thompson River [$N = 146$]), with peak out-migration occurring in late October. Highest predicted probabilities of Bull Trout out-migration occurred at lengths of 179 mm in Fishtrap Creek (30.4%) and 165 mm in West Fork Thompson River (29.3%). Only 13.5% of all Bull Trout that entered the Thompson River ($N = 192$) entered Thompson Falls Reservoir, with peak out-migration occurring in December. Median daily water temperature, minimum daily atmospheric pressure, and lunar illumination were weakly associated with an increase in the number of out-migrants. Radio-tagged out-migrants were randomly distributed throughout the Thompson River and exhibited long periods of site fidelity between intermittent downstream movements. Bull Trout demonstrated low out-migration rates in the Thompson River drainage and prolonged habitation of the mainstem Thompson River, which was contrary to the *a priori* hypothesis of clustered out-migration by subadult Bull Trout.

INTRODUCTION

Bull Trout *Salvelinus confluentus* are a species of char endemic to the northwestern regions of the United States and southwestern Canada. Current Bull Trout distribution includes much of inland Washington, inter-mountain Idaho and Montana, and British Columbia (USOFR 1999). Additionally, anadromous Bull Trout exist in the coastal regions of Washington and British Columbia (McPhail and Baxter 1996). In the Thompson River drainage, which is a tributary to the Clark Fork River in northwest Montana, Bull Trout are primarily found within the mainstem Thompson River and in tributary drainages such as Fishtrap Creek and the West Fork Thompson River (GEI and Steigers 2013).

Regional extirpations and range-wide population declines throughout the last century have resulted in a contracted Bull Trout distribution (Rieman and McIntyre 1993; Rieman et al. 1997; USOFR 1999). Human-induced habitat degradation, habitat fragmentation, exploitation, and introductions of non-native species have been implicated as factors associated with the reduced distribution and declining trends in abundance (Fraley and Shepard 1989; Rieman and McIntyre 1995; Baxter et al. 1999; Rieman and Allendorf 2001; Fredenberg 2002; Schmetterling 2003; McMahon et al. 2007). The effects of habitat alteration on Bull Trout populations are probably exacerbated by the narrow range of habitat requirements (i.e., cold water temperatures, minimal sedimentation in natal headwaters, complex habitat, and unobstructed migratory pathways) in which the species can survive (Rieman and McIntyre 1993; Baxter et al. 1999; Selong et al. 2001). Reductions in habitat connectivity can have strong negative effects on the long-term persistence of inland Bull Trout populations with a migratory (e.g., fluvial and adfluvial) component (Fraley and Shepard 1989; Rieman and McIntyre 1995; Neraas and Spruell 2001). As a result, Bull Trout have been designated as a threatened species under the U.S. Endangered Species Act (USOFR 1999).

Bull Trout are glacial relicts that evolved multiple life-history strategies and behaviors that allowed them to persist during times of glacial advance and to recolonize available habitat during times of glacial retreat (Power 2002). The diverse array of Bull Trout life-history strategies is probably an evolutionary adaptation to persist in highly variable environments (Northcote 1992; Power 2002). Consequently, patterns of migration (e.g., resident, fluvial, adfluvial, and anadromous) are regularly used to identify Bull Trout life-history strategies (Rieman and McIntyre 1993; McPhail and Baxter 1996). Despite this, mechanisms associated with the adoption of a particular life-history strategy have not been well-established for Bull Trout. Endogenous (i.e., fish size, genetics, growth rate, and condition) and abiotic (e.g., photoperiod, water temperature, discharge, lunar illumination, and atmospheric pressure) factors may promote the adoption of a specific life-history strategy (Smith 1985; Nelson et al. 2002). Identification of such factors remains complicated because inland populations of Bull Trout exhibit resident and migratory life-history strategies—cohabitating forms often existing within the same population (Rieman and McIntyre 1993; McPhail and Baxter 1996; Nelson et al. 2002). Migratory life-history strategies may be rapidly suppressed by isolation associated with the construction of passage barriers (Nelson et al. 2002).

A commonality among all Bull Trout, regardless of life-history strategy, is their use of headwater stream habitat for spawning and juvenile rearing. Resident Bull Trout typically use smaller headwater streams (< 4th order) to fulfill their life cycles and rarely attain total lengths greater than 400 mm (Rieman and McIntyre 1993; Nelson et al. 2002; Zymonas 2006). Conversely, migratory Bull Trout spawn in headwater streams and out-migrate to more productive riverine (fluvial) or lacustrine (adfluvial) habitats as subadults (100 – 300 mm) or adults (Fraley and Shepard 1989; Rieman and McIntyre 1993). Juvenile migratory Bull Trout tend to remain in natal headwaters from 1 to 4 years, with age and yearly timing of out-migration varying by drainage (Fraley and Shepard 1989; McPhail and Baxter 1996; Downs et al. 2006; Bowerman and Budy 2012).

Population-level declines of Bull Trout have occurred throughout the lower Clark Fork River watershed, including the Thompson River drainage (USOFR 2010). The construction of Thompson Falls Dam (in 1915), together with other dams on the Lower Clark Fork River, such as Cabinet Gorge (in 1953) and Noxon (in 1958), have blocked upstream fish movements and contributed to Bull Trout population fragmentation (Neraas and Spruell 2001). A U.S. Fish and Wildlife Service biological opinion concluded that the Thompson Falls hydroelectric project, as operated by PPL Montana (currently owned by NorthWestern Energy), has adversely affected Bull Trout (USFWS 2008). Furthermore, long-term habitat fragmentation caused by the Thompson Falls Dam probably had the largest negative influence on Bull Trout population growth in the Thompson River (PPL Montana 2010), ostensibly because of the proximity of the dam to the confluence of the mainstem Thompson River (10.1 km) and the duration (100 years) that fish migration has been disrupted by the dam (PPL Montana 2014). The installation of a fish ladder at Thompson Falls Dam in 2011, in conjunction with the manual transport of fish collected below the Cabinet Gorge and Noxon dams, has partially facilitated upstream migration in the Clark Fork River watershed. Despite this, few Bull Trout have used the fish ladder and recent evaluations by Montana Fish, Wildlife and Parks (MTFWP) concluded that the Bull Trout population in the Thompson River drainage has continued to decline (PPL Montana 2014). Habitat degradation is particularly problematic in the Thompson River drainage because natural habitat conditions restrict spawning and rearing activity to two tributary drainages, each of which has been subjected to extensive habitat alteration from road construction, logging, cattle grazing, and development of public camping sites in riparian areas (Whitehorse Associates 1997; GEI 2005; GEI and Steigers 2013).

Whereas the disruption of migration is the most obvious effect stemming from the construction of dams, river impoundments also alter habitat structure, food web dynamics, and fish assemblage composition (USFWS 2002; Scarnecchia et al. 2014). Additionally, it has been conjectured that expanding populations of introduced non-native species pose the greatest threat to Bull Trout recovery (USFWS 2002). Intentional or unplanned (i.e., accidental or illegal) introductions of non-native prey and predator species in adjacent reservoirs on the lower Clark Fork River have altered fish assemblages (Scarnecchia et al. 2014). Similarly, construction of Thompson Falls Reservoir reduced lotic habitat in the Clark Fork River and increased slow-moving lentic habitat, which allowed for the propagation and exchange of introduced non-native predators such as Northern Pike *Esox lucius*, Largemouth Bass *Micropterus salmoides*, Smallmouth Bass *Micropterus dolomieu*, Lake Trout *Salvelinus namaycush*, Brown Trout *Salmo trutta*, and Rainbow Trout *Oncorhynchus mykiss* (USFWS 2002; NWE 2016). Accordingly, Thompson Falls Reservoir may serve as a “predator trap” (McMahon and Bennett 1996) that increases predation risk to out-migrating Bull Trout (PPL 2008). Moreover, adfluvial Brown Trout and Rainbow Trout migrate into the mainstem Thompson River when subadult Bull Trout out-migrate. As such, non-native species probably prey on Bull Trout in the Thompson River drainage and Thompson Falls Reservoir (NWE 2016).

The distribution, seasonal migration patterns, and abiotic factors associated with migration and movement patterns of adult Bull Trout have been extensively studied; however, a paucity of information exists on the out-migration characteristics of juvenile and subadult Bull Trout (Muhlfeld and Marotz 2005; Monnot et al. 2008). The objectives of my study were to: 1) describe the out-migration timing, magnitude, and demographics of subadult Bull Trout in the Thompson River drainage, 2) identify abiotic parameters that influence fluvial and adfluvial out-migration of Bull Trout in the Thompson River drainage, and 3) assess movement characteristics (i.e., maximum distance, distribution, dispersal, rate of movement, and survival) of subadult Bull Trout in the mainstem Thompson River and Thompson Falls Reservoir. Documenting spatial and temporal variation in subadult Bull Trout out-migration characteristics in the Thompson River drainage will inform local conservation efforts and expenditures of limited restoration resources.

MATERIALS AND METHODS

Study Site

The Thompson River drainage is 163,169 ha in area and includes a 2,134-km stream network (Figure 1). The Thompson River originates in the Thompson Chain lakes and flows south for 72.4 km before merging with the lower Clark Fork River 10.1 km upstream of Thompson Falls Dam. Two unpaved roads follow the length of the Thompson River immediately next to each river bank for 29-km upstream of the confluence with the Clark Fork River (GEI and Steigers 2013). Whereas these roads benefit recreational activities (e.g., angling, hunting, camping) and industrial usage (i.e., logging and grazing), their close proximity to the river has resulted in extensive degradation of riparian and river habitat (USFWS 2008; GEI and Steigers 2013).

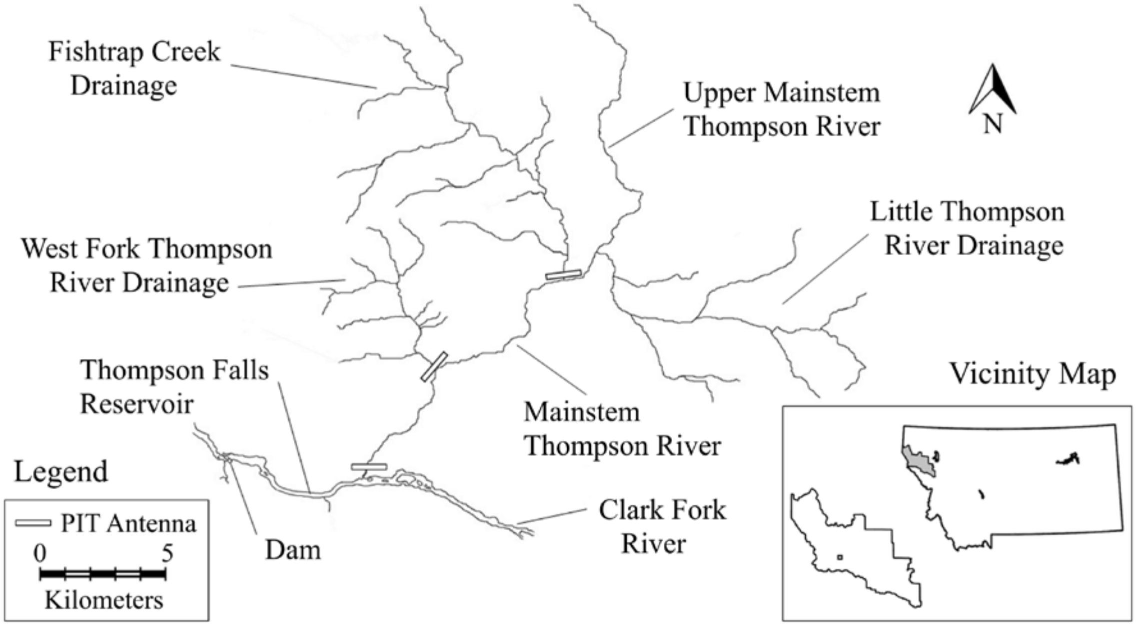

Figure 1. The Thompson River drainage near Thompson Falls, Montana, with locations of PIT antennas used to assess subadult Bull Trout out-migration characteristics.

The mainstem Thompson River has two distinct sections. The upper section includes about 45 km of the Thompson River from its origin to the confluence with the Little Thompson River drainage and is characterized by low gradient flows and warm water temperatures—warmest water temperatures occur immediately upstream of the confluence with Fishtrap Creek (Figure 1). The lower section of the mainstem Thompson River, which includes 27.4 km from the confluence with the Clark Fork River, is predominantly narrow-canyon habitat that results in high gradient flows. Inflow of several headwater tributaries into the lower mainstem Thompson River results in the Thompson River being near the confluence with the Clark Fork River. Accordingly, Bull Trout are predominantly found downstream of the confluence between the mainstem Thompson River and the Little Thompson River (GEI and Steigers 2013; PPL Montana 2014).

Fishtrap Creek and the West Fork Thompson River are tributary drainages to the lower section of the Thompson River (Figure 1). Fishtrap Creek drainage covers 24,307 ha and is predominantly owned by the U.S. Forest Service (74.2%) and Weyerhaeuser Timber Company (23.1%), with only minor state and private property holdings (Whitehorse Associates 1997; GEI 2005). Fishtrap Creek is characterized by high-gradient flows in the upper and lower reaches with a broadened valley floor in the middle of the drainage. Several small tributaries to the mainstem Fishtrap Creek contain Bull Trout, including West Fork Fishtrap Creek, Beatrice Creek, and Jungle Creek (Figures 1 and 2). From the late 1950s through 2005, over 15% of the Fishtrap Creek drainage was subject to timber harvest, which was facilitated by an extensive (938 km) road network

(GEI 2005). Particularly, 85.3% of the 180.5 km stream channel network in the Fishtrap Creek drainage is paralleled by unpaved roads (GEI 2005).

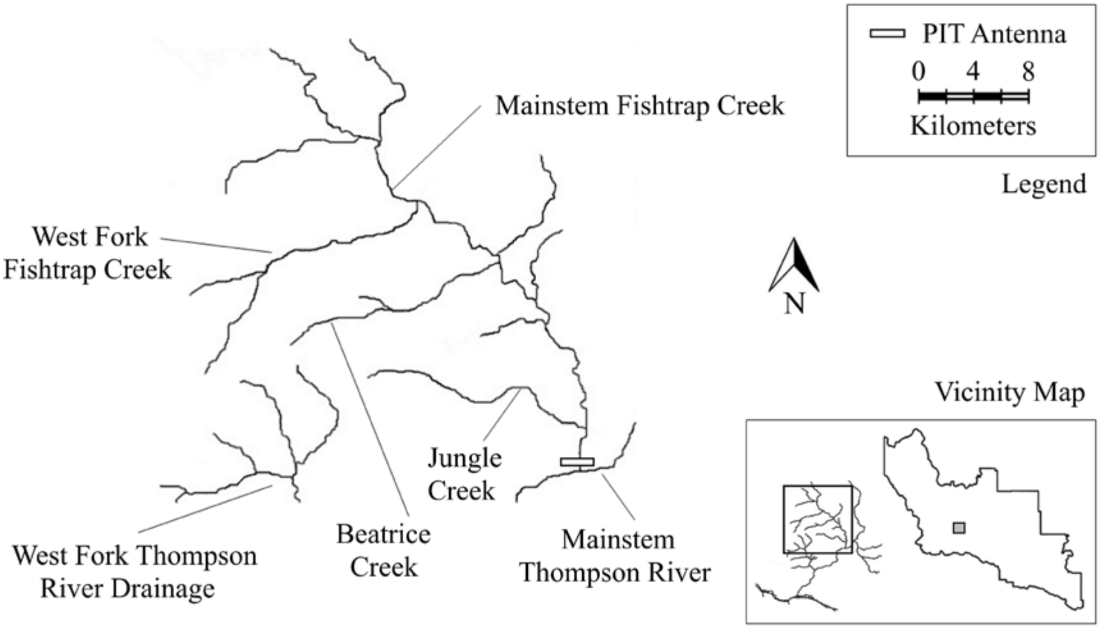

Figure 2. The Fishtrap Creek tributary drainage and headwaters of West Fork Thompson River to the mainstem Thompson River, Montana, with location of the PIT antenna used to assess subadult Bull Trout out-migration characteristics.

The West Fork Thompson River drainage is 9,219 ha in area and primarily within U.S. Forest Service property (Whitehorse Associates 1997; GEI 2005). The West Fork Thompson River is a relatively short drainage characterized by low-gradient habitat in the upper reaches that transitions to high gradient step-pool habitat 1.1 km from the confluence with the mainstem Thompson River. Previous land-use assessments determined that 11.3% of the West Fork Thompson River basin, including the riparian corridor, was directly affected by logging activity (GEI 2005; USFS 2008). Furthermore, 37.5% of the 53.9 km West Fork Thompson River stream channel has a non-paved road within the riparian area (GEI 2005).

Thompson Falls Reservoir is a run-of-the-river hydroelectric impoundment of the Clark Fork River located about 160 km northwest of Missoula, Montana (Figure 3). The 92.3-megawatt Thompson Falls hydroelectric project was completed in 1915 and is currently operated by NorthWestern Energy. Thompson Falls Reservoir is 11.2-km long, has a surface area of 607 ha, and a storage capacity of 18.53 hm^3 (USFWS 2008). Mean annual reservoir discharge is about 566 m^3/sec with a conservation pool elevation of 730.6 m above mean sea level (USFWS 2008).

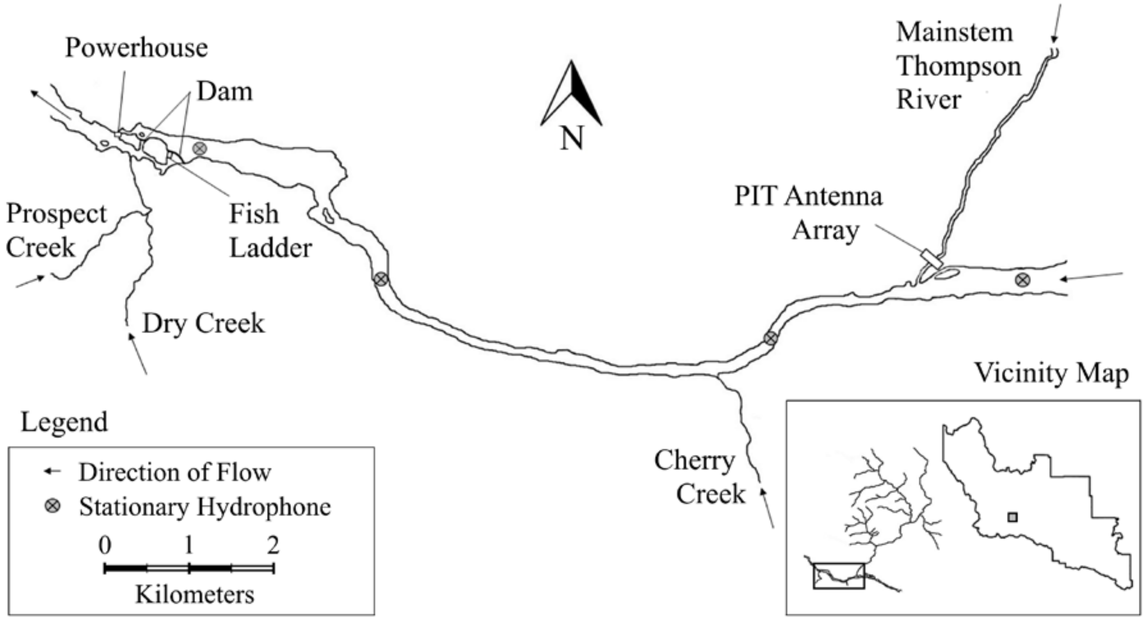

Figure 3. Thompson Falls Reservoir near Thompson Falls, Montana, with locations of mainstem Thompson River PIT antenna array and stationary acoustic data loggers.

The native fish assemblage in the Thompson River drainage includes Bull Trout, Columbia Slimy Sculpin *Cottus cognatus*, Largescale Sucker *Catostomus macrocheilus*, Longnose Dace *Rhinichthys cataractae*, Longnose Sucker *Catostomus catostomus*, Mountain Whitefish *Prosopium williamsoni*, Northern Pikeminnow *Ptychocheilus* *oregonensis*, Rocky Mountain Sculpin *Cottus bairdi*, and Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi*. The non-native fish assemblage in the Thompson River drainage includes Brook Trout *Salvelinus fontinalis*, Brown Trout, and Rainbow Trout. The native fish assemblage in Thompson Falls Reservoir includes Bull Trout, Columbia Slimy Sculpin, Largescale Sucker, Longnose Dace, Longnose Sucker, Mountain Whitefish, Northern Pikeminnow, Peamouth *Mylocheilus caurinus*, Redside Shiner *Richardsonius balteatus*, Rocky Mountain Sculpin, and Westslope Cutthroat Trout. The non-native fish assemblage in Thompson Falls Reservoir includes Black Bullhead *Ameiurus melas*, Brown Trout, Lake Trout, Lake Whitefish *Coregonus clupeaformis*, Largemouth Bass, Northern Pike, Pumpkinseed *Lepomis gibbosus*, Rainbow Trout, Smallmouth Bass, and Yellow Perch *Perca flavescens*.

Field Methods

Capture and Tagging

During autumn 2014, Bull Trout were sampled from seven randomly selected reaches within the lower 1.2 river kilometers (rkm) of the West Fork Thompson River (Figure 1). River kilometer delineations were measured from the confluence with the mainstem Thompson River. Reaches varied in length from 127 to 183 m, with length dependent on the presence of suitable ending points. The majority of sampling occurred from 3 October to 14 October, with one additional event occurring on 27 October. Two-pass electrofishing was used in most reaches because of low catch rates caused by the high-gradient step-pool conditions. Catch was optimized by use of electrofishing that proceeded downstream and terminated at a block-net. Backpack electrofishing (Smith-Root; Model LR-24) settings were established in a systematic manner, which began at 300 V and 30 Hz and were increased incrementally until fish were effectively immobilized (Dunham et al. 2009). Settings used spanned 300 – 550 V, 0.1 A, and 30 – 45 Hz depending on the reach-specific conductivity (89 – 132 µS/cm). Sampled Bull Trout were anaesthetized (40 mg/L MS-222), weighed to the nearest gram, and measured to the nearest millimeter of total length. Adhering to MTFWP and U.S. Fish and Wildlife Service standardized procedures that have been adopted in the lower Clark Fork River area, all Bull Trout greater than or equal to 100 mm were implanted with 134.2-kHz half-duplex (HDX) PIT tags measuring 12.0 × 2.1 mm that were injected into the dorsal sinus (Biomark, Inc., Boise, Idaho). Likelihood of detection at Biomark PIT antenna equipment was increased by also inserting 134.2-kHz full-duplex (FDX) PIT tags measuring 12.0 × 2.1 mm into the surgery incisions of all acoustically-tagged fish (see below). All out-migrating Bull Trout had multiple detections at the tributary-confluence PIT antenna, with dual-detections registered for fish with HDX and FDX PIT tags. Thus, tag-collision probably did not influence detection. A hand-held PIT tag reader (Biomark Inc.; Model 601 Handheld Reader) was used to check for existing tags in all Bull Trout showing evidence of recent surgery. Acoustic transmitters (Lotek Wireless; MAP6_1; 13 mm, 0.9 g in air) were surgically implanted into Bull Trout (*N* = 29) using methods modified from Brown et al. (2003), Deters et al. (2012), and Liedtke et al. (2012). Large subadult Bull Trout (> 44 g) required for adherence to the 2% rule were scarce in the lower section of the West Fork Thompson River. Thus, 17 fish were implanted with acoustic transmitters that exceeded the 2% tag to body-weight ratio (mean = 2.0%; minimum = 0.6 % and maximum = 2.9%). Implanted tags impart no negative effects until tag to body weight ratio reaches 4 to 7% (Liermann 2003; Jepsen et al. 2003; Zale et al. 2005; Brown et al. 2006; Cooke et al. 2012; Smirich and Kelly 2014).

During summer 2015, Bull Trout were sampled from the lower 5.0 rkm of the West Fork Thompson River, between rkm 5.0 and 18.5 in mainstem Fishtrap Creek, and the lower 3.0 rkm of West Fork Fishtrap Creek, Beatrice Creek, and Jungle Creek. All river kilometer delineations were measured from the confluence of the respective water body, with the confluence being normalized to zero. Random sampling, without replacement, was used in the West Fork Thompson River. Random stratified sampling, without replacement, was used in the Fishtrap Creek drainage, with the mainstem Fishtrap Creek and its tributaries being divided into separate strata. Strata were based on prior information regarding tributary size (e.g., headwater tributaries and mainstem tributary), and historic high catch rates (Ryan Kreiner, MTFWP, personal communication).

Individual sampling reaches in the West Fork Thompson River ($N = 10$) varied in length from 59 to 144 m and from 88 to 144 m in the Fishtrap Creek drainage ($N = 24$). As was the case in 2014, specific lengths of all sampling reaches were dependent on the presence of suitable starting and ending points. All sampling during summer 2015 occurred from 14 July to 6 August. Standardized backpack electrofishing methods were similar to 2014 with the exception of sample reach selection. Settings used spanned 250 – 680 V, 0.05 – 0.11 A, and 40 – 45 Hz depending on the reach-specific conductivity (58 –

234 µS/cm). Sampled Bull Trout were anaesthetized, weighed to the nearest gram, and measured to the nearest millimeter of total length. Likelihood of detection was maximized at Biomark PIT antennas through the use of FDX PIT tags. A 12-mm PIT tag was injected into the dorsal sinus of all sampled trout using a syringe-style implanter. Fin-clip samples collected from the ventral caudal lobe of Bull Trout (*N* = 116) for genetic sampling unrelated to this project served as secondary markers to PIT-tagged fish. A hand-held PIT tag reader was used to check for existing tags in all Bull Trout with caudal fin-clips. While recapture rates of PIT-tagged Bull Trout were low (*N* = 5) no fish with a caudal fin-clip were detected as having shed the injected 12-mm PIT tag. All PIT-tagged Bull Trout were placed in a metal-framed mesh cage and allowed to recover from anesthesia in fresh water until equilibrium could be maintained.

Throughout autumn 2015, out-migrating Bull Trout were sampled using directional weir traps that were deployed at the confluences of Fishtrap Creek and the West Fork Thompson River. Weirs were constructed of steel angle-iron frames with conduit pickets spaced about 1.25-cm apart; thus, maximizing the potential to capture out-migrating Bull Trout of target length (≥ 175 mm; ≥ 37 g) (Liermann 2003; Ryan Kreiner, MTFWP, personal communication). Trap boxes were covered with Vexar plastic mesh (12.7-mm bar width), and fitted with 16.5-cm conical entrances. Weir traps were installed on 22 September (after the post-spawn migration of adult fish) and operated continuously until 12 November. Traps were checked and pickets cleared of debris two to three times per day. All out-migrating Bull Trout sampled in the weir traps were temporarily held in a metal-framed mesh cage prior to FDX PIT tag injection (all fish ≥

100 mm) or tag implantation surgery. Weir-sampled Bull Trout greater than 37 g were implanted with a MAP6_1 acoustic transmitter or NTQ-3-2 radio transmitter (Lotek Wireless; 16 mm, 1.1 g in air), the order of which were randomly selected prior to sampling. Acoustic transmitters (N = 29) and radio-telemetry tags (N = 15) were surgically implanted into the peritoneal cavity of subadult Bull Trout using methods modified from Brown et al. (2003), Deters et al. (2012), and Liedtke et al. (2012).

PIT Antennae

Out-migration timing and magnitude were assessed in the Thompson River drainage using an array of pass-over PIT antennas in 2014 and 2015. All antennas were installed prior to sampling in both years. In September 2014, one stream-width PIT antenna array (Biomark Inc.; IS1001-MTS) consisting of seven integrated antennas was installed, and operated continuously throughout both field seasons, near the confluence of mainstem Thompson River (Figures 1 and 2). A multi-antenna system was selected for use in the mainstem Thompson River because the factory-quoted read-range (~ 45 cm) was greater than the depth of the designated build location; which was essential to ensure maximum detection efficiency of PIT-tagged fish. One PIT antenna (Biomark Inc.; IS1001-MTS) was installed in the West Fork Thompson River in September 2014 and July 2015, and one PIT antenna was installed in Fishtrap Creek near its confluence with the mainstem Thompson River in July 2015 (Figure 1). Detection efficiencies were evaluated with monthly *in situ* detection tests (Beeman and Hayes 2012). Average estimated detection efficiencies throughout 2015 were 98.8% (SD = 0.9) in Fishtrap

Creek, 98.9% (SD = 1.1) in the West Fork Thompson River, and 95.6% (0.9) in the mainstem Thompson River.

Abiotic Factors

Water temperature was measured (± 0.01 °C) in the Thompson River drainage at 15-minute intervals with stationary submersible data loggers (Onset, Inc.; HOBO UA-001-64 Pendant). Temperature loggers were placed in each tributary and the mainstem Thompson River adjacent to PIT antenna locations. Measurements from all data loggers were used to calculate minimum, maximum, median, and 24-hour change in daily temperatures. Reach-specific water level was measured (± 0.001 m) as an index to discharge at 15-minute intervals with submersible pressure sensors (Onset, Inc.; HOBO U20L-4) deployed at the confluences of Fishtrap Creek and the West Fork Thompson River. Pressure sensor measurements were calibrated using atmospheric barometric measurements generated by a reference pressure sensor. Observed water levels were periodically measured at each pressure sensor location to corroborate calculated values. Measurements from the reference pressure data logger were also used to calculate minimum, maximum, median, and 24-hour change in daily atmospheric pressure. Discharge (m^3/sec) data for the mainstem Thompson River was obtained from online records for the USGS monitoring station (USGS site: 12389500) and was used to calculate minimum, maximum, median, and 24-hour change in daily discharge. Surface level light intensity (kLux) was measured at 15-minute intervals with land-based light intensity data loggers (Onset, Inc.; HOBO UA-002-64). Patterns in diel light intensity were used to calculate median and maximum light intensity, and photoperiod length (hours of kLux/day > 0.0). Date-specific daily proportion of illuminated lunar surface, which varied from 0 (new moon) to 1 (full moon), was obtained from the U.S. Naval Observatory database (http://aa.usno.navy.mil/data/docs/MoonFraction.php).

Radio Telemetry

Radio-tagged Bull Trout were relocated a minimum of three times per week. The generally narrow and shallow characteristics of the mainstem Thompson River, combined with the presence of roads that parallel each bank downstream of the Fishtrap Creek confluence, allowed for detection of telemetered fish throughout the river. Coarse-scale relocations of radio-tagged Bull Trout were assessed from a vehicle using a mobile radio receiver (Lotek Wireless; Model SRX-400) with a roof mounted omni-directional antenna. Detection at a finer scale was achieved with a three-element handheld Yagi antenna. Location accuracy averaged 3 m (SD = 1.4) and was evaluated in blind tests ($N = 15$) conducted in sections of the mainstem Thompson River that had a depth of less than 0.63 m. For each fish relocation, a GPS point (UTM; NAD83) was recorded and the status of a given fish (alive, dead, predated on, or unknown) was established based on movement, or lack thereof, during successive detections. Individual status (alive or dead) of radio-tagged Bull Trout was obtained at the end of the field season by intentionally disturbing each fish. One stationary radio-telemetry recording station (Lotek Wireless; Model SRX400) operated continuously from 8 October to 12 December at a position adjacent to the confluence of the mainstem Thompson River to detect fish moving into Thompson Falls Reservoir. Individual relocations (N = 265) of radio-tagged Bull Trout were recorded from 24 September to 11 December (78 days). Data for movement analyses and kernel density maps only included individual Bull Trout that had been relocated alive during a period of time greater than two weeks (i.e., minimum of six relocations) in order to allow for potentially negative effects of surgery (e.g., transmitter loss, tagging site irritation, atypical behavior, or mortality) to manifest (Brown et al. 2003).

Acoustic Receivers

Four stationary hydrophone receivers (Lotek Wireless; Model WHS3050) were deployed to assess broad-scale movement of acoustically-tagged Bull Trout in Thompson Falls Reservoir. The stationary receiver matrix encompassed 11.2 rkm of the impounded Clark Fork River from a point 1.1 km upstream of the Thompson River confluence to immediately upstream of Thompson Falls Dam (Figure 3). Stationary receivers were moored to the riverbed with a 20-kg concrete anchor connected to a 30-cm (diameter) inflatable buoy; resulting in the hydrophone unit being suspended 2-3 m below the surface (Clements et al. 2005; Heupel et al. 2006). Horizontal placement of the stationary receivers in Thompson Falls Reservoir was determined based on *in situ* range testing to verify that environmental conditions did not affect transmitter signal detection (Clements et al. 2005; Heupel et al. 2006).

Data Analysis

Out-migration Characteristics

The number of subadult Bull Trout out-migrating was quantified by sampled tributary. Migration was defined as movement between at least two distinct habitat types (e.g., tributary drainage, mainstem river, and reservoir; Starcevich et al. 2012). The magnitude of out-migration of PIT-tagged Bull Trout into the mainstem Thompson River was characterized in 2014 (West Fork Thompson River) and 2015 (Fishtrap Creek drainage, West Fork Thompson River). Out-migration from the mainstem Thompson River was assessed from autumn 2014 through spring 2016.

A Wilcoxon signed-rank test was used to assess differences in mean total length between PIT-tagged fish that out-migrated from, and those that remained in, the West Fork Thompson River for the data collected in 2014. A Welch's two-sample t-test for unequal variance was used to evaluate whether mean total length of PIT-tagged Bull Trout that out-migrated from each tributary drainage (i.e., Fishtrap Creek drainage and West Fork Thompson River) differed during the 2015 field season.

For each year of sampling, a length-weight relationship for the sampled Bull Trout population was determined by least-squares regression of $\log_{10}W \times \log_{10}TL$. The exponentiated slope and intercept coefficients from each length-weight relationship equation were used to calculate relative condition factor (K_n) of each fish with the following equation:

$$(1) \qquad K_n = W/W',$$

where W is weight (g) and W' is the length-specific mean weight of an individual fish as predicted by the length-weight equation generated for the sampled population (Neumann et al. 2012). Diagnostic tests (Shapiro-Wilk for normality and Levene's for equal variance) were used to evaluate if parametric analyses were appropriate. A Wilcoxon signed-rank test was used to assess differences in K_n between PIT-tagged fish that out-migrated from, and those that remained in, the West Fork Thompson River for the data collected in 2014. A Welch's two-sample t-test for unequal variances was used to evaluate whether K_n of PIT-tagged Bull Trout that out-migrated from each tributary drainage (i.e., Fishtrap Creek drainage and West Fork Thompson River) differed during the 2015 field season.

The effect of total length, total length squared, and K_n on the probability of subadult Bull Trout out-migration were evaluated with binary logistic regression models. The squared term of total length was included in preliminary models because previous studies (Zymonas 2006) and the sampling of large (> 200 mm) subadult Bull Trout in both tributary drainages indicated that the effect of length on out-migration would not be constant for all fish. Backward likelihood-ratio selection resulted in a logistic regression model of Bull Trout out-migration being predicted by total length and total length squared but not K_n. Deviance goodness-of-fit and Hosmer-Lemeshow tests were used to evaluate whether the preferred logistic model was appropriate. The natural log odds that Bull Trout did or did not out-migrate were estimated using the following equation:

$$(2) \qquad \mathrm{logit}(\hat{p}) = \beta_0 + \beta_1(\mathrm{TL}) + \beta_2(\mathrm{TL}^2),$$

where $\mathrm{logit}(\hat{p})$ is the logistic probability of out-migration, β_i is the parameter estimate, and TL is total length of Bull Trout in millimeters. Using the estimated $\mathrm{logit}(\hat{p})$, the probability of out-migration across the length range of observed Bull Trout in each tributary drainage to the mainstem Thompson River was predicted as:

$$(3) \qquad \hat{p} = \frac{e^{\mathrm{logit}(\hat{p})}}{[1 + e^{\mathrm{logit}(\hat{p})}]}.$$

Date and time at initial detection for each PIT-tagged Bull Trout was used to describe out-migration rates and timing (seasonal and diel) in the Thompson River drainage. Dates of first and last detection of all Bull Trout were used to define the out-migration period. Peak of out-migration was calculated as the median date of all detections, and graphically represented with cumulative proportion of total out-migrants for each portion of the Thompson River drainage (Zimmerman and Kinsel 2010). Diel timing of out-migration, quantified as the hour-of-day where individuals were first detected by a PIT antenna, was characterized using frequency-histogram plots and the calculated mode of hourly detections. Potential differences in the proportions of observed out-migration from the Fishtrap Creek drainage and West Fork Thompson River was examined using a chi-square test.

Abiotic Cues to Out-migration

The influence of abiotic factors on the number of unique daily detections of PIT-tagged subadult Bull Trout was evaluated using Poisson regression models (Zuur et al. 2009). Abiotic factors in this assessment included all calculated daily statistics for: water temperature, discharge, atmospheric pressure, proportion of lunar illumination, surface light intensity, and photoperiod. Correlations between all abiotic variables were assessed by generating a Pearson’s correlation coefficient matrix. Highly correlated predictor variables ($\geq |0.60|$) were not simultaneously included during candidate model generation to avoid collinearity (Zuur et al. 2009). Candidate models were constructed based on speculated relationships between abiotic factors and Bull Trout out-migration. For each spatial component of the Thompson River drainage where out-migration was assessed, the number of abiotic parameters included in candidate models was limited to approximately one (1) parameter per 15 observed out-migrants to avoid model over-fitting (Harrell 2001). Akaike's Information Criteria corrected for small sample size (AICc), change in AICc (ΔAICc), over-dispersion, and pseudo-r^2 values were evaluated for each candidate model (Burnham and Anderson 2002; Heinzl and Mittlböck 2003). Model selection was used to identify the most parsimonious model (lowest AICc) and to identify biotic parameters that were associated with Bull Trout out-migration (Rogers and White 2007).

Movement Characteristics

Movement was assessed by evaluating timing, distance, distribution, and movement rate for each radio-tagged Bull Trout. Thus, individual fish, not individual detections, were the experimental unit of interest (Otis and White 1999). All geographic coordinates of fish relocations were indexed to river kilometer to allow for calculation of distances between relocations. Relocation data for radio-tagged fish was used to estimate minimum total and net movement (Rogers and White 2007). Daily movement rate (km/d) was quantified for individual fish throughout the autumn 2015 field season by calculating the distance moved between successive locations over the elapsed time. Net movement in the mainstem Thompson River was calculated weekly for all radio-tagged fish by subtracting their telemetered river kilometer location from the tributary confluence with the mainstem Thompson River. Thus, negative net movement indicated primarily upstream movement in the Thompson River while positive net movement indicated primarily downstream movement. Cumulative migration distance for radio-tagged Bull

Trout was calculated as the linear difference between the tagging location and the location where the fish was last detected at the end of the study (Starcevich et al. 2012).

Patterns of river use were graphically assessed with kernel density maps (Rogers and White 2007). Kernel density maps of the number of radio-tagged Bull Trout per one river kilometer block were constructed for each week of telemetry data using the R package ‘riverdist’ (Tyers 2016). Weekly relocations of each radio-tagged fish were standardized by randomly selecting one relocation per week to avoid pseudo-replication. As such, individual fish, not the number of weekly relocations, were maintained as the experimental unit of interest (Pollock 1987).

Ripley’s K-function analysis was used to graphically identify patterns of clustering and/or dispersion of radio-tagged Bull Trout in the mainstem Thompson River. A refinement of nearest neighbor analysis, K-function analysis is an estimated index of non-random distribution across a designated spatial scale (Dixon 2002). Thus, a K-function statistic can be defined as the average proportion of additional fish found within a given distance of each individual (Tyers 2016). Weekly K-function analyses were conducted on standardized weekly relocations using code extracted from the ‘riverdist’ package (Tyers 2016). To compare whether the K-statistic distribution for observed fish relocations was different from chance, a confidence envelope of average distances between randomly distributed locations was constructed by iterative bootstrapping (N = 1000). The distribution of radio-tagged Bull Trout were considered to be clustered if the average proportion of fish within a given distance was greater than would be expected from a random distribution (i.e., the observed line extended above the confidence envelope). Conversely, Bull Trout were considered to be dispersed if the average proportion of fish within a given distance were less than that expected from a random distribution (i.e., the line of observed relocation extended below the confidence envelope). Potential bias caused by the staggered entry of radio-tagged fish from two disparate points of origin was negated by only generating K-function plots based on data collected during the final six weeks of the telemetry period.

RESULTS

2014 Field Season

Sample Characteristics

Fifty-three subadult Bull Trout were sampled and PIT-tagged in the West Fork Thompson River in October 2014. The majority of Bull Trout (*N* = 51) were sampled from 3 October to 14 October, and two additional Bull Trout were sampled on 27 October. Bull Trout varied in length from 108 to 276 mm (mean = 180 mm; SD ± 33.5) (Table 1). Acoustically-tagged Bull Trout (*N* = 29) varied from 173 to 276 mm (mean = 201 mm; SD ± 26.6). The average tag- to body-weight ratio of acoustically-tagged Bull Trout varied from 0.63 to 2.87% (mean = 2.01%; SD ± 0.62).

Table 1. Sample size (*N*), total length, weight, and relative condition factor (K_n) descriptive statistics for all subadult Bull Trout sampled from the lower 1.2 river kilometers of the West Fork Thompson River, Montana, from 3 October to 27 October 2014.

		Total length (mm)		Weight (g)		K_n	
Tag type	*N*	Min - Max	Mean (SD)	Min - Max	Mean (SD)	Min - Max	Mean (SD)
PIT-tag only	24	108—174	154 (19.8)	10—39	28 (9.1)	0.90—1.19	1.01 (0.07)
Acoustic	29	173—276	201 (26.6)	37—176	63 (32.6)	0.91—1.18	1.00 (0.07)
Total	53	108—276	180 (33.5)	10—176	47 (30.2)	0.90—1.19	1.00 (0.07)

Out-migration Characteristics

Throughout the autumn and winter, 13.2% of all tagged subadult Bull Trout were detected out-migrating from the West Fork Thompson River into the mainstem Thompson River. Of the out-migrants, only one had an acoustic transmitter. Mean length of out-migrating subadult Bull Trout (mean = 189 mm; SD ± 17.7) was 10 mm greater than the mean length of Bull Trout that remained in the West Fork Thompson River (mean = 178 mm; SD ± 35.3) (Figure 4). However, total length of migratory Bull Trout did not significantly differ from fish remaining in the West Fork Thompson River (W = 114, P = 0.222). Mean relative condition factor of migratory Bull Trout from the West Fork Thompson River (mean = 0.96; SD ± 0.03) was only 0.05 less than that of non-migratory fish (mean = 1.01 mm; SD ± 0.07; Figure 5), but the distributions of each group were non-identical (W = 237.5, P = 0.046).

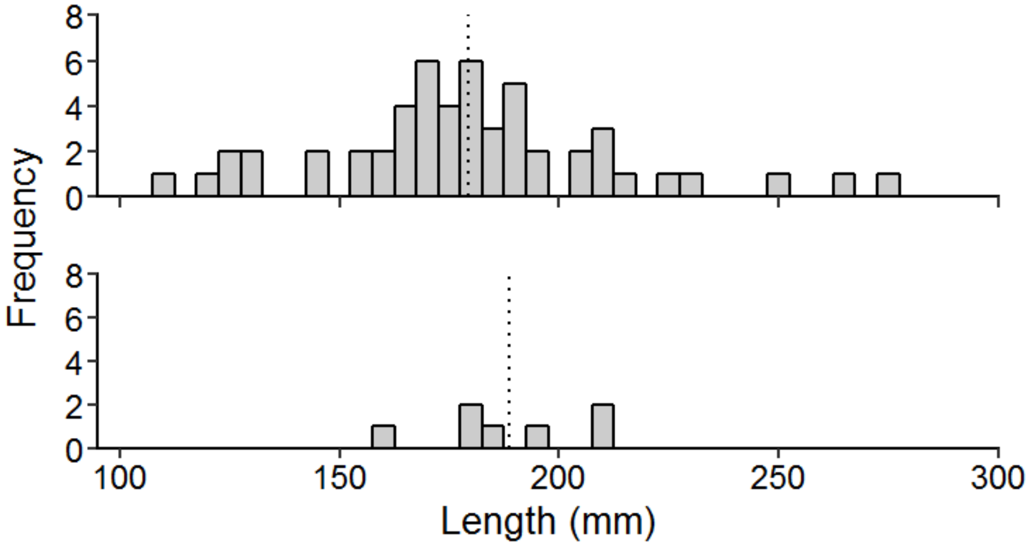

Figure 4. Length frequency of all subadult Bull Trout (top graph; *N* = 53) and Bull Trout that out-migrated (bottom graph; *N* = 7) from the lower 1.2 river kilometers of the West Fork Thompson River, Montana from October through December 2014. Dashed vertical lines delineate the group mean.

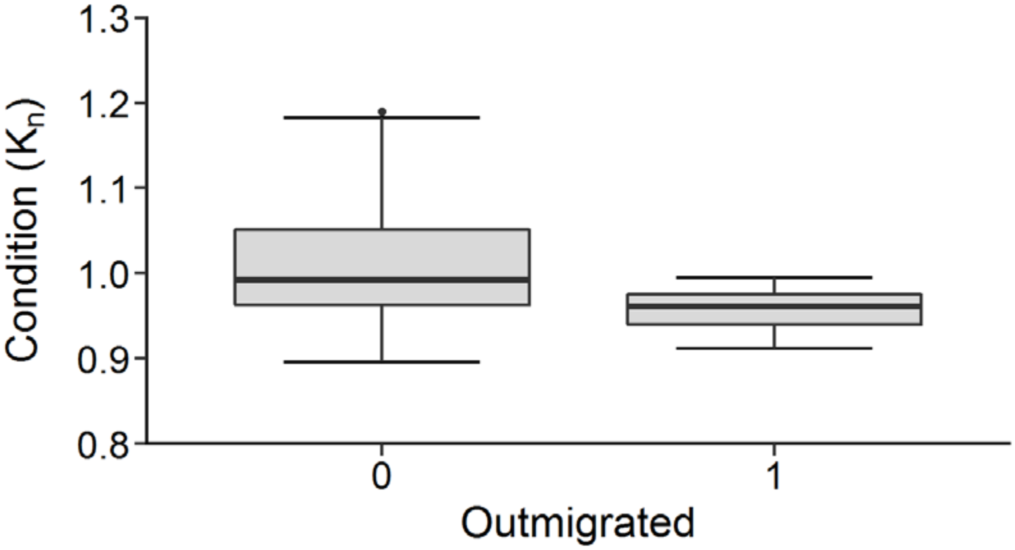

Figure 5. Box plot of realtive condition factor (K_n) for subadult Bull Trout that did not (0; *N* = 46) and did (1; *N* = 7) out-migrate from the lower 1.2 river kilometer of the West Fork Thompson River, Montana from October through December 2014. Horizontal bar within the box delineates the median, box delineates upper and lower quartiles, whiskers delineate largest and smallest values within 1.5 interquartile range of the quartile, and individual points delineate outliers.

Out-migration of subadult Bull Trout from the West Fork Thompson River occurred from 13 October to 5 December. Fifty-percent of the Bull Trout out-migrated from the West Fork Thompson River by 16 October. At a finer scale, the diel distribution of first recorded detections for PIT-tagged Bull Trout that out-migrated into the mainstem Thompson River followed a bimodal diel pattern. Diel out-migration timing from the West Fork Thompson River occurred predominantly during the night (86%). The majority of PIT-tagged Bull Trout were observed out-migrating between 1 and 2 hours after sunset and immediately after midnight with the lowest count occurring from four hours before sunrise to sunset (Figure 6).

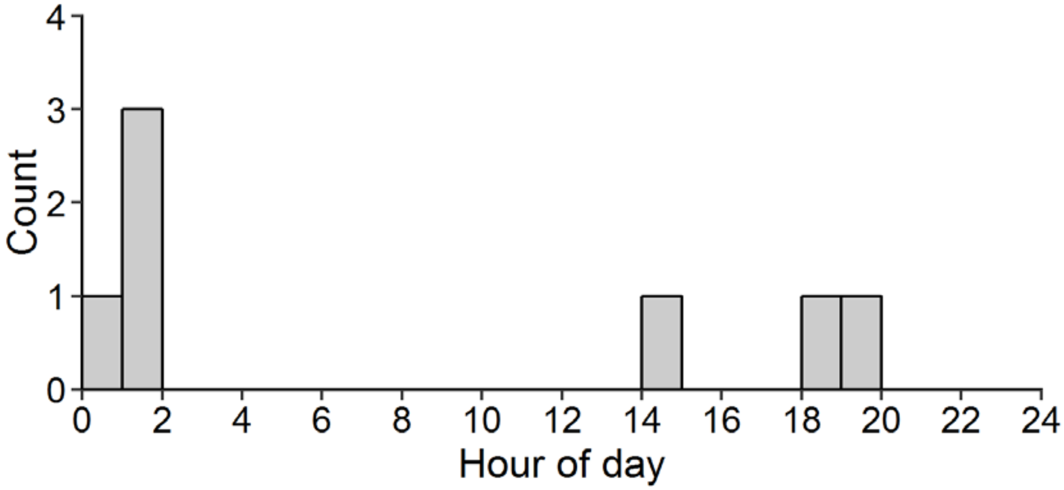

Figure 6. Hour of day associated with time of first detection for all out-migrating subadult Bull Trout (*N* = 7) at the tributary confluence PIT antenna in the West Fork Thompson River, Montana from 13 October to 5 December 2014.

Only one PIT-tagged Bull Trout (161 mm) was detected by the mainstem Thompson River PIT antenna array on 23 October, which represents an estimated minimum migration duration of 8.8 days between the West Fork Thompson antenna and the Thompson River antenna. Tributary out-migration of acoustically-tagged Bull Trout during autumn 2014 was limited (*N* = 3); none of which were detected by the Thompson River PIT antenna array as out-migrating into the reservoir. Furthermore, no Bull Trout were detected by the stationary hydrophone array in Thompson Falls Reservoir.

2015 Field Season

Sample Characteristics

During summer 2015, 566 subadult Bull Trout were PIT-tagged from tributary drainages to the mainstem Thompson River (Table 2). The largest subadult Bull Trout by length was sampled from West Fork Fishtrap Creek, but on average fish from mainstem Fishtrap Creek were larger (Table 2). Total length of Bull Trout PIT-tagged in the Fishtrap Creek drainage ($N = 420$) varied from 100 to 294 mm with a mean of 144 mm (SD ± 27.4), which was 7 mm less than fish sampled from the West Fork Thompson River (Table 2). Length distributions of subadult Bull Trout in the Fishtrap Creek and West Fork Thompson River drainages differed significantly ($t = -2.13$, $df = 564$, P = 0.034) (Figure 7). Subadult Bull Trout sampled from all tributaries in the Fishtrap Creek drainage weighed between 14 to 6 grams less than fish in the West Fork Thompson River. Mean relative condition factor of sampled Bull Trout was consistent among all sampled tributaries with fish from the West Fork Fishtrap Creek exhibiting the largest variability (Table 2). Mean relative condition factor of PIT-tagged Bull Trout did not differ significantly between drainages ($t = -0.003$, $df = 253.8$, P = 0.998).

Table 2. Sample size (*N*), total length, weight, and relative condition factor (K_n) descriptive statistics for subadult Bull Trout sampled in the West Fork Thompson River and Fishtrap Creek tributary drainages to the mainstem Thompson River, Montana from 14 July to 6 August 2015.

		Total length (mm)		Weight (g)		K_n	
Water	*N*	Min - Max	Mean (SD)	Min - Max	Mean (SD)	Min - Max	Mean (SD)
West Fork Thompson River drainage							
WF Thompson River	146	100—277	151 (44.8)	8—183	36 (35.8)	0.84—1.21	1.00 (0.07)
Fishtrap Creek drainage							
Fishtrap Creek	135	103—237	151 (27.2)	9—106	31 (17.7)	0.88—1.17	0.99 (0.06)
WF Fishtrap Creek	139	101—294	143 (34.2)	8—227	29 (27.0)	0.72—1.36	1.01 (0.08)
Beatrice Creek	107	111—243	140 (15.6)	12—110	24 (10.6)	0.85—1.16	1.01 (0.06)
Jungle Creek	39	100—192	137 (21.5)	7—55	22 (10.5)	0.80—1.16	0.96 (0.08)

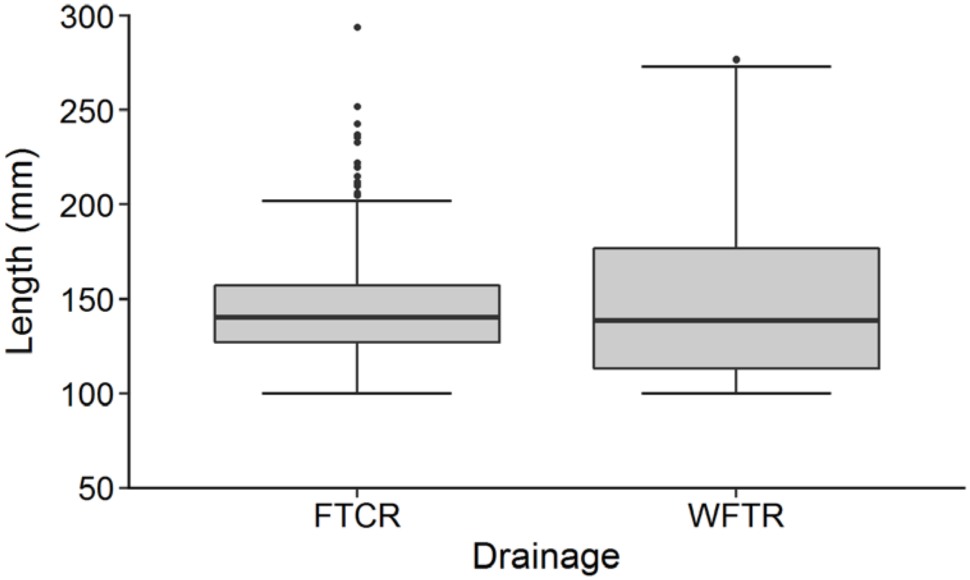

Figure 7. Box plot of total length (mm) for subadult Bull Trout sampled from the Fishtrap Creek drainage (*N* = 420) and West Fork Thompson River (*N* = 146) tributaries to the mainstem Thompson River, Montana, from 14 July to 6 August 2015. Horizontal bar within the box delineates the median, box delineates upper and lower quartiles, whiskers delineate largest and smallest values within 1.5 interquartile range of the quartile, and individual points delineate outliers.

Out-migration Characteristics

Only 11.4% of the Bull Trout PIT-tagged during the summer out-migrated from the Fishtrap Creek drainage, and 6.2% from West Fork Thompson River. Mean total length of out-migrating Bull Trout was slightly longer than all Bull Trout sampled during summer 2015 (Figures 8 and 9). Specifically, mean length of out-migrating PIT-tagged Bull Trout was 16.2 mm (95% CI: 10 – 22 mm) greater and differed significantly from fish that remained in the headwater tributaries ($t = 5.36$, $df = 96.95$, $P < 0.0001$). Total length of out-migrating Bull Trout PIT-tagged during summer 2015 varied from 113 to 199 mm, with 96.5% of out-migrants between 130 to 200 mm. Subadult Bull Trout within the size range most associated with out-migration (i.e., 130 to 200 mm) accounted for 61.4% of all Bull Trout PIT-tagged during summer 2015 (*N* = 566), with 16.4% of fish in this length group having out-migrated. In contrast, only 0.9% of all sampled subadult Bull Trout that were not within the 130 to 200 mm size range (*N* = 218) were detected out-migrating. Coincidentally, the mean total length of weir-sampled Bull Trout from the Fishtrap Creek drainage (*N* = 91) and West Fork Thompson River (*N* = 44) were also slightly larger than Bull Trout initially PIT-tagged during the summer 2015 (Figures 8 and 9). Total length of out-migrating Bull Trout sampled in the weir-traps varied from 115 to 222 mm with a mean of 165 mm (SD ± 20.6) in Fishtrap Creek, and 132 to 276 mm with a mean of 171 mm (SD ± 26.4) in the West Fork Thompson River (Table 3). Few Bull Trout from the summer sampling were recaptured by weir trapping in the Fishtrap Creek drainage (*N* = 5) and West Fork Thompson River (*N* = 2). There was no significant difference between the relative condition at time of tagging for Bull Trout that eventually out-migrated and those that did not out-migrate ($t = 0.263$, $df = 65.7$, $P = 0.794$). However, mean K_n of all Bull Trout PIT-tagged in summer and recaptured out-migrating in the autumn weir-trapping (*N* = 8; mean = 0.86; SD ± 0.06) was 0.17 lower than the overall mean K_n at time of tagging (mean = 1.03; SD ± 0.07). Despite this, no fish that remained in the tributary drainages were recaptured in the autumn to generate seasonal K_n comparisons.

Table 3. Sample size (*N*), length, weight, and relative condition factor (K_n) descriptive statistics by tag type for out-migrating subadult Bull Trout sampled using weir traps in the West Fork Thompson River and Fishtrap Creek tributary drainages to the mainstem Thompson River, Montana from 22 September to 12 November 2015.

		Total length (mm)		Weight (g)		K_n	
Tag type	*N*	Min - Max	Mean (SD)	Min - Max	Mean (SD)	Min - Max	Mean (SD)
West Fork Thompson River							
PIT-tag only	29	132—186	158 (13.1)	17—46	28 (6.6)	0.74—0.94	0.85 (0.05)
Acoustic	10	173—222	187 (13.4)	38—72	46 (10)	0.80—0.90	0.85 (0.03)
Radio	5	192—276	219 (33.4)	49—140	78 (36.7)	0.83—1.03	0.89 (0.08)
Total	44	132—276	171 (26.4)	17—140	38 (21.2)	0.74—1.03	0.85 (0.05)
Fishtrap Creek							
PIT-tag only	64	115—193	154 (13.2)	11—49	26 (6.1)	0.74—1.05	0.85 (0.07)
Acoustic	18	170—222	188 (14.3)	34—76	48 (12.5)	0.82—1.07	0.88 (0.05)
Radio	9	176—204	190 (11.6)	38—67	50 (10.8)	0.82—0.98	0.88 (0.05)
Total	91	115—222	165 (20.6)	11—76	33 (13.2)	0.74—1.07	0.85 (0.06)

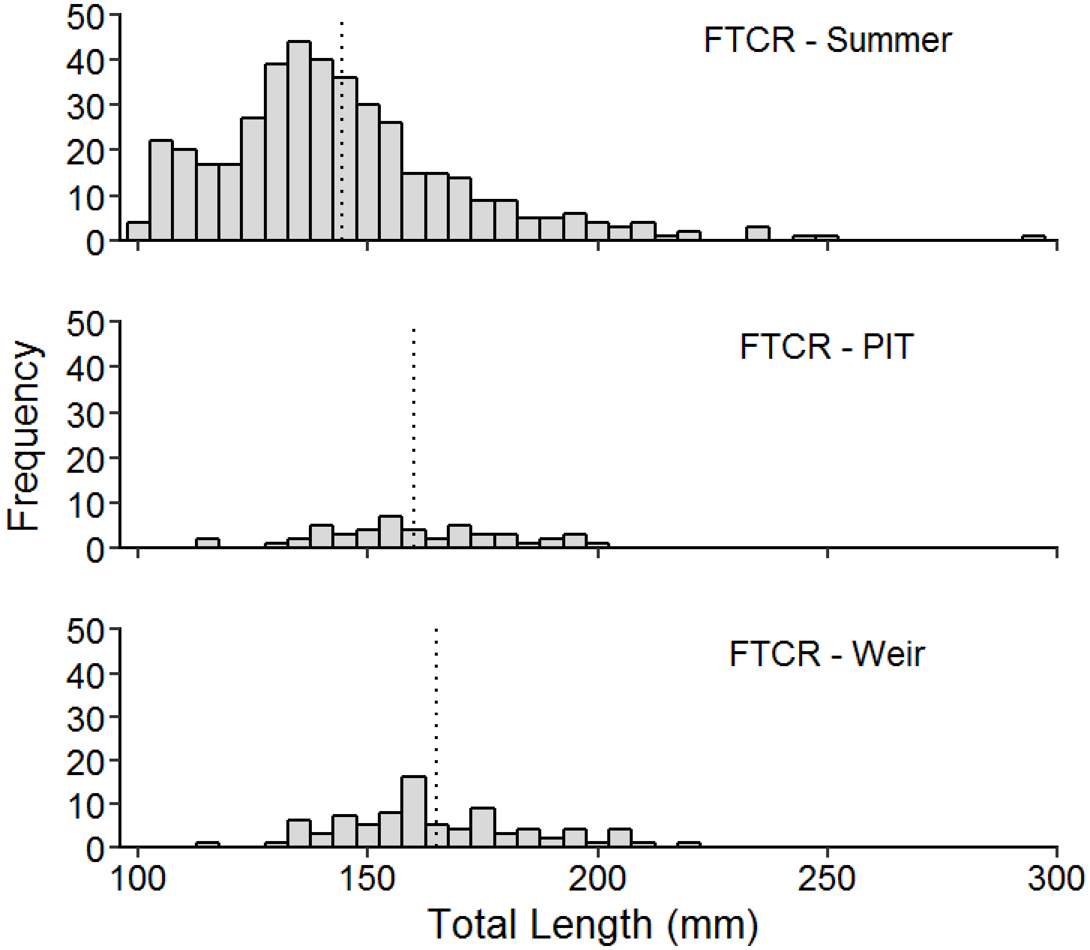

Figure 8. Fishtrap Creek drainage length-frequency histograms for subadult Bull Trout PIT-tagged during the summer (FTCR – Summer), all out-migrants detected at the confluence PIT reader (FTCR – PIT), and out-migrants sampled in weir traps (FTCR - Weir) in 2015. Dashed vertical lines delineate the group mean.

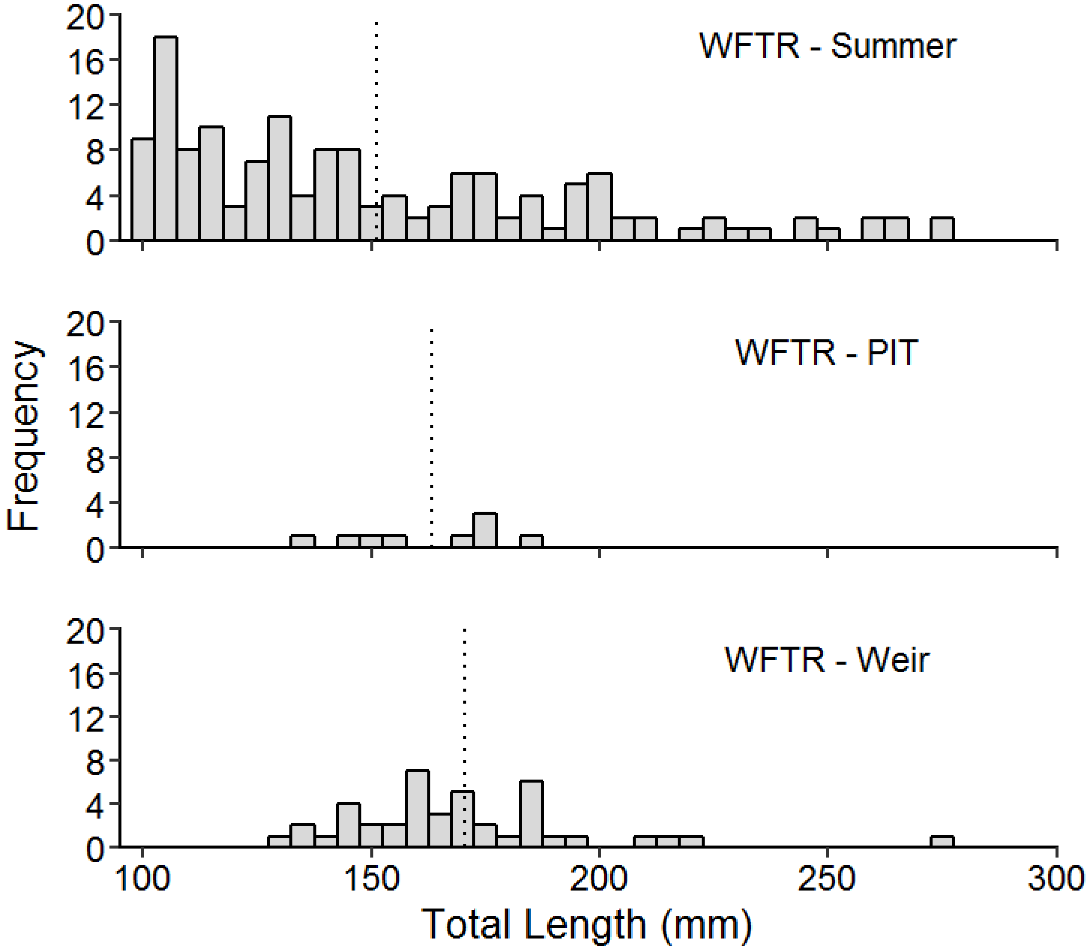

Figure 9. West Fork Thompson River length-frequency histograms for subadult Bull Trout PIT-tagged during the summer (WFTR – Summer), all out-migrants detected at the confluence PIT reader (WFTR – PIT), and out-migrants sampled in weir traps (WFTR - Weir) in 2015. Dashed vertical lines delineate the group mean.

Total length influenced the probability of out-migration from the Thompson River tributary drainages and the effect of total length was negatively parabolic. Relative condition and the interaction between length and K_n were not significant in either preliminary model ($P > 0.05$). Coefficient estimates for the model output associated with Fishtrap Creek out-migration were: $\beta_1 = 1.41$ TL (95% CI: 1.21 to 1.73) and $\beta_2 = 0.9990$ TL^2 (95% CI: 0.9984 to 0.9995). Coefficient estimates for the model output associated with West Fork Thompson River out-migration were: β_1 = 2.49 TL (95% CI: 1.38 to 6.81) and β_2 = 0.9972 TL^2 (95% CI: 0.9941 to 0.9990). The highest probability of Bull Trout out-migration was predicted to occur at a total length of 179 mm in Fishtrap Creek and 165 mm in West Fork Thompson River (Figure 10). Model prediction estimated a maximum subadult Bull Trout out-migration probability of 30.4% (95% CI: 21.5 to 41.0) in the Fishtrap Creek drainage and 29.3% (95% CI: 13.7 to 52.1) in West Fork Thompson River (Figure 10). Interestingly, the predicted probability of tributary out-migration associated with the observed mean length of weir-sampled Bull Trout in Fishtrap Creek (165 mm) was 26.7% and in the West Fork Thompson River (171 mm) was 27.3%.

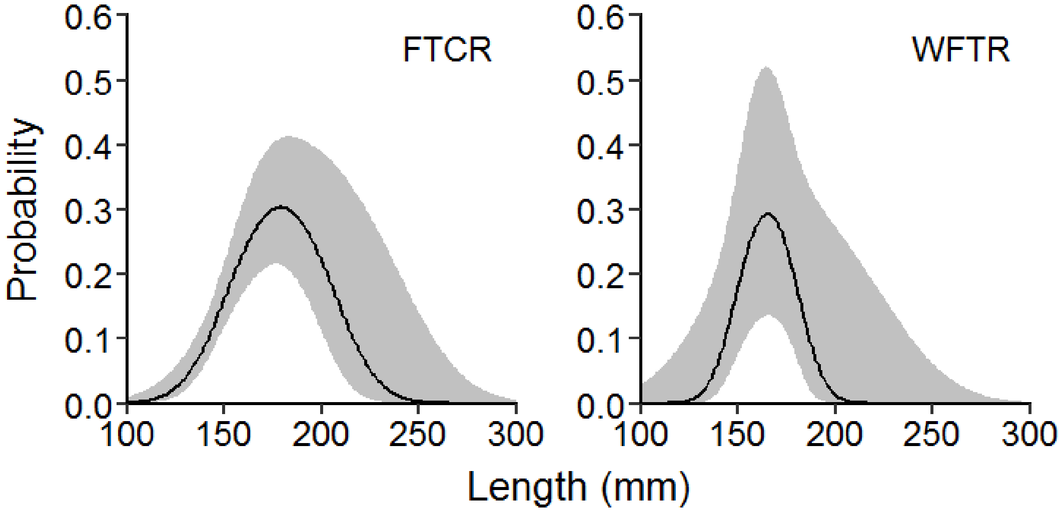

Figure 10. Predicted probability (black line) and associated 95% confidence intervals (grey band) of out-migration for subadult Bull Trout from the Fishtrap Creek (FTCR) drainage and West Fork Thompson River (WFTR), Montana in 2015.

Out-migration of subadult Bull Trout occurred from 8 August to 12 December in the Fishtrap Creek drainage and from 4 September to 13 December in West Fork Thompson River. The median date of Bull Trout out-migration was 10 October in the

Fishtrap Creek drainage and 18 October in West Fork Thompson River (Figure 11). At a finer scale, detections for PIT-tagged Bull Trout followed an approximately bimodal diel pattern. Diel timing of fluvial out-migration occurred primarily at night in the Fishtrap Creek (95.8%) and West Fork Thompson River (88.9%) drainages (Figure 12). The lowest observed counts of out-migrating Bull Trout occurred from sunrise to immediately before sunset, whereas the highest counts primarily occurred from 1 to 3 hours after sunset to immediately before sunrise.

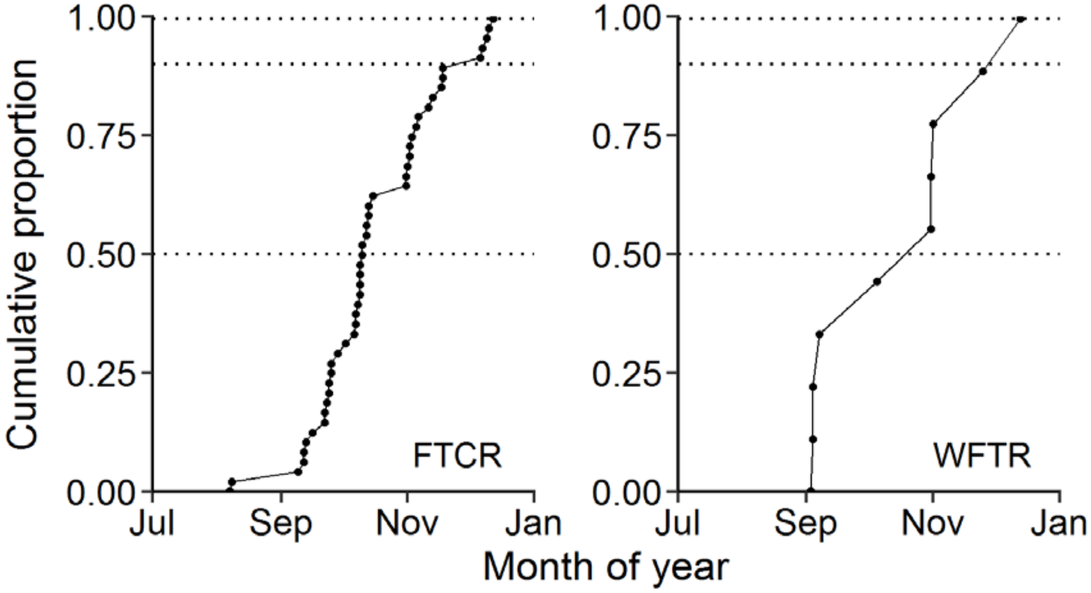

Figure 11. Cumulative proportion of subadult Bull Trout that out-migrated into the mainstem Thompson River after being PIT-tagged during the summer in Fishtrap Creek (FTCR; *N* = 48) and West Fork Thompson River (WFTR; *N* = 9), Montana from 8 July to 12 December 2015. Dotted horizontal lines indicate the points at which 50%, 90%, and 100% of fish out-migrated.

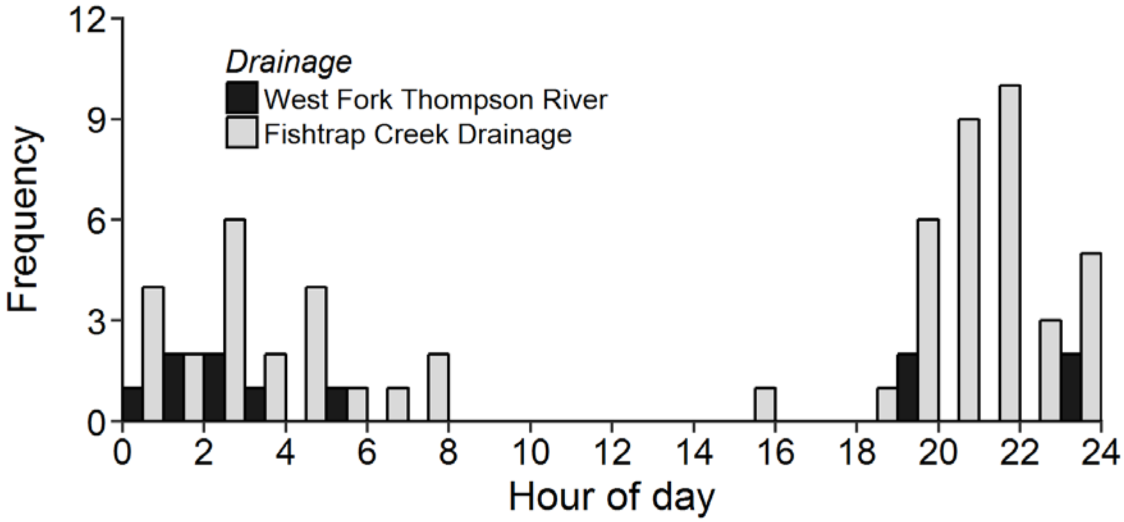

Figure 12. Diel timing of fluvial out-migration for PIT-tagged subadult Bull Trout from tributary drainages to the mainstem Thompson River, Montana from 8 July to 12 December 2015.

Of all Bull Trout that out-migrated (i.e., were detected at a tributary PIT antenna or sampled by weir-trap) into the mainstem Thompson River (*N* = 192), only 13.5% further out-migrated into Thompson Falls Reservoir. Specifically, only 0.7% of all out-migrants PIT-tagged in the summer (*N* = 57) and 16.3% of all out-migrants sampled at the weir-traps (*N* = 135) were detected at the mainstem Thompson River PIT antenna prior to 31 December. While all PIT-detected tributary out-migrants that entered the reservoir (*N* = 4) originated from the Fishtrap Creek drainage, 68.2% of weir-sampled Bull Trout that entered the reservoir (*N* = 22) had originated from the West Fork Thompson River.

The mean total length of Bull Trout sampled in each of the tributary drainage weir traps that further out-migrated into Thompson Falls Reservoir were similar. Bull Trout out-migrating from the mainstem Thompson River that originated in the Fishtrap Creek weir trap varied from 134 to 211 mm with a mean of 163 mm (SD ± 24.4) while fish originating in the West Fork Thompson River weir trap varied from 136 to 192 mm with a mean of 161 mm (SD ± 16.2).

Out-migration into Thompson Falls Reservoir occurred from 11 October to 22 December 2015. Median date of adfluvial out-migration for all Bull Trout that entered the mainstem Thompson River was 8 December (Figure 13). Out-migration primarily occurred at night (96.2%) from the mainstem Thompson River. The lowest observed counts of out-migrating Bull Trout occurred from sunrise to just before sunset, whereas the highest counts primarily occurred from 2000—0800 hours (Figure 14). A slight peak in the diel timing of out-migration into Thompson Falls Reservoir occurred between 2 and 3 hours after midnight.

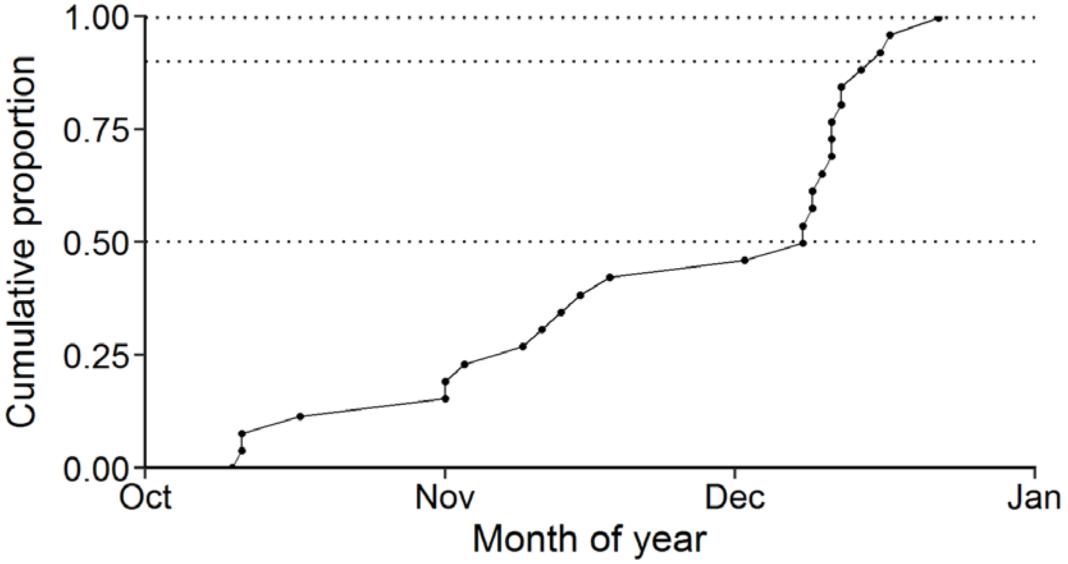

Figure 13. Cumulative proportion of all subadult Bull Trout (*N* = 26) that were detected by the mainstem Thompson River PIT antenna as out-migrating from the mainstem Thompson River, Montana, 2015. Dotted horizontal lines indicate the points at which 50%, 90%, and 100% of fish out-migrated.

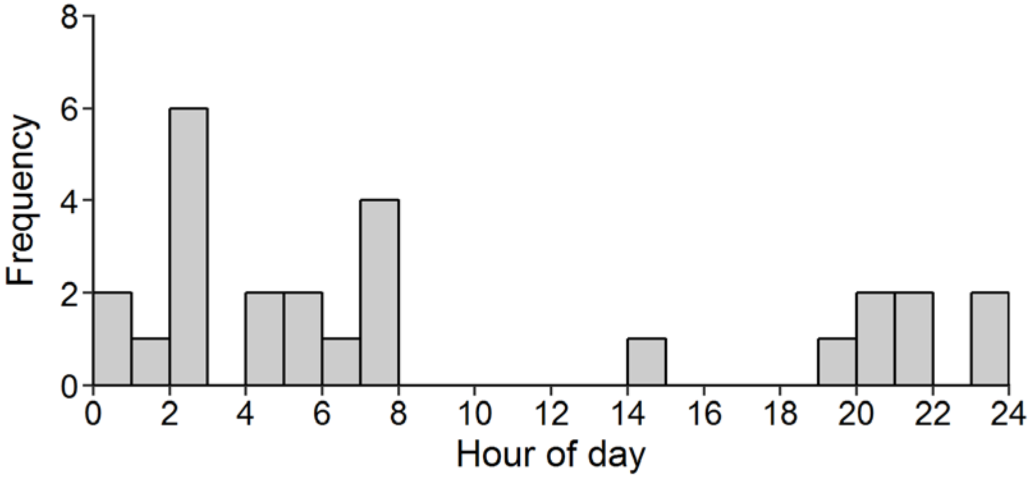

Figure 14. Diel timing of out-migration for PIT-tagged subadult Bull Trout from the mainstem Thompson River, Montana, from October to December 2015.

Abiotic Cues to Out-migration

The number of out-migrating Bull Trout in the Thompson River drainage was probably influenced by several abiotic factors that differed among tributary drainages and the mainstem Thompson River. Candidate model development for the Fishtrap Creek drainage was restricted to four predictor variables per model because of the moderate number of observed out-migrants from that tributary (*N* = 48). The top AICc-ranked model for the Fishtrap Creek drainage provided evidence of an association between the odds of out-migration and water temperature, lunar illumination, and atmospheric pressure (Table 4). While a drop in deviance test suggests that the preferred model fits the data well ($P = 0.912$), the estimated pseudo – r^2 value indicates that the model explains only 25% of the variation in the number of Fishtrap Creek drainage out-migrants. Thus, there was weak evidence that median water temperature ($Z = 3.69$, $P = 0.0002$), the square of median water temperature ($Z = -3.75$, $P = 0.0001$), proportion of lunar illumination ($Z = -2.15$, $P = 0.032$), and minimum atmospheric pressure ($Z = -1.94$, $P =$

0.050) influenced the odds of out-migration from the Fishtrap Creek drainage. Nevertheless, the combined effect of these abiotic factors is evident during when median water temperatures varied between 2.9 and 8.3 °C and periods of low lunar light occurred during a decrease in minimum atmospheric pressure (Figure 15). Specifically, the odds of out-migration from the Fishtrap Creek drainage increased by a factor of 16.12 (95% CI: 4.29—83.67) for every 1° C increase in median temperature above 0° C (although the negative squared term indicates that the effect of temperature declined by a factor of 0.80 [95% CI: 0.70—0.89] as median water temperature increased), to decrease by a factor of 0.37 (95% CI: 0.14—0.89) with increased lunar illumination, and to decrease by a factor of 0.61 (95% CI: 0.37—1.01) for higher values of minimum atmospheric pressure (Table 4). The inclusion of median temperature, the square of median temperature, and lunar illumination in each of the top four models of out-migration from Fishtrap Creek highlights the importance of these variables (Table 4).

Table 4. Summary of top-ranked Poisson regression models describing abiotic variables associated with the daily count of PIT-tagged subadult Bull Trout detected out-migrating from the Fishtrap Creek drainage, Montana, from July through December 2015. Variables include: model rank, sample size (*N*), median water temperature (T_{med}) in °C, square of median temperature (T^2_{med}) in °C, proportion of illuminated lunar surface (lunar), minimum atmospheric pressure (Ψ_{min}) in kPa, median calculated gage height ($\hat{G}_{med}$) in cm, 24-hour change in median gage height ($\Delta \hat{G}_{med}$) in cm. Model fit statistics include: estimated pseudo – r^2 value ($\sim r^2$), small-sample size corrected Akaike's information criterion value (AICc), difference in AICc from the preferred model (Δ AICc). Dash indicates that an independent variable was not included in the model.

			β						Model Fit			
Model	*N*	Intercept	T_{med}	T^2_{med}	Lunar	Ψ_{min}	$\hat{G}_{med}$	$\Delta \hat{G}_{med}$	df	$\sim r^2$	AICc	ΔAICc
1	48	37.27	2.78	– 0.22	– 1.01	– 0.50	-	-	5	0.25	186.86	0.00
2	48	– 12.62	3.05	– 0.25	– 0.98	-	0.11	-	5	0.24	187.73	0.87
3	48	– 7.95	2.61	– 0.21	– 1.04	-	-	0.09	5	0.24	188.21	1.35
4	48	– 7.25	2.40	– 0.20	– 1.05	-	-	-	4	0.22	188.43	1.57

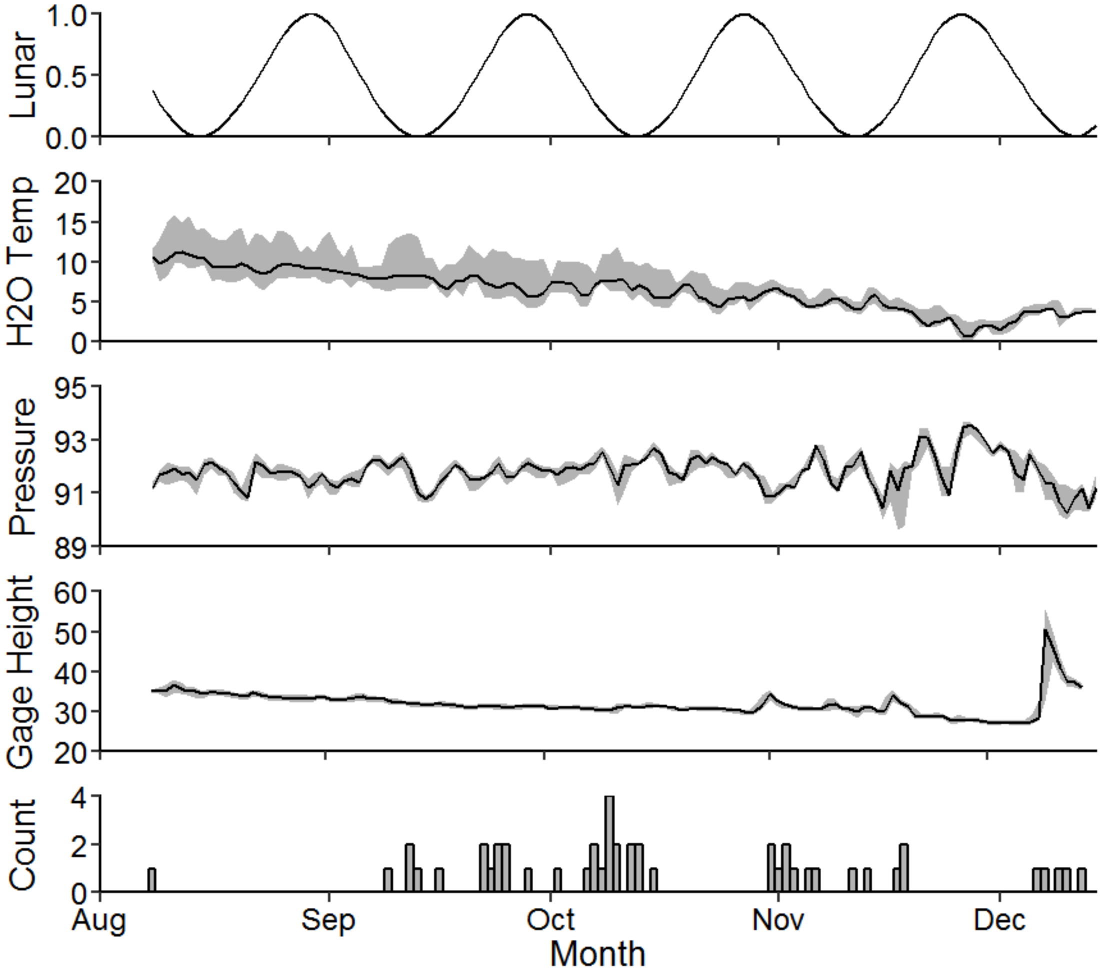

Figure 15. Abiotic factors associated with the top-ranked Poisson regression models for the daily count of PIT-tagged subadult Bull Trout (*N* = 48) detected out-migration from the Fishtrap Creek drainage, Montana, 8 August to 12 December. Abiotic factors include the proportion of lunar illumination, water temperature (°C), atmospheric pressure (kPa), and gage height (cm). Solid black line in water temperature, atmospheric pressure, and gage height graphs indicate the median and the grey bands delineate the minimum and maximum values.

Candidate model development for the West Fork Thompson River was restricted to one predictor variable per model because of the low number of observed out-migrants (*N* = 9). The top AICc-ranked model of the number of out-migrants from the West Fork Thompson River provided evidence that maximum atmospheric pressure (Z = –2.33, P =

0.020) was associated with the odds of out-migration (Table 5). Although a drop in deviance test suggests that this model fits the data well (P = 0.998), the estimated pseudo $-r^2$ value indicates that maximum atmospheric pressure explains only 11% of the variation in the number of West Fork Thompson River out-migrants. Specifically, the number of out-migrating Bull Trout decreased by a factor of 0.22 (95% CI: 0.06—0.77) with increased values of maximum daily atmospheric pressure (Table 5). Additional abiotic factors in the top-ranked models included median atmospheric pressure, maximum daily gage height (cm), and daily change in maximum daily gage height (cm) (Table 5). The effect of atmospheric pressure and gage height are evident during the first week of November when a period of low pressure occurred in conjunction with increased water levels (Figure 16).

Table 5. Summary of top-ranked Poisson regression models describing abiotic variables associated with the daily count of PIT-tagged subadult Bull Trout detected out-migrating from the West Fork Thompson River, Montana, from July through December 2015. Table includes: model rank, sample size (*N*), maximum atmospheric pressure (Ψ_{max}) in kPa, median atmospheric pressure (Ψ_{med}) in kPa, maximum calculated gage height ($\hat{G}_{max}$) in cm, 24-hour change in maximum gage height ($\Delta\hat{G}_{max}$) in cm. Model fit statistics include: estimated pseudo$-r^2$ value ($\sim r^2$), small-sample size corrected Akaike's information criterion value (AICc), difference in AICc from the preferred model (Δ AICc). Dash indicates that an independent variable was not included in the model.

			β				Model Fit			
Model	*N*	Intercept	Ψ_{max}	Ψ_{med}	$\hat{G}_{max}$	$\Delta\hat{G}_{max}$	df	$\sim r^2$	AICc	ΔAICc
1	9	138.50	– 1.53	-	-	-	2	0.11	66.90	0.00
2	9	94.95	-	– 1.06	-	-	2	0.07	68.94	2.04
3	9	-5.29	-	-	0.09	-	2	0.05	69.96	3.06
4	9	-2.72	-	-	-	0.13	2	0.04	70.6	3.69

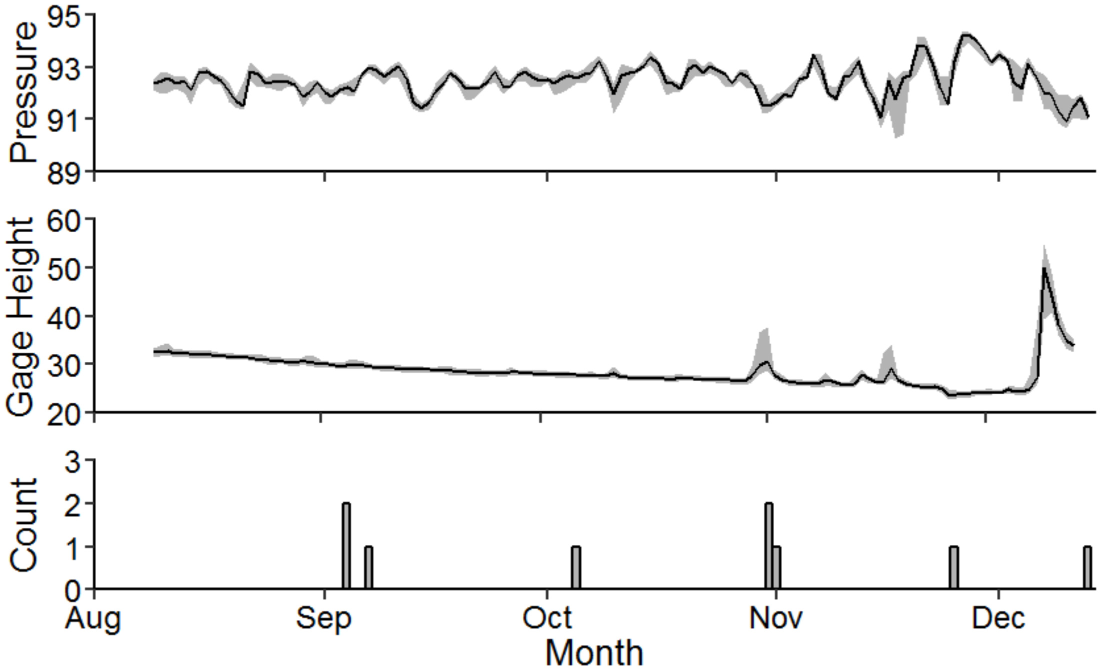

Figure 16. Abiotic factors associated with the top-ranked Poisson regression models for the daily count of PIT-tagged subadult Bull Trout (*N* = 9) detected out-migration from the West Fork Thompson River, Montana, 8 August to 12 December. Abiotic factors include atmospheric pressure (kPa) and gage height (cm). Solid black line in atmospheric pressure and gage height graphs indicate the median parameter values while grey bands delineate the range of minimum and maximum parameter values.

Candidate model development for mainstem Thompson River out-migration was restricted to two abiotic predictor variables per model because of the low number of observed out-migrants (*N* = 26). The top AICc-ranked model of the number of out-migrants from the mainstem Thompson River included the proportion of lunar illumination and minimum atmospheric pressure as predictor variables (Table 6). Although a drop in deviance test suggests that the preferred model fits the data well (P = 0.978), the estimated pseudo – r^2 value suggests that the model explains only 36% of the variation in the number of out-migrants. Thus, there was only moderate evidence that minimum atmospheric pressure (Z = – 3.348, P = 0.0008) and the proportion of lunar illumination (Z = – 2.40, P = 0.016) influenced the odds of out-migration from the mainstem Thompson River. Specifically, coefficient estimates suggest that the number of out-migrants decreased by a factor of 0.38 (95% CI: 0.21—0.67) with increased values of minimum atmospheric pressure and decreased by a factor of 0.10 (95% CI: 0.01—0.52) with increased amounts of lunar illumination (Table 6). Correspondingly, out-migration increased during each month of the study when low minimum atmospheric pressure occurred simultaneously with low lunar light (Figure 17). Mean and maximum daily discharge (m^3/sec) were also abiotic factors found in the top-ranked models (Table 6). The combined effect of abiotic factors found in the top-ranked models is particularly evident during the second week of December when a decrease in minimum atmospheric pressure occurred during a period of low lunar light and increased discharge (Figure 17).

Table 6. Summary of top-ranked Poisson regression models describing abiotic variables associated with the daily count of PIT-tagged subadult Bull Trout detected out-migrating from the mainstem Thompson River, Montana, from July through December 2015. Table includes: model rank, sample size (*N*), proportion of lunar illumination (Lunar), minimum atmospheric pressure (Ψ_{min}) in kPa, maximum atmospheric pressure (Ψ_{max}) in kPa, mean discharge (Q_{mean}) in m^3/sec, maximum discharge (Q_{max}) in m^3/sec. Model fit statistics include: estimated pseudo−r^2 value (~ r^2), small-sample size corrected Akaike's information criterion (AICc), difference in AICc from the preferred model (Δ AICc). Dash indicates that an independent variable was not included in a model.

			β					Model Fit			
Model	*N*	Intercept	Lunar	Ψ_{min}	Ψ_{max}	Q_{mean}	Q_{max}	df	~ r^2	AICc	ΔAICc
1	23	88.47	– 2.42	– 0.97	-	-	-	3	0.36	88.13	0.00
2	23	108.50	– 2.32	-	– 1.18	-	-	3	0.34	89.47	1.34
3	23	79.88	-	– 0.89	-	0.20	-	3	0.31	91.97	3.85
4	23	79.73	-	– 0.89	-	-	0.15	3	0.31	92.06	3.93

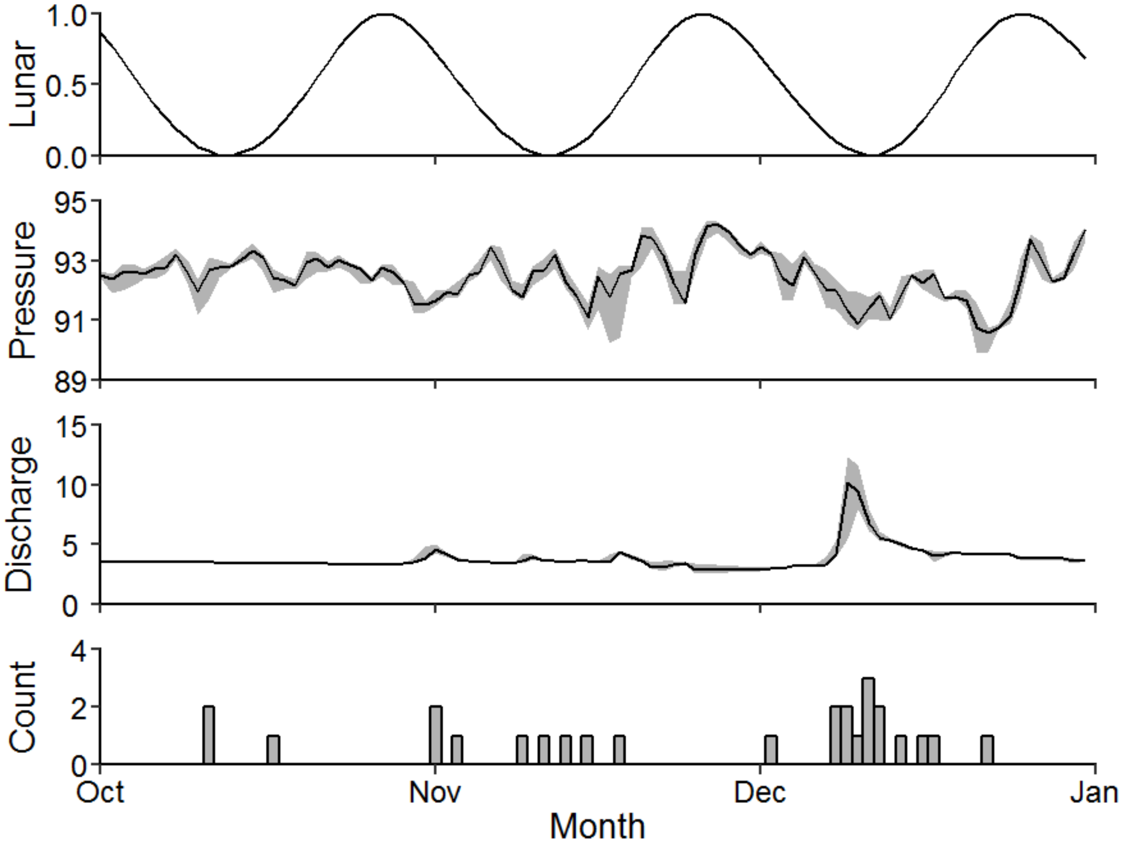

Figure 17. Abiotic factors associated with the top-ranked Poisson regression models for the daily count of PIT-tagged subadult Bull Trout (*N* = 26) detected out-migration from the mainstem Thompson River, Montana, 1 October to 31 December 2015. Abiotic factors include proportion of lunar illumination, atmospheric pressure (kPa), and discharge (m^3/sec). Solid black line in atmospheric pressure and discharge graphs indicates the median parameter value while grey bands delineate the range of minimum and maximum parameter values.

Movement Characteristics and Survival

Movement of radio-tagged Bull Trout in the mainstem Thompson River was almost exclusively downstream (Figure 18). Upstream movements were limited to less than 195 m and occurred only after periods of downstream movement. The majority of Bull Trout that survived until the end of the telemetry period (*N* = 9) moved between 3.9 and 10.9 km (mean = 6.9; SD ± 2.8). One fish tagged at the Fishtrap Creek drainage remained within 1 rkm of the confluence. Mean maximum distance moved varied between Bull Trout from the Fishtrap Creek drainage (mean = 4.5 rkm, SD ± 3.5) and West Fork Thompson River (mean = 7.5 rkm, SD ± 2.6).

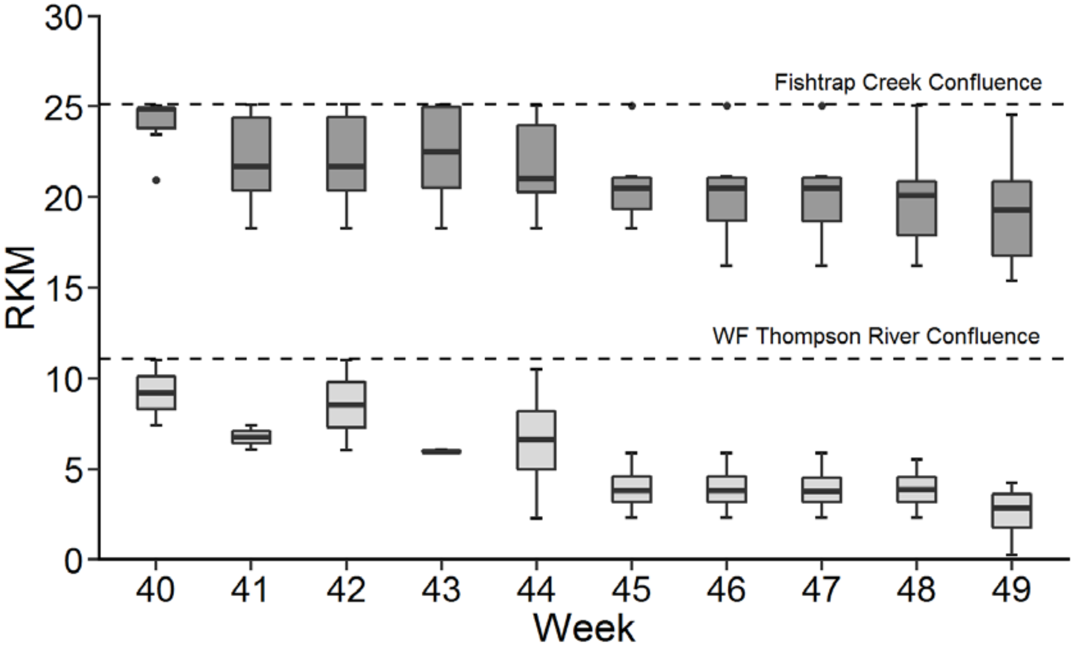

Figure 18. Distribution of radio-tagged subadult Bull Trout relocations by river kilometer (RKM) within the mainstem Thompson River by week of year (week 40 starts on 5 October 2015). Dashed horizontal lines delineate the RKM associated with identified tributary confluences. Radio-tagged Bull Trout from Fishtrap Creek and West Fork Thompson River did not intermix and remained downstream of the respective tributary-of-origin.

Mean movement rate for all radio-tagged Bull Trout, regardless of natal origin, was 0.18 km/day (SD ± 0.68). Mean rate of movement for Bull Trout originating from the Fishtrap Creek drainage was 0.14 km/day (SD ± 0.58) and mean rate of movement for fish originating from the West Fork Thompson River was 0.27 km/day (SD ± 0.85). Incremental downstream movement between stationary periods varied from 0.3 to 6.2 km with a mean of 2.9 km (SD ± 1.9). Number of days with nearly sedentary activity (< 200 m between relocations) varied from 1 to 76 with a mean of 21.0 days (SD ± 22.4).

Weekly kernel density maps indicated that the majority of fish originating from the West Fork Thompson River were located between rkm 1.7 and 6.7 of the mainstem Thompson River while radio-tagged Bull Trout originating from Fishtrap Creek drainage were predominantly located between rkm 15.1 and 23.3 (Figure 19). No radio-tagged Bull Trout were relocated between rkm 10.9 (West Fork Thompson River confluence) and rkm 15.2. Low movement rates and high site fidelity resulted in the distribution varying little over the final five weeks of the study (Figure 19). Consequently, 90% of the Bull Trout that survived until the end of the telemetry period (*N* = 10) remained in the mainstem Thompson River.

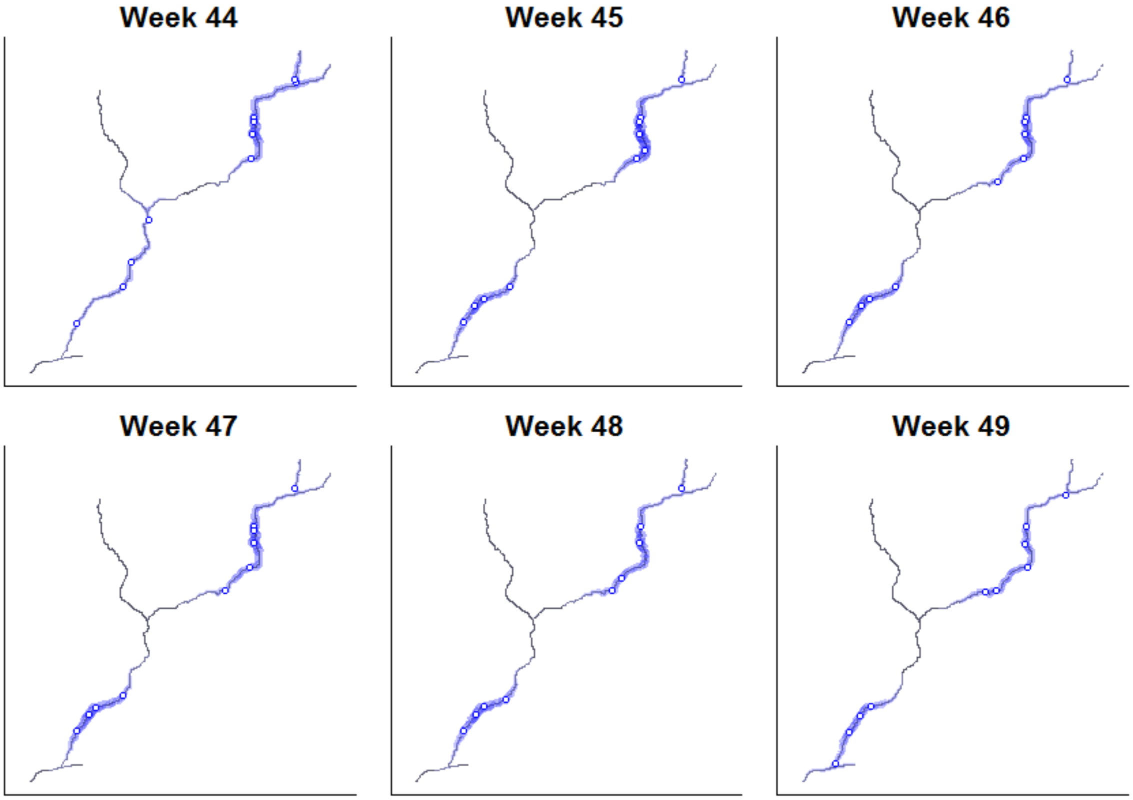

Figure 19. Kernel-density plots illustrating relocations of radio-tagged subadult Bull Trout in the Thompson River drainage during weeks 44 through 49 of 2015, with the start of week 44 corresponding to 2 November. Ten fish were tracked each week.

Despite the appearance of two clustered groups in the kernel-density plots (Figure 19), weekly K-function analyses indicated the observed distribution of all radio-tagged Bull Trout exhibited a random dispersion pattern (Figure 20). The overall lack of clustering observed among tagged Bull Trout, and the sporadic detections of out-migration at the Thompson River PIT antenna, suggest that Bull Trout in the Thompson River drainage do not exhibit concentrated pulses of out-migration.

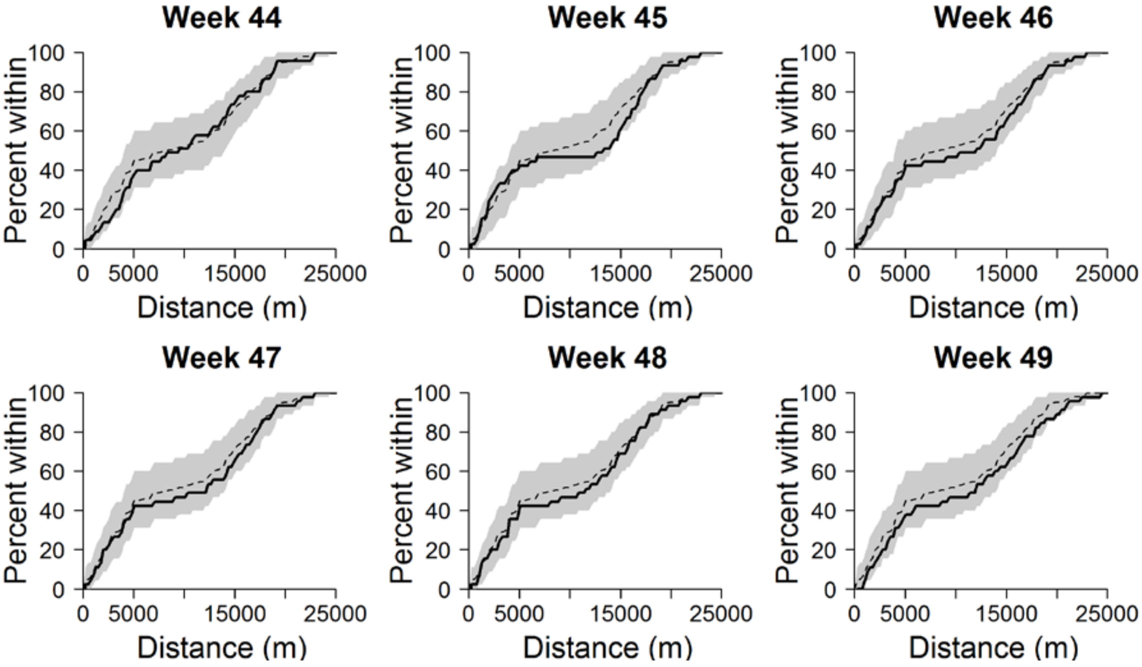

Figure 20. Ripley’s K-function plots of the percent of additional subadult Bull Trout in the Thompson River drainage that are within a given distance of each other from week 44 through 49 of the 2015 telemetry period—week 44 corresponds to 2 November. Ten fish were tracked each week.

Radio-tagged Bull Trout survival was 71.4% during the tracking period in the mainstem Thompson River. All recovered mortalities of Bull Trout that originated in the Fishtrap Creek drainage (*N* = 3) were recovered within 2.6 rkm of the tributary confluence. One radio-tagged Bull Trout mortality that originated from the West Fork Thompson River was recovered 3.7 rkm from the tagging location. All recovered Bull Trout mortalities (*N* = 4) showed direct (i.e., teeth marks) and indirect (i.e., chewed radio antennae, cache site, scat, foot print) evidence of American Mink *Neovison vison* predation. Incidentally, systematic searches conducted in areas of known Bull Trout mortality with a handheld PIT antenna yielded the remains of 12 additional fish with evidence of predation by mink, including untagged Bull Trout (*N* = 6), previously PIT-tagged Bull Trout (*N* = 2), Rainbow Trout (*N* = 2), and Brook Trout (*N* = 1).

DISCUSSION

Contrary to the predictions related to the objectives, the assessment of subadult Bull Trout out-migration characteristics and movement patterns indicates that few subadult Bull Trout emigrated from Thompson River tributary drainages and the mainstem Thompson River. Additionally, predicted probability of out-migration was marginal for Bull Trout of all sizes in the Thompson River drainage. Low probability of out-migration for fish of all lengths, in conjunction with observed spatial overlap between fish with migratory and resident life-history strategies, indicates that relying on size alone is not a good predictor of whether subadult Bull Trout in the Thompson River drainage will out-migrate. For Bull Trout that did out-migrate, peak out-migration was observed in the tributary drainages during October and in the mainstem Thompson River during December, and out-migration predominantly occurred at night. Furthermore, the majority of telemetered Bull Trout remained in the mainstem Thompson River, with out-migration into to the reservoir occurring only sporadically and with no indication of clustering.

Few PIT-tagged Bull Trout were detected out-migrating from the Thompson River tributaries, with only 13.2 % in 2014 and 10.1% in 2015. These findings are consistent with the lower end of estimates generated by a multi-year study of Bull Trout in the South Fork Walla Walla River of northeastern Oregon, which found that proportions of fluvial out-migration among the subadult size range varied from 12 – 23% (Al-Chokhachy and Budy 2008). At a finer scale, the proportion of PIT-tagged Bull Trout that out-migrated into the mainstem Thompson River in 2015 was slightly higher in the Fishtrap Creek drainage than West Fork Thompson River and corroborates the observation of minimal out-migration from the West Fork Thompson River in 2014. Previous studies in the region have also documented the existence of a largely resident population of Bull Trout in the West Fork Thompson River (Liermann 2003; Zymonas 2006) and a subset of the headwater tributaries to the Fishtrap Creek drainage (Huston 1994). Thus, both resident and migratory life-history strategies are probably present among Bull Trout of the Thompson River drainage.

Size alone was an insufficient predictor of whether Bull Trout would out-migrate from the tributary drainages and was probably confounded by other factors. Although Bull Trout towards either end of the subadult size classification (100–300 mm) were less likely to out-migrate than intermediately sized fish (160–180 mm), the maximum predicted probability of out-migration was always less than 52.1% (the upper bound of 95% confidence interval) regardless of size. Similarly, Al-Chokhachy and Budy (2008) found that Bull Trout in the 171 to 220 mm size range made up the highest proportion of subadult out-migrants in an assessment conducted in northeastern Oregon. Delayed emigration by smaller fish is most likely an adaptation for increased survival, while reduced emigration by larger subadult Bull Trout (> 200 mm) is probably attributable to the expression of a residential life-history strategy (Goetz 1989; Al-Chokhachy and Budy 2008). These results are similar to those reported in previous studies of Bull Trout in the Thompson River tributaries (Zymonas 2006) and the Rocky Mountain West (Rieman and McIntyre 1993; Goetz 1989; Al-Chokhachy and Budy 2008), which found that fish adhering to a resident life-history strategy rarely exceed 300 mm with some fish reaching sexual maturity by 152 – 178 mm (Huston 1994).

Relative condition was generally lower for out-migrating Bull Trout, particularly among fish assessed in 2014 and those sampled in the 2015 autumn weir sampling. While there was no significant difference between relative condition of migratory and resident Bull Trout at the time of tagging in 2015, relative condition values throughout the autumn weir-trapping were, on average, lower than those estimated for the population in summer (i.e., when resources are characteristically abundant and relative condition was probably highest). Previous assessments of salmonid species in similarly oligotrophic environments suggest that emigration may occur in conjunction with decreased individual size or energy reserves (Smith 1985; Goetz 1989; Forseth et al. 1999; Erhardt and Scarnecchia 2016). Although I did not evaluate growth, I speculate that energy reserves of fast-growing Bull Trout of the migratory life-history form, with increased metabolic demands, may diminish faster than that of slow-growing resident fish in response to resource constraints that typically occur in autumn and winter in oligotrophic streams (Huusko et al. 2007).

Minimal out-migration of subadult Bull Trout into Thompson Falls Reservoir was observed in this study. Only 20% of all tagged Bull Trout had been detected out-migrating as of spring 2016. This indicates that out-migrating juvenile and subadult Bull Trout probably use the mainstem Thompson River for extended periods of time if not indefinitely. A ‘stepwise’ out-migration with prolonged inhabitance within progressively larger aspects of the Thompson River drainage may allow for out-migrating Bull Trout to increase in size—the effect of which has been shown to increase out-migration survival of juvenile and subadult salmonids (Connor et al. 2000; Al-Chokhachy and Budy 2008;

Brown et al. 2013). Past sampling of the mainstem Thompson River by MTFWP primarily captured Bull Trout that were slightly larger than were observed out-migrating at PIT antennae or weir traps, which is consistent with the idea of prolonged residency in portions of the river that were widely believed to be migratory corridors (Huston 1994; R. Kreiner, MTFWP, personal communication). Additional assessments have also shown that small Bull Trout use suspected migratory corridor habitats differently than would be predicted by adult fish (Muhlfeld and Marotz 2005; Homel and Budy 2008; Monnot et al. 2008). In particular, Monnot et al. (2008) indicated that small migratory Bull Trout inhabited fluvial habitat for periods of time that extended through winter, which contrasted with transient use by larger fish during pre- and post-spawning migrations.

Seasonal and diel out-migration by subadult Bull Trout was not uniform. Despite sporadic out-migration being observed throughout the study, activity increased in the tributaries during October and in the Thompson River during December. Similar patterns of continuous out-migration that peaked in autumn have been observed in previous assessments conducted in Fishtrap Creek and the West Fork Thompson River (Liermann 2003; Zymonas 2006) and other studies in the Rocky Mountain West (Fraley and Shepard 1989; Nelson et al. 2002; Muhlfeld and Marotz 2005; Downs et al. 2006; Monnot et al. 2008; Homel and Budy 2008; Bowerman and Budy 2012). For example, Monnot et al. (2008) observed that peak tributary out-migration activity occurred between mid-September and late-November, with peak activity during October. While a slight increase in Bull Trout out-migration, typically of age-0 fish < 70 mm (Downs et al. 2006; Bowerman and Budy 2008), has been observed during spring freshets in previous studies (Downs et al. 2008; Homel and Budy 2008), this evaluation focused on larger (>100 mm) subadult fish that were able to be PIT-tagged. Furthermore, in addition to decreased capture efficiency during spring freshets, out-migration of small age-0 Bull Trout has been shown to contribute minimally to the number of migratory adults (Downs et al. 2006). In addition to out-migrating during the late autumn and early winter, the majority of Bull Trout in the Thompson River drainage performed nocturnal migrations, with most occurring just after sunset and before sunrise. Similar patterns of nocturnal migratory activity have been observed for other populations of Bull Trout (Jakober et al. 2000; Thurow 1997; Homel and Budy 2008) and salmonid species (Smith 1985). Nocturnal timing of out-migration of subadult Bull Trout may reduce the predation risk by visual predators (Clark and Levy 1988) while also increasing foraging opportunities for out-migrants (Muhlfeld et al. 2003; Homel and Budy 2008).

The number of out-migrating subadult Bull Trout was weakly associated with several abiotic factors. These results were not surprising given the complexity associated with life-history strategy expression, the lack of multi-year data collected in this study, and low sample size of observed out-migrants. While extensive research has been conducted to identify the influence of abiotic factors on the migration of juvenile anadromous salmonids (Mason 1975; Jonsson 1991; Spence and Dick 2014; Forsythe et al. 2012; Aldvén et al. 2015), research on Bull Trout migration has become increasingly focused on the assessment of water temperature, discharge, and habitat availability (Swanberg 1997; Jakober et al. 2000; Muhlfeld and Marotz 2005; Homel and Budy 2008). Interestingly, increased Bull Trout out-migration in Thompson River drainage during periods of low lunar illumination has also been reported for other juvenile salmonid species (Mason 1975; Jonsson 1991; Spence and Dick 2014; Forsythe et al. 2012; Aldvén et al. 2015) and, similar to the benefits of nocturnal out-migration, may be an evolutionary adaptation to decrease detection risk from visual predators (Clark and Levy 1988; Muhlfeld et al. 2003). Furthermore, fish in shallow river environments probably experience physiological responses to changes in barometric pressure, which has been shown to influence rates of fish movement (Guy et al. 1992) and may serve as an adaptation to anticipate the onset of instream flow pulses and changing environmental conditions that result from inclement weather (Peterson 1972; Smith 1985).

No acoustically-tagged Bull Trout were detected entering the Thompson Falls Reservoir at a time that coincided with the operation of stationary acoustic receivers. This further indicates prolonged residency in the mainstem Thompson River by out-migrating Bull Trout, which is consistent with observations of radio- and PIT-tagged fish. Manual tracking was not logistically feasible for acoustically-tagged fish that remained in the mainstem Thompson River because hydrophone use is rendered ineffective in shallow lotic environments, particularly for benthic-oriented fish such as Bull Trout (Thurow 1997; Jakober 2000; Muhlfeld et al. 2003), because of signal attenuation (e.g., absorption caused by entrained air, plant-life, woody debris, etc.), signal interference, and signal deflection (Pincock and Johnston 2012).

In contrast with an *a priori* expectation of a clustered ‘pulse’ of out-migration into Thompson Falls Reservoir, minimal and sporadic out-migration of telemetered individuals into Thompson Falls Reservoir was observed in this study. Although radio-tagged Bull Trout from each tributary remained spatially separated, and kernel density plots showed two clustered groups of radio-tagged fish, spatial analysis provided no evidence for overly clustered or dispersed out-migration. These seemingly contradictory results may stem from the increased distance that existed between low numbers of radio-tagged fish, which would inflate the measured distance between any two individuals. While not significantly clustered, different radio-tagged Bull Trout were consistently found in a limited number of areas within the mainstem Thompson River throughout the study—the frequent use of which might be attributable to “habitat bottlenecks” caused by degradation. Aggregation of fish at habitat bottlenecks sites could, ostensibly, have negative impacts on the migratory component of the population by increasing competition for resources and exposure to predators (Orpwood et al. 2004).

Although this study was not designed to measure predation, I observed that mink killed 29% of radio-tagged Bull Trout. Predation may have been facilitated by tagging, but I surmise this is unlikely given: 1) healthy recapture of multiple acoustic (2014 and 2015) and radio-telemetered (2015 only) Bull Trout, 2) lack of negative effects observed in surviving radio-tagged Bull Trout, and 3) a high number (N = 12) of untagged or PIT tag only fish found with evidence of mink predation. Observations from this and other studies provide evidence that mink may have a considerable influence on the mortality of fish in the Thompson River Drainage and other areas where the species overlap (Heggenes and Borgstrøm 1988; Jakober 1995; Liermann 2003; Lindstrom and Hubert 2004). While no other species was found predating on Bull Trout in this study, several other top-level predators exist in Thompson River drainage that may affect the survival of subadult Bull Trout.

The magnitude and timing of out migration by Bull Trout observed in this study may have been reduced because of uncharacteristically low discharges and warm water temperatures. Mean daily discharge observed in 2015 approached record lows when compared to historic (1957-2015) discharge data. However, when truncating the data for the last 15 years, the median daily discharge recorded for 2014 and 2015 were within the increasingly variable bounds of what has been observed throughout recent history (see Appendix for table and figure). Thus, direct comparisons between historic and current discharge data in the Thompson River drainage may be misrepresentative of more recent trends (i.e., 2014 and 2015 represent a ‘new normal’).

Management and Research Recommendations

Documentation of subadult Bull Trout out-migration characteristics in the Thompson River drainage has increased our understanding of the local population and provided information for management recommendations and additional research.

1. Continue facilitation of upstream migration into the Thompson River drainage for spawning adults in Noxon and Cabinet Gorge Reservoirs, and Lake Pend Oreille through the currently implemented trap-and-transport program and fish ladder operation at the Thompson Falls Dam. Ultimate success of these programs, and the augmentation of the migratory component of the population, may be further improved through the identification and removal of barriers to

migration (i.e., extensive log jams, unused beaver dams, anthropogenic activity) throughout the drainage (Nelson et al. 2002).

2. Continue PIT-tagging efforts and yearly out-migration monitoring in the Thompson River drainage to evaluate if conclusions from the present study – namely those regarding the relative contribution of Bull Trout by Thompson River tributary drainages – are representative over a greater temporal scale.
3. Identification of potential habitat bottlenecks in the mainstem Thompson River and evaluation of whether bottlenecks are associated with increased success of predator species and human-instigated habitat degradation (i.e., roads along river banks, riparian damage, etc.). Subsequent management actions, such as the improvement of potential migratory corridors and habitat complexity in the mainstem Thompson River, should then be assigned based on the future findings.
4. Initiation of a predation study to assess the effect of terrestrial and aquatic species on different life-stages of Bull Trout in the mainstem Thompson River.

REFERENCES CITED

Al-Chokhachy, R., and P. Budy. 2008. Demographic characteristics, population structure, and vital rates of a fluvial population of bull trout in Oregon. Transactions of the American Fisheries Society 137:1709–1722.

Aldvén, D., E. Degerman, and J. Höjesjö. 2015. Environmental cues and downstream migration of anadromous brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) smolts. Boreal Environment Research 20:35–44.

Baxter, C. V., C. A. Frissell, and F. R Hauer. 1999. Geomorphology, logging roads, and the distribution of bull trout spawning in a forested river basin: implications for management and conservation. Transactions of the American Fisheries Society 128:854–867.

Beeman, J. W., and B. Hayes. 2012. Detection probability of an in-stream passive integrated transponder (PIT) tag detection system for juvenile salmonids in the Klamath River, Northern California, 2011. U.S. Geological Survey Open-File Report 2012–1001.

Bowerman, T., and P. Budy. 2012. Incorporating movement patterns to improve survival estimates for juvenile bull trout. North American Journal of Fisheries Management 32:1123–1136.

Brown, R. S., S. J. Cooke, G. N. Wagner, and M. B. Eppard. 2003. Methods for surgical implantation of acoustic transmitters in juvenile salmonids: a review of literature and guidelines for technique. U.S. Army Corps of Engineers, Portland District, Portland, Oregon.

Brown, R. S., D. R. Geist, K. A. Deters, and A. Grassell. 2006. Effects of surgically implanted acoustic transmitters >2% of body mass on the swimming performance, survival and growth of juvenile sockeye and Chinook salmon. Journal of Fish Biology 69:1626–1638.

Brown, R. S., E. W. Oldenburg, A. G. Seaburg, K. V. Cook, J. R. Skalski, M. B. Eppard, and K. A. Deters. 2013. Survival of seaward-migrating PIT and acoustic-tagged juvenile Chinook salmon in the Snake and Columbia rivers: an evaluation of length-specific tagging effects. Animal Biotelemetry 1(10):1–9.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York.

Clark, C. W., and D. A. Levy. 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. The American Naturalist 131:271–290.

Clements, S., D. Jepsen, M. Karnowski, and C. B. Schreck. 2005. Optimization of an acoustic telemetry array for detecting transmitter implanted fish. North American Journal of Fisheries Management 25:429–436.

Connor, W. P., R. K. Steinhorst, and H. L. Burge. 2000. Forecasting survival and passage of migratory juvenile salmonids. North American Journal of Fisheries Management 20:651–660.

Cooke, S. J., S. G. Hinch, M. C. Lucas, and M. Lutcavage. 2012. Biotelemetry and biologging. Pages 819–881 *in* A. V. Zale, D. L. Parrish, and T. M. Sutton, editors. Fisheries techniques, 3rd edition. American Fisheries Society, Bethesda, Maryland.

Deters, K. A., R. S. Brown, J. W. Boyd, M. B. Eppard, and A. G. Seaburg. 2012. Optimal suturing technique and number of sutures for surgical implantation of acoustic transmitters in juvenile salmonids. Transactions of the American Fisheries Society 141:1–10.

Dixon, P. M. 2002. Ripley’s K function. Pages 1796–1803 *in* A. H. El-Shaarawi and W. W. Piegorsch, editors. Encyclopedia of Environmetrics. John Wiley & Sons Ltd., Chichester, England.

Downs, C. C., D. Horan, E. Morgan-Harris, and R. Jakubowski. 2006. Spawning demographics and juvenile dispersal of an adfluvial bull trout population in Trestle Creek, Idaho. North American Journal of Fisheries Management 26:190–200.

Dunham, J. B., and B. E. Rieman. 1999. Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. Ecological Applications 9:642–655.

Dunham, J. B., A. E. Rosenberger, R. F. Thurow, C. A. Dolloff, and P. J. Howell. 2009. Coldwater fish in wadeable streams. Pages 119–138 *in* S. A. Bonar, W. A. Hubert, and D. W. Willis, editors. Standard methods for sampling North American freshwater fishes. American Fisheries Society, Bethesda, Maryland.

Erhardt, J. M., and D. L. Scarnecchia. 2016. Growth model selection and its application for characterizing life history of a migratory bull trout (*Salvelinus confluentus*) population. Northwest Science 90(3):328–339.

Forseth, T., T. F. Nesje, B. Jonsson, and K. Hårsaker. 1999. Juvenile migration in brown trout: a consequence of energetic state. Journal of Animal Ecology 68: 783–793.

Forsythe, P. S., K. T. Scribner, J. A. Crossman, A. Ragavendran, E. A. Baker, C. Davis, and K. K. Smith. 2012. Environmental and lunar cues are predictive of the timing of river entry and spawning-site arrival in lake sturgeon *Acipenser fulvescens*. Journal of Fish Biology 81:35–53.

Fraley, J. J., and B. B. Shepard. 1989. Life-history, ecology and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lake and River systems, Montana. Northwest Science 63:133–143.

Fredenberg, W. A. 2002. Further evidence that lake trout displace bull trout in mountain lakes. Intermountain Journal of Sciences 8:143–151.

GEI (GEI Consultants, Inc.). 2005. Lower Clark Fork River drainage habitat problem assessment. Report to Avista Corporation, Spokane, Washington.

GEI and Steigers (GEI Consultants, Inc. and Steigers Corporations). 2013. Thompson River bull trout enhancement and recovery plan. Thompson Falls Project No. 1869. Thompson Falls, Montana.

Goetz, F. 1989. Biology of the bull trout, *Salvelinus confluentus*, a literature review. Eugene, Oregon, U.S. Department of Agriculture, Forest Service, Willamette National Forest.

Goetz, F. 1991 Bull trout life history and habitat study. U.S. Department of Agriculture, Forest Service, Deschutes National Forest, Bend, Oregon.

Guy, C. S, R. M. Neumann, and D. W. Willis. 1992. Movement patterns of adult black crappie, *Pomoxis nigromaculatus*, in Brant Lake, South Dakota. Journal of Freshwater Ecology 7(2): 137–147.

Harrell, F. E. Jr. 2001. Regression modeling strategies with applications to linear models, logistic regression, and survival analysis. Springer, New York.

Heggenes, J., and R. Borgstrøm. 1988. Effect of mink, *Mustela vison* Schreber, predation on cohorts of juvenile Atlantic salmon, *Salmo salar* L., and brown trout, *S. trutta* L., in three small streams. Journal of Fish Biology 33:885–894.

Heinzl, H., and M. Mittlböck. 2003. Pseudo R-squared measures for Poisson regression models with over- or underdispersion. Computational Statistics and Data Analysis 44(1–2):253–271.

Heupel, M. R., J. M. Semmens, and A. J. Hobday. 2006. Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. Marine and Freshwater Research 57:1–13.

Homel, K., and P. Budy. 2008. Temporal and spatial variability in the migration patterns of juvenile and subadult bull trout in northeastern Oregon. Transactions of the American Fisheries Society 137:869–880.

Huston, J. E. 1994. Northwest Montana coldwater stream investigations, species of special concern segment. DJ Project F-46-R-7. Report. Montana Fish, Wildlife and Parks, Thompson Falls.

Huusko, A., L. Greenberg, M. Stickler, T. Linnansaari, M. Nykanen, T. Vehanen, S. Koljonen, P. Louhi, and K. Alfredsen. 2007. Life in the ice lane: the winter ecology of stream salmonids. River Research and Applications 23:469–491.

Jakober, M. J. 1995. Autumn and winter movement and habitat use of resident bull trout and westslope cutthroat trout in Montana. Master's thesis. Montana State University, Bozeman, Montana.

Jakober, M. J., T. E. McMahon, and R. F. Thurow. 2000. Diel habitat partitioning by bull charr and cutthroat trout during fall and winter in Rocky Mountain streams. Environmental Biology of Fishes 59:79–89.

Jepsen, N., C. Schreck, S. Clements, and E. B. Thorstad. 2003. A brief discussion on the 2% tag/body mass rule of thumb. Pages 255–261 *in* M. T. Spedicato, G. Lembo, and G. Marmulla, editors. Aquatic telemetry: advances and applications, FAO/COISPA, Rome.

Jonsson, N. 1991. Influence of water flow, water temperature and light on fish migration in rivers. Nordic Journal of Freshwater Research 66:20–35.

Liedtke, T. L., J. W. Beeman, and L. P. Gee. 2012. A standard operating procedure for the surgical implantation of transmitters in juvenile salmonids. Open-file report 2012–1267. U.S. Geological Survey.

Liermann, B. W. 2003. Thompson River fishery investigations: comprehensive report 2000–2002. Avista Corporation, Noxon, Montana.

Lindstrom, J. W., and W. A. Hubert. 2004. Mink predation on radio-tagged trout during winter in a low-gradient reach of a mountain stream, Wyoming. Western North American Naturalist 64(4):551–553.

Mason, J. C. 1975. Seaward movement of juvenile fishes, including lunar periodicity in the movement of coho salmon (*Oncorhynchus kisutch*) fry. Journal of the Fisheries Research Board of Canada 32:2542–2547.

McMahon, T. E., and D. H. Bennett. 1996. Walleye and northern pike: boost or bane to northwest fisheries? Fisheries 21(8):6–13.

McMahon, T. E., A. V. Zale, F. T. Barrows, J. H. Selong, and R. J. Danehy. 2007. Temperature and competition between bull trout and brook trout: a test of the elevation refuge hypothesis. Transactions of the American Fisheries Society 136:1313–1326.

McPhail, J. D., and J. S. Baxter. 1996. A review of bull trout (*Salvelinus confluentus*) life-history and habitat use in relation to compensation and improvement opportunities. British Columbia Ministry of Environment, Lands and Parks, Fisheries Branch, Fisheries Management Report 104, Victoria.

Monnot, L., J. B. Dunham, T. Hoem, and P. Koetsier. 2008. Influences of body size and environmental factors on autumn downstream migration of bull trout in the Boise River, Idaho. North American Journal of Fisheries Management 28:231–240.

Muhlfeld, C. C., S. Glutting, R. Hunt, D. Daniels, and B. Marotz. 2003. Winter diel habitat use and movement by subadult bull trout in the upper Flathead River, Montana. North American Journal of Fisheries Management 23:163–171.

Muhlfeld, C. C., and B. Marotz. 2005. Seasonal movement and habitat use by subadult bull trout in the upper Flathead River system, Montana. North American Journal of Fisheries Management 25:797–810.

Nelson, M. L., T. E. McMahon, and R. F. Thurow. 2002. Decline of the migratory form in bull charr, *Salvelinus confluentus*, and implications for conservation. Environmental Biology of Fishes 64:321–332.

Neraas, L. P., and P. Spruell. 2001. Fragmentation of riverine systems: the genetic effects of dams on bull trout (*Salvelinus confluentus*) in the Clark Fork River system. Molecular Ecology 10:1153–1164.

Neumann, R. M., C. S. Guy, and D. W. Willis. 2012. Length, weight, and associated indices. Pages 637–676 *in* A. V. Zale, D. L. Parrish, and T. M. Sutton, editors. Fisheries techniques, 3rd edition. American Fisheries Society, Bethesda, Maryland.

Northcote, T. G. 1992. Migration and residency in stream salmonids – some ecological considerations and evolutionary consequences. Nordic Journal of Freshwater Research 67:5–17.

NWE (NorthWestern Energy). 2016. 2015 annual report, fish passage project. Thompson Falls Hydroelectric Project, FERC Project Number 1869, Butte, Montana.

Orpwood, J. E., S. W. Griffiths, and J. D. Armstrong. 2004. Effect of density on competition between wild and hatchery-reared Atlantic salmon for shelter in winter. Journal of Fish Biology 65:201–209.

Otis, D. L., and G. C. White. 1999. Autocorrelation of location estimates and the analysis of radiotracking data. Journal of Wildlife Management 63:1039–1044.

Peterson, D. A. 1972. Barometric pressure and its effect on spawning activities of rainbow trout. The Progressive Fish-Culturist 34:110–112.

Pincock, D. G., and S. V. Johnston. 2012. Acoustic telemetry overview. Pages 305– 337 *in* N. S. Adams, J. W. Beeman, and J. H. Eiler, editors. Telemetry techniques: a user guide for fisheries research. American fisheries Society, Bethesda, Maryland.

Pollock, K., 1987. Experimental design of telemetry projects. Journal of Raptor Research 21(4):129–131.

Power, G. 2002. Charrs, glaciations, and seasonal ice. Environmental Biology of Fishes 64:17–35.

PPL Montana. 2010. Thompson Falls Hydroelectric Project FERC project number 1869. 5-year reservoir monitoring plan, 2011–2015. Public. Submitted to Federal Energy Regulatory Commission, Washington D.C.

PPL Montana. 2014. 2013 Annual report fish passage project Thompson Falls Hydroelectric Project, FERC project number 1869. Submitted to FERC, Washington D.C.

Rieman, B. E., and F. W. Allendorf. 2001. Effective population size and genetic conservation criteria for bull trout. North American Journal of Fisheries Management 21:756–764.

Rieman, B. E., D. Isaak, S. Adams, D. Horan, D. Nagel, C. Luce, and D. Myers. 2007. Anticipated climate warming effects on bull trout habitats and populations across the interior Columbia River basin. Transactions of the American Fisheries Society 136:1552–1565.

Rieman, B. E., D. C. Lee, and R. F. Thurow. 1997. Distribution, status, and likely future trends of bull trout within the Columbia River and Klamath River basins. North American Journal of Fisheries Management 17:1111–1125.

Rieman, B. E., and J. D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. U.S. Forest Service, Intermountain Research Station, General Technical Report INT–302, Ogden, Utah.

Rieman, B. E., and J. D. McIntyre. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. Transactions of the American Fisheries Society 124:285–296.

Rogers, K. B., and G. C. White. 2007. Analysis of movement and habitat use from telemetry data. Pages 625–676 *in* Guy C. S. and M. L. Brown, editors. Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda, Maryland.

Scarnecchia, D. L., Y. Lim, S. P. Moran, T. D. Tholl, J. M. DosSantos, and K. Breidinger. 2014. Novel Fish Communities: Native and non-native species trends in two run-of-the-river reservoirs, Clark Fork River, Montana. Reviews in Fisheries Science and Aquaculture 22(1):99–111.

Schmetterling, D. A. 2003. Reconnecting a fragmented river: movements of westslope cutthroat trout and bull trout after transport upstream of Milltown Dam, Montana. North American Journal of Fisheries Management 23:721–731.

Selong, J. H., T. E. McMahon, A. V. Zale, and F. T. Barrows. 2001. Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerance in fishes. Transactions of the American Fisheries Society 130:1026–1037.

Smirich, M. G., and J. T. Kelly. 2014. Extending the 2% rule: the effects of heavy internal tags on stress physiology, swimming performance, and growth in brook trout. Animal Biotelemetry 2:16.

Smith, R. J. F. 1985. The control of fish migration. Springer-Verlag, Berlin.

Spence, B. C., and E. J. Dick. 2014. Geographic variation in environmental factors regulating outmigration timing of coho salmon (*Onchorhynchus kisutch*) smolts. Canadian Journal of Fisheries and Aquatic Sciences 71:56–69

Starcevich, S. J., P. J. Howell, S. E. Jacobs, and P. M. Sankovich. 2012. Seasonal movement and distribution of fluvial adult bull trout in selected watersheds in the mid-Columbia River and Snake River basins. PLoS ONE 7:e37257.

Swanberg, T. R. 1997. Movements of and habitat use by fluvial bull trout in the Blackfoot River, Montana. Transactions of the American Fisheries Society 126:735–746.

Thurow, R. F. 1997. Habitat utilization and diel behavior of juvenile bull trout (*Salvelinus confluentus*) at the onset of winter. Ecology of Freshwater Fish 6:1–7.

Tyers, M. B. 2016. riverdist: river network distance computation and applications. Package version 0.13.0, available: https://CRAN.R-project.org/web/package=riverdist

USFS (U.S. Forest Service). 2008. Fishtrap: final supplemental environmental impact statement. Lolo National Forest Plains/Thompson Falls Ranger District, Sanders County, Montana.

USFWS (U.S. Fish and Wildlife Service). 2002. Bull trout (*Salvelinus confluentus*) draft recovery plan. U.S. Fish and Wildlife Service. Portland, Oregon.

USFWS (U.S. Fish and Wildlife Service). 2008. Biological opinion for Thompson Falls Hydroelectric Project bull trout consultation. Federal Energy Regulatory Commission Docket No. 1869-048 – Montana. PPL Montana, LLC, Licenses. Prepared by USFWS Montana ES Field Office, Helena.

USOFR (U.S. Office of the Federal Register). 1999. Endangered and threatened wildlife and plants; determination of threatened status for bull trout in the coterminous United States. Federal Register 64:210(November 1, 1999):58910–58933.

USOFR (U.S. Office of the Federal Register). 2010. Endangered and threatened wildlife and plants; revised designation of critical habitat for bull trout in the coterminous United States, final rule. Federal Register 75:200(October 18, 2010):63897–64070.

Whitehorse Associates. 1997. Ecological classification Thompson River basin Montana. Prepared for Plum Creek Timber, Columbia Falls, Montana.

Zale, A. V., C. Brooke, and W. C. Fraser. 2005. Effect of surgically implanted transmitter weights on growth and swimming stamina of small adult westslope cutthroat trout. Transactions of the American Fisheries Society 134:653–660.

Zimmerman, M. S., and C. Kinsel. 2010. Migration of anadromous juvenile bull trout in the Skagit River, 1990–2009. Washington Department of Fish and Wildlife, Olympia.

Zuur, A., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York.

Zymonas, N. D. 2006. Age structure, growth, and factors affecting relative abundance of life history forms of bull trout in the Clark Fork River drainage, Montana and Idaho. Master’s thesis. Montana State University, Bozeman.

APPENDIX A

PAST THOMPSON RIVER DISCHARGE DATA

Table A1. Overall monthly minimum, median, and maximum discharge rates (m^3/s) of the Thompson River, near Thompson Falls, MT, for a 15 year period (1999 – 2013) compared to that of 2014 and 2015 fall field seasons where values in parentheses indicate the percentage of change (relative to that of the 15 year period). All data were obtained from the U.S. Geological Survey (monitoring site 12389500) and converted from ft^3/s prior to summary analysis.

		Year(s)				
Month	m^3/s	1999 - 2013	2014		2015	
September	Min	3.00	4.87	(62.26)	3.51	(16.98)
	Median	4.47	5.15	(15.19)	3.68	(-17.72)
	Max	7.31	5.58	(-23.64)	4.39	(-39.92)
October	Min	2.94	4.50	(52.88)	3.34	(13.46)
	Median	4.22	5.15	(22.15)	3.43	(-18.79)
	Max	6.88	5.58	(-18.93)	4.08	(-40.74)
November	Min	2.55	4.25	(66.67)	2.55	(0.00)
	Median	4.06	4.70	(15.68)	3.54	(-12.89)
	Max	17.56	18.04	(2.74)	4.64	(-73.55)
December	Min	1.56	4.02	(158.18)	2.92	(87.27)
	Median	3.96	7.90	(99.29)	4.11	(3.57)
	Max	10.96	9.80	(-10.59)	9.63	(-12.14)

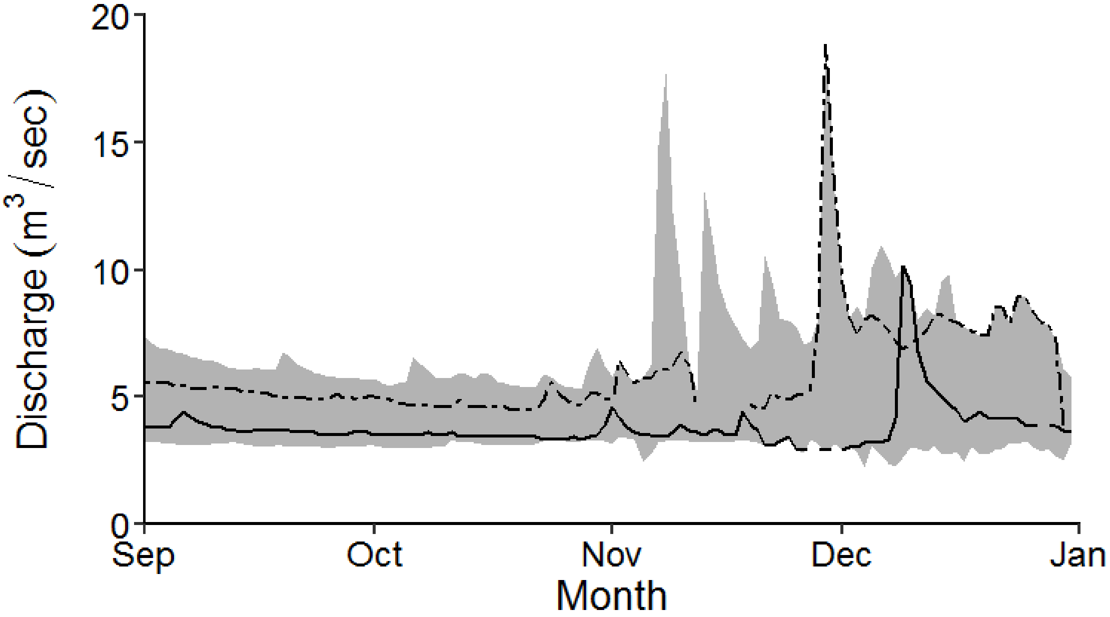

Figure A1. Median daily discharge values for 2014 (dashed black line) and 2015 (solid black line) compared to the observed range of median discharge values beginning in 2000 (grey ribbon).